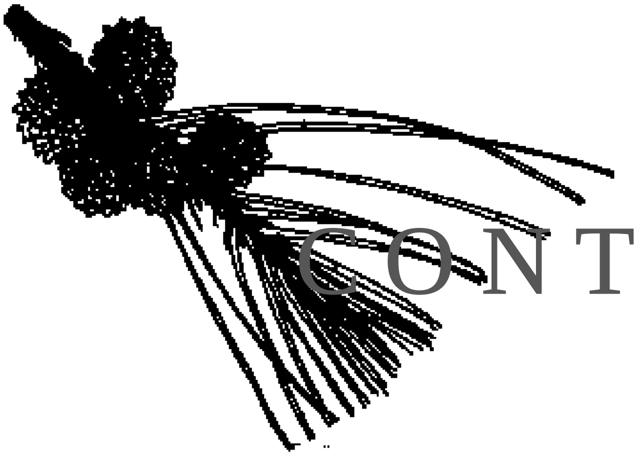
J.A. VOZZO

Tropical Tree
SEED MANUAL

United States Department of Agriculture

Forest Service



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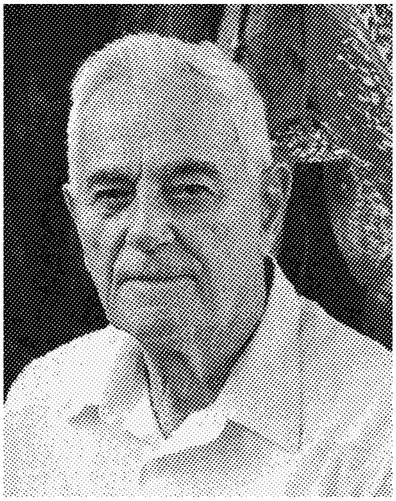


Dr. Frank H. Wadsworth has been actively and continuously researching tropical silviculture for the U.S. Department of Agriculture Forest Service since 1942.

Before his impressive career in the Tropics began, Dr. Wadsworth investigated forest succession at the confluence of the Koyukuk and Yukon rivers in Alaska. After brief assignments with the USDA Forest Service in Nebraska and Arizona, he began his tropical focus with a dissertation on the management of the Caribbean National Forest in Puerto Rico. This dissertation earned him a Ph.D. from the University of Michigan.

Dr. Wadsworth was Research Officer for the Tropical Forest Experiment Station in Rio Pedras, PR until 1956, when it became The Institute of Tropical Forestry (ITF) and he was appointed Director. He remained Director until 1978. Under his leadership, the ITF staff researched and reported on hundreds of tropical tree species, planted species on diverse and degraded sites, supported 16 annual 3-month tropical forestry courses for international participants, and published *The Caribbean Forester*—a trilingual, quarterly journal that disseminates information pertaining to technical forestry.

When ITF became IITF—International Institute for Tropical Forestry—in 1978, Dr. Wadsworth became head of Special Studies for International Cooperation, where he remains as an active researcher and consultant. As a leading consultant in every country of tropical America, Dr. Wadsworth has published more than 100 scientific articles, authored both reference and technical books on tropical forestry, and remains in demand as a speaker relating his experiences with and opinions about technology transfer.

I have personally known Dr. Wadsworth since July 1964 when he was an advisor for my own research dissertation in Rio Piedras, PR. I continue to seek and value his advice.

I am proud to dedicate this *Tropical Tree Seed Manual* to Dr. Frank H. Wadsworth as further recognition of his distinguished career in tropical forestry.

J.A. Vozzo
Research Plant Physiologist

ACKNOWLEDGEMENT

The *Tropical Tree Seed Manual* (TTSM) is the product of international cooperation and contributions. In 1990, the members of the North American Forestry Commission of the United Nations Food and Agriculture Organization authorized compilation of a tropical tree seed reference manual for use among its membership in Canada, the United States, and Mexico. Under the direction of Dr. J. L. Whitmore, USDA Forest Service (Forest Service), the project was later expanded to include tropical tree species found in all of tropical America from Canada to Colombia. Since work on the project began in April 1996, 63 scientists from 19 countries have responded by providing species descriptions, chapters, translations, drawings, herbarium specimens, and references both unpublished and published.

The Forest Service supported the project by permitting employees to establish international contacts, compile the data, and oversee production and by funding the botanical drawings, Spanish-English translations, operations, editing, and printing of the English edition. Specifically, I want to thank the National Reforestation, Nurseries, and Genetic Resources (RNGR) Team and the Washington Office Cooperative Forestry group for their support with the English-Spanish translations. I value the advice and counsel of Dr. George Hernandez, Dr. Tom Landis, and Dr. Ron Overton of the Forest Service.

The TTSM would not have been produced without the help of all of these people. My sincere gratitude goes especially to Dr. James M. Guldin, USFS; the Red de Herbarium de Mesoamerica y el Caribe, particularly Dr. Mireya Correa A., Lic. AnaLu E. de MacVean; Dr. Cyril Hardy Nelson Sutherland; Dr. Ricardo Rueda; and M.Sc. Jeanine Velez Gavilan. I thank Gustavo Serrano for the original botanical drawings of all species, and Francisco Hodgson for the illustrations in Chapter 1. Special thanks to Maria Arun Kumar for her patience with the Spanish-English translations, and to Brenda Grebner for the draft and final versions of all submissions. I also thank Pamela Bowman, a technical editor with the Forest Service, Sonja Beavers, Mary Jane Senter, USFS, and George Avalos, USDA for their invaluable comments and suggestions. Dr. K.F. Connor and Mrs. Penny Byler made available additional Forest Service resources to complete this project.

Dr. Rosa Elena Molina Achecar de Vozzo warrants special mention for her many hours of patience, cooperation, and translations…all volunteered.

The greatest fault of this manual will not be misspelled words, unintentionally erroneous data reports, or negligent omissions. It will be my inability to acknowledge all the people and institutes who helped make TTSM possible.

J.A. Vozzo
Research Plant Physiologist

ABSTRACT

The *Tropical Tree Seed Manual* is a one-volume reference manual for students, technicians, and scientists that provides comprehensive, internationally compiled data about tropical trees. The emphasis is on species of the Americas; however, a number of tropical tree species from other countries are also included. The manual is divided into two parts. The first part consists of nine chapters written by authorities in each area. The second part presents descriptions of 197 botanically and economically important tropical tree species. The manual is published in both English and Spanish. It contributes to the academic and scientific communities by collating and organizing a wealth of internationally significant research and practical data into one publication. It should be used with similar references on seed technology and handling to give students, technicians, and scientists a thorough understanding of tropical tree seeds.

Keywords: collection, ecology, ethnobotany, germination, pathology, recalcitrance, seeds, storage, tropical forestry

INTRODUCTION

The North American Forestry Commission (NAFC) is a component of the United Nations Food and Agriculture Organization that addresses international forestry. The NAFC members (Canada, Mexico, and the United States) initiated a proposal to improve forestry applications by providing guidelines on tropical tree seed handling to nursery and plantation managers. The project was approved with the implied support of each member country. The NAFC chairperson, Jacob L. Whitmore of the USDA Forest Service, secured authorization in April 1996 for the Forest Service to proceed with the planning and organization of a tropical tree seed reference manual.

The concept was later expanded to include a technical section and descriptions of tropical tree species in the Neotropics and tropical Asia, Africa, Australia, and India, and a compiler was identified to coordinate the project. There was no intent to include all tropical tree species, only those of economic or biologic interest to forestry applications in Canada, Mexico, the United States, and Central America.

The information published here resulted primarily from previously known data; however, much of it had not been reported outside its area of origin. Through experience, nursery and plantation managers have learned about the biology and handling techniques of their significant species, but they lack information about species they have not planted. The *Tropical Tree Seed Manual* (TTSM) provides them with a reference for investigating the feasibility of introducing new species into their economies. It also provides a practical starting point for comparative morphology and literature references for those scientists conducting research within tropical forestry. Finally, students will find the technical chapters useful as an introduction to and a current review of the issues involving tropical tree seeds.

The TTSM is intended as a useful reference for practical and academic ventures into tropical forestry. It is a one-volume reference manual for nursery and plantation managers, scientists, and students that provides comprehensive, internationally compiled data. By including previously unpublished reports, data, illustrations, and international references in a single book, time-consuming literature searches will be reduced or eliminated.

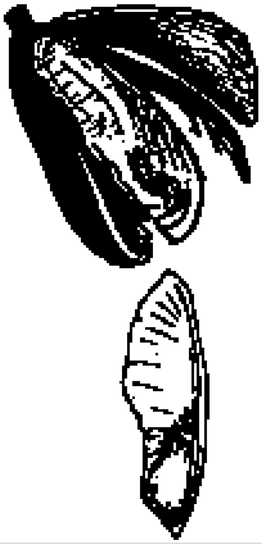
The first part consists of nine technical chapters written by authorities in each subject: biology, collection, storage, orthodox and recalcitrant seeds, dormancy and germination, pathology, ecology, ethnobotany, and dendrology. Each chapter provides an independent and comprehensive discussion, but together they form a single, complete text solely dedicated to tropical tree seeds. The current and historical information thus provided can be used for both teaching and research.

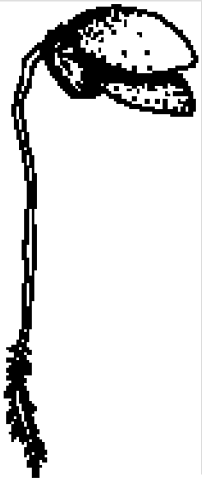
The second part of the manual presents descriptions of 197 botanically and economically important species in a standard format. The most widely used and well-known species are described in depth, while lesser known species are not. Authors have attempted to include all known information on each species, thus absence of information indicates limited knowledge about a species. All nomenclature is according to references from the Missouri Botanical Gardens.

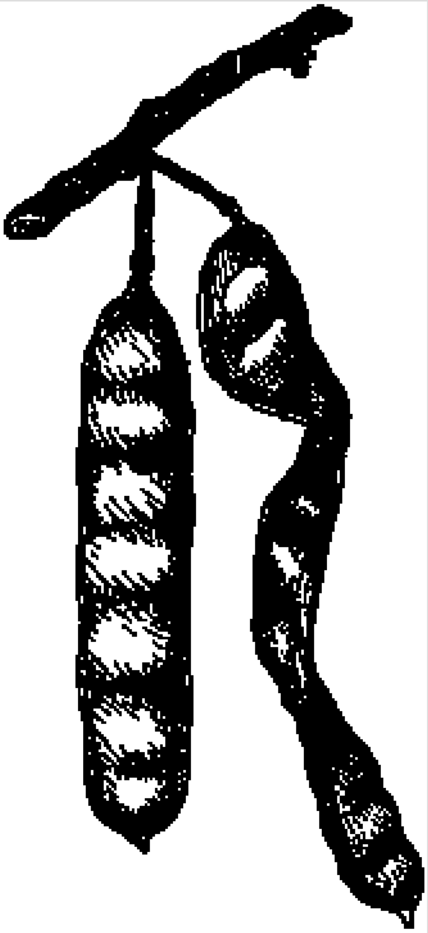
For practicality and easy searching, the referenced literature in TTSM is listed in one separate section. Common names, synonyms, and associated organisms are also cross-referenced. The international effort to produce the TTSM is represented by 63 contributors from 19 countries, and brief autobiographies of contributors are included.

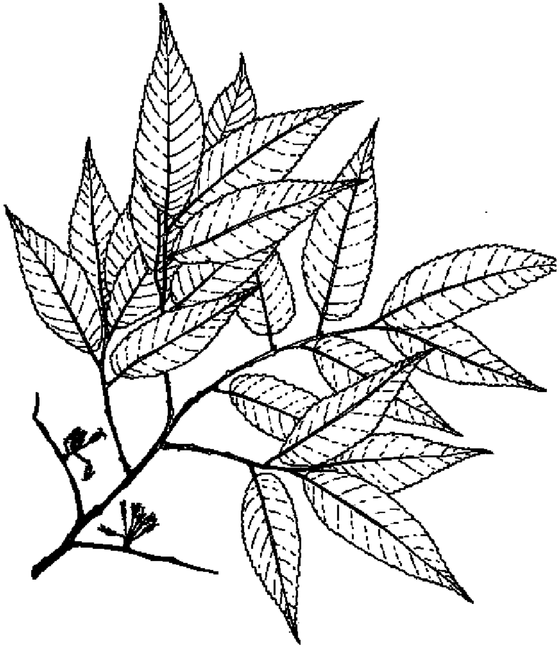
The TTSM is published in both English and Spanish. Particular styles in both languages are mediated into chapters and species descriptions for a common, but bilingual, volume. For example, all units are in metric values and a conversion table is included. Common names are not limited to English and Spanish, but also include names in any language indigenous to a country with a particular species.

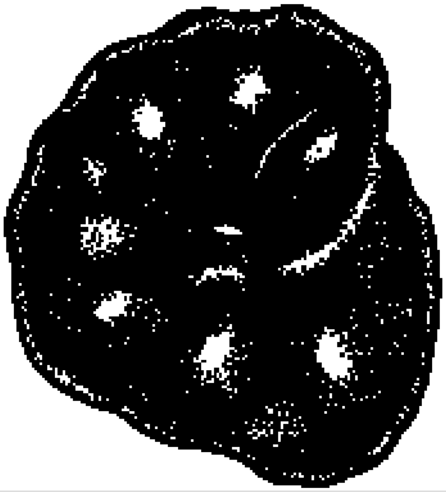
The TTSM contributes to the academic and scientific communities by collating and organizing an internationally significant research and practical subject into one reference. It should be used with similar references on seed technology and handling to give students and technicians a thorough understanding of tropical tree seeds.

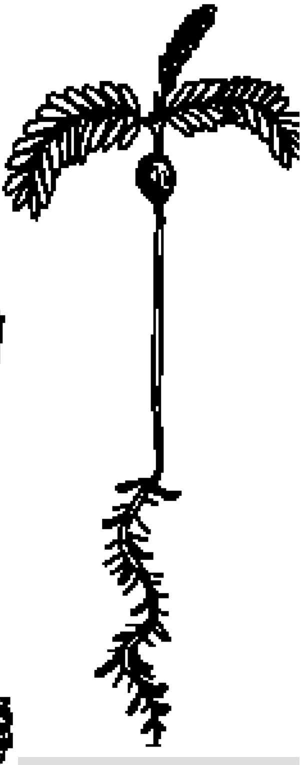


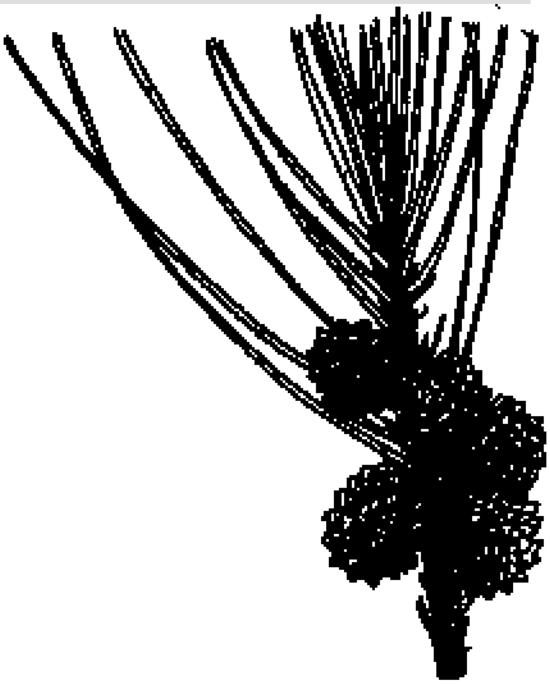












PART I

TECHNICAL CHAPTERS

The nine technical chapters were selected to give a comprehensive overview of current tropical tree seed technology as written by internationally recognized authorities. All chapters together offer a supplement text for the study or reference of tropical tree seeds. However, each chapter may be used alone to pursue a specific field of interest. This objective necessarily produces an overlap of subjects between chapters. The overlap is not as repetitive as it is descriptive from the viewpoints of the authors as they develop dominant research references.

CHAPTER 1

Seed Biology

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Seeds have been associated with human development since prehistoric times. In the post-glacial gathering era, Paleolithic people depended upon seed plants for their existence. They collected wild berries, nuts, and many edible seeds capable of providing nutrients and useful products (Baker 1965, Schery 1952). Since ancient times, seeds have been symbolic in the religious creeds of human groups. In ancient Egypt, for example, seeds symbolized the mysteries of death, resurrection, and life after death. Mummies were buried with a vessel of viable seeds to fill the food requirements in a new life (Evenari 1980/1981). Seed symbolism continues to be a part of religious rituals and ceremonies practiced by numerous people. The Bribri Indians of Costa Rica believe that grave-diggers and women are responsible for maintaining a basic seed stock because the Bribri are born as cocoa trees and a dead Indian is comparable to a dead tree since both of them leave seed (Bozzoli 1979). Because the Bribri god Sibö gave rise to the trees when Earth was created, Bribris believe they are immortal, everlasting, and perpetuated through the fruits and seeds they produce (Bozzoli 1979).

With the birth of agriculture, this symbol of resurrection and life became a necessity for the development of civilization. Gathering, storing, selecting, and sowing seeds capable of producing good crops became an art and an obligation: human food security was dependent on seeds. Throughout the centuries, seeds have been a means to reproduce species and a source of nutrients upon which all developing civilizations have been built. Seeds have ultimately produced fibers, carbohydrates, proteins, essential oils, insecticides, beverages, alkaloids, phytoestrogens, animal fodder, and other less important products (Hughes 1988).

Agricultural development and the recognition that seeds are the primary base for obtaining good crops promoted the study of seed biology in crops. Traditionally, this study focused on cereal, grain, and other seeds basic to the human diet such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), corn (*Zea mays*), barley (*Hordeum vulgare*), rye (*Secale cereale*), beans (*Phaseolus vulgaris*), peanuts (*Arachis hypogaea*), and soybeans (*Glycine max*). The study and research of these basic seeds continues to grow, especially when demographic explosion and climatic global change undermine our confidence that we have the capacity to feed present and future human populations.

Widely studied seeds include those of plants that produce commercial trichomes such as cotton (*Gossypium hirsutum, G. arboreum*); fibers such as flax (*Linum usitatissimum*) or ramie (*Boehmeria nivea*); oil such as the coconut (*Cocos nucifera L.*) or the oil palm (*Elaeis guianeensis, E. oleifera*); nuts such as the cashew (*Anacardium occidentale*), the Brazilian (*Bertholletia excelsa*), the American hazel (*Corylus americana*), the pecan (*Carya illinoinensis*), and the Queensland or Australian (*Macadamia ternifolia*); beverages such as coffee (*Coffea arabica*) and cocoa (*Theobroma cacao*); and spices and condiments such as nutmeg, mace (*Myristica fragrans*), and pepper (*Pimenta dioica*). Among the drug-producing plant seeds studied are some species of the genus *Strychnos*, which produce strychnine and brucine; the quinas (*Cinchona*), which produce quinine; and the coca (*Erythroxylum coca*), which produces cocaine.

Because of the importance of biodiversity conservation, natural forest management, reforestation, agroforestry, and agro-silvo-pasture systems, our study of forest tree seeds in the Tropics is only the beginning.

FOREST TREE SEEDS INTEREST AND STUDY

The systematic study of tropical forest tree seeds is becoming increasingly important as we realize that the forest and forest trees are not a boundless resource, and as we realize the value of treating the forest as a crop. The exhaustive, indiscriminate, and haphazard use of forest resources gradually limits the supply of traditional woods and other forest products important in national and international markets. Resource reduction also hastens the loss of a multiple use resource that beneficially affects soils, hydric regimes, biodiversity, landscapes, and microclimates. Additionally, the forest mass fixes CO_2, diminishes atmospheric contamination and deterioration, and contributes to sustaining human survival (Reynolds and Thomson 1988).

Today, increasing the existing knowledge about forest dynamics, trees as basic and essential units, and seeds and seedlings as indisputable factors of regeneration has become important. Challenging issues include generating new knowledge; developing effective techniques that promote conservation, management, and rational use of remaining forests; and implementing successful reforestation programs.

Most tropical tree pioneers, that is those typical of early forest succession, have small orthodox and dormant seeds. Easily dispersed, these seeds may form seed banks on the forest floor and may be photoblastic or thermoblastic. Germination of most of these seeds is stimulated by environmental alterations or disturbances, such as natural or artificial clearings in the canopy, on different spatial or chronological scales. Changes in the rates of red/far-red light or temperature fluctuations produced by vegetation removal may increase the germination rate (Bazzaz 1991). In contrast, a large number of climax species have big recalcitrant or intermediate seeds. Recalcitrant seeds germinate quickly, an advantage in terms of avoiding insect predation and preventing lipid degradation from diverse microorganism action (Whitmore 1990). A recalcitrant seed lacks maturation drying and its development is uninterrupted; however, the speed of embryo development (growth and differentiation) varies greatly among species. Diaspore permanence on the forest litter or substrate before root protrusion may vary from days to months. For example, root protrusion in *Dipteryx panamensis* (Pittier) Record & Mell and *Pentaclethra macroloba* (Willd.) Kuntze occurs 8 to 10 days after sowing; in *Virola koschnyi* Warb., 11 to 14 days; in *Carapa guianensis* Aubl., 14 to 16; in *Calophyllum brasiliense* Cambess., 15 to 18; in *Lecythis ampla* Miers, 45 to 48; in *Ocotea austinii* C.K. Allen, 50 to 55; and in *Minquartia guianensis* Aubl., 150 to 160 (5 months or more) (Flores 1992a, 1992c, 1994a, 1994b, 1994d, 1994e, 1994f). While pioneer species such as *Cecropia*, *Goethalsia meiantha* (Donn. Sm.) Burret, *Hampea platanifolia*, *Heliocarpus appendiculatus*, and *H. americanus* form seed banks on the forest floor, the species with recalcitrant seeds form seedling banks. The seedlings that remain until advanced stages of forest regeneration are, in many species, more important than the seed banks as a source of regeneration (Bazzaz 1991).

Regeneration includes dormancy types and germination times and types that are all obviously related to the morphology, physiology, and ecology of seeds (Grübb 1977). Consequently, the study of these aspects is becoming increasingly important to understanding seed behavior and predicting the regeneration capacity of the trees and the forest. The completion of a life cycle or the regeneration of a plant community depends on the production of physiologically independent individuals, which happens through seed or vegetative reproduction. Establishment of the species reproduced by seeds is dominant in communities in early succession after strong disturbances, and in forests of intermittent regeneration, throughout a vegetation mosaic (Ashton 1984, 1989; Bazzaz and Ackerly 1991; Hall and others 1994; Harris and Silva-López 1992; Hilty 1980).

The genotype of a tree seed is the result of the evolutionary forces operating on the species for centuries. It is adapted to the present environmental conditions but not to those of the future, especially when environmental conditions are being drastically modified by accelerated global change. Even if scientific and technological knowledge could be increased, the forests of the past and those of today cannot be replicated tomorrow. The natural processes that gave rise to the species, communities, and ecosystems we want to preserve have been built over a long period of time and in large spaces (Pickett and others 1992). To preserve and reproduce tree species by seed, we must know the limits imposed on the ecophysiology of seeds by nature through the evolutionary process. The genetic combinations able to survive through environmental changes have intrinsic value and must be carefully selected.

Seed germination is also influenced by the environmental conditions during seed development and maturation while on the parent tree. Day length, temperature, parental photothermic environment, light quality, and elevation are factors that significantly influence germination capacity (Dorne 1981; Fenner 1991, 1992; Foster 1986; Grime and Jeffrey 1965; Gütterman 1991; Kigel and others 1977). Additional factors include the inflorescence position on the parent tree, seed position in the fruit or infrutescence, and parent tree age during floral induction (Gütterman 1991).

These factors, plus others, explain the strong variation found in seed parameters (weight, color, water content, germinability) among seed groups and among seeds in the same group.

To most people, the concept of "seed" is deceptively simple. It is compared to a pill, isolated from the environmental impact, replicated many times, and capable of producing a plant (Janzen and Vásquez-Yáñez 1991). However, a seed is attached to a long and complex evolutionary and physiological history, and it is also conditioned to the variations of a long and complex future. The study of seeds has many facets and should not be limited to collection, storage, and sowing.

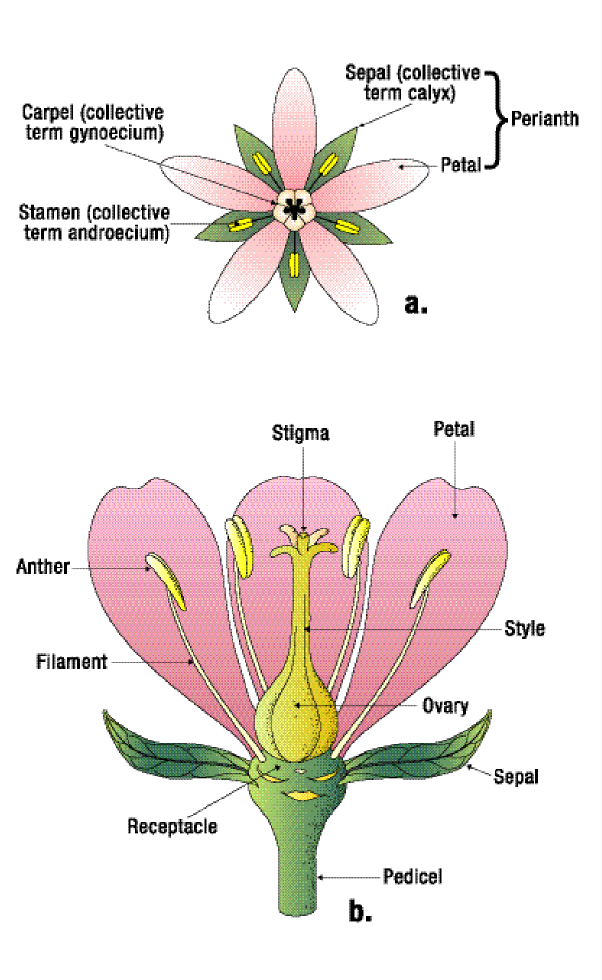


Fig. 1. Perfect flower. a, viewed from above; b, longitudinal section.

REPRODUCTIVE BIOLOGY IN TROPICAL TREES

SEXUAL STRUCTURES IN ANGIOSPERMS

The flower is the reproductive structure in angiosperms. The classic flower has a pedicel, floral receptacle, calyx (group of sepals), corolla (group of petals), androecium (ensemble of stamens), and gynoecium (ensemble of carpels) (fig. 1). The androecium and the gynoecium are the fertile organs; the remaining organs are sterile (vegetative structures).

Most flowers have a specific numeric arrangement of organs. In monocotyledons, the flowers generally have three pieces: three sepals, three petals, and usually three stamens or a multiple of three stamens; these flowers are called trimerous. The dicotyledons have flowers built in an array of four or five pieces and are called tetramerous or pentamerous. The flower plan is more evident in petals and sepals, and to some degree in the stamens; the plan is not applied to carpels. In the flower, the sepals alternate with the petals and the petals frequently alternate with the stamens. Groups of inner stamens may alternate with groups of outer stamens; sometimes the carpels are opposite to the sepals.

When all of the typical organs—petals, sepals, stamens and carpels—are present in a flower, it is complete; if one or more organs are missing, the flower is incomplete. A nude flower lacks a perianth; a flower is apetalous if it lacks a corolla (e.g., *Roupala montana*, *Macadamia integrifolia*, *Oreomunnea pterocarpa*, *Sterculia apetala*, *Alfaroa costaricensis*, *Hyeronima alchorneoides*).

The terms regular and irregular are commonly used in reference to flowers. These terms generally involve the perianth (corolla + calyx); the reproductive organs are occasionally included. A regular, or actinomorphic, flower (e.g., *Coccoloba tuerckheimii*, *Terminalia amazonia* (J.F. Gmel.) Exell, *Ocotea austinii*, *Magnolia poasana*, *Gustavia hexapetala*) has perianth pieces of similar shape and size. The flower can be divided into equal halves by a vertical plane in several directions. This flower has radial symmetry (polysymmetric) (fig. 1). Bisymmetric flowers have two planes of symmetry (bilateral flowers; typical in Brassicaceae) (Strasburger and others 1908, Weberling 1989). The irregular, or zygomorphic, flowers are dor-

Fig. 2.

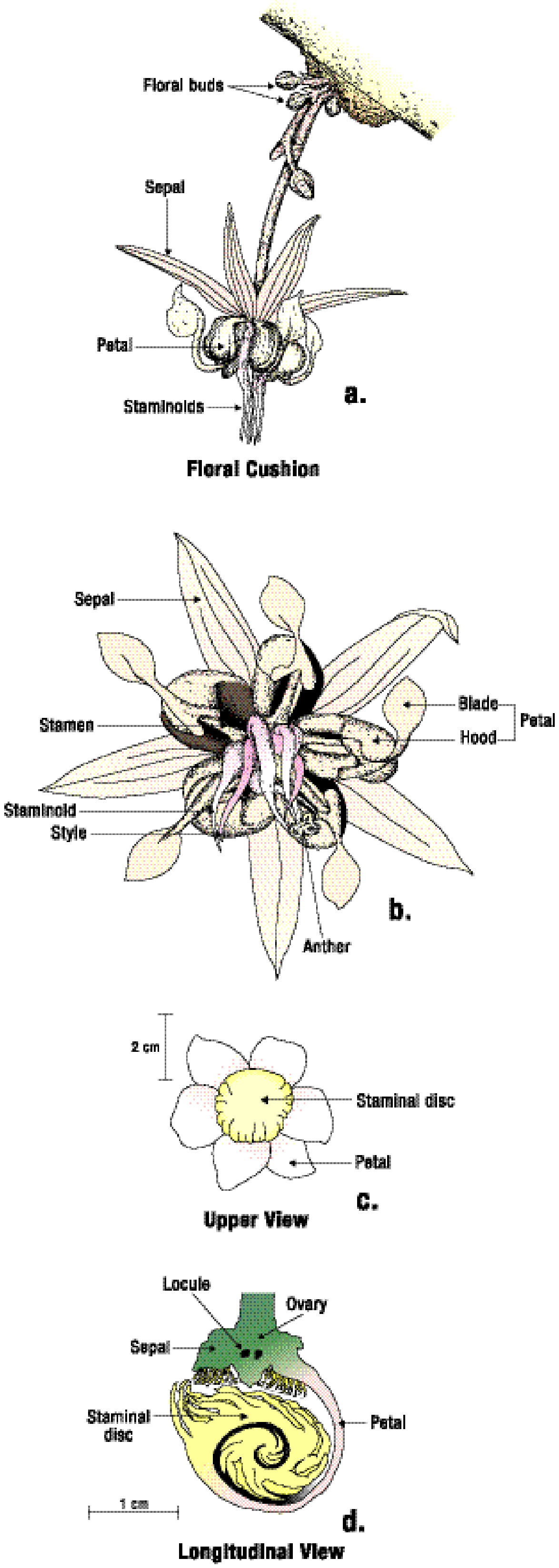


Fig. 3. Zygomorphic flower. a,b, *Theobromoa cacao* (Sterculiaceae); c,d, *Eschweilera sp.* (Lecythidaceae).

siventral or monosymmetric (e.g., *Andira*, *Diphysa americana* (Mill.) M. Sousa, *Dipteryx panamensis*, *Erythrina*, *Gliricidia*, *Hymenolobium mesoamericanum*, *Theobroma cacao*, *Bertholletia*, *Cariniana*, *Couratari*, *Lecythis*, *Eschweilera*, *Qualea paraensis* [figs. 2 and 3]) (Strasburger and others 1908, Weberling 1989). The irregularity usually involves the petals, but the sepals and the perianth as a whole could be included. There are also asymmetric flowers. This asymmetry must be produced by organ reduction, multiplication, or modification (e.g., *Vochysia*, and typical in *Canna* and *Maranta*) (Strasburger and others 1908, Weberling 1989).

Floral reduction can occur in one or several organs simultaneously. By reduction, organs may change their shape, structure, and function. The transformation of petals and stamens in glands, or of stamens in staminoids or petals, is the most common change. Stamen reduction may occur in different degrees, from anther abortion to organ disappearance. Carpel reduction usually refers to reduction in size and ovule number; for example, the achene is a fruit with only one ovule. Ovule reduction and loss is usually gradual; it may take place in acropetal direction, retaining only the distal ovule(s), or proceed in basipetal direction; in this case only the basal (proximal) ovule(s) remain (Eames 1961, Flores 1999).

The receptacle resembles a shoot in ontogeny and structure. It has nodes, internodes, and appendages; the nodes are crowded due to internode reduction or suppression. The fertile and sterile floral organs arise at the receptacle nodes and are grouped in spirals or verticils.

The calyx and corolla are vegetative structures and collectively constitute the perianth (fig. 4). They are easily distinguished in many flowers (e.g., *Xylopia sericophylla*, *Cananga odorata*, *Annona*, *Drimys granadensis*, *Guajacum sanctum L.*); in other flowers the perianth parts are indistinguishable and are named *tepals* (e.g., *Cecropia*, staminate flowers; *Allocasuarina*, staminate flowers; *Hernandia didymantha*, *Magnolia poasana*, *Gyrocarpus*). In many flowers, the sepals and petals are modified leaves.

In many flowers, the calyx and corolla may be reduced, vestigial, or missing. Reduced sepals may be toothed, scaly, bristled, or ribbed. Petals are usually laminar and bigger than sepals. They vary widely in size and shape. Flowers with large and elaborate petals can be found in families such as Fabaceae-Caesalpinioideae (*Cassia grandis* L.f.), Hippocastanaceae (*Billia*), Lecythidaceae (*Lecythis*, *Eschweilera*, *Grias cauliflora*), Fabaceae-Papilionoideae (*Dipteryx oleifera*, *D. panamensis*, *Hymenolobium mesoamericanum*, *Hymenaea courbaril* L.), and Vochysiaceae (*Vochysia*, *Qualea paraensis*). Those with small, reduced, vestigial, or no petals are in families such as Betulaceae (*Alnus acuminata* Kunth in H.B.K.), Casuarinaceae (*Allocasuarina*), Euphorbiaceae (*Hyeronima*), Fagaceae (*Quer-*

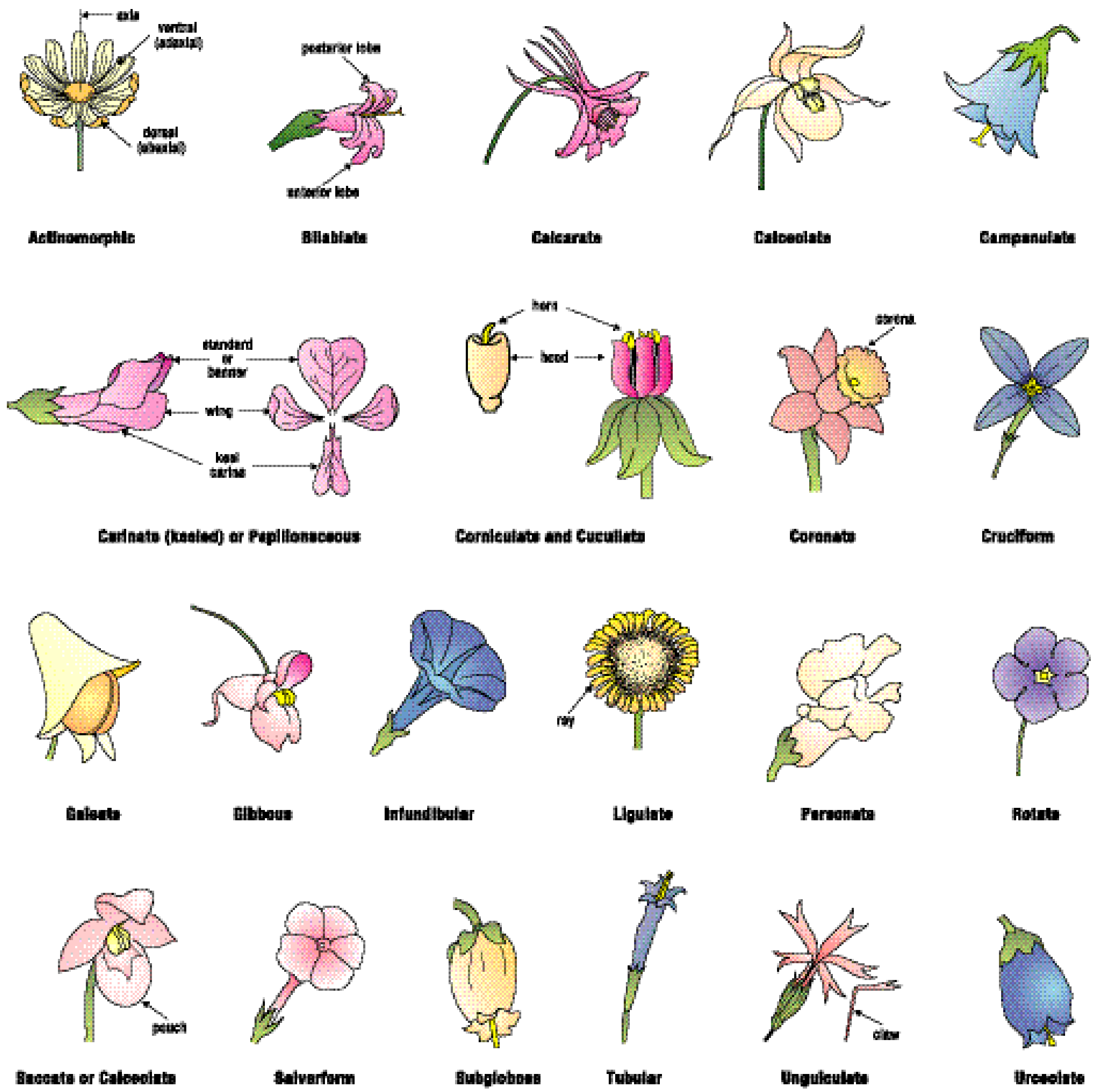


Fig. 4. Perianth structural types.

cus), Juglandaceae (*Alfaroa costaricensis* Standl.), Moraceae (*Brosimum*, *Maclura tinctoria* [syn. *Chlorophora tinctoria*], *Castilla elastica*, *Naucleopsis naga*), Myristicaceae (*Virola*, *Myristica fragrans*, *Otoba novogranatensis* Moldenke), Salicaceae (*Salix*), and Ticodendraceae (*Ticodendron incognitum*). When reduced, the petals may form scales, bristles, or glands of varied size and shape.

The position of the calyx and corolla pieces in the floral bud (aestivation) sometimes persists in the mature flower. There are several aestivation types (fig. 5); the following classification follows that of Radford and others (1974):

Alternate. Two rows or series of organs or structures where the margins of the inner group are overlapped by a margin from each adjacent outer piece.

Cochleate. A hollow or helmet-shaped structure encloses or surrounds the other pieces.

Contorted or regular. Several structures or organs in a whorl or close spiral have one margin covering the margin of the adjacent structure.

Convolute. A leaf or perianth piece partly rolled in another, commonly twisted distally.

Imbricate or irregular. Piece margins overlap.

Induplicate. Piece margins fold inward, touching the margins of the adjacent structures.

Quincuncial. Five pieces: two are interior and two exterior; the fifth piece has one margin covering the interior pieces while the other margin is covered or surrounded by one margin of the exterior pieces.

Valvate. Margins of the adjacent structures touch at edges without overlapping.

Vexillate. Large piece surrounds other minor pieces, parallel-oriented with respect to the outer piece semilimbs.

Perianth aestivation has taxonomic value; for example, the corolla aestivation is a feature distinguishing Caesalpinioideae from Papilionoideae.

The androecium is the ensemble of stamens. The typical stamen has the anther and the filament, which connects the anther to the floral axis or another organ (fig. 6). The anther comprises four elongated microsporangia (pollen sacs), where pollen develops. The androecium is outside the gynoecium and inside the corolla; the stamens are sometimes attached to or inserted upon the petals, the corolla (epipetalous), or the gynoecium (gynandrous). The stamens may be united through coherent or connate filaments in a single group (monadelphous), in two groups (diadelphous), or more (polydelphous) or by union of their anthers into a ring (syngenesious; fig. 6); (Porter 1967).

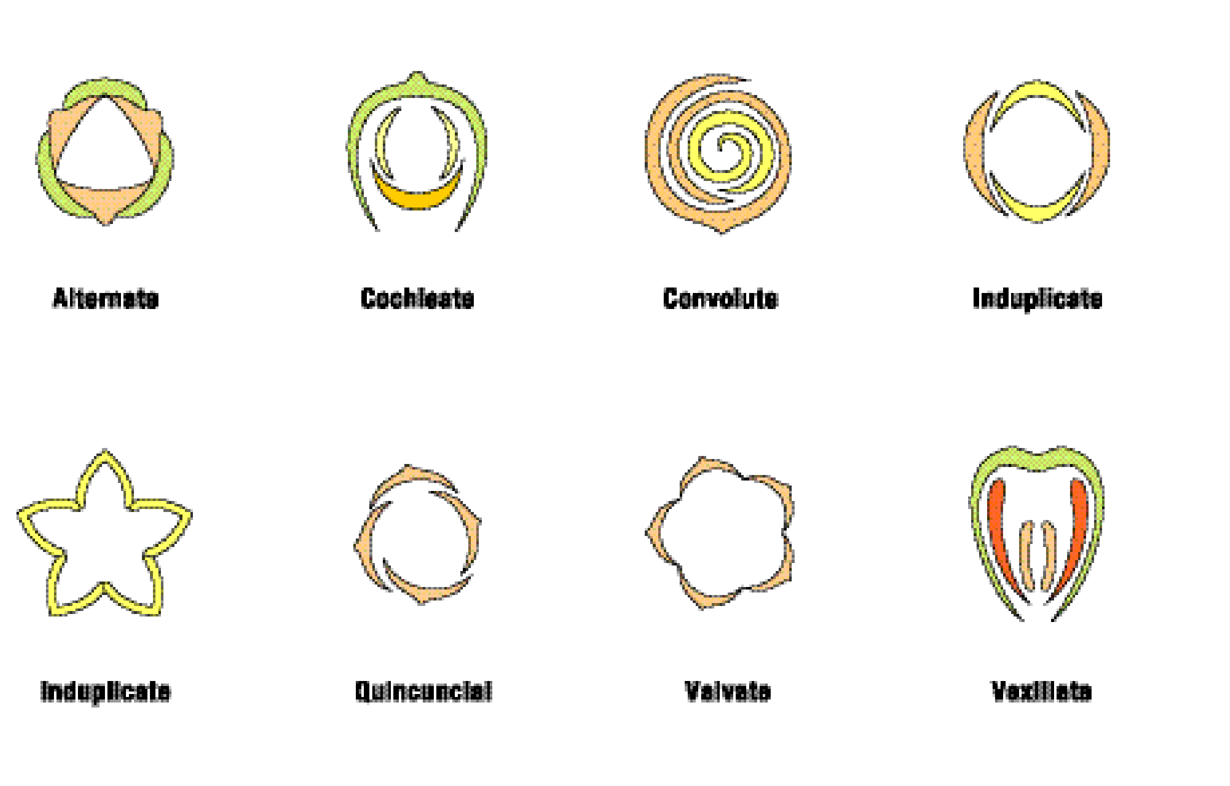


Fig. 5. Perianth aestivation types.

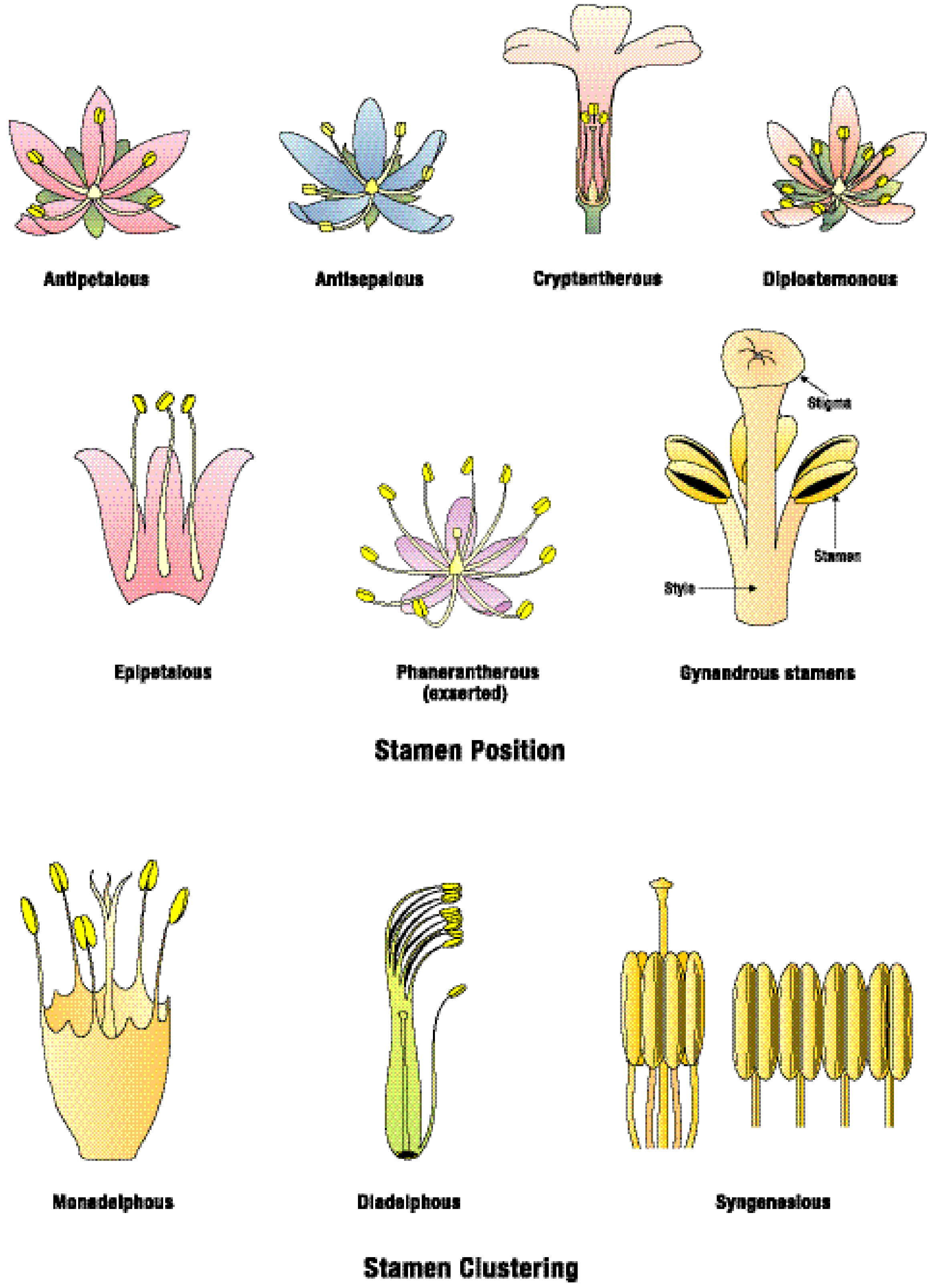


Fig. 6. Stamen position and clustering.

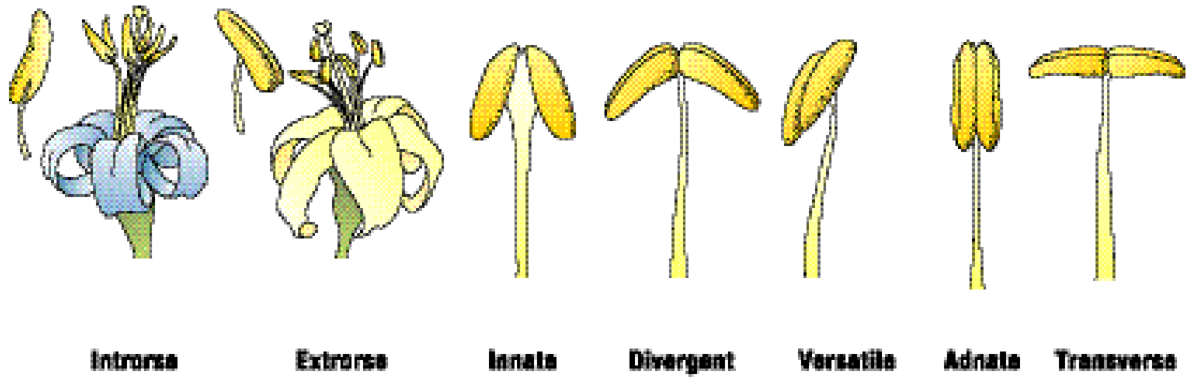


Fig. 7. Anther Attachment.

The attachment of the anther to the filament (fig. 7) is innate when the microsporangia are terminal and the filament is continuous between the microsporangia. It is adnate when the microsporangia are elongated and attached lengthwise to the filament. When the anther is attached by its middle, with both ends free, it is versatile. Dorsifixed anthers are attached dorsally and medially to the filament tip, while basifixed anthers are attached distally to the filament. In some species the microsporangia are in a transverse position.

The number of stamen in a flower ranges from one to many, and from an indefinite number to a defined one (Eames 1961). The arrangement on the receptacle could be spiral (helical), whorled (verticillated), or fasciculate (clustered); the fascicles are commonly in whorls. The spirally arranged stamens represent a primitive condition from which the whorled and fasciculate types developed (Eames 1961). The fascicles have various numbers of stamens and are formed by aggregation and conation of individual stamens to different degrees. When the stamens are in one whorl the androecium is haplostemonous. When the stamens are distributed in two whorls and the members of the outer verticil alternate with the petals, the androecium is diplostemonous; if the members of the outer whorl are opposite the petals, the androecium is obdiplostemonous. An androecium with more than two stamen whorls is polystemonous (Eames 1961).

The stamens may vary in size and shape, but before dehiscence all anthers have two pairs of microsporangia in the anther lobules. The microsporangia are separated by a zone of sterile tissue called intervenal connective. In some species only one microsporangia develops; however, many bisporangiate anthers are truly tetrasporangiate. At maturity the two contiguous sporangia of each side flow together because the partition separating them breaks down.

All stamen parts can be modified in the evolutionary process. The filament length is variable and may be missing. The microsporangia may be reduced and sterile, and the stamens become staminodia. The zygomorphic flowers have only modified stamens or a reduced number of them.

The gynoecium has a central position and may have one to several free or connate carpels (fig. 8). Each free carpel or gynoecium formed by several carpels has a stigma (structure receiving the pollen), a style (narrow portion below the stigma), and an ovary (wide base containing one or more ovules) (figs. 1 and 8). Some gynoecia lack styles (e.g., *Clusia*, Clusiaceae), but ovaries and stigmas are always present. In the gynoecium, the ovules develop from the placenta. When the gynoecium has individual carpels, the flower is apocarpous (e.g., *Magnolia*); if carpels are connate, the flower is syncarpous (e.g., *Oreomunnea*).

Ovaries have at least two zones: the wall and the locule(s). Multilocular ovaries have a third zone: the septa or partitions (fig. 8). Each carpel has two placentas on the adaxial surface near the margins. When reduction of the carpelar margins is accentuated, the contiguous placentas join and sometimes fuse.

Placentation is the type of ovule distribution in the carpels forming the gynoecium (fig. 9). Carpels are located in the ovary. The primitive, free, laminar carpel has submarginal placentation because ovules develop in the placenta between the dorsal and ventral bundles. The closed carpel usually has laminar placentation such as in Mimosoideae, Caesalpinioideae, and Papilionoideae. When the ovule develops close to the ovary base it is basal even when it is morphologically pseudobasal (e.g., *Calophyllum brasiliense*, *Virola koschnyi*). The suspended ovules are near the distal end of the ovary (e.g., *Allocasuarina*, *Roupala montana* Aubl., *Terminalia amazonia*). When the carpels

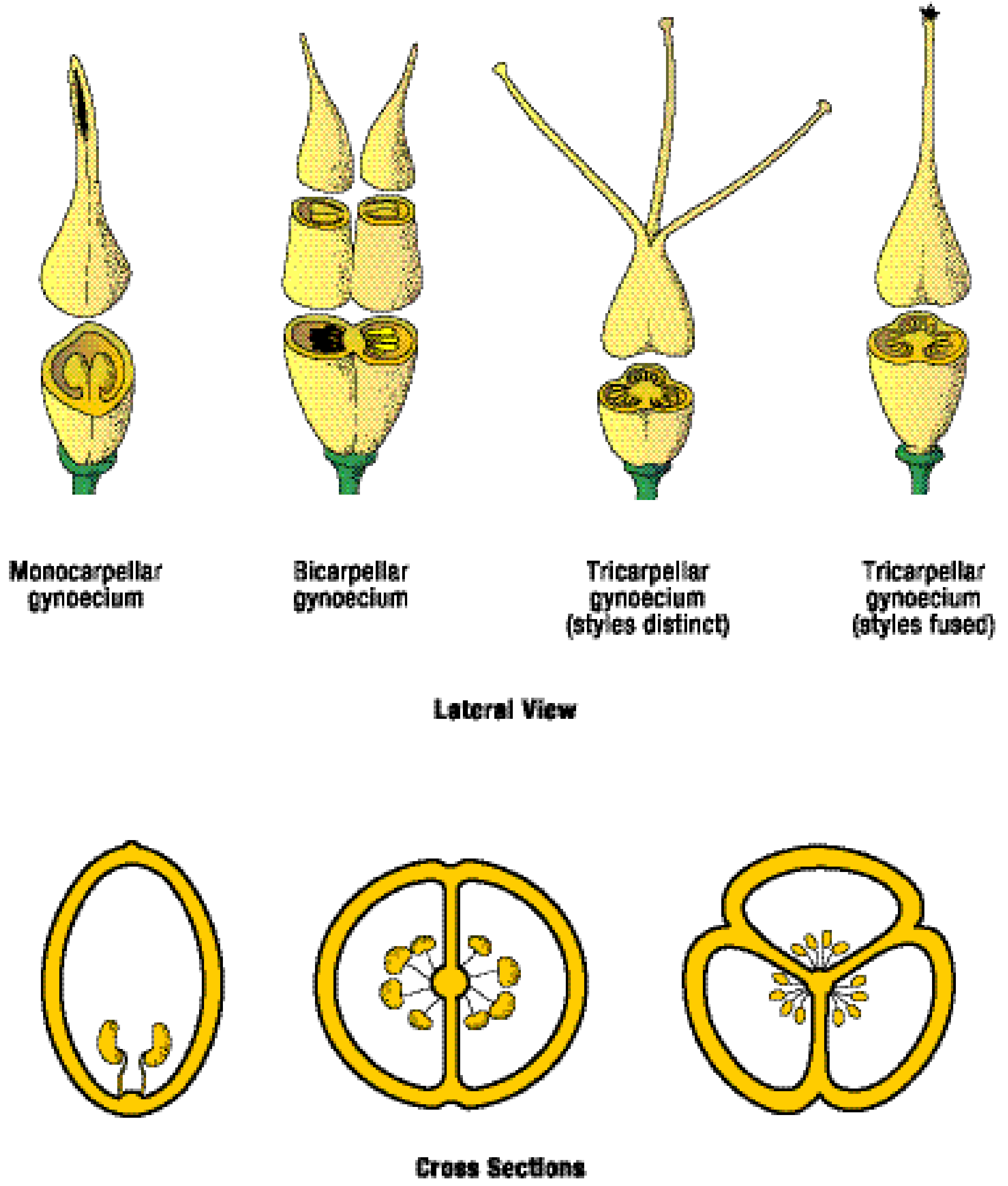


Fig. 8. Different gynoecium types.

are open and connate (syncarpous), placentation is parietal (e.g., *Bixa orellana*, *Escallonia myrtilloides, Hasseltia floribunda, Homalium racemosum*, *Casearia arborea*); if the carpels are closed and connation occurred after closing, placentation is axilar (e.g., *Lecythis ampla*, *Vochysia*, *Luehea seemannii* Triana & Planch., *Pseudobombax septenatum*, *Swietenia macrophylla* King, *Cedrela odorata* L.). In some cases, the carpel walls or septa dividing the ovary in locules are destroyed during development. A central column appears in the ovary, and the ovules appear attached to it. This placentation is free-central (e.g., *Theobroma cacao).* If the carpels forming a syncarpous gynoecium were open before connation, usually only a central locule forms. Generally, a carpel has three vascular bundles: a dorsal (median) vein and two ventral (lateral, marginal) veins. Many

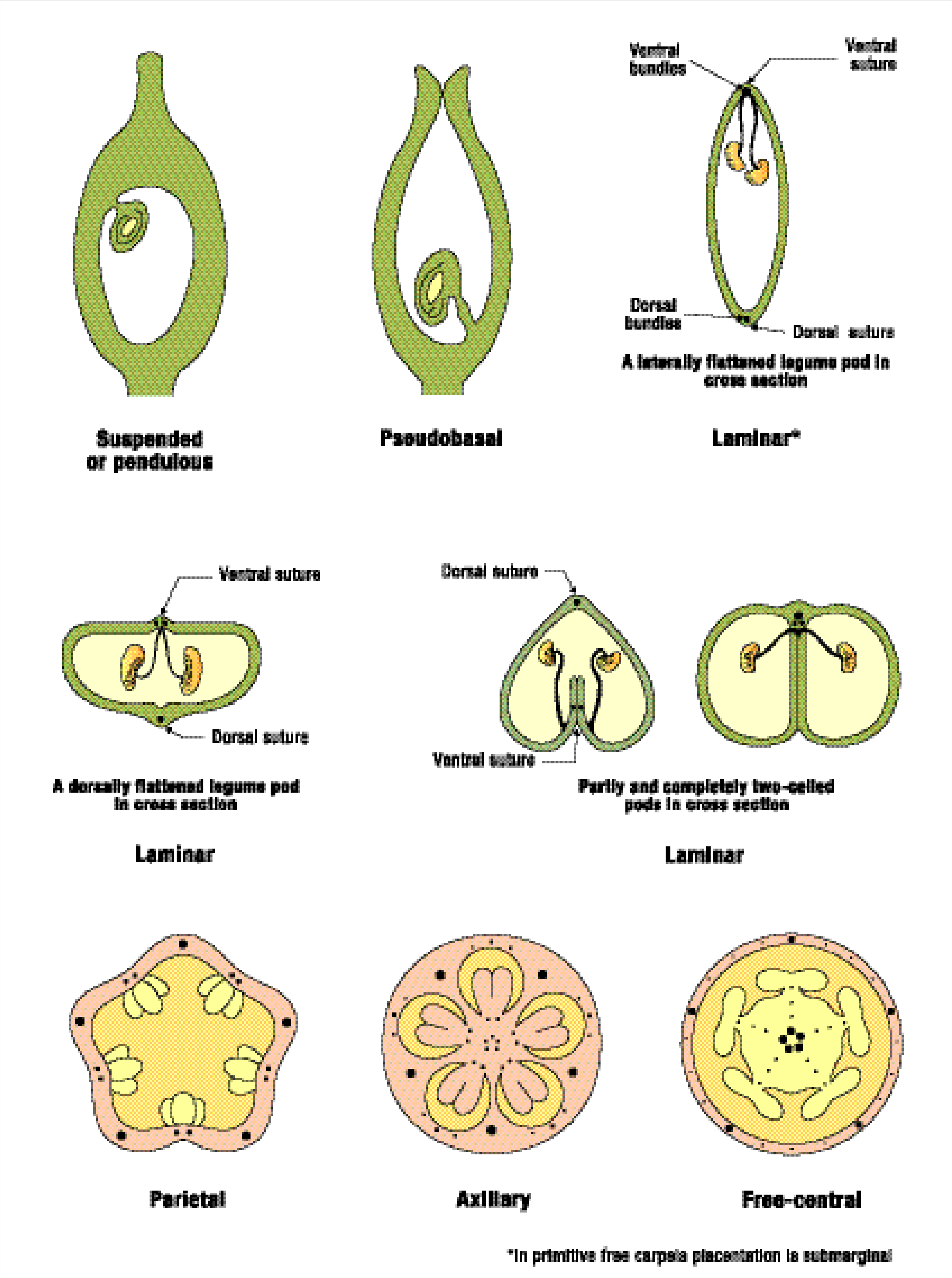


Fig. 9. Placentation types.

carpels have additional veins while others have lost veins by reduction and have fewer than the basic three.

When the gynoecium is in the distal end of the floral axis, the ovary is superior and the flower hypogynous (fig. 10). When the gynoecium occupies the lowest level in the floral axis and its wall is adnate to the floral tube or hypanthium to which the other floral organs (perianth and androecium) are attached, the ovary is inferior and the flower is epigynous. Some flowers have the perianth and androecium attached to the floral tube or hypanthium surrounding the ovary without fusing to it. These flowers are perigynous and the ovaries are semi-inferior. They are transitional forms to epigyny. More complicated classifications include several subtypes (see Radford and others 1974).

The style is the narrow carpel zone located between the ovary and the stigma. In the syncarpic gynoecia that bear a single style, tissues of the carpels integrating the gynoecium form the style. The carpels may be partially fused distally, where the style is a single structure at the base and a compound one at the top. The style may have stylar branches (stylodes); usually, one stylode per carpel (e.g., *Hibiscus*), and the styles or stylodes can be solid or have a central canal (hollow).

The stigma is the receptive surface that captures the pollen grains. It is formed by specialized surface cells that connect to the stylar tissues. Style and stigma morphology is diverse; it depends on flower structure and pollination type (fig. 10). The stigma captures and accepts the pollen and provides a suitable environment for pollen germination. The stigma can provide nutrients to the pollen and orient pollen tube growth; it also helps regulate flower metabolism (Van Went and Willemse 1984). The stigmatic surface must provide balanced osmolarity and the necessary water supply to promote pollen germination. Frequently, changing environmental conditions delay pollination, and the style and stigma must maintain the vitality to continue functioning.

The pollen wall and the stigmatic surface are involved in the cellular reception and recognition of signals or stimuli. Some of the macromolecules involved in this mechanism are allergic substances, stigmatic antigens, carbohydrates, proteins, gycoproteins, and glycosphingolipids (Ferrari and others 1985, Flores 1999, Shivanna and Sastri 1981).

Stigmas are divided into two categories: wet stigmas, with a copious fluid secretion; and dry stigmas, with a slight fluid secretion. The dry stigmas have receptive cells dispersed in multiseriate stylodes or concentrated in ridges, zones, or heads. Those with specialized reception areas may be separated into papillate and nonpapillate stigmas (Van Went and Willemse 1984). Wet stigmas have a receptive surface with small or medium-sized papillae. The binucleate pollen grains seem correlated to wet and dry stigmas, while trinucleate pollen grains are associated more with dry stigmas (Van Went and Willemse 1984).

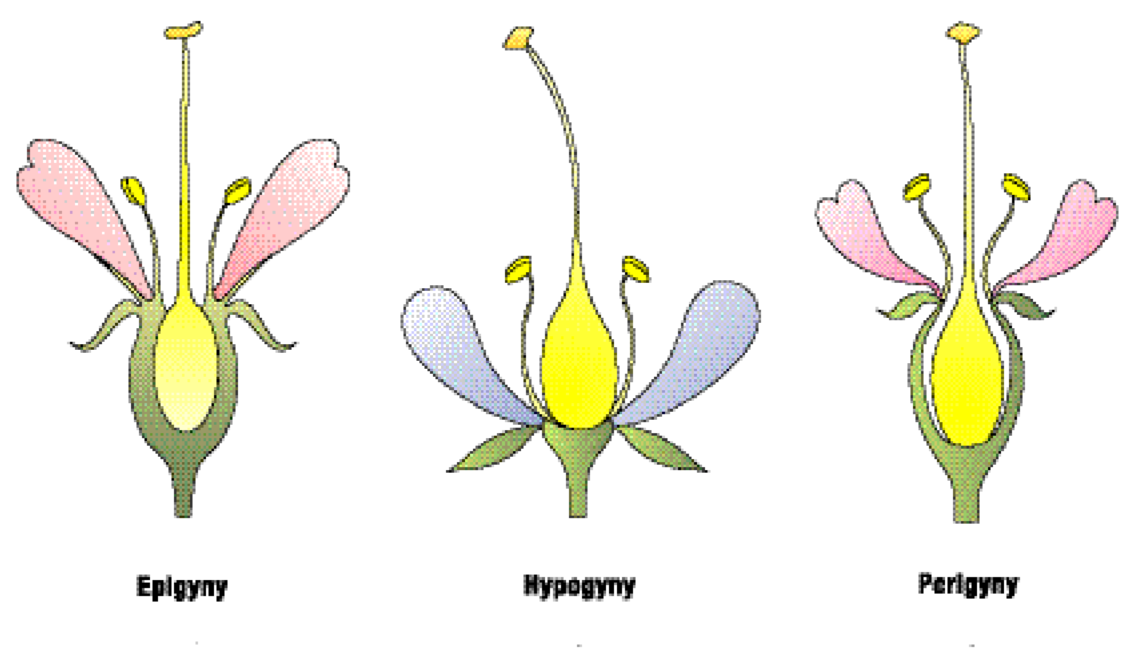


Fig. 10. Ovary position and flower types.

Sexual Expression in the Flower, the Inflorescence, and the Sporophyte

The morphology and physiology of the flower in tropical trees are varied and are associated with pollination and the sexual systems of the species. Plants can be either self- or cross-pollinated; however, sex separation in space or time, as well as self-sterility (homogamy) are frequent mechanisms used to favor cross-pollination. In the individual flower the separation of sexes in space has three modalities (fig. 11a):

Perfect, bisexual, or hermaphrodite. Flowers with pistillate (gynoecium) and staminate (androecium) organs. Examples include: *Persea americana* Mill., *Dipteryx panamensis, D. oleifera, Samanea saman, Stryphnodendron microstachyum, Vochysia guatemalensis* Donn. Sm., *Pentaclethra macroloba, Terminalia amazonia, Lecythis ampla,* and *Sideroxylon persimile.*

Unisexual. Single-sex flowers with androecium or gynoecium. Examples include *Brosimum alicastrum* Sw., *Diospyros nicaraguensis*, *Hura crepitans* L., *Hyeronima alchorneoides* Allemao., and *Virola koschnyi*. In species such as *Carapa guianensis* Aubl., the flowers are unisexual (male or female) but maintain vestiges of the other sex. There are two subtypes of unisexual flowers:

(1) **Staminate or male**—Flowers with an androecium but no gynoecium. For example: *Batocarpus*, *Casuarina*, *Hyeronima*, *Otoba novogranatensis,* and *Virola.*

(2) **Pistillate, carpellate, or female**—Flowers with a gynoecium but no androecium. For example: *Batocarpus, Casuarina, Hyeronima, Otoba novogranatensis, and Virola.*

Neutral or agamic. Sterile flowers with abortive or no sexual organs.

In the inflorescence, the spatial separation of sexes may have numerous variations and combinations (fig. 11b). In the individual tree, the sexual expression must be as follows:

Hermaphrodite or monoclinous. Tree with only hermaphrodite flowers (bisexual). For example: *Pentaclethra macroloba, Stryphnodendron microstachyum*, and *Terminalia amazonia.*

Monoecious or diclinous. Tree with both staminate and pistillate flowers. For example: *Artocarpus*, *Carapa guianensis*, *Hernandia didymantha*, *Poulsenia armata*, and *Ricinus communis.*

Dioecious. Tree with only one type of unisexual (imperfect) flowers. For example: *Virola*, *Hyeronima*, and *Batocarpus.* There are two subtypes:

(1) **Gynoecious, pistillate, or female**—Trees with only pistillate flowers. For example: *Guarea rhopalocarpa*, *Hampea*, *Virola*, and *Hyeronima*.

(2) **Androecious, staminate, or male**—Trees with only staminate flowers. For example: *Ilex*, *Myristica fragrans*, *Siparuna grandiflora*, *Virola koschnyi*, and *Hyeronima alchorneoides.*

Androdioecious. Some trees with hermaphrodite flowers and others with staminate or male flowers.

Andromonoecious. Tree with both hermaphrodite and staminate flowers. For example: *Calophyllum brasiliense*, *Parkia bicolor*, and *Schefflera*.

Gynodioecious. Some trees with hermaphrodite flowers and others with pistillate or female flowers. For example: *Ocotea tenera.*

Gynomonoecious. Tree with both hermaphrodite and pistillate flowers.

Polygamous or trimonoecious. Tree with hermaphrodite, pistillate, and staminate flowers. For example: *Aesculus hippocastanum* and *Gyrocarpus jatrophifolius.*

Polygamo-dioecious. Staminate, pistillate, and hermaphrodite trees in the same species. For example: *Coccoloba uvifera* (L.) L.

In many plants, a mechanism under genetic control prevents the ovules being fertilized by pollen from the same tree. In these species, the pollen may reach the stigma of its own flower but fertilization does not occur. In dioecious species, cross-pollination is the only alternative; in monoecious species, the separation of sexes into different flowers promotes but does not guarantee cross-pollination.

The separation of sexes by time prevents self-pollination in hermaphrodite flowers; the stamens and stigmas mature at different times, diminishing the possibility of self-pollination. The separation of sexes by time is known as dichogamy. There are two modalities of dichogamy:

Protandry (protandrous flowers). Stamens mature first and pollen release occurs before stigmas are receptive.

Protogyny. Stigmas mature first and are receptive and functional before anther dehiscence and pollen release.

Protandry is common in legumes (Fabaceae) and Malvaceae; protogyny is frequent in many families including

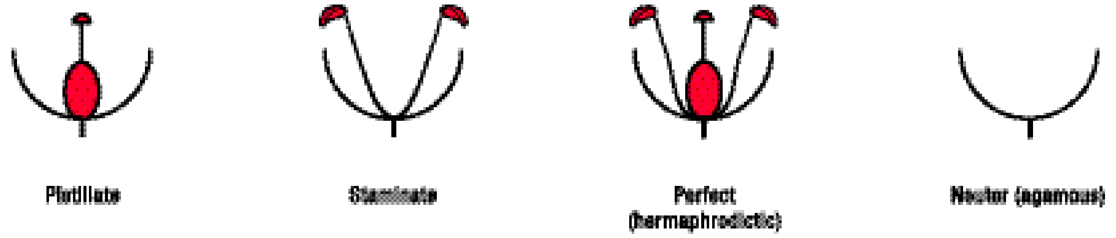


Fig. 11a.

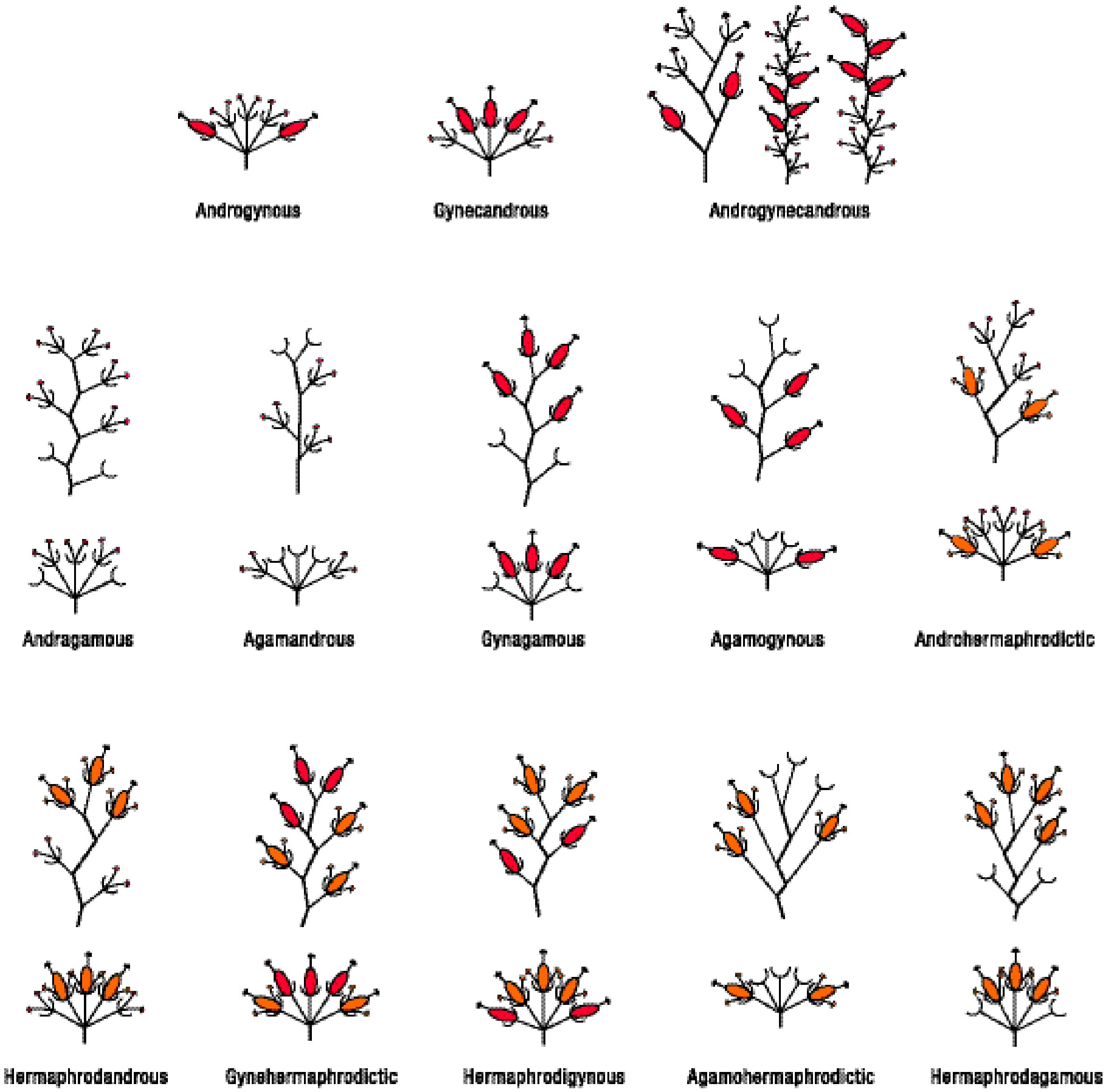


Fig. 11b. Inflorescence sex. (Redrawn from Radford *et al.* 1974).

Moraceae (*Ficus*), Rosaceae, Annonaceae (some *Annona*), Chrysobalanaceae, Combretaceae, and Lauraceae.

In Lauraceae, the flowers are protogynous (proterogynous) and the floral mechanism in the family is the synchronized dichogamy (Frankel and Galun 1977, Kubitzki and Kurz 1984). In the family, the species have two types of flowering in different individuals. In some, the flowers have receptive stigmas (opening of the female phase) in the early morning, ceasing activity at noon (closing of the female phase). In the afternoon of the same day or the following day, the stamens release pollen (opening of the male phase), ceasing activity at dusk (closing of the male phase). In other trees, the flowers have receptive stigmas in the afternoon and cease activity at dusk. The following morning, the stamens release pollen. This mechanism preventing self-pollination and cross-pollination becomes obligatory (Frankel and Galun 1977, Kubitzki and Kurz 1984). If the rhythm is disturbed by changing climatic conditions, the flower could be pollinated and fertilized by pollen coming from another flower in the same tree (geitonogamy), but the fruits undergo an early abscission. A postzygotic mechanism of incompatibility has been suspected (Kubitzki and Kurz 1984). Dichogamy has also been documented in Annonaceae [*Annona squamosa, A. cherimolia, A. reticulata, Cananga odorata, Rollinia membranacea* (syn. *R. jimenezii*), Betulaceae (*Alnus acuminata*) and Combretaceae (*Terminalia amazonia*)] (Deroin 1988; Flores 1994g; Flores and Sandí 1995; Gottsberger 1989a, 1989b, 1993; Kubitzki 1993). *Terminalia amazonia* has protogynous flowers. It is believed that the flowers are pollinated by pollen coming from the flowers of other trees (xenogamy); however, sporadic geitonogamy appears to occur. In this species, a postzygotic mechanism of incompatibility has also been suggested (Flores 1994g, Flores and Sandí 1995).

In numerous species, the dichogamy is partial and the second sexual phase begins before the first sexual phase is over. The flowers are functionally unisexual in the initial phase and bisexual (hermaphrodite) in their terminal phase (Faegri and Van der Pijl 1971, Frankel and Galun 1977). For example, the flowers of *Symphonia globulifera* L.f. are protandrous, with a bisexual phase in which the stigma is receptive and the anthers release pollen (Pascarella 1992).

The homogamous (self-sterile) hermaphrodite flowers release and accept pollen at the same time; nevertheless, they are not always autogamous. Both morphological (heteromorphic autoincompatibility) and physiological (homomorphic autoincompatibility) mechanisms may prevent self-pollination, self-fertilization, or seed development, thus promoting self-sterility (Faegri and Van der Pijl 1971, Frankel and Galun 1977).

Heteromorphic self-incompatibility is characterized by intraspecific differences in floral structure, reinforcing cross-pollination and cross-fertilization. Floral heterostyly is the most typical mechanism. In this case, two or three floral morphs exist. A distylous species has two floral morphs; in some flowers the styles are long, in others they are short. In the flowers with long styles, the stamens are found below the stigma level while in those with short styles, the stamens are above the stigma level. Other features are usually associated with style length. Morphs with long styles and short stamens have small pollen grains and long stigmatic papillae; morphs with short styles and long stamens have big pollen grains and small stigmatic papillae (Boshier 1995). These features favor cross-pollination between the two floral morphs. However, some species have a diallelic mechanism of incompatibility, lacking stylar and staminal polymorphism, and others have a polymorphism that is reduced to the style (Ganders 1979).

The homostyly of neotropical laurel [*Cordia alliodora* (Ruiz & Pav.), Boraginaceae] flowers has been described repeatedly (Johnston 1950, Miller 1985, Opler and others 1975); however, the species has a kind of heteromorphy restricted to stylar variation, and the small flower size may hinder differentiation between style and stigma (Boshier 1995). Additionally, two tree groups exist in which intercrossing is possible but intracrossing is not. The low variation in stylar length must be associated with a diallelic incompatibility system in the sporophyte (Boshier 1995).

Heterostyly is a type of genetically controlled polymorphism shared by at least 25 families of angiosperms (Ganders 1979), e.g., *Byrsocarpus, Rudgea, Psychotria, Turnera ulmifolia, Erythroxylum coca*, and *Cratoxylum* (Barrett and Richards 1990, Bawa 1992, Bawa and Beach 1983, Bawa and others 1985a, Bawa and others 1990). In distylous species, the polymorphism acts in conjunction with a diallelic incompatibility system to prevent self- and intramorphic fertilization (Boshier 1995).

Homomorphic autoincompatibility can be divided into two subtypes (Radford and others 1974):

Gametophytic. Fertilization is inhibited as a result of genetic action in the pollen grain (male gametophyte) when the pollen tube protrudes through the stigmatic-stylar tissues (e.g., *Tectona grandis* L.f.).

Sporophytic. Inhibition of pollen germination or pollen tube growth is imposed by genetic action of the sporophytic tissues such as the stigma, the style, and sometimes the embryo sac; e.g., *Dalbergia retusa* Hemsl., *Dalbergia miscolobium, Dipteryx panamensis, Myrospermum frutescens* and probably *Terminalia amazonia* (Barrett and Richards 1990, Bawa and Beach 1983, Flores and Sandí 1995).

The incompatibility systems share a common factor: both maintain a high degree of genetic heterozygocity in the species population. With a few exceptions, the incompatibility system operates at the stigma or style level. Because both structures have diploid tissues and a sporophyte genome (parent tree), the incompatibility reaction is controlled by the genome of the parent tree. The male gametophyte (pollen grain) has in part the genome of the sporophyte in which it develops and some sporophytic components. Thus, the incompatibility reaction of the pollen can be controlled by the gametophyte itself or by the sporophytic components carried with it. In the gametophytic incompatibility the haploid genome of the pollen and the diploid genome of the stigma/style genetically control the pollen-stigma/style interaction. Incompatibility that occurs in the embryo sac is haploid-haploid (Frankel and Galun 1977). The sporophytic incompatibility is determined by the genome reaction of the paternal sporophyte from which the pollen grain originated.

In some species, homogamous flowers can be cleistogamous. In these flowers, pollen release and stigma receptivity are synchronized before floral perianth opening. Species with this type of flower include *Annona muricata*, *Cyathocalyx*, *Dasymaschalon*, *Goniothalamus* sp. in Annonaceae (Kessler 1993), *Lithospermum caroliniense* (Levin 1972), and *Coffea arabica* (Rubiaceae). If the maturation and functioning of the unisexual flowers (staminate and pistillate) in a monoecious tree are not synchronized, cross-pollination is obligatory. In dioecious species, cross-pollination and cross-fertilization are obligatory. The forests in the lowlands of the Atlantic coast in Costa Rica show dominance of species with hermaphrodite flowers in the canopy and subcanopy; dioecious species have a lower representation and monoecious species are scarce (Bawa and others 1985a, b).

Inflorescence Types

Because the traditional nomenclature used to describe inflorescences, which shows morphological inconsistencies, is widely used, descriptions and definitions follow. The stem bearing the inflorescence is the peduncle, while that bearing the flower is the pedicel. The flowers develop in the bract axil; if the inflorescence lacks bracts it is ecbracteate. The groups or whorls of bracts form an involucre; secondary involucres, as in the compound umbels, are involucels of bractlets. When a single conspicuous bract subtends a floral group (usually a fleshy spike or spadix), it is called a spathe.

The most common types of traditional inflorescences are the following (see fig. 12):

Dichasium. Peduncle with a terminal flower and a pair of branches, each producing a single flower. The central flower matures first. The simple dichasium can be repeated as a unit several times giving rise to a compound dichasium. The dichasium has been named cyme, but the term is used indiscriminately and its use is inappropriate.

Monochasium. Peduncle with a terminal flower and a basal lateral branch bearing a single flower. The simple monochasium can be replicated several times giving rise to a compound monochasium, which may form the following subtypes:

(1) **Bostryx (helical monochasium)**—Flower distribution spirally coiled around the main axis.
(2) **Cincinnus**—Flowering alternately to one side and then the other along one side of the axis, the whole inflorescence often coiling downward.
(3) **Rhipidium**—A bostryx is extended in one plane, and the inflorescence is sometimes fan-shaped.
(4) **Drepanium**—A cincinnus bears all the branches on one side. The inflorescence extends in one plane and coils downward to one side.

Panicle. Inflorescence with a central axis giving rise to lateral branches that are themselves branched. The minor ramifications can be dichasial. A crowded, nearly cylindrical panicle is called a thyrse.

Raceme. Inflorescence with a central axis, along which simple pedicels of similar length are located. The blooming usually proceeds upwards, although it may be irregular.

Spike. Elongated inflorescence with an unbranched central axis with sessile or subsessile flowers. The blooming usually proceeds upwards. The spikelet or locusta is the basic unit of the inflorescence in grasses and sedges.

Corymb. Flat-topped inflorescence with a central axis giving rise to branches of unequal length. The lateral branches may branch further or be simple pedicels. Blooming usually begins in the external flowers and proceeds centripetally, but can also be irregular.

Head (capitulum). A determinate or indeterminate, rounded or flat-topped cluster of flowers placed at the same level. The flowers can be sessile or subsessile and are placed on a wide receptacle. Blooming usually begins at the periphery and proceeds centripetally. Heads may be solitary or form diverse aggregates. Each bract of the involucre is a phyllary.

Umbel. Inflorescence with several branches arising from a common point, in the distal end of the peduncle. If each branch ends in a single terminal flower, the umbel is simple; if

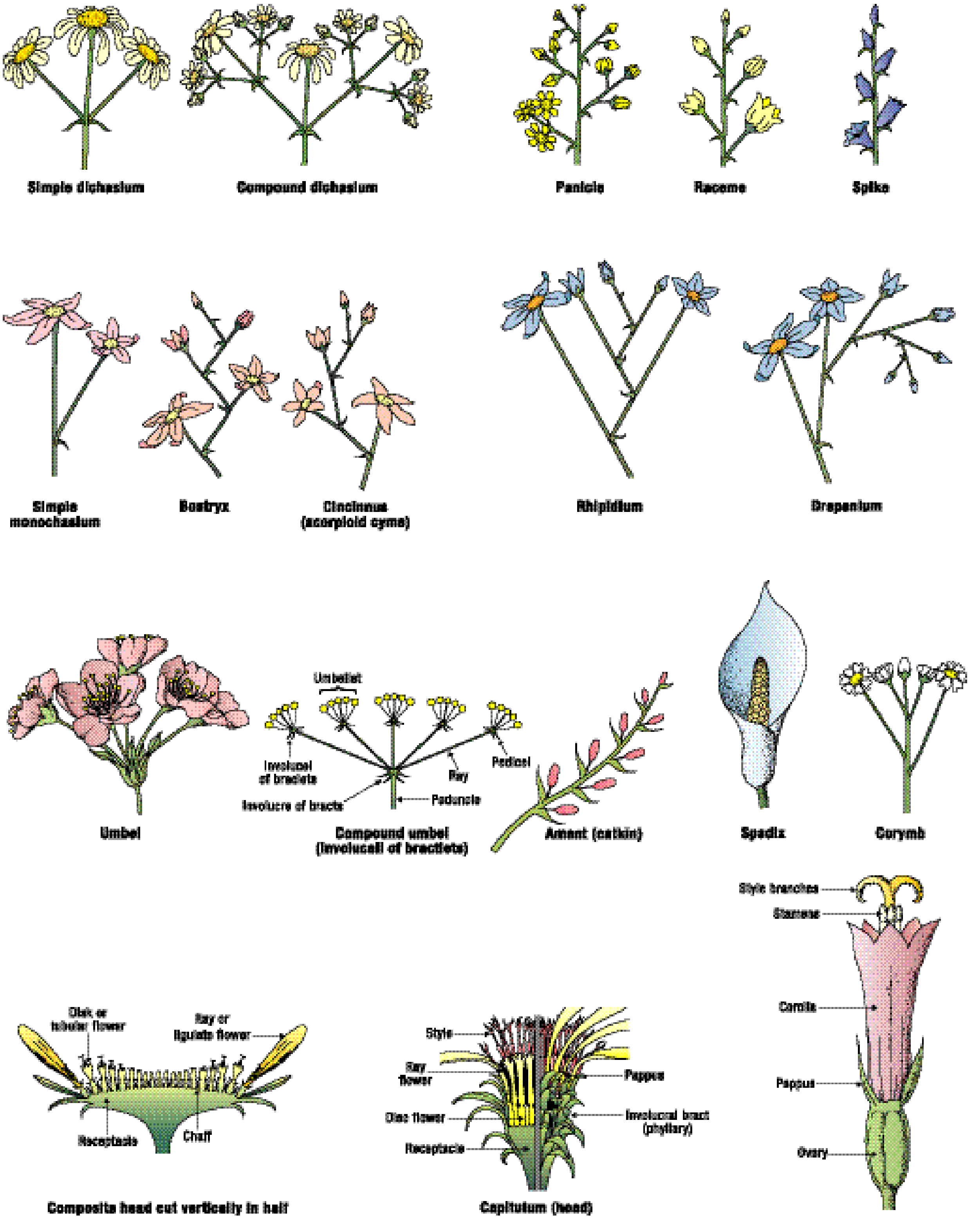


Fig. 12. Morphological inflorescence types

it ends in a secondary umbellate, the umbel is compound. Flowering usually begins in the peripheral flowers and proceeds centripetally. The umbel may have an involucre at the peduncle distal end. If the umbellates have similar whorls of bracts, they are involucels and each bract is a bractlet. The main branches of a compound umbel are rays, and the corresponding members of the umbellate are pedicels.

Ament (catkin). Spike, raceme, or dichasium of apetalous unisexual flowers. It can be long or short, erect or hanging. The flowers are usually very small and subtended by a scaly, small bract.

Spadix. Spike with a thick, fleshy apex, surrounded by a large, usually colored bract (spathe). Frequently, the flowers are very small and unisexual.

Siconium (hypanthodium). Inflorescence with small flowers on the wall of a concave head.

Other inflorescence types include:

Glomerule. Inflorescence formed by an indeterminate cluster of sessile or subsessile flowers.

Verticillaster. A group of whorled dichasia at the nodes of an elongated axis.

Pseudanthium. Inflorescence with several flowers simulating a single flower but composed of more than a single axis bearing subsidiary flowers. The pseudanthium is subtended by an involucre: scapose, with a single flower or inflorescence on a leafless peduncle; or scape, usually arising from a basal rosette.

Reproductive Cycle

During the flowering period of angiosperms, the tree or sporophyte produces microspores forming microgametophytes or pollen grains, and megaspores producing megagametophytes or embryo sacs inside the ovules (Flores 1999). In most angiosperms the entire reproductive cycle, from floral inception to fruit and seed maturation, occurs in one season (fig. 13); however, there are exceptions such as the red oak (*Quercus* subg. *Quercus*) (Bonner and others 1994) and *Allocasuarina* (Flores 1976, Flores and Moseley 1982).

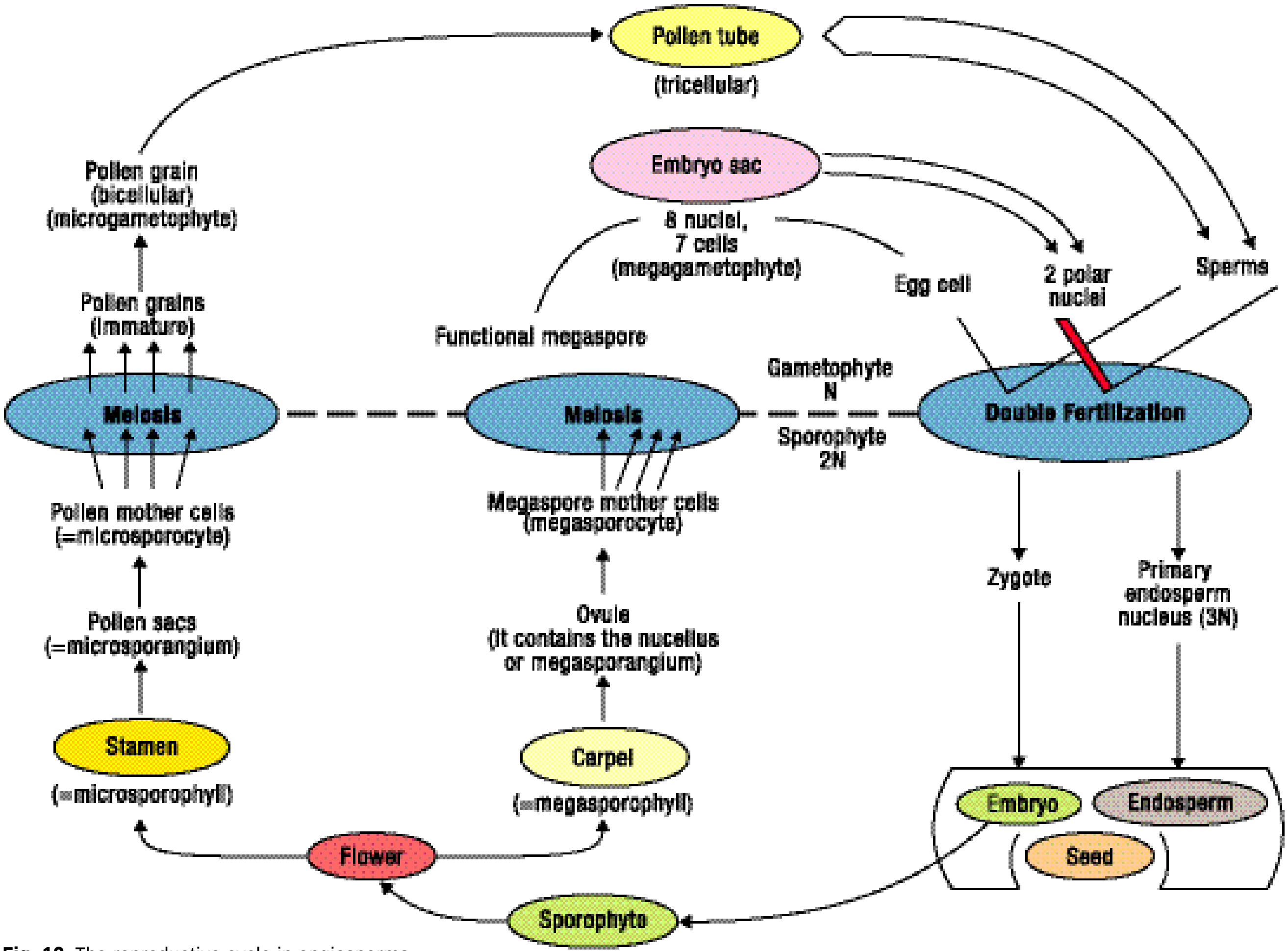


Fig. 13. The reproductive cycle in angiosperms.

Pollen

The embryonic anther has a mass of fundamental tissue surrounded by a protodermis. This layer forms the epidermis of the anther. In the four corners of the developing anther, two to four hypodermal cells are formed; each group divides periclinally forming a series of primary parietal cells and primary sporogenous cells (internal layer). Figure 14 shows the histogenesis of a typical anther; figure 15 illustrates the structure of a mature anther. In the mature anther the outer layer or epidermis covering the microsporangium wall may remain intact in families such as Lauraceae, Magnoliaceae, and Winteraceae. In others, such as Moraceae and Ulmaceae, the epidermal cells restrain or fall down during anther maturation. In some species, the epidermis has trichomes; in others, it develops fibrillar bands and is called an endothecium. If the epidermis falls down, the underlying layer substitutes for it. This layer is commonly called the endothecium or fibrous layer because it has cell wall thickenings; these thickenings are absent in the stomium.

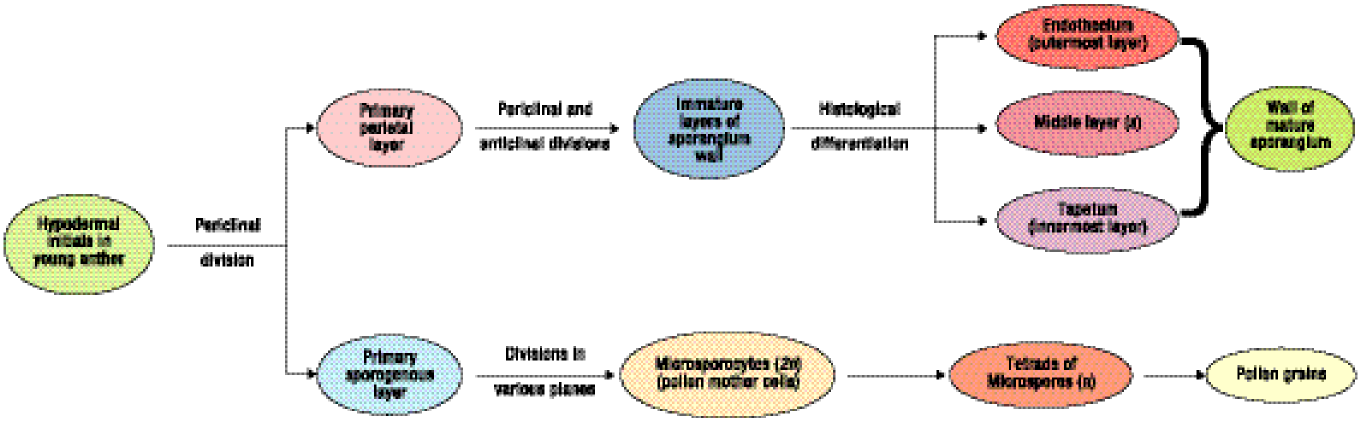


Fig. 14. General pattern of development of the microsporangium in the angiosperms.

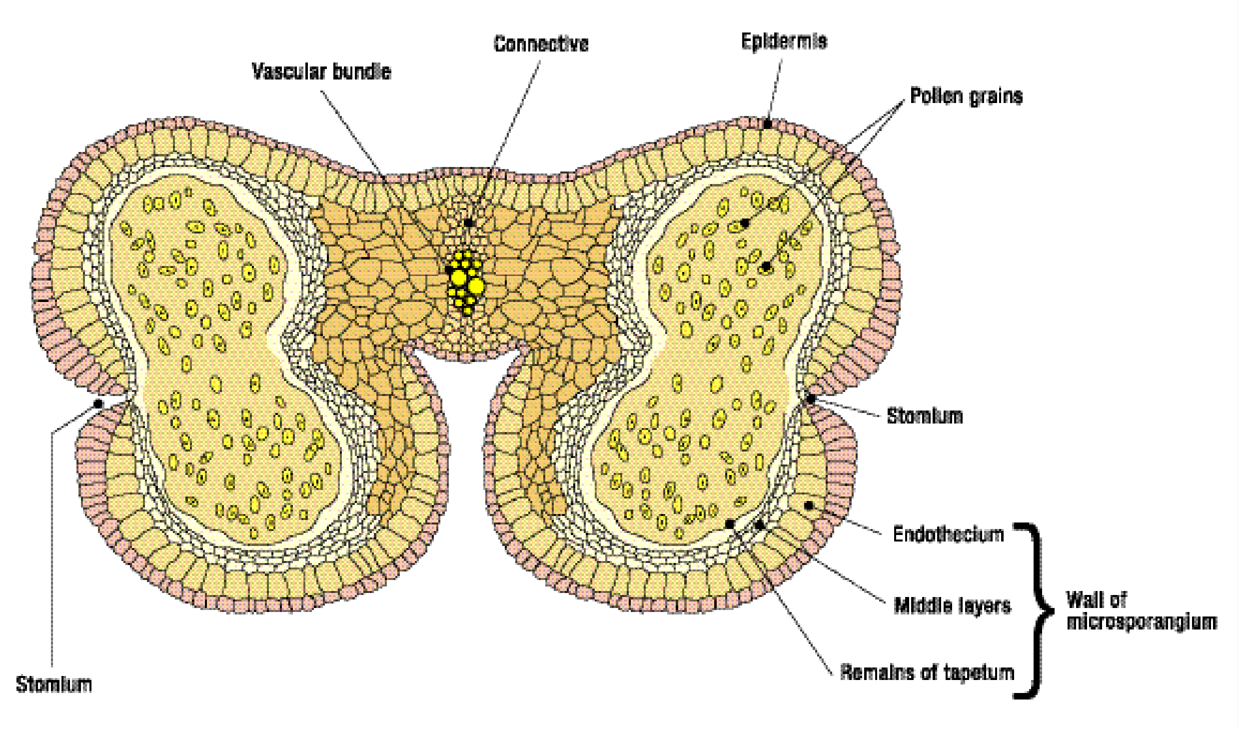


Fig. 15. Mature anther.

Middle layers consist of one or several layers of tubular cells with thin walls beneath the endothecium. These layers are compressed or crushed during microspore formation. The inner layer of the microsporangium wall is the tapetum. It seems to accomplish three functions: microspore nutrition, exine formation, and synthesis of some materials contributing to pollen grain wall formation (tryphine and pollenkitt). In angiosperms the tapetum can be glandular (secretory) or periplasmodial (amoeboid). In the first case, the cells remain intact and persist in situ; in the second, the cell walls break down and the protoplasts mingle. The protoplasmic mass forms a multinucleate periplasmodium, which becomes mixed with the pollen mother cells.

The cells in the primary sporogenous layer can divide before microsporogenesis, or directly become the microsporocytes or pollen mother cells. These, through meiosis, produce haploid microspores (n) which later differentiate as pollen grains. The cells in the primary parietal layer form, through periclinal and anticlinal divisions, a variable number of layers concentrically placed, which differentiate and become the several layers of the mature sporangium wall (Flores 1999).

Meiosis of the pollen mother cells in the tapetum is the time of the synthesis of substances such as starch, lipids, and tryphine. The tapetum is involved in numerous activities. It keeps a delicate balance with the differentiation of the sporogenous tissue, and any alteration in it induces the degradation of pollen. Some evidence indicates that, through physical or physiological factors, the tapetum may induce the abortion of pollen. The endothecium or the vascular bundle of the filament may influence the abortion process. The carotenoids and carotenoid esters formed in the tapetal cells participate in the formation of the sporopollenin, a major component of the pollen wall. The pollenkitt (Pankow 1957) formed by lipids, glycolipids, glycoproteins, monosaccharides, flavonoids and carotenoids synthesized in the tapetum, gives adhesiveness, order, and color to the pollen grain (Heslop-Harrison 1968, 1979a, 1979b; Hesse 1979). Its probable functions are insect attraction, pollen protection against ultraviolet radiation, and adhesion to insects' bodies; the last function contributes to pollen dispersal (Heslop-Harrison 1968, 1979a, 1979b).

The pollen grain is the structure containing the male gametes. It is formed by a vegetative cell (tube cell) and a generative cell immersed in the vegetative cell cytoplasm (bicellular pollen grain or microgametophyte); both cells are haploid (Brewbaker 1967). If the generative cell divides mitotically and gives rise to the spermatic cells during pollen maturation and before pollen tube development, the pollen grain is tricellular (fig. 16). The nucleus of the vegetative cell controls the pollen tube's metabolism as well as its initial growth after germination. The spermatic cells have self-motility, are structurally different, and may have different patterns of cytoplasmic genetic transmission (Flores 1999, Knox 1984, Russell and Cass 1983).

The pollen grain covering is complex and is formed by the exine (external layer formed by sporopollenin and charac-

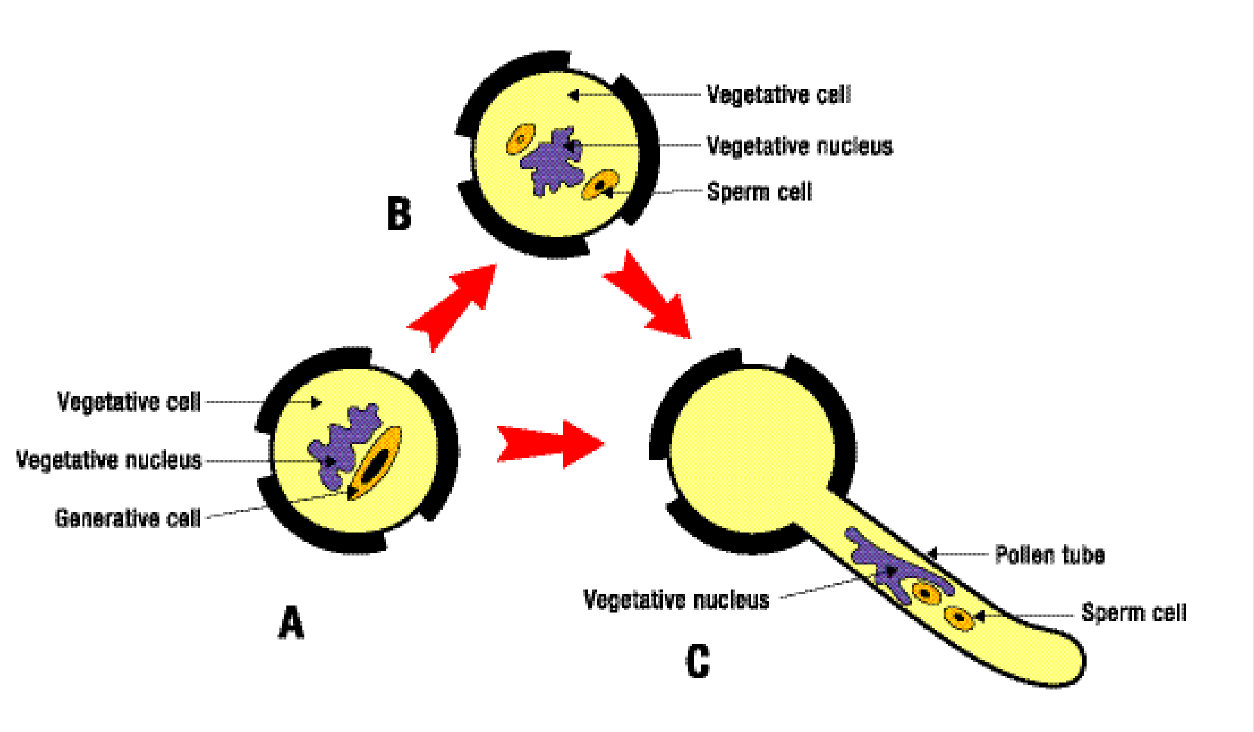


Fig. 16. Pollen grain types and pollen germination. a, Bicellular pollen grain; b, Tricellular pollen grain; c, Pollen germination and tube development.

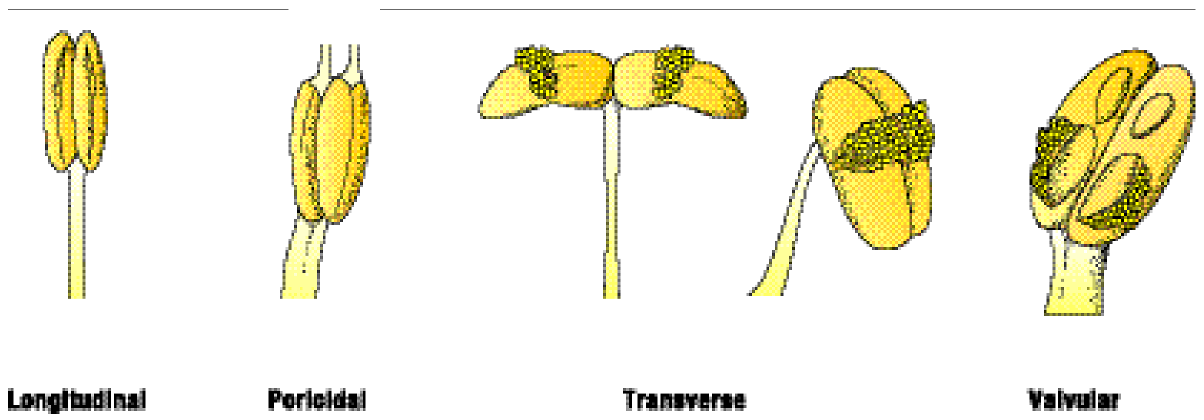


Fig. 17. Anther dehiscence.

terized by a specific ornamentation) and the intine (smooth inner layer made of polysaccharides). The layers are chemically, morphologically, and ontogenetically different (Knox 1984). Cell wall formation follows different patterns in different species, as an adaptation to various factors including cellular environment, pollination method, and potential interactions with the different pollination vectors.

The correlation between exine structure and pollination method has been corroborated in diverse families pollinated by both wind and animal vectors (Knox 1984). The transportation methods and the structures expediting pollen adhesion to the stigma are adaptations; for example, exine thickness and ornamentation, aperture type, and wall adhesives (Heslop-Harrison 1968, 1979a, 1979b; Heslop-Harrison and others 1973). Pollen-stigma recognition and the allergic reaction in humans (pollen wall proteins and glycoproteins) are also adaptations. Pollen germination and pollen tube growth throughout the style involve the action of specific enzymes and heterotrophic nutrition; these conditions represent a high degree of specialization.

The pollen of most angiosperms is a free cellular structure (monad), but in some families there are compound grains. Compound grains can be arranged in tetrads (a microsporocyte product), polyads of grains, or complex masses *(*pollinia). The tetrads may have zero to four fertile grains mixed with a remnant of abortive grains. Pollen shape, a genetically determined feature, is influenced by three factors: microspore position in the tetrad, number and disposition of germinal apertures, and differential cellular expansion during microspore and pollen grain development.

Anther dehiscence is the mechanism of pollen release. In some families the pollen is released through a small opening usually placed at the distal end of the anther. This type of dehiscence is poricide (e.g., *Hyeronima alchorneoides*, *Conostegia*, *Miconia*, *Gustavia*). In most species, however, the anther dehisces longitudinally along the stomium (longitudinal dehiscence; e.g., *Vochysia*, *Alnus acuminata*) (fig. 17). If the anther is oriented outward and dehisces longitudinally to the exterior, it is called extrorse; if it is oriented inward and dehisces longitudinally to the interior, it is introrse (*Lacandonia*). In other species the anther opens transversely (transverse dehiscence; e.g., *Brosimum alicastrum*). Although the force opening the stomium seems to be generated in the endothecium, this issue is still a matter of discussion. The dehiscence is not always produced by changes in the fibrous layers; in many anthers, especially those of the poricide type, this layer is missing.

Anthers with a complex shape are usually associated with special types of poricide dehiscence and have tubular projections in the pollen sac ends, through which the pollen is released. The anthers with elongated, narrow openings may have a valve. This type of dehiscence is valvular and occurs in Hernandiaceae (*Hernandia stenura*), Lauraceae (*Ocotea*, *Nectandra*), and Monimiaceae (*Mollinedia*, *Siparuna*) (fig. 17). The valve opens at the base and projects outward and backward, carrying the pollen mass outside (Flores 1999). The number and distribution of valves has taxonomic value in Lauraceae.

Ovule

The nucellus (megasporangium), integument(s), chalaza, and funiculus form the typical ovule (fig. 18). The nucellus occupies the central part of the ovule and is surrounded by the integuments. These leave a passage (micropyle) for pollen tube penetration. The integuments protect and nourish the nucellus. After fertilization, they form the seedcoat, the raphe, and the chalaza. The ovules can be bitegmic, unitegmic or ategmic. In some Annonaceae *(Cananga odorata*, *Cleistopholis patens*, *Cyathocalyx sumatranus*, *Guamia mariannae*, *Mezzetia leptopoda*, *Mezzettopsis creaghi*) a third integument, placed between the testa and the tegmen, has been proposed (Corner 1976, Kubitzki 1993). The third integument in the Opuntieae (Cactaceae) is a funicular covering surrounding the seed (Flores and Engleman 1976). The funiculus is an extension, usually filamentous, that unites the ovule with the placenta. The funiculus has a vascular bundle transporting nutrients from the sporophyte to the megagametophyte (Bouman 1984, Flores 1999, Maheshwari 1950).

Frequently, the ovule has special structures:

Hypostase. Usually cupuliform, formed by differentiation of nucellar and chalazal tissues. It is located on the chalazal vascular bundle and can be a cell mass or a discoid cell plate. It is found in the ovules of the Anacardiaceae, Bixaceae, Euphorbiaceae, and Lauraceae. It is considered a physical barrier to retain embryo growth and a bridge connecting the chalazal vascular bundle with the embryo sac, which facilitates nutrient transfer to the embryo sac (Bouman 1984, Flores 1999, Tilton 1980). Other functions include producing enzymes and hormones and maintaining water balance in dormant seeds.

Podium. A nucellar remnant, resistant to the absorbing activity of the embryo sac. This structure is located at the nucellar base and is cupuliform in shape. When it is located near the micropylar end, it is epistase. After fertilization, it generally precludes the micropyle (Bouman 1984, Flores 1994a).

Obturator. Formed by funicular, placental, or funicular-placental tissues. It is a protuberance covered by secretory trichomes or epidermal papillae, functioning as transfer cells. The obturator surface extends to the micropyle or enters through it. In general, it is continuous with the ovarian, stylar, and stigmatic tissues through which the pollen tube penetrates. After pollination, the obturator degenerates (Bouman 1984, Flores 1999).

The ovules have different forms and degrees of curvature: athropous (orthotropous), anatropous, campylotropous,

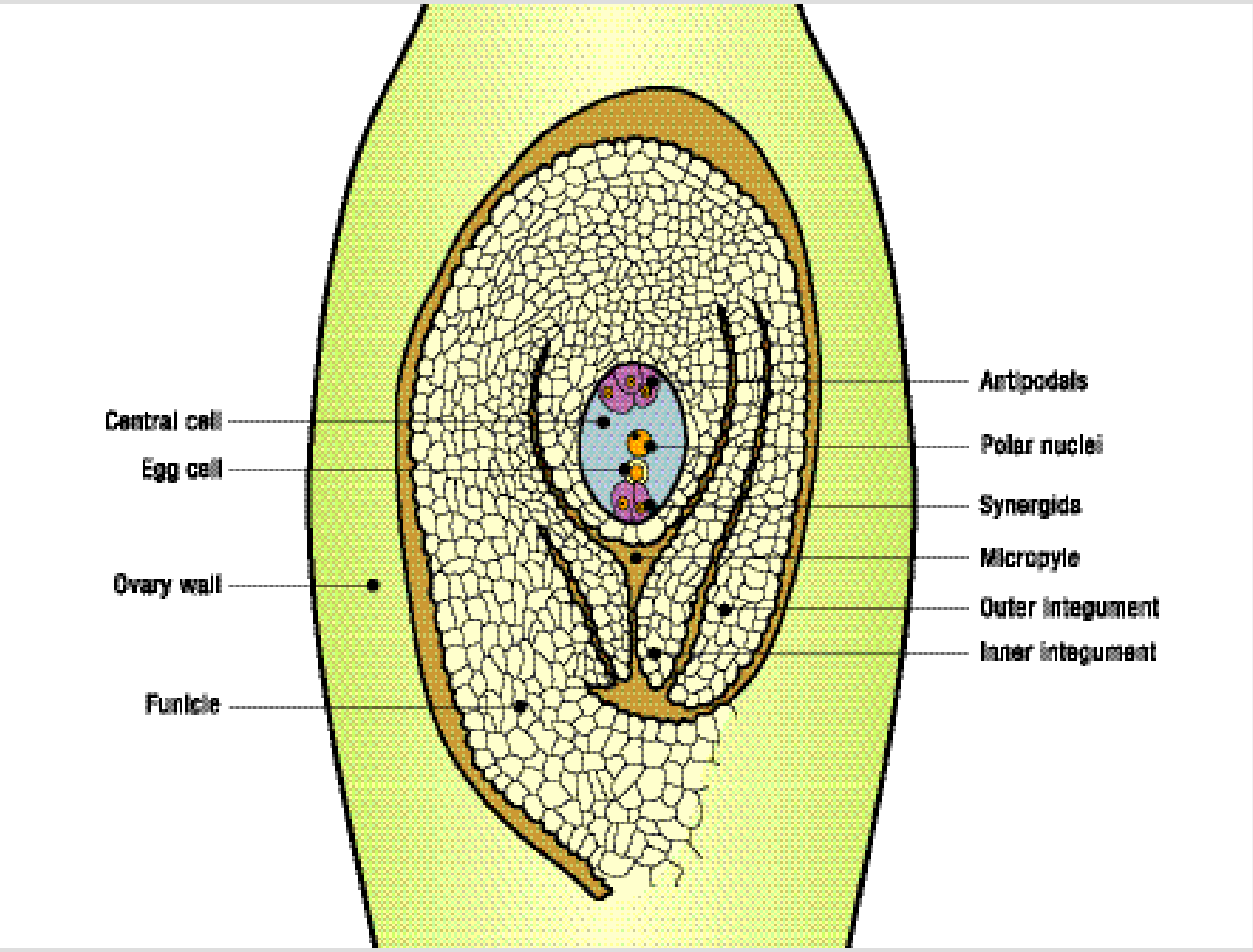


Fig. 18. Bitegmic ovule showing the common embryo sac in angiosperms (*Polygonum type*).

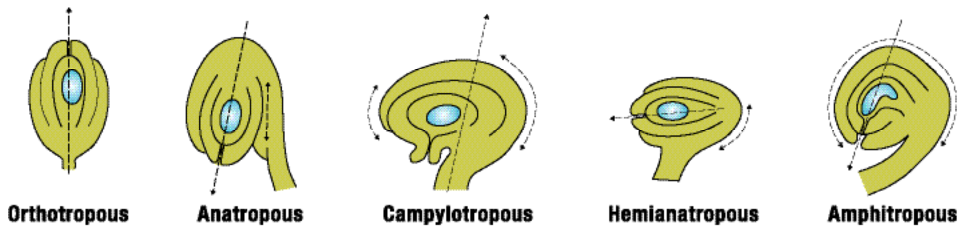


Fig. 19. Ovule types (Redrawn from Flores 1994a).

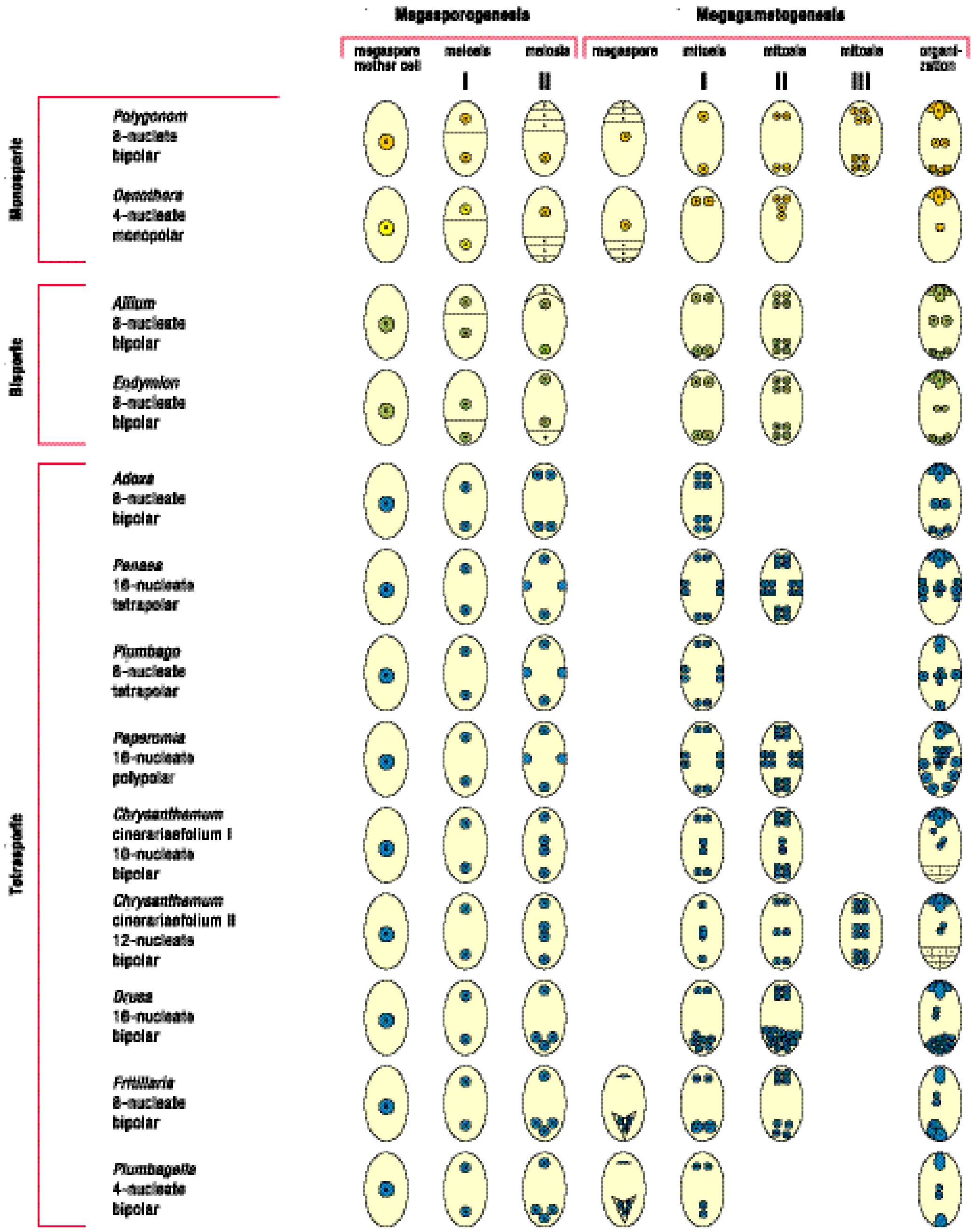


Fig. 20. Schematic representation to show the origin and development of different types of embryo sacs.

hemianatropous, or amphitropous (fig. 19). In general, the differential growth is in the funiculus-chalaza area. The integuments and the nucellus cause the differences in shape and curvature exhibited by the ovules and the mature seeds (Flores 1999, Flores and Engleman 1976). In many cases, the curvature shown by an ovule during the floral anthesis is different and usually smaller than that shown by the mature seed. After fertilization, the differential growth occurring in the different parts of the ovule may increase or diminish the ovule curvature. The seed curvature is correlated to embryo shape, micropyle position, and hilum length.

During ovule development, the archesporial cell differentiates in the nucellus. This cell originates, directly or indirectly, in the megasporocyte, meiocyte, or megaspore mother cell. The latter divides by meiosis and gives rise to four haploid megaspores. There are many variations in the megasporogenesis (fig. 20), but in most cases only the chalazal megaspore is functional. Mitotic divisions of the functional megaspore produce the monosporic megagametophyte (embryo sac). This type is common in the angiosperms. In other cases, no cell wall forms during the second mitotic division and a dyad is formed. The binucleate cell serves as a starting point for the formation of the embryo sac (bisporic). There are species in which no wall forms during the meiosis and a coenomegaspore with four nuclei is formed; it serves as the starting point for embryo sac formation (tetrasporic) (Bouman 1984, Flores 1999, Maheshwari 1950, Willemse and Van Went 1984).

Approximately 60 to 70 percent of angiosperms have an embryo sac (fig. 21) with eight nuclei and seven cells: the egg, two synergids, a central cell (binucleate), and three antipodals (Bouman 1984, Eames 1961, Flores 1999, Willemse and Van Went 1984). The egg cell and the synergids are big cells located in the micropylar end of the embryo sac and forming a structure called the egg apparatus. The synergids are partially surrounded by a wall that is thick at the micropylar end; this thickening forms the filiform apparatus. The central cell occupies the middle of the embryo sac and contains two polar nuclei or a fusion nucleus; the cell wall is partial and is restricted to the chalazal end. The cell membrane or plasmalemma has the typical invaginations of a transfer cell at the micropylar end. The antipodals are small cells with a varied structure, and may be ephemeral or persistent after fertilization. They transport nutrients from the nucellus to the central cell and store nutrients for future endosperm. These cells may also serve a secretory function including secretion of growth regulators involved in endosperm development (Bouman 1984, Flores 1999, Willemse and Van Went 1984).

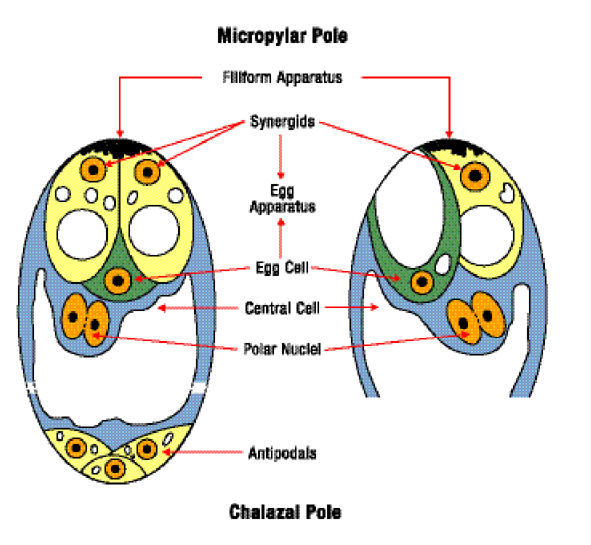


Fig. 21. Embryo sac (*Polygonum* type).

FLOWER POLLINATION AND FERTILIZATION

Pollination Vectors

In angiosperms, pollination can be biotic or abiotic; most species participate with more than a single vector. For example, in *Mabea fistulifera* (Euphorbiaceae), pollination occurs through diurnal (passerine birds, bees) and nocturnal (bats and *Didelphis marsupialis*) pollinators (Vieira and Carvalho-Okano 1996). The adaptation to pollination mechanism is controlled by numerous evolutionary principles. Floral morphology is related to the most efficient pollinator, and evolutionary adaptation is parallel between the pollination vector and the structural, spectral, and olfactory specifications of the flower (Faegri and Van der Pijl 1971, Frankel and Galun 1977, Gottsberger 1993, Kalin-Arroyo 1978).

Biotic pollination must be carried out by different vectors such as insects (entomophily), birds (ornithophily), and bats (chiropterophily). Several mammals contribute to a minor degree, including prosimians, marsupials, rodents, giraffes, reptiles such as lizards, and invertebrates such as snails and slugs (malacophily). Biotic pollination provides mutual benefits: the vector obtains a reward (nectar, fragrances, oils, or pollen) and the plant disperses the pollen (Buchman 1987, Frankel and Galun 1977, Walter 1983).

The abiotic agents are gravity, wind [air movements or air currents (anemophily)], and water [movements or currents (hydrophily)]. Pollination by gravity is unidimensional and, in general, results in species autogamy. Dispersal by wind is tridimensional; by water it can be bidimensional if it occurs on the surface or tridimensional if large water volumes or drops are involved (Frankel and Galun 1977).

The different pollination vectors are associated with floral syndromes or groups of characteristics displayed by the diversity of flowers to attract and reward them. The most common means of attraction are colors and fragrances (Brantjes 1973, 1978). For example, most hymenopterans have similar vision systems of color, with three kinds of receptors (ultraviolet, blue, and green) and only some species have tetrachromic vision (Menzel and Backhaus 1989, Menzel and Shmida 1993). Floral color is not restricted to the perianth; it may be found in bracts [*Bougainvillea* (Nyctaginaceae), *Euphorbia pulcherrima* (Euphorbiaceae)], stamens, and gynoecium. The colors can be produced by light refraction on physical structures and surfaces or by absorption of a defined light wavelength by the pigments. The carotenoids, which are aliphatic compounds, produce colors varying from light yellow to dark red. The flavonoids (anthocyanins, flavones, flavonols, aurones) produce a color scope that ranges from light yellow in the flavones to purple and blue in the anthocyanins. Most color displays and chemical mechanisms use a limited number of anthocyanins (flavonoids) and include the anthocyanin color loss and the participation of a copigment (Gottsberger 1993). The most common anthocyanins are the magenta cyanidine, the purple delphinine, and the red pelargonin. The betalains are alkaloids producing a group of colors varying from red to light ivory (Faegri and Van der Pijl 1971, Flores 1999). The color changes produced by age can be an indicator for vector visits, but the vector does not always discriminate on this basis (Gottsberger 1993).

Nectar production influences vector behavior in the pollinating process. Nectar is composed of monosaccharides (glucose, fructose) and disaccharides (maltose, melobiose), amino acids, proteins (enzymes), lipids, alkaloids, phenols, antioxidants (ascorbic acid), organic acids, saponins, dextrins, and inorganic substances (Baker and Baker 1983). The nectar can be directly ingested by the visitor (birds, bats, lepidopterans, dipterans) or carried to the nest to feed the larvae (hymenopterans). A strong correlation exists between the concentration of sugars and amino acids in the nectar and the type of pollinator (Baker and Baker 1983, Koptur 1994). In addition to pollinator reward, the nectar may have other functions. In some plants it serves as substrate for pollen grain germination; in others, inhibiting yeasts present in the nectar may inhibit pollen germination. The nectar also attracts insects to protect the plant against predators, a phenomenon present in the Neotropics (Bentley and Elias 1983, Koptur 1994, Vinson and others 1997). Flowers with elaiophores offer oils (Faegri and Van der Pijl 1971, Gottsberger 1993). The oils are formed in epithelial glands of the calyx (most New World Malpighiaceae) and released as an exudate exploited by bees such as *Centris* (e.g., *Byrsonima crassifolia* (L.) Kunth, *B. crispa*, some *Bunchosia*) and Krameriaceae. These oil-producing flowers are pollinated by oil-collecting bees (Vinson and others 1997). The plant may use mechanisms, such as inflorescence size, floral morphology, anthesis patterns, nectar production, and dichogamy, to restrict pollen remotion.

Pollinating insects can be coleopterans [beetles (cantharophily)], hymenopterans (symphytophily), wasps (vespophily), ants (phormicophily), bees (melittophily), flies (myophily), butterflies (psychophily), and moths (palaenophily) (Faegri and Van der Pijl 1971, Frankel and Galun 1977, Gottsberger 1993, White and others 1994). Some insects have mechanisms to answer the optical signals sent by the anthers, confirming that stamens and their mimetism are common signals for pollinating insects. Fragrances also attract insects; for example, the osmophores of the neotropical orchid *Stanhopea* and other genera, such as *Clowesia* and *Polycnis*, produce floral scents that attract euglossine bees (Buchman 1987, Curry 1987, Stern and others 1987, Williams 1983). These scents consist of several compounds such as monoterpenes and benzenoids (Williams and Whitten 1983). The production of heath-promoting aroma volatilization to attract pollination vectors has been corroborated in numerous tree species. For example, the flowers of *Annona muricata* and other species in the genus have thermogenic respiration which, combined with strong fragrances, attract dynastid insects (Armbruster and Berg 1994; Gottsberger 1989a, 1989b; Kessler 1993). The male euglossine bees (*Euglossa*, *Eulaema*) collect fragrances from flowers, mix them with the labial glandular secretions, and probably biochemically modify the fragrances to attract females for mating (Armbruster and Berg 1994, Knudsen and Mori 1996, Whitten and others 1989, Williams and Whitten 1983). The scent has a daily cycle, probably influenced by the thermal environment (Armbruster and Berg 1994). These variations may influence insect distribution and mating systems (Corbet 1990). Some insects can change their preference for scents with the season (Gottsberger 1993, Knudsen and Mori 1996, Walter 1983). The entomophilous species usually have large, spherical pollen grains (more than 300 ?m) and a thick, ornamented exine which facilitates the adhesion to insects and stigmatic surfaces. Many pollen grains also have an adhesive cover or lipid seal (pollenkitt) (Flores 1999, Frankel and Galun 1977, Knox 1984).

The coleoptera are a primitive group and cantharophily has been associated with the most primitive angiosperm families; nevertheless, in some families such as the Annonaceae, Calycanthaceae, Eupomatiaceae, and Magnoliaceae, the cantharophily is derived, secondary, and parallel to floral specialization (Gottsberger 1989a, 1989b, 1993). In those groups, the flowers are open, have no structural restrictions to insect access, and produce an excess of organs and tissues that are

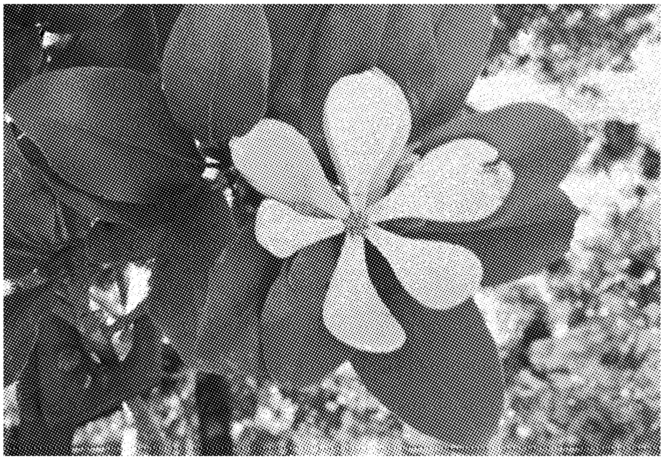


Fig. 22.

Fig. 23.

Fig. 24.

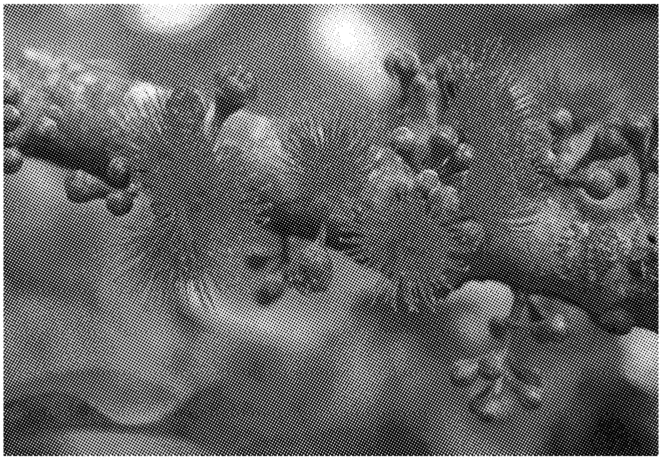


Fig. 25.

eaten by the beetles (figs. 22 and 23). Only exceptional cases have flowers with nectar (Faegri and Van der Pijl 1971, Gottsberger 1993, Knox 1984). The Myristicaceae from southeast Asia (*Myristica, Horsfeldia, Knema, Gymnacranthera*) also seem to be pollinated by coleoptera even when they have a floral structure that strongly differs from that of the annonaceous flowers. The flowers are whitish or creamy, have a nocturnal scent, and lack nectaries or defined secretory structures. They are unisexual and the fused perianth forms a small urn that restricts insect access; the gynoecium of the pistillate flower also has a single ovule (Armstrong and Drummond 1986). Curiously, in the Melastomataceae, with flowers having stamens with poricide dehiscence, the coleopteran squeezes the anther and extracts the pollen.

Psychophilous and palaenophilous flowers have sacarose concentrations in the nectar varying from 1 to 40 percent; the higher percentages are in the palaenophilous (Faegri and Van der Pijl 1971, Gottsberger 1993). Butterflies have diurnal activity and are usually attracted by small flowers with deep colors and soft, agreeable scents. The corolla is trumpet-shaped with a narrow base and stands in a vertical position; sometimes the flowers are not attractive but the bracts are intensely colored (*Godmania, Mussatia*). The anthesis is diurnal, but the flower usually does not close at night (De Vries 1985, 1988; Faegri and Van der Pijl 1971). Moths are the most important lepidopteran pollinators in the Neotropics, especially sphingids; with their elongated proboscis they easily reach pollen (Faegri and Van der Pijl 1971). The flowers are white or poorly colored, sometimes red; the tubular or lobulated corolla maintains a horizontal position or is hanging (*Leucocalantha, Tanaecium*). The anthesis is nocturnal, the anthers are versatile, and the scent is sweet and strong (Faegri and Van der Pijl 1971). Many species have the brush syndrome: very small flowers clustered, each with many stamens and stigma above the perianth level. These features attract large pollinators like sphingids. The species pollinated by moths include *Enterolobium cyclocarpum* (Jacq.) Griseb., *Samanea saman* (Jacq.) Merr., *Pseudosamanea guachapele* (Kunth) Harms, *Cojoba arborea* (L.) Britton & Rose., *Abarema adenophora* (Ducke) Barneby & J.W. Grimes, *Albizia niopoides* (Spruce ex Benth.) Burkart, and *Inga* (Fabaceae-Mimosoideae); *Cedrela odorata* and *Guarea* (Meliaceae); *Cordia alliodora* (Boraginaceae); and *Quararibea asterolepis* (Bombacaceae) (Bawa and others 1985a, Koptur 1994) (figs. 24-25). The *Symphonia globulifera* (Clusiaceae) species

Fig. 26.

has been considered ornithophilous and pollinated by hummingbirds, although pollination is carried out by lepidoptera. The hummingbirds remove nectar (Pascarella 1992).

Melittophily is the most common type of entomophily in the Neotropics. Bees may be generalists or specialists and some may detect differences in the pollen availability of diverse flowers (Gottsberger 1993). The most important families are the Anthophoridae (*Xylocopa*, *Centris*) and the Apidae (social bees). *Centris* frequently pollinate flowers such as *Byrsonima crassifolia* that produce abundant lipids but lack nectar (Vinson and others 1997). In the Subfamily Meliponidae (Family Apidae) the genera *Trigona* and *Melipona* are important; in the Subfamily Bombinae (Family Apidae) the euglossine bees are the best pollinators (*Bombus*). The morphological diversity found in the group enables pollination of zygomorphic and actinomorphic flowers (Knudsen and Mori 1996). Tropical trees pollinated by bees include *Aspidosperma megalocarpon* (Apocynaceae), *Mabea fistulifera* (Euphorbiaceae), *Copaifera camibar* Poveda, Zamora & Sanchez (Fabaceae), *Andira inermis* (W. Wright) Kunth ex DC., *Dipteryx oleifera*, *D. panamensis* (Fabaceae-Papilionoideae), *Laetia procera* (Poepp.) Eichler. (Flacourtiaceae), *Couratari scottmori*, *Eschweilera*, *Grias*, *Gustavia*, *Lecythis ampla* (Lecythidaceae), *Cespedesia macrophylla* (Ochnaceae), and *Qualea paraensis* (Vochysiaceae) (figs. 26 and 27).

Because Vespidae have high nutritional requirements, especially for carbohydrates, they collect and store nectar. Almost all species of *Ficus* are pollinated by Agaonidae wasps when they oviposit the syconium. Several wasp families may pollinate the *Ficus* species (Berg 1989, Kerdelhué and others 1997). Because ants (formicophily or mirmecophily) require sugars and proteins, they collect nectar and eat anthers. They are considered nectar thieves and it is impossible to characterize the flower type with which they are associated. Presumably, ants and wasps visit the same kinds of flowers. Flies and gnats visit several types of flowers. The flowers pollinated by Vespidae are small, whitish, greenish, or yellowish, such as *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels, *Mangifera indica* L., *Tapirira guianensis*, *T. mexicana* (Anacardiaceae), *Bursera simaruba* (L.) Sarg.(Burseraceae), *Simarouba amara* Aubl. (Simaroubaceae), and *Goethalsia meiantha* (Tiliaceae) (figs. 28 and 29). The group has many pollinators. The cocoa

Fig. 27.

Fig. 28.

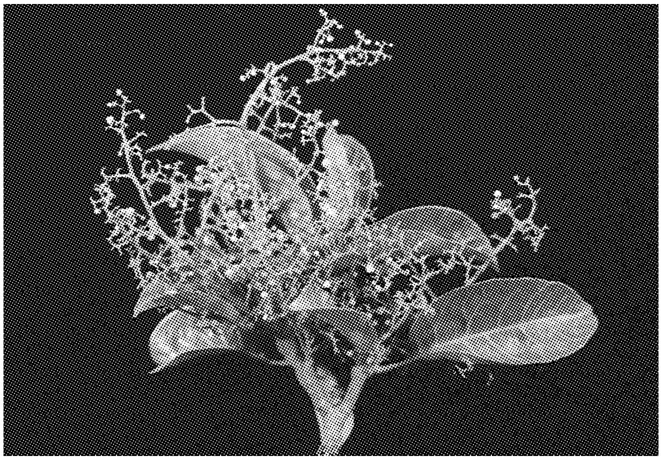


Fig. 29.

(*Theobroma cacao*) is pollinated by several species of Diptera, and flies pollinate *Monadera myristica* flowers (Kessler 1993).

Birds either pollinate the flowers while eating nectar or are opportunistic. Flowers are usually red, orange, or deep purple, with narrow tubes, thick texture, and no odor. Anthers are exserted or subexserted and the calyx is long and loose. The pollination of *Myrrhinium atropurpureum* (Myrtaceae) flowers illustrates an interesting case. Flowers are grouped in dichasia and placed in horizontal branches. They lack nectar and scent but the red petals are thick, fleshy, juicy, and sugary; they change in color and shape during the phases of the anthesis (pink, red, purple, black, purple). The stamens have a long filament (15 mm) and each anther contains around 8,000 pollen grains. The style is 12 to 20 mm long. Pollen presentation starts when sugar concentration in the petals is 4 ± 1 percent weight/weight and the petals are red-violaceous in color. This floral syndrome attracts passerine birds, which are the main pollinators; petal color attracts the birds, petal color variation indicates sugar variation, while the long filaments expose the anthers (Roitman and others 1997).

In the Neotropics the most specialized pollinators are the hummingbirds (Family Trochilidae), although there are other minor groups such as the Icteridae (Brosset and Erard 1986, Stiles 1985, Stiles and Skutch 1989). Bird pollination is common in epiphytes and the plants of forest clearings and secondary forests (Stiles 1985). Hummingbirds are very important pollination vectors in the upper levels of the mountain ranges (Stiles and Skutch 1989). The birds discriminate among ultraviolet radiations. Most have weak olfactory systems which are, however, sensitive enough to detect odors in the environment that can lead them to food. The anthocyanidic pigments are a typical syndrome of flowers pollinated by birds, although exceptions are found in Australia and New Zealand (Gottsberger 1993).

The flowers usually pollinated by hummingbirds may be odorless, and strongly colored, with the red, yellow, and orange colors dominant. The corolla is tubular, sometimes hanging, and lacks a lip or margin turned backward. There are nectaries at the base of the floral tube with an abundance of nectar. The filaments are rigid or fused, frequently stipitate. The position of sexual organs facilitates nectar gathering, pollen collecting, and pollen transference from one flower to another. The

Fig. 30.

anthesis is diurnal (Faegri and Van der Pijl 1971). The pollen is usually deposited in the beaks or head feathers of birds. Most pollen grains are light colored (white or pale yellow), spherical, smooth, and puverulent; sometimes the exine has spinules which expedite pollen adherence to bird feathers. In the Myrtaceae, the pollen deposited in bird beaks is smooth, spherical, or triangular and has a viscous brown, blue, or black covering (Inouye 1975, Knox 1984). Ornithophily is common in the Fabaceae-Mimosoideae (some species of *Inga*), Fabaceae-Papilionoideae (*Erythrina cochleata, E. crista-galli, E. poeppigiana* (Walp.) O.F. Cook), Rubiaceae (*Psychotria elata, Hamelia patens*), and Malvaceae (*Malvaviscus arboreus*). Hummingbirds pollinate these species (Bawa and others 1985a). *Vochysia* flowers, usually pollinated by bees and butterflies, are sometimes pollinated by small hummingbirds (De Vries 1988) (figs. 30 and 31). Birds are not always specific pollinators; for example, several passerine birds are diurnal pollinators of *Mabea fistulifera* (Euphorbiaceae) (Vieira and Carvalho-Okano 1996).

Nectarivorous bats are the most important group of mammalian pollination vectors. They are nocturnal, blind to color, and have a well-developed olfactory system. Because their sonar is weakly developed, bats have trouble flying in foliage. They may use their claws to hang from flowers or fly in front of the flowers like hummingbirds. The tongue is long and well adapted to extracting nectar from the flowers. The bats feed on flowers that produce abundant pollen and sticky or mucilaginous nectar. The corolla is usually wide distally and the nectar very accessible (Grünmeier 1990, Steiner 1981). The flowers pollinated by bats usually stand out in the tree crown, have a special position (cauliflory), are hanging (penduliflory), or have long pedicels. The corolla is campanulate or infundibular, whitish or creamy, greenish, purpuraceous or pinkish, and the flower has glandular tissues exuding unpleasant odors (butyric acid); the anthesis is nocturnal. They can be individual or be grouped in inflorescences. The pollen is transported from one flower to another in the bat hairs, which have scales resembling those of the bee abdomen (Eisenberg 1989, Vogel 1968).

Plant families such as Bombacaceae are pollinated primarily by bats (e.g., *Bombacopsis quinata* (Jacq.) Dugand, *Ceiba pentandra* (L.), *Pachira aquatica* Aubl., *Ochroma pyramidale* (Cav. ex Lam.) Urb. (fig. 32)). A high number of Bignoni-

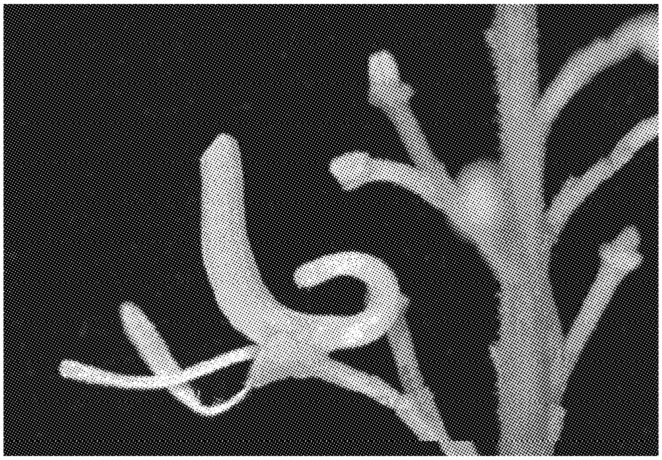


Fig. 31.

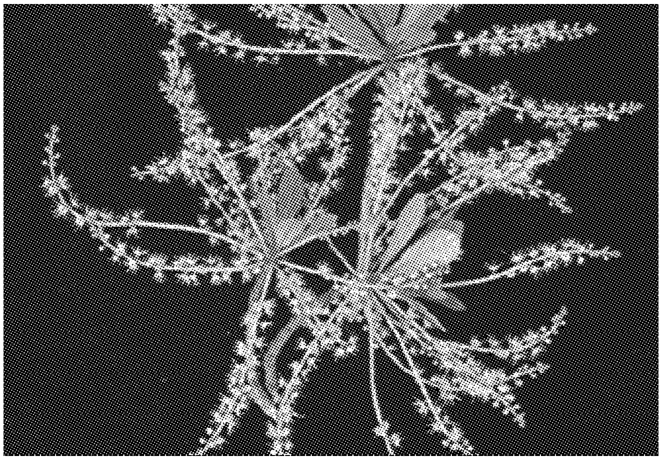


Fig. 33.

Fig. 32.

aceae (*Crescentia cujete* L., *Amphitecna sessilifolia*), Capparidaceae (*Capparis*), Caryocaraceae (*Anthodiscus chocoensis, Caryocar costaricense* Donn. Sm.), Euphorbiaceae (*Mabea*), Fabaceae-Mimosoideae (*Inga leiocalycina, Parkia pendula* (Willd.) Benth. ex Walp., and Fabaceae-Caesalpinioideae (*Peltogyne purpurea* Pittier), are also pollinated by bats. Both bats and sphingid insects pollinate some species, such as *Capparis pittieri.*

Wind pollination is difficult to detect because many flowers are also visited by diverse insects or other pollination vectors. Pollination by wind and insects (ambophily) is very common (Bullock 1994, Silberbauer-Gottsberger 1990). In general, the wind is the pollination vector of species with unisexual flowers that have reduced or no perianth and lack substances that attract birds and other animals (Faegri and Van der Pijl 1971). The anthers are exposed and have long filaments. Air-dispersed pollen grains are small (± 16 to 50 µm), light, and spherical; the exine is thin, sometimes reticulate, striate-reticulate, echinate, scabrous, psilate, sometimes rugose, geminate or discontinuous, puberulent and nonadhesive (Bullock 1994, Faegri and Van der Pijl 1971). The pollenkitt covering is restricted to the exine arcs. Pollen production is abundant in the species (Bullock 1994, Hesse 1979, Knox 1984, Rohwer 1993). Conditions that favor wind pollination include the absence of rain, low relative humidity, and good air movement (wind pollination is frequent in dry tropical forests) (Bullock 1994).

In the Neotropics, several families have species that are partially or exclusively wind-pollinated (Bullock 1994, Kubitzki 1993). These species include *Astronium graveolens* Jacq., *Tapirira guianensis, T. mexicana* (Anacardiaceae), *Alnus acuminata* (Betulaceae), *Terminalia amazonia* (Combretaceae), *Bernardia, Croton* (Euphorbiaceae), *Quercus* (Fagaceae), *Xylosma intermedia* (Flacourtiaceae), *Alfaroa costaricensis* (Juglandaceae), *Maclura tinctoria, Sorocea, Trophis racemosa* (Moraceae), *Forestiera* sp. (Oleaceae), *Agonandra racemosa* (Opiliaceae), *Zanthoxylum* (Rutaceae), *Ulmus mexicana* (Liebm.) Planch. (Ulmaceae), *Myriocarpa longipes*, and *Urera caracasana* (Urticaceae) (fig. 33). Anemophily is also present among gymnosperms such as *Podocarpus guatemalensis* (Podocarpaceae) and *Pinus* (Pinaceae).

The pollen dispersed by water has different shapes: spherical grains surrounded by mucilage; ellipsoid grains, in linear tetrads enclosed in mucilage tubes; or filiform grains lacking exine, with an intine layer resembling that of the terrestrial pollen (Knox 1984).

The tropical trees of lowlands and coastal plains have low population densities and are pollinated primarily by animals. Pollination mechanisms, pollinators, and sexual systems vary among angiosperms. Insects are the most common pollinators and large and medium-sized bees are the most frequent vectors, followed by moths, wasps, other insects, and small bees (Bawa and others 1985a). The pollination vectors of almost one-half of the plant species forage over a wide range. The highest diversity in pollination systems occurs in the subcanopy, where hummingbirds and sphingid insects are the most active. Bats and wind are minor pollinators. Pollination systems are more uniform in the canopy, where bees and small insects dominate.

Most tropical trees have incompatible bisexual flowers (perfect or hermaphrodite). Some are dioecious (pistillate and staminate trees) and cross-pollination is obligatory; however, the strength of the incompatibility barrier varies in a population (Bawa and Krugman 1991). In forest management, the degree of individual crossing is vital to determining the genetic quality of the seed. The degree of endogamy depends not only on the genetic tendency to individual self-pollination but also on the spatial distribution of the individuals (Bawa and Krugman 1991).

Dispersal from the site of origin promotes gene displacement throughout a population or to new populations. In species with cross-pollination, the paternal genes move twice in each generation, first during pollination and second during seed dispersal. The maternal genes move only once; therefore, the paternal genes move farther in each generation (Willson 1992).

The pattern of dispersal contributes to structure population, to potential genetic drift, and to natural selection. The occasional gene transference from one population to another conspecific population is important to maintaining the genetic diversity of the recipient population (Willson 1992). The invasion and colonization of new lands permits the formation of monospecific populations. Natural or artificial monospecific populations are at high risk for diseases and infestations of parasites. The damage produced by the shootborer of the Meliaceae (*Hypsipyla grandella*) in populations of mahogany (*Swietenia*

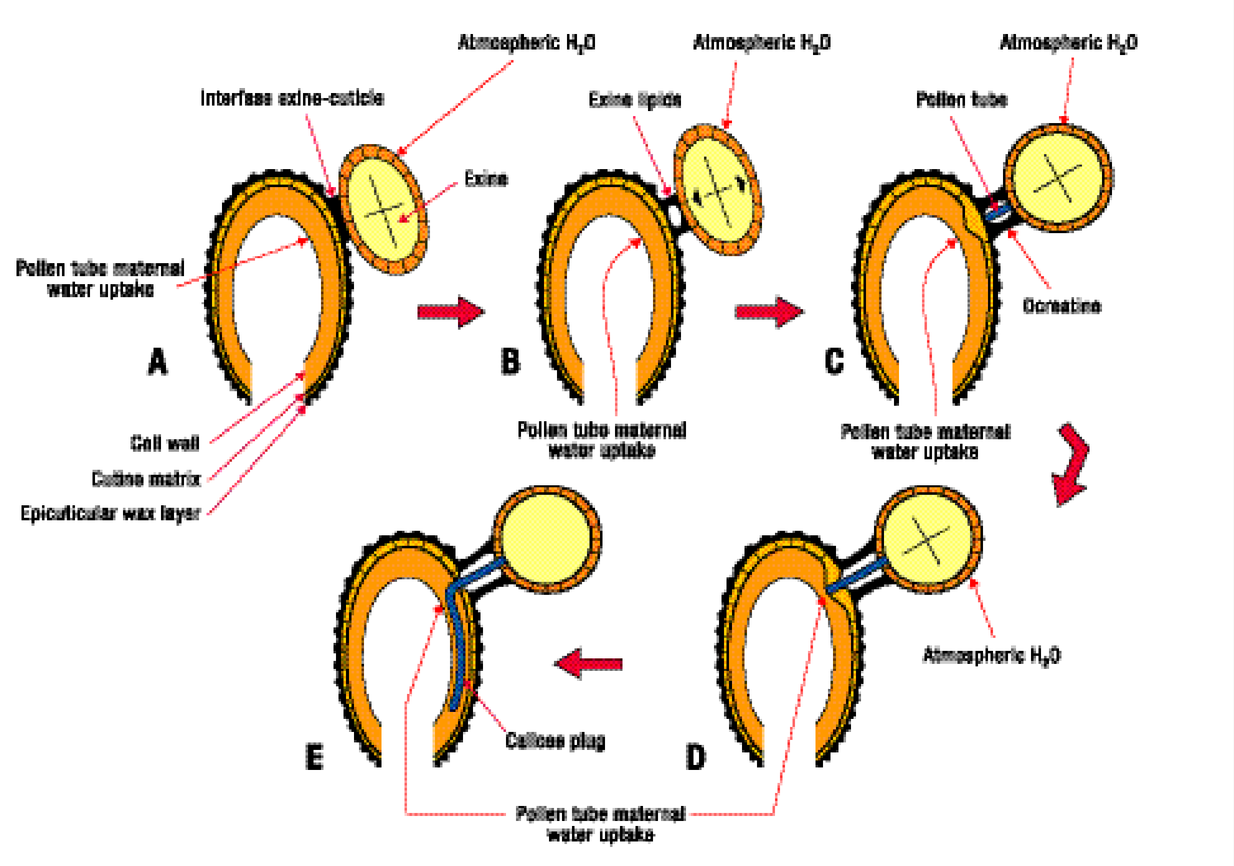


Fig. 34. Pollen-stigma interactions; a, initial contact (pollen capture); b, early stage of secondary binding reaction; c, later stage of secondary binding (pollen tube emergence); d, pollen tube penetrates the cuticle; e, pollen tube growth down. (Redrawn from Ferrari et al., 1985).

macrophylla, S. mahogani), Spanish cedar (*Cedrela odorata*), and other Meliaceae with economic value illustrates this risk.

Pollination

Climatic factors such as wind, rain, moisture, temperature, light intensity, and spectral quality are the stimuli that determine the floral anthesis and the activity of the pollination vectors (Frankel and Galun 1977). The constancy or continuous change of these factors, the graduation or abruptness of any change, and the diurnal or seasonal periodicity of changes can delay or impede pollination. The covering of the pollen and the stigma are involved in the intercellular recognition of signals and stimuli.

The first interaction of pollen and stigma is the capture of pollen by the stigmatic surface, usually 30 to 60 seconds after the initial contact (fig. 34). The epicuticular waxes of the stigmatic surface and the unsteady oils of the exine are placed strategically to function as the initial lipophilic intercellular bond between the matrices of the exine (pollen) and the cutin (stigma). Selective capture of compatible pollen is not apparent in this initial interaction (Ferrari and others 1985).

The second cellular interaction is slower and takes place between pollen and stigma compatibles. When the pollen and the papillae or stigmatic surface come into contact, they form rigid convex surfaces tangentially between them (fig. 34); the macromolecular distances are long and varied. The hydrolysis and polysterification of the substances (oils and waxes) that made the initial contact connect the pollen exine with the cutin matrix. The enzymes of the cuticle (cutinase, estearase) catalyze the process. Usually 15 to 30 minutes after pollination, a tubular connection is established between the pollen and the stigmatic surface. This connection has a diameter double the size of the orifice left by the pollen tube when it crossed the cuticle. The pollen tube develops between the connection, tube, or ocreatine and goes through the cuticle of the stigma (Ferrari and others 1985). Pollen hydration and ocreatine formation may be inhibited when the pollen is incompatible. The pollen tubes of a species show strong phenotypic differences during their growth through the styles of different species. The apical end shows cytological anomalies when there are specific incompatibilities in the stigma, style, or embryo sac.

Fertilization

Fertilization in angiosperms is a two-part process: one sperm fuses with the egg cell, giving rise to the zygote, a process called syngamy by Strasburger and others (1908); another fuses with the two polar nuclei of the central cell, creating the endosperm (triple fusion).

Usually the pollen tube enters the ovule through the micropyle (porogamy), through the chalaza (chalazogamy), or through the integuments (pleurogamy). The sperm fertilizing the egg cell first penetrates through the filiform apparatus. The sperm is then transferred to a synergid cell and later to the egg cell. The fusion between the sperm and the egg cell plasmalemma results in a bridge through which the sperm enters the egg cell. The fusion of one sperm nucleus with the egg produces a diploid zygote; the fusion of another sperm nucleus with the nuclei of the central cell produces the triploid endosperm, typical in 60 to 70 percent of the dicotyledons (monosporic embryo sac of the *Polygonum* type) (fig. 21). In the other embryo sac types, the endosperm varies from 2n (*Oenothera* type) to 3n in the *Allium* and *Adoxa* types. The remaining embryo sac types develop a polyploid endosperm (Flores 1999, Maheshwari 1950). The double fertilization transforms the ovule into the seed.

Fertilization can occur within the same flower (autogamy), between two flowers on the same tree (geitonogamy), or between flowers of different individuals (allogamy or xenogamy). Some species can have autogamy and allogamy on the same tree; this phenomenon is called alautogamy (Radford and others 1974).

SEXUAL STRUCTURE IN GYMNOSPERMS

The gymnosperm, which means naked seed, is a group of superior vascular plants in which the ovules and seeds are not enclosed within a carpel. They are exposed on *scales* or similar structures, equivalent to sporophylls (Foster and Gifford 1974).

Among the gymnosperms, the Coniferales are the dominant group. Coniferales are a primarily perennial, woody species, many of which have economic value. In the Neotropics, species of frequent use and economic value are numerous, including *Pinus oocarpa* Schiede ex Schltdl., *P. montezumae* Lamb., *P. caribaea* Morelet, *P. maximinoi* H.E. Moore, *P. patula* Schiede & Schltdl. & Cham., *P. ayacahuite* C. Ehrenb. ex Schltdl., *Abies guatemalensis* Rehder, *A. religiosa* (Kunth) Schltr. & Cham. (Pinaceae), and the ciprecillos (*Podocarpus guatemalensis, P. costaricensis, P. macrostachyus, Prumnopitys standleyi* (Buchholz & Gray) de Laub., Podocarpaceae).

Coniferales are predominantly monoecious and have ovules and pollen grains clustered in strobiles or cones of different shapes and sizes. All the species of Pinaceae are monoecious, but some families, such as Cupressaceae and Podocarpaceae, have both dioecious and monoecious species (Bierhorst 1971, Foster and Gifford 1974, Sporne 1965). The strobile has a central axis with numerous imbricate sporophylls (2n), called scales or bracts, distributed in a closed spi-

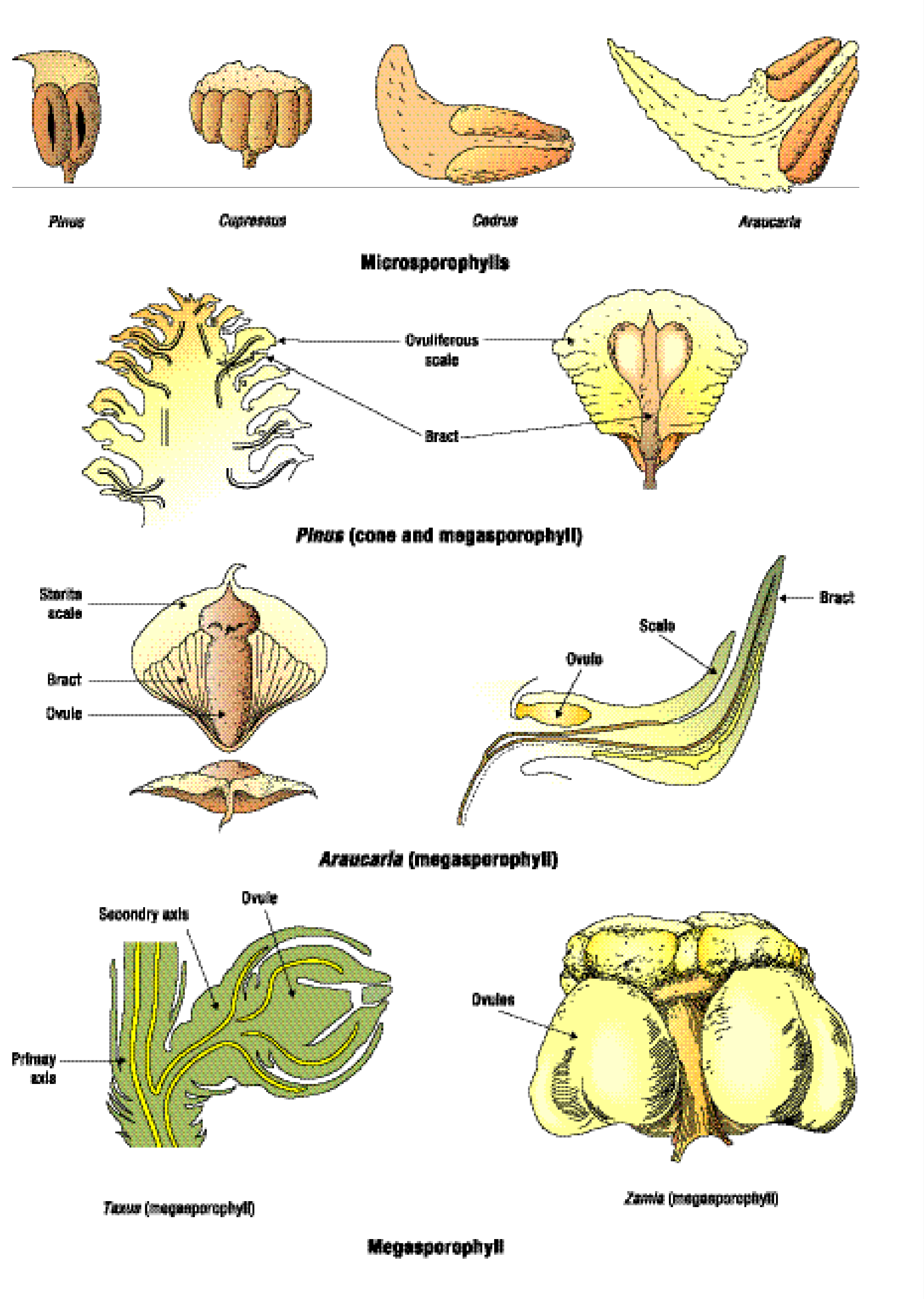


Fig. 35. Micro and megasporophylls in several gymnosperms.

ral (fig. 35). The male strobile (androstrobile) has microsporophylls; usually each microsporophyll has two pollen sacs (microsporangia) in the abaxial (lower) surface. However, *Cycas media* may produce more than 1,000 sacs, *Zamia floridana* several dozen, the Taxodiaceae 2 to 9, the Cupressaceae 3 to 6 (sometimes more), the Taxaceae 2 to 8, and the Araucariaceae 5 to 20 (Foster and Gifford 1974).

In families such as Pinaceae, the female strobile (gynostrobile) has megasporophylls and each has two ovules inverted in the adaxial (upper) surface. Other families have more or fewer ovules per megasporophyll; for example, the Taxodiaceae have two to nine and the Cupressaceae two to many, while Araucariaceae, Podocarpaceae, and Taxaceae have a single ovule (Foster and Gifford 1974, Sporne 1965).

The numerous male strobiles have a short life span; when mature they may have a yellowish, purplish, or reddish coloration. The less numerous female strobiles also show variations in color. The color is genetically determined and can vary with elevation; for example, the white fir (*Abies concolor*) has light green or dark purple cones. The morph with green cones is more common in low elevations, while the morph with dark purple cones becomes more numerous with increases in elevation (Sturgeon and Milton 1980).

Reproductive Cycle

Figure 36 illustrates the reproductive cycle in a gymnosperm. Anther dehiscence permits pollen release, and scale opening in the cone permits pollen entrance. The period of postpollination-prefertilization may last from weeks to years. In the

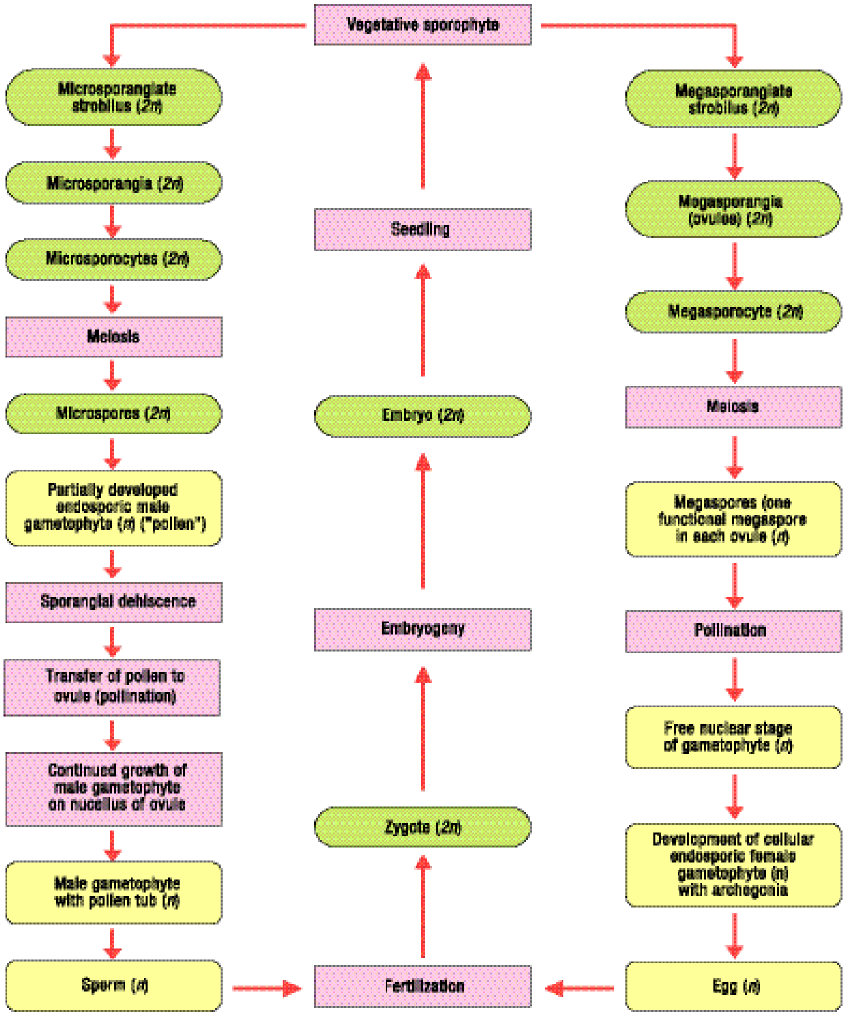


Fig. 36. The reproductive cycle in gymnosperms.

species *Pinus*, the period from ovule inception to seed dispersal can last 2.25 years (Krugman and others 1974, Bonner and others 1994) (fig. 37). This period includes pollen germination, pollen tube growth, and penetration of the nucellus, as well as archegonium and gamete development (Owens and Morris 1990).

Pollen

The microsporangium (2n) or pollen sac has wall, tapetum (in many species), and sporogenous cells. The latter give rise to the microspore mother cells or microsporocytes, each producing four microspores (n) by meiosis. The microspores remain inside the microsporocyte wall for variable periods of time depending on the species (figs. 36-38). During this period, the microspore divides three times and forms the microgametophyte or partially developed pollen grain. The latter has two prothallic cells (they die early), a generative cell, and a tube cell. Pollen sac opening and pollen grain release usually occur in this stage. After pollination, the pollen grain germinates and develops the pollen tube, which penetrates through the nucellus to the archegonium, absorbing nutrients from nucellar origin. Usually, the generative cell divides during pollen tube penetration, giving rise to two or sometimes more sperm. In the cycads and *Ginkgo*, the sperm are multiflagellate; the conifers lack flagella and are steady (Bold 1967, Foster and Gifford 1974, Jensen and Salisbury 1972, Sporne 1965).

In genera such as *Pinus*, *Podocarpus guatemalensis*, and *Prumnopitys standleyi*, the pollen has air vesicles or wings (Torres-Romero 1988); in others, such as *Pseudotsuga*, the pollen grains are spherical or oval with a smooth wall and lack wings. The pollen is yellow and abundant (Bierhorst 1971, Foster and Gifford 1974, Krugman and others 1974).

Ovule

The ovule has one integument fused to a multicellular body called the nucellus (functionally equivalent to the megasporangium). In the apex (distal end) the integument forms the micropyle (figs. 36-39). The proximal end, opposite the micropyle, is the chalaza. In the micropylar end of the megasporangium, a megasporocyte or megaspore mother cell (2n)

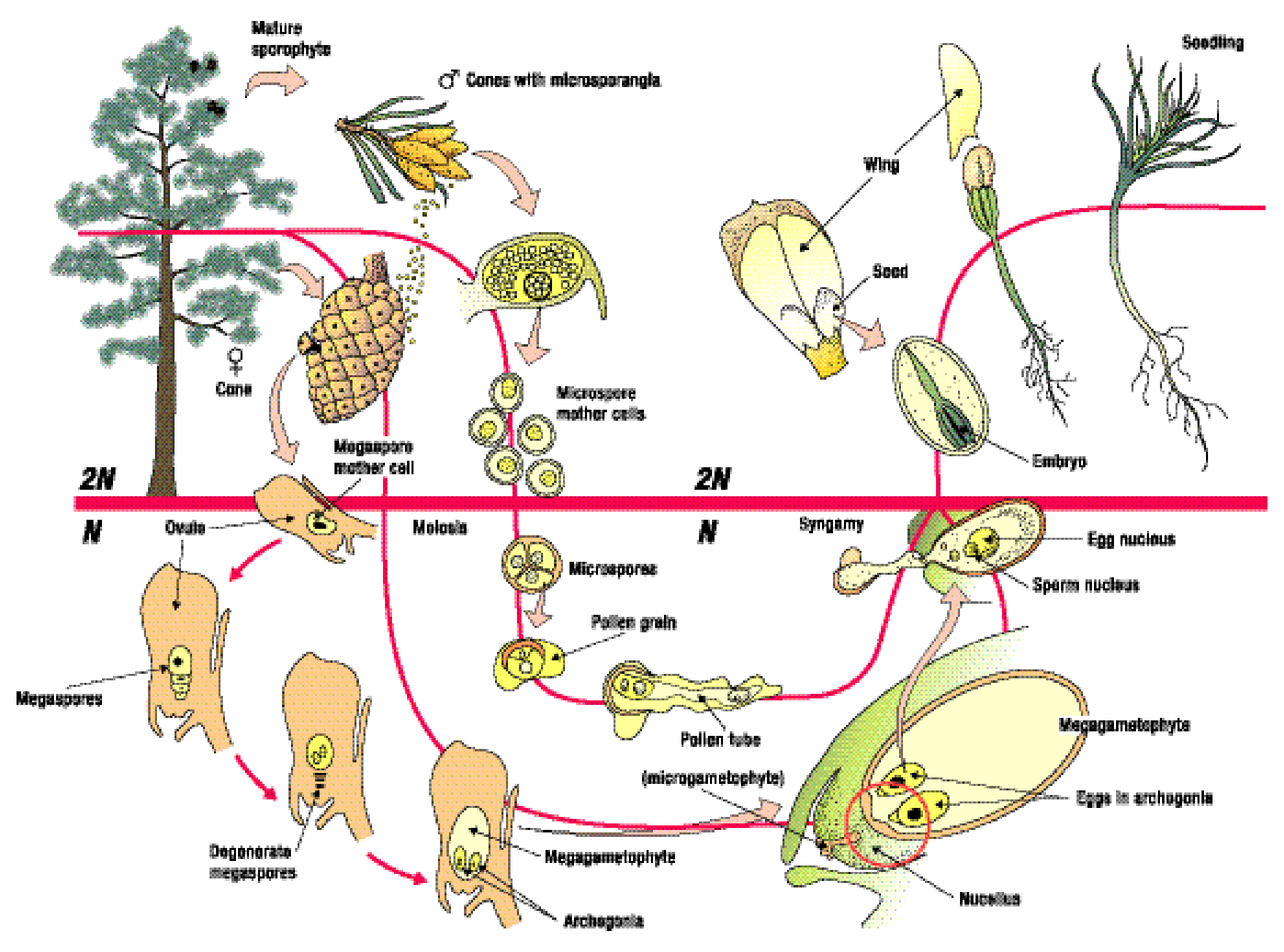


Fig. 37. The reproductive cycle of *Pinus*. (Redrawn from Jensen & Salisbury. 1972).

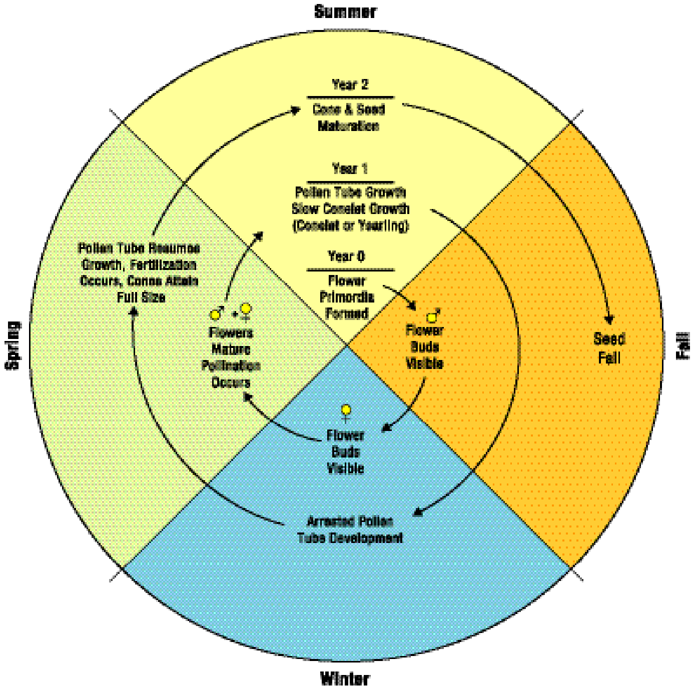


Fig. 38. Life cycle of a gymnosperm (*Pinus* sp.).

(Redrawn from Bonner, Vozzo, Elam & Land. 1994).

develops. Through meiosis, this cell originates a linear tetrad of megaspores (n); only the innermost megaspore is functional. Inside the functional megaspore, numerous free nuclear divisions occur (e.g., up to 2,000 nuclei in the Pinaceae); cell wall formation occurs later. It begins in the periphery and proceeds centripetally. A cellular megagametophyte forms and is surrounded by the megaspore wall, which frequently increases in thickness (Sporne 1965). The megagametophyte cells are rich in nutrients. During or after cell wall deposition, some surface cells in the megagametophyte, usually placed at the micropylar end, form varying numbers of archegonia (e.g., 2 to 6 in *Pinus*, 2 in *Ginkgo*, up to 60 in *Sequoia*). A jacket of sterile cells enclosing and protecting an egg cell placed at the canal base forms each archegonium.

Pollination and Fertilization

Pollination is the transport of the partially developed endosporic microgametophyte (pollen grain) from the pollen sac to the micropyle. The developmental stage in which polli-

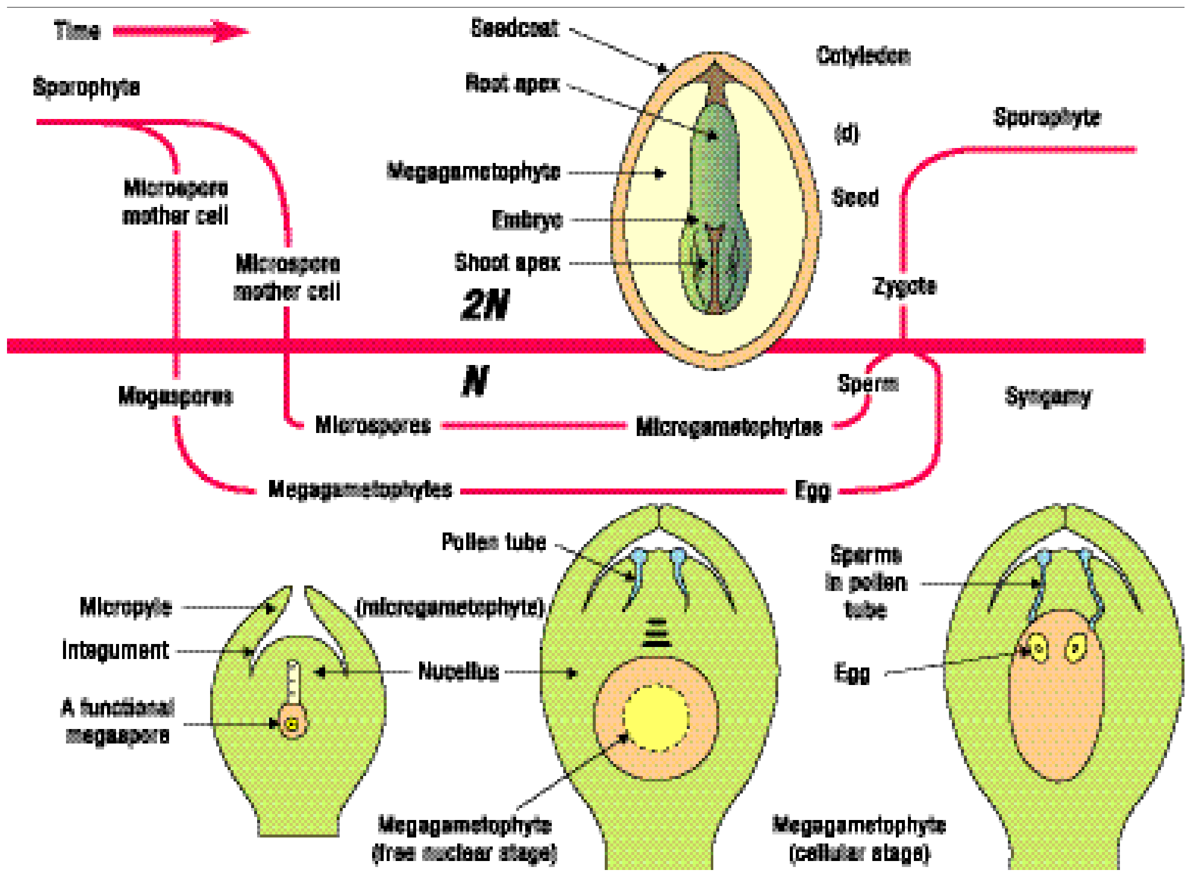


Fig. 39. The development of the megagametophyte and the seed of the gymnosperms. (Redrawn from Jensen & Salisbury. 1972).

nation occurs in gymnosperms varies. In most conifers, taxads, and *Ginkgo* it occurs when the ovule has only sporogenous cells or megaspore mother cells (Singh and Johri 1972). During the prepollination phase the micropyle is open and many cell divisions occur in the ovule. In many species, a pollen chamber is formed at the micropilar end through degeneration of nucellar cells (Singh and Johri 1972).

The wind is the main pollination vector, although several species are entomophilous. Coleopterans and hymenopterans are the most frequent agents. Examples of entomophily include *Zamia pumila* (Tang 1987), *Macrozamia communis* (Chadwick 1993), and *M. riedlei* (Connell and Ladd 1993). The angiostrobiles of some cycads release a strong odor, which helps to attract the insects (Chamberlain 1935). Many conifers, such as *Pinus*, have pollen adhering to the integument and floating later in the liquid exuded by the ovule (pollination drop). While the drop evaporates, the pollen is mobilized to the base of the micropylar canal where it finds the egg cell (Owens and Blake 1985, Singh and Johri 1972). In other species, such as *Larix occidentalis* and *Pseudotsuga menziesii* (Mirb.) Franco, the pollen is captured and detained by a stigmatic extension with many trichomes. The trichomes produce a small secretion that contributes to the initial development of the pollen tube (Owens and Molder 1979, Owens and Morris 1990). The pollen tube enters the megaspore wall and elongates to reach the archegonium where it establishes (Foster and Gifford 1974, Owens and Morris 1990). Usually, a long period of time elapses between pollination and fertilization. In this period the ovule undergoes several changes: the closing of the micropylar canal and the increasing in size, through cell division and activation, of the spongy tissue or tapetum. The latter originates from sporogenous cells not functioning as spore mother cells or from nuclear cells surrounding the sporogenous tissue. Later, this tissue degenerates and collapses (Singh and Johri 1972).

The primary difference between gymnosperms and angiosperms is that fertilization in the former is not a two-part process. A single fertilization occurs in which one sperm fuses with the egg cell and the zygote (2n) develops. The remaining sperms degenerate and no true endosperm is formed. Usually, the egg cells of several archegonia are fertilized; however, only a single embryo develops. The reserve materials stored in the female gametophyte nourish the embryo. The ovule is usually the same size as the mature seed. *Ginkgo* and the cycads have an haustorial pollen tube (Sporne 1965). Double fertilization has reportedly occurred in several gymnosperms such as *Ephedra*, *Gnetum*, *Pseudotsuga*, *Thuja*, and *Welwitschia*; nevertheless, double fertilization has been corroborated only in *Ephedra nevadensis* (Friedman 1986, 1987, 1990).

THE FRUIT

THE ANGIOSPERM FRUIT

Structure, development, and ripening

The fruit is the structure containing the seed. It develops from the gynoecium of the flower, which is frequently associated with other floral organs. The process of fruit development has four stages:

(1) Initiation and development of the floral bud leading to the formation of the mature flower, with one or several ovules in the gynoecium (Nitsch 1965).

(2) Cessation of cellular division and elongation during pollination, pollen tube development, and ovule fertilization (Nitsch 1965). After pollination, many flowers close the corolla or undergo a fast collapse of the corolla and the other floral organs. Floral collapse is correlated to increasing respiration and ethylene production (Flores 1999, Leopold and Kriedemann 1975).

(3) Postfertilization events:

> Growth of the ovary wall and associated tissues, by cell elongation and ovary wall transformation into the fruit wall or pericarp.
>
> Seed development from the fertilized ovule; however, some fruits may develop without fertilization or seed development (parthenocarpy). In general, seed development and perianth and stamen withering and abscission are simultaneous (Flores 1999, Leopold and Kriedemann 1975, Nitsch 1965).

(4) Fruit ripening followed by senescence and, sometimes, dehiscence and abscission.

The pericarp can be more or less differentiated and frequently shows two or more different layers. If the layers are distinguishable, they are called (from the outside to the inside): exocarp (epicarp), mesocarp, and endocarp. These terms are used for descriptive purposes and do not relate to the ontogenetic origin of the layers.

Numerous fruits have sigmoid growth patterns, which start with an exponential increase in size, diminishing later to adjust to a sigmoid pattern. Other fruits have more complex growth patterns involving periods of growth with an interval of reduction or detention of growth. The fruits of many tropical trees have the latter type, as well as some crops with edible drupes (Leopold and Kriedemann 1975).

Fruit growth requires cell division and cell elongation. The range of cell division differs from one fruit to another. Some complete division during pollination while others extend it into the postpollination period (Leopold and Kriedemann 1975). The reserves stored by fruits are synthesized in the leaves and transported by the phloem. The existence of haploid, diploid, and triploid tissues (sporophyte 2n, embryo 2n, but differing from the sporophyte genome; the endosperm usually 3n, and the perisperm 2n) complicates the growth pattern. During fruit development, the differential growth follows different directions in the distinct parts and tissues of the fruit.

Normally, fruit development depends on and is controlled by growth regulators synthesized in the developing seeds. The seeds produce auxins, gibberellins, cytokinins, abscissic acid, and ethylene. The relationships between these substances are very complex but the most important fact is the balance of regulators at the different stages of development (Kozlowski 1971, Leopold and Kriedemann 1975, Nitsch 1965). In many species a fruit lacking seeds can develop well; for example, the empty and filled fruits (samaras) of *Terminalia amazonia* and *T. oblonga* (Ruiz & Pav.) Steud. are indistinguishable externally (Flores 1999, 1994h). Generally, the extraction of fertilized ovules from a developing fruit stops development.

Fruit shape usually reflects the internal distribution of the seeds (e.g., *Cojoba arborea*), and seed shape frequently reflects the number of seeds inside the fruit (e.g., *Carapa guianensis* (Flores 1994a), *Eschweilera panamensis*, *E. costaricensis*). Seed number inside the fruit and final fruit and seed size are correlated. In many cases, the fruit shape reflects the internal pressures exerted by the overgrown seed(s) developing inside it; in this case, embryo growth is limited by the pericarp (e.g., *Prioria copaifera* Griseb., *Dipteryx panamensis*). Fruit maturation is the ensemble of processes associated with the attainment of maximal size and the qualitative transformation of the tissues. The latter involves tissue softening as a product of hydrolytic conversions of stored reserves, as well as changes in pigmentation, production of tastes, and disappearance of astringent substances (e.g., *Achras*, *Elaeoluma*, *Manilkara*, *Micropholis*, *Pouteria*, Sapotaceae).

The hydrolytic changes in the reserve materials result in the production of sugars by starch and lipid chemical transformation. Proteins follow an opposite tendency; their synthesis intensifies during the process of ripening (Biale 1950, 1964; Sacher 1973). Enzymes present in the tissues soften the fruit tissues and the process requires that pectic substances present in the cell walls become soluble.

Fruit ripening promotes drastic changes in the respiratory rate. The increase in respiration known as climacteric respiration is related to ethylene concentration. Other events associated with fruit ripening include the increase in ribonucleic acid (RNA) and the change in cellular permeability. Climatery is the developmental period of certain fruits (especially fleshy fruits) in which many biochemical changes occur that determine the transition from growth to senescence and ripening. These changes are promoted by the autocatalytic production of ethylene (Smith and Parker 1966).

Fruit Abscission

Abscission is the organized separation of cells resulting in tissue separations; this occurs in leaves, flowers, fruits, and stems (Leopold and Kriedemann 1975). Abscission occurs during the opening of many types of fruits (fruit dehiscence). The actions of growth regulators cause abscission at different stages of fruit development. When it occurs at maturity, the fruits may contain seeds (indehiscent fruits; e.g., *Minquartia guianensis*, *Prioria copaifera*). The fruit usually lacks seeds if the dehiscence precedes abscission (e.g. *Cedrela*).

The abscission zone varies in the different fruits and a fruit may have more than one zone. For example, apples abscise at the base of the pedicel, while *Prunus* (prunes), *Calophyllum brasiliense*, and *Minquartia guianensis* first separate at the fruit base and then at the pedicel base.

The degree of cell differentiation in the abscission zone also varies from one fruit to another. Abscission is an active process involving the separation of the middle layers of the cell walls in the abscission line, under enzymatic action. Usually a cellulase and a polygalacturonase are involved. The abscission process requires the synthesis of proteins; e.g., the ethylene stimulates the abscission and induces the synthesis of enzymes in the cell wall (Biale 1950, Leopold and Kriedemann 1975, Sacher 1973, Wilson and Hendershott 1982).

Dehiscence

The spontaneous breaking of the pericarp allowing seed dispersal is known as dehiscence. Methods of dehiscence are diverse (fig. 40). If the ovary derives from a single carpel, the pericarp may break longitudinally along the ventral suture (suture joining the carpel margins), along the dorsal suture (midvein line), or along both sutures. In ovaries with two or more carpels, tissue separation takes place along the lines (septa) joining contiguous carpels; this type of dehiscence is called septicidal. Rupture along the carpel backs (middle of the

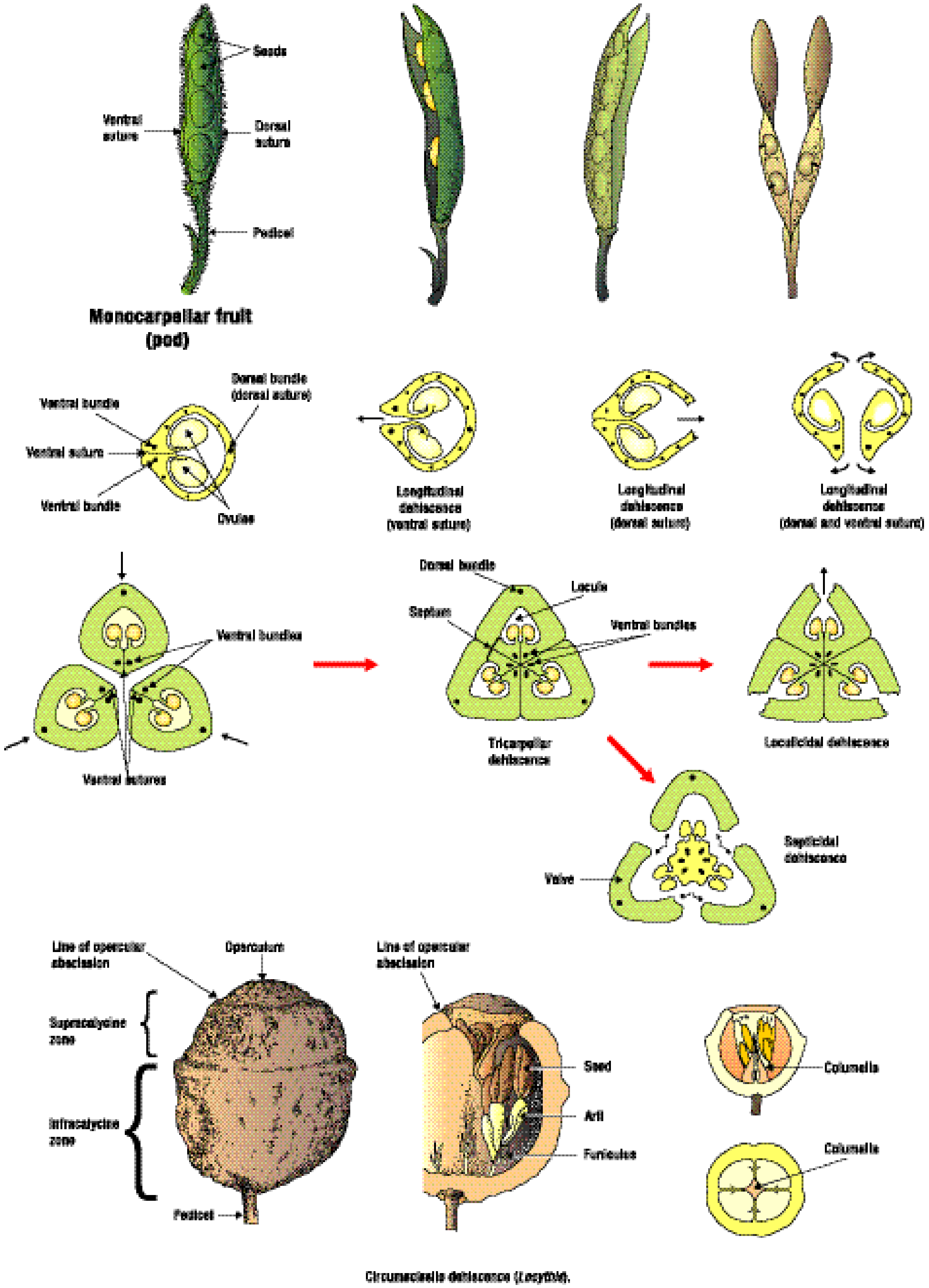


Fig. 40. Types of fruit dehiscence.

loculus) where the dorsal bundles are located is loculicidal dehiscence. In some fruits the dehiscence that occurs along a horizontal ring involving all carpels is known as circumscissile dehiscence. Dehiscence can also take place along one or several pores (poricide dehiscence) which sometimes have an operculum (poricidal-operculate dehiscence).

Classification of Fruits

Flower organization in terms of carpel number, distribution, degree of fusion, and structure influences fruit size, shape, texture, and anatomy (Flores 1999). Fruit classifications are artificial and emphasize certain anatomical and biological characteristics, such as fruit texture (dry or fleshy) and dehiscence (dehiscent and indehiscent). Although these characteristics are valid for classification purposes they lead to juxtapositions and duplications of types in some classification systems (Flores 1999, Foster and Gifford 1974). The classification system described in this chapter is very simple and oriented to tree species; it omits the subtypes not found in tree fruits such as the caryopsis typical of grasses and the cypsela common in the Asteraceae. The fruits are separated into three categories: simple, aggregate, and multiple. A simple fruit is originated by a single gynoecium, unicarpellar or syncarpic. The aggregate fruit is derived from an apocarpic gynoecium; each carpel keeps its identity until ripening. The multiple fruit derives from an inflorescence; that is, from a combination of the gynoecia of many flowers, which are sometimes coalescent. If any of these fruits has extracarpellar tissue it is an accessory fruit (Flores 1999, Foster and Gifford 1974).

Simple Fruits

Pericarp texture is the basis used to categorize the simple fruits into dry (dehiscent and indehiscent) and fleshy fruits.

Dry Indehiscent Fruits

Those fruits that remain closed at maturity. They usually arise from ovaries in which only a single seed develops, although in some cases more seeds are present. This category includes several types of fruit (fig. 41):

Achene. Small fruit bearing one seed fused to the fruit wall at a single point; it derives from a superior ovary with only one locule; e.g., the sunflower (*Helianthus annuus*, Asteraceae).

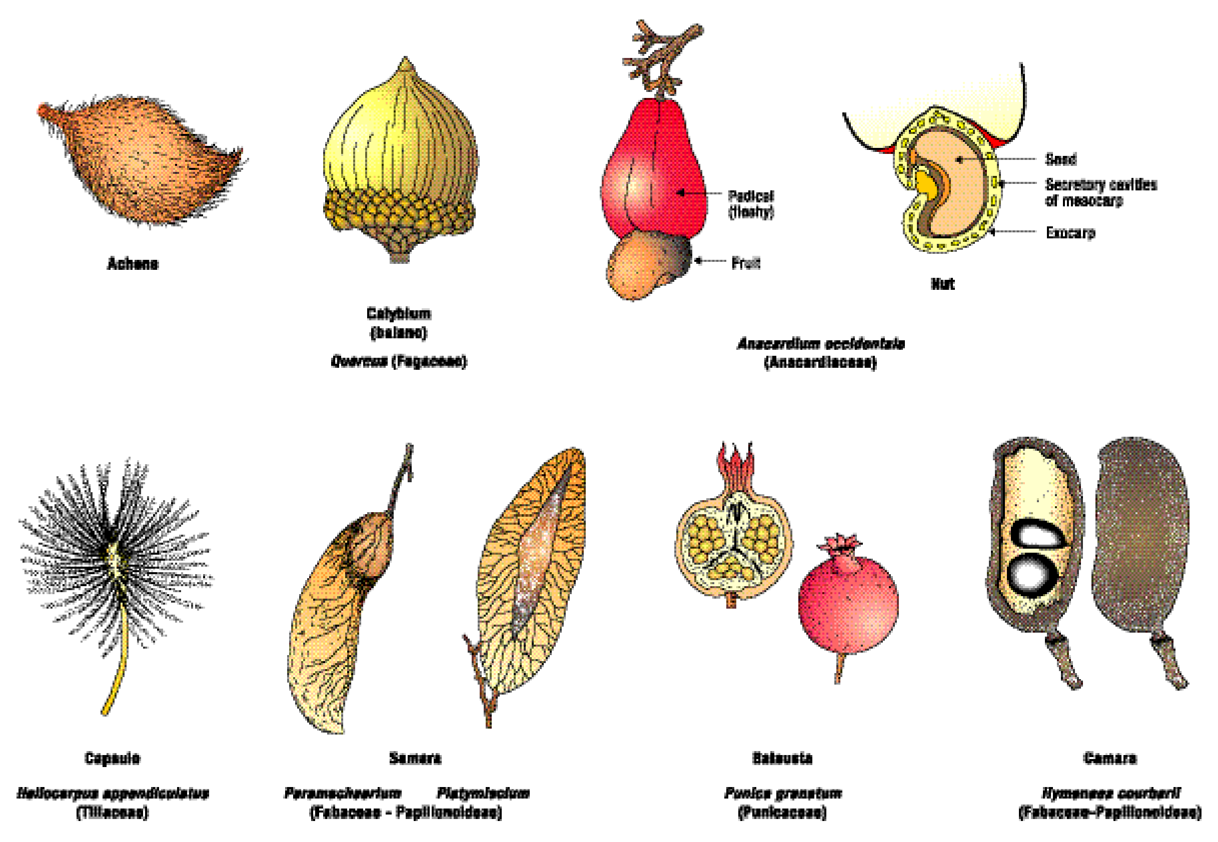


Fig. 41. Dry indehiscent fruits.

Fig. 42.

Fig. 43.

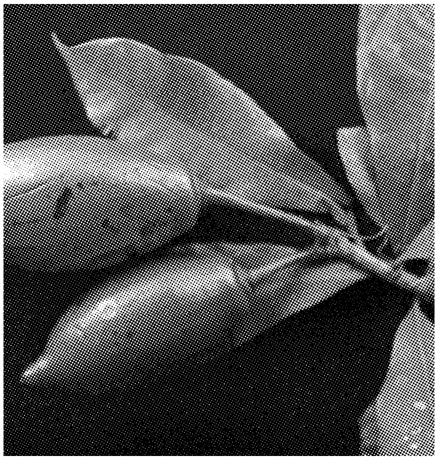


Fig. 44.

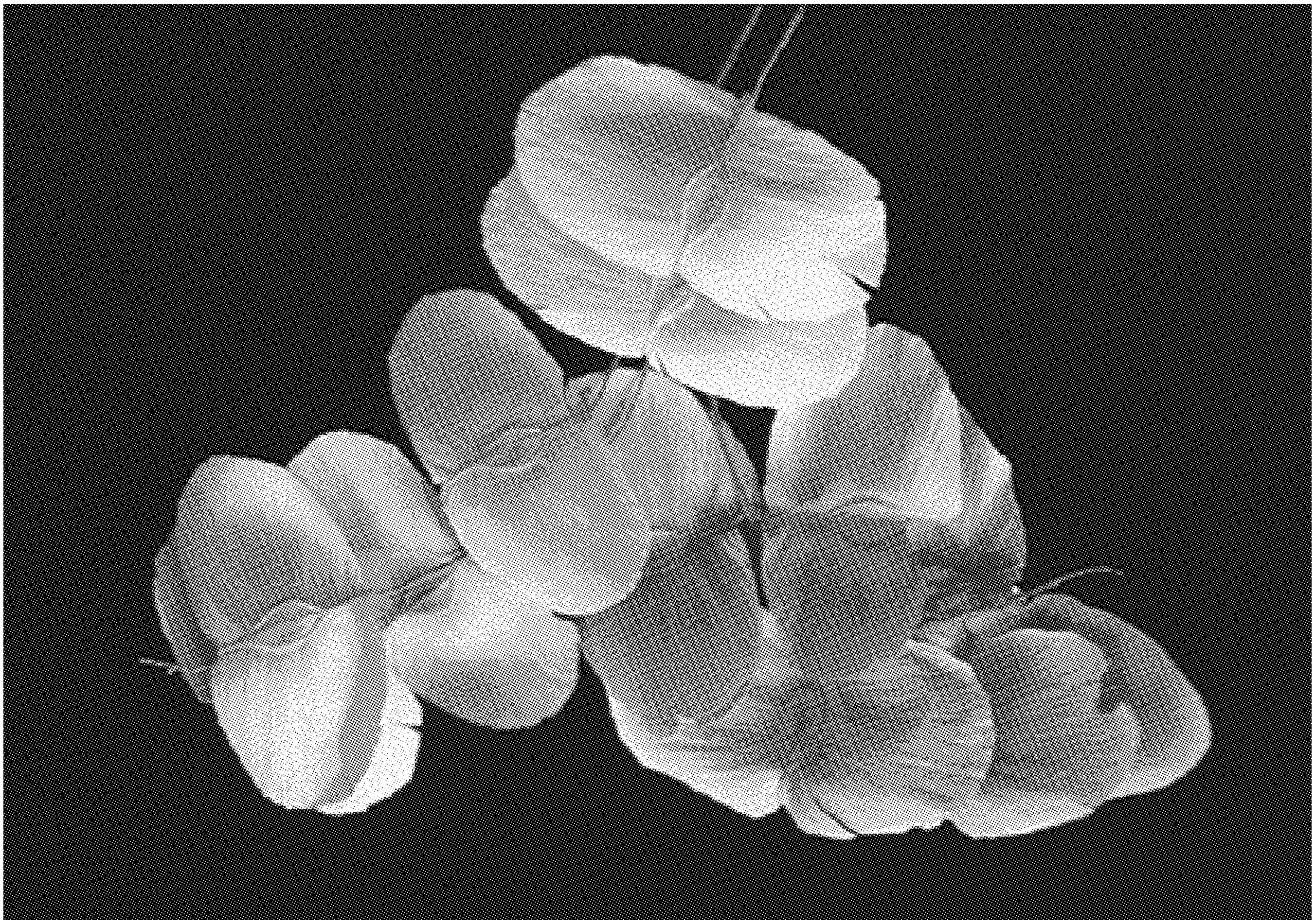


Fig. 45.

Balausta. Fruit with numerous locules and numerous seeds; the pericarp is coriaceous; e.g., *Punica granatum* (Punicaceae).

Calybium (balano). Hard fruit with only one locule developed in the mature fruit (figs. 41 and 42). The calybium derives from an inferior ovary; e.g., the oaks (*Quercus*, Fagaceae). The oaks have tricarpellar, trilocular flowers with two ovules per locule, but only one locule and one seed develop (Abbe 1974). The *Quercus* fruits have a dry, cupuliform involucre; because of that the fruit is sometimes classified as an accessory fruit under the name of cupule or glans.

Indehiscent capsule. Fruit derived from an ovary with two or more locules (figs. 41 and 43-44); e.g., *Crescentia cujete*, *Amphitecna sessilifolia* (Bignoniaceae); *Catostema fragrans* (Bombacaceae); *Apeiba tibourbou*, *Heliocarpus appendiculatus* (Tiliaceae); and *Simira maxonii* (Rubiaceae).

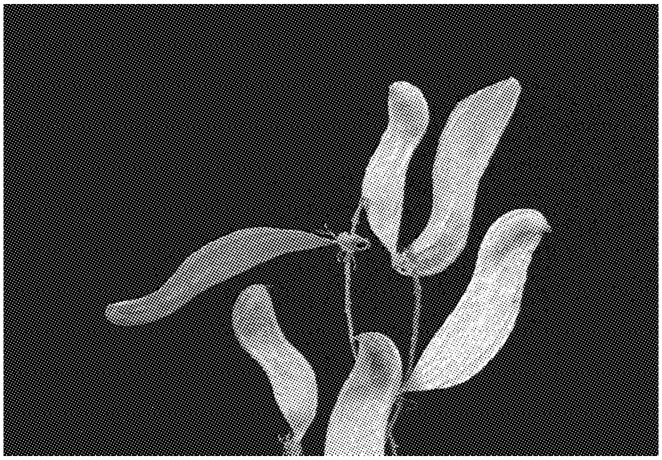


Fig. 46.

Fig. 47.

Fig. 48.

Nut. Fruit with only one seed. The pericarp is hard. Usually the nut derives from a unilocular ovary; e.g., *Anacardium excelsum* and *A. occidentale* (Anacardiaceae). In *A. occidentale* the fleshy structure corresponds to the pedicel (fig. 41).

Samara. Winged fruit or diaspore (figs. 41 and 45-48); e.g., Anacardiaceae (*Astronium graveolens*), Bombacaceae (*Cavanillesia platanifolia*), Combretaceae (*Terminalia amazonia*, *T. oblonga*), Oleaceae (*Fraxinus uhdei* (Wenz.) Lingelsh.), Fabaceae-Caesalpinioideae (*Sclerolobium costaricense*, *Tachigali versicolor*), Fabaceae-Papilionoideae (*Dalbergia retusa*, *Hymenolobium mesoamericanum*, *Platymiscium pinnatum* (Jacq.) Dugand, *P. pleiostachyum*, *Myrospermum frutescens*, *Myroxylon balsamum* (L.) Harms, *Paramachaerium gruberi*, *Pterocarpus hayesii*), Polygonaceae (*Triplaris surinamensis*), and Ulmaceae (*Phyllostylon brasiliensis* Capan. Ex Benth. & Hook f.). Some authors call the samara of different Fabaceae samaroid pods.

Fig. 49.

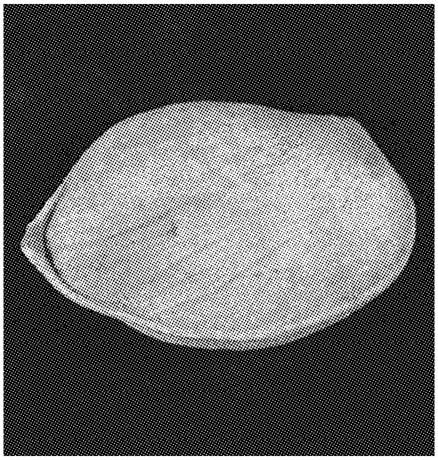


Fig. 50.

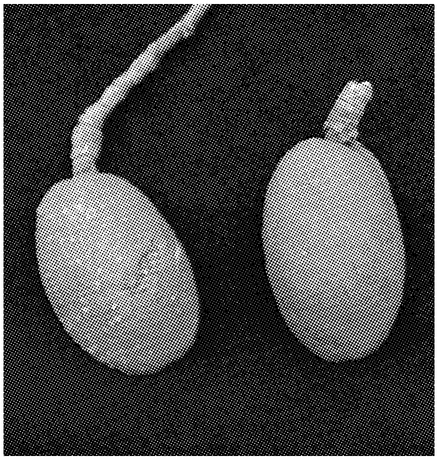


Fig. 52.

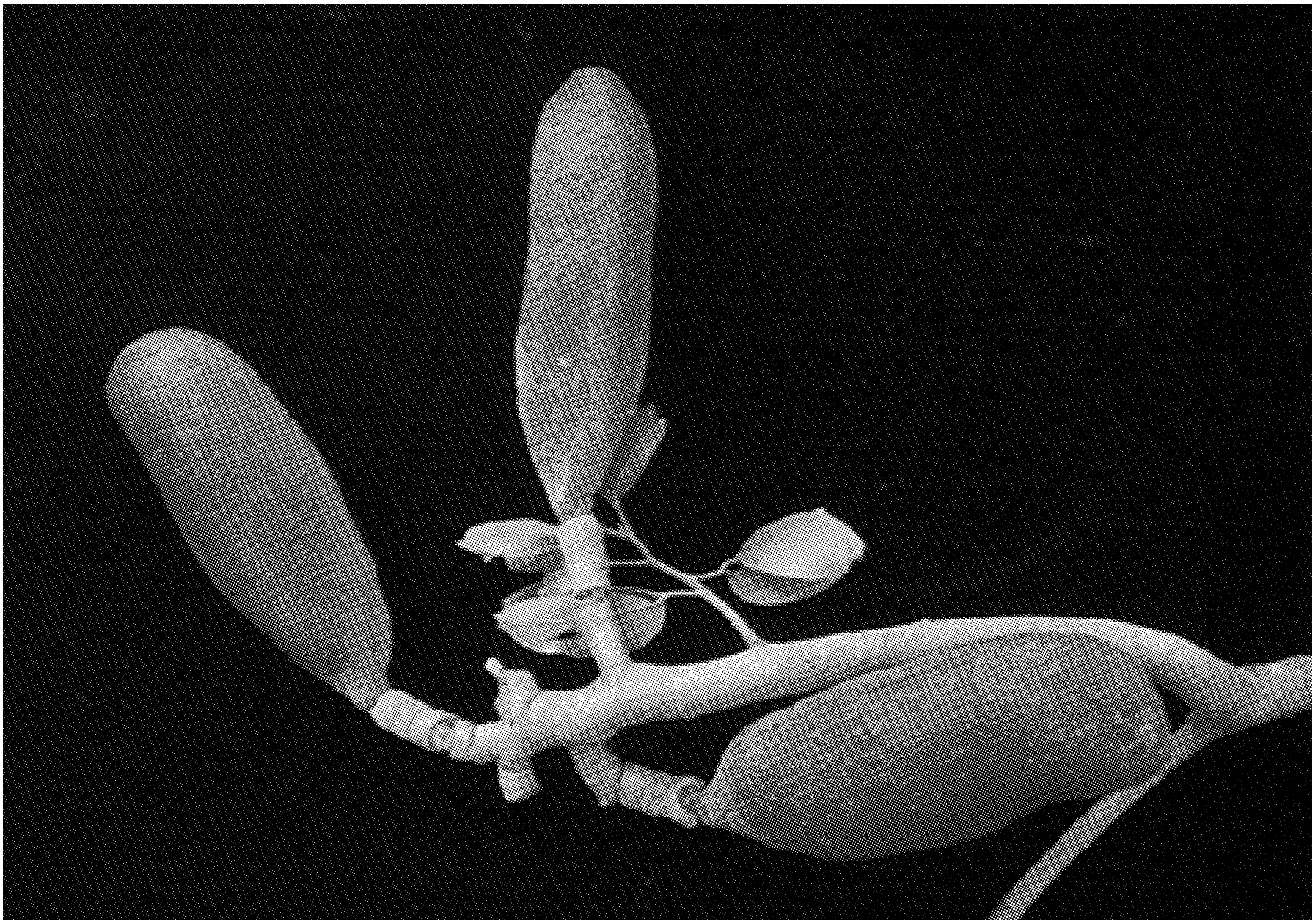


Fig. 51.

Camara. Unicarpellar fruit, indehiscent or late dehiscent. The fruit pericarp and the seedcoat are independent (figs. 41 and 49-52). Frequent in legumes and commonly described as an indehiscent pod; e.g., Fabaceae-Caesalpinioideae (*Cassia grandis, Hymenaea courbaril, Prioria copaifera, Tamarindus indica* L.), Fabaceae-Mimosoideae (*Enterolobium cyclocarpum* (Jacq.) Griseb.), Fabaceae-Papilionoideae [*Andira inermis, A. surinamensis, Diphysa americana* (with air chambers in the pericarp), and *Dipteryx panamensis* (late dehiscence)].

Dry Dehiscent Fruits

These are fruits that open at maturity. The following types are found in this category (fig. 53):

Capsule. Fruit derived from an ovary with two or more carpels. The pericarp opens along predetermined lines as the result of tensions produced by tissue drying. Several kinds of capsules exist:

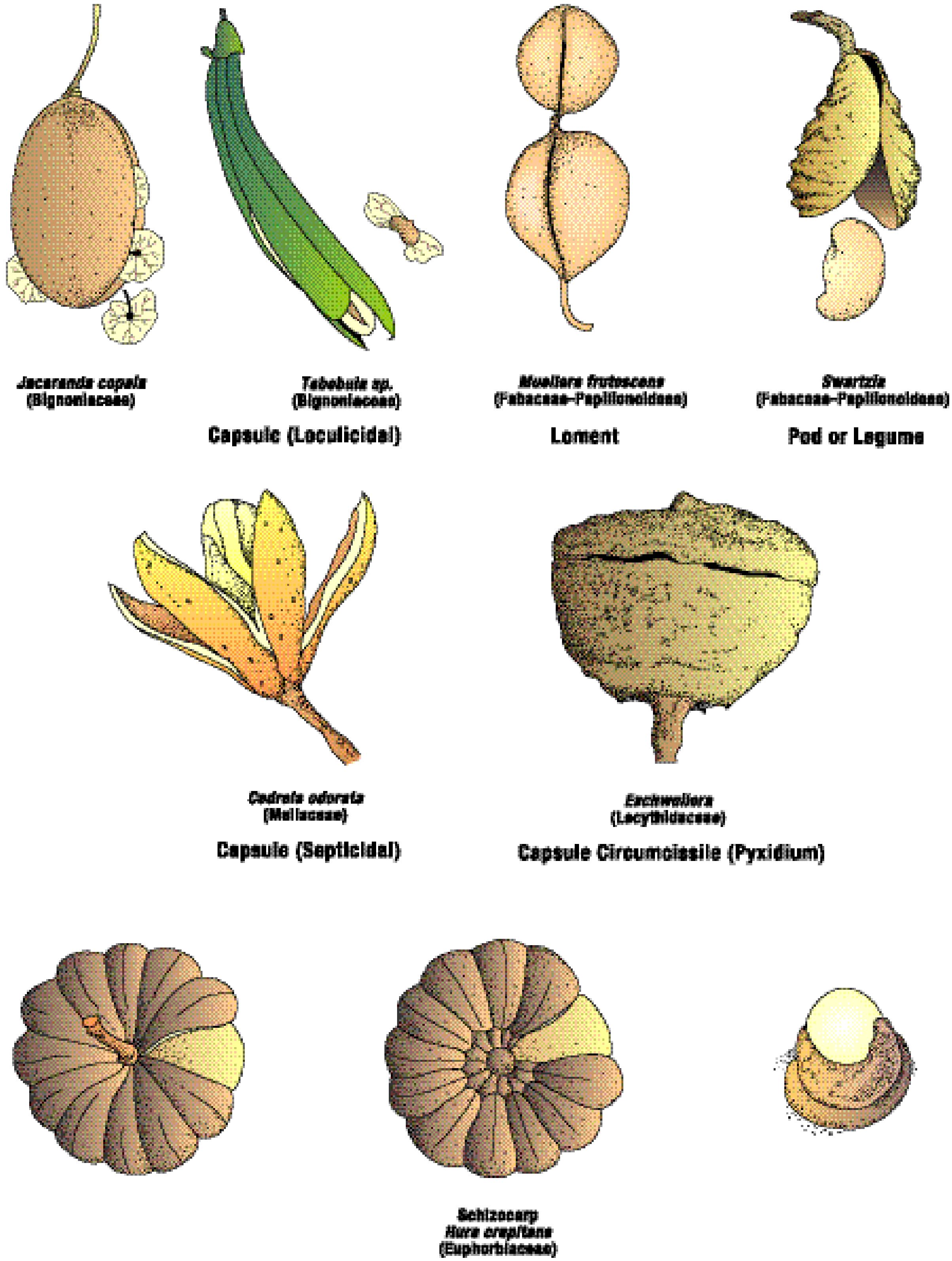


Fig. 53. Dry dehiscent fruits.

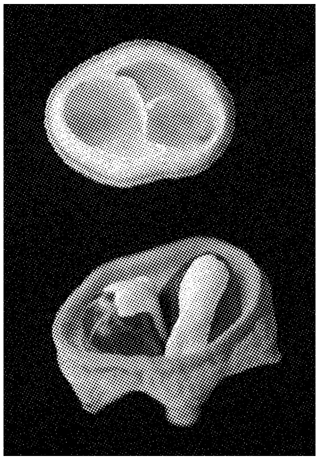


Fig. 54.

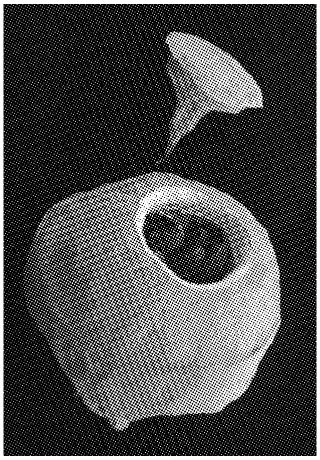


Fig. 55.

Fig. 56.

Fig.57.

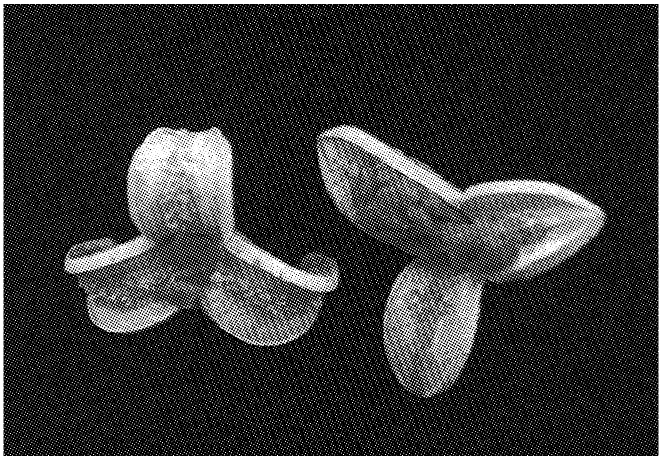


Fig. 58.

Fig. 59.

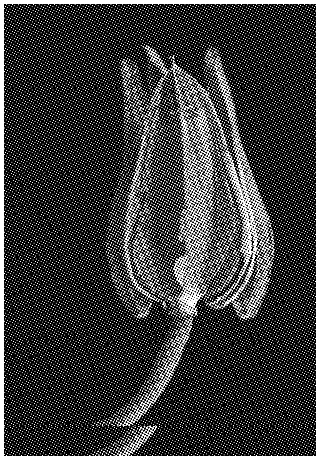


Fig. 61.

Fig. 62.

Acrocidal: The capsule opens through fissures or specific openings; e.g., *Gossypium hirsutum*.

Circumscissile (pyxidium): The cover is named operculum and the dehiscence line is a well-defined circumference. It is common in Lecythidaceae (figs. 53-55); e.g., *Lecythis ampla, Eschweilera panamensis, E. costaricensis,* and *Couratari guianensis* Aubl.

Loculicidal: The capsule opens longitudinally in the locule cavity (carpel midvein region) (figs. 53 and 56-59); e.g., Tiliaceae (*Luehea seemannii*), Bixaceae (*Bixa orellana*), Bignoniaceae (*Jacaranda copaia* (Aubl.) D. Don, *Tabebuia rosea* (Bertol.) DC., *T. chrysantha*), Elaeocarpaceae (*Sloanea faginea, S. latifolia*), Loganiaceae (*Placospermum buxifolium*), Meliaceae (*Guarea, Trichilia*), Sapindaceae (*Cupania*), and Turneraceae (*Erblichia odorata*).

Poricidal: The capsule opens through a pore. If the pore has an operculum the capsule has poricidal-operculate dehiscence; e.g., *Triodanis*.

Fig. 60.

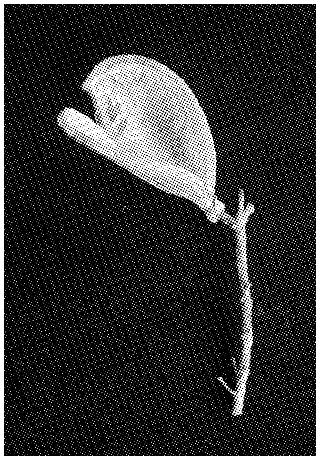


Fig. 63.

Fig. 64.

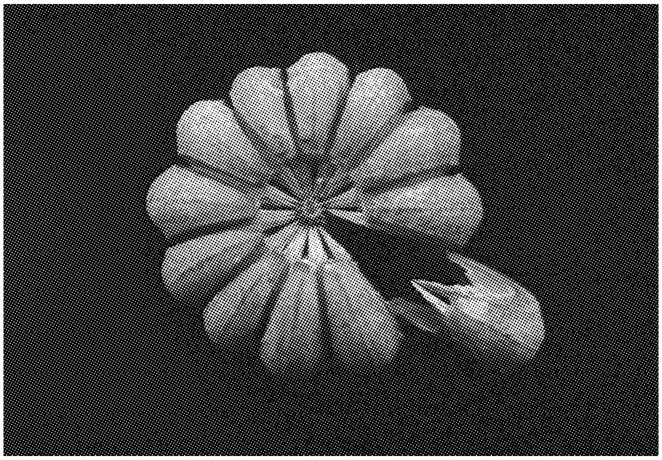


Fig. 65.

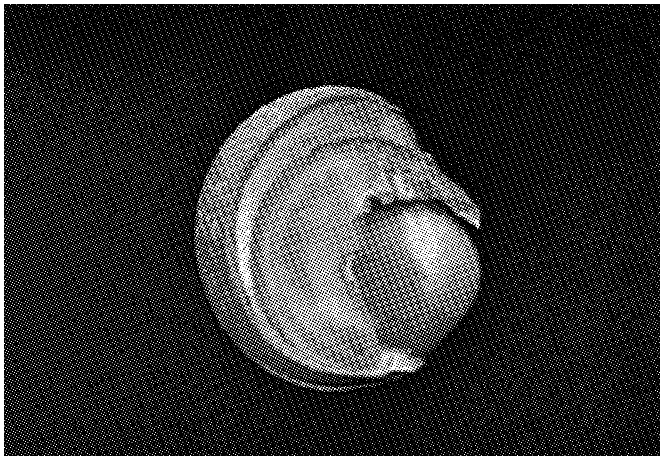


Fig.66.

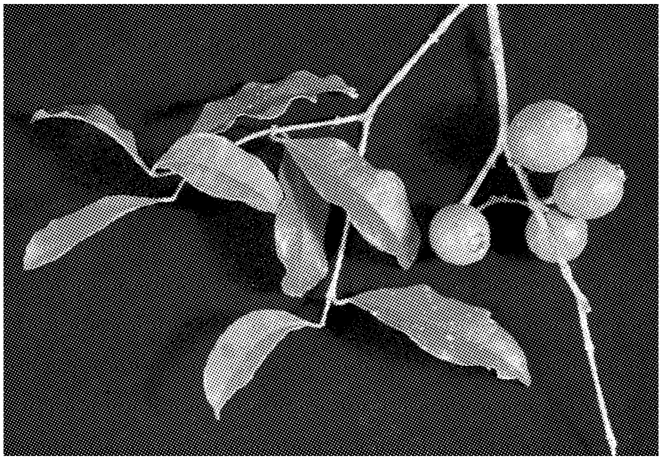


Fig. 68.

Fig.69.

Fig. 70.

Septicidal: The capsule opens longitudinally through septa (figs. 53 and 60-62). It is common in Meliaceae (*Cedrela, Carapa guianensis, Swietenia*), and Myristicaceae (*Virola, Otoba, Myristica fragrans*).

Follicle. Fruit derived from a carpel opening along a suture (fig. 63); e.g., Proteaceae (*Roupala montana, Macadamia integrifolia*).

Legume or pod. Coriaceous fruit derived from a monocarpellar gynoecium. It opens along the ventral and dorsal sutures (figs. 53 and 64). Typical fruit in the Fabaceae-Caesalpinioideae (*Copaifera aromatica* Dwyer, *Peltogyne purpurea*), and Fabaceae-Mimosoideae (*Cojoba arborea, Abarema macradenia*). The dehiscence is explosive in *Pentaclethra macroloba* (Fabaceae-Mimosoideae) and *Gliricidia sepium* (Fabaceae-Papilionoideae).

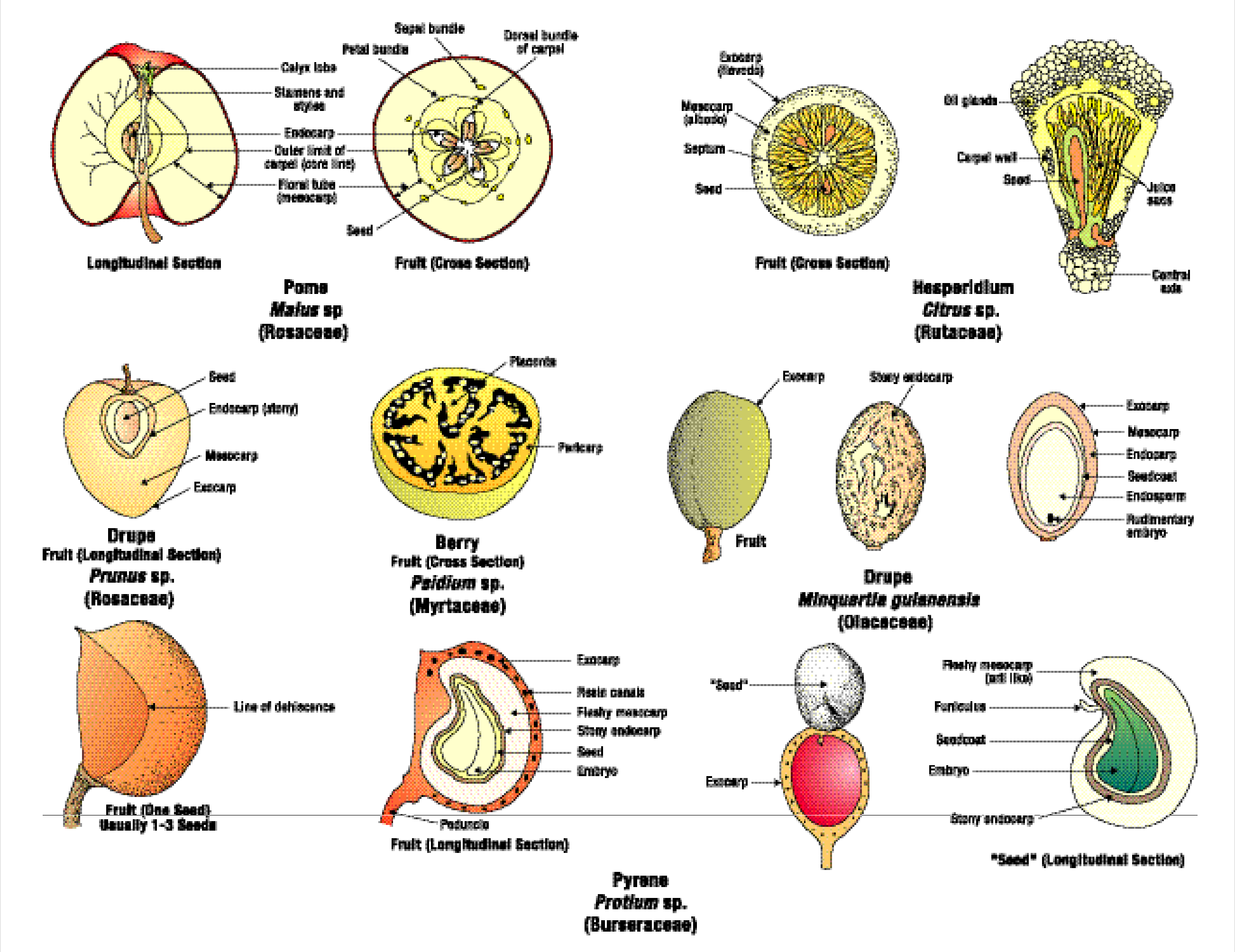


Fig. 67. Types of fleshy fruits.

Loment. Pod or legume splitting into segments each containing a seed (fig. 53); e.g., *Muellera frutescens* (Fabaceae-Papilionoideae) and *Senna skinneri* (Fabaceae-Caesalpinioideae). The last species is extremely specialized; the pod has deep constrictions in the break sites.

Schizocarp. Fruit splitting into units or fruitlets containing the seeds (figs. 53 and 65-66); e.g., *Hevea brasiliensis* Müll Arg. and *Hura crepitans* (Euphorbiaceae). The mericarp (cremocarp, carpopodium) are the units; if the unit is equivalent to half a carpel it is called a carcerule.

Fleshy Fruits

Those fruits derived from a monocarpellar or multicarpellar gynoecium (fig. 67). The pericarp has carpellar or extracarpellar tissue (hypanthium, perianth, androecium, peduncle, bracts) (Fahn and Werker 1972). The pericarp can be fleshy in the external or internal parts; in some fruits both zones are fleshy. In some fruits the placenta and the partitions of multilocular ovaries are also fleshy. The principal fleshy fruits follow:

Pome. Fruit derived from a gynoecium with two or more carpels and an inferior ovary. The receptacle and hypanthium are adnate to the ovary and form most of the fleshy tissues. The endocarp is cartilaginous (fig. 67); e.g., Rosaceae (*Pyrus malus*, *Pyrus communis*, *Cydonia oblonga*).

Berry. Fruit with a succulent pericarp (figs. 67-70), e.g., Myrtaceae (*Psidium friederichsthalianum*, *P. guajava*, *Syzygium jambos*, *Myrcianthes fragrans*), Clusiaceae (*Calophyllum brasiliense*, *Symphonia globulifera*), Lauraceae (*Ocotea*, *Nectandra*, *Persea*), and Rubiaceae (*Posoqueria*).

Fig. 71.

Fig. 72.

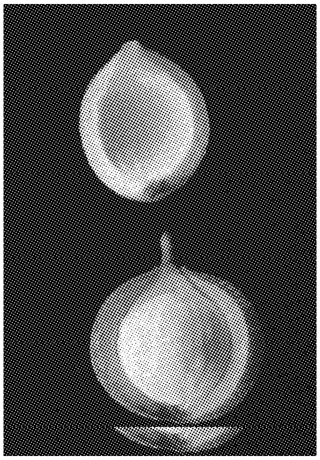


Fig. 73.

Drupe. Fruit with a hard endocarp (figs. 67 and 71-73); e.g., Anacardiaceae (*Spondias purpurea*, *S. mombin*, *Mangifera indica*, *Tapirira*), Caryocaraceae (*Caryocar costaricense*), Chrysobalanaceae (*Licania*), Euphorbiaceae (*Hyeronima*), Malpighiaceae (*Byrsonima crispa*), Olacaceae (*Minquartia guianensis*), Sapindaceae (*Meliccocus bijugatus*), and Verbenaceae (*Vitex cooperi*).

Hesperidium. Septicidal berry with a thick pericarp (fig. 67). Most of the fruit is derived from glandular trichomes. It is typical of the Rutaceae (*Citrus*).

Aggregate Fruits

Several types of aggregate fruits exist (fig. 74):

Achenacetum. Cluster of achenia; e.g., the strawberry (*Fragaria vesca*).

Baccacetum *or etaerio*. Aggregate of berries; e.g., Annonaceae (*Asimina triloba*, *Cananga odorata*, *Uvaria*). The berries can be aggregate and syncarpic as in *Annona reticulata*, *A. muricata*, *A. pittieri* and other species.

Drupacetum. Aggregate of druplets; e.g., *Bursera simaruba* (Burseraceae).

Folliacetum. Aggregate of follicles; e.g., Annonaceae (*Anaxagorea crassipetala*, *A. phaeocarpa*, *Xylopia aromatica*, *X. frutescens*, *Cymbopetalum costaricense*, *C. torulosum*, *Guatteria*), Illiciaceae (*Illicium verum*, *I. anisatum*), Apocynaceae (*Aspidosperma*, *Prestonia surinamensis*, *Stemmadenia*, *Tabernaemontana*), Magnoliaceae (*Magnolia poasana*, *Talauma gloriensis*), and Sterculiaceae (*Helicteres guazumaefolia*, *Sterculia*). *Desmopsis bibracteata* (Annonaceae) has aggregate follicles with constrictions between successive seeds, similar to those found in loments.

Samaracetum. Aggregate of samaras (fig. 74); e.g., Aceraceae (*Acer pseudoplatanus*), Magnoliaceae (*Liriodendron tulipifera* L.), Sapindaceae (*Thouinidium dodecandrum*), and Tiliaceae (*Goethalsia meiantha*).

Multiple Fruits

Multiple fruits are found along a single axis and are usually coalescent. The most common types follow:

Bibacca. Double fused berry; e.g., *Lonicera*.

Sorosis. Fruits usually coalescent on a central axis; they derive from the ovaries of several flowers; e.g., Moraceae (*Artocarpus altilis*).

Syconium. Syncarp with many achenia in the inner wall of a hollow receptacle (fig. 74); e.g., *Ficus*.

THE GYMNOSPERM FRUIT

Fertilization stimulates the growth of young gynostrobiles which in species such as *Pinus* are more than 1 year old. Many genera have woody gynostrobiles (*Pinus*, *Picea*, *Pseudotsuga*); others have fused scales forming a berry-like structure around the seeds (*Juniperus*). In some species, such as *Taxus* and *Torreya*, the seeds develop inside fleshy arils (Foster and Gifford 1974, Krugman and others 1974, Sporne 1965). In *Podocarpus*

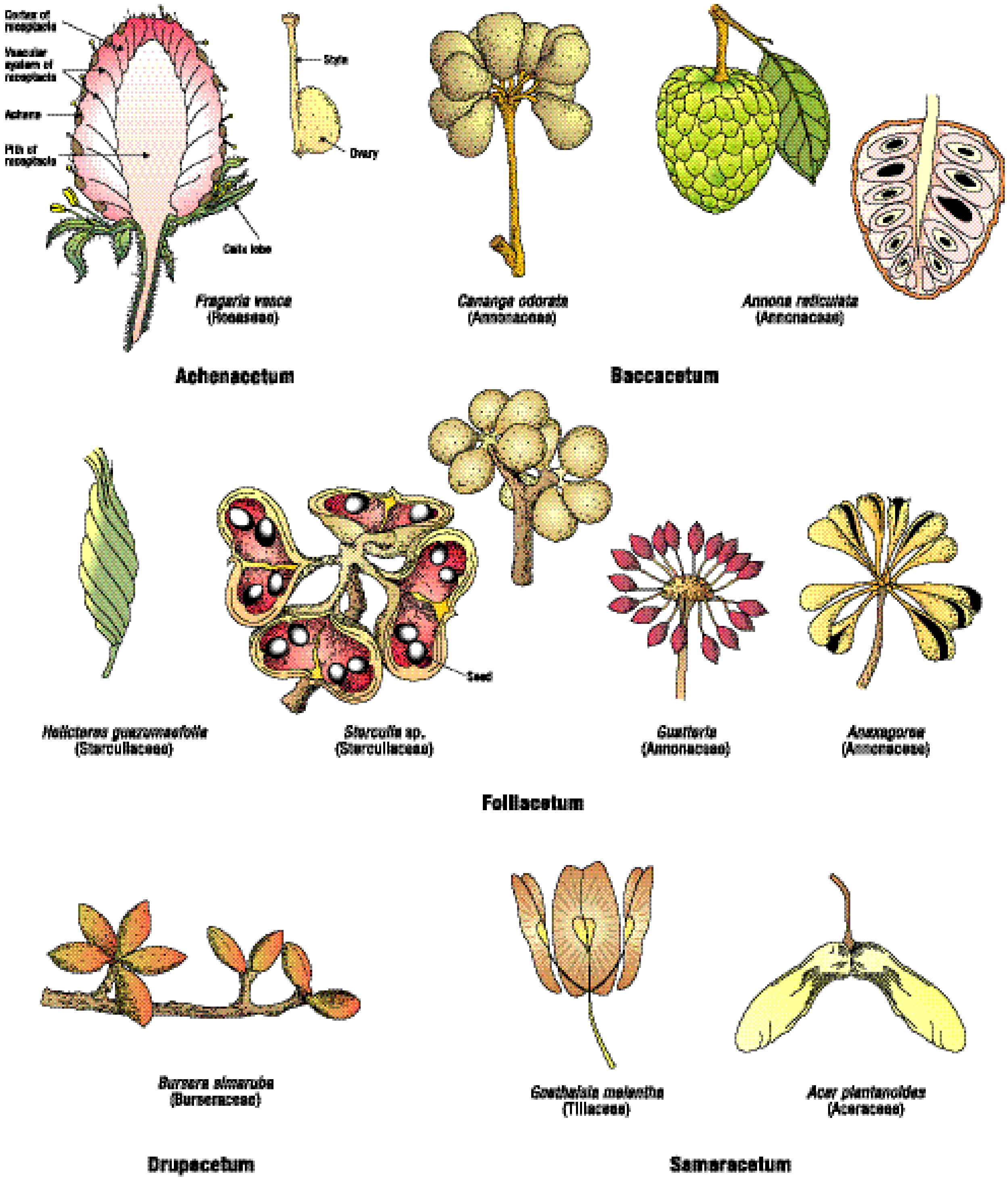


Fig. 74. Aggregate and accessory fruit types.

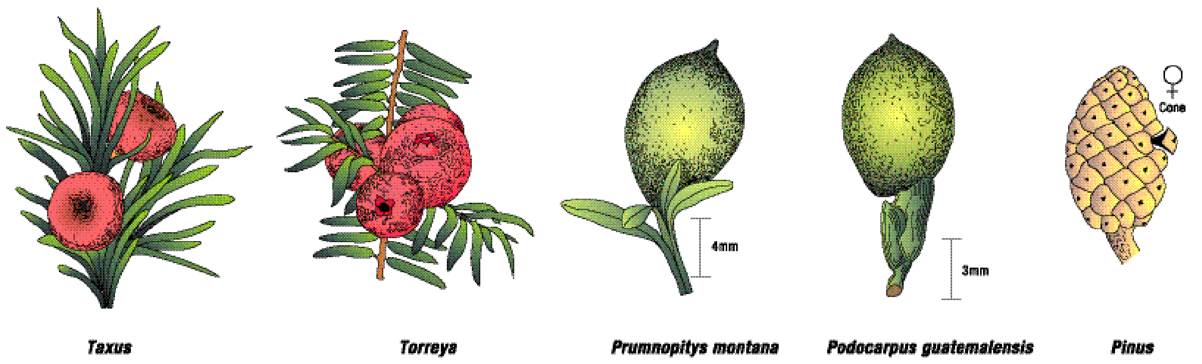


Fig. 75. Fruits of several gymnosperms.

and *Prumnopitys*, the ovuliferous scale forms a fleshy covering called epimatium, which surrounds the seed (fig. 75). This structure can be partially or totally fused to the ovule integument and even to the bract subtending the ovuliferous scale (Sporne 1965).

The pre- and postfertilization development of the strobile shows many facets similar to those of angiosperm fruits. Parameters such as size and moisture content show daily fluctuations as a consequence of variations in the moisture level, increasing dry weight, high respiratory rates, and storage of carbohydrates and minerals. However, in the last stages of maturation the moisture content decreases. Weight may be lower, respiration is lower, and nutrients are mobilized to the seed. The metabolic activity declines with strobile dehydration and the scales become open (Krugman and others 1974, Singh and Johri 1972).

THE SEED

The seed is the site of a partial development of the sporophyte (*embryo*) and the linkage between successive generations. It is a critical intermediate stage in the life cycle of angiosperms and gymnosperms, which guarantees the propagation and survival of the species.

Seeds are dynamic and tridimensional entities, and their morphology is the result of the physiological and environmental processes involved in their development. The physical configuration (size, shape, distribution, and structure of tissues and organs) influences, at different ontogenetic stages, the nature and efficiency of the functional activities.

THE ANGIOSPERM SEED

Seed Development

The ovule, whose embryo sac was fertilized twice, is the starting point for seed development (Bhatnagar and Johri 1972). In some cases, the process is long and complicated; in others, it is short and simple.

In seed development, three functional phases can be identified:

(1) Cell divisions produce the tissues that will form the seedcoat, the endosperm, and the embryo (early embryogenesis); this stage is characterized by a fast increase in fresh weight.

(2) Ontogenetic changes guarantee the success of the offspring as an independent unit, through the storage of reserves. They lead to an increase in dry weight.

(3) Maturation drying leads to a stage of metabolic quiescence, interpolated between the end of seed development and the beginning of germination. In this stage, fresh weight decreases. Many studies suggest that this period of dehydration is important to the transition of activities from seed development (especially embryo) to germination-seedling development (Bewley and Black 1982, 1994; Kermode 1990, 1995, 1997; Kermode and Bewley 1985a, 1985b, 1986; Kermode and Jiang 1994; Kermode and others 1989).

Maturation drying guarantees the permanent inactivation of seed metabolism during seed dispersal and the period before germination. The reduction of water content in the tissues, the impermeability of the seedcoat, and the presence of inhibitors cause seed inactivity. The influence of these factors varies from one species to another, but many seeds do not germinate if they are removed from the maternal plant before this stage. However, a precocious germination may be induced through a dessication-rehydration period (Bewley and Black 1994, Kermode and others 1989). The maturation drying stops seed development and irreversibly stunts the germination-seedling development. A dramatic reduction in the synthesis of storage proteins occurs. Synthesis of reserves stops and synthesis of proteins related to germination-seedling development is introduced (e.g., enzymes related to reserve mobilization). The change in genetic expression seems to act at the transcription and post-transcription (mRNA) levels. The drying suppresses the production of messages to synthesize proteins for development. When the seeds rehydrate, the messages to synthesize proteins used in development and growth increase (Kermode and Jiang 1994, Kermode and others 1989).

Growth regulators present in the tissues of developing seeds (indol acetic acid, IAA), gibberellins (GAs), cytokinins, and abscisic acid (ABA) seem to be involved in several processes. These processes are development of the seed (growth: cell division and elongation) and cellular differentiation (qualitative differences between cells, tissues, and organs), including the arrest of growth prior to seed germination; accumulation of the storage reserves; development of the extraseminal tissues (growth and cell differentiation); and several physiological effects on tissues and organs close to the developing fruit (Bewley and Black 1994).

The biologically active gibberellins show high concentrations during the growth (mainly cell division) of the embryo and the endosperm. Abscissic acid plays an important role in the development and maturation of seeds. It is associated more with the reduction of embryo growth than with its promotion; in many cases, it can be present in the normal embryogenesis but not in the germination and longitudinal extension of the embryo axis. Abscissic acid concentration also appears to influence the deposition of proteins and other reserves and, in many species, the highest content of ABA is coincident with the highest rate of reserve synthesis (Bewley and Black 1994). It also induces dehydrine expression (LEA), which is the accumulation of proteins during the last stages of seed maturation (late embryogenesis). However, the entire role of ABA is not yet well comprehended. Dehydrine expression finishes when germination starts (Farrant and others 1993). Water loss during the process of maturation is common to many seeds, which may diminish to less than 5 to 10 percent of their fresh weight.


Fig. 76.


Fig. 77.

In temperate zones, and especially in the tropics, many seeds do not undergo drying, do not experience reduced cellular metabolism, and do not exhibit a clear end to seed development (Côme and Corbineau 1996a, 1996b; Corbineau and Côme 1988; Finch-Savage 1992a, 1992b, 1996; Finch-Savage and Blake 1994; Kermode 1997). During fruit dehiscence and dispersal, seed development is followed by germination-seed development without interruption. In some species, the seedling develops when the seed is still inside the fruit and is attached to the parent tree. These seeds are called *viviparous,* and it has been demonstrated experimentally that the inhibition of their development requires high concentrations of ABA (Bewley and Black 1994). Mangroves growing on protected tropical coasts are the best-known examples of viviparous seeds. Common on the American coasts are *Rhizophora racemosa* (Rhizophoraceae), *Pelliciera rhizophorae* (Theaceae), *Avicennia germinans* (L.) L., *A. bicolor* (Verbenaceae), and *Laguncularia racemosa* (L.) C.F. Gaertna. (Combretaceae). *Inga paterno* Harms (Fabaceae-Mimosoideae) also has a viviparous seed (fig. 76). *Cojoba arborea* and *C. costaricensis* (Fabaceae-Mimosoideae) show an incipient viviparity (fig. 77). The overgrown seeds described by Corner (1951, 1953), which have a continuous embryo development limited by a hard and indehiscent pericarp or a late dehiscence pericarp (*Dipteryx panamensis*, *D. odorata*, *Prioria copaifera*), seem to be an intermediate type. In these seeds, the cotyledons fold and become disfigured because space is inadequate. The plumule, which is well developed, usually has an incipient epicotyl and several foliar primordia in different stages of development.

Embryogenesis

Embryo development includes two fundamental processes: the establishment of a precise spatial organization of the cells derived from the zygote (pattern of formation), and the generation of cell diversity inside the developing embryo (cytodifferentiation). These processes are coordinated to develop a recognizable morphological structure, regulated by the embryogenic pattern of the species. Although in plants most organogenesis occurs in the postembryonic stage, the embryonic pattern reveals coordinated growth and development during the process of development (Flores 1999, Lindsey and Topping 1993).

Early Embryogenesis

The pattern of embryogenic formation has three levels: pattern of cellular organization, pattern of protein accumulation, and pattern of gene expression (Lindsey and Topping 1993).

The unicellular zygote evolves into a multicellular embryo with differentiated organs and the potentialities of the adult plant. This occurs through a programmed sequence of events (pattern of embryogenesis). In angiosperms, the embryo is located at the micropylar end of the embryo sac. Its basal end is attached to the embryo sac wall and its apical end faces the central cell. After fertilization the zygotic cell polarizes (establishes structural and physiological differences). The endoplasmic reticulum and the cellular organelles reorganize around the nucleus. During mitosis, the polarized zygote divides, forming two daughter cells that have cytoplasmic elements differentially distributed. This fact has a strong effect on the embryogenesis. In most angiosperms the zygote divides transversely, producing a chalazal or apical cell (ac) and a basal cell (bc); in several exceptional cases, cell division is longitudinal or oblique as in Piperaceae and Dipsacaceae (Flores 1999, Natesh and Rau 1984). The cells derived from the apical cell contribute to form most of the proembryo and embryo (usually the plumule and the cotyledons); the basal cell and its derivatives commonly form the hypocotyl and the suspensor.

The variations in cell wall orientation and the sequence of cell divisions in the embryo are the basis for classification of embryonic types (fig. 78). The separation of types, except the piperad, is based on the destiny of the proembryo apical cell during the second and subsequent cell divisions, and in the contribution of the basal cell to the embryo organs.

In the onagrad type, a vertical division in the apical cell (ac) and a transversal division in the basal cell (bc) result in a tetrad of cells forming a “T”. The ac and its derivatives form most of the embryo (cotyledonar zone, apical meristem, hypocotylar zone). The bc forms the radical cortex, the root cap, and the suspensor. The proembryo in the asterad type is formed through a vertical division in ac and a transverse division in bc. In some taxa, the ac divides obliquely and when the quadrant is formed, one of the cells forms the epiphysis. Through further growth, the epiphysis produces the epicotyl. The remaining cells in the quadrant develop into the cotyledons. In this type, bc contributes to form a considerable portion of the embryo (hypocotylar region, radical cortex, root cap, suspensor). The solanad type forms a linear tetrad of cells. The two cells derived form ac from most of the embryo; bc does not take part in embryo organization but forms the root cap and the suspensor. The chenopodiad type also has a linear tetrad; ac produces the cotyledonar region, the apical meristem, and a hypocotyl half, while bc provides the other hypocotyl half, the radical cortex, the root cap, and the suspensor. The caryophyllad type differs from the other types. Here, the bc does not divide and the ac originates the embryo. The piperad type includes those cases in which the zygote divides in a longitudinal plane (Natesh and Rau 1984).

The time and the fixation mechanism of the polar axis in the zygote are very important in morphogenesis. The establishment of the polarity, and the zygote and proembryo histodifferentiation occur in the absence of cell movement due to the rate and planes of cell division and subsequent cellular elongation. As a result, the regions giving rise to the apical and radical meristems are formed (Flores 1999, Steward 1970, Steward and others 1970). These changes mark the beginning of mRNA synthesis in the zygote during early embryogenesis (Flores 1999).

During the zygotic, proembryonic and embryonic stages, coordination exists at the biochemical level. A specific pattern also exists for the synthesis of proteins, lipids, and carbohydrates in the embryo and other seed structures. The three types of protein involved in this synthesis are as follows: enzymes involved in reserve mobilization, structural proteins associated with the membranes and the ribosomes, and storage proteins in which the LEA or dehydrines are critical.

The activation and expression of genes during embryogenesis, especially those regulating specific aspects of development, are the subject of increasing research. Lindsey and Topping (1993) identified a gene in *Arabidopsis* that expresses in the basal region of the proembryo when the latter is in the heart stage, and in the radical meristem when in the adult

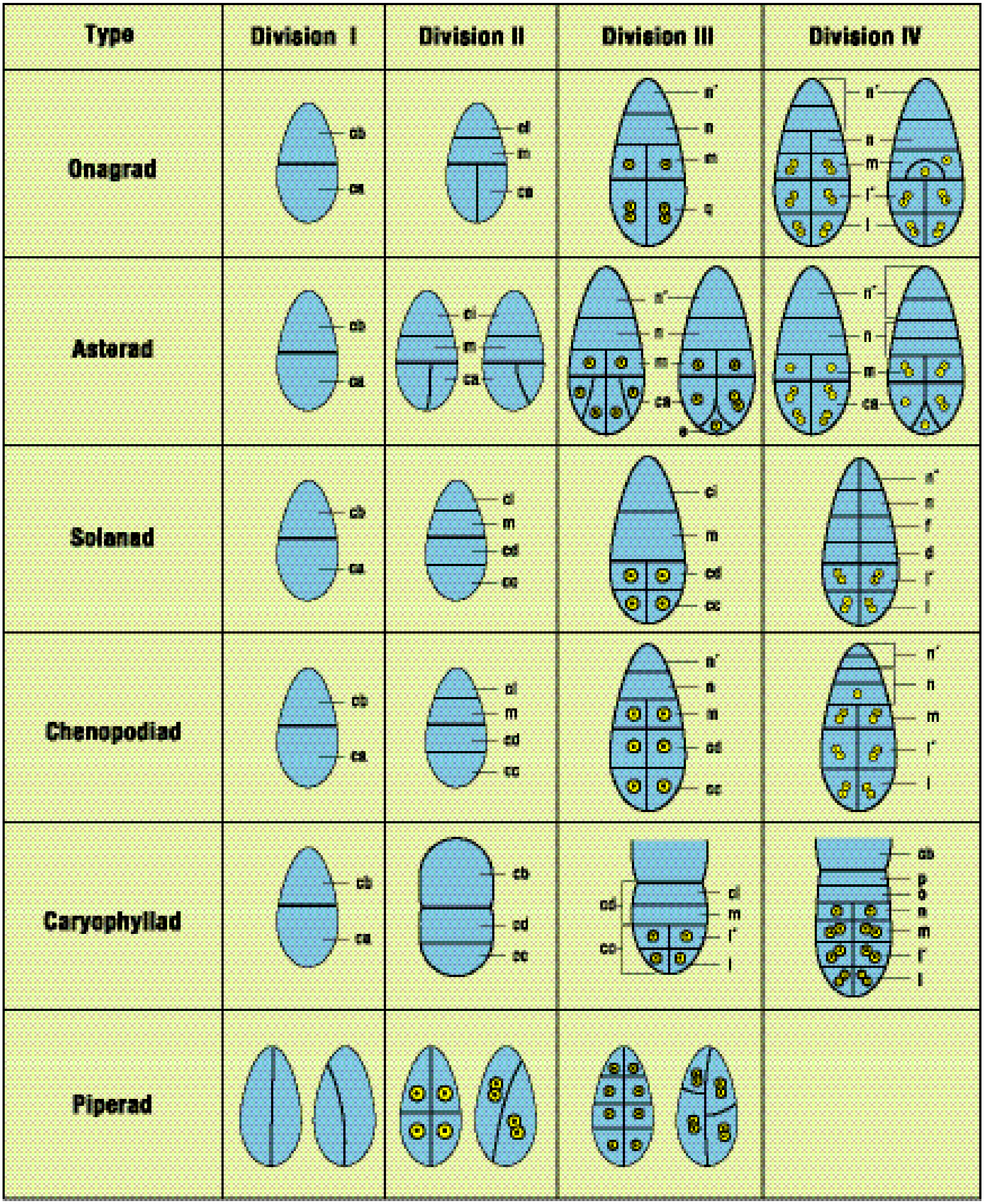


Fig. 78. Main types of embryogeny. (Redrawn from Natesh & Rau. 1984).

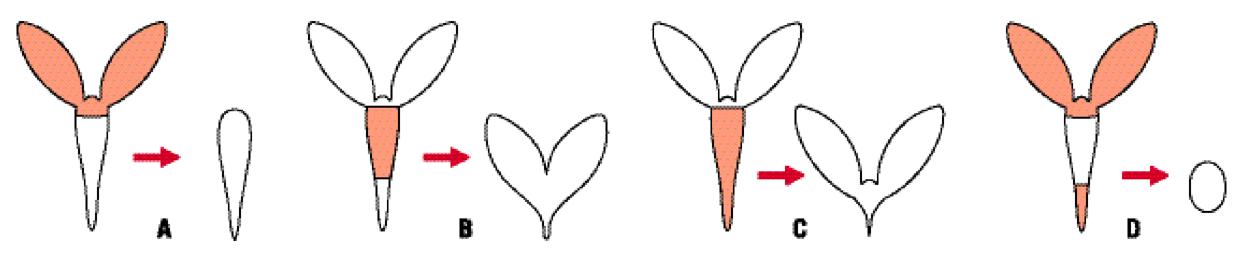


Fig. 79. Origin and final form of apical-basal pattern mutants.

(Redrawn from Lindsey & Topping. 1993).

stage. By studying mutants, researchers have proven that numerous loci control the diverse aspects of embryogenesis. Processes such as cell division and morphogenesis per se, and the establishment of polarity, embryo, and endosperm shape are determined by genes that can be recognized easily. Figure 79 depicts some mutants of the apical-basal pattern in *Arabidopsis* (Mayer and Shain 1974, Mayer and others 1991). In the mutant a, the apical cell does not form the plumule, and the cotyledons resemble the embryo of some Lecythidaceae such as *Lecythis ampla* (Flores 1994d, 1999). Perhaps the embryology of *L. ampla* will reveal similarities to that found in mutant *a*. Figure 80 shows the hierarchies proposed by Lindsey and Topping (1993) in the embryonic gene expression regulating cell division and cytodifferentiation during the embryogenesis.

Embryo Differentiation

The tridimensional growth of the embryo begins with the formation of vertical walls in the derivatives of the apical cell. Further divisions in several planes produce a globular embryo. Cell differentiation begins in this stage with the establishment of the cotyledonar and epicotylar loci in the shoot pole; the hypocotyledonar region and the radical pole with the hypophysis are also distinguished. Loci organizations are not strictly related to cell lineage or row systems. The cotyledonar, epicotylar, hypocotyledonar, and hypophysial regions are identified after the growth and differentiation of the incipient organ. The hypocotyledonar region contributes to the embryo axis formation through cell division and elongation. This phase of differential growth in the embryo leads to the establishment of the meristems and accentuates the differences between shoot and root (Natesh and Rau 1984).

Embryo histogenesis in seeds without maturation drying is similar in its early stages to that of seeds with maturation drying; however, accentuated variations appear in late embryogenesis. Many seeds without maturation drying are large, with very well developed embryos such as those of *Aesculus hippocastanum* (Tompsett and Pritchard 1993), *Dipterocarpus* (Tompsett 1987), *Quercus robur* (Finch-Savage 1992a, 1992b), *Hevea brasiliensis* (Chin and others 1981), *Calophyllum brasiliense* (Flores 1994b), *Mangifera indica* (Corbineau and Côme 1988, Corbineau and others 1987), and *Sclerocarya birrea* (Gamené 1996). Other seeds are large but have a small, rudimentary embryo such as those of *Hyeronima alchorneoides* (Flores 1993c). All these seeds increase in dry weight until fruit dehiscence, with slight or no loss in fresh weight; however, a decreasing loss in water content is characteristic of several seeds without maturation drying (Finch-Savage 1996). Embryo growth may continue (increasing in dry weight) after dehiscence in the absence of enough water to promote germination (Finch-Savage 1996); however, in the tropical forest, with very high rain regimes, the seeds or fruits (diaspores) fall down on very humid soils, sometimes inundated, and continue hydrating.

Dicotyledons and monocotyledons have similar types of embryonic development (Lakshmanan 1972). During early embryogenesis–the stages of quadrant and octant and the formation of the globular embryo–the cells in both groups are similar in lineage and configuration. The fundamental differences arise during differentiation of the globular embryo. The organization of the shoot apex follows different morphogenetic patterns. In dicotyledons, the axial cells forming the epiphysis grow slower than the circumaxial cells. In monocotyledons, one-half of the terminal cell and its derivatives grow slowly while the remaining half, which forms the cotyledonar locus, grows rapidly. The apparent lateral position of the shoot apex in late stages is due to the rapid growth of the single cotyledon in monocotyledons. The epicotyl and the cotyledon of monocotyledons develop from the same layer of terminal cells (Lakshmanan 1972). The two loci differentiate through a vertical wall in the terminal layer. The differences found in the terminal region are conspicuous during the quadrant stage (Lakshmanan 1972). In the dicotyledons, two cells opposite the terminal quadrant form the cotyledons; in the monocotyledons the number of cells forming the cotyledon in the quadrant stage is variable (Lakshmanan 1972). Despite these variations, the changes occurring in the different ontogenetic stages

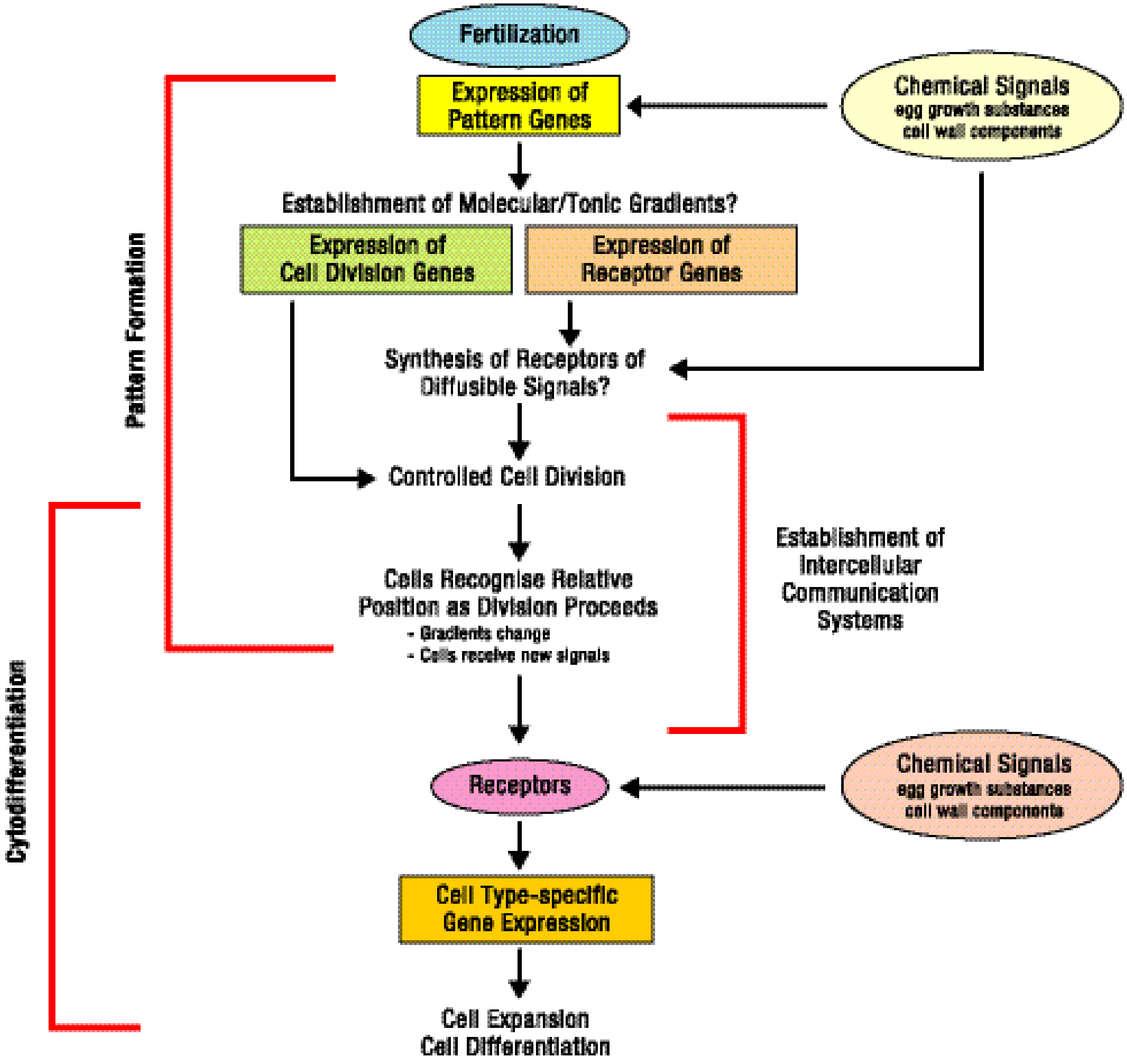


Fig. 80. Hierarchies in embryonic gene expression.

(Redrawn from Lindsey & Topping. 1993).

result in an organized morphogenetic system from which the future tree evolves (Natesh and Rau 1984).

Structure and Function of the Suspensor

The suspensor plays an active and dynamic role during embryogenesis (Alpi and others 1975; Natesh and Rau 1984; Newcomb 1973; Schulz and Jensen 1968a, 1968b, 1969; Singh and Dathan 1972; Yeung and Cutler 1978). The suspensor has a stable cell number and its rate of growth is higher during the early stages of embryogeny. In many species it has transfer cells, suggesting an active role in the absorption and exchange of nutrients for embryo growth. During the late stages of the embryogeny, the suspensor degenerates and seems to be digested by the embryo (Natesh and Rau 1984).

The suspensor seems to accomplish two functions: (1) nutrient absorption from the surrounding somatic tissues and transportation to the developing embryo (Schulz and Jensen 1968a, 1968b, 1969); and (2) a source of nutrients and growth regulators for the developing embryo (Schulz and Jensen 1986a, 1986b, 1969). In vitro, gibberellic acid can partially replace the suspensor; therefore, the suspensor must be a source providing this growth regulator to the developing embryo. The suspensor also contains auxins and cytokinins; the concentrations of these substances have the same fluctuation pattern as those of gibberellic acid (Alpi and others 1975, Natesh and Rau 1984, Yeung and Cutler 1978).

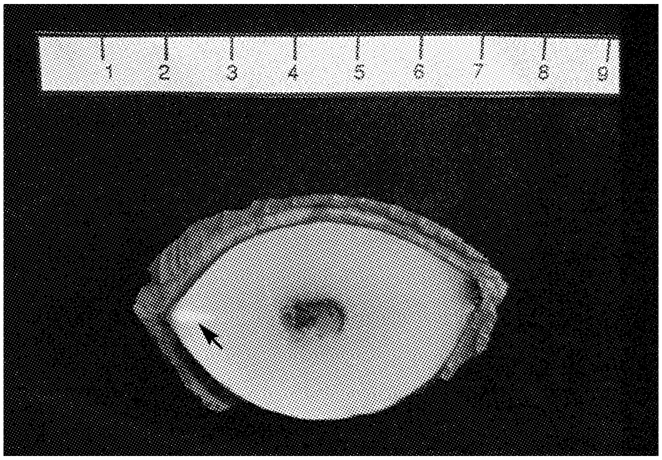


Fig. 81.

The embryo of some taxa (*Tilia*) do not have a suspensor; others have a reduced structure (*Euphorbia*, *Ruta*). Usually, the taxa with haustorial endosperm do not have a suspensor or have one that is reduced and ephemeral. Families such as Rubiaceae have a massive and haustorial suspensor (Natesh and Rau 1984). In Fabaceae, the suspensor may be missing or may form a massive structure, filamentous or tubercular.

Embryogenic Deviations

In some parasite and saprophyte taxa, as well as in some forest trees [Olacaceae (*Minquartia guianensis*), Myristicaceae (*Virola koschnyi*, *V. sebifera*, *Otoba novogranatensis*), Icacinaceae (*Calatola costaricensis*), Piperaceae (*Piper*, *Peperomia*)] minute embryos are found (fig. 81). Frequently they are also rudimentary (Flores 1992c, 1994c, 1994e, 1996, 1999). Other embryos have deviated since their origin. Some deviations are formed by apomixis (asexual process); they may derive from the unfertilized egg cell (haploid parthenogenesis) or from another cell from the gametophyte (haploid apogamy). In many cases, there is no meiosis and a diploid gametophyte is formed, leading to diploid parthenogenesis or diploid apogamy.

Endosperm Development

The fusion of the sperm nucleus with the central cell nuclei forms the primary endosperm cell. Through successive mitosis, this cell forms the endosperm. This tissue does not have a significant role at the proembryo stage, but it is important to embryo nutrition during embryo development and seed germination. In most dicotyledons the endosperm is reabsorbed during seed maturation and storage proteins accumulate in the tissues of the embryo. During seed development, the interactions between endosperm and embryo are essential to insure reproductive success. The formation of the endosperm, its reabsorption, and the transference of reserves to the embryo are genetically established (Lindsey and Topping 1993).

Three types of endosperm are recognized: nuclear, cellular, and helobial. Many free nuclear divisions before cell wall formation characterize the nuclear type; its formation varies from one species to another. The endosperm is consumed before partial or total wall formation occurs in many species. The seeds of other species, such as *Virola koschnyi*, *V. sebifera*, *V. surinamensis*, and *Compsoneura sprucei*, have nuclear endosperm when they are dispersed (Flores 1999). Several species have haustorial endosperm (Vijayaraghavan and Prabhakar 1984).

In the cellular endosperm, each cell division is followed by cell wall formation; this type of endosperm is frequently haustorial. The helobial endosperm has a different development: the first endosperm cell divides and gives rise to a pair of unequal chambers; usually, the micropylar chamber is bigger. It undergoes free nuclear divisions before cell wall formation; in contrast, the nucleus of the chalazal chamber does not divide or undergo division before giving rise to a coenocyte. Sometimes cell wall deposition takes place later. The helobial endosperm is typical of the monocotyledons (Vijayaraghavan and Prabhakar 1984).

The Mature Seed

The mature seed generally has a seedcoat (product of one or both ovule integuments), an endosperm, and an embryo (fig. 82). Some mature seeds retain a remnant of nucellar tissue called a perisperm. The degree to which these structures continue their development, are reduced or reabsorbed, or disappear during the late stages of seed development leads to distinct structural patterns associated with physiological differences.

Seedcoat

In bitegmic seeds the seedcoat has a testa (former outer integument) and a tegmen (inner integument). Each integument has its own opening at the seed's distal end; the opening

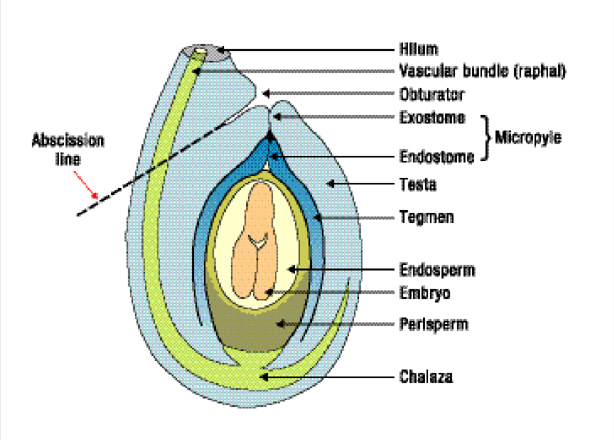


Fig. 82. Typical seed (longitudinal section).

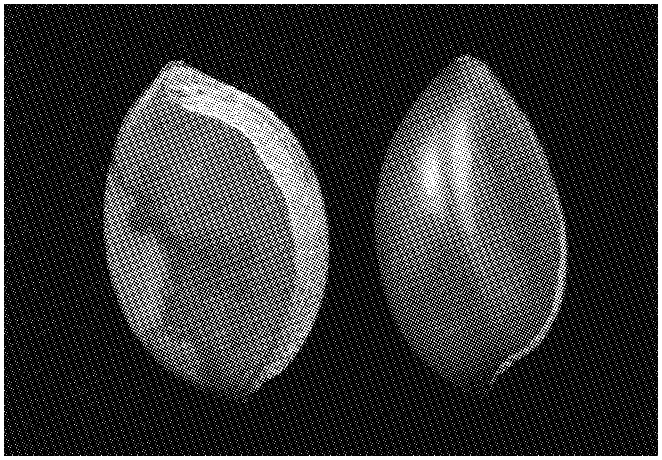


Fig. 83.

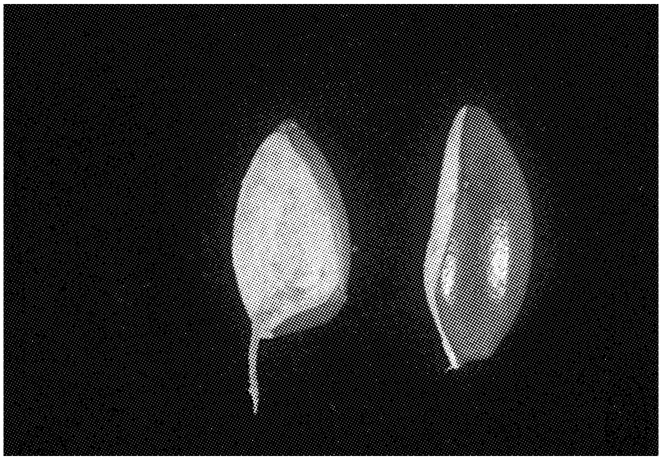


Fig. 84.

in the outer integument is the exostome while that of the inner integument is the endostome. The exostome and the endostome form the micropyle. Unitegmic seeds have only one opening (micropyle) and the seedcoat is called the testa. The seedcoat has a funicular scar called the hilum, indicating the point at which the funiculus separates from the seed. This zone has a different structure and often includes the micropyle. Frequently, a longitudinal ridge (raphe) formed by differential growth of the funiculus is found near the hilar zone. It forms as a result of a curvature of about 80 degrees that occurs during the ontogeny of the anatropous ovules. The hilar zone may extend and be a significant part of the seedcoat as observed in the Sapotaceae (*Manilkara chicle*, *M. zapota* (L.) P., *Micropholis crotonioides*, *Pouteria congestifolia*, *P. viridis*), or may combine its extension with an extension of the chalazal zone (pachychalaza) as seen in the Meliaceae (*Carapa*, *Guarea*), and Hippocastanaceae (*Aesculus*, *Billia columbiana*, *B. hippocastanum*) (figs. 83-84). Other seeds have only a chalazal extension (*Cupania glabra*). A funicular protuberance close to the chalaza is found in many seeds (numerous Cactaceae in the Subfamily Cereaneae). The vascular bundle supplying the ovule follows its course along the raphe—a characteristic easily observed in the seeds of Fabaceae-Papilionoideae (*Erythrina*).

The seedcoat is formed not only by the integument tissue(s) but also by the chalazal and raphal tissues. When the outer layer of the outer integument differentiates as a layer for mechanical protection (exotesta), the outer layer of the raphe and the chalaza undergo an equivalent differentiation. The same happens with the formation of the mesotesta (middle layers) and the endotesta (inner layer of the outer integument). In small seeds, the integument cells undergo mitosis sporadically after fertilization, and their elongation and differentiation form the seedcoat. Many large seeds have complex seedcoats as a result of many anticlinal and periclinal divisions in the integument cells. When periclinal divisions are dominant and more cell layers are formed, the integument is multiplicative (Magnoliaceae, Myristicaceae, Annonaceae, Clusiaceae, Fabaceae, Bombacaceae). If the seedcoat extends primarily by anticlinal cell division and does not develop more cell layers, the integument is nonmultiplicative (Corner 1976). Frequently, multiplicative integuments form seedcoats with many layers (Corner 1976). The periclinal divisions may be diffused or localized in the outer integument. The testa can be soft-textured (*Cojoba arborea*, *C. costaricensis*), hard (*Enterolobium cyclocarpum*, *Samanea saman*, *Tamarindus indica*), or fleshy (*Inga*, *Guarea*, *Punica granatum*, *Carica papaya*, *Magnolia*). The fleshy testa is the sarcotesta. In general, the outer integument is the fleshy and juicy part; however, in *Magnolia* and other related species as well as in *Punica granatum*, the sarcotesta originates only from the mesotesta. In Connaraceae, Meliaceae, and Sapindaceae the fleshy pachychalaza is similar to the aril. It may have lipids, sugars, and attractive color.

The presence of a multiplicative mesotesta is common; these layers may form an aerenchyma (Burseraceae, Bombacaceae, Meliaceae, Simaroubaceae, Fabaceae). Usually the endotesta divides anticlinally. An endotesta with multiple layers is common in the zoochorous seeds. In most species, the inner integument is thin and slightly specialized; it collapses in early stages and is then partially or totally reabsorbed. In exceptional cases, it forms multiplicative middle layers that produce the aerenchyma (e.g., many Euphorbiaceae), although in several families those layers disintegrate during seed maturation (Boesewinkel and Bouman 1984).

The seedcoat may have cell layers or cell groups with tannins, oils, crystals, mucilage, cork, sclerenchyma, or collenchyma cells. The parenchyma may serve as storage tissue, as chlorenchyma, or as aerenchyma. The tannins form in vacuoles, and are formed by polyphenoles and substances of hard metabolic transformation. The presence of tannins serves as a requisite for alkaloid deposit and probably protects the plant against herbivore predators (insects), pathogens (bacteria, fungi), and light. They also increase seed hardness and provide

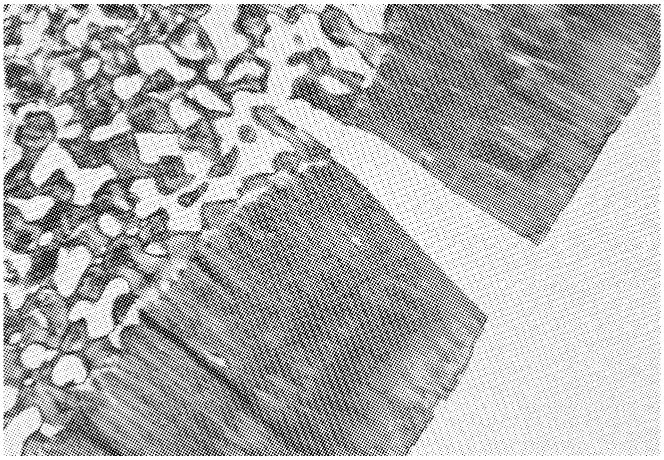


Fig. 85.

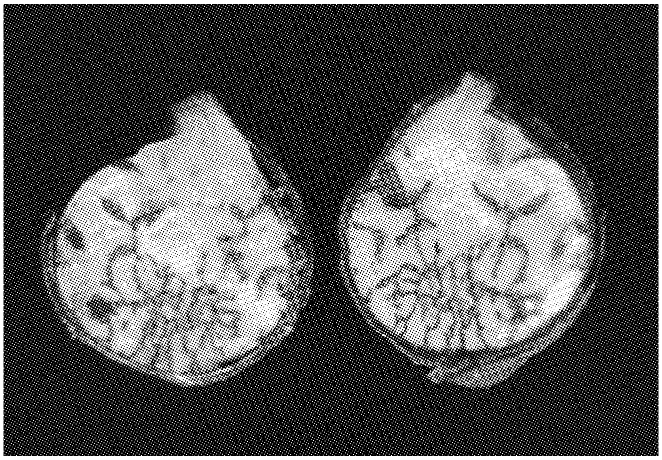


Fig. 86.

color. The crystals are variable in shape and are formed by calcium oxalate, calcium carbonate, or silica (Flores 1999). The mucilage cells are found primarily in the epidermal cells of the exotesta. They form by hydration of substances in the secondary walls of the cells. Some species in Sterculiaceae have mucilage sacs in the testa and tegmen. In Ebenaceae, these sacs are restricted to the tegmen (Boesewinkel and Bouman 1984). Mucilage secretion (myxospermy) appears to help seeds adhere to animals and fix in the soil. Other proposed functions of myxospermy include water retention, germination regulation, oxygen barrier, storage substance, and covering lens (Boesewinkel and Bouman 1984).

Sclerenchyma and collenchyma cells provide mechanical strength. In some seeds, cell walls impregnated with suberin serve as a barrier in the chalazal zone and seal the testal or tegmic layers. These cell walls are also found in the integuments of the hydrochorous seeds and in mucilaginous epidermal cells (Corner 1976). The sclerenchymatic cells (fibers or sclereids) provide hardness and rigidity to the seedcoat. Additionally, the lignin protects against herbivore and pathogen attacks. The more typical macrosclereids are the Malpighi cells of the exotesta in Fabaceae (fig. 85). These cells are elongated radially, have a linea lucida (light line), and in early stages deposit a wall of irregular thickness, which is sometimes lignified. The apical region shows suberized incrustations reinforcing the walls and influencing water permeability. The linea lucida is not involved in cell wall permeability and shows a high density of cellulose microfibrils without interfibrillar spaces. The seeds of Rhamnaceae and Elaeagnaceae have a linea lucida in the external epidermis of the testa. The structure is also present in the external epidermis of the tegmen (Boesewinkel and Bouman 1984, Corner 1976).

When the sclerenchymatous layer forms in the external epidermis of the testa, the seedcoat is called exotestal. The mesotestal seeds have sclerenchyma in the testal middle layers; the endotestal, in the epidermis of the testa. If the sclerenchyma differentiates in the tegmen, the seeds are exotegmic, mesotegmic, and endotegmic respectively. In families with dry indehiscent fruits or drupaceous fruits (e.g., Anacardiaceae), there is a marked tendency toward seeds with a slightly differentiated testa, sometimes lacking mechanical layers. In extreme cases, the mature seed lacks a seedcoat, as in parasites, some Apocynaceae, and Rubiaceae (Boesewinkel and Bouman 1984, Corner 1976).

The seedcoat has an external cuticle on the external epidermis of the testa, a middle cuticle between testa and tegmen (if both exist), and an inner cuticle between the epidermis of the inner integument and the nucellus (Flores 1999). The cuticles contribute to the impermeability of the seedcoat (to water and gases) and may influence the metabolism and growth of the embryo.

The external surface of the seedcoat has characteristics of taxonomic value. Its morphology sometimes shows the influence exercised by the endocarp of the fruit or by arilar structures (e.g., Myristicaceae). Characteristics such as cell distribution, form, surface (conic, papillate, reticulate, striate, micropapillate, or hairy external wall), and epicuticular waxes (scarce) define the external surface of the seed. In many species, the seeds have stomata localized in the external epidermis of the testa.

Some families, such as Myristicaceae, have seeds with an irregular tegmen producing invaginations inwards; these invaginations protrude into the endosperm. This type of endosperm is ruminate (fig. 86). The seeds with a network of lobules in the endosperm are labyrinthine. The lobulation can be the result of the invagination of the tegmen and the folding of the embryo cotyledons (Vijayaraghavan and Prabhakar 1984).

The testa has special structures such as the caruncle, strophiole, and aril (figs. 54 and 62). The caruncle is a fleshy protuberance or swelling arising in the exostome (*Ricinus*,

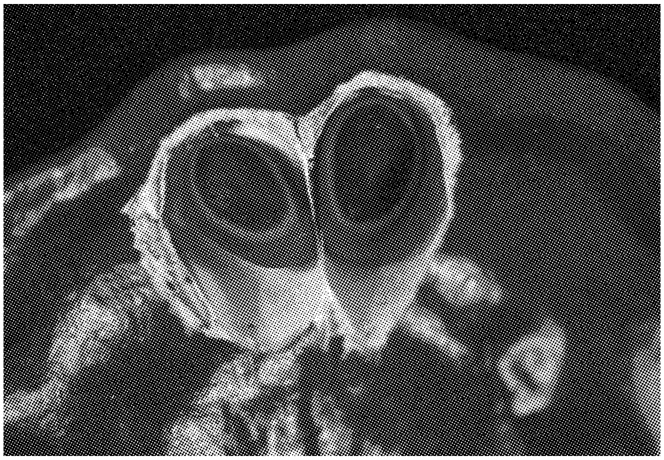


Fig.87.

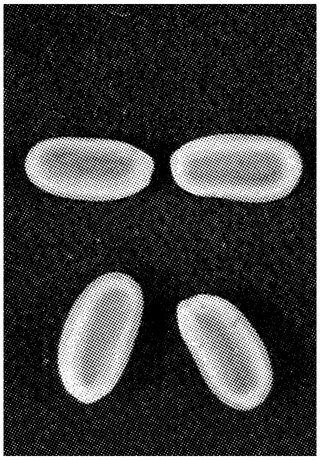


Fig. 88.

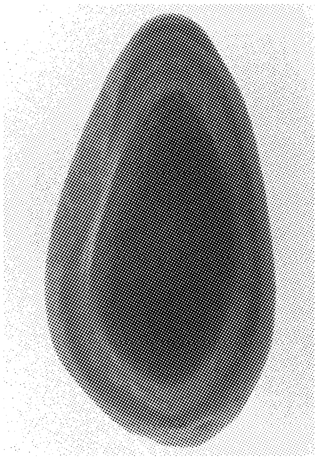


Fig. 89.

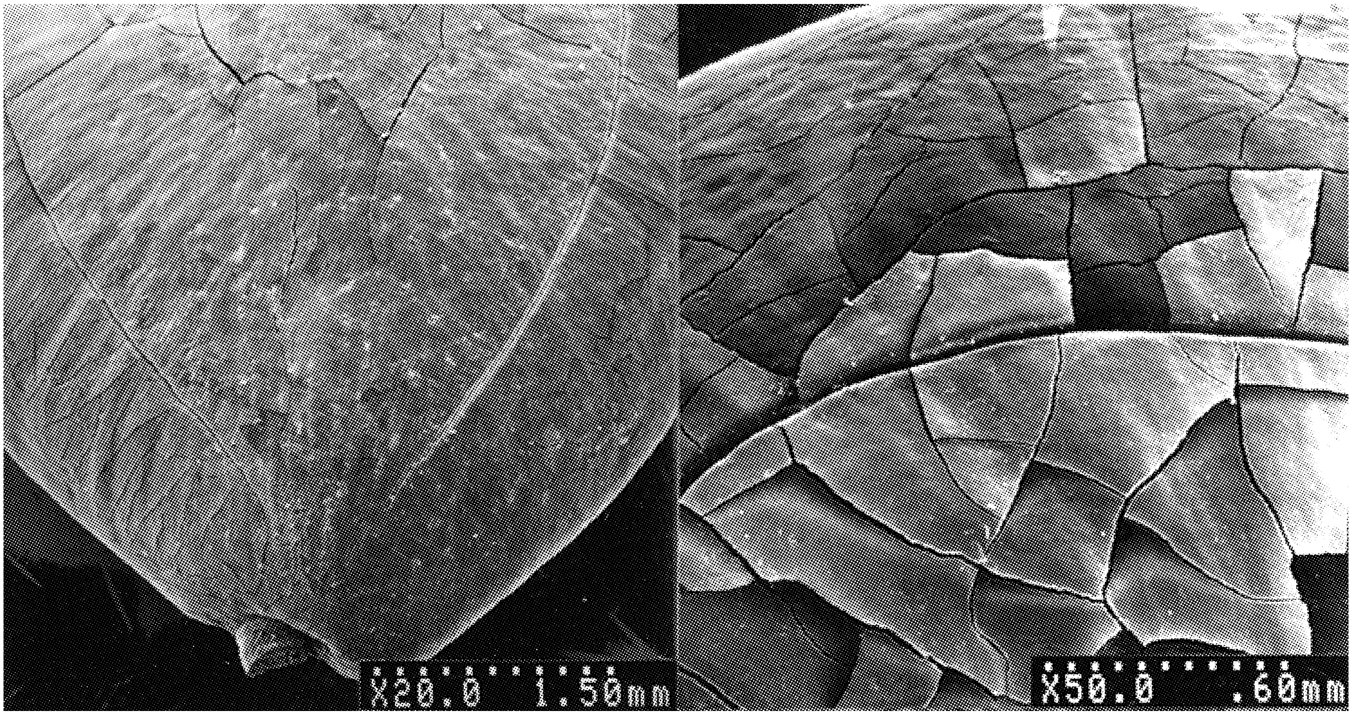


Fig. 90.

Euphorbia). Some caruncles (elaiosomes) are oily, or rich in ricinoleic acid (e.g., *Turnera*). These caruncles are white or yellow, fleshy, and edible and are detached, eaten, and dispersed by ants. The strophiole is an outgrowth of the raphe. The aril is a funicular or hilar outgrowth and may cover the whole testa (complete) or part of it (incomplete; e.g., *Stemmadenia, Lecythis ampla, Phitecellobium dulce*). Some arils are reticulate or have frimbriate projections (frimbriate arils; e.g., *Myristica fragrans, Virola, Otoba*). The aril develops after fertilization. When complete, the aril may cover the micropyle. Morphologically the caruncle is considered an exostomic aril and the strophiole a raphal aril (Boesewinkel and Bouman 1984; Flores 1999; Van der Pijl 1957, 1972).

Many seeds of Fabaceae-Mimosoideae (*Albizia niopoides* (Spruce ex Benth.) Burkart, *Entada, Enterolobium cyclocarpum, Pseudosamanea guachapele* (Kunth Harms, *Stryphnodendron microstachyum, Samanea saman*) are laterally compressed and have a special mark on each lateral surface called a pleurogram (Corner 1951) and a fissure (linea sutura or linea fissura) delimiting the pleurogram. The linea fissura is parallel to the raphe-antiraphe line and breaks to the hilar end (figs. 87-90). The linea fissura seems to be associated with the gradual dehydration of the seed during maturation and storage, and the slow imbibition of the seed during germination.

Fig. 91.

Fig. 93.

Fig. 94.

Fig. 92.

The wings or hairs found on many seeds seem to be devices for anemochorous dispersal (figs. 91-94). Some winged seeds (*Vochysia, Qualea, Cedrela, Swietenia, Bernoullia flammea*) have one to several testal extensions that form wings; in many seeds the wing is circular or oval in outline (e.g., *Tabebuia rosea, Jacaranda copaia*). Other seeds have a tuft of trichomes at one end (*Macrohasseltia macroterantha*) or hairs distributed at random. The crowned seeds have a crown of hairs at one end, and the crestate seeds have one or several ridged excrescences. There are also punctate seeds covered by small excrescences or depressions, round umbonate seeds with a central or lateral umbo, and warty seeds with wart-like foldings.

Vascular System of the Seed

The vascular system of the ovule is formed by procambial or partially differentiated vascular strands. The differentiation of the vascular system occurs during the development of the seed. The vascular system supplying the seed is formed by placental, raphal, and funicular vascular bundles. These bundles transport nutrients to the developing seed. The larger seeds have a more extensive and well-developed vascular system; the small seeds have partially differentiated or no vascular bundles. The large seeds usually have a massive or compound raphal vascular bundle, well differentiated, which ends at the chalaza. Some seeds have additional vascular bundles extending from the chalaza to the outer integument; these are called postchalazal vascular bundles. Some seeds are encircled by a postchalazal vascular bundle along the median plane (Annonaceae, Polygalaceae) and others have a chalazal vascular plexus and a network of vascular bundles. Through intercalar growth, this plexus may replace the seedcoat locally (e.g., *Guarea*). Vascular ramifications in the tegmen are common. In the seeds of species such as the Myristicaceae, the vascular branches enter the tegmen invaginations, increasing the contact with the endosperm. In *Virola koschnyi*, *Otoba novogranatensis*, and *Compsoneura sprucei* the vascular branches found in the tegmen invaginations have transfer cells (Flores 1999).

Storage of Reserves

Seeds contain many substances. Some are typical to cells and tissues and others contribute to nourishing the embryo (before and after germination) and the developing seedling (in its early stages). Seeds store energy in the form of lipids, carbohydrates, and proteins to fulfill the needs of the seed during germination. They are a source of precursors for carbon skeletons and a source of energy when assembling precursors.

The seeds are perispermous if the reserves are stored in the perisperm, endospermous or albuminous if the nutrients accumulate in the endosperm, cotyledospermous if the thick and fleshy cotyledons store the reserves, hypocotylospermous or macropodial when the hypocotyl is the storage organ, and chalazospermous if the nutrients are stored in the chalaza. The cell walls of different seed tissues may also store nutrients.

Lipids, which appear as lipidic bodies in the endosperm and the embryo, are a greater source of nourishment than the carbohydrates. The amount of lipids in a seed varies: 30 percent for the sunflower *Helianthus annuus* and 50 percent for *Ricinus communis*, *Zea mays*, and *Arachis hypogaea*. In the coconut (*Cocos nucifera*) and the African oil palm (*Elaeis guianeensis*) the lipid content is higher. The seeds without maturation drying are rich in lipids. For example, the lipid content in fresh seeds of *Virola koschnyi* is approximately 41 percent, in *Calophyllum brasiliense* 38 to 39 percent, in *Minquartia guianensis* 37 to 38 percent, and in *Lecythis ampla* 40 percent (Flores 1996). The dried cotyledons of the embryo of *Carapa guianensis* have 65 to 70 percent of unsaturated lipids in the storage parenchyma (Flores 1994g); the endosperm of *Otoba novogranatensis* has about 69 percent of lipids (dry weight) (García-Barriga 1974).

Carbohydrates are stored as starch or in thick cell walls rich in hemicelluloses. Cereals contain 70 to 80 percent starch, legumes ± 50 percent (Boesewinkel and Bouman 1984, Vijayaraghavan and Prabhakar 1984). The predominant types of carbohydrates stored in cell walls are mannans, xyloglucans, and galactans. The three types of mannans–pure mannans, glucomannans, and galactomannans–are restricted to the endosperm cell walls. The pure mannans are found in the date (*Phoenix dactylifera*), the ivory nut or tagua (*Phytelephas macrocarpa*), the coffee bean (*Coffea arabica*), and *Carum carvi*. The galactomannans are found in the endosperm of the legume seeds (Grant-Reid 1985, Higgins 1984). The mannans and glucomannans are crystalline and insoluble; they confer an extraordinary hardness to the endosperm. The xyloglucans are amiloid and are found in the endosperm or the embryo of approximately 2,600 species, among them *Tamarindus indica* and *Annona muricata*. The galactans are stored in the cotyledons of the embryo of numerous legumes (Boesewinkel and Bouman 1984, Vijayaraghavan and Prabhakar 1984).

Nearly all seeds contain proteins as reserve. Proteins supply the nitrogen needed by the plant in early stages of development (Higgins 1984). The storage proteins are found as protein bodies (aleurone). These grains are the primary source of proteins and minerals, and in addition to the homogeneous protein matrix they contain crystals of proteins and calcium oxalate. Several cations (K, Mg, Ca, Fe, Ba, Mn) are also found as globoid crystals. The protein bodies are found in the embryo as the endosperm or are restricted to a specialized layer (Poaceae, Fabaceae). This layer is active only during germination. Protein reserves are necessary to synthesize the enzymes involved in starch digestion. Nuts are about 40 percent proteins (Higgins 1984). The following species have seeds with a high protein content: *Aesculus hippocastanum*, *Billia columbiana*, *Bertholletia excelsa*, *Lecythis ampla*, *Enterolobium cyclocarpum*, *Leucaena leucocephala* (Lam.) de Wit, and *Entada scandens*.

The seeds with maturation drying accumulate disaccharides, such as the saccharose and oligosaccharides, in the form of stachyose and raffinose. Some propose that these sugars are associated with tolerance to desiccation (Leopold and Vertucci 1986, Leopold and others 1992, Leopold and others 1994); however, some seeds sensitive to desiccation also accumulate sugars and saccharose (*Avicennia marina*) or saccharose and raffinose (e.g, *Quercus robur*) (Farrant and others 1993, Finch-Savage and Blake 1994).

Structural Variation

Diversity is great in the internal and external structure of seeds. This diversity is related primarily to the wide range of methods of dispersal and germination. The morphological variations include differences in size, form, texture, color, and presence or absence of special structures such as arils of exostomic (elaiosome, caruncle), raphal (strophiole), or funicular origin (Boesewinkel and Bouman 1984, Flores 1999). Anatomical variations include the presence, absence, or position of the storage tissues; the size, form, and position of the embryo; the form and size of the chalazal zone, and the structure of the seedcoat.

The size and position of the embryo vary among seeds (Bernhardi 1832). The area occupied by the embryo is inverse to that used by the endosperm, perisperm, or both. A larger embryo has a smaller endosperm or perisperm, and vice versa. The classification system in this chapter is based on the size, position, and form of the embryo. It represents a modification of the classification system proposed by Martin (1946). Although some types overlap, the taxonomic usefulness of the classification is maintained (Duke 1969). Types must be identified immediately after fruit dehiscence, especially in seeds with no maturation drying where embryo development is continuous. For example, in *Virola koschnyi* seeds, the foliaceous, haustorial, and divergent cotyledons begin to develop inside the seed after seed dispersal, and because space is limited the cotyledonar blade folds (Flores 1992c). In *Compsoneura sprucei* the cotyledonar development is faster and the foldings are more conspicuous.

The following classification system divides seed embryos into three primary types: basal, peripheral, and axile. Basal is further divided into four subtypes and axile into seven (fig. 95).

Basal Embryos

Embryos are usually small, nonperipheral, and restricted to the inferior half of the seed, except in the lateral type. The seeds are medium to large, with abundant endosperm, starchy or oily. The rudimentary and broad subtypes are found in the monocotyledons and dicotyledons; the capitate and lateral subtypes are typical of the monocotyledons (fig. 95).

(1) Rudimentary: The embryo is small and globular to oval-oblong. Cotyledons are rudimentary or obscure, sometimes evident, simulating miniatures of the linear or spatulate types; e.g., *Ilex skutchii* (Aquifoliaceae), *Calatola costaricensis* (Icacinaceae), *Magnolia poasana* (Magnoliaceae), *Compsoneura sprucei*, *Myristica fragrans*, *Otoba*, *Virola* (Myristicaceae), *Minquartia guianensis* (Olacaceae).

(2) Broad: The embryo is as wide or wider than it is high, and very fleshy. It could be globular or lenticular, peripheral or nearly so. This type is common in dicotyledons and monocotyledons that are quite primitive, aquatic, marshy, or parasitic.

(3) Capitate: The embryo expands distally into a head-like form (turbinate); e.g., *Tradescantia* (Commelinaceae), *Dioscorea* (Dioscoreaceae).

(4) Lateral: The embryo is basal-lateral or lateral, inclined to expand in the plane of the periphery. The embryo is usually less than one-half of the seed (inferior half) but can be larger. Typical in Poaceae.

Peripheral Embryos

Embryos are usually elongated and large. The embryo occu-

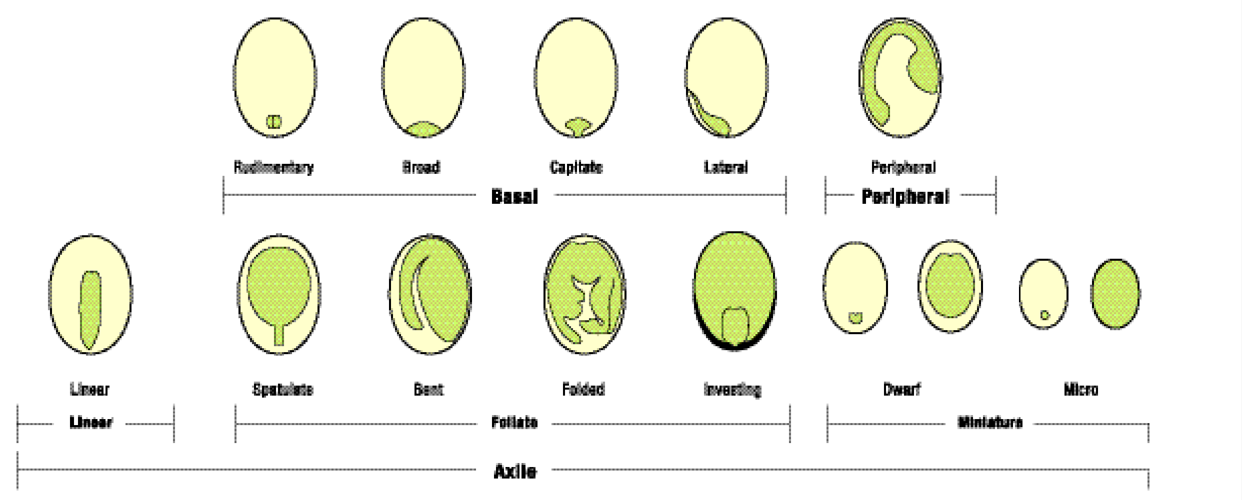


Fig. 95. Seed types and embryo position.

(Redrawn from Martin. 1946).

pies one-quarter to three-fourths of the seed (fig. 95). It is partially contiguous to the seedcoat and often curved, central or lateral, with cotyledons narrow or expanded. The endosperm or perisperm is starchy. As is typical in dicotyledons, one cotyledon can be smaller or abortive (*anisocotyly*); e.g., *Pereskia* (Cactaceae).

Axile Embryos

Embryos range from small (occupying only part of the seed's lumen) to large (occupying the whole lumen), central (axile), straight, curved, coiled, bent, or folded (fig. 95). The endosperm can be oily or starchy. Found in gymnosperms, dicotyledons, and monocotyledons.

(1) Linear: The embryo is usually several times longer than it is wide. It can be straight, curved, or coiled. The cotyledons are small, not expanded or not developed. Seeds are not minute. Examples include *Annona* (Annonaceae), *Tovomita*, *Tovomitopsis*, *Garcinia intermedia* (Clusiaceae), *Elaeocarpus*, *Sloanea* (Elaeocarpaceae), *Muntingia calabura* (Tiliaceae), *Garrya laurifolia* (Garryaceae), *Bertholletia excelsa*, *Eschweilera*, *Lecythis* (Lecythidaceae), *Ardisia brenesii* (Myrsinaceae), and *Zizyphus* (Rhamnaceae).

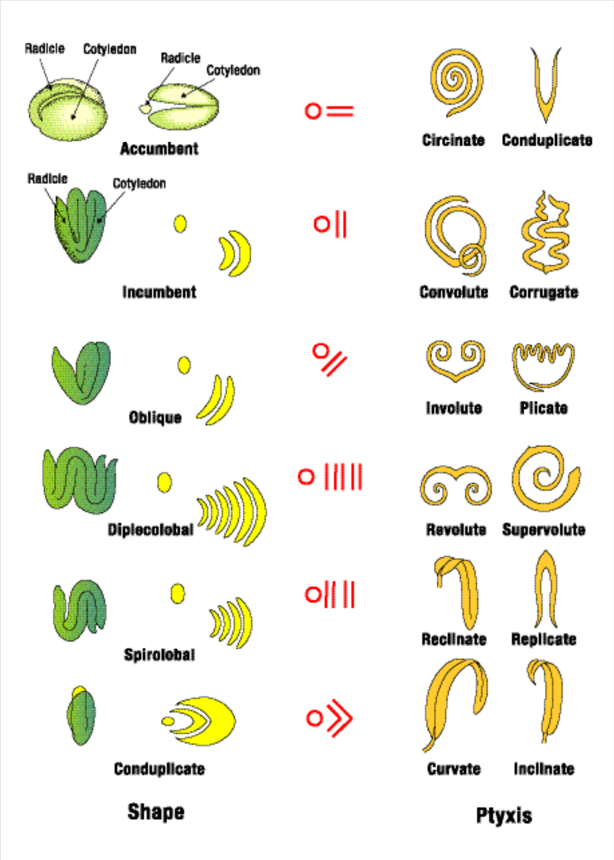


Fig. 96. Embryo shapes and cotyledonar ptyxis.

(2) Miniature: Embryos stocky or minute in small-to-minute seeds. Seedcoats are delicate, often reticulate; the endosperm is not starchy. Two types exist:

(a) Dwarf: The embryo is variable in relative size, small to total (whole seed lumen). It is commonly oval, elliptic, or oblong, with incipient cotyledon development. The embryo is frequently stocky. Seeds are small at 0.3 to 2.0 mm long; e.g., *Clethra* (Clethraceae), *Buddleja americana* (Loganiaceae), several Ericaceae.

(b) Micro: The embryo is minute or total (whole seed lumen), globular, and usually undifferentiated. Seeds are small, commonly less than 0.2 mm long; e.g., Orchidaceae.

(3) Foliate: The embryo is large, one-fourth to all of the seed lumen, central rather than peripheral. Cotyledons are expanded and the endosperm is not starchy. Seeds are medium to large. Four types exist:

(a) Spatulate: The embryo is straight, and cotyledons are variable, from thin to thick and from expanded to broad; e.g., *Aspidosperma*, *Tabernaemontana* (Apocynaceae), *Bixa orellana* (Bixaceae), *Cornus disciflora* DC. (Cornaceae), *Diospyros* (Ebenaceae), *Hyeronima*, *Sapium* (Euphorbiaceae), *Casearia*, *Xylosma* (Flacourtiaceae), *Cedrela*, *Melia azedarach* (Meliaceae), *Genipa americana*, *Simira maxonii*, *Psychotria* (Rubiaceae), *Zanthoxylum kellermanii* P. Wilson (Rutaceae), *Manilkara zapota*, *Chrysophyllum cainito* (Sapotaceae), *Goethalsia meiantha* (Tiliaceae), *Guajacum sanctum* (Zygophyllaceae).

(b) Bent: The embryo is bent and spatulate and usually has thick cotyledons, planoconvex, bent on the hypocotyl (fig. 96). The latter is partially immersed in the area of cotyledon overlapping. In the most common type, the curvature occurs in the plane of the cotyledons [(o =), accumbent, pleurorhizal]. The curvature also can be against the cotyledonar plane (o |), incumbent, notorhizal; or can be oblique (o //) if it is intermediate between accumbent and incumbent. The fourth subtype is the orthoplocal: the cotyledons are incumbent and conduplicate (o >>) as seen in *Avicennia*. The spirolobal embryos (o | |) have incumbent cotyledons, folded once, while diplecolobal embryos have two or more folds (o | | |). The convolute cotyledons are present in *Terminalia* (Duke 1969). Examples include *Acer pseudoplatanus* (accumbent, Aceraceae), *Ceiba pentandra* (bent, Bombacaceae), *Crataeva religiosa* (spirolobal, Capparidaceae), *Caryocar costaricense* (accumbent, Caryocaraceae), *Sapindus saponaria* (Sapindaceae), *Ficus*, *Maclura tinctoria* (bent, Moraceae), and *Myrcianthes fragrans* (accumbent, Myrtaceae).

(c) Folded: The embryo has thin cotyledons, expanded and folded in several ways (fig. 96). Embryos with conduplicate cotyledons are frequent in Sapindales and Malvales (Duke 1969). In Vochysiaceae, the cotyledons are foliaceous, large, and convolute as seen in *Vochysia*, *Qualea*, and *Calycanthus occidentalis* (Calycanthaceae) (Corner 1976; Flores 1993a, 1993b). Examples of folded embryos include *Bursera simaruba* (L.) Sarg. (Burseraceae), *Couratari*, *Couroupita* (plicate; Lecythidaceae), *Tilia americana* (Tiliaceae), *Myrcia splendens* (conduplicate; Myrtaceae), and *Pimenta guatemalensis* (involute; Myrtaceae).

(d) Investing: The embryo is erect; the cotyledons are thick, overlapping, and encase a small hypocotyl. The endosperm is missing or very reduced. The embryo may be confused with bent or spatulate embryos. It can be associated with cryptocotylar seedlings. Examples include *Alnus acuminata* (spatulate-investing; Betulaceae), *Calophyllum brasiliense* (Clusiaceae), *Prioria copaifera* (Fabaceae-Caesalpinioideae), *Pentaclethra macroloba* (Fabaceae-Mimosoideae), *Dipteryx oleifera* (Fabaceae-Papilionoideae), *Quercus* (Fagaceae), *Ocotea*, *Nectandra* (Lauraceae), *Carapa guianensis*, *Guarea* (Meliaceae), *Nephelium lappaceum*, *Cupania* (Sapindaceae), and *Quassia amara* (Simaroubaceae). The total or partial fusion of the cotyledons along the adaxial surfaces is common in seeds with cryptocotylar germination such as *Calophyllum*, *Carapa*, and *Guarea* (Flores 1994c, 1994g).

RELATIONSHIPS BETWEEN SEED STRUCTURE AND STORAGE BEHAVIOR

Some seeds lose water during maturation drying and gradually acquire tolerance to desiccation, while others maintain a high water content, do not experience a reduced cellular metabolism, and are sensitive to desiccation and temperature decreases. The tolerance/intolerance to desiccation shown by the seeds in their natural environment is also exhibited when they are stored.

Sensitivity to desiccation limits a seed's storage potential, genetic conservation, and use in trade. Roberts (1973) defined two types of seeds based on sensitivity to desiccation: orthodox seeds (those that undergo maturation drying) and recalcitrant seeds (those that do not undergo maturation drying).

The ability to tolerate desiccation by orthodox seeds is associated with metabolic changes such as respiration decrease, increase of some carbohydrates or oligosaccharides, and accumulation of dehydrines (LEA proteins). During germination the seeds lose this tolerance, frequently several hours after radicle protrusion. Dehydration at this stage leads to irreversible damage, in which the peroxidation of lipids and free radicals has an important role (Côme and Corbineau 1996a, 1996b; Finch-Savage 1996). However, mature orthodox seeds can be dehydrated without damage to very low levels of moisture (1 to 5 percent) and in a variety of conditions (Kermode 1997). Bound water (structural) is less easily frozen than free water. Bound water seems to be a crucial component to tolerating desiccation, and in the orthodox seeds all water is bounded (Leopold and Vertucci 1986, Leopold and others 1992). In storage, the longevity of seeds increases with a reduction of the water content in a predictable and quantifiable manner. Bonner and Vozzo (1990) subdivide these seeds into (a) true orthodox, which "can be stored for long periods at seed moisture contents of 5 to 10 percent and subfreezing temperatures" and (b) suborthodox, which "can be stored under the same conditions, but for shorter periods due to high lipid content or thin seedcoats."

Recalcitrant seeds are rich in free water and neither tolerate nor survive desiccation. They die when the water potential reaches levels similar to those of permanent withering in many growing tissues (-1,5 to 5,0) (Pritchard 1991, 1996). The dehydration of intolerant tissues (recalcitrant) provokes membrane deterioration (plasmalema and mitochondria), protein denaturalization, and reduction of both the respiratory rate and the ATP level (Leopold and others 1992). The oxidative processes and the free radical seem to be involved in cellular and molecular deterioration (Côme and Corbineau 1996a, 1996b). The seeds show a strong resistance to rehydration and the loss of cellular integrity leads to a loss of viability. Recalcitrant seeds are present in at least 70 percent of tropical trees. Their sensitivity to temperature lowering is due to the high water content.

Because some seeds did not fit readily into either orthodox or recalcitrant categories, Ellis and others (1990a) proposed a third category: the intermediate seeds. These seeds survive desiccation at intermediate moisture levels but not to the degree of orthodox seeds. This last category can be considered arbitrary, and the existence of a recalcitrance gradient throughout the different species has been suggested (Finch-Savage 1996, Flores 1996).

Variations in the sites of water storage and the gradual damage observed in the seed's tissues when it dehydrates, can be illustrated by the seeds of the following species: *Calophyllum brasiliense* (Clusiaceae), *Otoba novogranatensis* (Myristicaceae), *Minquartia guianensis* (Olacaceae), *Caryocar costaricense* (Cary-

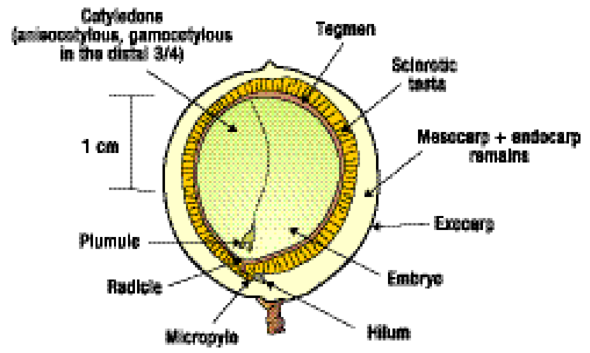


Fig. 97. Berry of *Calophyllum brasiliense* enclosing the overgrown seed, (longitudinal section).

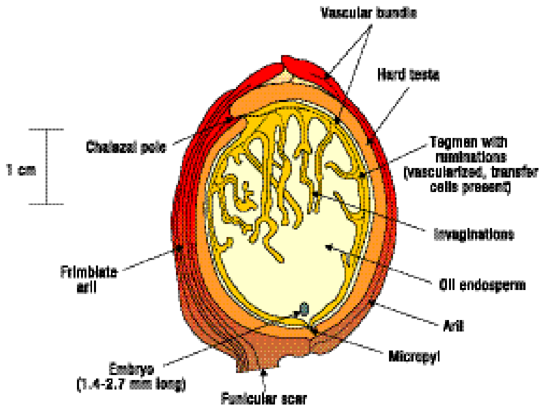


Fig. 98. Seed of *Otoba novogranatensis*, (longitudinal section).

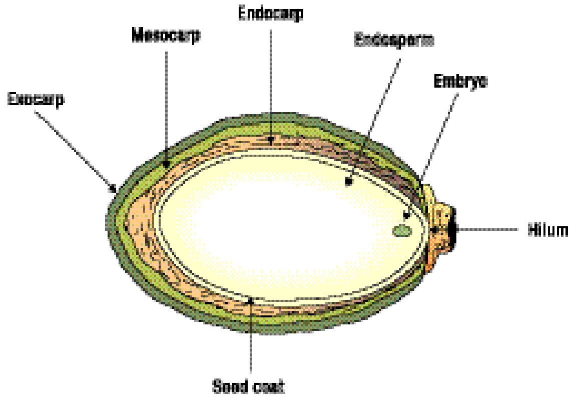


Fig. 99. Drupe of *Minquartia guianensis* enclosing the seed.

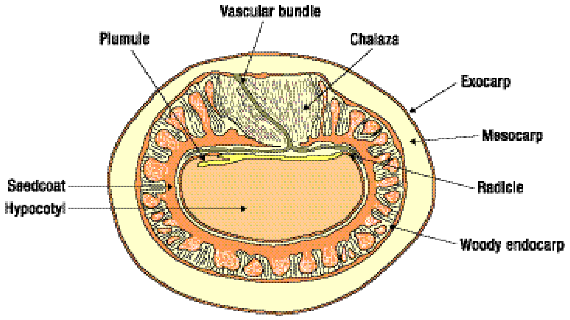


Fig. 100. Drupe of *Caryocar costaricense* enclosing the seed.

ocaraceae), and *Lecythis ampla* (Lecythidaceae) (figs. 97-101, Table 1).

How does dehydration affect seeds? In *Calophyllum brasiliense* the seedcoat is hard and resists desiccation; water loss is slow. Once the seedcoat dehydrates, the water loss directly affects the embryo, with the exposed radicle being the most rapidly affected. The thick cotyledons enclose the small plumule and it dehydrates last. In species with minute, rudimentary embryos (*O. novogranatensis*, *M. guianensis*), the sequence of dehydration is seedcoat ¢ peripheral endosperm and radicle ¢ remaining embryo ¢ inner endosperm. Seed viability deteriorates rapidly upon embryo dehydration. *Otoba novogranatensis* is more sensitive to desiccation than *Minquartia guianensis*, due to endosperm rumination and tegmen vascularization. *Caryocar costaricense* has a curved, accumbent embryo and the plumule and radicle dehydrate immediately after endo-

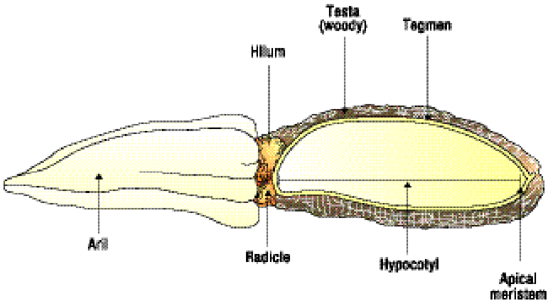


Fig. 101. Seed of *Lecythis ampla* (longitudinal section).

Table 1

Structural variation of five recalcitrant seeds from neotropical species during seed dispersal

	Species				
Structure	*Calophyllum brasiliense*	*Otoba novogranatensis*	*Minquartia guianensis*	*Caryocar costaricense*	*Lecythis ampla*
Fruit	Berry	Septicidal Capsule	Drupe	Drupe	Pyxidium
Type of diaspore	Fruit	Seed	Fruit	Fruit	Seed
Endocarp surrounding the mature seed	Soft, thin, crushed	Absent	Drupe, hard endocarp	Drupe, hard endocarp	Absent
Seedcoat	Hard	Hard	Soft	Papyraceous	Hard
Testa	Hard	Hard	Soft	Soft	Hard
Tegmen	Thin, soft	Thin, ruminate	Soft, fragmentary	Thin, soft	Remnants
Endosperm	Absent in mature seed	Massive, nuclear-cellular	Massive, cellular	Absent in mature seed	Absent in mature seed
Perisperm	—	—	—	—	—
Embryo	Massive, complete	Minute, rudimentary	Minute, rudimentary	Massive, complete	Massive, undifferentiated
Cotyledons	Massive, fused	Differentiate and develop during germination	Differentiate and develop during germination	Small, scaly	Differentiate and develop during germination, small, scaly
Hypocotyl	Thick, massive	Differentiate and develop during germination	Differentiate and develop during germination	Thick, massive	Thick, massive
Epicotyl	Very small	Differentiate and develop during germination	Differentiate and develop during germination	Very small	Differentiate and develop during germination
Radicle	Thick, small	Differentiate and develop during germination	Differentiate and develop during germination	Thick, small	Rudimentary
Reserves location	Cotyledons, hypocotyl	Endosperm	Endosperm	Hypocotyl	Hypocotyl
Water storage	Whole embryo	Mainly endosperm	Mainly endosperm	Hypocotyl	Hypocotyl

carp dehydration. The dehydration of *Lecythis ampla* seeds first affects the seedcoat and then the meristematic poles (radical and apical); they die instantly after seedcoat dehydration.

The seeds enclosed in berries (*C. brasiliense*) or drupes (*C. costaricense*, *M. guianensis*) are protected by the pericarp tissues, which help maintain seed moisture. In these cases, the functional unit is the fruit and dehydration is slower.

The moisture level below which a seed loses its viability varies from one seed to another. Variations are found among seeds collected from the same tree as well as from different trees, zones, seasons, or years. The recalcitrant behavior seems to be genetically determined and its genetic base is still not well understood. The variations found can be explained if the seed history from flower inception to seed dispersal and germination is analyzed carefully (Flores 1994i, 1996).

The difference found between temperate and tropical recalcitrant seeds must be added to the gradient found in recalcitrance manifestation. Bonner and Vozzo (1990) established two categories: temperate recalcitrant seeds and tropical recalcitrant seeds. The first cannot be dried but can be stored for 3 to 5 years at near freezing temperatures; the latter cannot be dried and are killed by temperatures below 10 to 15 ºC, depending on the species.

Unfortunately, very limited information exists on the tissular, cellular, and biochemical alterations produced by dehydration in the recalcitrant seeds, as well as on the appropriate strategies and mechanisms to manage them under storage conditions. The diversity of types found in recalcitrant seeds is preliminary and further complicates the issue. The problem of cellular desiccation is complex; it seems to involve genetic components that lead to mechanisms of cellular protection. These mechanisms limit the cell damage produced by seed dehydration and promote cellular repair, reversing the changes induced by water loss (Kermode 1997). The accumulation of protecting substances in the tolerant tissues is quite possible (Kermode 1997). The dehydrines, disaccharides (sacarose), and oligosaccharides (raffinose and stachyose) may have an important role in the stabilization and maintenance of the

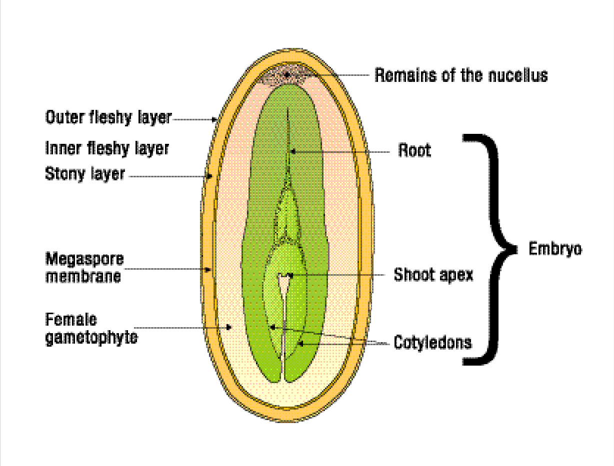


Fig. 102. *Pinus* seed (longitudinal section).

(Redrawn from Foster & Gifford, 1974).

membrane system and other sensitive systems (Kermode 1997, Leopold and others 1992).

THE GYMNOSPERM SEED

The gymnosperm seed initiates with the fertilization of the egg cell. The zygote forms the embryo (2n), which remains immersed in the nutritious tissue (endosperm) of the megagametophyte (n). The integument gives rise to the seedcoat (2n, part of the tissues of the maternal tree).

Embryo Development

The gymnosperms have a phase of free nuclear division in early embryogeny unlike most angiosperms. The exceptions include *Sequoia sempervirens*, *Gnetum*, and perhaps *Welwitschia* (Foster and Gifford 1974, Maheshwari and Vasil 1961). The number of free diploid nuclei varies within species; some cycads may have about 1,000, while *Pinus* has 4 (Foster and Gifford 1974). The free nuclear division phase is followed by a cellular phase in which cell walls are formed and the suspensor, the apical meristem, the radicle, the hypocotyl, and the cotyledons are gradually differentiated.

The mature embryo is linear except in *Ephedra*, although some are slightly spatulate (fig. 102). *Zamia* and *Gingko* have large, expanded cotyledons covering the small embryo axis. The cotyledon number varies among and within the species. Conifers have 3 to 18 small, narrow cotyledons organized in a whorl; for example, *Pseudotsuga* has 4 to 12; *Abies,* 2 to 10; *Tsuga*, 2 to 7; *Thuja, Juniperus,* and *Taxus,* 2 (Chowdhury 1962, Martin 1946). The average in *Pinus* is 8.1 (Butts and Buchholz 1940). In conifers, the embryo may be physiologically mature when seed dispersal occurs, although there are exceptions such as *Pinus cembra*, *P. sylvestris* L., and *Picea abies*. The last has a rudimentary embryo that continues its development if the dispersed seed reaches a suitable environment (Krugman and others 1974, Stokes 1965). Most gymnosperms have a tendency to polyembryony because more than one archegonia can be fertilized. In conifers, certain cells of the incipient embryo can separate and form four or more embryos. Some species show a conjugation of both types of polyembryony, although competition eliminates all embryos except one; this one develops and reaches physiological maturity (Foster and Gifford 1974).

Seedcoat

The seedcoat derives primarily from the chalazal tissue in cycads and pines, and from integumentary tissue or from both chalazal and integumentary tissues in *Gnetum*, *Ephedra*, and cypresses. In Podocarpaceae (*Podocarpus costaricensis*, *P. guatemalensis*, *P. macrostachyus*, and *Prumnopitys standleyi*), the epimatium forms a fleshy covering surrounding the seed; this coriaceous covering has a single crest or umbo (Torres-Romero 1988). The seedcoat of *Gnetum* has three integuments while *Ephedra* and *Welwitschia* have only one (Singh and Johri 1972). The seedcoat may be thin and soft or thick and hard. In *Pinus*, the seedcoat has a layer of sclerenchyma derived from the integument. The fleshy layer degenerates during seed development (Foster and Gifford 1974). Some seeds have mucilage canals (cycads) or resin ducts (*Abies*, *Tsuga*, *Libocedrus*), the contents of which impregnate the seeds, making them sticky (Krugman and others 1974, Singh and Johri 1972). The seeds have wings of different sizes and shapes; these wings sometimes fall off early. However, the seed wings of some species, such as *Taxodium* and *Pinus,* may be persistent (Krugman and others 1974).

Endosperm

In early embryogeny the central part of the nucellar tissue (megagametophytic), called the endosperm, disintegrates and forms the corrosion cavity. The suspensor pushes the embryo into this cavity, where it absorbs nutrients (Singh and Johri 1972). The endosperm disorganizes completely at the end of embryogenesis; only a papyraceous layer remains at the micropylar end. The seed matures in two to three seasons. The content, behavior, and fluctuation of growth regulators are similar to those of the angiosperms (Krugman 1966, Krugman and others 1974). The lipid content in the seeds is high, although carbohydrates and proteins are also present. Some pines contain up to 50 percent lipids stored in the endosperm (Krugman and others 1974, Singh and Johri 1972).

FRUIT AND SEED DISPERSAL

Seed dispersal is one of the critical stages in the life cycle of the species. It transports physiologically independent individuals to the habitat occupied by their parents or to new suitable territories, where the seeds may colonize if environmental conditions are favorable (Howe and Smallwood 1982, Willson 1992). The unit of dispersal receives the generic name of diaspore, propagule, or diseminule, and can be formed by the embryo, the seed, the fruit, or the fruit and associated parts of the modified perianth, the receptacle, or both (Harper 1977, Van der Pijl 1972).

Diaspores can be dispersed in space and time. Dispersal in space is the transport from one site to another, usually far from the parent tree. Dispersal in time is the quiescence or inactivity of diaspores for a variable period of time after which they activate under the action of environmental stimuli, unchaining the germination process (Harper 1977). This dispersal of diaspores from the source (parent tree) and commonly around it is called the seed shadow (Janzen 1971a) (seed = diaspore in this context). The source can be the parent tree or a nucleus of multiple parents. Four processes interact to generate the seed shadow which eventually becomes the seedling shadow: seed production, predation, dispersal and quiescence or dormancy (Janzen and Vásquez-Yáñez 1991). The seed shadow, which can be asymmetrical, is affected by two factors: the relationship of density to distance and the direction of dispersal in respect to the source. The relationship density (seed number)-distance in respect to the source reaches a peak and has a tail; the direction has an important ecological value (Janzen 1971a). Outside the peak, the number of seeds decreases centrifugally and forms a negative exponential curve. Habitat fragmentation and other factors such as the behavior of the dispersal agents, the environment, and the genetic constitution can change the conventional form of the curve (Willson 1992).

The expectation is that the dispersed offspring live and breed, but the seed shadow is modified and reduced by predation, lack of germination, and seedling mortality. In general, the lack of natural enemies (predators, pathogens, parasites, and herbivores), the absence of unfavorable interactions, and the probability of finding a favorable site favor natural dispersal.

TYPES OF DISPERSAL

The dispersal of diaspores can be biotic (zoochorous) or abiotic (azoochorous) and their morphology is related to the method of dispersal. In biotic dispersal the vectors are numerous: invertebrates [flies, dung insects and ants (myrmecochory), earthworms, and snails], herbivorous fish (ichthyochory), marine turtles, lizards and desert iguanas (saurochory), birds (ornithochory), and mammals including human beings (mammaliochory). When the mammals dispersing fruits are rodents, the process is called dyszoochory; if the vectors are bats the process is called chiropterochory. Abiotic dispersal is by wind (anemochory), water (hydrochory) or the tree itself (autochory). The last is achieved by active ballistics (tension generated by the dehydration of hygroscopic tissues), passive ballistics (movements of the seeds enclosed in the fruit), and creeping diaspores and barochory (dispersal by weight) (Carlquist 1966; Flores 1994a; Gautier-Hion 1990; Gottsberger 1978; Howe 1990; Terborgh 1986, 1990; Van der Pijl 1972; Van Roosmalen 1985).

In tropical forests most dispersal is achieved by the vertebrates, which obtain food from the seeds and other edible parts of the fruit. The dominance of zoochorous dispersal has been demonstrated in several places. In the French Guiana and Surinam, 6 percent of the diaspores produced by woody forest trees are dispersed by autochory, 11 percent by anemochory, 9 percent by hydrochory, and 74 percent by zoochory. Most diaspores dispersed by water come from riparian species and are typical in marshes or mangrove vegetation, while those dispersed by wind grow at forest edges. In primary forests, zoochory may increase to 87 or 90 percent (Van Roosmalen 1985). Some investigators consider that zoochorous dispersal in the tropical rain forest is about 80 percent (Croat 1975, 1978; Frankie and others 1974; Gentry 1982, 1993; Levey 1987; Levey and others 1994; Opler and others 1980; Stiles 1985; Willson and Thompson 1982; Willson and others 1989).

Most diaspores are polychorous and their morphology indicates the mechanisms of general dispersal, although an obvious modification does not preclude the existence of alternative mechanisms (Bawa and others 1985a, 1985b; Flores 1992b, 1992c, 1993a, 1993b, 1993c, 1994b, 1994f; Howe and Smallwood 1982). The Fabaceae, for example, are dispersed by birds, bats, rodents, Perissodactyla, Artiodactyla, carnivores, water, skin, feathers, wind, ballistics, or gravity (Howe and Smallwood 1982, Van der Pijl 1972, Van Roosmalen 1985), while the Lauraceae are dispersed by birds, bats, monkeys, rodents, carnivores, fish, gravity, and water (Flores 1999). The specificity of disperser or dispersers is uncommon and most fruits and seeds are used and dispersed by several or many vectors, which may include consumers, commensals, predators, commensals and dispersers, or predators and dispersers.

Biotic or Zoochorous Dispersal

Biotic dispersal occurs in three ways. Dispersal is epizoochorous if the transport of diaspores is passive, external, and occurs through diaspore adhesion to animal skin (hairs) or feathers. Biotic dispersal is synzoochorous when animals, eating part of the seeds but not ingesting them, actively transport the diaspores. This type of dispersal extends to predators who store and bury the seeds, thus providing an opportunity for the survival and germination of some seeds. Dispersal is endozoochorous if the diaspore containing the seed, or the seed itself, is ingested and eventually regurgitated or defecated intact (Gottsberger 1983, Van der Pijl 1972). Zoochorous dispersal requires nutritious tissues (aril, pericarp, testa) in the diaspore, chemical attractants (elaiosomes, stale scent), mimetism (seedcoat coloration), or adhesive structures (viscous materials, hooks) (Howe and Smallwood 1982, Van der Pijl 1972). About 80 percent of the vertebrates (50 percent birds, 30 percent other mammals) feed on fruits (Howe and Smallwood 1982, Janson 1983, Janson and Emmons 1990, Levey and others 1994, Terborgh 1986). The most common types of biotic dispersal are described in the following paragraphs.

Ornithochory

Birds have a poor olfactory sense and very well developed vision. To be dispersed by birds, diaspores must have an edible part with an agreeable taste, external protection against premature ingestion, embryo protection (a hard seedcoat, hard endocarp, or both), attractive colors, and a fixed position. The fruits or seeds dispersed by birds are odorless, small, and usually spherical or oval (Levey 1987, Levey and others 1994, Morden-Moore and Willson 1982, Sorensen 1983, Van der Pijl 1972, Wheelwright 1985, Willson and Thompson 1982, Willson and Whelan 1990). Crop size, distance from other fruiting trees, and the nutritious content of other available fruits also affect bird predation and dispersal (Howe 1977, 1981, 1982; Howe and DeSteven 1979; Howe and Richter 1982; Jordano 1983, 1988; Levey and others 1994; Sargent 1990; Stapanian 1982). Nonflying birds also disperse fruits and seeds; for example, the ñandú *Rhea americana* and *Pterocnemia* (Rheidae) and the Tinamidae (*Crypturellus*, *Nothocercus*, *Rhynchotus*, *Tinamus*) feed on fleshy diaspores (Gottsberger 1983, Stiles and Skutch 1989). Parakeets, parrots, macaws (Psittacidae), toucans, and toucanets (Ramphastidae) eat fruits and seeds that can be swallowed entirely. They also split and eat hard fruits that other birds are unable to consume (Gottsberger 1983; Loiselle 1987, 1990, 1991; Loiselle and others 1996; Stiles and Skutch 1989). The Icteridae, Picidae, Trogonidae, Tyrannidae, Turdidae, and Funaridae also feed on fruits (Gottsberger 1983; Loiselle 1987, 1990, 1991; Stiles and Skutch 1989). The following paragraphs describe the fruits birds prefer.

Fruits with bright color (brown, green, yellow, or orange), fleshy but sufficiently dry, with a woody or semiwoody exocarp, a few large seeds, and a fleshy mesocarp rich in lipids are frequently consumed (Janson 1983, Johnson and others 1985, Van der Pijl 1972, Van Roosmalen 1985). The fruits are usually green drupes, berries, or camaras (e.g., many Anacardiaceae (*Astronium*), Burseraceae (pyrenoid drupe in *Protium*, *Tetragastris*, *Trattinickia)* (figs. 72-73), Combretaceae (*Buchenavia*), Clusiaceae (*Calophyllum brasiliense*, *Symphonia globulifera*), Lauraceae (*Aniba*, *Licaria*, *Nectandra*, *Ocotea*, *Persea*) (fig. 70), and Fabaceae-Papilionoideae (*Dipteryx panamensis)* (fig. 52). Specialized frugivorous birds such as toucans, toucanets, caracaras, cotingas, and quetzals consume these fruits (Avila and others 1996; Bonaccorso and others 1980; DeSteven and Putz 1984; Flores 1992a, 1994a, 1994f, 1999; Gentry 1993; Van Roosmalen 1985). For example, 63 percent of the fruits eaten by the quetzal *Pharomachrus mocinno* (Trogonidae) are lauraceous; the remaining 37 percent are the fruits of the Myrsinaceae, Araliaceae, Verbenaceae, Solanaceae, Myrtaceae, Melastomataceae, Moraceae, and Clusiaceae (Avila and others 1996). The quetzal is a highly specialized, frugivorous bird and an excellent disperser of fruits and seeds, especially during the nonreproductive season when it may range over many kilometers (Avila and others 1996).

Drupes and berries with bright color (red, pink, white, black, blue, purple, orange, yellow, or greenish yellow), membranaceous or slightly coriaceous exocarp, fleshy mesocarp, watery, rich in sugars, poor in lipids and proteins, and fast-rotting are highly appreciated by birds (Levey 1987, Moermond and Denslow 1985, Sorensen 1983, Van der Pijl 1972, Van Roosmalen 1985, White 1974). Examples include Anacardiaceae (*Spondias*, *Tapirira*), Araliaceae (*Dendropanax*), Boraginaceae (several species of *Cordia*), Cecropiaceae (*Cecropia*, *Pourouma*), Malpighiaceae (*Byrsonima, Tetrapodenia*), Melastomataceae (*Conostegia*, *Miconia*), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia*, *Marliera*, *Myrcia*, *Psidium*, *Syzygium*) (fig. 68), Olacaceae (*Minquartia guianensis*) (fig. 71), Piperaceae (*Piper*), Rosaceae (*Prunus*), Rubiaceae (*Alibertia*, *Coussarea*, *Faramea*, *Genipa*), Solanaceae (*Brunfeldsia guianensis*, *Cestrum*), Simaroubaceae (*Picramnia*), Theaceae (*Symplococarpon*), Ulmaceae (*Trema micrantha*), and Verbenaceae (*Citharexylum mocinnii*), (Flores 1994e, Gentry 1993, Herrera and Jordano 1981, Van Roosmalen 1985).

Dehiscent fruits (follicles, pods, etc.) and seeds with special structures (arils, elaiosomes, caruncles, strophioles, and funicles) or sarcotestas rich in lipids, sugars, or mucilage feed birds. The testas or sarcotestas are usually black, white, red, orange, or yellow and the arils are red, white, yellow, or orange (Van der Pijl 1972, Van Roosmalen 1985). The funicles are fre-

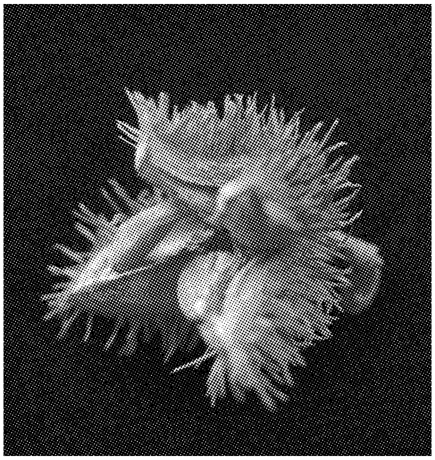


Fig. 103.

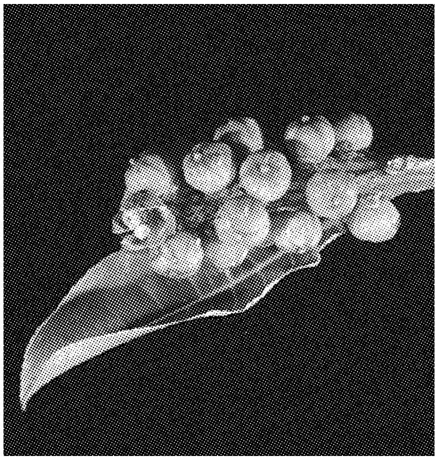


Fig. 104.


Fig. 106.

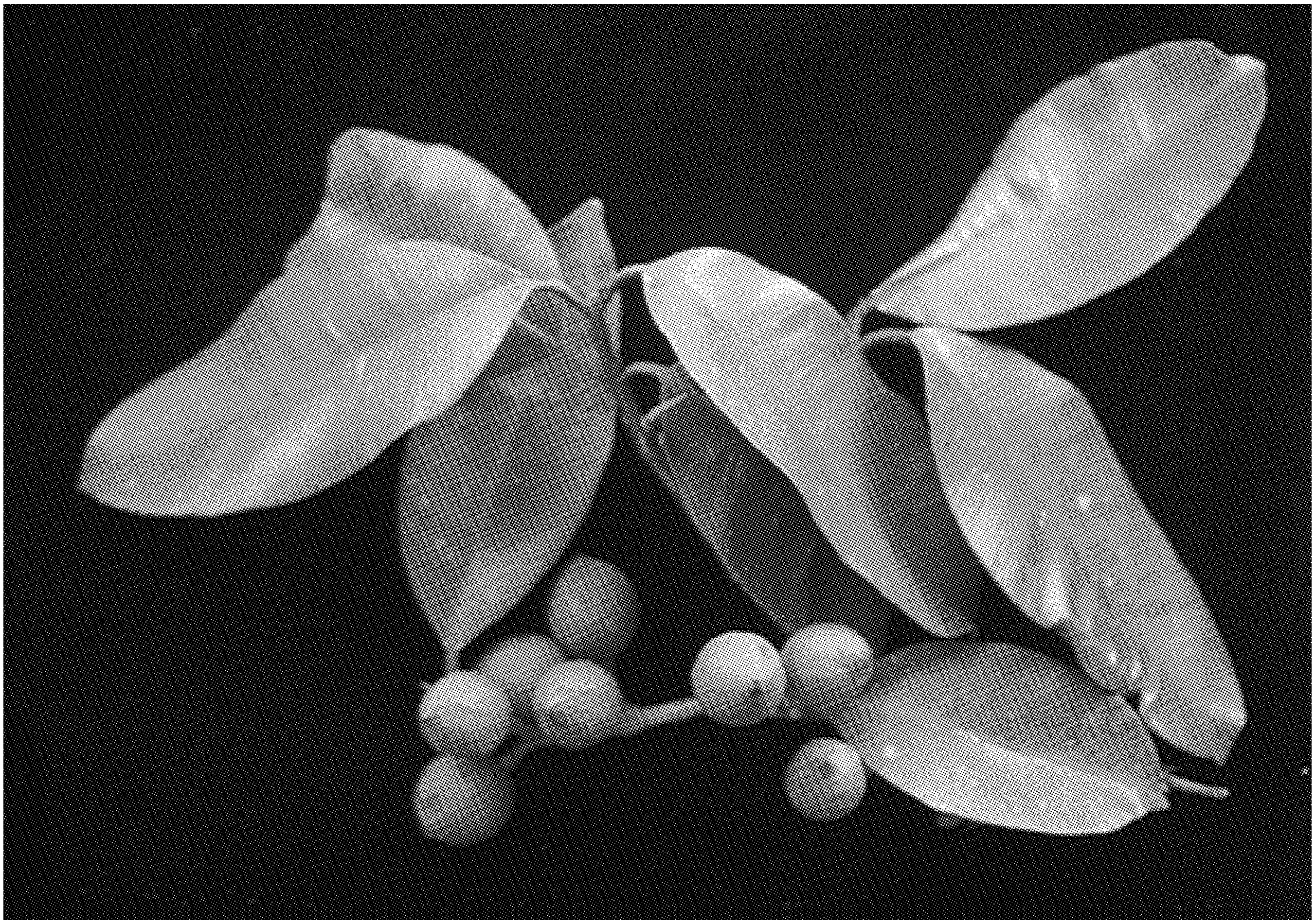


Fig. 105.

quently long and the seeds hang (Van der Pijl 1972). The color of the seedcoat combines with that of the aril and frequently the endocarp and exocarp to create an attractive display eliciting ornithochory. Examples include several Annonaceae (*Xylopia*), Apocynaceae (*Stemmadenia*), Bixaceae (*Bixa orellana*), Fabaceae-Caesalpinioideae (*Dialium guianense*), Clusiaceae (*Clusia*), Connaraceae (*Connarus, Rourea*), Dilleniaceae (*Curatella, Davilla*), Elaeocarpaceae (*Sloanea*) (fig. 103), Euphorbiaceae (*Sapium*) (fig. 104), Flacourtiaceae (*Casearia arborea*, *C. decandra*, *C. guianensis*), Magnoliaceae (*Magnolia*), Meliaceae (*Guarea*, *Trichilia*) (fig. 56), Fabaceae-Mimosoideae (*Acacia*, *Cojoba*) (fig. 64), Myristicaceae (*Virola*, *Compsoneura*, *Otoba*) (fig. 62), Sapindaceae (*Cupania*) (fig. 59), and Zygophyllaceae (*Guaiacum sanctum*) (Flores 1992c, 1996, 1999; Gentry 1993; Howe 1981; Howe and DeSteven 1979; McDiarmid and others 1977; Van Roosmalen 1985; Wendelken and

Martin 1987). When the follicles of *Xylopia aromatica* open, blue seeds contrasting with the reddish interior of the endocarp are revealed. The sarcotesta of the seeds and the white aril attract different birds which swallow seeds intact (Gottsberger 1993). The black seeds of *Connarus* are partially covered by a yellow, fleshy aril contrasting with the red or orange inner surface of the open follicle; the display attracts birds which swallow or remove the seeds, eating the aril and discarding the seed (Van Roosmalen 1985).

Capsules, nuts, or other types of fruits with fleshy floral structures attached are also preferred. Examples are Moraceae (pseudofruits of *Brosimum*, *Morus*), Ochnaceae (fleshy receptacle in *Ouratea*), and Polygonaceae (succulent perianth tube in several species of *Coccoloba*) (Flores 1996, 1999; Gentry 1993; Van Roosmalen 1985).

Finally, mimetic seeds are swallowed and transported by mistake because the colored exocarp or testa resembles an aril (Howe and Smallwood 1982, Van Roosmalen 1985). Examples include many Fabaceae-Mimosoideae (*Adenanthera*, *Cojoba*), Fabaceae-Papilionoideae (*Erythrina*, *Ormosia*), Meliaceae (some *Guarea* in which the testa imitates a sarcotesta) (Corner 1953).

Numerous birds eat fruits or seeds, digest the mesocarp or the aril, and defecate or regurgitate the seed, which is often surrounded by a hard endocarp. In many cases, the gastric juices scarify the testa, the endocarp, or both, and facilitate the germination of the seeds. The seeds of various species of the genera *Cordia*, *Virola*, *Protium*, *Tetragastris*, *Xylopia*, and others are dispersed in this way (Flores 1992c; Howe 1977, 1990; Howe and Ritcher 1982; Howe and Vande-Kerckhove 1981).

Mammaliochory

Dispersal by mammals is more developed in the tropical zones. The diaspores dispersed by mammals have characteristics similar to those dispersed by birds; other groups, such as bats, often eat the same fruits (Van der Pijl 1972).

Chiropterochory

The presentation of diaspores eaten by bats is similar to or the same as that exhibited by those consumed and dispersed by birds; however, the diaspores dispersed by bats are usually green, brown-yellow, brown, purple, black, or variegated and are found at the ends of the branches. The color is not important because bats are nocturnal and blind to color, but their olfactory sense is well developed. Bats prefer a stale odor and many consume diaspores that have this odor (butyric acid), which is produced by substances in fermentation, usually in the tissues of the fleshy mesocarp (Flores 1994e, 1999; Van der Pijl 1972). The taste of preferred diaspores varies from insipid to acid or sweet, and the consistency is soft to semihard. Bats also consume the arils of the seeds of dehiscent fruits, which are commonly rich in lipids (Flores 1994d). The frugivorous bats of the Paleotropics (tropics of Asia and Africa), which belong to Megachiroptera, are important seed dispersors; in the American tropics, bats are members of the Phyllostomidae (Microchiroptera). The major consumers and dispersors are found in the Subfamily Stenoderminae (*Artibeus jamaicensis*, *A. lituratus*, *Dermanura*, *Sturnira*). Those of the Subfamilies Carollinae (*Carollia brevicauda*, *C. castanea*, *C. perspicillata*) and Glossophaginae (*Anoura*, *Glossophaga*) follow as important dispersers (Fleming 1988; Fleming and Heithaus 1981; Timm and others 1989; Van der Pijl 1957, 1972).

Bats are commensals and, in many cases, dispersers. When fruit size exceeds their transport capacity, bats consume the fleshy mesocarp of drupes and berries, and drop the remaining tissues under the tree crown. Smaller fruits are transported to the feeding and resting roosts where the bats drink the mesocarp juice (Bonaccorso 1979; Bonaccorso and others 1980; Fleming and Heithaus 1981; Flores 1992a, 1994e, 1999; Heithaus and Fleming 1978). The fruits of *Calophyllum brasiliense* (Clusiaceae) (fig. 105), *Ocotea austinii* (fig. 70), and *Minquartia guianensis* are transported to feeding and resting roosts. Frequently, populations of seedlings are found on the ground below the roosts (Flores 1994b, 1994e, 1999).

Bats disperse the diaspores of several species in the following families: Anacardiaceae (*Mangifera indica*, *Spondias*), Annonaceae (*Annona*), Bombacaceae (*Quararibea*), Fabaceae-Caesalpinioideae (*Aldina*, *Cynometra*, *Hymenaea*), Caryocaraceae (*Caryocar*), Cecropiaceae (*Cecropia*, *Pourouma*), Chrysobalanaceae (*Couepia*, *Licania*, *Parinari*), Clusiaceae (*Calophyllum*, *Clusia*) (fig. 105), Lauraceae (*Licaria*, *Nectandra*, *Ocotea*, *Persea*), Lecythidaceae (arils, *Lecythis*, *Eschweilera*, *Gustavia*) (figs. 54 and 106), Fabaceae-Mimosoideae (*Inga*, *Cojoba*) (figs. 64 and 76), Monimiaceae (*Siparuna*), Moraceae (*Ficus*, *Brosimum*, *Maclura*), Myrtaceae (*Psidium*), Olacaceae (*Minquartia guianensis*) (fig. 71), Fabaceae-Papilionoideae (*Andira inermis*, *Cassia grandis*, *Dipteryx*, *Lecointea*, *Swartzia*) (figs. 50 and 51), Piperaceae (*Piper*), Rubiaceae (*Genipa*, *Palicoure*a), Sapindaceae (*Matayba*), Sapotaceae (*Achras*), Sterculiaceae (*Theobroma*), and Verbenaceae (*Vitex orinocensis*) (August 1981; Fleming 1981; Fleming and Heithaus 1981; Flores 1992a, 1994b, 1994d, 1994e, 1999; Foster 1978, 1990; Gentry 1993; Gottsberger 1983; Janzen 1971a, 1971b; Janzen and others 1976; Levey and others 1994; Morrison 1978; Timm and others 1989; Van der Pijl 1957, 1972; Van Roosmalen 1985).

Primates

As recent colonizers, primates are fundamentally predators that eat all the fruits available but disperse few diaspores. Monkeys prefer fruits with hard pericarp bearing arillate seeds (Van der Pijl 1972). Commonly they eat numerous fruits of the

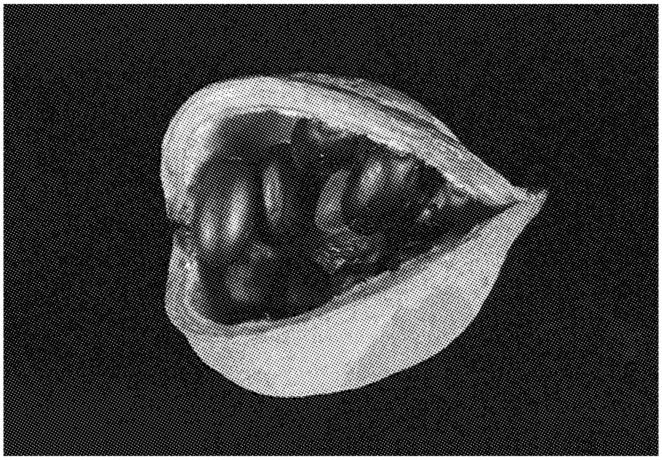


Fig. 107.

following families: Annonaceae (*Annona*, *Guatteria*, *Rollinia*), Anacardiaceae (*Spondias*), Apocynaceae (*Stemmadenia*), Araliaceae (*Dendropanax*), Boraginaceae (*Cordia bicolor*), Burseraceae (*Bursera simaruba, Tetragastris, Trattinickia*), Fabaceae-Caesalpinioideae (*Cassia grandis*, *Hymenaea courbaril*, *Prioria)* (fig. 50), Capparidaceae (*Capparis*), Caryocaraceae (*Caryocar*), Cecropiaceae (*Cecropia*, *Pourouma*), Chrysobalanaceae (*Couepia, Hirtella, Licania, Parinari*), Clusiaceae (*Garcinia, Vismia*), Euphorbiaceae (*Euphorbia*), Flacourtiaceae (*Casearia, Zuelania*), Lauraceae (*Ocotea*, *Nectandra*, *Persea*), Lecythidaceae (*Bertholletia*, *Gustavia*, *Lecythis*, *Eschweilera*) (figs. 54 and 106), Melastomataceae (*Miconia*, *Mouriri*), Meliaceae (*Guarea*, *Trichilia*) (fig. 56), Fabaceae-Mimosoideae (*Enterolobium*, *Inga*) (fig.76), Monimiaceae (*Mollinedia*, *Siparuna*), Moraceae (*Brosimum*, *Ficus*, *Helicostylis*, *Maquira*, *Perebea*), Myristicaceae (*Compsoneura, Irianthera, Virola, Otoba*) (fig. 62), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia*, *Marliera*, *Myrcia*, *Psidium*, *Syzygium*) (fig. 68), Nyctaginaceae (*Neea*), Olacaceae (*Minquartia guianensis*) (fig.71), Opiliaceae (*Agonandra*), Fabaceae-Papilionoideae (*Dipteryx*, *Swartzia*) (figs. 51-52), Polygonaceae (*Coccoloba*), Quiinaceae (*Lacunaria*), Rhamnaceae (*Ziziphus cinnamomum*, *Z. chloroxylon*), Rubiaceae (*Alibertia, Coussarea, Faramea, Genipa, Gonzalagunia, Guettarda, Palicourea*, *Psychotria*, *Simira*), Rutaceae (*Citrus*), Sapindaceae (*Cupania*) (fig. 59), Sapotaceae (*Chrysophyllum*, *Manilkara, Pouteria*), Simaroubaceae (*Picramnia, Simarouba amara*), Sterculiaceae (*Guazuma ulmifolia*, *Sterculia*, *Theobroma*) (fig. 107), Tiliaceae (*Apeiba*, *Muntingia calabura*) (fig. 43), Ulmaceae (*Trema micrantha*), and Verbenaceae (*Citharexylum*, *Vitex stahelii*) (Chapman 1989; Croat 1978; Eisenberg 1983; Estrada and others 1984; Flores 1992a, 1992b, 1994d, 1994e, 1999; Gentry 1993; Hladik and Hladik 1969; Howe 1980, 1982; Levey and others 1994; Milton 1980; Van der Pijl 1972; Van Roosmalen 1985; Yumoto and others 1995; Zhang and Wang 1995). Gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and mandrills (*Papio anubis*) also eat several of these fruits (Yamagiwa and others 1993, Yumoto and others 1995).

Humans are active seed dispersers. They gather fruits and use seeds to obtain food, fibers, essential oils, insecticides, beverages, alkaloids, drugs, phytoestrogens, animal fodder, and other products. Seeds are also used to start plantations (see Ethnobotany Chapter).

Other Mammals

Rodents are frequently predators but may behave as commensals and dispersers (dyszoochory). Some eat the diaspore pulp while rejecting the remaining tissues and the seed; some swallow the diaspore and defecate the seeds at other sites; some bury the diaspores to feed on later. However, mammal-diaspore relationships are very complex (Janzen 1983a, 1983c, 1983d, 1983f; Janzen and Wilson 1983). *Microsciurus*, *Sciurus*, *Orthogeomys*, *Heteromys*, *Liomys*, *Proechimys*, *Hesperomys*, *Thmasomys*, *Agouti*, *Dasyprocta*, and *Myoprocta* are active rodents in Neotropical forests; they forage, destroy, bury, and store several diaspores (Fleming 1983a, 1983b; Gottsberger 1983; Paschoal and Galetti 1995; Timm and others 1989). *Sciurus* forages first on the ground and only later climbs the tree to gather additional fruits (Bonaccorso and others 1980, Heaney 1983). The mammals that climb the trees and those that feed on the discarded diaspores attract *Agouti*, *Dasyprocta*, and *Proechimys*. Rodents usually eat the mesocarp and frequently the seed or a part of it. Some seeds with woody endocarps, intact or partially damaged, are transported to different areas or are swallowed and defecated at other sites. Some seeds remain viable and eventually germinate. *Myoprocta exilis* and *Dasyprocta leporina*, dispersal vectors of *Vouacapoua americana* seeds, bury many seeds. These seeds produce seedlings with a higher capacity to survive than those that germinate on the forest floor under the tree crown, where they perish from weevil and termite attacks (Forget 1997).

Among the marsupials, *Philander opossum*, *Didelphis marsupialis*, and *Caluromys derbianus* are active dispersers of fruits and seeds; *Didelphis marsupialis* is the most efficient disperser (Medellín 1994, Timm and others 1989). Some of the diaspores dispersed are those of *Piper*, *Cecropia*, *Dipteryx*, and *Virola.*

All carnivores, except *Lutra* and *Felis*, are frugivorous (Janzen 1983a) and all are potential dispersers of adhesive diaspores (epizoochory) (Gottsberger 1983). *Nasua narica*, *Potos flavus*, and *Eira barbara* are sporadic dispersers of diaspores (Brosset and Erard 1986, Janzen 1983c, Jordano 1983, Kaufmann 1983). *Chrysocyon* and *Cerdocyon*, species from the fauna of the Brazilian cerrado, feed on seeds and fruits (Gottsberger 1983, Vieira and Carvalho-Okano 1996). The tapirs (*Tapirus bardii*, Perissodactyla) bury part of the seeds, promoting the creation of new seedling populations (Janzen 1983f).

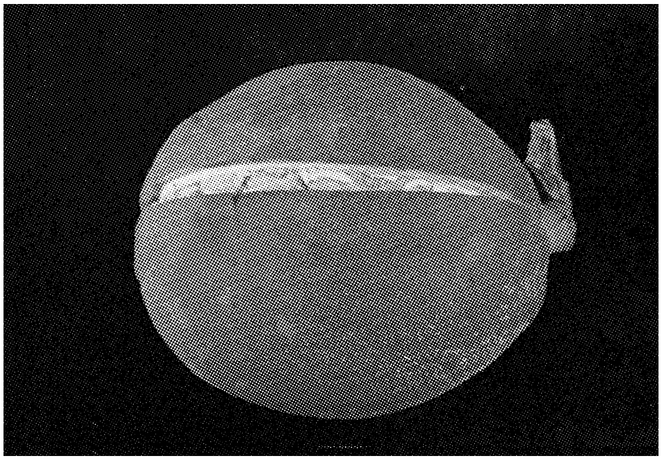


Fig. 108.

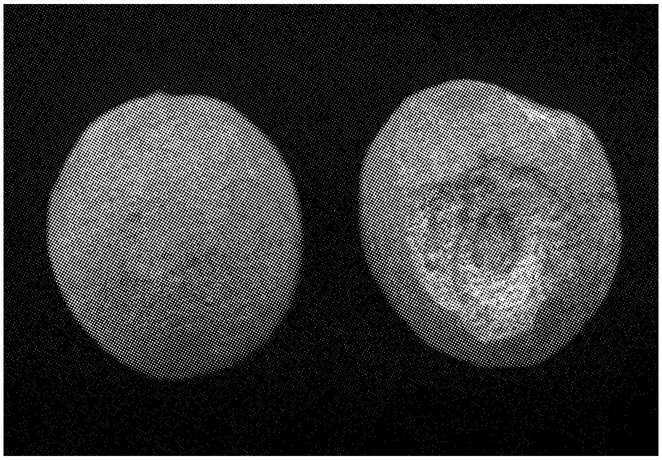


Fig. 109.


Fig. 110.

Tayassu tajacu (Artiodactyla) eat, bury, and defecate seeds thus contributing to seed dispersal (Kiltie 1981, Sowls 1983). *Odocoileus virginianus* (Artiodactyla, Cervidae) eat diaspores of several species but do not swallow the seeds; they are ejected when the soft tissues are chewed (Janzen 1983d). All mammals consume diaspores with attractive color, and scarce pulp, but with tissues very rich in lipid content such as the fruit mesocarp or the sarcotesta, embryo, and endosperm from the seed. They also eat hard, indehiscent, nonedible fruits with no attractive color. These fruits contain from one to several seeds rich in lipids (Van Roosmalen 1985).

Elephants are efficient dispersers of diaspores (Alexandre 1978, Gautier-Hion and others 1985, White and others 1993, Yumoto and others 1995). They prefer fruits with dry, fibrous pericarp and well-protected seeds. These fruits are dull brown, yellow-brown, blackish-brown, light brown, yellow-orange, or green (Gautier-Hion 1990, Gautier-Hion and others 1985). Examples of diaspores dispersed by elephants include *Antrocaryon nannanii* (Anacardiaceae), *Anonidium mannii* (Annonaceae), *Mammea africana* (Clusiaceae), *Uapaca guineensis* (Euphorbiaceae), *Tetrapleura tetraptera* (Fabaceae-Mimosoideae), *Treculia africana* (Moraceae), *Omphalocarpum* (Sapotaceae), *Klainedoxa gabonensis* (Simaroubaceae), *Grewia milbraedii* (Tiliaceae), and *Cissus dinklagei* (Vitaceae) (Yumoto and others 1995).

The following are fruits and seeds commonly consumed and dispersed by mammals: Anacardiaceae (*Spondias*), Annonaceae (*Duguetia*), Bombacaceae (*Pachira*) (fig. 108), Boraginaceae (*Cordia*), Burseraceae (*Protium*), Caryocaraceae (*Anthodiscus*, *Caryocar*), Chrysobalanaceae (*Couepia*, *Licania*, *Parinari*), Combretaceae (*Terminalia cattapa* L.), Euphorbiaceae (*Croton floribundus*, *Dalechampia pentaphylla*), Fabaceae-Caesalpinioideae (*Cynometra*, *Hymenaea*), Fabaceae-Papilionoideae (*Andira*, *Dipteryx*) (figs. 51 and 52), Fagaceae (*Quercus*), Humiriaceae (*Humiriastrum*, *Sacoglottis*, *Vantanea*) (fig. 109), Juglandaceae (*Alfaroa*, *Juglans*) (fig. 110), Lauraceae (*Ocotea*), Lecythidaceae (*Bertholletia*, *Couroupita*, *Eschweilera*, *Gustavia*, *Lecythis*) (figs. 54 and 106), Malpighiaceae (*Byrsonima crassifolia*, *Dicella bracteosa*), Meliaceae (*Cabralea canjereana*, *Carapa*, *Guarea grandifolia* DC.) (fig. 56), Fabaceae-

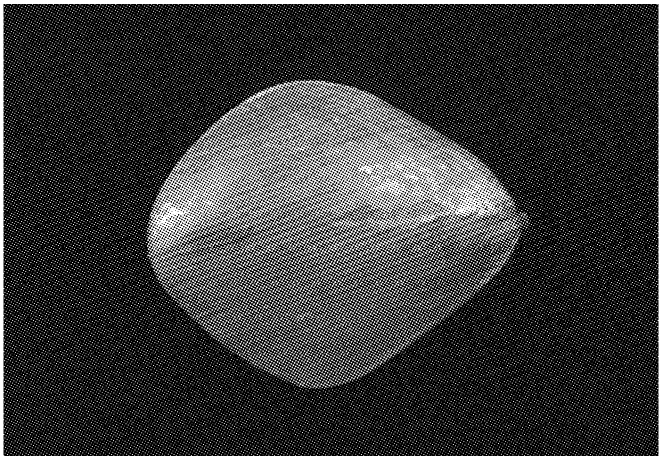


Fig. 111.

Mimosoideae (*Enterolobium*, *Pentaclethra macroloba*, *Stryphnodendron*) (fig. 111), Moraceae (*Brosimum*, *Ficus*), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia ligustrina*), Polygalaceae (*Diclidanthera laurifolia*), Rubiaceae (*Alibertia*), Sapotaceae (*Achras*, *Chrysophyllum cainito*, *Manilkara*), Sterculiaceae (*Guazuma ulmifolia*, *Luehea*, *Sterculia*) (figs. 108 and 112), Ulmaceae (*Celtis iguanae*), and Verbenaceae (*Citharexylum*, *Vitex*) (Fleming 1983a, 1983b; Gentry 1993; Janzen 1983a, 1983c, 1983d, 1983f; Kaufmann 1983; Paschoal and Galetti 1995; Van Roosmalen 1985).

Myrmecochory

Ants do not play an important role in the dispersal of diaspores (Van der Pijl 1972). Ant-dispersed fruits are small, and dehiscent with seeds having an elaiosome rich in lipids; usually these seeds are too small to attract birds (Thompson 1981, Van der Pijl 1972, Van Roosmalen 1985). Some species move the seeds 1 to 2.5 m. Frequently, ants deposit seeds in their nests, and many of these germinate and develop into healthy seedlings (Passos and Ferreira 1996).

Saurochory

Several reptiles are frequent diaspore dispersers in the Tropics. The turtle *Rhinoclemmys annulata*, the lizard *Basiliscus basiliscus*, and the iguana *Iguana iguana* eat and transport fruits and seeds of species such as *Spondias* (Anacardiaceae), *Cordia* (Boraginaceae), *Sloanea* (Elaeocarpaceae) (fig. 103), *Macrolobium*, *Swartzia* (Fabaceae-Caesalpinioideae), *Inga* (Fabaceae-Mimosoideae) (fig. 76), *Ficus*, *Brosimum* (Moraceae), and *Ardisia* (Myrsinaceae) (Berg 1975, Ernst 1983, Gottsberger 1978, Rand 1978, Van Devender 1983).

Ichthyochory

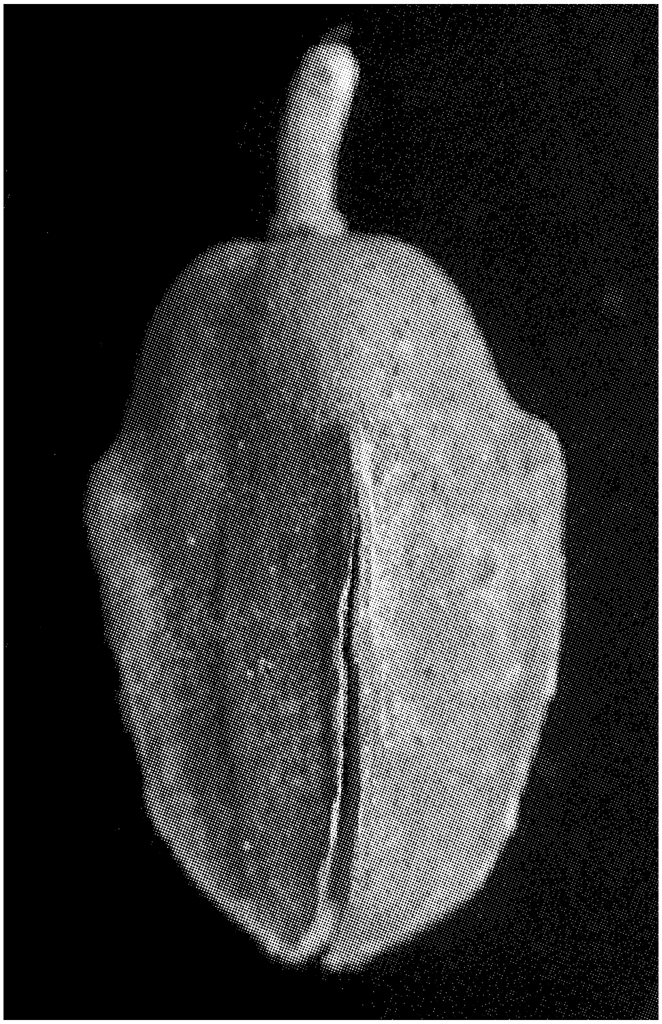


Fig. 112.

The proportion of diaspores dispersed by fish in the riparian and inundated forests is high, although it has not been precisely quantified (Gottsberger 1978, Goulding 1980, Howe and Smallwood 1982). Fish dispersed 16 forest tree species and destroyed 17 species in the varzea forests (riparian plains, rivers with clear waters) of the Brazilian Amazon. Gottsberger (1978) proposed that ichthyochory is an archaic method of dispersal and that the incidence is high in waters poor in nutrients, a finding that suggests fish depend on nutritious fruits and seeds.

In the varzea and the igapó (riparian plains and rivers with dark waters), peak fructification coincides with the period of flooding. In the inundated forests almost all diaspores fall into the water where they are eaten by fish, with variable rates of destruction. Ichthyochory can be facultative or obligatory (Kubitzki and Ziburski 1994).

Ichthyochoric diaspores can have ariloid structures (*Annona*, *Virola*). Some have protective structures such as a hard pericarp (*Cecropia*), woody endocarp (*Licania*, *Astrocaryum*), hard seedcoat (some Elaeocarpaceae, *Unonopsis*), sarcotesta, and fleshy tissues with agreeable taste or attractive infrutescence (Gottsberger 1978) (fig. 62). Many of the diaspores dispersed by fish or water and fish have structural adap-

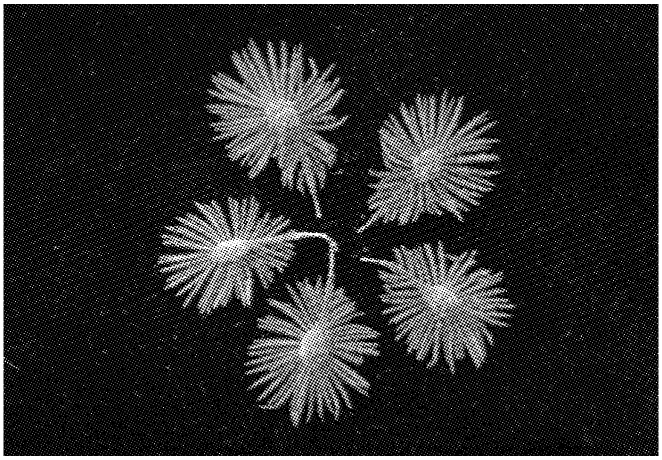


Fig. 113.

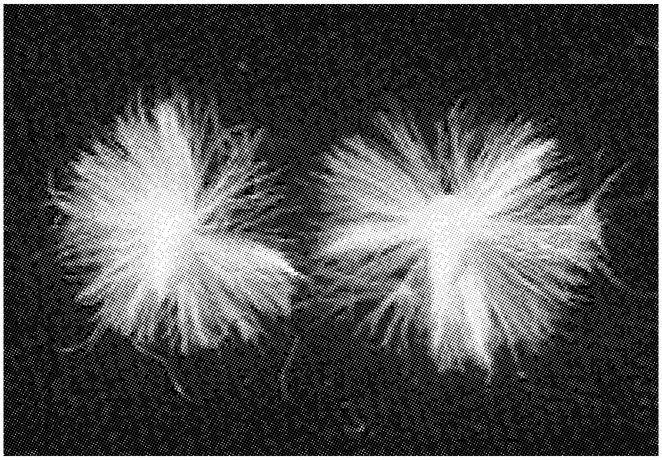


Fig. 114.

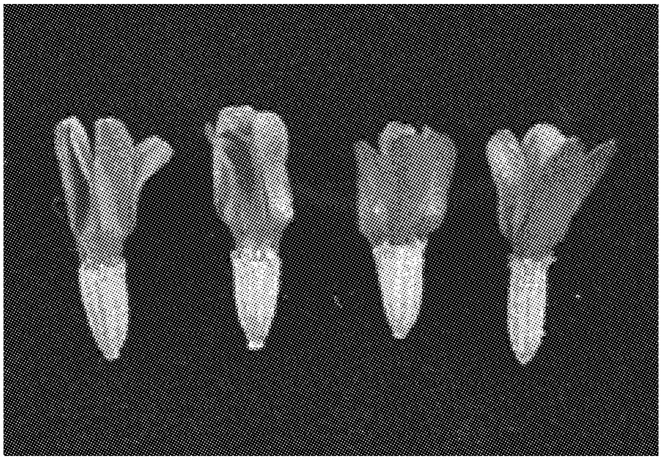


Fig. 115.

tations for staying afloat for long periods in inundated forests. Finally, they sink and germinate near the end of the immersion period (Kubitzki and Ziburski 1994).

Neotropical rivers contain many species of disperser fish: *Cichlasoma* (Cichlidae), *Brycon* (Characidae, highly predatory), *Rhamdia* (Pimelodidae), *Colossoma* (Characidae), *Cytocharax* (Characidae), *Leporinus* (Curimatidae), *Lithodoras dorsalis* (Doradidae); they feed on the diaspores that fall into the water (Flores 1992c, 1999; Gottsberger 1978). These fish contribute to dispersal of seeds of the following trees: *Anacardium* (Anacardiaceae); *Annona hypoglauca, Annona, Duguetia, Unonopsis* (Annonaceae); *Crescentia amazonica, Tabebuia barbata, T. palustris* (Bignoniaceae); *Pseudobombax* (Bombacaceae); *Protium* (Burseraceae) (figs. 72 through 73); *Crataeva benthamii* (Capparidaceae); *Cecropia membranacea, C. latiloba* (Cecropiaceae); *Buchenavia oxycarpa* (Combretaceae); *Sloanea* (Elaeocarpaceae) (fig. 103); *Hevea spruceana* (Euphorbiaceae); *Aldina latifolia, Crudia amazonica, Cynometra, Macrolobium, Mora oleifera, M. paraensis* (Fabaceae-Caesalpiniodeae); *Swartzia* (Fabaceae-Papilionoideae); *Laetia corymbulosa, L. suaveolens* (Flacourtiaceae); *Aniba, Licania, Nectandra, Ocotea* (Lauraceae) (fig. 70); *Eschweilera ovalifolia, E. tenuifolia, Lecythis* spp. (Lecythidaceae) (figs. 54 and 106); *Byrsonima* (Malpighiaceae); *Carapa guianensis, Guarea, Trichilia* (Meliaceae) (fig. 56); *Brosimum, Ficus* (Moraceae); *Virola, Otoba* (*Myristicaceae*) (fig. 62); *Genipa, Randia* (Rubiaceae); and *Vitex cymosa* and *V. cooperi* (Verbenaceae) (Flores 1992c, 1999; Gottsberger 1978; Kubitzki and Ziburski 1994).

Sometimes fish drop the seeds and the streams transport them long distances; eventually the seeds reach a riverbank where they sometimes germinate (Flores 1992c, 1999). In the Brazilian Amazon, fish play an important role as dispersers (Gottsberger 1978, Goulding 1980). Preliminary information on the role of fish in the Atlantic lowlands of Mesoamerica leads one to similar conclusions.

Abiotic or Azoochorous Dispersal

The three types of abiotic dispersal are discussed in the following sections.

Anemochory

Tropical trees produce a great variety of wind-dispersed diaspores (Van der Pijl 1972). Light fruits can have a winged pericarp (*Terminalia amazonia*, Combretaceae; *Hymenolobium, Sclerolobium*) (fig. 45) or filiform projections (*Heliocarpus appendiculatus*, Tiliaceae) (fig. 113). Some seeds have a winged seedcoat (*Tabebuia rosea*, Bignoniaceae; *Cedrela odorata, Vochysia guatemalensis*) (figs. 91-93); other seeds are pubescent and lanate (*Bombacopsis quinata*, Bombacaceae; *Macrohasseltia macroterantha*, Flacourtiaceae) (fig. 114). Some units of dispersal (fruit + modified floral organs such as androecium, perianth, and receptacle) have additional floral parts to aid in dispersal. Examples include *Oreomunnea pterocarpa* (Juglandaceae) (fig. 115) with a nut surrounded by a modified perianth; *Triplaris americana* and *Coccoloba tuerckheimii* (Polygo-

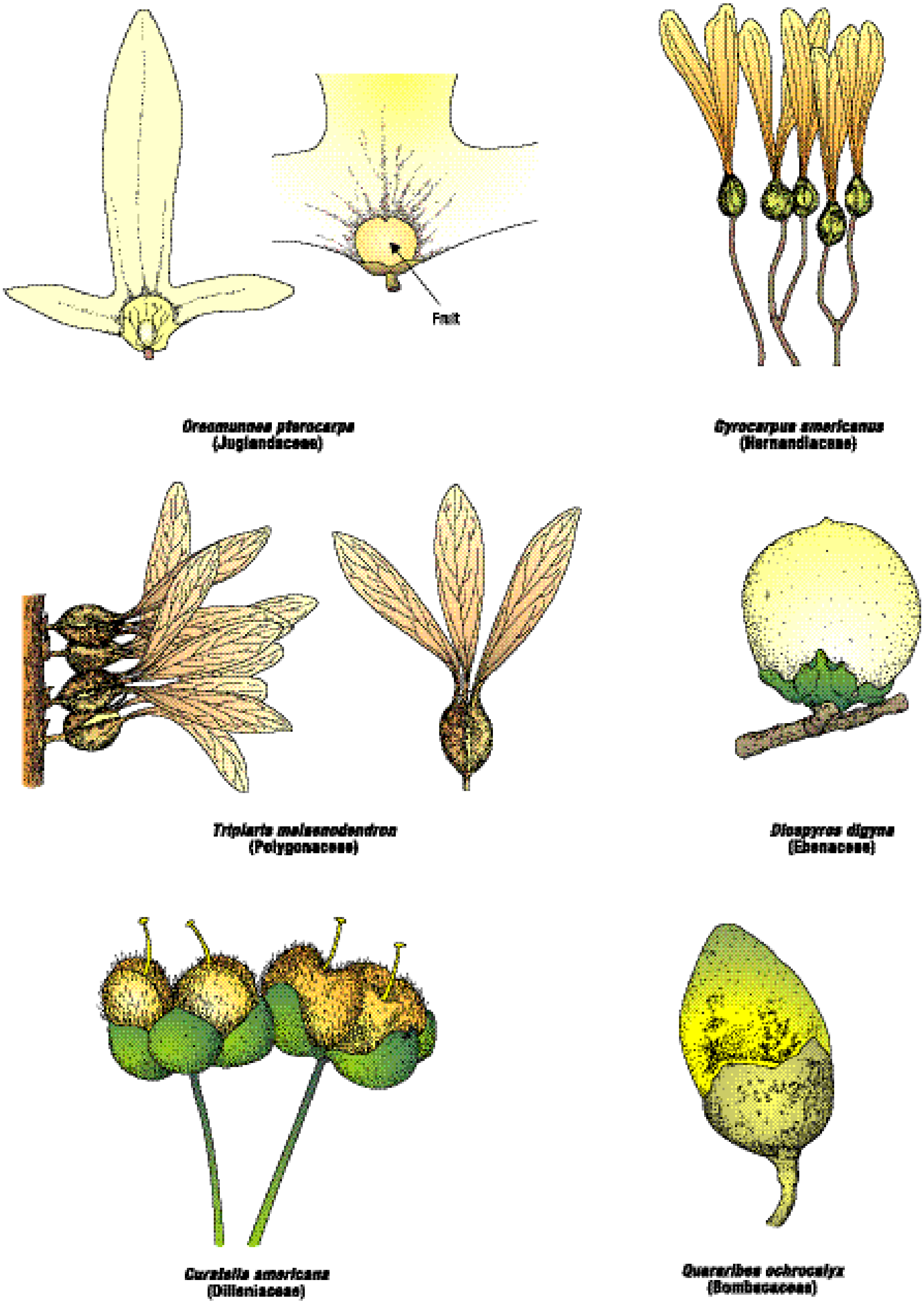


Fig. 116. Different types of diaspores.


Fig. 117.


Fig. 118.

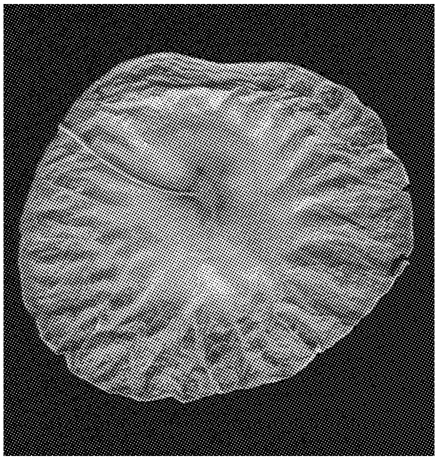


Fig. 119.

naceae) with a nut enclosed in an acrescent perianth that extends after fertilization; *Gyrocarpus jatrophifolius* and *Hernandia didymantha* (Hernandiaceae) with a nut immersed in a cup formed by perianth tissues; *Astronium graveolens* (Anacardiaceae) with a drupe surrounded by a winged calyx growing in the postfertilization stages and masking the petals; and *Curatella americana* (Dilleniaceae) (fig. 116), *Diospyros nicaraguensis* (Ebenaceae), and *Cordia alliodora* (Boraginaceae) (fig. 116), with a conspicuous calyx, acrescent and persistent.

The morphological design of wind-dispersed diaspores seems to slow their descent and increase their exposure to horizontal or gusty winds (Augspurger 1986, Rabinowitz and Rapp 1981). The rate of descent is correlated with the wing loading (weight/area) of the diaspore (Green 1980). Horizontal winds disperse the diaspores over a wide area, with potential dispersal and area inverse to the descent rate (Augspurger 1986). The consistency in direction, intensity, and speed of the wind also affects the seed shadow.

Using the morphology of the diaspore, the rotatory movement, and the rate of descent, Green (1980) established two categories of wind-dispersed diaspores: rolling samaras, which autorotate around the longitudinal axis of the diaspore and autogyrate around one end of the diaspore, and autogyros, or nonrolling samaras, including the samaras that only autogyrate. For a determined wing loading the first have a higher descent rate (Augsburger 1986, Green 1980, Norberg 1972). The morphology and the aerodynamic behavior led Augsburger (1986) to group the wind-dispersed diaspores studied into six types:

(1) The floater is a diaspore that floats downward in a vertical line; e.g., *Bombax*, *Bombacopsis*, *Ceiba*, *Ochroma*, *Pseudobombax* (Bombacaceae), *Trichospermum* (Tiliaceae).

(2) The rolling autogyro is a diaspore that rotates on two axes: around the longitudinal axis of the diaspore and around one end of the diaspore in a closed spiral (rolling samara, per Green 1980); e.g. *Cespedesia* (Ochnaceae); *Couratari* (Lecythidaceae); Dalbergia, *Hymenolobium*, *Lonchocarpus*, *Machaerium*, *Platymiscium* (Fabaceae-Papilionoideae); *Lafoensia punicifolia* (Lythraceae); *Sclerolobium*, *Tachigali* (Fabaceae-Caesalpinioideae); *Terminalia amazonia*, *T. oblonga*, *T. bucidoides* (Combretaceae); and *Vochysia*, *Qualea* (Vochysiaceae) (figs. 45-46, 91, 117-118).

(3) The autogyro is a diaspore that rotates closely around the diaspore end containing the seed; e.g. *Loxopterygium sagotii* (Anacardiaceae); *Cedrela*, *Swietenia* (Meliaceae); *Luehea* (Tiliaceae); *Myroxylon*, *Vatairea* (Fabaceae-Papilionoideae) (figs. 92 and 112).

(4) The undulator is a diaspore that glides and undulates but not with accumulative forward motion; its gliding is discontinuous or it oscillates fugaciously (nonrolling samara, per Green 1980); e.g. *Aspidosperma* (Apocynaceae), *Pterocarpus* (Fabaceae-Papilionoideae), and *Jacaranda* (Bignoniaceae) (figs. 47 and 119).

(5) The helicopter is a diaspore that spins tightly around a vertical line; it is similar to the autogyro with additional wings; e.g. *Astronium graveolens* (Anacardiaceae), *Cordia alliodora* (Boraginaceae), *Triplaris* (Polygonaceae), and *Macrohasseltia* (Flacourtiaceae) (figs. 114-116).

(6) The tumbler is a diaspore that tumbles with an inconsistent axis, at random. It can also rotate around a vertical line in an open and extended spiral; e.g. *Cavanillesia* (Bombacaceae).

The unclassified diaspores include those with variable behavior; e.g., *Tabebuia* (Bignoniaceae) (fig. 93).

Fig. 120.

Hydrochory

Hydrochory is carried out by rain-wash (*ombrohydrochory*), rivers, or marine streams (*nautohydrochory*). It plays an important role in the dispersal of riparian, marshy, or coastal tree diaspores (Kubitzki and Ziburski 1994, Van der Pijl 1972). In some cases the diaspores float; in others, they submerge. The seeds of *Astrocaryum*, *Cocos nucifera* (Arecaceae), *Tabebuia palustris* (Bignoniaceae), *Calophyllum brasiliense* (Clusiaceae), *Hevea brasiliensis* (Euphorbiaceae), *Aldina latifolia*, *Crudia amazonica*, *Cynometra*, *Eperua*, *Macrolobium*, *Mora oleifera*, *M. paraensis* (Fabaceae-Caesalpinioideae), *Parkia discolor* (Fabaceae-Mimosoideae), *Pterocarpus*, *Swartzia* (Fabaceae-Papilionoideae), *Bertholletia excelsa*, *Eschweilera* spp., *Grias cauliflora*, *Gustavia superba* (Lecythidaceae), *Carapa guianensis* (Meliaceae), and *Calatola costaricensis* (Icacinaceae) can be dispersed by river or rivulet streams or by inundation of riparian plains (figs. 105 and 120). To increase their floating capacity, the seeds are dispersed primarily by hydrochory, which reduces the specific gravity, increases the surface area, and deposits a thick cuticle on the outer surface. The existence of aerenchyma is a common device.

Autochory

Several taxa use autochoric dispersal. The fruit wall commonly dictates use of this mechanism. The explosive release of seeds is an ancient characteristic (Van der Pijl 1972). Autochory is frequent in arid zones (Van der Pijl 1972), but it is also observed in tropical forest trees, e.g., some Fabaceae.

Active Ballistics

The active ballistics of diaspores occurs when tension increases in hygroscopic, dead tissues. Tension in dead tissues is present in *Croton priscus, Hevea brasiliensis,* and *Hura crepitans* (Euphorbiaceae); some species of *Cassia* and *Crudia* (Fabaceae-Caesalpinioideae); and several species of *Calliandra*, *Mimosa*, and *Pentaclethra macroloba* (Fabaceae-Mimosoideae) (figs. 65-66).

Passive Ballistics

This occurs when an external agent (wind, rain, or animal) releases the inner tension of the fruit and provides the necessary energy for the opening of the fruit. The mechanism is common in herbaceous species (Van der Pijl 1972).

Creeping Diaspores

In creeping diaspores the movement of the adhesive structures is provoked by weather changes (moistness-dryness). It is common in Asteraceae and Poaceae (Van der Pijl 1972).

Barochory

This is dispersal by weight (Van der Pijl 1972); e.g., *Billia hippocastanum*, *B. columbiana* (Hippocastanaceae), *Quercus* (Fagaceae), *Rhizophora* (Rhizophoraceae), *Juglans* (Juglandaceae), *Carapa*, *Guarea* (Meliaceae), *Mora* (Fabaceae-Caesalpinioideae), *Dipteryx* (Fabaceae-Papilionoideae), *Achras*, *Manilkara* (Sapotaceae) (figs. 42, 52, and 56).

GERMINATION

Germination is, in a nutshell, the process unchained by seed hydration (imbibition) and the beginning of radicle expansion (Evenari and others 1957). Embryogeny and germination are, then, successive stages in the development of the new sporophyte, separated by a period of relative metabolic inactivity called quiescence (Bewley and Black 1978, 1982, 1994; Flores 1999).

The process of germination involves the transition of cells from a dehydrating stage and low metabolic activity to a hydrated and metabolically active stage. Water is absorbed by many seeds in a triphasic way: imbibition, germination sensu stricto, and embryo development (Bewley and Black 1994, Tissaoui and Côme 1975). Imbibition corresponds to the rapid absorption of water leading to a regular increment in the respiratory activity. Germination sensu stricto is the process of embryo activation, not accompanied by any apparent morphological change. Embryo development is marked by the initiation of radicle elongation and a significant change in the physiology of the embryo (Côme and Corbineau 1996a, 1996b). The crucial phase is the germination sensu stricto, because seedling development depends on it. In most cases, the seed germinates only if the respiration and production of adenosine 5’-triphosphate (ATP) are adequate, creating an oxygen requirement (Côme and Corbineau 1996a, 1996b).

Germination culminates with radicle development (basically cellular elongation) and its protrusion into the adjacent tissues. In recalcitrant seeds with minute, rudimentary embryos or large embryos with a rudimentary radicle (reduced to a radical meristem), the development of the radicle implies cell division and elongation.

ENVIRONMENTAL INFLUENCES

The external environmental factors regulating the activity of the maternal tree during seed maturation include temperature, light, photo- and thermoperiod, relative air moisture, and water potential in the soil. The internal parameters, that is, the water potential of the maternal tree and its nutritional and hormonal state, and the position of the seed on the tree also affect seed maturation. Other environmental factors involved directly in the process of germination are temperature, light, and gas (Bewley and Black 1994, Bonner 1966).

Water

In seeds undergoing maturation drying, water imbibition is the first requirement for germination because it permits metabolic reactivation and restoration of the entire system of membranes and organelles. Activation of the enzymatic system, respiration, and synthesis of RNA and proteins are fundamental. The enzymes participating in the process are found in the dehydrated seed or are synthesized during imbibition. In most cases, the water imbibing the seed is equivalent to two or three times the dry weight of the seed. The net diffusion occurs in a descendent gradient of water potential (or energetic state of the water i); in other words, from pure water to water containing solutes (Bewley and Black 1994). The potential of a cell inside a seed is determined by the osmotic potential (c_p), determined by the concentration of solutes (more solutes = less osmotic potential), the matric component (c_c), determined by the hydration of matrices (cell walls, starch, protein bodies), and the pressure potential (c_p), permitting water intake and putting pressure on the cell wall (Bewley and Black 1994, Leopold and Kriedemann 1975). In the water potential of the soil, only c_c has an important function. Water absorption has three phases:

(1) A rapid phase of initial imbibition that is strongly influenced by the matric forces. This phase occurs in both viable and nonviable seeds, because the water potential of the mature seed is lower than that of the surrounding humid soil. In this phase, energy is liberated as heat; the gases of colloidal adsorption and the solutes are released as sugars, organic acids, ions, amino acids, and proteins. The solutes may stimulate the growth of bacteria and the fungi of the soil. An imbibitional pressure is also created through protein hydration (colloid formation) (Bewley and Black 1994, Bonner and others 1994).

(2) A phase of slow water intake, in which the matric component (c_c) is not important and the water potential of the seed (c) is determined by $c_{\check{s}}$ and c_p. This is the phase when metabolic activity begins. Dormant seeds are also metabolically active; the length of this phase is correlated with the intensity of the dormancy (Bewley and Black 1994, Bonner and others 1994).

(3) The last phase occurs only in nondormant seeds involved in active germination. It is a rapid phase intensified by metabolism activation; in many cases, it coincides with the breaking of the seedcoat and the beginning of the elongation and protrusion of the radicle (Bewley and Black 1994, Bonner and others 1994). In orthodox seeds, the endosperm and the cotyledons do not expand if the seedlings are cryptocotylar. In recalcitrant seeds with rudimentary embryos, cotyledon development frequently precedes radicle development (e.g., *Virola*) or both develop concurrently (e.g., *Minquartia guianensis*). Seeds with nuclear endosperm may finish cell wall deposition in this stage, and endosperm disintegration either in the middle or around the embryo occurs (fig. 81).

Reserve mobilization and enzymatic activation depend on hydration; the best germination occurs with a low moisture tension (0.005 to 0.500 bars). If the tension is zero, the water pellicle around the seed inhibits the absorption of oxygen (Bonner and others 1994, Mayer and Shain 1974). During reserve mobilization, the insoluble forms are transformed into soluble forms. The amylases are the first enzymatic system involved in the transformation of starch into soluble sugars. The lipases enfold the lipids in fatty acids and glycerol. The fatty acids are b-oxidated to acetyl-coenzyme A, which enters the glyoxylate cycle and eventually forms carbohydrates. Some proteins are important as sources of nutrients and are converted to soluble forms. The movement of substances inside the embryo is vital. In many species the stimulus controlling the amylase activity arises in the radicle; other stimuli arise in the cotyledons (Bewley and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975, Mayer and Shain 1974, Stanwood and McDonald 1989).

Temperature

The effect of temperature is difficult to separate from the effects of light and water. Under natural conditions, temperature determines the capacity and rate of germination, removing the primary and inducing secondary dormancy (Bewley

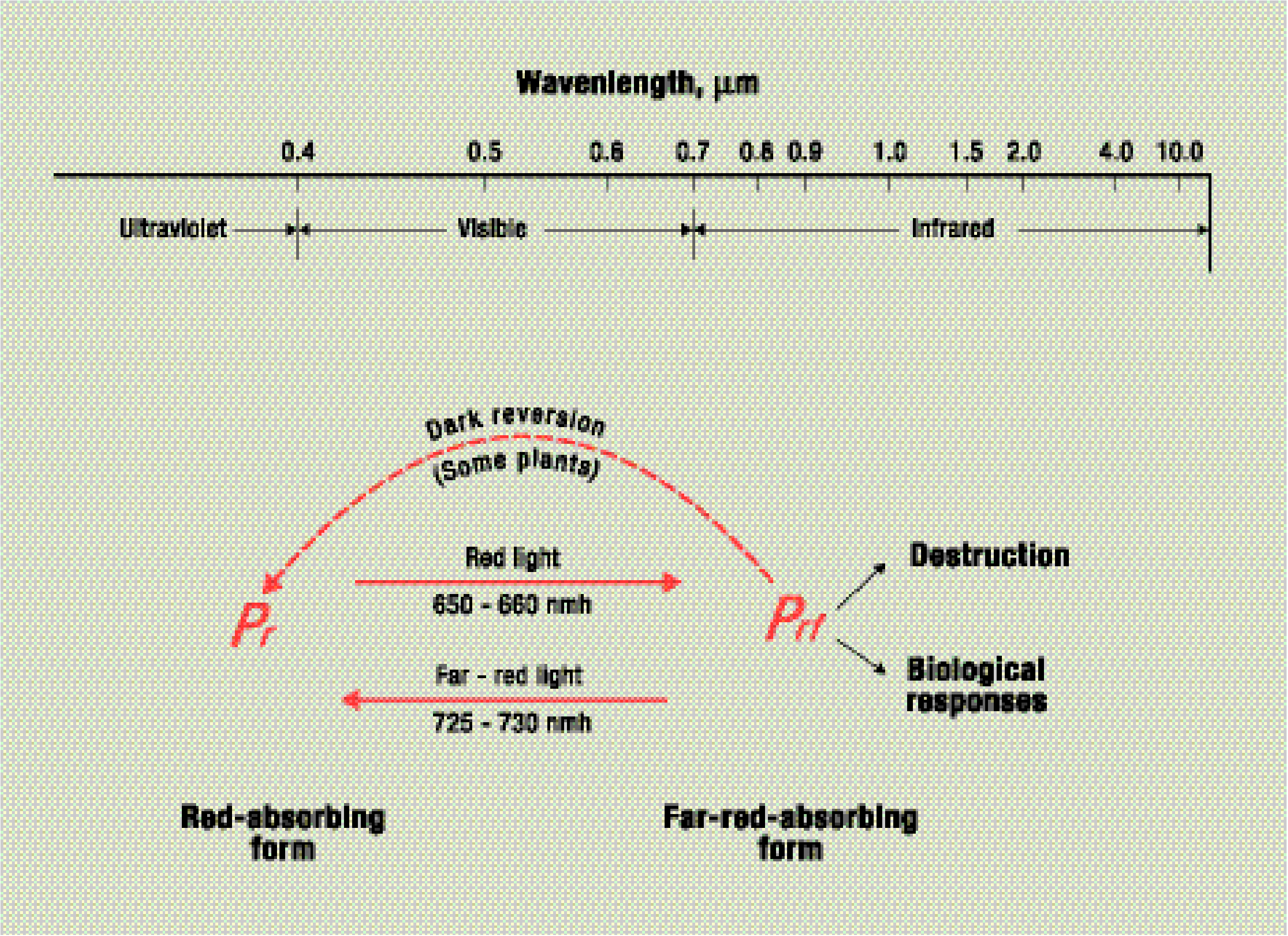


Fig. 121. Light spectral composition and exposure of phytochrome to red light and conversion to the far-red-absorbing form and viceverse.

and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975, Mayer and Shain 1974, Stanwood and McDonald 1989). For germination, the upper limit is about 45 °C and the lower 3 to 5 °C. Many species germinate at about 40 °C, but the seedlings are abnormal; others can germinate near the lower temperature limit but they rarely produce normal seedlings (Bonner and others 1994). The regimes of alternating temperature (20 °C at night and 30 °C during the day) seem optimal for species from temperate zones, although similar results are obtained with constant temperatures of 25 °C (Bonner and others 1994). In tropical species the best range is usually 25 to 30 °C.

Light

Light stimulates germination, but it is not strictly necessary for most seeds; however, some pioneer tropical species typical of areas in early succession, such as *Cecropia* and *Heliocarpus*, have photoblastic seeds. A pigment called phytochrome is involved in the photocontrol of the germination; it exists in two reversible forms. The *Pr* form (red light) has a maximal absorbency of 660 nmh and stimulates germination; the *Pfr* form (far-red light) has a maximal absorbency of 730 nmh and inhibits germination (fig. 121) (Bonner 1966, Hendricks and Borthwick 1967, Hillman 1969). The far-red light can reverse the effects of the red light. If seeds are exposed to red and far-red light consecutively, failure to germinate depends on which light was used. Exposure to red light for less than a second can produce the stimulus to unchain germination; this effect is magnified if infrared light is applied later. When the treatment is reversed, the seed does not germinate (Bonner 1966, Kozlowski 1971, Leopold and Kriedemann 1975).

When the *Pr* is illuminated with red light, it changes to *Pfr*; if the latter absorbs far-red light it converts to *Pr* (fig. 121). Inside the seed, the *Pfr* is converted metabolically to *Pr* even in darkness. The *Pfr* can also be metabolically destroyed and the *Pr* resynthesized (Bonner 1966, Kozlowski 1971, Leopold and Kriedemann 1975).

Light sensitivity is influenced by pretreatment with temperature. With an increment of cold pretreatment, seed germination can be increased in darkness and the sensitivity to far-red light decreased. The requirement of light for germination varies with the amount of imbibed water (Bonner and others 1994, Kozlowski 1971).

GENETIC INFLUENCE

A factor always neglected and one that has not been well evaluated is how the genome received by the diaspore controls germination. Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seedcoat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore. For example, the genes expressed in the megagametophyte play a role in the induction of seed development, primarily in embryo and endosperm development (Angenent and Colombo 1996, Ray 1998). The endogenous annual rhythm of the germinability of the seed and the internal mechanisms regulating it are not well known either.

SEED RESPIRATION

Respiration permits the acquisition of energy. It requires oxygen and the removal of CO_2. High levels of CO_2 can inhibit germination, and a lack of oxygen has the same effect although some species can germinate in anaerobic conditions (Bewley and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975).

The inhibited seed has three active routes of respiration: glycolysis, pentose-phosphate, and the citric acid cycle (Krebs cycle). Glycolysis–catalyzed by cytoplasmic enzymes–and the Krebs cycle (inside the mitochondria) are essential for the production of ATP. The Krebs cycle produces ATP through the cyclic metabolism of organic acids. The pentose phosphate route is a source of reduced nicotine adenine dinucleotide phosphate (NADPH); it acts as a hydrogen and electron donor in reductive biosynthesis, especially of fatty acids. Intermediate compounds, which initiate other biosynthetic processes producing energy, also exist in this route (Bewley and Black 1994, Leopold and Kriedemann 1975).

According to Bewley and Black (1994), the respiratory process in the orthodox seed involves three or four stages:

(1) High oxygen (O_2) consumption and a linear increment in respiration during tissue hydration (hydration and activation of mitochondrial enzymes in the Krebs cycle and the electron chain).

(2) Decrease in the respiration proportional to the stabilization of O_2 intake. The seed is hydrated and the enzymatic system is active. Between stages (2) and (3), the radicle protrudes through the surrounding tissues (it coincides with phases (2) and (3) of the imbibition process). The seedcoat (or seedcoat + endocarp or pericarp) can be a physical barrier limiting O_2 intake.

(3) Respiratory reactivation due to activation of the embryo axis and meristems and mobilization of stored reserves. The breaking of the seedcoat may contribute to increasing the intake of O_2.

(4) Respiration restricted to storage tissues whose reserves are being degraded and removed.

The dicotyledon embryo can be complete, large or small, differentiated, partially differentiated, rudimentary, or not differentiated. Cell activation in all embryo tissues appears sequential and in numerous cases it begins in the hypocotyl and extends to the embryonic poles. In the embryo, gradients of activation are at all levels. The sequence of activation in the cotyledons is quite complex and varies with the species (Bewley and Black 1982, 1994). The differentiation of the preexisting cellular organelles and the synthesis of new complementary ones occurs during early germination. The endosperm disintegration takes place in late germination and seems to be regulated by the gibberellins produced in the embryo.

LONGEVITY, VIABILITY, AND DORMANCY

The regeneration of plant communities depends on the seeds reaching a suitable place at the right time. They must have an adequate physiological state to germinate and develop seedlings when the opportunity to regenerate or colonize is available. In some cases, the requirements are satisfied by a strategy of germination in which the seeds germinate as soon as they reach the ground; in other cases, the seeds remain for long periods of time in the ground forming seed banks (pioneers or typical of early succession), with part of the population germinating intermittently. Some seeds live a long time in the soil (Murdoch and Ellis 1992). The period of time in which the seed remains viable in the ground is called longevity. Viability is the germinative capacity; its loss is the final stage of seed deterioration. Seed aging produces a gradual declination of many seed capacities such as germination rate, culminating in seed death (Bewley and Black 1994, Murdoch and Ellis 1992). Species from wet tropical forests tend to lose viability rapidly; perhaps 60 to 70 percent lose it in 3 to 6 months. Some species lose viability in days or weeks (Nichols and González 1991).

To survive in the ground, seeds must maintain viability during the time in which germination is inhibited by dormancy or quiescence. Dormancy is the suppression of germination under favorable environmental conditions. An estimated 10 percent of tropical species show dormancy (Nichols and González 1991). Several conditions cause dormancy: the presence of rudimentary embryos or physiologically immature embryos, mechanical resistance or impermeable seedcoats, endogenous growth regulators inhibiting germination, or inadequate storage; some dormancies are the product of multifactorial interactions (Bewley and Black 1994, Bonner and others 1994, Murdoch and Ellis 1992).

Dormancy can be innate or induced. Innate dormancy (primary) prevents the germination of seeds during their development and maturation in the maternal tree and usually some time after dispersal or collection (Karssen 1980/1981). Dormancy is innate external (primary external) when the seedcoat is hard, impermeable to gases or water, or mechanically resistant (e.g., *Ilex*, *Magnolia*, *Enterolobium cyclocarpum*, *Samanea saman*, *Stryphnodendron microstachyum*) (Murdock and Ellis 1992, Werker 1980/1981). This phenomenon also applies to seeds enclosed by a hard, woody pericarp or endocarp. According to Murdoch and Ellis (1992), the hard seeds are innately quiescent and the environment can reinforce the quiescence. When the embryo contains inhibitory substances or it is physiologically immature, the dormancy is innate internal or primary internal (e.g., *Juniperus virginiana*) (Bewley and Black 1994, Bonner and others 1994, Murdoch and Ellis 1992).

The heritability of dormancy is complex because the distinct parts of the seed are genetically different. Innate dormancy varies with both the genotype and the environment at maturation (Fenner 1992). Seeds produced in hot, dry summers are less dormant than those produced in cold, humid summers. Those maturing inside green tissues tend to be more sensitive to light than those in which the chlorophyll decreases in the early stages of maturation (Murdoch and Ellis 1992). The innate dormancy declines before or after dehiscence. This period is called postmaturation dormancy (Murdoch and Ellis 1992).

Induced dormancy (secondary) develops after the dispersal or collection of nondormant seeds or seeds emerging with partial or total primary dormancy (Karssen 1980/1981). Essentially, it reflects no sensitivity to germination inductors, internal or external. The main causes inducing dormancy in buried seeds are the level of humidity, the insufficiency or lack of light and oxygen, the presence of volatile or allelophatic inhibitors, and the high level of CO_2 (anaerobiosis or insufficient air) (Karssen 1980/1981, Murdoch and Ellis 1992). Germination can be inhibited by exposing the seeds to long periods of white light, especially to densities of high radiant flows or far-red light. Dormancy can also be prevented, delayed, or reduced by intermittent light of low intensity (Murdoch and Ellis 1992). Innate dormancy is absent in the recalcitrant seeds of the Tropics.

The induction of primary dormancy while the seed is on the parent tree, or the induction of secondary dormancy in the independent seed, can be complete or relative (partial). In a state of true or complete dormancy, the seed does not germinate under any environmental condition; if the dormancy is partial or relative, germination is restricted to a certain range of environmental conditions (Karssen 1980/1981, Vegis 1964). Seed dormancy is subjected to constant changes; the increasing of dormancy is caused by cyclic changes following a seasonal pattern (Karssen 1980/1981). The dormancy that persists when the seed returns to favorable environmental conditions is reinforced or induced (Roberts 1972a).

The emergence from dormancy is frequently regulated by a promoter-inhibitor system, where the principal promoter is gibberellic acid (GA_3) and the main inhibitor is abscissic acid (ABA). Low levels of inhibitor and high levels of promoter induce germination. According to some studies, it is not possible at present to determine the precise function of ABA in the induction of dormancy (Bewley and Black 1994, Bonner and others 1994).

THE SEEDLING

The term seedling has not been precisely defined and its conceptualization varies among authors. Seedling is defined in this chapter as the youngest stage of the new sporophyte, from radicle protrusion through total liberation of the protective structures and abscission of the cotyledons, until the plant reaches a length of 50 cm. The numerous variations among seedlings of different species and the continuity among the programs of seed development-germination-seedling development in seeds lacking maturation drying make it difficult to establish the limits of this term. The definition provided establishes at least some minimal limits.

SEEDLING AND GERMINATION TYPES

Since Caesalpinius first defined seedling morphology in 1583, many have proposed different ways to classify seedlings. To alleviate confusion, to simplify the classification, and to deal with the numerous variations in tropical seedlings, two types of germination (epigeal and hypogeal) and two types of seedlings (phanerocotylar and cryptocotylar) are used in this chapter. The types of germination refer to the process of germination

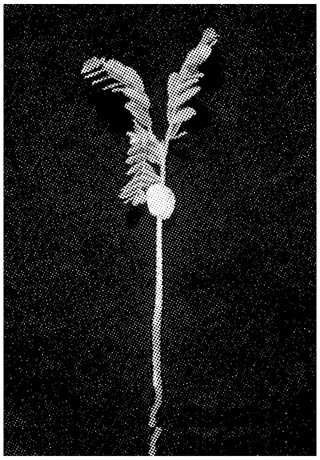


Fig. 122.

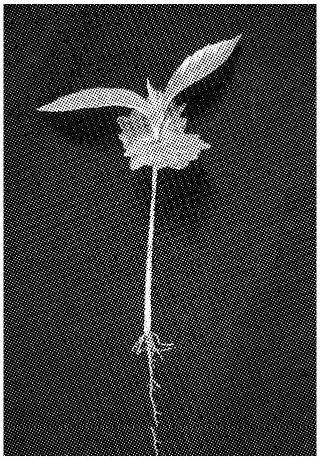


Fig. 124.

Fig. 123.

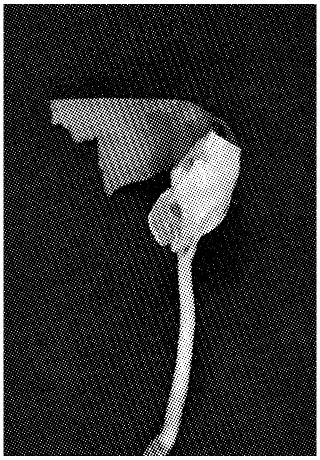


Fig. 125.

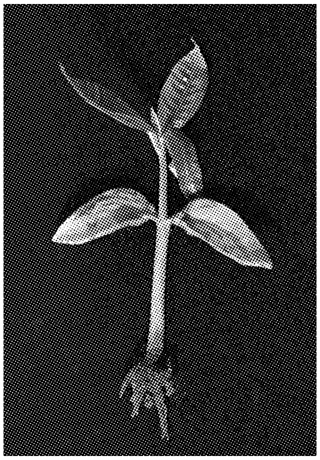


Fig. 126.

while the seedling types emphasize cotyledon location.

Many seedlings have epigeal germination. The cotyledons (free or inside the seed, seed plus endocarp, or seed plus pericarp) and the cotyledonar node are affected by the distance to the soil level due to hypocotyl development. In hypogeal germination, the cotyledons and the cotyledonar node remain on the soil level, partially or totally immersed but seldom buried. The hypocotyl is very small or vestigial, sometimes not observable. In most cases, the cotyledons remain inside the seed. This type of germination is common in tropical trees and frequent in large, recalcitrant seeds.

In the phanerocotylar seedling the cotyledons are outside the seedcoat. The cotyledons are free. In the cryptocotylar seedling, the cotyledons remain enclosed in the seedcoat (or seedcoat plus endocarp, or seedcoat plus pericarp). It does not matter whether they are large or small, storing or haustorial, free or fused, etc. This classification allows a combination of germination and seedling types.

Epigeal germination-phanerocotylar seedling—Examples include the seeds and seedlings of the following species: *Acacia, Adenanthera, Albizia, Cassia grandis, Dipteryx, Diphysa, Enterolobium, Erythrina, Gliricidia, Haematoxylum, Hymenaea courbaril, Hymenolobium, Parkia, Parkinsonia, Pterocarpus, Samanea saman, Sclerolobium, Tamarindus, Vatairea, Ormosia velutina, Stryphnodendron, Casuarina, Annona, Cymbopetalum, Mollinedia, Bernoullia, Cordia alliodora, Laetia, Psychotria, Simira maxonii, Palicourea, Guettarda, Genipa americana, Myrcia, Stemmadenia, Tetrapteryx, Vochysia, Qualea, Hyeronima, Capparis, Terminalia amazonia, T. oblonga, Guajacum sanctum, Cedrela, Melia, Zizyphus, Meliosma, Anacardium excelsum, Crescentia, Tabebuia, Jacaranda, Ulmus, Ilex, Casearia, Homalium, Rapanea, Dendropanax, Elaeocarpus, Vitex, Couratari, Couroupita,* and *Cariniana* (figs. 122-126). *Calatola costaricensis* (Icacinaceae) presents a problem of ubication. The germination is epigeal, but initially the plumule remains enclosed within the seedcoat plus the endocarp. Later, the endocarp splits along two fissures and the two valves are dropped. The plumule continues its development inside the papyraceous seedcoat and continuously absorbs nutrients from the endosperm. The seedcoat remains intact until it explodes under the pressure of the expanding plumule. The plumule is several centimeters

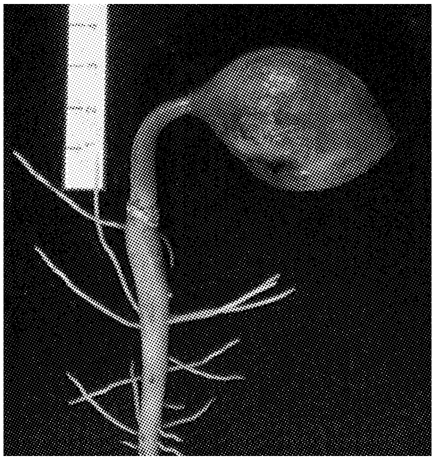


Fig. 127.

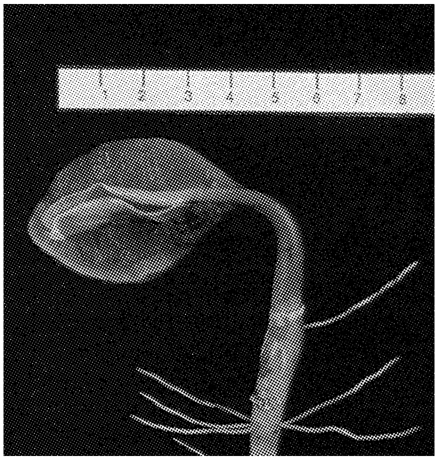


Fig. 128.

Fig. 129.

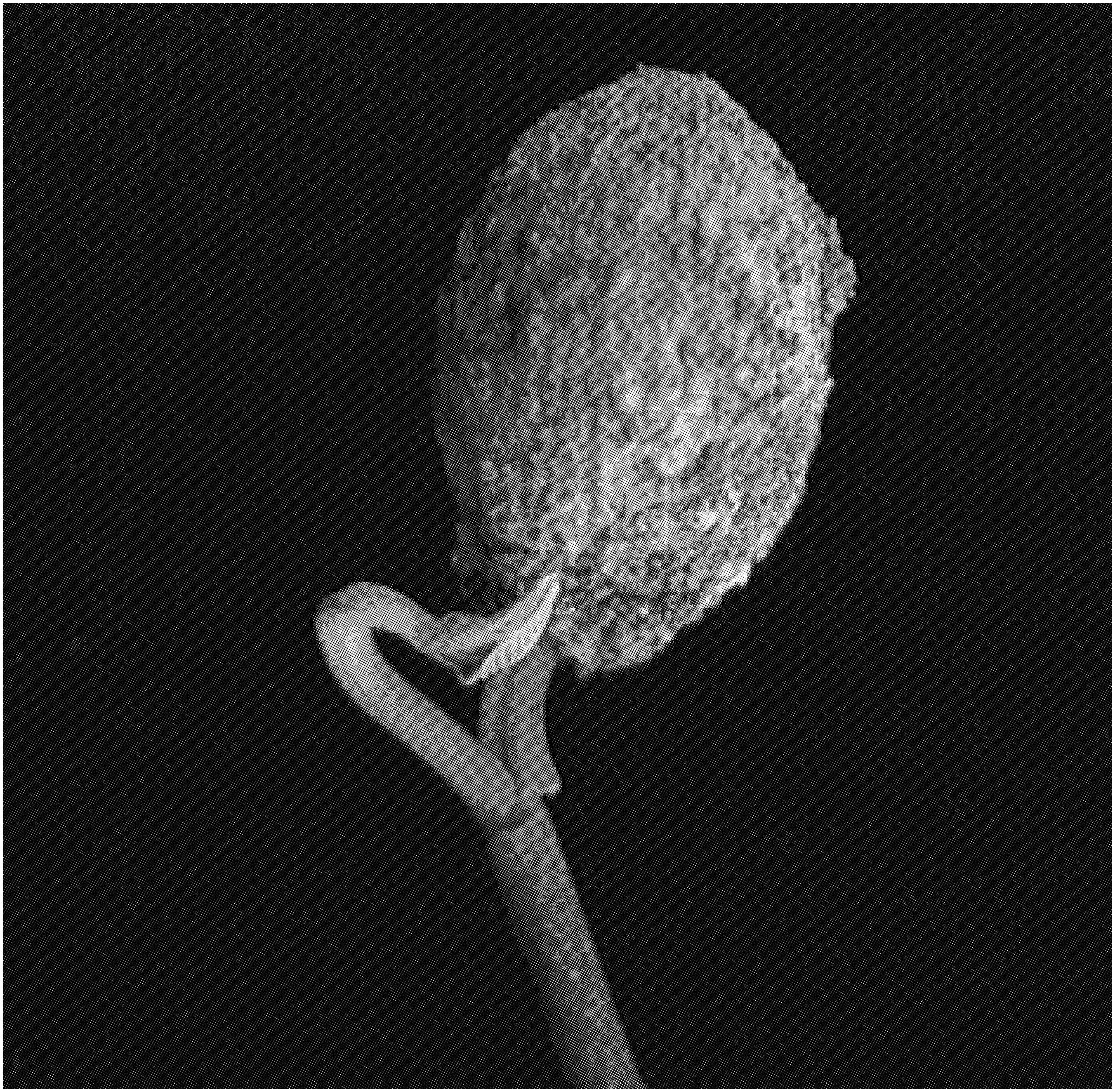
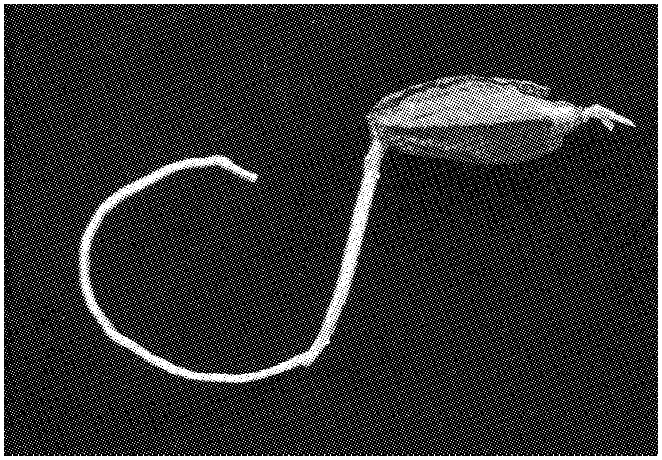


Fig. 131.

Fig. 130.

Fig. 132.



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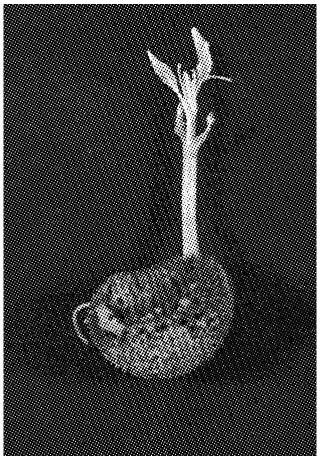


Fig. 134.

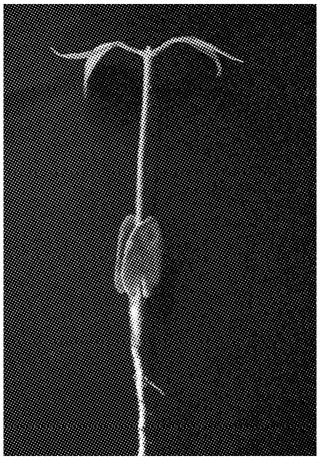
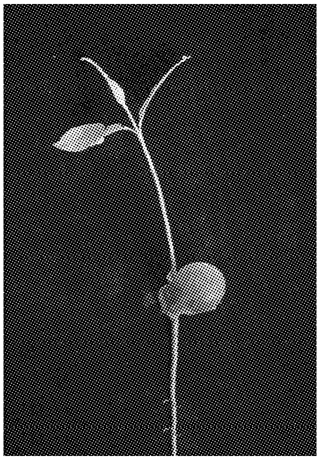


Fig. 135.

long and has a pair of large, green cotyledons and several young, developing leaves (figs. 127-129).

Epigeal germination-cryptocotylar seedling—Examples include *Virola, Otoba, Minquartia guianensis, Ximenia, Hura, Faramea, Omphalea, Sterculia apetala,* and *Durio* (figs. 130-132).

Hypogeal germination-phanerocotylar seedling—Examples are: *Allantoma, Lecythis, Barringtonia, Eschweilera, Grias, Bertholletia, Careya,* and *Corythophora* (the hypocotyl remains inside the seedcoat; the cotyledons are two free cataphylls), *Inga,* (destroyed sarcotesta), *Garcinia* (reduced, free cotyledons, sometimes seen as fleshy warts), and *Caryocar* (cotyledons free, scaly) (figs. 133-135).



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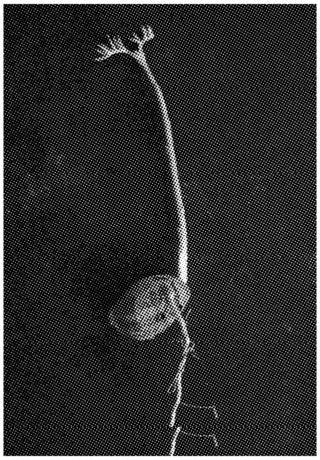

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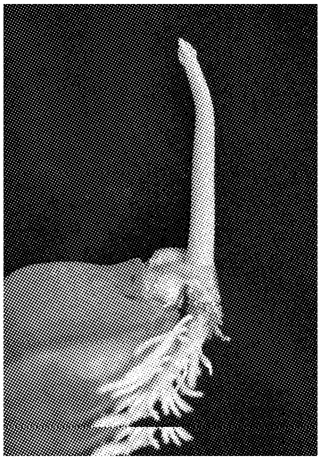


Fig. 139.

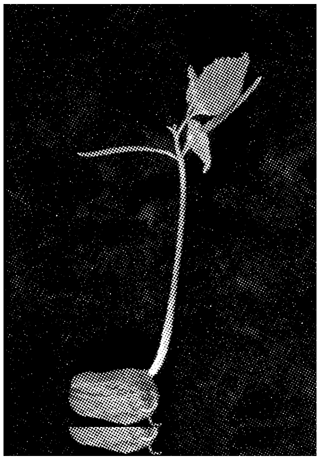


Fig. 140.

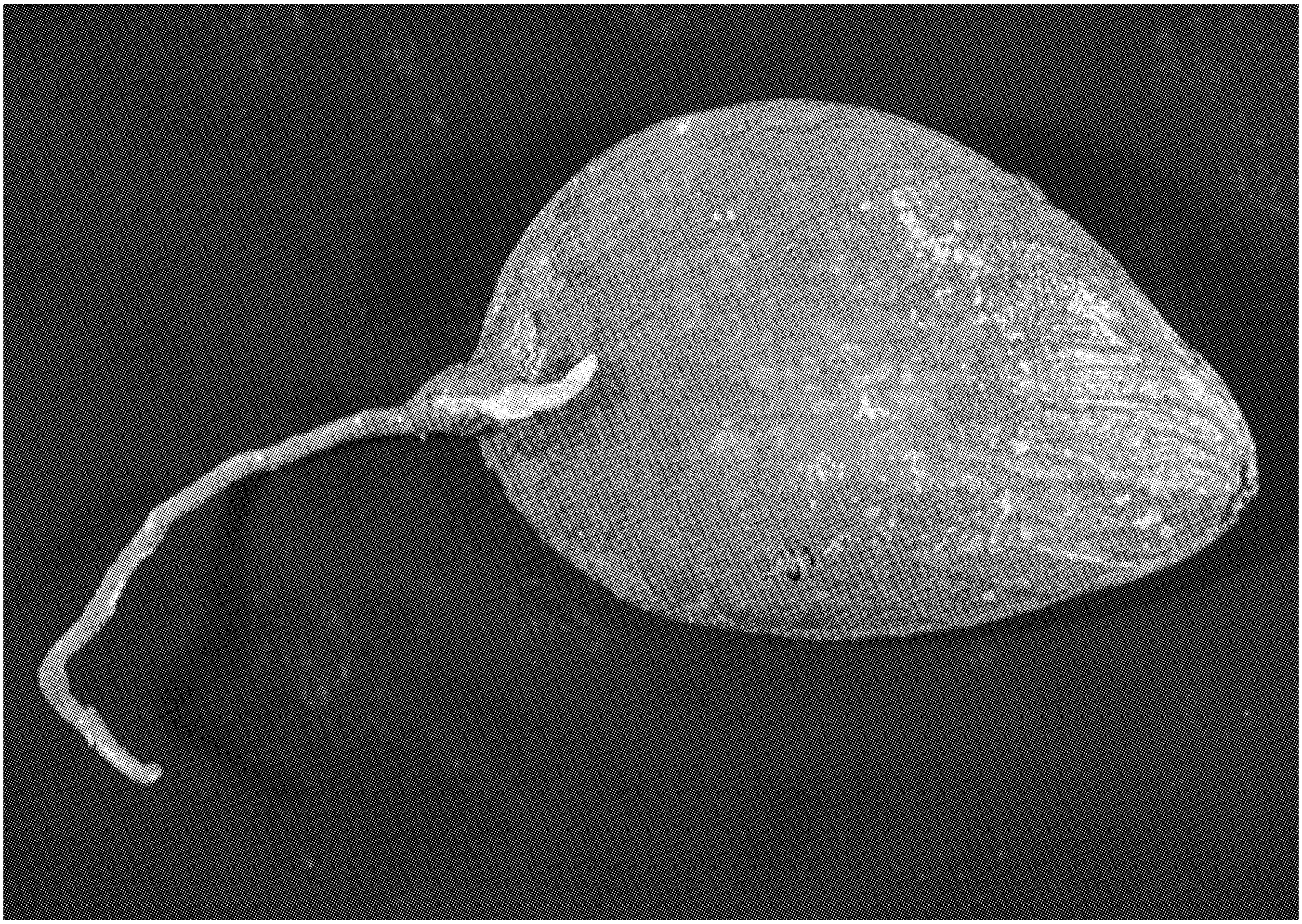
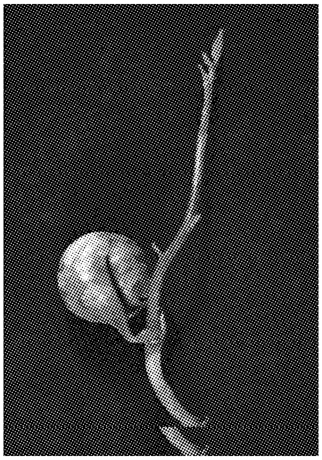


Fig. 138.

Hypogeal germination-cryptocotylar seedling—Examples are *Calophyllum, Andira, Cynometra, Cojoba, Sophora, Spondias, Prioria, Mora oleifera, Myroxylon, Swartzia, Pentaclethra, Ocotea, Licaria, Nectandra, Persea, Swietenia, Carapa, Guarea, Trichilia, Brosimum, Poulsenia, Pseudolmedia, Mappia, Cupania, Gustavia, Eugenia, Syzygium, Lacmellea, Hernandia, Rourea, Hirtella, Chrysobalanus, Licania, Parinari, Prunus, Pachira aquatica, Sapindus saponaria, Melicoccus, Nephelium, Quararibea, Cavanillesia, Terminalia catappa, Pouteria, Quercus, Gynocaryum, Oreomunnea,* and *Alfaroa* (figs. 136-146).



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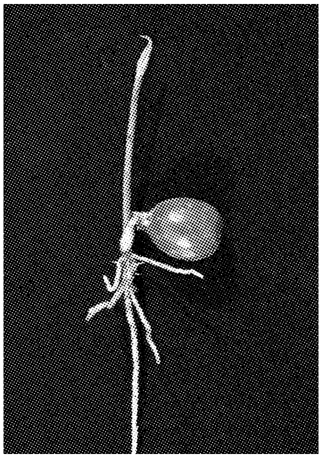

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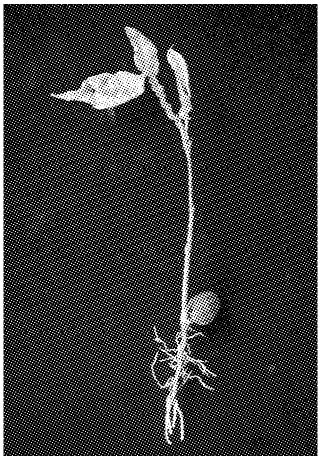

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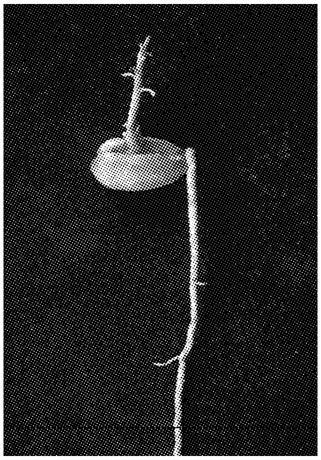

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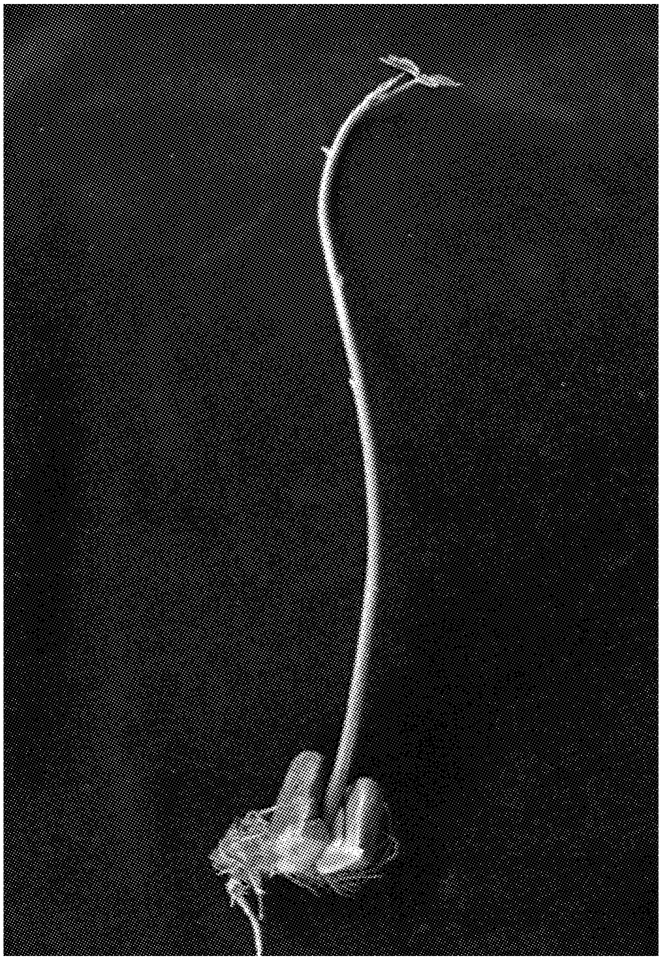

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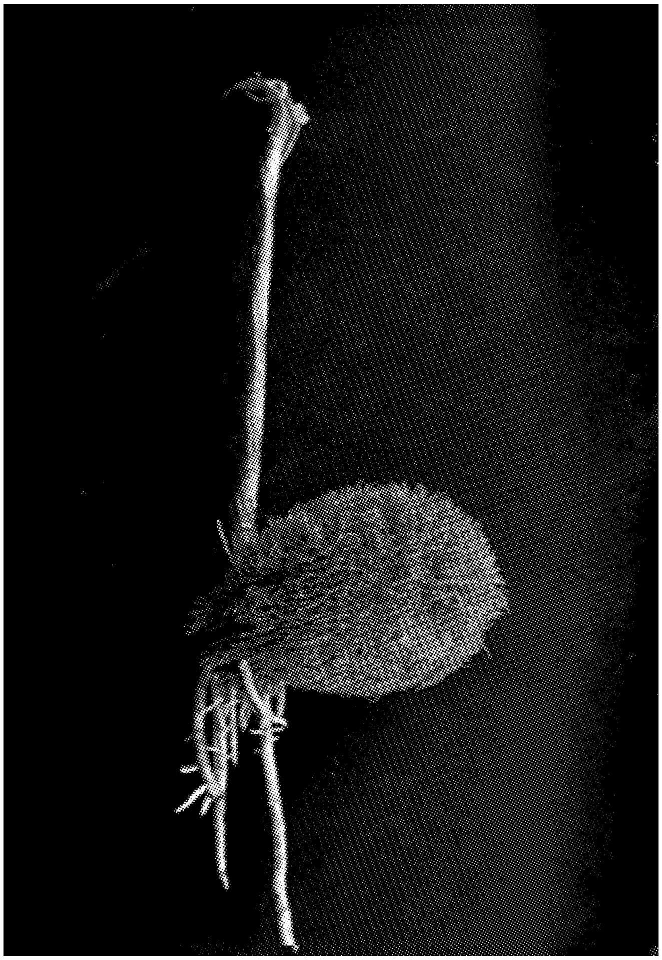

Fig. 143.

SEEDLING STRUCTURE

The seedling is formed by the root (radicle in the embryo); the hypocotyl; one, two, or several cotyledons (embryonic leaves); the epicotyl; and the leaves arising at the nodes of the epicotyl. The plumule, a term frequently used, is the embryonic shoot of the embryo or seedling, located above the cotyledonar node (Flores 1999). It includes the incipient epicotyl, the foliar primordia, and the apical meristem. Figures 147 through 151 show the structure of the seedlings in different species.

Root

The radicle of the embryo can be oriented facing the hilum (syntropous) or in the opposite direction (antitropous). In most seeds the radicle emerges through the micropyle; in some, the embryo pushes the seedcoat, fragments it, and protrudes through it at a specific point. This point or opening is called the operculum, embryostega, or plug (Flores 1999). Opercula vary in ontogeny, structure, and opening mechanism. Opercula are formed by the micropylar and hilar regions, by the exostome and endostome, or by only the endostome. The operculum is more common in monocotyledons (Boesewinkel and Bouman 1984, Jacobson 1984).

In numerous species, root emergence is more complicated because it requires going through the tissues of the seedcoat, the fruit, or the diaspore. This phenomenon is frequent in legumes with winged diaspores (*Hymenolobium mesoamericanum*, *Sclerolobium*, *Myroxylon balsamum*, *Myrospermum frutescens*, *Pterocarpus hayesii*, *P. officinalis* Jacq.), indehiscent fruits with hard pericarp (*Andira inermis*, *Prioria copaifera*), drupes with a woody endocarp enclosing the seed(s) as a physical barrier (*Dipteryx panamensis*, *Calatola costaricensis*, *Minquartia guianensis*, *Caryocar costaricense*, *Licania platypus*), and diaspores in which the perianth pieces are hard and enveloping (*Oreomunnea*, *Dipterocarpus*).

In some seeds, root protrusion coincides with the liberation of characteristic odors and, sometimes, a change in seedcoat color. The seedcoat of *Balizia elegans* (Fabaceae-Mimosoideae) is peculiar because it changes from the original greenish color to purplish on the lateral surfaces as soon as the seed is imbibed, and also exudes a strong sulphur odor. The seedcoat of *Schizolobium parahyba* (Fabaceae-Caesalpinioideae) liberates tannins when root protrusion starts. In *Stryphnodendron microstachyum* and *Abarema adenophora*, the root leaches sulfuring substances, liberating a strong odor. The root of *Abarema adenophora* has nodules a few days after root protrusion.

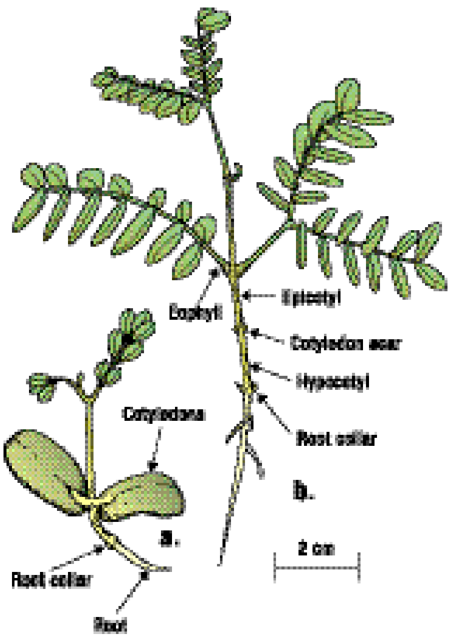

Fig. 147. *Stryphnodendron microstachyum* seedlings.

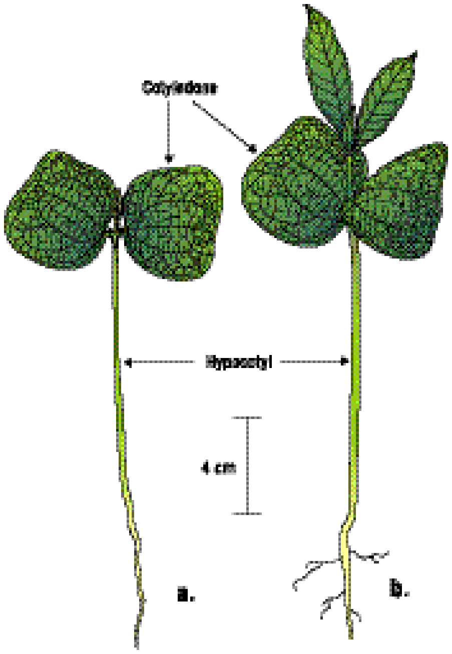

Fig. 148. *Vochysia guatemalensis* seedlings.

The root is the organ that supports (anchors) the seedling and absorbs, conducts, and sometimes stores water and nutrients. Allorhizy is the process through which the seedling develops an embryonic root (radicle) as a pivotant or typical root. The first root is called the primary root. In the dicotyledons and the gymnosperms this root penetrates directly into the soil and gives rise to the secondary or lateral roots. The older roots are found near the root collar (zone of transition hypocotyl-root) (fig. 147). When a primary root is missing and the main root is adventitious, as happens in the pteridophytes, the seedling has primary homorhizy. In the monocotyledons and some dicotyledons, the primary root dies in early stages and the radical system is formed by adventitious roots forming a fibrous or fascicled root system in which no root dominates (secondary homorhizy). Typically, primary roots penetrate deeper in the soil than fibrous roots. Nevertheless, the superficiality of the fibrous roots and the toughness with which they adhere to the soil particles enable them to reduce soil erosion (Flores 1994b).

The root has several zones of growth–meristem or quiescent center, zone of cell division, region of elongation, and region of maturation. The radical hairs form in the maturation zone and their development can be inhibited by very wet or dry soils. The number of radical hairs varies among species and

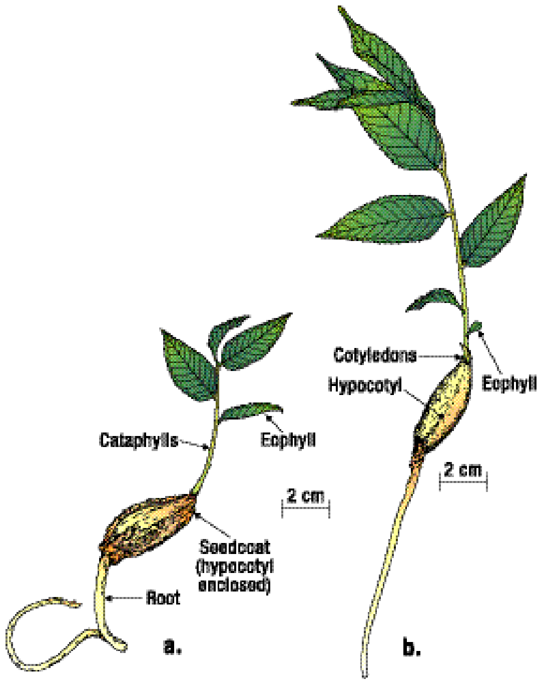

Fig. 151. *Lecythis ampla* seedlings.

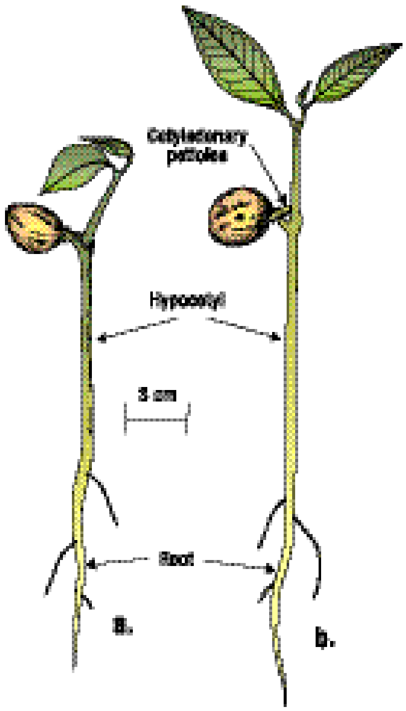

Fig. 149. *Virola koschnyi* seedlings.

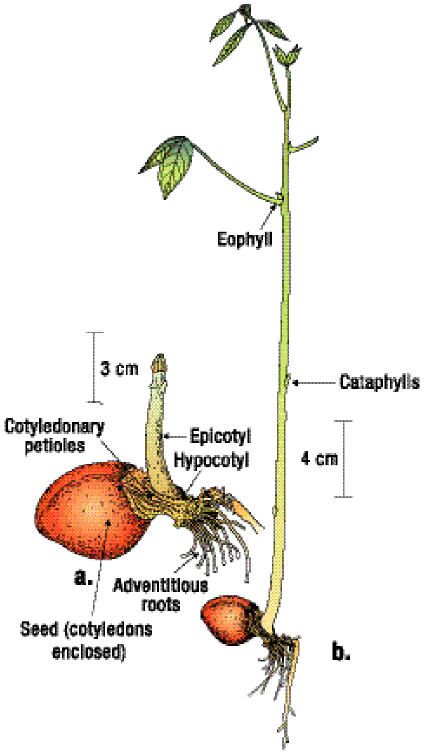

Fig. 150. *Carapa guianensis* seedlings.

they can be absent in groups such as the Lauraceae (*Ocotea, Nectandra, Persea*) and Olacaceae (*Minquartia guianensis*) (Flores 1994b, 1994e). They have a short life, but in some woody species they may suberize or lignify, persisting for months or years (Kramer and Kozlowski 1979). The center for the perception of gravity seems to be located in the root cap.

The extension of a radical system (depth and lateral extension) depends on factors such as humidity, temperature, and soil composition. Most absorbent roots are localized in the first meter of depth (juvenile forms and adults) and condensed in the upper 15 cm, which usually coincides with the richest organic matter. The lateral extension of the radical system usually coincides with that of the aerial system (Flores 1999).

During growth, the balance between photosynthates (manufactured substances) and the water and minerals being absorbed by the roots is essential. During seedling establishment, the total of water and minerals absorbed generally exceeds that of the photosynthates produced. The balance is gradually reached with age, but transplanting seedlings always alters this process. The thinnest absorbing roots break when the plant is removed from the soil; pruning contributes to reestablishing the balance of shoot to root. Fungi, bacteria, and insects that attack the shoot or the root may also affect the balance between the shoot and the root (Flores 1994b, 1999).

Approximately 90 percent of the trees and, in general, the higher vascular plants, are associated with soil fungi (mycorrhizas). They have a symbiotic relationship. The two main categories established are the ectomicorrhizas and endomycorrhizas, which are based on the morphology of the mycorrhiza and the fungus involved. Seedlings lacking mycorrhizas grow slower and are frequently feeble. The mycorrhizic fungi with their extramatricial hyphae increase the survival and growth of the seedlings; the hyphae increase the area of root absorption for the intake of water and soil elements such as P, Cu, and Zn (especially P). The surface covered by the hyphae goes farther than that covered by the radical hairs. The mycorrhizic associations also protect against pathogens (Harley and Smith 1983, Perry and Amaranthus 1990). Seedlings with few radical hairs are highly dependent on mycorrhizas. Seedlings bearing mycorrhizas are also more tolerant to heavy toxic metals, pathogens attacking the roots, dryness, high soil temperatures, saline soils, adverse pH, and transplant. Frequently, species growing in marshes do not have mycorrhizas but when they grow in noninundated soil the mycorrhizic association becomes indispensable. The mycorrhizic rhizosphere is rich in bacteria, diatoms, and other fungi (Azcon and Barea 1980, Englander 1982, Flores 1999, Schenck 1982).

Mycorrhizic fungi depend on zoochorous dispersal. Animals may ingest sporocarps willingly or unwillingly, transporting the spores (Cazares and Trappe 1994, Cork and Kenagy 1989, Kotter and Farentinos 1984, Reddell and others 1997, Trappe 1988, Trappe and Schenck 1982). The ingested spores maintain their viability through the digestive tracts of invertebrate and vertebrate vectors (Reddell and Spain 1991, Reddell and others 1997). Some propose that the spores' passage through the digestive tracts of mammals promotes germination (Claridge and others 1992, Lamont and others 1985). The sporocarps of diverse fungi are also part of the diet of numerous local fauna (Reddell and others 1997).

Other root associations common in the Tropics, and especially in legumes of the subfamilies Papilionoideae and Mimosoideae, are those established with nitrogen-fixing bacteria (bacterial nodules). The most common bacteria involved in root nodulation is *Rhizobium*. The bacterial symbiosis permits the fixation of atmospheric N and its conversion to ammonium, a soluble form of N that is easy to use and important for increasing forest productivity (National Research Council 1979). Numerous tree legumes have bacterial nodules, for example: *Abarema, Abrus, Acacia, Afzelia, Albizia, Anadenanthera, Andira, Baphia, Cedrelinga, Centrosema, Cojoba, Dalbergia, Detarium, Dialium, Dipteryx, Enterolobium Erythrina, Gliricidia, Indigofera, Inga, Lonchocarpus, Machaerium, Parkia, Pentaclethra, Piptadenia, Pithecellobium, Prosopis, Pterocarpus, Sclerolobium, Stryphnodendron, Swartzia, Tephrosia*, and *Platymiscium* (Flores 1994b, Kirkbride 1984, Okigbo 1984). The presence of bacterial nodules has also been documented for *Alnus, Coriaria, Elaeagnus, Hippophaë, Shepherdia, Comptonia,* and *Purshia* (Allen and Allen 1965). Some gymnosperms, such as *Podocarpus* (Burger 1972), *Libocedrus, Agathis,* and *Araucaria* (Kozlowski 1971), also have bacterial nodules.

Some semiparasitic species such as *Ximenia* (Olacaceae) have haustorial roots (Heckel 1898) and some evidence exists of the parasitic behavior of the roots of *Minquartia guianensis* (Olacaceae) (Flores 1994e).

Hypocotyl

The hypocotyl is the part of the seedling axis that extends from the cotyledonar node downward to the root collar. The latter can be conspicuous or inconspicuous. Morphologically, it is the zone of transition between the root (with a radial distribution of alternating bundles of xylem and phloem) and the epicotyl, with vascular bundles formed by xylem and phloem (Compton 1912, Eames 1961).

In the species with epigeal germination (phanerocotylar or cryptocotylar seedlings), the hypocotyl is well developed and its thickness, color, and indumentum distinguish it from the root when the collar root is not conspicuous (figs. 125, and 131). The seedlings with hypogeal germination (and phanerocotylar or cryptocotylar seedlings) usually have a small or vestigial hypocotyl (*Calophyllum*, *Carapa*, *Cojoba*, *Pentaclethra*, *Quercus*, *Swietenia*) that is barely observable (figs. 136, and 139). In several cases, the hypocotyl is a massive, storing organ, occupying the interior of the seed almost completely and remaining in the seed during germination. It remains hidden for weeks or months, thickens and enlarges slowly, and finally breaks the surrounding seedcoat or seedcoat and endocarp (*Eschweilera*, *Lecythis*, *Caryocar*). This last type of seed is recognized because the root and the epicotyl emerge at opposite ends of the seed. Frequently, these seeds produce one or several adventitious roots at the epicotyl base or near the cotyledonar node. *Garcinia* and other Clusiaceae illustrate this kind of seedling development. However, *Calophyllum* (Clusiaceae) differs from this pattern. In this species, the cotyledons are fused in the distal three-quarters and seedling development follows the hypogeal-cryptocotylar pattern instead of the hypogeal-phanerocotylar pattern followed by other Clusiaceae.

Epicotyl

The epicotyl is the part of the seedling axis that is distal to the cotyledons (above the cotyledonar node). It develops from the activity of the apical meristem. It is well developed in many seeds of Fabaceae, Fagaceae, and other families. Usually, it is easily distinguished after germination and differs from the hypocotyl in thickness, texture, and color.

Foliar Succession in the Shoot

Plants have four types of leaves: cotyledons, protophylls, metaphylls, and prophylls.

Cotyledons

The first leaf (or leaves) of the plant are the cotyledons. The most common condition is dicotyly, present in dicotyledons and some gymnosperms. Polycotyly (three or more cotyledons), syncotyly (gamocotyly or cotyledons partly or totally fused), schizocotyly (cotyledon division), pseudomonocotyly (false monocotyly due to cotyledonar fusion), monocotyly (one cotyledon), and anisocotyly (cotyledons of different sizes) represent the extremes of modification of the simple dicotyly (Duke 1965, 1969; Eames 1961). Polycotyly is quite common. *Acer*, *Juglans*, and *Coffea* frequently present three cotyledons (Duke 1969, Eames 1961). Numerous gymnosperms present the same phenomenon [e.g., *Tsuga* (2 to 7), *Abies* (2 to 10), *Pseudotsuga* (4 to 12), and *Pinus* (3 to 18)] (Chowdhury 1962). *Qualea paraensis* (Vochysiaceae) may present three or four cotyledons in some seedlings. Syncotyly is also common. For example, *Calophyllum*, *Swietenia*, *Guarea*, and *Carapa* have cotyledons fused distally. If the fusion is less than half the cotyledon length, they are called hemisyncotylous or amphisyncotylous. The presence of unequal cotyledons (anisocotyly) is frequent in such diverse seeds as those of *Calophyllum*, *Peperomia*, *Brosimum*, and other legumes.

Syncotyly is one of the primary causes impeding cotyledon emergence during the germination of seeds enclosed in hard seedcoats, fruits with hard endocarps, or diaspores with other tissues attached. In these seeds the emergence of the epicotyl requires intercalary growth at the base of the cotyledons, leading to petiole formation. The elongation of the cotyledonary petioles displaces the cotyledonar node outside the seedcoat. Once outside, those petioles open backwards. Their concave adaxial surfaces provide space for the development of the plumule enclosed at the cotyledonary node base. In species that are syncotylous, with hypogeal germination and a cryptocotylar seedling, the cotyledonary petioles are thick, sometimes short, woody or corky, and have a different color, but they are always adaxially channeled (figs. 136 and 139). If the germination is epigeal and the seedling is cryptocotylar, those petioles are longer, flexible, and with a softer texture (figs. 130-132). In some groups, the cotyledons have lobules. Sometimes the lobules are so deep that they suggest a possible schizocotyly.

Form, size, and thickness of cotyledons vary widely. Terms to describe cotyledon form include linear, reniform (*Hymenolobium*), cordate or auriculate (Bignoniaceae), elliptic (*Guaiacum*), lanceolate (*Annona*), obovate (*Casuarina*), oblong (*Erythroxylum*), scaly (cataphylls, *Lecythis*), trifoliate (*Bursera simaruba*), and oblong and planoconvex (*Dipteryx*). Many cotyledons have a petiole, but others are sessile or semisessile.

De Vogel (1980) proposed three types of cotyledons from a functional point of view: storing, haustorial, and photosynthetic during germination. Numerous cotyledosperm seeds have large, fleshy cotyledons, rich in stored reserves (e.g., *Anacardium*, *Aspidosperma*, *Brosimum*, *Calophyllum*, *Carapa*, *Cojoba*, *Dipteryx*, *Enterolobium*, *Guarea*, *Hymenaea*, *Hymenolobium*, *Mangifera*, *Manilkara*, *Nectandra*, *Ocotea*, *Pachira*, *Pentaclethra*, *Persea*, *Prioria*, *Quercus*, and *Sclerolobium*). In many cases, the embryo stores nutrients in the cotyledons and the hypocotyl and the whole embryo is thick and fleshy.

The existence of *haustorial cotyledons* associated to hypogeal germination (cryptocotylar seedlings) was well documented by Heckel (1898), who describes the germination of *Ximenia americana* (Olacaceae). This type of cotyledon is present in many families (Celastraceae, Olacaceae, Myristicaceae). In *Myristica*, *Virola*, and *Otoba*, the rudimentary embryo develops divergent cotyledonar blades that are large, very thin, and highly vascularized (Flores and Rivera 1989a; Flores 1992c, 1999). The vascular bundles have numerous transfer cells for rapid transport. In *Compsoneura*, the cotyledons are haustorial but their structure is more complex. The Olacaceae (*Ximenia*

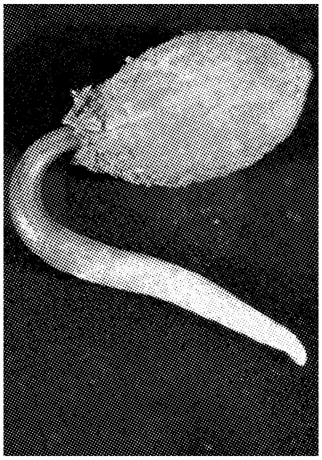

Fig. 154.

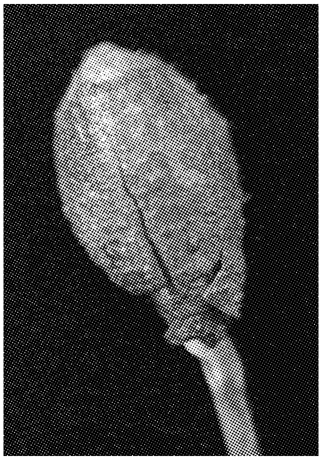

Fig. 155.

Fig. 156.

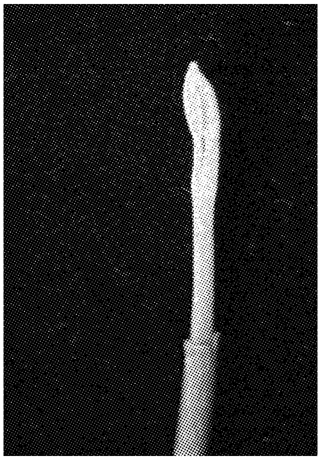

Fig. 158.

americana, Minquartia guianensis) have minute embryos which develop haustorial cotyledons with a large blade, well vascularized and usually colored pink or violaceous (figs. 154-158).

Green cotyledons are common in many seeds (Dahlgren 1980, Janzen 1982, Yakolev and Zhukova 1980). Janzen (1982) found in his study of 74 species in the dry tropical forest of Costa Rica that 55 percent of the developing embryos from trees, shrubs, and herbs were chlorophyllous. The cotyledons, the radicle, and the hypocotyl were green. The seedcoats were white and transparent and the fruit pericarp was green. In seeds with maturation drying and dormancy, the embryos became nonchlorophyllous at the end of the maturation period. Janzen (1982) suggests that the chlorophyllous stage is important in embryo development and adds several variables to the complex interaction of fruit to seed(s), because fruit and seed form are selected to increase the exposure of the embryo to sunlight. *Astronium graveolens*, *Bursera simaruba*, *Terminalia oblonga*, *Ateleia herbert-smithii*, *Enterolobium cyclocarpum*, *Samanea saman*, *Gliricidia sepium*, *Haematoxylum basiletto* H. Karst., *Piscidia carthagenensis*, *Licania arborea*, *Calycophyllum candidissimum*, and *Simarouba glauca* DC. are examples of trees that have seeds with chlorophyllous embryos. In some species (e.g., *Inga*, *Dipteryx*), the embryos with fleshy cotyledons are green during germination. In others, foliaceous cotyledons become chlorophyllous when germination begins. In many cases they increase in size (e.g., *Vochysia* , *Qualea*, *Simira maxonii*) (figs. 112 and 132). In *Pentaclethra macroloba* (hypogeal germination-cryptocotylar seedling), the cotyledons break the seedcoat and open like valves. The seedcoat remains attached to the abaxial surface of the cotyledons but the adaxial turns green and photosynthetic. These cotyledons have two functions: storage and production of photosynthates. When they assume the photosynthetic function, the cotyledons increase in size, change in texture, and develop stomata at the distal end of the cotyledon blade (Flores and Rivera 1989a). *Simira maxonii* (Rubiaceae) shows a different pattern. The embryo is spatulate and whitish, but when germination starts, the cotyledonar blade extends and turns green. As the cotyledonar blade expansion progresses, they begin to corrugate because the seedcoat limits their extension. Finally, the pressure they exert on the seedcoat causes it to break and the cotyledons become free (figs. 152-153).

Fig. 152.

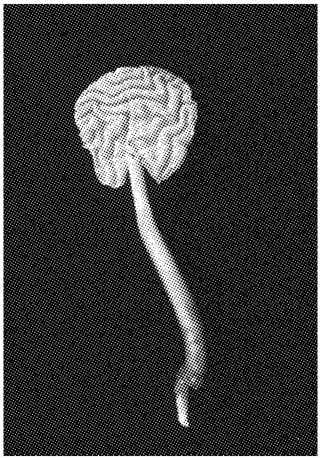

Fig. 153.

In most species, the cotyledonar buds may develop if the epicotyl is damaged by herbivory or other factors. This phenomenon is frequent in Meliaceae (*Carapa*, *Guarea*), Fabaceae (*Cojoba*, *Pentaclethra*), and Fagaceae (*Quercus*). However, some species have more than a single axillary bud (e.g., *Swietenia*, *Carapa*, and *Pentaclethra macroloba*). The cotyledon axils and the leaves of *P. macroloba* have descendent series of accessory buds, which develop in a predetermined order to generate a shoot that assumes apical dominance (Flores and Rivera 1989b). These buds have ecological significance because they guarantee a high rate of seedling survival even in the limiting conditions imposed by predation and other factors in the low strata of the forest.

A peculiar case requiring further research is the capacity of the cotyledons of *Gustavia superba* (Lecythidaceae) to regenerate (Harms and others 1997). The cotyledons removed from

Fig. 157.

young seedlings were able to regenerate root and shoot. This capacity represents an advantage for the species because rodents predate the fruits and seeds and the seedlings, like most Lecythdaceae seedlings, are exposed to a high rate of herbivory on the forest floor.

Protophylls

These are the juvenile leaves of the plant. In seedlings, they are called cataphylls, or eophylls.

Cataphylls—This term, derived from the Greek *cataphyllum*, means the lower leaves. The cataphylls are the inferior leaves, between the cotyledons and the eophylls. They are reduced forms, simpler than the metaphylls and, in general, are squamiform, membranaceous, hyaline or coriaceous, and brown. Usually, they lack chlorophyll. The scales of the invernating buds or perules, as well as those of the subterranean stems, are also called cataphylls (Font Quer 1977). Cataphylls are frequently found in the epicotyl of many plants (e.g., *Carapa*, *Swietenia*, *Pentaclethra*, *Lecythis*, *Eschweilera*, *Calophyllum*, *Pseudolmedia,* and *Mappia*). Their size, shape, and structural complexity usually increase along the axis in an acropetal direction. In many species they drop off early in the plant's development.

Eophylls—The term means precocious or juvenile leaves. Tomlinson (1960) defined eophylls as the first leaves with a green and expanded blade. In many seedlings, one or several cataphylls precede the eophylls. Families such as the Anacardiaceae, Bignoniaceae, Fabaceae (Caesalpinioideae, Mimosoideae, Papilionoideae), Meliaceae, and Sapindaceae have seedlings with a transitional series of leaves between the eophylls and the metaphylls. The variation (heterophylly) in the series can be constant or can vary among seedlings of the same species. Abrupt change and lack of seriation is typical in species such as *Guajacum sanctum* (Zygophyllaceae). The seedlings of this species and *Hymenolobium mesoamericanum* (Fabaceae-Papilionoideae) have paripinnate eophylls, similar to the metaphylls (Duke 1969). Certain other species, such as *Bursera simaruba*, have trifoliate cotyledons, simple eophylls, and complex metaphylls. Still others, such as *Tilia,* have lobed cotyledons followed by eophylls and metaphylls with simple blades (Duke 1969). Some seedlings have eophylls that are more dentate or lacerate than the metaphylls (*Cordia*, *Casearia*, *Hasseltia*, *Poulsenia*, *Quercus*, and *Rapanea*).

Metaphylls

These are the typical leaves of the adult plant, usually morphologically different from protophylls. The typical leaf has a blade or limb, a foot or petiole, and a foliar base. The petiole can be missing (sessile leaf) or can be short and reduced (semisessile leaf). The petiole participates in the transport of substances, supports the foliar blade, and situates it in a position favorable to receiving sunlight. In several species the blade does not develop and the petiole may bear thorns, creeping organs, or tendrils. In some species, laminar petioles (phyllodes) substitute for the foliar blade. *Acacia heterophylla* and *A. mangium* Willd. show a series of transitions from leaf to phyllode.

Leaves can be simple or compound. In simple leaves, the blade does not divide into minor units. In compound leaves, the blade divides into folioles or pinnae (fig. 159). The foliar blade varies in size, form, texture, and other characteristics. Shapes range from linear to circular, with a great richness of variation in blade, margin, base, and apex (figs. 160-163). Families such as the Casuarinaceae (*Allocasuarina*, *Casuarina*) have whorled metaphylls, gamophyllous (congenital concrescence), reduced, and scaly. The gymnosperms have several types. The best known is the acicule (needle) typical of *Pinus*. In other gymnosperms the leaves are larger and have different shapes. The Podocarpaceae have lanceolate, linear, or oval leaves. The cycads have pinnate leaves; *Bowenia* have bipinnate, and those of *Ginkgo biloba* are fan-shaped.

In compound leaves, the folioles or pinnae may grow from a central point, as in *Tabebuia* or *Ceiba*, forming palmate-compound leaves; if they arise in pairs along a rachis, as in *Spondias*, *Simarouba*, *Enterolobium*, and *Samanea saman*, the leaf is pinnate-compound. The leaf with a terminal pinna is imparipinnate; if a terminal pinna is missing, the leaf is paripinnate. When the compound leaf has more complex subdivisions, the secondary axes arising at the rachis are called rachillae and the small foliar blades are called foliolules or pinnules. The folioles or pinnules can be sessile, semisessile, or have a petiolule. In the petiole base a basal thickening called pulvinus can be found; the petiolule can have a pulvinulus. In some species, the petiole has a double pulvinus (e.g., *Sloanea*, Elaeocarpaceae). The petiolule can have double pulvinuli as in *Protium* (Burseraceae). The pulvini and pulvinuli are common in Fabaceae and are related to nyctinasty (Satter and Galston 1981; Satter and others 1997; Satter and others 1981; Simon and others 1976a, 1976b).

The texture or consistency of the leaf blade can be cartilaginous (hard, tough, flexible), crustaceous (hard, thin, brittle), coriaceous (hard, thick, leathery), chartaceous (papery, opaque, thin), membranous (thin, semitranslucent, membrane-like), or hyaline (thin, translucid). Some cotyledons and leaves lack trichomes and are called glabrous; others have indument or vestiture. Those with trichomes can be pubescent (hairs or trichomes short and soft), pilose (soft, shaggy trichomes), puberulent (minutely pubescent, like dust), velutinous (dense, straight, long and soft trichomes), floccose (dense, appressed trichomes in patches or tufts), hirsute (long,

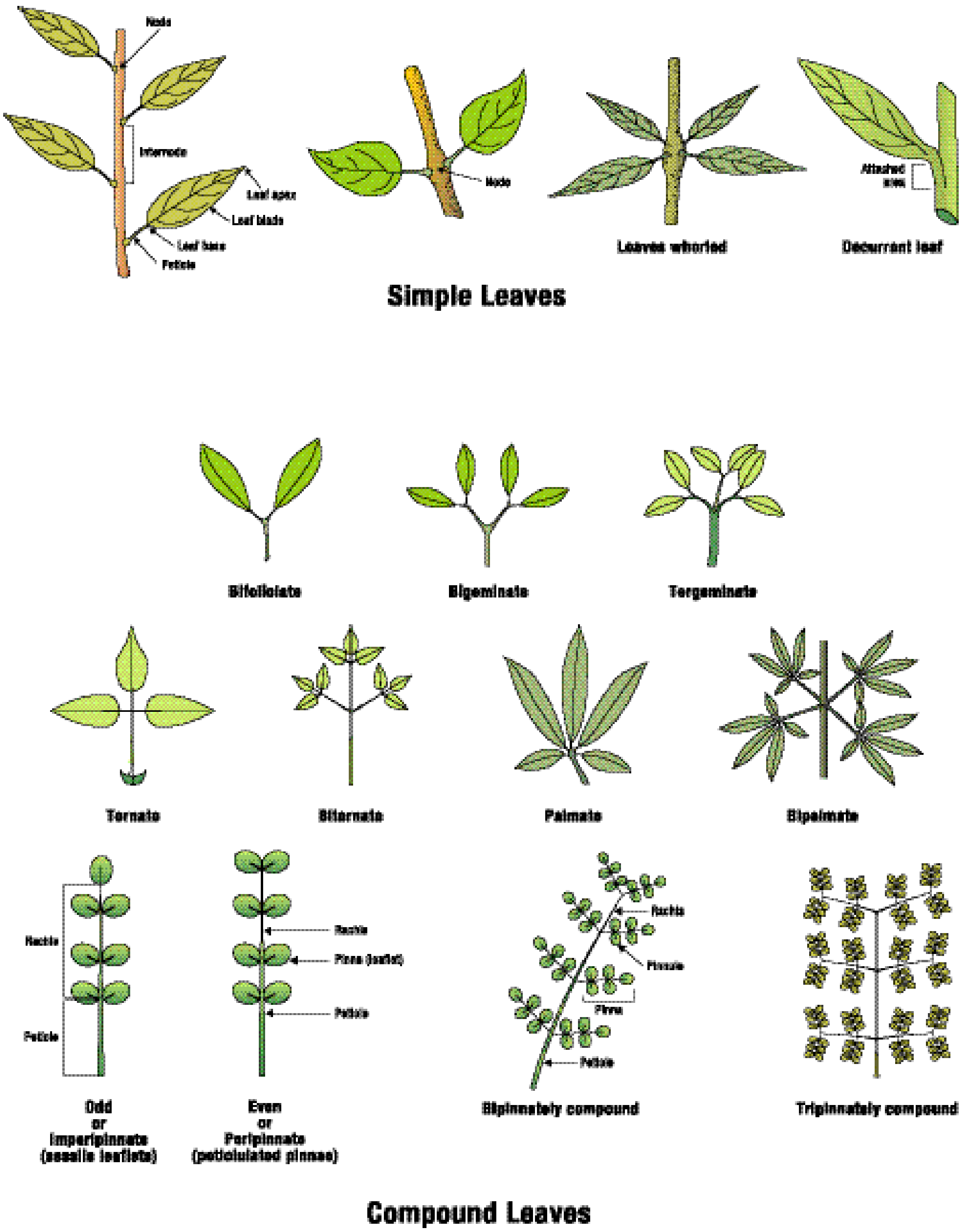

Fig. 159. Simple and compound leaves.

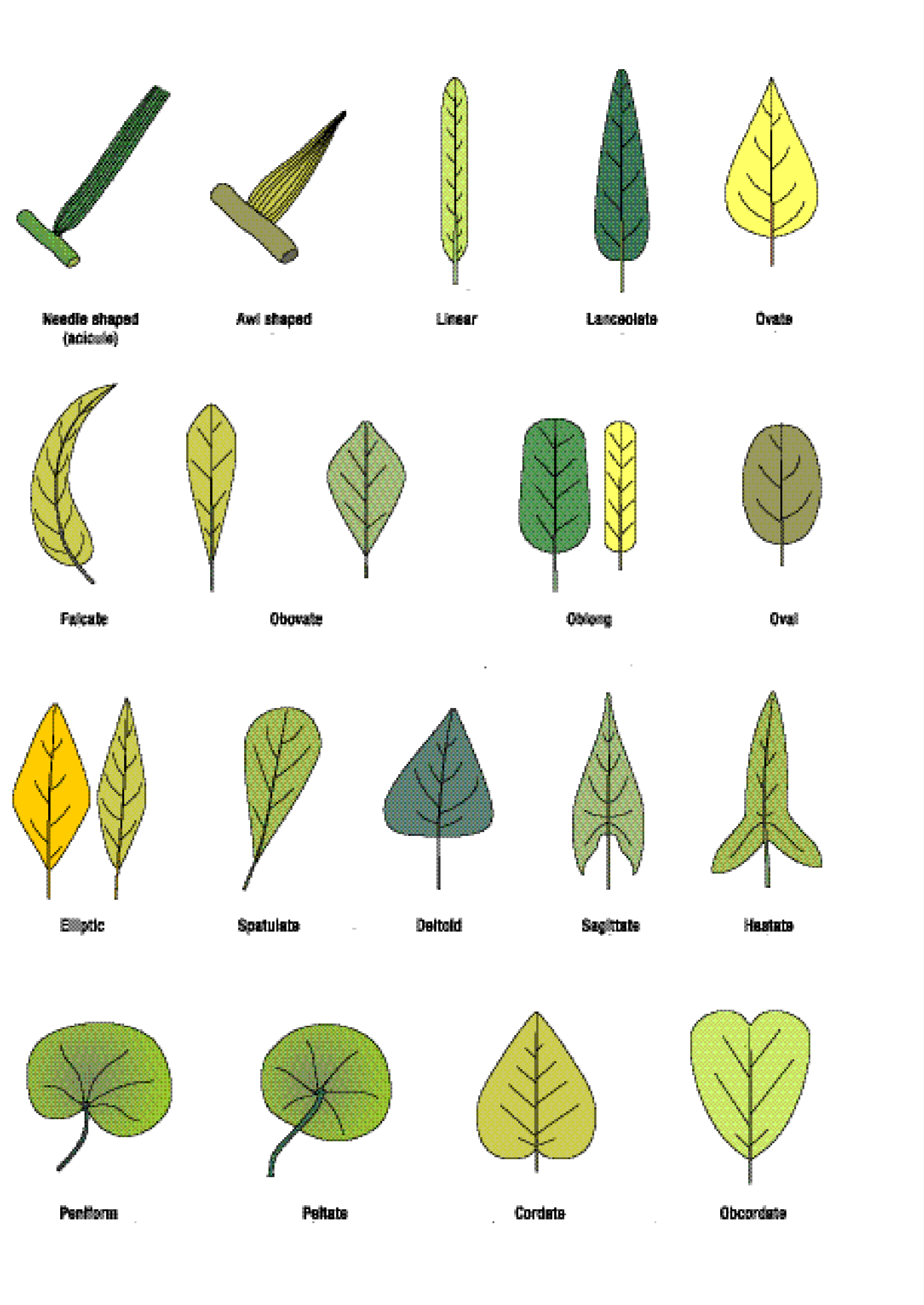

Fig. 160. Leaf shapes.

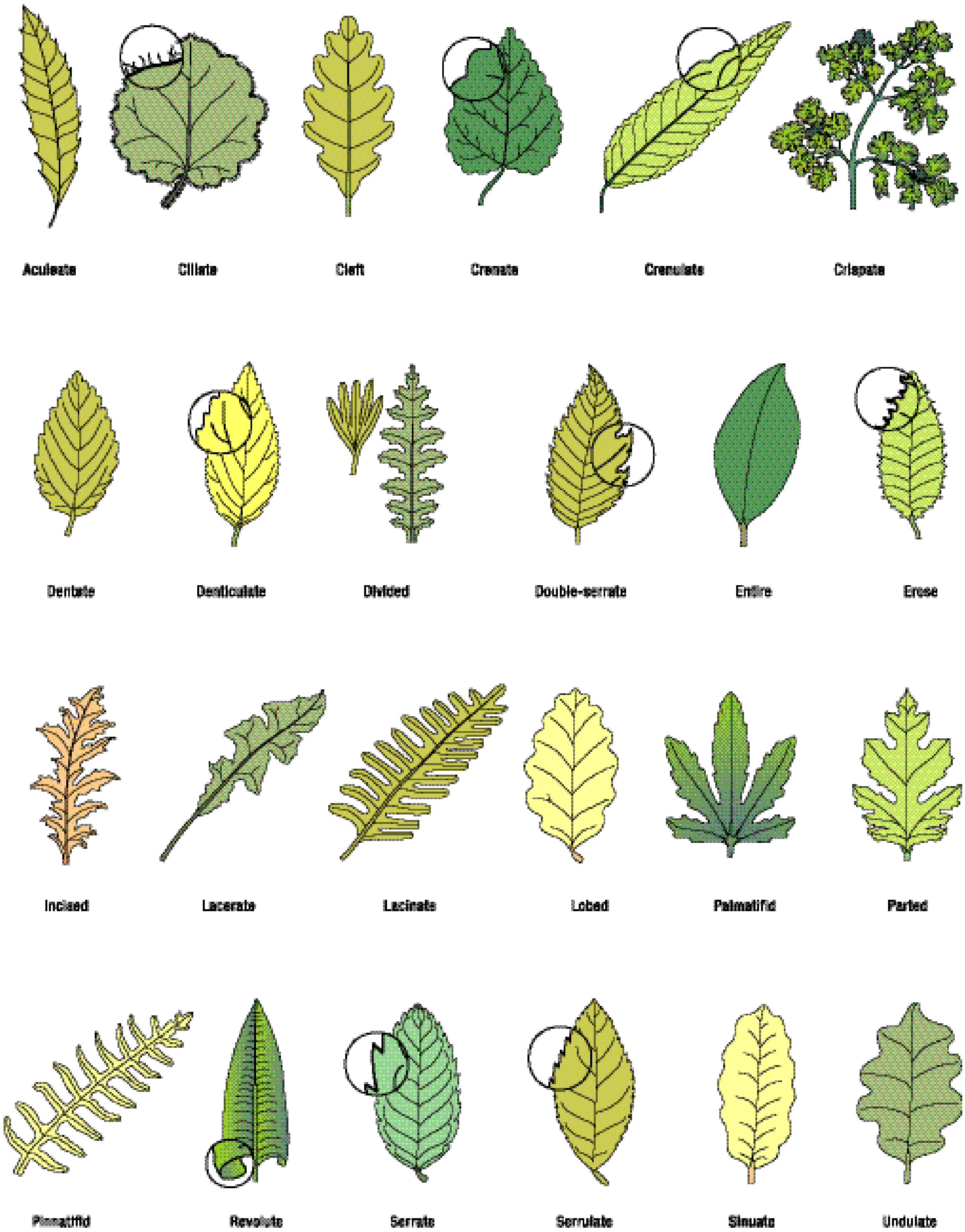

Fig. 161. Leaf margins.

rather stiff trichomes), hispid (very long, stiff trichomes), lanate (long, intertwined trichomes), papillose (with papillae), sericeous (long, silky trichomes, commonly appressed), strigose (sharp, coarse, bent trichomes with wide bases), tomentose (dense, interwoven trichomes). The type of trichome can be used for taxonomic purposes. The indument can be ferruginous, whitish, grayish, golden, reddish, or colorless.

The cotyledons and metaphylls can be stipulate or exstipulate. The stipules are lateral appendages emerging from both sides of the foliar base. Their development often precedes the foliar blade development. They can be connected to the foliar base (*adnate*) or be free. Most are small and scaly, but some are foliaceous, or modified as thorns (*Robinia*, *Acacia*), and some form glands. When the leaves are opposite or whorled, the contiguous stipules fuse and form an interpetiolar stipule as in Rubiaceae (*Coffea*, *Randia*, *Hamelia*, *Cinchona*, and *Psychotria*), or an ocreate (ocreate base) by congenital concrescence and longitudinal elongation as in Polygonaceae (fig.

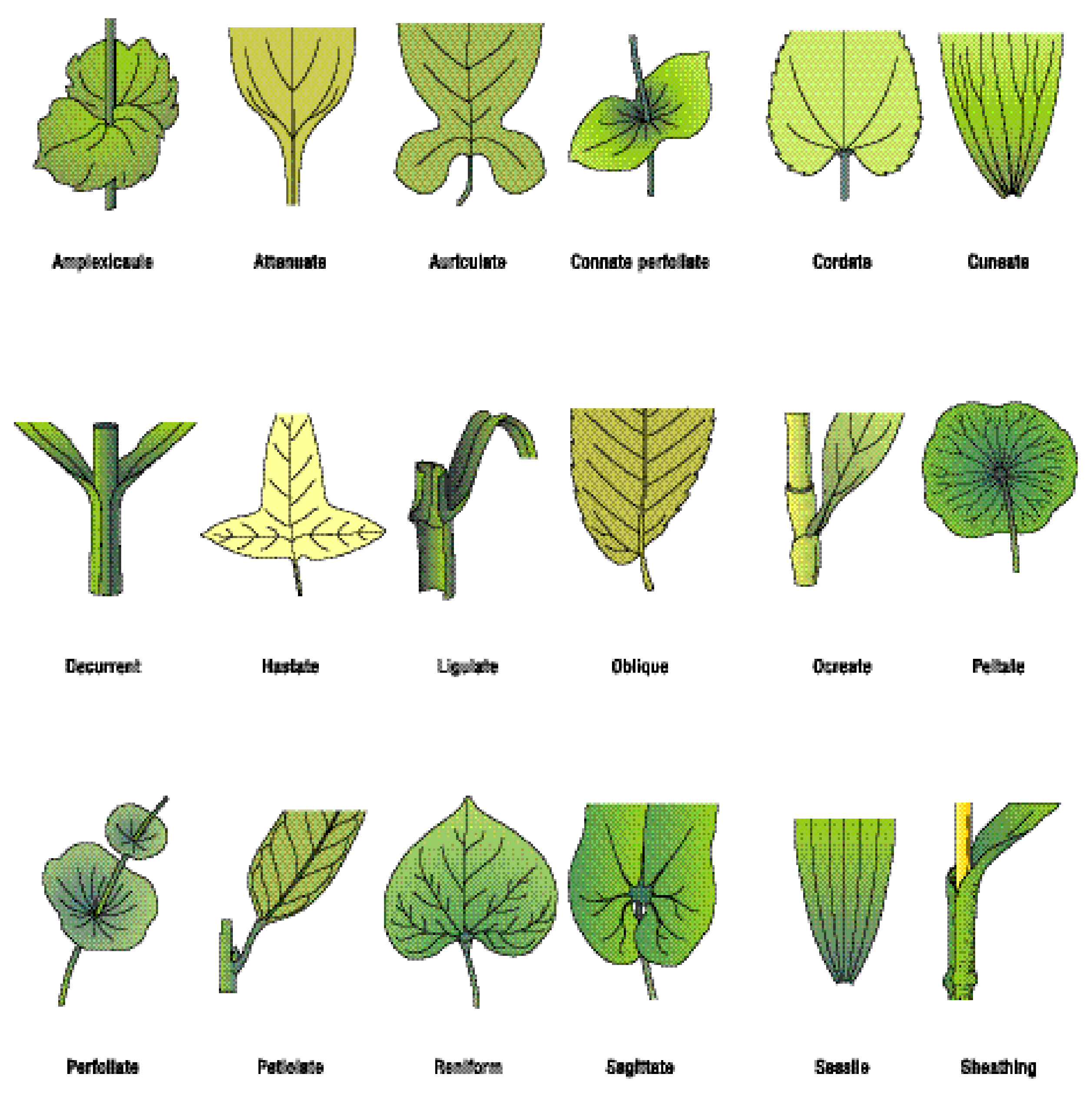

Fig. 162. Leaf bases and attachments. (Redrawn from Bradford *et al.* 1974).

162). The deciduous stipules leave stipular scars on both sides of the leaf base. When the stipules are narrow and have an acute apex they are lacinate.

Prophylls

The prophylls are the first leaves of the lateral buds giving rise to branches. The dicotyledons have a pair of prophylls transverse to the branch axis; the monocotyledons have one parallel to the principal axis. The pair of prophylls in the dicotyledons are usually opposite and can have reduced forms, sometimes squamiform. In adult trees, some species with floral branches have concrescent prophylls that may form special structures such as the cupule in Fagaceae.

Leaf Venation

The leaf venation is formed by a system of vascular bundles or veins distributed throughout the whole leaf blade in close relation with the mesophyll. The venation of the leaf blade has

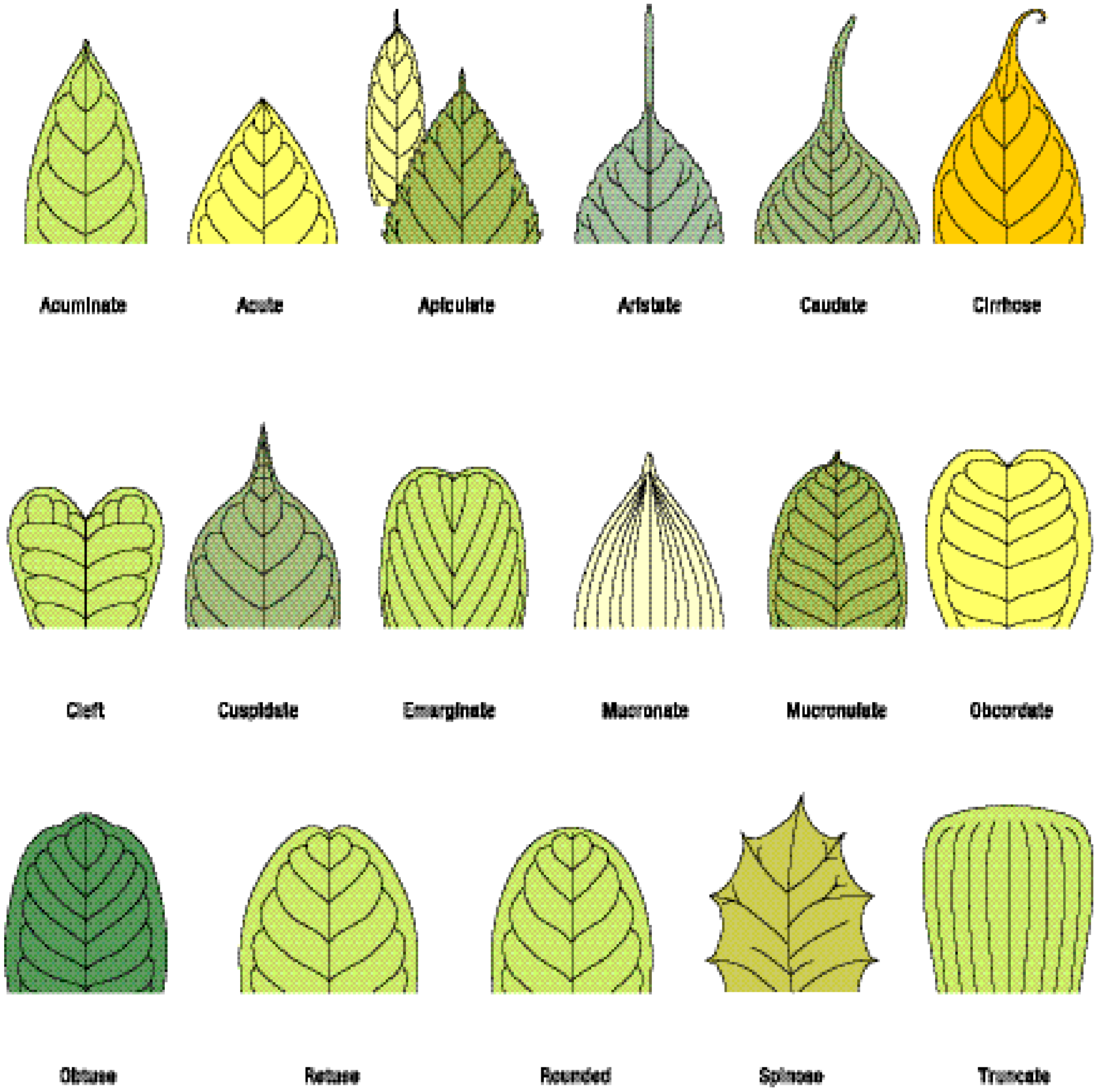

Fig. 163. Leaf apices. (Redrawn from Bradford *et al.* 1974).

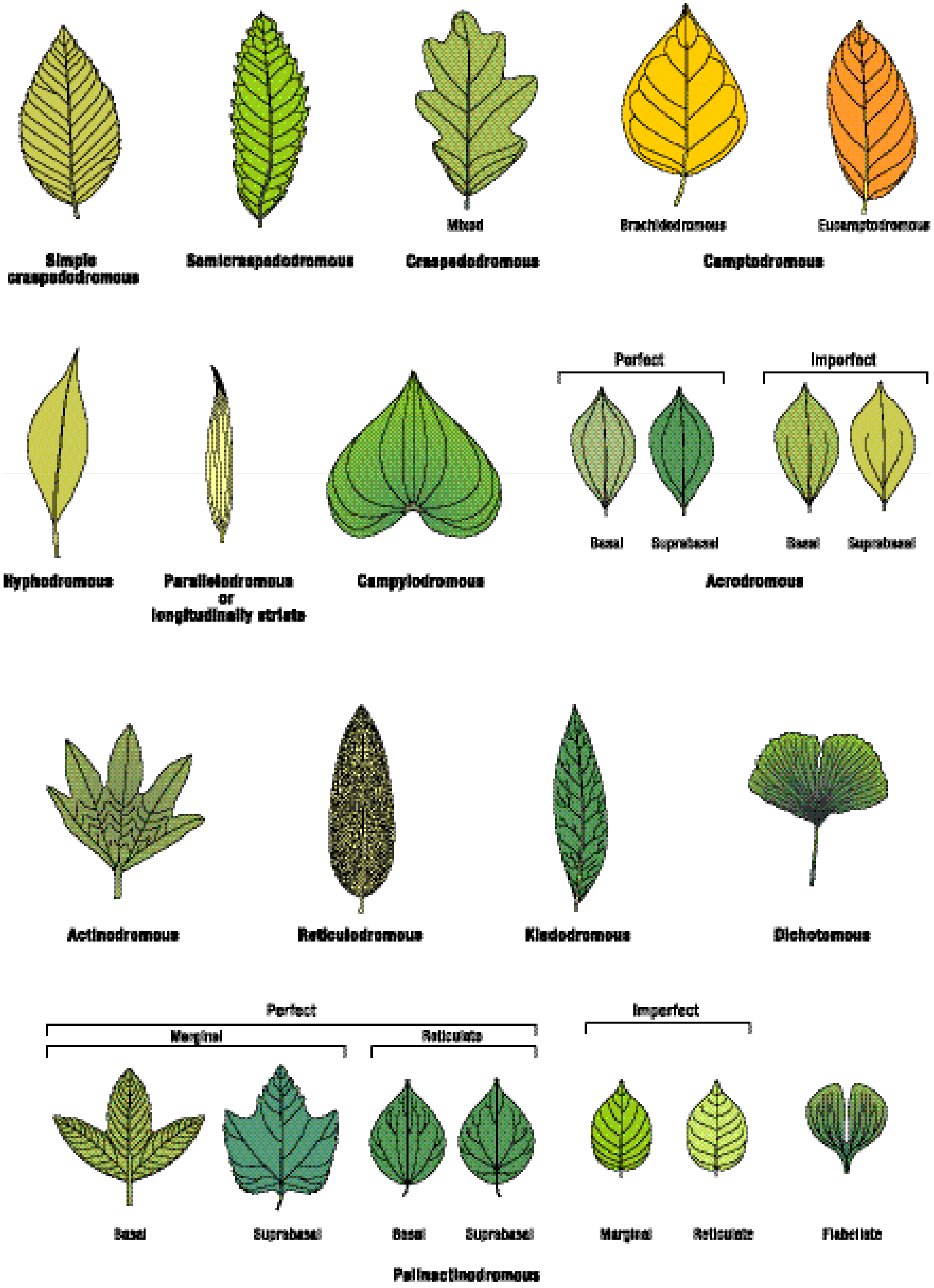

Fig. 164. Venation patterns in dicotyledons. (Redrawn from Hickey, 1974).

taxonomic value. The leaves of most dicotyledons have a midvein and a network of veins progressively smaller, arranged in a reticular pattern. Close inspection of the minor veins reveals that the areole or islets–small areas of mesophyll limited by intersecting veins–contain small, single, or ramified veins ending freely in the mesophyll. The following classification is modified from Hickey (1974) (fig. 164).

Pinnate

A midvein is the origin of the major lateral veins.

Craspedodromous: All secondary veins end at the leaf margin. It can be simple (all of the secondary veins and their branches ending at the margin), semicraspedodromous (secondary branches within the margin, one branch terminating at the margin, the others joining the superadjacent secondary), or mixed (a combination of the two former subtypes).

Camptodromous: The secondary veins do not end at the margin. These are of four types.

(1) Brochidodromous: The secondary veins are joined together in a series of prominent arches, forming a pseudo-marginal vein.

(2) Eucamptodromous: The secondary veins arch upwards, gradually diminish distally inside the margin, connecting to the superadjacent secondary veins through a series of cross veins without forming conspicuous marginal loops.

(3) Reticulodromous: The secondary veins lose their identity towards the leaf margin due to repeated branching, forming a reticulum.

(4) Kladodromous: The secondary veins branch freely toward the margin.

Hyphodromous: Only a primary vein (midvein) is present. It can be rudimentary or concealed.

Striatodromous

This type was called parallelodromous by Hickey (1974); however, as in the venation described by Troll (1957) for the monocotyledons, the major veins arising at the foliar base are not equidistant along their course and are progressively anastomose toward the leaf apex. This type of venation was called closed striate by Troll.

Campylodromous

Several primary veins or their branches arise in or near a single point and extend upwards, forming recurved arches before converging at the leaf apex.

Acrodromous

Two or more well-developed primary or secondary veins extend in convergent arches toward the leaf apex. Their origin at the leaf base can be basal or suprabasal; the development of the lateral veins can be perfect or imperfect (incomplete).

Actinodromous

Three or more primary veins diverge radially from a single point.

Palinactinodromous

The primary veins have one or more subsidiary points of radiation above the lowest point. They can be basal or suprabasal. The development can be perfect (marginal or reticulate), imperfect (marginal, reticulate) or flabellate.

The most common type in the leaves of the monocotyledons is the closed striate. In some families the lateral veins diverge and form a striate-arcuate pattern, in others a pinnate-striate pattern (fig. 165). The acicular leaves of gymnosperms have one or two vascular bundles. In others with pinnate leaves, the pinnae can have a single vein as in *Cycas*, a pinnate venation as in *Stangeria*, or a ramified dichotomous venation as in *Ceratozamia mexicana*. Some species, such as *Ginkgo biloba*, *Circaeaster*, and *Kingdonia*, have dichotomous venation (Foster and Gifford 1974) (fig. 164).

The cotyledons may have any of the former types; frequently, their venation is simpler and can differ from the type found in the metaphylls. The eophylls may have intermediate or transitional types.

VARIATIONS IN SEEDLING DEVELOPMENT

The timing of visible and invisible (inside seed before root emerges) events of seedling development vary among species. The following five examples show the numerous chronological and morphological variations that exist in seedling development, and although general patterns are established, each seed and each seedling is unique.

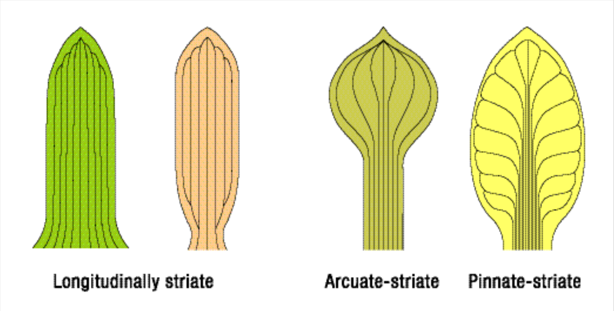

Fig. 165. Types of striate venatin in the leaves of monocotyledons. (Redrawn from Foster & Gifford 1974).

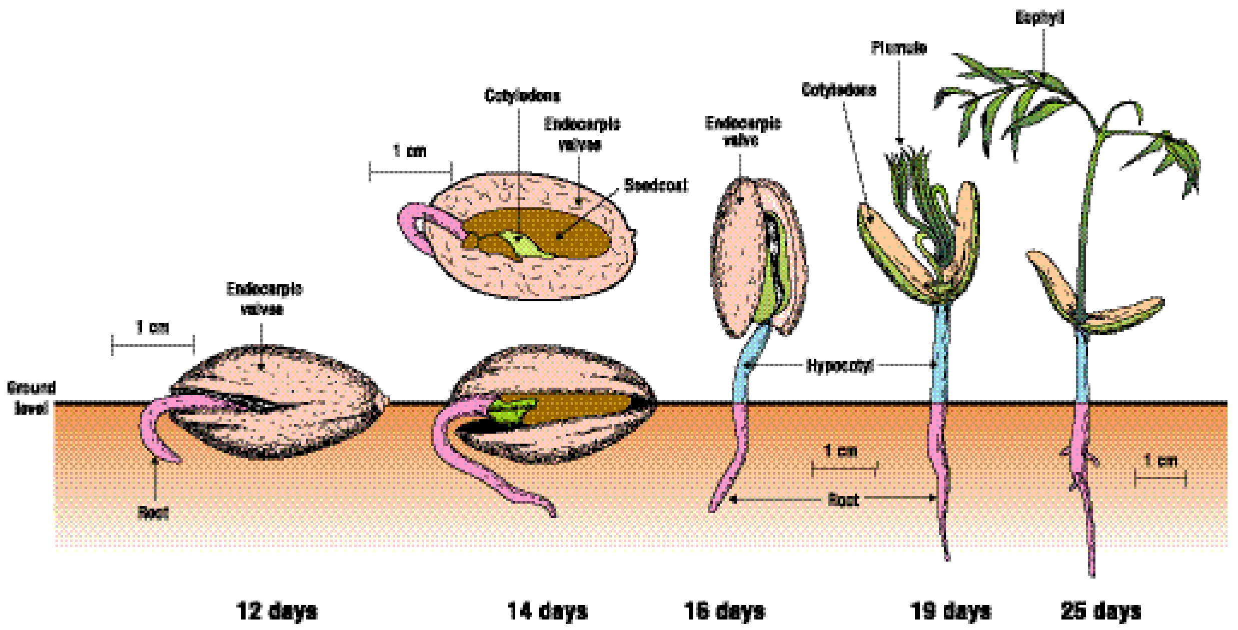

Fig. 166. Seedling development in *Dipteryx panamensis*.
Germination in epigeal; the seedling is phanerocotylar.

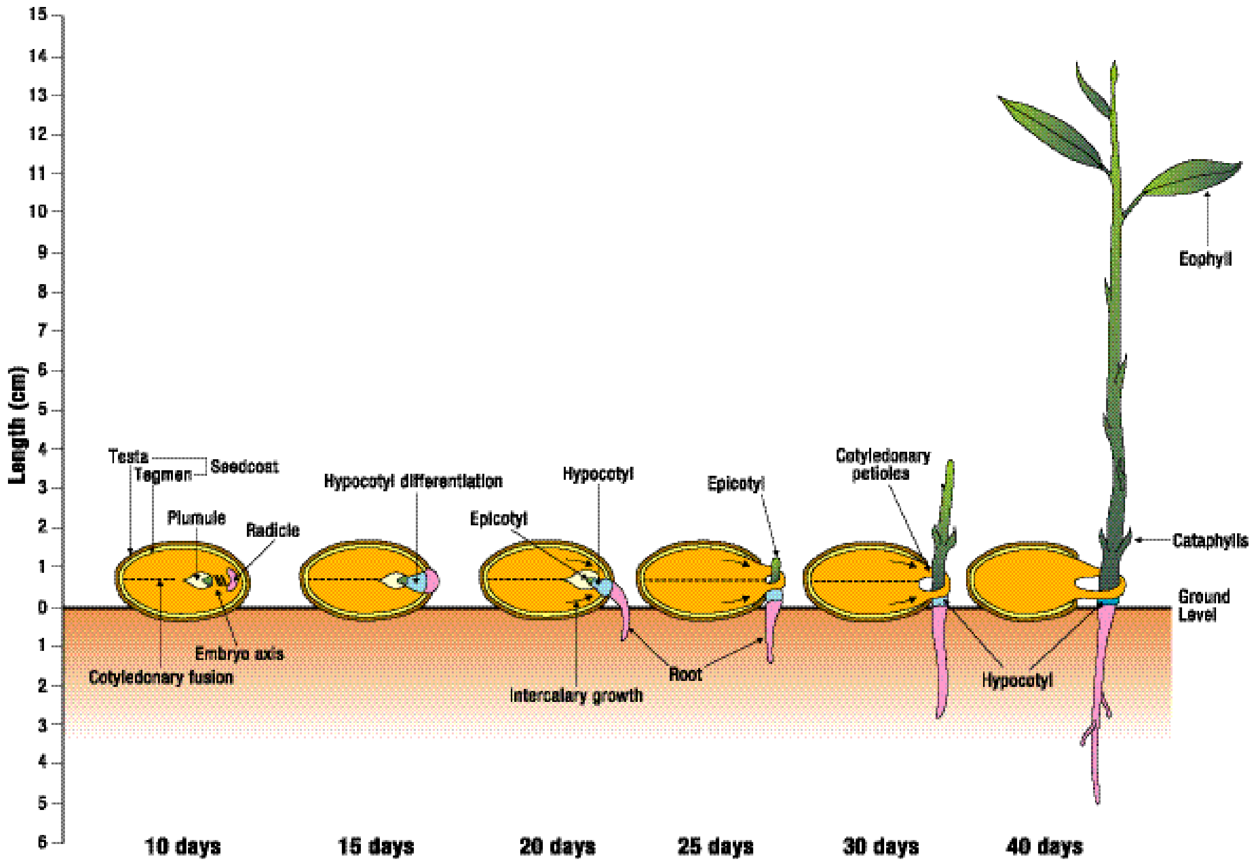

Fig. 167. Seedling development in *Calophyllum brasiliense*.
Germination is hypogeal; the seedling is cryptocotylar.

Dipteryx panamensis has a large embryo and the plumule is well developed. Visible germination (root emergence) begins at 10 days (fig. 166). The two endocarpic valves open along the dorsal and ventral sutures and the seedcoat splits along the raphe-antiraphe line. The greenish hypocotyl begins its development at 13 to 15 days and elevates the plumule which is enclosed inside the partially open valves. The eophylls are compound and pinnate with stipellate folioles. Germination is epigeal, and the seedling is phanerocotylar (Flores 1992a).

Calophyllum brasiliense has a large, well-developed embryo, with cotyledons that are gamocotylous in the distal three-quarters and concave adaxially in the basal quarter. The plumule is enclosed within this small cavity. The embryo axis is poorly developed. Visible germination begins between 16 and 18 days, and plumule emergence requires the formation and extension of cotyledonar petioles (fig. 167). The hypocotyl is vestigial. The epicotyl produces several deltoid cataphylls before developing the eophylls. Germination is hypogeal, and the seedling is cryptocotylar (Flores 1994b).

Virola koschnyi and *Minquartia guianensis* have a minute embryo and a massive endosperm, rich in lipids (figs. 168-169); in *V. koschnyi* the endosperm is ruminate. In both species, the embryo has a long, intense period of development inside the seed before the root emerges. Both embryos devel-

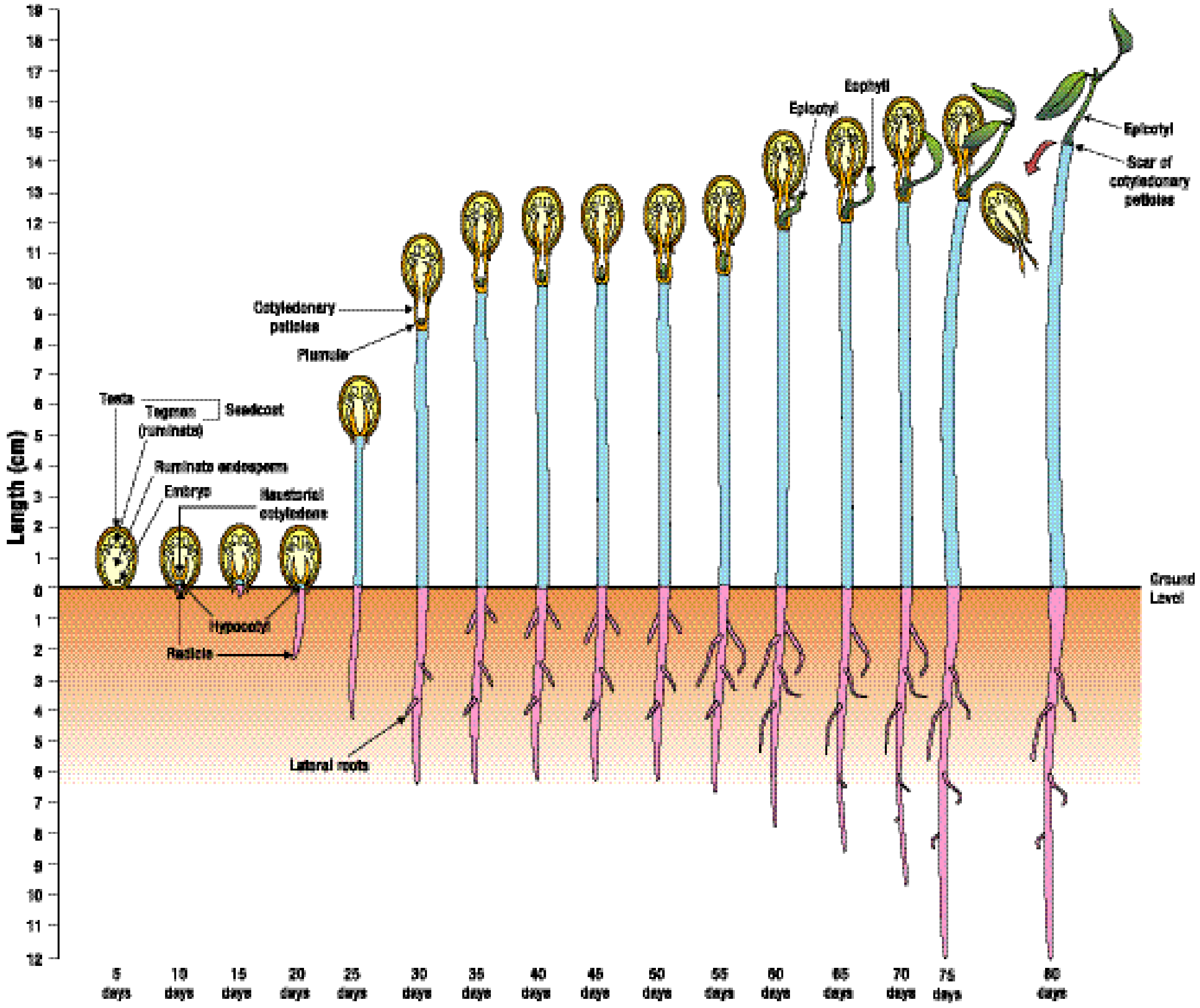

Fig. 168. Seedling development in *Virola* spp. Germination is epigeal; seedling cryptocotylar. (Most Myristicaceae studied share this pattern.)

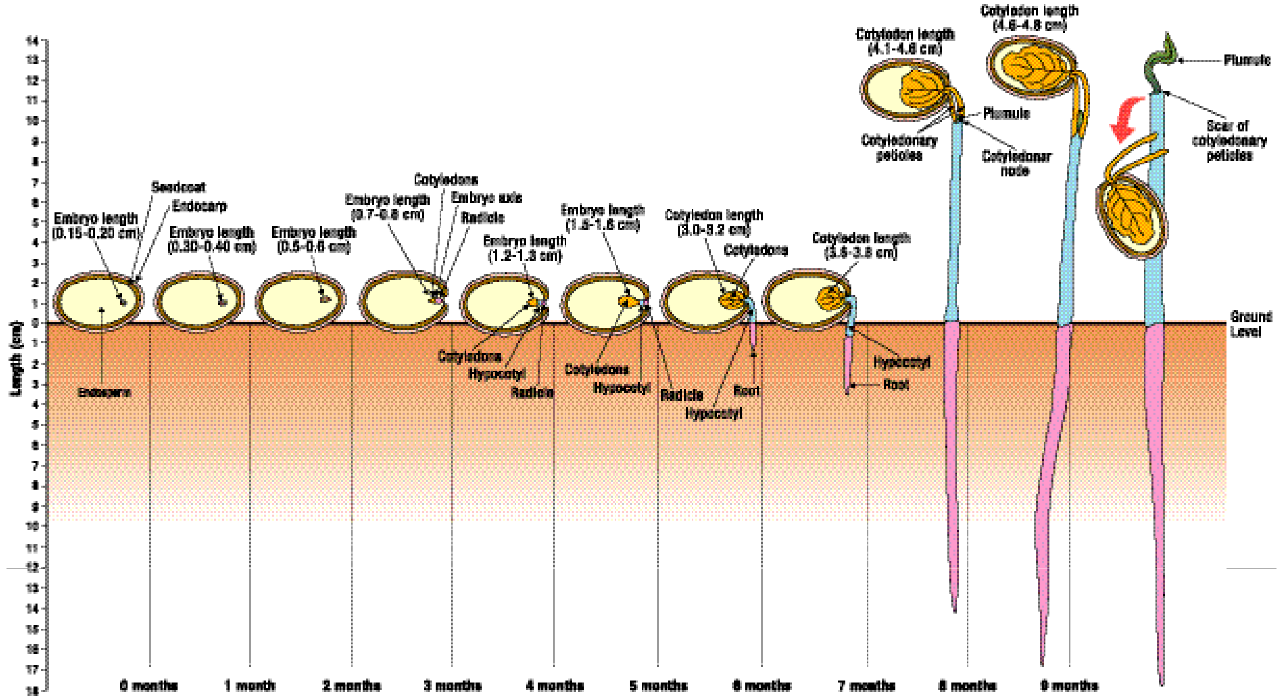

Fig. 169. Seedling development in *Minquartia guianensis*. Germination is epigeal; the seedling is cryptocotylar.

op haustorial cotyledons and cotyledonar petioles that propel the plumule. Both species have cryptocotylar seedlings. Although the process is similar in both species, *V. koschnyi* seedlings develop faster. In both, germination is epigeal and the seedling is cryptocotylar (Flores 1992c, 1994e).

Lecythis ampla seedlings develop very slowly. The embryo is large and the entire seed cavity is filled by a massive hypocotyl. The radicle and the plumule are reduced to a small mass of meristematic cells at opposite ends of the hypocotyl. The radicle forms 35 to 40 days after sowing, and the root

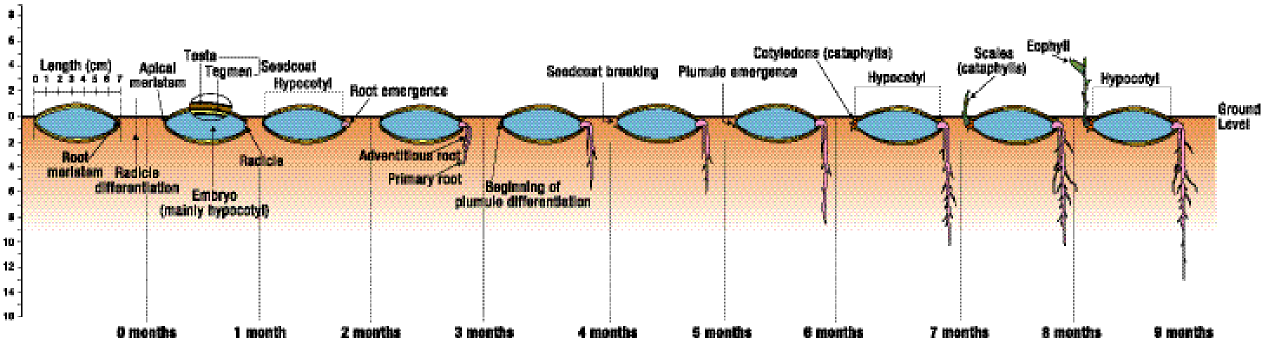

Fig. 170. Seedling development in *Lecythis* spp.. Germination is hypogeal; the seedling is phanerocotylar although the hypocotyl remains inside the seedcoat.

emerges at 45 days. Sometimes an adventitious root emerges before the primary root. Plumule development begins at 7 months and is very slow. The cotyledons are green, squamiform structures (fig. 170). Several cataphylls are produced before the eophylls. Germination is hypogeal, and the seedling is phanerocotylar.

SEEDLING ECOLOGY

Seedling ecology is only partially known and many factors affect seedling development and survival. These factors include spectral composition of light, presence of shade, type of soil, extent of herbivory, and association of bacteria and fungi.

The spectral composition of light affects seed germination and seedling development. In the forest, the canopy trees modify the spectral composition because the leaves absorb the photosynthetically active radiation (400 to 700 nm) but allow the near-infrared radiation (700 to 3000 nm) to penetrate to the lower strata (Fetcher and others 1994). The red far-red radiation ratio (R/FR) decreases with clearings at 1.22, forest gaps at 0.90, sunflecks in the understory at 0.87, and diffuse light in the understory at 0.40 (Fetcher and others 1994). The canopy also provides differences in temperature and moisture in the different microenvironments of the forest (Fetcher and others 1994).

The seedlings of many tropical trees do not tolerate shade (heliophytes) and develop only in forest clearings and gaps; others are indifferent to shade and may develop under full shade (tolerant, sciophytes). Some are partially tolerant to shade (partial sciophytes); these can survive under shade but need light to develop fully (Barton 1984, Clark 1994, Clark and Clark 1984, Finegan 1991). The heliophytes of the natural forest can be ephemeral or durable. The ephemeral are pioneers with a short life; they have light, soft wood and rapid growth, and occupy forest clearings (*Ochroma*, *Cecropia*). Approximately 10 years later, durable heliophytes begin to dominate. These species live longer and produce better wood. The partial sciophytes are established next, followed by the sciophytes (Finegan 1991). The sciophytes grow slower and live longer than partial sciophytes. The incidence of shade-intolerant species is high in the different strata of the forest and increases toward the canopy. Shade-intolerant species comprised 71 percent of the species in the canopy, 48 percent in the subcanopy, and 39 percent in the understory in La Selva, Sarapiquí, Costa Rica (Hartshorn 1980).

Although seedling behavior in the forest is very important to consider for natural forest management and forest regeneration, the vastly different ecology of the plantation evokes very different and often unexpected responses, which often limit success. Twenty-three native species planted in experimental blocks near a community of San Miguel de Sixaola, Talamanca, Costa Rica, showed that the seedlings of some species did not survive under the shade of the forest; some experienced high mortality rates under full sunlight; and others were indifferent to light level and quality, flourishing in all treatments. Under full sunlight, most seedlings show higher longitudinal growth and higher increments in diameter. Species such as *Dalbergia retusa*, *Dipteryx panamensis*, *Rollinia pittieri*, *Virola koschnyi*, *Genipa americana*, *Terminalia amazonia*, and *T. oblonga* grew better under full sunlight; under moderate shade, the juveniles were smaller and thinner but still survived well. *Cordia alliodora* was the only species that grew best under partial shade; however, it did not survive under full shade. *Virola sebifera* was the only species that grew well under partial or total shade (Rodríguez and Van Andel 1994).

Many of the species that grow best under full sunlight in plantations behave as partial sciophytes in the natural forest. Under natural conditions, they cannot compete with climbers, weeds, or other pioneer trees or shrubs in open spaces; in plantations, competition is reduced by periodic ground clearings three to four times per year). In the forest, the species survive well under partial shade but their growth is slower (in height and diameter). Heliophytes, on the other hand, compete with climbers and weeds by natural pruning (autopruning), growing a dense crown and exfoliating bark early. These differences demonstrate why seedling behavior must be studied in the natural forest, the greenhouse, the nursery, and the different types of plantations.

Soil type, especially in natural habitats, also influences seedlings. Some grow well in acid (oxylophytes) or saline (halophytes) soils, others in sandy (psammophytes) or rocky (lithophytes, chasmophytes) soils. The differences in soil can affect seed germination; seedling vigor; the size, strength, and woodiness of the stem; the depth of the radical system; the pubescence; the susceptibility to dryness, cold, or pathogens; and, eventually, the flowering and fructification of the mature tree (Daubenmire 1974). Seedlings can be deeply influenced by minor differences in soil composition produced by forest clearing or by the local effect of the canopy trees on the soil (Brandani and others 1988). Some species have very specific soil requirements; for example, *Vochysia ferruginea* Mart., *V. guatemalensis* and *V. allenii* Standl. & L.O. Williams may form monospecific stands or patches with *Dipteryx panamensis* and *Pentaclethra macroloba* in clayey, acid soils (pH 5.0 to 6.0), with high concentrations of iron and bauxite (Flores 1992a, 1993a, 1993b, 1994f).

Herbivory plays an essential role in maintaining diversity in the tropical forest (Marquis and Braker 1994). Herbivores reduce seed establishment under the maternal tree through intense predation (Connell 1971, Janzen 1970). The greater the density of the seedlings under the conespecific adult trees, the greater the predation by herbivores and pathogens (Connell 1971, Janzen 1970). This density-dependent mortality can be common to many species in the forest, but the strategies of growth vary among species and affect the structure of the populations (Henriques and Sousa 1989, Oliveira-Filho and others 1996). In species such as *Xylopia brasiliensis* (Annonaceae), variations in phenological patterns and fruit availability define the forage patterns, which in turn affect the patterns of seed dispersal (Loiselle and others 1996, Oliveira-Filho and others 1996). The real influence of herbivory on species diversity in the forest can be determined only by studying the process dynamics; the restriction of the census to spacing patterns is insufficient (Clark and Clark 1984).

In the plantations of several neotropical forest tree species, herbivory intensifies and seedlings come under greater fungal attack. *Colletotrichum* sp. produces the derrite of the apex in *Dipteryx panamensis*; *Phomopsis,* the foliar spots of *Virola koschnyi* leaves; and *Nectria,* the seedling death of *Stryphnodendron microstachyum*. Rodents and other mammals in forests and plantations can also predate seedlings (e.g., deer eat the shoots of seedlings of *Dipteryx panamensis,* provoking stem bifurcation).

The influence of bacteria (nodules) and fungi (mycorrhiza) associations on seedling survival and development is only partially known. John (1990) proposes that mycorrhizic symbiosis promotes seedling development and increases transplant survival. Because symbiotic fungi are probably lacking in the areas being restored, inoculation of seedlings may be the best alternative (John 1990). Future research on these associations would increase information about what bacteria and fungi to use in tropical plantations.

A FINAL COMMENT

Trees must have pollinators and dispersers of diaspores (Janzen and Vásquez-Yáñez 1991, Kress and Beach 1994). The state of health and the physiological maturity of the tree are important. Sexual expression in the flowers can be affected by tree age, by environmental conditions [mineral nutrition, edaphic factors, light (hours of light, intensity, quality), by the temperature (high temperature promotes maleness, while low temperature promotes femininity)], or by the application of growth regulators (auxins, gibberellins) able to produce sex alteration (Jackson 1981, Janzen and Vásquez-Yáñez 1991, Kress and Beach 1994)

The selection of seed trees in the forest is complicated. The correct shape, size, and bole; the phytosanitary conditions; and other morphological parameters are all necessary but insufficient. Many species are cross-pollinated and more than one tree is required to obtain seeds. Some hermaphrodite or pistillate trees never produce fruits and seeds or are unproductive during long periods of time; for example, *Hymenolobium mesoamericanum* produce flowers and fruits every 7 or 8 years. The presence of fruits and seeds before or after logging could be the only accurate indicator of fertility.

The production of new sporophytes requires a long and complex series of events, beginning with floral inception, followed by fruit and seed production and dispersal, and then germination. The maintenance of the remaining tropical forests, the restoration of altered areas, and the use of native species in plantations all depend on knowledge about the biology of tropical trees, their spatial distribution, their population dynamics, and their interrelationships with other elements of the ecosystem.

CHAPTER 2

Collection

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One of the most important differences between tropical and temperate forests is the high degree of species diversity in tropical forests. While a tract of temperate forest might contain 25 tree species, a tropical forest of similar size might easily support 10 times that number. Indeed, there are probably more than 50,000 arborescent species in the Tropics. As byproducts of this vast biological diversity and a broad range of climate, economic conditions, and political systems, tropical tree nurseries and seed-collecting organizations vary enormously in structure and in methods employed to collect and process seeds. These nurseries and organizations range from the most sophisticated and mechanized operations to tiny nurseries that use only hand labor and locally manufactured materials. All use valid and necessary means to solve the unique problems of each local situation.

Seed collection and processing operations are molded by the objectives driving them. Industrial objectives, such as supplying raw material to a productive mill or satisfying the demands of an export contract, require the production of abundant quantities of relatively high-quality seeds of one or a very small number of species. Usually great care is taken to select or produce seeds from highly productive genotypes. Most of these seed-collection organizations have generous budgets and a high degree of mechanization.

Seed suppliers that produce seed for sale both within their own countries and for export are required to produce the highest quality product possible. It must contain little debris and be free of insects and weed seeds. Superior genotypes bring premium prices, but all lots must be forest-run (representing the average for wild trees) or collected from trees of selected phenotypes. There is constant pressure to offer as many species as possible, but costs tend to escalate with the number of species maintained in collections. These operations may employ one to many people, have varying degrees of mechanization, and be government affiliated or private.

The most common objective of seed collection in the Tropics is to support local tree nurseries. These nurseries are the principal source of tree seedlings for homeowners, cities, farmers, and conservation and forest management organizations who use the seedlings for ornamental, agricultural, agroforestry, conservation, and silvicultural purposes. They typically maintain a relatively large inventory of the few species that are in continual demand (all of which are reliable seed producers) and a group of other species that changes as seed collection opportunities present themselves. Seeds are usually collected by nursery employees or purchased from local seasonal collectors. Seeds are rarely stored for more than 1 year. Seed quality and handling are highly variable. Because wages are low in most of the Tropics and in some places the objective of providing employment supersedes that of producing seedlings, labor is often substituted for equipment or improvements requiring capital investment. Unfortunately, product quality and efficiency may decrease.

Collection and processing problems are species-driven. Hence, the greater the number of species handled, the greater the number of problems that must be solved. Unfortunately, some species are planted because their seed collection and management are easy, not because they are the best species available to meet the need. Many superb species are rarely or never planted because their seeds are difficult to collect or use. As experience in seed collection and management increases, many exciting species will be added to plantation inventories. Increasing the number of species we are able to successfully reproduce by seed will facilitate the difficult task of rehabilitating damaged ecosystems. This chapter reviews some of the challenges to seed collection and processing in the Tropics and the approaches to meeting these challenges.

SEED COLLECTION

GENERAL METHODS

It is important to remember that fruit characteristics evolved to facilitate a seed dispersal strategy. Often a seed collection, extraction, or germination technique has simply mimicked the natural process.

From the Ground

The mainstay of seed collection is and will remain the picking up of the fruits or their seeds from the ground after they fall. This method is especially convenient for species with large or conspicuous fruits or seeds such as *Melia azedarach* L.,*Ormosia krugii* Urban,and *Terminalia catappa* L. Protective pods enable collection of fruits of such species as *Crescentia cajute* L., *Hymenaea courbaril* L., *Pterocarpus macrocarpus* Kurz, and *Senna spectabilis* (DC.) Irwin and Barneby, weeks to months after fruit-fall. Even the seeds or fruits of relatively small-seeded species, such as *Bucida buceras* L. and *Petitia domingensis* Jacq., can be collected from the ground if it is bare or paved, or if a tarp is placed under the tree just before fruit-fall. In those circumstances, vacuuming or sweeping can sometimes speed the collection process.

From the Tree

Another common means of collecting fruits and seeds is picking them from the trees. It is faster in many cases than collecting from the ground and it keeps the seeds cleaner. In addition, the seeds of many species are too small to pick up from the ground, and others are dispersed widely or consumed by animals and insects before they fall. Short trees may allow hand picking. Production can be accelerated by flailing into a basket attached to a picker’s waist.

Picking must occur between physiological ripening (timed so the fruits will ripen in storage) and release by the tree or consumption by predators or dispersers. Ripeness is usually indicated by a color change of the fruit from some shade of green to an indicator color such as brown or red. In some cases, animal predation indicates ripeness. The sight of cockatoos feeding on the seeds indicates that *Agathis* seeds are ripe (Whitmore 1977). The seeds of many species, such as *Albizia lebbeck* (Kunth) Harms and *Melia azedarach* L., remain in their fruits on the trees for weeks or months, greatly facilitating collection. Many of the eucalypts carry large quantities of fruits for extended periods that open quickly after fires (Cremer and others 1978) These fruits will also open after the clipped twigs dry. Species with serrotinous cones, such as *Pinus patula* Schiede & Deppe, produce cones that remain on the tree with viable seeds 1, 2, or more years after ripening (Wormald 1975).

SPECIAL CHALLENGES

Tall Trees

Most species are too tall for hand picking. Pole pruners provide a convenient and inexpensive way to collect fruits from 2 m to about 9 m above the ground. Stepladders and easily portable, straight or extension ladders up to 7 m are also used. Fruits or seeds that shatter or detach easily, or seeds that are ejected from their fruits, can be collected by placing a tarp under the tree and flailing the tree with a long pole. In similar approaches, trees are shaken by hand (if small), by mechanical shaker, or by attaching a chain or rope to the trunk as high as convenient and to a vehicle or another tree, then jumping up and down on the chain or rope or pulling back and forth with a vehicle. A particular benefit of collecting seeds by shaking is that for species such as *Cordia alliodora* (Ruiz & Pavon) Oken, in which all the fruits or seeds do not mature at the same time, shaking releases the mature fruits while the immature fruits remain on the tree (Greaves and McCarter 1990).

When short-statured species, such as *Acasia farnesiana* (L.) Willd., *Hibiscus tiliaceus* L., and *Moringa oleifera* Lam., and precociously flowering species such as *Spathodea campanulata* Beauv., invade cleared areas, they are short enough to pick by hand or pole pruner. Trees planted in open-grown situations sometimes grow low enough for easy harvest. Open-grown *Swietenia* spp. will usually bear many of its fruits within 9 m of the ground but does not do so in closed forests. Many species will continue to bear fruits after pruning to a low crown. Fruit trees, including *Mangifera indica* L. and *Citrus* spp., are routinely managed this way. Crown-shaping trials with many tropical forest species should be conducted.

The seeds of timber trees in natural forests are often borne near the tops of very tall trees. Traditionally, these seeds are collected from trees felled by logging operations. The method is excellent, if available. However, felling can shatter seed clusters and produce enough slash to hinder fruit retrieval. In some areas, trees have been destructively felled to obtain the seeds (Britwum 1973). Generally considered unacceptable ecologically and economically, this method may be beneficial if the seed trees are scheduled for removal to improve the stand.

The challenge of collecting seed from tall trees has inspired a number of approaches. Small quantities of seed, usually intended for breeding or provenance trials, have been collected by shooting down limbs with rifles or shotguns. Slingshot pellets and thrown sticks have been used to shatter small quantities of seed. Arrows have been used to draw lines over limbs to cut down or shake down small quantities of seed. Traditionally, local climbers were hired to ascend the trees and pick the desired seed in quantity with little or no safety equipment. Any conscientious collector would now require the use of safety harnesses and belts, safety lines, and helmets. Tree-climbing spurs, tree bicycles, tethered sectional ladders, and other climbing aids can greatly accelerate an ascent up the tree bole. Once up the tree, a collector often uses a pruning pole to clip fruits on the ends of limbs or to saw off fruit-bearing limbs. Finally, seed collectors with generous budgets use high-lift buckets on hard and nearly level ground to collect fruits from tall trees.

Widely Scattered Seed Trees

In tropical moist forests, seed trees of many species grow more than 1 km apart. Seed-producing adults of heavily exploited and rare species can often be very difficult to find. Random searches can be incredibly time consuming. Traditionally, seed collectors maintain a mental inventory of known seed trees or potential seed trees they have sighted during excursions through the forest over the years. Although it takes many years to accumulate this degree of experience, the system works well as long as these inventories are handed down to succeeding generations of collectors. The alternative is to maintain a written inventory of potential seed trees of at least the critical species along with maps of their locations. Modern technology can add efficiency and accuracy to this time-consuming process through the use of computer data bases and global positioning satellite (GPS) technology.

Genetic Impurity

A number of species hybridize freely with members of the same genus or varieties within the same species to produce undesirable or unpredictable offspring. The *Swietenia*s have hybridized freely in Puerto Rico and the seeds of *Eucalyptus robusta* Sm., obtained from Brazil many years ago, introduced many hybrids that were generally inferior to the pure species. The timber tree *Hibiscus elatus* Sw. has been reported to hybridize with the shrubby *Hibiscus pernambucensis* Arruda in Jamaica (Adams 1971). In the case of *Swietenia*, the hybrid seedlings can usually be separated from the parent species by leaf size. With *E. robusta*, sorting is impossible. The problem is solved by collecting from well-identified and isolated seed trees.

Unknown or Unpredictable Fruiting Seasons

In that portion of the Tropics with a strong wet-dry seasonal cycle, almost all species flower and fruit in certain well-defined seasons. Phenological studies can document these seasons and seed collection can be planned accordingly. However, in many species the flowering and fruiting dates may vary somewhat (Greaves 1978) and the level of fruiting may vary tremendously from year to year, depending on seasonal rainfall amounts and patterns, and other factors such as wind or insect damage. Seed years are theoretically predictable from climatic conditions and can be successfully predicted from flowering and fruit set for a few species, such as *Pinus caribaea* sensu Small, non Morelet, which flowers one year and bears seeds the next.

In those portions of the Tropics with a relatively even distribution of rainfall, many species, such as *Roystonea* spp., *Ficus citrifolia* P. Miller, and *Hibiscus elatus* Sw., flower and fruit irregularly throughout the year. Some species, such as *Leucaena leucocephala* (Lam.) de Wit, bear seed more or less continuously in moist habitats, but seasonally in habitats with a strong wet-dry cycle. *Vochysia hondurensis* Sprague in Costa Rica bears fruit twice per year (Nichols and González 1992a, 1992b). Fruiting in some species is thoroughly unpredictable; individual trees fruit irregularly from year to year and by seasons and are not synchronized with others of their species. However, this can be an advantage. If seeds are unavailable on one tree, they may be present on the next tree; or if seeds are unavailable in one locality, they may be available a few kilometers away. *Byrsonima spicata* (Cav.) Kunth, *Cordia sulcata* DC., and *Buchenavia tetraphylla* (Aubl.) Howard illustrate this behavior. Although *Swietenia macrophylla* G. King is usually seasonally synchronized even outside its native range, a few unsynchronized individuals produce some seeds during most of the year. Continuous flowering and fruiting and discontinuous/irregular year-round fruiting is a natural strategy to avoid overloading the demand for pollinators and seed dispersers. Moreover, having a small percentage of the population out of synchrony helps avoid loss of regeneration to irregularities in normal rainfall patterns. To solve the problem of collecting from species with this diverse behavior, phenology should be recorded and collection activities should be planned by species. Collectors should not become discouraged by a few failures.

Delayed and Rare Fruiting

Many species, such as *Bertholletia excelsa* Humb. & Bonpl., do not bear fruit until they become large canopy dominants, a process that may take 50 years or more. In plantations, the process can be shortened to 15 to 25 years and grafted stock will bear fruits in as little as 6 years (Ferraz 1991). Seed orchards exploit the tendency for open-grown trees to bear fruit more quickly and prolifically than forest trees. The abundance and ease of collection from open-grown trees has often led to excessive collection from phenotypically unproven trees in pastures and along streets. *Lagerstroemia speciosa* (L.) Pres. begin fruiting in as little as 3 years, but do not bear viable seeds until about 15 years (Food and Agriculture Organization 1957). Most species of *Bambusa* flower and fruit in regional synchrony only once every few decades, and *Corypha umbraculifera* L., a palm, flowers once at the end of its long life and then dies.

The advantages to collecting seeds of species that can be stored during bumper crop years are numerous. The cost per unit of seed is lower; fewer seeds are damaged by insects; and the seed usually germinate at higher rates (Lamb 1993). A number of healthy exotic trees, such as *Araucaria heterophylla* (Salisb.) Franco in Puerto Rico, do not produce seeds in their new habitats (Francis 1987), and seeds must be imported each season. Ringing, shallow girdling, stem strangulation, stem bending, root pruning, and water supply restriction has shown some promise in promoting seed production, although these methods ultimately injure the trees (Rudolf and others 1974).

Animal Predation

Rodents, monkeys, birds, bats, and grazing animals can quickly eliminate a seed crop in a limited area. Parrots in Central America can consume an entire seed crop of *Acacia aneura* F. Muell. before it ripens (Willan 1995). Although fences, screens, scarecrows, reflectors, and noise makers can successfully reduce or eliminate seed predation, they are usually practical only for seed orchards or concentrations of seed trees. Sometimes seeds can be harvested after they have become viable but before they or the fruits become attractive or accessible to animals. When forest species are scattered, collecting more widely and intensively appears to be the only way to obtain the needed seed stocks. In temperate areas, squirrel caches can be robbed; and in the Tropics, seeds are separated from the manure of predators that have been feeding on the fruit of the desired species.

Insect Infestation

Most species are attacked to some degree by seed insects. Occasionally, species such as *Prosopis juliflora* (Sw.) DC. and *Triplochiton scleroxylon* K. Schum. are so seriously attacked by insects that propagation is limited (Brookman-Amissah 1973, Marrero 1949). In some cases, insecticides can be used to prevent attack and assure good seed crops. *Zanthoxylum flavum* Vahl seeds in Puerto Rico are reduced to $\leq$5 percent viability by a seed weevil (Francis, personal communication 1994; Marrero 1949). A conservation organization was able to produce seeds free of insects and with good germination by spraying with insecticide (Rivera, personal communication). Many types of seeds should also be treated by fumigation, cold treatment, or insecticide application to eliminate insect damage during drying and storage.

Short Period of Availability

For various reasons, fruits or seeds of many species are ripe and available on trees for a very short time, often just a few days. The fruits of *Hyeronima oblonga* Muell. Arg. and *H. alchornioides* Allem. Diss. fall 3 to 4 days after maturity (Nichols and González 1992a, 1992b). In the final stage of ripening, *Pinus caribaea* sensu Small, non Morelet cones change color from green to brown, the cones open, and the seeds are dispersed quickly (Greaves 1978). Frequent field checks are essential to best time seed collection. Because individual trees of a species are often not closely synchronized, collecting from tree to tree can extend the collection season. Often, the collector can lengthen the period of seed collection by moving up an elevational gradient or across a moisture gradient. Some species, such as *Maesopsis eminii* Engl. and *Pouteria* spp., picked up just before ripening, ripen in storage; thus the picking season is lengthened by a few days. The collector must know the species' traits, because some species, such as

Cordia alliodora (Ruiz & Pavon) Oken, stop ripening as soon as they are detached from the tree (Greaves and McCarter 1990). The collector should also study how long seeds of critical species will remain viable on the ground after fruitfall. Collecting diptocarp seeds from the ground, for example, must be carefully timed because a delay of a few days can result in loss of viability (Domingo 1973).

SEED PROCESSING

The basic method of removing seeds from fruit structures by hand is useful for research quantities of seed, and even highly productive for a few species such as *Swietenia* spp., but is too slow for most applications. Traditional methods such as flailing, trampling, grinding with a mortar and pestle, winnowing, floating, or screening are used to clean seeds of some species such as *Albizia procera* (Roxb.) Benth, *Casuarina* spp., *Eucalyptus* spp., *Leucaena leucocephala* (Lam.) deWit, and *Melaleuca* spp. Seeds in clusters and in brittle pods or capsules, such as those of *Acacia farnesiana* (L.) Willd., *Cassia javonica* L., *Parkinsonia aculeata* L., and *Zanthoxylum martinicense* (Lam.) DC., can often be cleaned by using standard research thrashing machines or by breaking them up by gentle hammermilling followed by screening and blowing. Usually, each stage of the operation is adjusted to accommodate the many seed sizes, shapes, and densities.

CHALLENGES TO PROCESSING

Seed Cleaning Difficulties

The seeds of *Ochroma pyramidale* Cav. are covered with a silky wing ("silk") that is time consuming to remove by hand. In an innovative solution, the seeds were thinly spread over a large mesh screen and set on fire. As the silk burned, the seeds fell through and were scarified in the process (Holdridge 1940b). It is often adventitious to de-wing or eliminate other dry parts from seeds or fruits to reduce the bulk for storage or shipping. De-winging machines designed for *Pinus* spp. have also been used to de-wing other species and to remove some unwanted tissue, such as scale tissue and bract points in *Araucaria cunninghamii* Aiton ex D. Don (Haines and Nickles 1987). Because the seeds of *Swietenia* spp. are large and fragile, they are de-winged by hand, but other more resistant seeds, such as *Tectona grandis* L.f., may be cleaned by working sacks of seed against the ground with a foot, then removing debris by blowing.

Many species, such as *Dalbergia sissoo* Roxb., *Guazuma ulmifolia* Lam., *Prosopis juliflora* (Sw.) DC., Lam., and *Tectona grandis* L.f., have very tough pods or capsules. Some, such as *Pterocarpus macrocarpus* Kurz., have fragile seeds within. Others have fruit structures that tightly adhere to the seeds, as in some *Araucaria*s. These seeds can sometimes be separated by hand using knives or clippers but not by any machines currently available. Usually, the pods or capsules are broken into small units and planted as seeds (FAO 1955). When seeds cannot be separated from fruits or debris, they can be planted within their fruits or mixed with debris. This method frequently requires thinning any resulting seedlings that appear in clusters (Francis 1989c). Sometimes, increased germination will justify hand cleaning small lots of seed (Dabral 1976), especially if the seeds are scarce or expensive or if labor is abundant. One ingenious method of cleaning the seeds of sweet podded legumes, such as *Acacia* spp., *Enterolobium cyclocarpum* (Jacq.) Griseb., and *Samanea saman* (Jacq.) Merril, involves feeding the pods to cattle or goats and extracting the cleaned (and scarified) seeds from the manure (National Academy of Sciences 1980).

Another class of cleaning problems occurs when the seeds are encased in fleshy fruits. When the fruit is thin, seeds may sometimes be dried within the fruit and planted with the adhering fruit residues without affecting germination (Food and Agriculture Organization 1955, Stein and others 1974). In some species, adhering fruit can be removed or loosened by promoting rotting or allowing consumption by insects. If the fruits of *Acrocomia media* O.F. Cook are incubated under mulch for several months, the fleshy fruit is reduced to a husk and the seeds are not damaged. This method also afterripens the seeds (Francis 1993a). The same process, with a shorter duration, may be used with *Juglans jamaicensis* C. DC. (Francis and Alemañy 1994).

However, fruit must usually be removed soon after collection to facilitate storage and planting and to prevent damage to the seeds during putrification of the fruit (Pleva 1973). Numerous methods and machines for cleaning fleshy fruits are used. In many nurseries, most fleshy fruits are separated by hand, washed over screens, and dried. This method is the most rapid way to clean many large-seeded species such as *Mammea americana* L. and *Persea americana* Miller. Sometimes soaking the fruits in water for a period of time facilitates separating the seeds (FAO 1955). In wet sieving, the fruits are hand macerated against a screen just small enough to retain the seeds. The fruit pulp is continuously washed away by running water or by swirling the screen in standing water. The cleaned seed is then dried before storage. In a variation of this method, the fruits are pulped with a hand tool or machine before wet sieving. Flotation is also frequently used to separate fruit pulp, debris, and hollow seeds from filled seeds that sink (Stein and others 1974).

Inconvenient Seed Sizes

The most familiar example of giant seed size is *Cocos nucifera* L. These giant seeds must remain in the husk, which limits human carrying to about 10 seeds and requires a great deal of storage and nursery space. Other species, such as *Caryocar villosum* (Aubl.) Pers. and *Mammea americana* L., have large seeds that also may be inconvenient to transport and store in large quantities. Despite these problems, the abundant stored reserves of large seeds often compensate for the inconveniences of size with their excellent germination and impressive early growth.

Very small seeds can also present problems. Because the seeds of *Eucalyptus* ssp. and *Melaleuca quinquenervia* (Cav.) Blake are so small, the fruits must be collected and transported before they open and disperse their seeds. Cleaning dry, small seeds is easy, but cleaning very fine seeds embedded in fleshy fruits, such as *Ficus* spp. and *Muntingia calabura* L, can be difficult. These seeds are usually cleaned by wet sieving and drying, sometimes followed by dry sieving or blowing.

Perishable Seeds

Although usually thought of as a storage and seed handling problem, the short viability (as little as a few days) of some species (Food and Agriculture Organization 1955, National Academy of Sciences 1980) must be considered during collection to facilitate rapid processing and planting or dispatch of seed to the intended user. Another class of seeds, known as recalcitrants, lose their ability to germinate upon drying. They are especially prevalent in humid forests and are more commonly associated with fleshy fruits. The process of germination often begins as soon as the fruit matures. Whenever possible, seed operations with recalcitrant species, such as *Andira inermis* (W. Wright) Kunth ex DC., *Inga vera* Willd., *Persea americana* Miller, and *Thespesia grandiflora* DC., should harvest, clean, and plant the seeds on the same day or within a very short time. If these seeds are to be stored a short time at room temperature, they should be placed in a plastic bag or under wet sacks. Most of the species will withstand refrigeration and can be stored for one to several weeks. An alternative to seed storage is to germinate the seeds and maintain the seedlings in the nursery until needed. Although this is impractical with fast-growing species, slow-growing species such as *Guaiacum officinale* L. can be maintained an extra year in the nursery without difficulty.

Physical and Chemical Defenses

The fruits and seeds of a few species, such as *Pterocarpus angolensis* DC., are armed with spines or bristly hairs that make picking and extraction difficult. Using gloves and other protective clothing and possibly singeing (Kimariyo 1973) or milling the fruits or seeds can facilitate seed handling. In some species, such as *Comocladia* ssp., *Hippomane mancinella* L., and *Sapium laurocerasus* Desf., all parts are toxic, at least when green and especially to sensitive individuals. Others, such as *Sterculia apetala* (Jacq.) Karst., have irritating or allergenic hairs (Little and Wadsworth 1964). A large number of toxic and irritating species are scattered throughout the Tropics. Complete avoidance of these species by sensitive individuals and the use of disposable gloves, gauze masks, and other protective clothing by those who must work with them is strongly recommended.

CONCLUSIONS

A high degree of diversity is common in the Tropics, especially in the humid lowlands. In single-species operations, such as the extensive plantations of *Pinus* spp., natural diversity is irrelevant. But organizations that service a wide variety of users with diverse needs, and ecosystem restoration projects where nature dictates the species to plant, cannot ignore diversity. Poorly known species and species with difficult reproductive characteristics must be accommodated. With a good understanding of biology and ecology, innovative thinking, and a little luck, most of these new species can be collected and grown. In some cases research can provide answers, but for a few species, and for a variety of reasons, consistent collection and processing of viable seeds may be impossible. In a 14-year study of species suitable for revegetation of bauxite mine lands in Trombetas, Brazil, 600 species were evaluated and 160 were grown and outplanted; only 89 taxa demonstrated acceptable survival and growth during the first two years (Knowles and Parrotta 1995).

If diversity is a distinguishing feature of tropical forests, diversity also characterizes seed collection methods in the Tropics. Because the number of species collected is large and the objectives and budgets of seed collecting organizations are varied, a wide array of collection methods must be used. Redundancy is an important feature of high biodiversity; often several alternative species are available to fill any particular need. Seed collectors may not always be successful in harvesting seeds of all the species desired, but by using all the tools available, by taking advantage of seed opportunities as they arise, and by substituting species with similar properties, they can consistently offer an adequate range of seeds and seedlings to users.

CHAPTER 3

Storage

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The importance of seed storage to mankind has been recognized since prehistoric times (Priestley 1986). Most seed storage practices have developed empirically, often as a result of a combination of chance observation and pragmatic decisions on what can be achieved most easily by way of environmental control or modification. In agriculture, for example, the driving force for such empirical knowledge has been the simple practical requirement to store seeds reliably from harvest to the next production season. In silviculture, similarly, advice on storing tree seeds has long been available. For example, one and a half millenia ago it was recommended with regard to chestnut (probably *Castanea mollissima*) that "the fresh seeds should be stored in damp soil placed in the house, and during transport the seeds should be packed in a leather bag, because chestnut seeds will die when exposed to sun and wind" (Ssu-Hsieh Chia 535).

In discussing tree seed storage, we need to consider four principal factors: seed survival (i.e. viability, the ability of a seed to remain alive so that, when required, it will germinate and produce a seedling capable of autotrophic growth); storage environment; storage duration; and the species (actually five factors if variation among seed lots within a species is also considered).

One structure for such an essay would be to emphasize the duration of seed storage required. It is often convenient to classify such requirements into three, somewhat arbitrary, categories: short-term storage, typically from a matter of a few days to perhaps 6 or 9 months; medium-term storage, typically 1 to 5 years (for example, in order to carry stocks of seeds to avoid seed shortages after poor seed-production years); and long-term storage, typically 10 to very many more years (principally for genetic resources conservation). However, long-term seed storage is currently feasible only for species with certain characteristics. Consequently, we believe it is helpful to structure this essay around the principal differences in seed storage behavior among species. While most readers of this essay will be concerned solely with the seeds of trees, literature on other species is also cited here where helpful, since the principal differences among species in seed storage behavior that have been identified apply to all species of higher plants.

CLASSIFICATION OF SEED STORAGE BEHAVIOR

Although far from complete, the world literature includes several comprehensive compendia which provide information on tree seed storage (table 1). Some compendia on seed storage behavior were based on the duration of seed survival (whether air-dried or in soil or water) without considering the role of

Table 1

Collation of Several Compendia of Information on Seed Storage of Tree Species

Reference	Range of Species	Comments
Ewart (1908)	2,371 species of weeds, crops, and trees	Information on seed survival in relation to storage duration in soil, water, air-dry storage (mostly open storage at ambient temperature)
Dent (1948)	244 species of forest trees of India	Information on seed survival in relation to storage duration (mostly open storage at ambient temperature)
Holmes and Buszewicz (1958)	170 species of temperate forest trees	Information on seed survival in relation to storage duration and environment
Altman and Dittmer (1972)	123 species of weeds, crops, and trees of temperate climate	Information on seed survival in relation to storage duration and environment
Harrington (1972)	857 species of weeds, crops, and trees of temperate climate	Information on seed survival in relation to storage duration and environment
Wang (1974)	48 species of temperate forest trees	Information on seed survival in relation to storage duration and environment
King and Roberts (1979)	77 species (mostly trees) with recalcitrant seed storage behaviour	Information on seed survival in relation to storage duration and environment of recalcitrant seeds
Hofmann and Steiner (1989)	211 species (mostly trees) with recalcitrant seed storage behaviour	Updated list of species with recalcitrant seeds
Gordon (1992)	40 genera of temperate forest trees	Advice on medium-term tree seed storage environments
Tompsett and Kemp (1996)	120 species within 29 genera of tropical forest trees	Summary of authors' results of studies in seed desiccation and/or storage
Hong and others (1996)	6,914 species within 2,069 genera and 251 families including crops, and trees all over the world	Classification of seed storage behavior with information on seed survival in relation to desiccation and storage

environmental factors on seed longevity (e.g. Altman and Dittmer 1972, Ewart 1908, Harrington 1972). It was later found that certain species' seeds classified initially as "microbiotic" by Ewart (1908) or "short-lived" seeds (e.g. Harrington 1972) can in fact be stored for long periods of time under more suitable conditions. Therefore, later compendia have classified species on the basis of seed desiccation tolerance and/or the response of seed survival or longevity to environment (Hong and others 1996, King and Roberts 1979, Tompsett and Kemp 1996).

In this article we consider seed survival and longevity in the context of the response to environment, three different, discrete categories having been identified: orthodox seed storage behavior (Roberts 1973); recalcitrant seed storage behavior (Roberts 1973); and intermediate seed storage behavior (Ellis and others 1990a).

ORTHODOX SEED STORAGE BEHAVIOR

Orthodox seeds can be dried without damage to low moisture contents and, over a wide range of environments, their longevity increases with decreases in seed storage moisture content and temperature in a quantifiable and predictable way (Roberts 1973). The latter is defined by the seed viability equation

$$v = K_i - p / 10^{K_E - C_W \log_{10} m - C_H t - C_Q t^2}, \qquad (1)$$

where v is probit percentage viability after p days in storage at m percent moisture content (w.b.), t°C, K_i is a constant specific to the seed lot, and K_E, C_W, C_H and C_Q are species viability constants (Ellis and Roberts 1980). The constant K_i indicates the initial viability (in probits) of the seed accession when placed in storage. The value of K_i may vary considerably among different seed lots within a species, for example as a result of differences in seed production environment, time of harvest, or genotype (e.g. Ellis and others 1993).

The constants C_H and C_Q together describe the response of seed longevity to temperature. The particular form of the relation between longevity and temperature is a negative curvilinear semi-logarithmic relation whereby the relative benefit to longevity of each 10 °C reduction in temperature (i.e. Q_{10}) declines, the cooler the temperature (Dickie and others 1990, Ellis and Roberts 1981). A comparison of contrasting species, which included one tree species, found that the values of the temperature terms C_H and C_Q did not differ significantly among species (Dickie and others 1990). Similarly, the values of C_H and C_Q determined for four forest tree species (*Liquidambar styraciflua* L., *Pinus elliottii*, *Pinus taeda*, and *Platanus occidentalis*) by Bonner (1994) were 0.0306-0.0508 and 0.000328-0.000976, respectively, and thus close to the common estimates for diverse species of 0.0329 and 0.000478, respectively, determined previously (Dickie and others 1990). This suggests that seed longevity in all orthodox species may well show a similar quantitative response to storage temperature.

At one temperature, the gradient of the negative logarithmic relation between seed moisture content (m) and longevity provides the value of the constant C_W. Thus the value of this constant quantifies the effect of moisture content on longevity. The value of C_W differs considerably among species. For example, the values of C_W collated by Hong and others (1996) for 53 species from 24 families vary from 0.983 for *Pinus elliottii* (Bonner 1994) to 6.305 for *Sorghum bicolor* (Kuo and others 1990). In general, species having seeds with a high starch content, e.g. cereals, have high values for C_W (around 6) but in oily seeds it is much lower, e.g. between 3.5 and 4 for onion (*Allium cepa*) and soyabean (*Glycine max*). Since tree seeds are generally rich in oil in the embryo and/or endosperm (Tompsett and Kemp 1996), tree species tend to have lower values for C_W, e.g. 0.983 for *Pinus elliottii* (Bonner 1994) and 4.23 for Norway maple (*Acer platanoides*) (Dickie and others 1991). In one comparison of estimates of C_W, the mean value for forest tree species was 2.8 compared with a mean value of 4.72 for herbaceous species (Tompsett 1994). One consequence is that to obtain the same relative increase in longevity it is necessary to dry orthodox tree and oily seeds more than starchy seeds from a given initial moisture content.

As a consequence of the negative logarithmic relation between seed moisture content and longevity, the relative benefit to longevity becomes greater for each successive reduction in moisture content. For example, based on the viability parameters estimated for *Ulmus carpinifolia* seeds by Tompsett (1986), the effect of a reduction from 7 percent to 5 percent moisture content provides about a 2.7-fold increase in longevity whereas a reduction from 5 percent to 3 percent in seed moisture content increases seed longevity about 4.5-fold. There appears, however, to be a common response of longevity to equilibrium relative humidity among contrasting crop species, at least, whereby longevity increases by a factor of about 2.2 for each 10 percent reduction in equilibrium relative humidity (Ellis and others 1990c, Zanakis and others 1993). However, we do not yet know whether this generalization for seeds of arable and horticultural crops also applies to tree seeds.

There are two limits to the negative logarithmic relation between seed moisture content and seed longevity (Roberts and Ellis 1989). One is an upper limit, above which seed longevity in hermetic storage is no longer reduced with further increases in moisture, and above which in aerated storage seed longevity increases with further increase in moisture content (Roberts and Ellis 1982). The other is a lower limit, below which further reduction in moisture content no longer increases longevity in hermetic storage (Ellis and others 1988, 1989, 1990b, 1990c, 1992). The upper moisture-content limit appears to be 11 to 12 percent in pine (*Pinus elliottii* and *Pinus taeda*) (Bonner 1994), 22 percent in elm (*Ulmus carpinifolia*) (Tompsett 1986) and *Araucaria columnaris* (Tompsett 1984a), and between 15 percent in lettuce (*Lactuca sativa*) (Ibrahim and Roberts 1983) to about 26 percent in durum wheat (*Triticum durum*) (Petruzzelli 1986) for crop species. Despite wide variation among species in terms of moisture content, these values coincide with a water potential of about -14 MPa (Roberts and Ellis 1989, Zewdie and Ellis 1991), i.e. the upper moisture-content limit to the viability equation occurs when seed moisture contents are in equilibrium with about 90 percent relative humidity (r.h.) at 20 °C. The lower limit varies substantially between crop species, e.g. between about 6 percent moisture content for pea (*Pisum sativum*) and mungbean (*Vigna radiata*), and about 2 percent for sunflower (*Helianthus annuus*) (Ellis and others 1988, 1989). However, these variant moisture contents coincide with 10 to 12 percent equilibrium relative humidity at 20 °C (Ellis and others 1988, 1989, 1992) or with a seed water potential of about -350 MPa at this temperature (Roberts and Ellis 1989). We do not yet know whether this lower limit also applies to forest tree seeds.

In open storage (i.e. where seeds are exposed directly or indirectly to ambient relative humidity; e.g. in a paper bag, cloth bag, or thin, unsealed polythene bag which permits seed moisture content to be influenced by ambient relative humidity) at ambient temperature the longevity of orthodox seeds varies considerably. For example, viability of *Salix* spp. cannot be maintained beyond 10 days in open storage (Brinkman

1974b) while seeds of *Cassia multijuga* were capable of 100 percent germination when tested after 158 years in open storage at room temperature in a Mediterranean climate (Becquerel 1934). For the maintenance of viability in long-term storage, *Salix* spp. require hermetic storage at low moisture contents and cool temperatures, e.g. sub-zero temperatures and moisture contents in equilibrium with 10 to 30 percent r.h. (relative humidity) (Zasada and Densmore 1977). Clearly, seeds of *Cassia multijuga* do not need such precise control of the storage environment in order to maintain viability in storage over the long term.

Provided estimates of the viability constants are available, the viability equation can be applied to determine suitable air-dry storage environments for a given duration of storage for a particular orthodox species. Since the same storage life can be achieved by different combinations of storage temperature and seed moisture content–the precise values depending upon species–there can be considerable flexibility. Since the relative benefit to longevity from reducing temperature becomes less the lower the storage temperature, while the relative benefit to longevity from reducing moisture content becomes greater the lower the moisture content (within the wide range of environments over which the viability equation applies) (Ellis and Roberts 1980), it is often more cost-effective to reduce seed moisture content than to lower storage temperature. This approach is of particular importance for seed storage centers where refrigeration to zero and sub-zero temperatures cannot be provided. In such situations it has been recommended that the seeds be dried to moisture contents in equilibrium with 10 to 12 percent r.h. at 20 °C and then stored hermetically at ambient or (preferably) cooler temperatures (Ellis and others 1989). This low-technology approach has been described by some as "ultra-dry" seed storage (International Board for Plant Genetic Resources 1992). Results from a 5-year investigation have shown that the longevity of ultra-dry seed at ambient temperatures is greater than that of crop seeds stored at 5 to 6 percent moisture content, at least for several crops (Ellis and others 1996). Similarly, over a much longer duration, 90 percent germination of seeds of barley (*Hordeum vulgare*) was reported when tested after 110 years in ultra-dry storage (3.1 percent moisture content) at 10 to 15 °C (Steiner and Ruckenbauer 1995). However, to date, ultra-dry seed storage has not been applied to tree seeds to our knowledge.

Successful storage of orthodox tree seeds over the long term under the FAO/IPGRI preferred conditions, i.e. 3 to 7 percent moisture content and -18 °C (Food and Agriculture Organization/International Plant Genetics Resources Institute 1994), has been realized for more than two decades in the Royal Botanic Gardens' Kew Seedbank (Linington 1994) and for about 7 years at the International Institute of Tropical Agriculture (Ng and others 1993). For example, seeds of *Rhus verniciflua* and *Acacia tortilis* stored in the Kew Seedbank since 1970 and 1974, respectively (Linington 1994), showed 100 percent germination in recent tests (Hong and others 1996).

Long-term storage of orthodox tree seeds has also been achieved by cryopreservation (or cryostorage) at ultra-low temperatures from -80 °C to -196 °C with liquid nitrogen (Pence 1991b, Stanwood 1985, Touchell and Dixon 1993, Wang and others 1993). For example, no loss in viability was reported for *Pinus ponderosa*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla* following 3 years of cryopreservation in liquid nitrogen (Stanwood 1985). An essential first step in seed cryopreservation is the determination of optimum (safe) moisture contents for each orthodox species, particularly those with oily seeds. Wang and others (1993) collated information on the cryopreservation of orthodox tree seeds; it suggests that moisture contents between 3.8 and 11 percent are safe for at least short periods of time (from 4 days to 3 years). However, a loss in viability of about 10 percent following 14 days storage in liquid nitrogen at 6 to 8 percent moisture content was reported for seeds of certain tree species (Wang and others 1993). One possible cause of problems with liquid nitrogen seed storage is the requirement to optimize both the rate of cooling and the subsequent rate of warming; these must be determined empirically (Meryman and Williams 1981). Pretreatment with cryoprotectants sometimes improves seed survival in liquid nitrogen, but in some circumstances can be damaging (Touchell and Dixon 1993). Mechanical injury to seed by direct immersion into liquid nitrogen causing loss in viability has also been reported for some species (Pritchard and others 1988, Wang and others 1993). Finally, despite suggestions of infinite seed longevity by cryopreservation in liquid nitrogen, there is no firm evidence that reducing seed storage temperatures much below -20 °C results in further significant benefits to longevity, at least for tree seeds (Stanwood 1985; Tompsett 1986, 1994). For example, Tompsett (1986) found similar longevity for *Ulmus carpinifolia* seed stored at -13 °C and -75 °C.

For the maintenance of viability over the medium term, i.e. a period of 2 to 10 years or so, hermetic storage in a wide range of contrasting environments can be successful. For example, with relatively high moisture contents (in the air-dry range) combined with cool temperatures, e.g. 8 to 10 percent moisture content and 0 to 10 °C for most leguminous trees (Albrecht 1993), or low moisture contents combined with relatively warm temperatures, e.g. 3 to 7 percent moisture content and 10 °C to ambient temperatures, e.g. Barton (1961) reported 33 percent germination for *Ulmus americana* L. seeds following 4 years of hermetic storage at 3 percent moisture content at room temperature. Ultra-dry seed storage may be applicable to tree seeds for medium-term storage at ambient temperatures. For example, Joseph (1929) and Brinkman (1974a) recommended that seeds of *Betula* spp. be stored at moisture contents as low as 0.6 to 1 percent at room temperature. For practical advice on medium-term tree seed storage see Gordon (1992).

In addition to air-dry storage over a very wide range of different environments, successful storage of orthodox seeds over the short-term, from a few months to 1 or 2 years, can also be achieved by moist storage at cool temperatures. This approach is commonly used for tree species that exhibit strong dormancy such as those adapted to temperate climates (i.e. temperate latitudes and high altitudes of the Tropics) since prechilling during storage can remove dormancy. For example, several orthodox tree species of temperate climates, such as *Carya* spp., *Chionanthus virginicus*, *Euonymus* spp., *Hamamelis virginiana*, *Ilex* spp., *Juglans* spp., *Juniperus* spp., *Liriodendron tulipifera*, *Nyssa* spp., *Picea* spp., and *Taxus* spp. can be stored moist at 3 to 5 °C (Schopmeyer 1974). Similarly, orthodox seeds of several species that are native to high altitudes in the Tropics and show considerable dormancy can also be stored moist at 3 to 5 °C. For example, seeds of *Prunus africana*, native to high mountains between 900 m and 3400 m in Africa (Albrecht 1993), and *Michelia champaca* L. and *Michelia compressa*, native to high mountains of Asia (Lin and Wu 1995), can be stored moist at 4 °C for 1 year (Albrecht 1993, Lin and Wu 1995). In addition, seeds of some pioneer forest trees that have an absolute requirement for light in order to germinate can also be stored moist in the absence of light at ambient temperature for long periods of time. For example, seeds of *Piper aequale* can be maintained for 7 years fully imbibed in darkness without loss in viability (Vázquez-Yanes and Orozco-Segovia 1996).

RECALCITRANT SEED STORAGE BEHAVIOR

Recalcitrant seeds cannot be dried without damage (Roberts 1973) and so their longevity does not respond to air-dry environment in the manner described by the seed viability equation (1). When freshly harvested recalcitrant seeds are dried, viability is at first slightly reduced as moisture is lost, but then begins to be reduced considerably at a certain moisture content, termed the "critical moisture content" (King and Roberts 1979) or "lowest safe moisture content" (Tompsett 1984b). If drying continues further, viability is eventually reduced to zero.

Critical moisture contents for loss of viability on desiccation vary greatly among the recalcitrant species (Chin 1988, King and Roberts 1979), among cultivars and seed lots (Chin 1988, King and Roberts 1979), and depending upon the stage of seed maturity at time of collection (Finch-Savage and Blake 1994, Hong and Ellis 1990). The critical moisture content may also vary with the method of seed drying (Farrant and others 1985, Pritchard 1991, Pritchard and Prendergast 1986). The values of the "lowest safe moisture content" vary between extremes of about 23 percent for cocoa (*Theobroma cacao*) (Mumford and Brett 1982) to 61.5 percent for *Avicennia marina* (Farrant and others 1986). Despite this variation, these moisture contents are equivalent to a relatively narrow band of relative humidities of 96 to 98 percent, or seed water potentials of about -1.5 MPa to -5 MPa (Dickie and others 1991, Poulsen and Eriksen 1992, Pritchard 1991, Roberts and Ellis 1989, Tompsett and Pritchard 1993).

There is no satisfactory method of maintaining the viability of recalcitrant seeds over the medium and long term. Since they cannot be dried neither can they be stored at subzero temperatures, because they would be then killed by freezing injury resulting from ice formation. The longevity of recalcitrant seeds is short, from a few weeks to a few months for species adapted to tropical environments (King and Roberts 1979), and up to about 3 years for several species adapted to temperate environments (Suszka and Tylkowski 1981, 1982). However, if the optimum storage environments are carefully determined, longevity of several tropical recalcitrant seeds can be extended to 3 years, at least for species of *Symphonia globulifera* (Corbineau and Côme 1989).

The principle of successful moist seed storage for recalcitrant seeds is that seeds must be maintained at moisture contents close to that at which they are shed, with continuous access to oxygen; these circumstances minimize seed deterioration since repair mechanisms can operate (Villiers 1975). Under these conditions (high seed moisture and available oxygen), however, seeds tend to germinate. Clearly it is also essential that the conditions should prevent or at least delay germination. It is therefore easier to store recalcitrant species with dormant seeds (either primary dormancy or induced dormancy) than with nondormant seeds under such conditions. For nondormant seeds, as shown by most tropical tree seeds at maturity (King and Roberts 1979), low temperatures can reduce the rates of both seed deterioration and germination provided they remain above the value that results in chilling damage or the lower value at which ice crystallization occurs. For example, chilling injury occurs at between 5 and 10 °C for *Shorea roxburghii*, 5 and 12 °C for *Symphonia globulifera* and *Hopea odorata* Roxb. (Corbineau and Côme 1988). Determination of the optimum temperature for imbibed seed storage is required for each recalcitrant species. A suggested protocol for determining these values has been described elsewhere (Hong and Ellis 1996). The optimum temperature appears to be that at which nondormant seeds remain alive but are unable to germinate, i.e. the base temperature for germination (Corbineau and Côme 1988, Pritchard and others 1996). For example, the optimum storage temperatures determined in this way are 10 °C for *Shorea roxburghii*, 12 °C for *Mangifera indica*, and 15 °C for *Hopea odorata* and *Symphonia globulifera* (Corbineau and Côme 1988). However, recalcitrant seeds of species adapted to temperate climates (including high altitudes in the Tropics) show considerable dormancy which requires long periods of prechilling at 2 to 5 °C to overcome. Furthermore, seeds of many temperate species with recalcitrant seed storage behavior have the ability to germinate at 2 to 5 °C, and thus moist storage of such recalcitrant seeds at 0 to 10 °C may result in germination during storage. In such cases, germination may be prevented by reducing seed moisture content slightly (by about 5 percent below that of fresh seeds), or either reducing the storage temperature to below the optimum prechilling temperature (e.g. 0 to -3 °C) (Suszka 1978) or increasing it to the base temperature for germination of dormant seeds (Pritchard and others 1996). For example, the viability of seeds of sycamore (*Acer pseudoplatanus*) and *Quercus robur* can be maintained for 3 years at 24 to 32 percent and 40 to 45 percent moisture content, respectively, at -1 to -3 °C (Suszka 1978, Suszka and Tylkowsky 1981, Tylkowsky 1989), and horsechestnut (*Aesculus hippocastanum*) for 3 years if moist dormant seeds are stored at 16 °C, although in this case subsequent prechilling is required to remove dormancy (Pritchard and others 1996).

In practical terms, species with recalcitrant seeds can therefore be divided into two subcategories (Bonner 1990, Hong and Ellis 1996): those adapted to tropical climates, and those adapted to temperate climates (i.e. temperate latitudes, or high altitudes in the Tropics). In general, the viability of recalcitrant seeds can be maintained (albeit only for limited periods in aerated conditions) at moisture contents just less than fully imbibed, i.e. about 2 to 5 percent below those of fresh seeds, or in equilibrium with 98 to 99 percent r.h., at optimum storage temperatures which vary from about 7 °C to 17 °C among species adapted to tropical climates, and between about -3 °C and 5 °C among many of those adapted to temperate climates (Hong and others 1996). Maintaining recalcitrant seeds fully imbibed or subimbibed, with continuous aeration, and at the same time preventing germination and fungal contamination, is difficult. Aeration can result in loss of seed moisture, and respiration can quickly deplete oxygen. The storage medium is therefore very important for recalcitrant seeds. It should fulfill two functions: first, to maintain seed moisture constant at high values; second, to allow diffusion of sufficient oxygen to the moist seeds. The storage of moist recalcitrant seeds in damp charcoal, sawdust, or moist sand is generally reported to be more efficient than storage in polyethlene bags. Storage at or near the harvest moisture content in media such as sawdust (at 16 percent moisture content) or perlite (at 0 to 4 percent moisture content) within suitable containers, such as open-weave sacks or bags, placed in a high-humidity room has been recommended (Tompsett and Kemp 1996). Coating recalcitrant seeds with alginate or alginate with ABA was also reported to extend seed lifespan by a factor of up to 3 or 4 (Pammenter and others 1997).

Cryopreservation of zygotic embryos has been reported to be successful for a number of tree species that show orthodox, intermediate, or recalcitrant seed storage behavior (Engelmann and others 1995b). For successful cryopreservation, excised embryos or embryonic axes must survive desiccation below the threshold freezable moisture content (Hor and others 1990) of about 18 to 33 percent (see Hong and others 1996), below which value there is no freezable water for ice formation in ultra-low temperatures. Embryos and embryonic axes of some recalcitrant species are able to survive desiccation to lower moisture contents than are the whole seeds (Chandel and others 1995, Chin 1988, Finch-Savage 1992a, Normah and others 1986). For example, fresh seeds (36 percent moisture content) of *Hevea brasiliensis* tolerated desiccation to 20 percent moisture content, but no seeds survived further desiccation to 15 percent moisture content (Chin and others 1981). However, after desiccation to 16 percent moisture content followed by 16 hours cryopreservation in liquid nitrogen, 87 percent and 69 percent, respectively, of the excised embryonic axes (55 percent moisture content) survived (Normah and others 1986). Unfortunately, embryos of many recalcitrant seeds are damaged by desiccation before seed moisture content is reduced below those values at which ice crystallization no longer occurs, and so the cryopreservation of excised embryos of these species results in death, either by ice formation for embryos at moisture contents above the threshold freezable moisture content, or by desiccation to moisture contents below that threshold (Hor and others 1990).

Fast drying (also termed “flash” drying) may allow excised embryos to survive desiccation to lower moisture contents than those dried more slowly within intact seeds (Finch-Savage 1992a, Normah and others 1986, Pammenter and others 1991, Pritchard 1991, Pritchard and Prendergast 1986). Excised embryos or embryonic axes can be dried quickly in a laminar airflow cabinet at room temperature (e.g. Normah and others 1986) or under a flow of compressed air at about 9 liters min^{-1} (Pammenter and others 1991). After flash drying of embryonic axes extracted from mature seeds of *Landolphia kirkii* reduced moisture content from 67 percent to 23 percent in 30 minutes, 90 percent of the excised embryonic axes were able to germinate (Pammenter and others 1991). Fast drying with silica gel or with an aseptic air current has allowed excised embryonic axes to survive desiccation to a lower value than that achieved by vacuum drying (Fu and others 1993). The stage of maturity of the seeds from which the embryos are excised is an important factor influencing survival following desiccation: embryos excised from mature seeds not only survived desiccation to lower moisture contents than immature embryos, but also survived subsequent cryopreservation in liquid nitrogen (Chandel and others 1995, Engelmann and others 1995b). Fast freezing can allow desiccated embryos to better survive cryopreservation in liquid nitrogen (Berjak and Pammenter 1997). In contrast, slow freezing with immature excised embryos of cocoa has been reported to be more successful than fast freezing (Pence 1991a). The specimen to be frozen must be as small as possible, and pretreatment of embryos with cryoprotectants, such as DMSO, proline, sucrose, and glycerol (Assy-Bah and Engelmann 1992, Dumet and Berjak 1997, Pence 1991a), are important factors influencing the survival of excised embryos (or embryonic axes) in liquid nitrogen.

Results reported for *Aesculus* spp. (Pence 1990, 1992), *Araucaria hunsteinii* (Pritchard and Prendergast 1986), *Artocarpus heterophyllus* Lam. (cited by Engelmann and others 1995b), *Castanea sativa* (Pence 1990, 1992), *Citrus hystrix* (Normah and Serimala 1997), *Coffea liberica* (Hor and others 1993, Normah and Vengadasalam 1992), *Cocos nucifera* (Assy-Bah and Engelmann 1992, Chin and others 1989), *Dimocarpus longan* (Fu and others 1990, 1993), *Hevea brasiliensis* (Normah and others 1986), *Landolphia kirkii* (Vertucci and others 1991), *Quercus* spp. (González-Benito and Perez-Ruiz 1992; Jorgensen 1990; Pence 1990, 1992), *Trichilia dregeana* (Dumet and Berjak 1997) and *Theobroma cacao* (Pence 1991a) have shown the feasibility of the cryopreservation of excised embryos or embryonic axes of recalcitrant seeds. However, others have reported a lack of success using the same species. For example, experiments with excised embryos of *Artocarpus heterophyllus* (Dumet and Berjak 1977), *Landolphia kirkii* (Dumet and Berjak 1977), and *Quercus robur* (Poulsen 1992, Chmielarz 1997) found that none survived cryopreservation in liquid nitrogen.

INTERMEDIATE SEED STORAGE BEHAVIOR

Although the term "intermediate seed storage behavior" was introduced only at the beginning of this decade, this third category of seed storage behavior was hinted at more than eight decades ago. Elliott (1912, cited by Baldwin 1942) divided temperate forest tree seeds into three classes: (i) those that can be dried, (ii) those that can survive partial drying, and (iii) those that can rarely be dried at all. The first and third classes are more or less equivalent to the orthodox and recalcitrant categories of seed storage behavior defined in detail by Roberts (1973), respectively; the second class is equivalent to the "intermediate seed storage behavior" defined by Ellis and others (1990a).

The definition of intermediate seed storage behavior is based on the response of longevity to storage environment. In seeds showing intermediate seed storage behavior, the trend toward increasing longevity the lower the seed storage moisture content (within the air-dry range) is reversed at a comparatively high moisture content, whereby at lower moisture contents longevity is reduced (Ellis and others 1990a, 1991a, 1991b, 1991c). But in such species it is also often (but not always) observed that seeds may be damaged immediately by desiccation to relatively low moisture contents, about 7 to 12 percent moisture content depending on species. The critical moisture contents of intermediate seeds below which more rapid loss in viability occurs during hermetic storage varies considerably with species, degree of maturity, and method of seed extraction and/or postcollection handling. In general, seeds extracted from fruits at maturity tolerate desiccation to moisture contents in equilibrium with about 40 to 50 percent r.h., i.e., about 10 percent moisture content for arabica coffee (*Coffea arabica*) (Ellis and others 1991a, Hong and Ellis 1992a) and 7 percent moisture content for *Citrus* spp. (Hong and Ellis 1995). A further feature of intermediate seeds of tropical origin is the fact that the longevity of dry seeds (7 to 10 percent moisture content) is reduced with reduction in storage temperature below about 10 °C (Ellis and others 1990a, 1991a, 1991b, 1991c; Hong and Ellis 1992a). In such cases, then, there is an optimum air-dry storage environment for the maintenance of seed viability. In arabica coffee this is about 10 °C with 10 to 11 percent moisture content (Hong and Ellis 1992a).

It is now known that seeds of neem (*Azadirachta indica* A. Juss) (Gaméné and others 1996; Hong and Ellis 1998; Sacandé and others 1997a, 1997b), *Cinnamomum subavenium* (Lin 1996), several *Citrus* species (Hong and Ellis 1995), *Coffea arabica* (Ellis and others 1990a, 1991a; Hong and Ellis 1992a), robusta coffee (*Coffea canephora*) (Hong and Ellis 1995), oil palm (*Elaeis guineensis*) (Ellis and others 1991c), *Khaya senegalensis* (Hong and Ellis 1998), *Lindera megaphylla* (Lin 1996), *Neolitsea parvigemma* (Lin 1996), and *Swietenia macrophylla* (Hong and Ellis 1998, Pukittayacamee and others 1995) show intermediate seed storage behavior. Among about 7,000 species examined in a recent survey, about 134 species are believed to show intermediate seed storage behavior (Hong and others 1996). Many of these species are trees of tropical origin, but a few are herbaceous (Hong and others 1996). For example, that survey suggests that the following important tree species may show intermediate seed storage behavior: *Acer macrophyllum*, *Afrocarpus gracilior*, *Agathis* *macrophylla*, *Araucaria columnaris*, *A. nemorosa*, *A. rulei*, *A. scopulorum*, *Bertholettia excelsa*, *Bixa orellana*, *Chrysophyllum cainito*, *Dacrycarpus dacrydioides*, *Dipterocarpus alatus* Roxb. & G. Don, *D. intricatus*, *D. tuberculatus*, *Dipteryx odorata*, *Rhapidophyllum hystrix*, and *Virola surinamensis* (Hong and others 1996).

From the point of view of optimum air-dry seed storage environments, it may be helpful to distinguish between species with intermediate seed storage behavior adapted to tropical environments and those adapted to temperate environments (including high altitudes in the Tropics). For example, intermediate seeds of tropical origin such as arabica coffee (Bendana 1962, Wellman and Toole 1960) and papaya (*Carica papaya*) (Bass 1975) can be stored at moisture contents in equilibrium with 50 percent r.h. (9 to 10 percent moisture content) and 10 °C for up to 5 and 6 years, respectively, without loss in viability. The viability of intermediate seeds of temperate origin is also maintained well at moisture contents in equilibrium with about 50 percent r.h., but at cooler temperatures of 5 °C to -10 °C. For example, seeds of *Corylus avellana* can be stored hermetically at -5 °C with 10 to 13 percent moisture content (Degeyter 1987). Species showing intermediate seed storage behavior can be stored successfully over the medium term, therefore, provided optimum environments have been defined and can be maintained.

Like orthodox seeds, intermediate seeds can also be stored moist at cool temperatures if germination is either prevented or delayed. For example, seeds of arabica coffee (Van der Vossen 1979) and tea (*Camellia sinensis*) (Amma and Watanabe 1983) were stored moist at 15 °C and 1 °C, respectively, for 2.5 and 6 years, respectively, with little loss in viability.

The situation regarding the cryopreservation of intermediate seeds is a little confused. Despite reports of the immediate death of (whole) seeds of species with intermediate seed storage behavior following cryopreservation in liquid nitrogen, e.g. arabica coffee (Becwar and others 1983), *Corylus avellana* (Normah and others 1994), *Corylus cornuta* (Stanwood and Bass 1981), oil palm (Grout and others 1983), and *Roystonea regia* (Kunth) O.F. Cook (Ellis and others 1991c), there have been several reports of the survival of dry seeds of species with intermediate seed storage behavior following immersion in liquid nitrogen, e.g. *Camellia sinensis* (Hu and others 1994), *Carica papaya* (Becwar and others 1983, Chin and Krisnapillay 1989), *Citrus aurantifolia*, and *Citrus halimii* (Normah and Serimala 1997). This implies that it may be possible to improve cryopreservation techniques to make them suitable for intermediate seeds.

Since the whole seeds of species with intermediate seed storage behavior tolerate desiccation to relatively low moisture content (7 to 10 percent), desiccated embryos may have a greater chance to survive cryopreservation in liquid nitrogen than is the case for recalcitrant seeds (see above). Reports of successful cryostorage of excised embryos of *Azadirachta indica* (Dumet and Berjak 1977), *Camellia sinensis* (Chandel and others 1995; Chaudhury and others 1990, 1991; Dumet and Berjak 1977; Wesley-Smith and others 1992), *Citrus aurantifolia* and *Citrus halimii* (Normah and Serimala 1997), *Coffea arabica* (Abdelnour and others 1992), *Corylus avellana* (González-Benito and Pérez 1994, Normah and others 1994, Pence 1990, Reed and others 1994), *Elaeis guineensis* (Engelmann and others 1995a, 1995b; Grout and others 1983), *Howea forsteriana* (Chin and Krishnapillay 1989, Chin and others 1988), *Poncirus trifoliata* (Radhamani and Chandel 1992), and *Veitchia merrilli* (Chin and Krishnapillay 1989, Chin and others 1988) have shown the potential for long-term seed storage under such conditions.

DESICCATION TOLERANCE AND POTENTIAL SEED LONGEVITY IN DEVELOPING AND MATURING SEEDS

Application of the seed viability equation (1) reveals that initial seed quality (K_i)–potential longevity–plays an important role in ensuring good seed survival in storage. The higher the value of K_i the longer the period of viability for a given storage environment. During seed development and maturation, the value of the seed lot constant K_i–so the potential longevity of orthodox seeds–increases markedly. There is now good evidence in a wide range of contrasting orthodox crop species that potential longevity continues to increase during the period after the end of seed filling, as seeds mature (Demir and Ellis 1992, 1993; Ellis and others 1993; Ellis and Pieta Filho 1992; Pieta Filho and Ellis 1991a, 1991b; Sanhewe and Ellis 1996; Zanakis and others 1994). There is also good evidence that the ability of orthodox seeds to tolerate desiccation to very low moisture contents also improves considerably during the late stages of seed maturation, and indeed one study has, therefore, shown a strong association in developing and maturing seeds between potential longevity (K_i) and the ability of seeds to tolerate desiccation to very low moisture contents (Ellis and Hong 1994).

The ability of seeds to tolerate enforced rapid desiccation has been reported to increase during seed development and maturation of tree seeds with orthodox (Hong and Ellis 1990, 1992b, 1997a), intermediate (Ellis and others 1991a, Hong and Ellis 1995), and recalcitrant seed storage behavior (Finch-Savage 1992a, Hong and Ellis 1990, Tompsett and Pritchard 1993). Orthodox seeds of several crop, wild herb, and tree species are not able to tolerate rapid enforced desiccation to low moisture contents (4 to 5 percent) until some time after mass maturity [defined as the end of the seed-filling phase (Ellis and Pieta Filho 1992)] once maturation drying has reduced seed moisture content on the mother plant substantially (Ellis and Hong 1994; Fischer and others 1988; Hay and Probert 1995; Hong and Ellis 1990, 1992b, 1997a; Wechsberg and others 1993). Maximum tolerance of rapid enforced desiccation occurs some time after mass maturity, probably at natural dehiscence (Hay and Probert 1995; Hong and Ellis 1990, 1992b, 1997a; Sanhewe and Ellis 1996; Wechsberg and others 1993). In addition, the slow desiccation of immature seeds harvested before mass maturity, and well before maturation drying occurs naturally, enables tolerance of rapid desiccation to be acquired (Dasgupta and others 1982, Hay and Probert 1995, Hong and Ellis 1997a, Kermode and Bewley 1985a, Sanhewe and Ellis 1996). For example, in Norway maple (*Acer platanoides*), rapid drying (by reducing moisture content from 57.3 percent to 9 percent within 1 day, and to 5 percent within 4 days) of the seeds harvested at mass maturity reduced viability from 100 percent to 61 percent and 38 percent at 8.1 percent and 4.7 percent moisture content, respectively, while for seeds that were first dried slowly for 32 days, during which period seed moisture content was reduced from 57.3 percent to 29.9 percent, subsequent rapid drying to 3.5 percent moisture content (within 4 days) resulted in 93 percent viability (Hong and Ellis 1997a). The slow drying of seeds or fruits harvested before or at mass maturity has also been reported to increase seed vigor and potential longevity in several crop and wild species (Hay and Probert 1995, Sanhewe and Ellis 1996, TeKrony and Egli 1997).

In addition, desiccation tolerance also decreases when seeds are initially subjected to conditions under which germination is initiated. For example, prechilling, moist storage, presoaking, fermentation treatment for seed extraction, and seed priming can reduce desiccation tolerance, and hence alter seed storage behavior (see Hong and others 1996). Similarly, seeds that are produced in unfavorable environments may show reduced desiccation tolerance to low moisture contents. For example, seeds of a japonica rice (*Oryza sativa* subsp. *japonica*) produced in a hot environment of 32/24 °C (day/night) showed consistently poorer desiccation tolerance at each stage of maturation drying than those produced in a cooler environment of 28/20 °C (Ellis and Hong 1994).

The above implies that considerable care should be taken when collecting, extracting, and subsequently handling tree seeds. It also implies that further improvements in the success of tree seed storage, particularly in the Tropics, can be expected if greater attention is paid to the timing of seed collection, and to postcollection practices.

PREDICTION OF SEED STORAGE BEHAVIOR

Methods, and indeed feasibility, of seed storage depend upon the seed storage behavior shown by a particular species. A simple, two-stage protocol to determine seed storage behavior has been suggested elsewhere (Hong and Ellis 1996). This task is, however, considerable given that there are about 250,000 species of flowering plants. Estimation of likely seed storage behavior would therefore be helpful, and several approaches to doing this have been developed (Hong and Ellis 1996, 1997b, 1998; Hong and others 1996). No single criterion can provide a satisfactory estimation of likely seed storage behavior, but combining information for at least four of the six factors described below may be worthwhile (Hong and Ellis 1996).

PLANT ECOLOGY

There appears to be an association between plant ecology and seed storage behavior (Roberts and King 1980; Tompsett 1987, 1992). From information on seed storage behavior collated for almost 7,000 species from 251 families (Hong and others 1996), it is evident that species that show recalcitrant seed storage behavior do not occur naturally in (i.e. originate from) arid habitats, that is desert and savanna. In such environments, the majority of plant species show orthodox seed storage behavior, while a few may show intermediate seed storage behavior. It is clear, however, that further generalizations are not possible. In particular, for example, at the other ecological extreme it is quite clear that not all species native to moist habitats, rain forests, flooded forests, or aquatic environments show recalcitrant seed storage behavior; all three categories of seed storage behavior can be found among the species native to such moist environments.

TAXONOMIC CLASSIFICATION

Orthodox seed storage behavior can be found in all species within a few families (e.g. Chenopodiaceae, Combretaceae, Compositae, Labiatae, Solanaceae, Pinaceae), or almost all species in others with only a few exceptional species (e.g. Leguminosae, Graminae, Cucurbitaceae, Cruciferae and Rosaceae). However, most families of flowering plants including tree species have species with two (e.g. Anacardiaceae, Dipterocarpaceae, Euphorbiaceae, etc.) or three different categories of seed storage behavior (e.g. Meliaceae). Furthermore, seed storage behavior can differ among species within a genus (Hong and Ellis 1995, Tompsett 1983), or even among sections (Hong and Ellis 1997b).

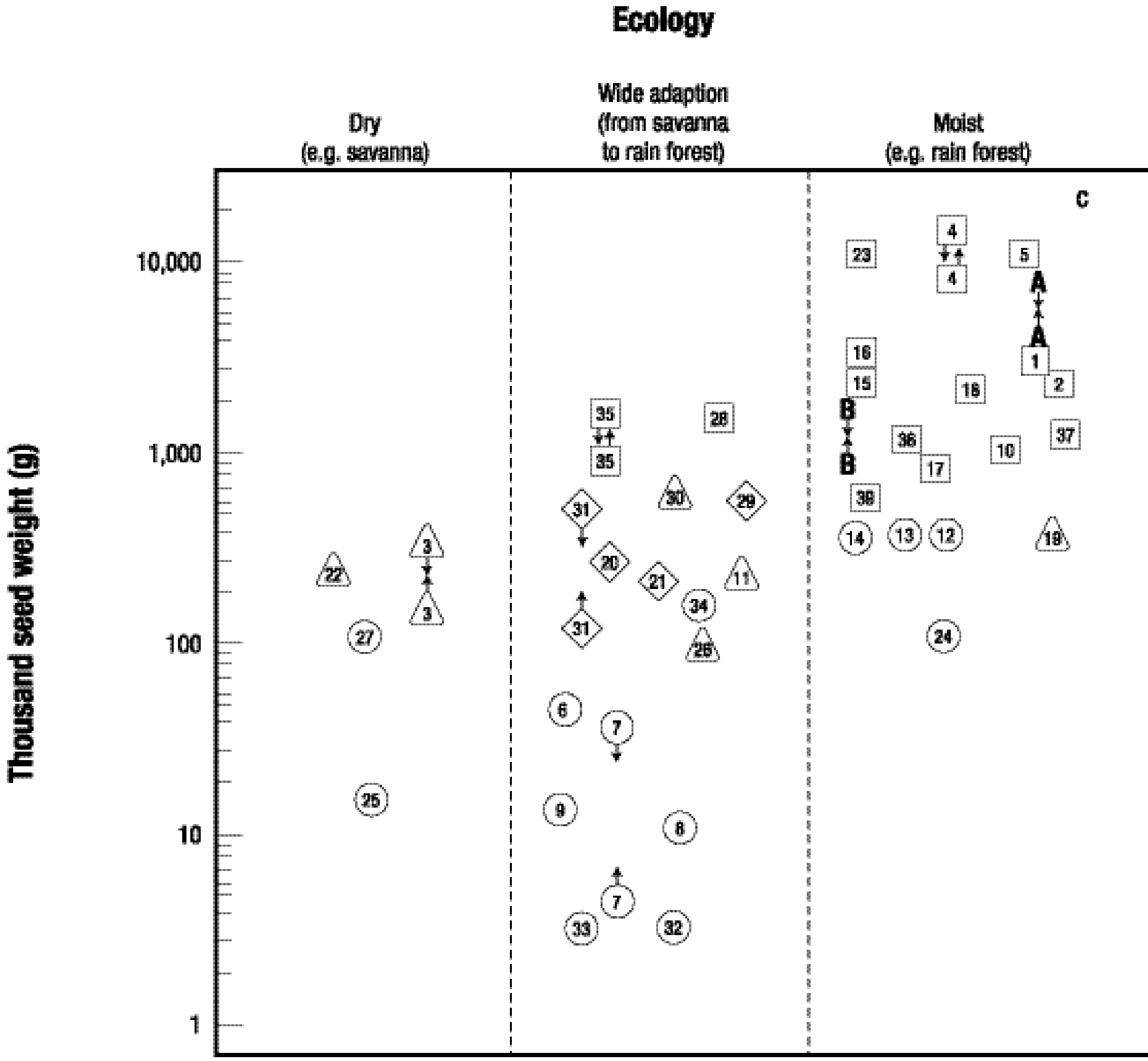
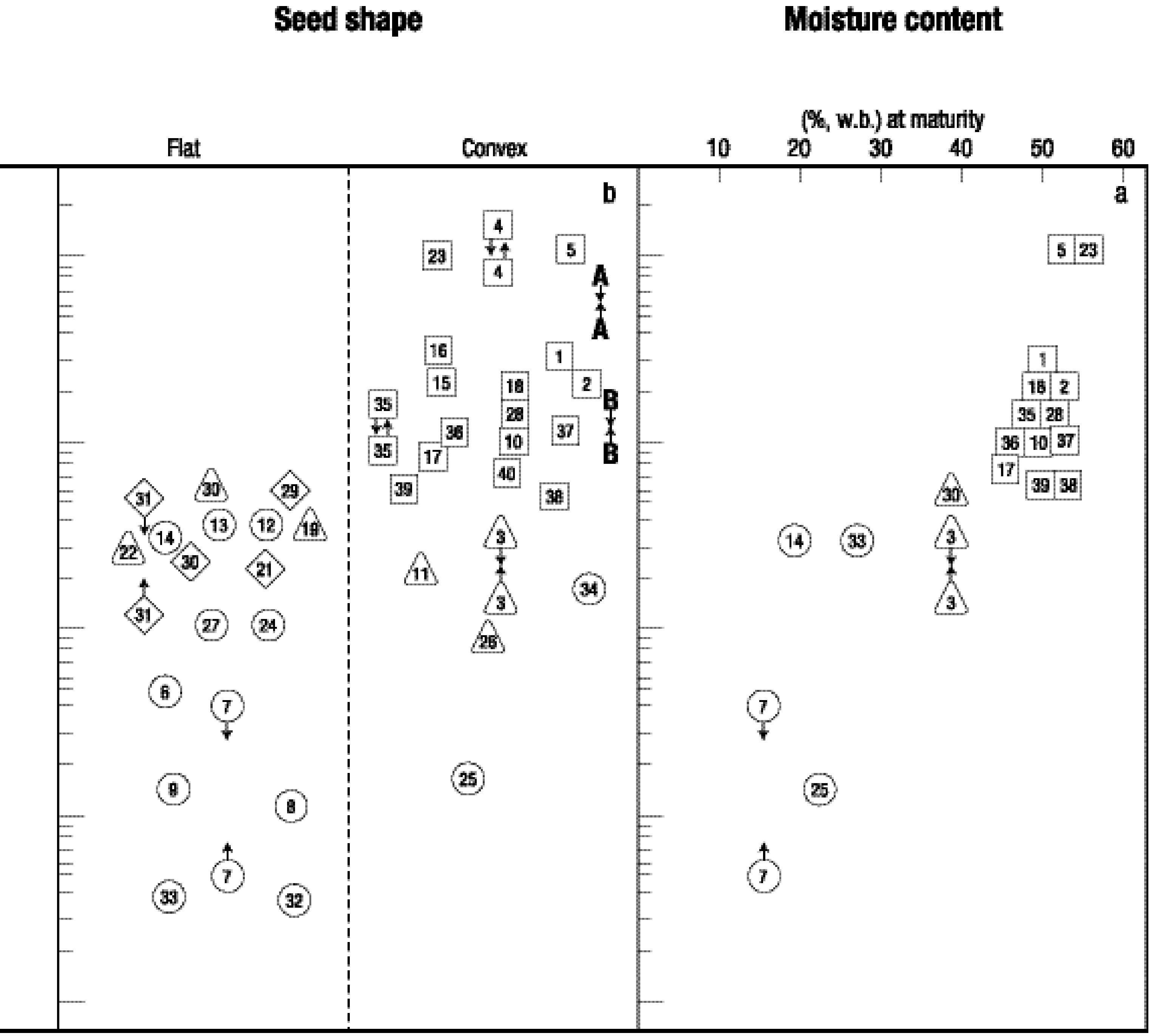


Fig. 1. Variation in thousand seed-weight (logarithmic scale) with that for seed moisture content at maturity or shedding (a), or seed shape (b), or ecology (c) and seed storage behaviour among 40 species of Meliaceae. Seed storage behaviour is classified as orthodox (s), intermediate or probably intermediate (n), recalcitrant or probably recalcitrant (u), or uncertain but not recalcitrant (e). The positions **A** and **B** for *Amoora wallichii* and *Turraeanthus africanus*, respectively, in both of which species seed storage behaviour is unknown, are included in order to test the prediction of seed storage behaviour (see text). Key to species: 1, *Aglaia clarkii*; 2, *Azadirachta excelsa*; 3, *Azadirachta indica*; 4, *Carapa guianensis*; 5, *Carapa procera*; 6, *Cedrela mexicana*; 7, *Cedrela odorata*; 8, *Cedrela toona*; 9, *Chukrasia tabularis*; 10, *Dysoxylum*



cauliflorum; 11, *Ekebergia senegalensis*; 12, *Entandrophragma angolense*; 13, *Entandrophragma candollei*; 14, *Entandrophragma utile*; 15, *Guarea cedrata*; 16, *Guarea sp.*; 17, *Guarea sp. nov (G. glabra)*; 18, *Guarea thompsonii*; 19, *Khaya anthothean*; 20, *Khaya grandiofoliola*; 21, *Khaya ivorensis*; 22, *Khaya senegalensis*; 23, *Lansium domesticum*; 24, *Lovoa trichiloides*; 25, *Melia azedarach*; 26, *Pseudobersama mossambicensis*; 27, *Pseudocedrela kotschyi*; 28, *Sandoricum koetjape*; 29, *Swietenia humilis*; 30, *Swietenia macrophylla*; 31, *Swietenia mahagoni*; 32, *Toona australis*; 33, *Toona ciliata*; 34, *Trichilia americana*; 35, *Trichilia emetica*; 36, *Trichilia martineaui*; 37, *Trichilia megalantha*; 38, *Trichilia monadelpha*; 39, *Trichilia prieuriana*; 40, *Trichilia tessmannii*. From Hong and Ellis 1998.

PLANT, FRUIT, OR SEED CHARACTERISTICS

Certain generalizations appear possible concerning associations between fruit and seed characteristics and seed storage behavior (Hong and others 1996). For example, orthodox seed storage behavior is shown by species that produce achenes, many-seeded berries, many-seeded dehiscent capsules, many dry-seeded pods (but not arillate), many dry-seeded follicles, schizocarps, and utricles (Hong and others 1996). Most species that produce siliques (one exception) and caryopses (three known exceptions) also produce orthodox seeds. On the other hand, however, all three categories of seed storage behavior can be found among species that produce one seed or a few large seeds (from 1 to 10 seeds) per fruit, or many arillate seeds per fruit, among drupes, pods, capsules, berries, and nuts.

SEED SIZE

Recalcitrant seeds often tend to be larger than intermediate seeds, which in turn tend (on average) to be larger than orthodox seeds. However, there is a very wide range of seed weights or sizes over which seeds of different species show all three types of seed storage behavior (Hong and Ellis 1996).

SEED MOISTURE CONTENT AT SHEDDING

A recent survey shows that seed moisture contents at maturity or shedding for species with recalcitrant, intermediate, and orthodox seed storage behavior overlap considerably. No generalization on seed storage behavior is possible for species in which seeds at maturity or shedding have between about 25 percent and 55 percent moisture content (Hong and Ellis 1996).

SEED SHAPE

There appears to be a weak association between seed shape and seed storage behavior. For example, recalcitrant seeds are often spherical or oval (Chin 1988). Seeds that are thin and flat, shapes that aid natural maturation drying, tend to show orthodox seed storage behavior (Tompsett 1994). Flat seeds tend to show orthodox seed storage behavior in *Acer* spp. (Hong and Ellis 1997b), but show both orthodox and intermediate seed storage behavior in Meliaceae (Hong and Ellis 1998). The spherical form is present in all three categories of seed storage behavior (Hong and Ellis 1997b, 1998).

All of the single criterion suggested above are not sufficiently reliable to be very useful as indicators of likely seed storage behavior. However, it may be possible to develop a multiple-criteria predictive framework in order to suggest likely seed storage behavior (Hong and Ellis 1996). For example, combining information on the four criteria–seed weight, seed moisture content at shedding, seed shape, and taxonomy (section)–can form the basis of a guide to likely seed storage behavior among *Acer* spp. (Hong and Ellis 1997b). Similarly, the four criteria of seed weight, seed moisture content at maturity, seed shape, and plant ecology may provide a guide to the estimation of seed storage behavior in Meliaceae (fig. 1). For example, from the two positions designated A in figure 1 for seed weight (TSW = 4300 to 7700 g), ecology (moist evergreen forest of India), seed shape (convex, fleshy aril) of *Amoora wallichii*–information from Luna (1996)–we suggest that this species is likely to show recalcitrant seed storage behavior. Similarly, from the two positions designated B for seed weight (TSW= 1000 to 1400 g [FAO 1975]), seed shape (convex, fleshy aril), and ecology (rain forest of East Africa) (Styles and White 1991) of *Turraeanthus africanus*, we suggest that recalcitrant seed storage behavior is likely in this species also. Furthermore, the information available on natural habitat of the two species can also be used to suggest likely suitable moist seed storage conditions. Given that the *Amoora wallichii* tree is described as “frost-hardy” (Luna 1996), and that *Turraeanthus africanus* grows at an altitude of 1525 m (Styles and White 1991), we suggest that chilling injury is unlikely if the seeds of both species are stored moist at about 10°C.

We propose that a collaborative investigation by seed scientists worldwide may realize larger, more accurate multiple-criteria keys to estimate seed storage behavior and so suitable environments for seed storage. We believe that the approach summarized here is particularly useful for tree seed storage, and that such a collaborative venture is urgently required.

CHAPTER 4

Orthodox and Recalcitrant Seeds

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The seeds of many species cannot be classified as orthodox, and this is particularly so in the case of tropical tree seeds. The views presented here favor a continuum of seed behavior that is based on a variety of characteristics. A suite of mechanisms or processes is discussed that embodies the properties currently thought to promote the acquisition of desiccation tolerance and to ensure survival of the desiccated condition in orthodox seeds. These include: cellular and intracellular physical characteristics; intracellular de-differentiation; the "switching off" of metabolism; the presence and efficient operation of antioxidant systems; the accumulation and roles of putatively protective molecules, including late embryogenic accumulating/abundant proteins (LEA's), sucrose, and certain oligosaccharides; deployment of amphipathic molecules; an effective peripheral oleosin layer around lipid bodies; the occurrence and operation of repair mechanisms during rehydration; and others yet to be identified. The presence of some of the mechanisms/processes, or their absence or partial expression, is considered in the context of the varied responses to dehydration shown by nonorthodox seeds. The factors that determine distinct variations in the behavior of recalcitrant seeds of individual species under the same conditions is given attention, with the effects of drying rate (i.e. the rate of water loss from tissues of desiccation-sensitive seeds) being stressed. Two different factors are distinguished in this regard: (1) damage that occurs at low water contents when nonfreezable water, which is held to stabilize intracellular structures and macromolecules, is removed, which is desiccation damage in the strict sense; and (2) damage that occurs during slow dehydration, when metabolic imbalances are proposed to cause the generation of damaging chemical species, e.g. free radicals, which is termed metabolic damage. Desiccation damage, in the strict sense, is attributed to the lack or inadequate operation of the processes/mechanisms held to protect desiccation-tolerant seeds in the dry state, while metabolic damage is considered in the context that nonorthodox seeds (especially those that are truly recalcitrant) do not possess the suite (or full suite) of mechanisms/processes that facilitate the acquisition and maintenance of desiccation-tolerance as exhibited by maturing and mature orthodox seed-types.

INTRODUCTION

Orthodox seeds (Roberts 1973) acquire desiccation tolerance during development and may be stored in the dry state for predictable periods under defined conditions. Unless debilitated by zero-tolerant storage fungi, orthodox seeds should maintain high vigor and viability at least from harvest until the next growing season (Berjak and others 1989) or for many decades at -18 °C (IBPGR 1976). Generally, such seeds undergo a period of drying during their maturation and are shed at low water content which is in equilibrium with the prevailing relative humidity (r.h.). The equilibrium water content at any particular r.h. is determined by seed composition, but all orthodox seeds can withstand dehydration to around 5 percent (0.053 g H_2O g^{-1} dry material [g g^{-1}]), even when maturation drying is not completed prior to shedding. *Any seed that does not behave this way is not orthodox*, and, in fact, the seeds of a great number of tropical species may accordingly be *nonorthodox*. Nonorthodox seeds have so far been described as either being *recalcitrant* (Roberts 1973) or *intermediate* (Ellis and others 1990a) according to their storage behavior.

Recalcitrant seeds are those that undergo little, or no, maturation drying and *remain desiccation sensitive* both during development and after they are shed. The situation is, however, far more complex than this because of the wide range of variability among recalcitrant seeds of different species and, indeed, of individual species under different conditions (Berjak and Pammenter 1997). Such seeds are shed hydrated, but the water content can generally be anywhere in the range from 0.43 to 4.0 g g^{-1}, which is 30 to 80 percent on a wet mass basis (wmb). Shedding water content is partly species characteristic, depending on the degree of dehydration that occurs late during seed development; this has been suggested to be correlated with the *degree of desiccation tolerance* developed by individual species (Finch-Savage 1996).

Recalcitrant seeds are not equally desiccation sensitive, in that variable degrees of dehydration are tolerated depending on the species. This implies that the processes or mechanisms (see below) that confer desiccation tolerance are variably developed or expressed in the nonorthodox condition. As diverse mechanisms have been suggested to be involved in the acquisition of desiccation tolerance and maintenance of the integrity of dehydrated orthodox seeds, it should be appreciated that any one of these may be absent, or present but ineffective, in recalcitrant seeds. Another important consideration is that desiccation tolerance is probably controlled by the *interplay* of mechanisms or processes, *and not by any one, acting in isolation*. Thus, the absence or incomplete expression of any factor proposed to confer dehydration tolerance could have profound consequences on the ability of a seed species to withstand a measure of dehydration below a particular level of hydration.

Differential desiccation sensitivity among recalcitrant seeds of various species is clearly shown by their different responses when subjected to the same drying regime–those of some species tolerating only a slight degree of dehydration, but others surviving to far lower water contents. There are also marked differences in the rates at which water will be lost from seeds of various species under the same dehydrating conditions (Farrant and others 1989). Other factors, too, influence the postharvest responses of recalcitrant seeds, e.g. developmental status (Berjak and Pammenter 1997, Berjak and others 1992, Berjak and others 1993, Finch-Savage 1996, Finch-Savage and Blake 1994) and chilling sensitivity (Berjak and Pammenter 1997).

In terms of desiccation sensitivity alone, therefore, it is not merely that a seed species *is* recalcitrant, but rather, *how recalcitrant* it is. This fact led to the proposal of a continuum of recalcitrant seed behavior, from species that are highly desiccation–and probably also chilling–sensitive, to those that will tolerate drying to the lowest water content still commensurate with recalcitrant seed behavior and will also tolerate relatively low temperatures (Farrant and others 1988).

The concept of a continuum of postharvest seed behavior (that is, dependent on preshedding developmental events) extends beyond the category of recalcitrant seeds. The continuum grades from extreme desiccation-sensitive types through the minimally recalcitrant types, to the intermediate seed species that do not react adversely to low temperatures, through those that are chilling sensitive when dehydrated (Hong and Ellis 1996), and finally to orthodox seeds that will tolerate less or more extreme dehydration (Vertucci and Roos 1990). It is also possible that there are seed species that behave in a manner that characterizes them as lying *between* the hitherto-defined categories: recalcitrant, intermediate, and orthodox. The idea of an extended continuum of seed behavior from the most desiccation tolerant of orthodox species, to the recalcitrant species that are most sensitive to even slight water loss, embodies many properties of seeds and their responses (Berjak and Pammenter 1994, 1997). It has its foundations in an appreciation of the physiological status of seeds at various water potentials (Vertucci 1993, Vertucci and Farrant 1995, Vertucci and Roos 1990) and the properties of water at the various hydration levels corresponding to specified water potential ranges (Vertucci 1993, Vertucci and Farrant 1995). It is more meaningful to consider seed responses to dehydration in terms of water potential rather than water content, but, since these two measures can be loosely correlated (Vertucci and Farrant 1995), the more familiar water content terminology is used here.

According to Vertucci and Farrant (1995): "Discrete changes in metabolic activity with moisture content are hypothesized to be associated with discrete changes in the physical properties of water… Thus upon the loss of water with certain properties, an essential function provided by [that] water is no longer possible. A tissue that is not damaged by the removal of a certain type of water has developed mechanisms to tolerate or avoid that particular stress." While the discussion that follows is not dependent on the reader's appreciation of the differences in the types of intracellular water, the basis of the arguments presented is that sequential removal of water with specific properties will have particular damaging effects on seed tissues that are not possessed of the appropriate mechanisms or processes to counteract that damage. We will, however, focus on the mechanisms or processes themselves.

MECHANISMS IMPLICATED IN DESICCATION TOLERANCE

It is most expedient to consider the processes or mechanisms listed below, which might confer protection against desiccation, and their deficiency or absence, which could contribute to the *relative degrees of desiccation sensitivity*.

- Intracellular physical characteristics such as
    - — reduction of the degree of vacuolation,
    - — amount and nature of insoluble reserves accumulated,
    - — integrity of the cytoskeleton,
    - — conformation of the DNA, chromatin, and nuclear architecture.
- Intracellular de-differentiation, which effectively results in the minimization of surface areas of membranes and probably also of the cytoskeleton.
- "'Switching off" of metabolism.
- Presence, and efficient operation of, antioxidant systems.
- Accumulation and roles of putatively protective molecules, including late embryogenic accumulating/abundant proteins (LEA's), sucrose and certain oligosaccharides, or galactosyl cyclitols.
- Deployment of certain amphipathic molecules.
- An effective peripheral oleosin layer around lipid bodies.
- The presence and operation of repair mechanisms during rehydration.

In the discussion that follows comparisons are made, as far as is possible, between desiccation-sensitive and orthodox seeds, and of the status of the processes or mechanisms that have been suggested to contribute to desiccation tolerance. Although the interrelationships among them are far from being resolved, these processes or mechanisms are those that have been implicated to date in the acquisition and maintenance of desiccation tolerance. However, it is important to realize that additional properties that contribute to the ability of seeds to withstand extreme dehydration are likely to be elucidated.

INTRACELLULAR PHYSICAL CHARACTERISTICS

Vacuolation and Reserve Deposition

In 1957, Iljin had already identified one of the major requirements of cells of desiccation-tolerant plant material: the ability to withstand mechanical stress. Vacuole volume reduction, whether by the shrinkage of the space occupied by these usually fluid-filled organelles or by their becoming filled with insoluble reserve material, is one of the mechanisms that would contribute to increased mechanical resilience of cells to dehydration. This aspect was examined by Farrant and others (1997) for (1) *Avicennia marina*, the highly recalcitrant seeds of which can withstand very little dehydration either before or after they are shed; (2) *Aesculus hippocastanum*, a temperate recalcitrant species, the seeds of which overwinter in the hydrated condition during which the necessary stratification occurs to facilitate germination the following spring; and (3) *Phaseolus vulgaris*, a typical orthodox seed that attains a low water content prior to shedding and is long-lived in this condition.

Avicennia marina seeds lose no water during development, and are as sensitive to dehydration before shedding as after abscission (Farrant and others 1992b). These seeds, at best, are unable to surive water contents lower than 0.5 g g^{-1} (33 percent wmb). The vacuoles ultimately occupy almost 60 percent on average of the volume across the cells of all axis tissues, and 90 percent of the cotyledonary cells when mature. At no stage do either the axial or cotyledonary vacuoles contain insoluble reserves, the little insoluble reserve material occurring as plastid starch. Seeds of *A. hippocastanum* naturally undergo a measure of dehydration during development, accompanied by an increase in relative desiccation tolerance (Tompsett and Pritchard 1993). The mature seeds are more desiccation tolerant than those of *A. marina*, being able to withstand dehydration to water contents in the range of 0.42 to 0.25 g g^{-1} (30 to 20 percent wmb). Vacuoles ultimately constitute only a small fraction of the intracellular volume, particularly in the axis cells at maturity. The cotyledonary cells contain many large, starch-filled plastids and protein bodies and are considerably less vacuolate than those of *A. marina*. In *P. vulgaris* seeds, which are orthodox and able to tolerate low water contents, vacuolar volume is reduced to an insignificant proportion in axis cells, and vacuoles in cotyledonary cells accumulate an amorphous, presumably insoluble, material. The differential degree of vacuolation and insoluble reserve deposition among the three species, in both developing and mature seeds, correlates with their degree of desiccation sensitivity. This is in accord with the concept that a high degree of vacuolation can lead to lethal mechanical damage upon dehydration (Farrant and others 1997).

Reaction of the Cytoskeleton

The cytoskeleton, the major components of which are microtubules and microfilaments, is not only an integrated intracellular support system, it also plays a major role in imposing organization on the cytoplasm and also the nucleus. Microtubules consist of polymerized a-tubulin, and microfilaments are composed of F-actin, which is a polymer of G-actin. We are presently investigating the status of the actin microfilaments in hydrated and variously dehydrated embryonic axes of seeds of *Quercus robur*, a temperate recalcitrant species. In the hydrated state, there is an extensive microfilamentous network in the cells of the root tip, which becomes dismantled as the seeds are increasingly dehydrated–a feature that is expected for orthodox seeds as well. In such desiccation-tolerant seeds, orderly reassembly of the elements of the cytoskeleton accompanies imbibition, but once the water content falls to damagingly low levels in *Q. robur*, the microfilaments are not reassembled when the seeds are subsequently rehydrated (Mycock and others 2000). The resultant lack of the intracellular support and structural organization afforded by the cytoskeleton would obviously be a major damaging factor upon rehydration of recalcitrant seeds. Additionally, certain cytomatrical (cytoplasmic) enzyme systems exist as multienzyme particles in plant cells (Hrazdina and Jensen 1992), the formation of which could occur because of the binding of key or anchor enzymes to the microfilaments of the cytoskeleton, as illustrated for glycolysis by Masters (1984). Thus, failure of the cytoskeleton to reassemble following deleteriously low levels of dehydration would have physiological as well as structural consequences in the cells of desiccation-sensitive seed tissues.

DNA, Chromatin, and Nuclear Architecture Conformation

Maintenance of the integrity of the genetic DNA material in the desiccated condition in orthodox seeds, and/or its rapid repair when seeds are rehydrated, is considered to be a fundamental requirement for desiccation tolerance. There is, however, little information on which to draw. DNA assumes different conformational states depending on water activity and, although this has not yet been demonstrated for seeds, it is considered that as water is lost (i.e. water activity is lowered) such conformational changes will occur (Osborne and Boubriak 1994). According to information reviewed by those authors, there is an increase in the number of base pairs per turn of the DNA helix as water is lost from the individually hydrated phosphate groups, and water bridges are formed instead as the conformation changes from the B to the Z form. Osborne and Boubriak (1994) have suggested that protein glycation (i.e. the nonenzymic addition of reducing sugars to [*i.a.*] histone proteins) is likely to occur, which could increase the incidence of DNA conformations appropriate to the dehydrated state. Those authors also discuss the possibility of nonenzymic methylation of cytosine occurring, which would favor the Z-form of the DNA.

However, besides the postulated necessity of conformational changes in the DNA occurring as desiccation-tolerant material is dehydrated, the structure of the chromatin itself must also be stabilized. The highly condensed state of the chromatin in dry, orthodox seeds (e.g. Crévecoeur and others 1976, Sargent and others 1981), which is reversed at the stage in germination when desiccation sensitivity ensues (Deltour 1985), is thought to be a visible manifestation of its stabilized condition. A major factor in chromatin stabilization in the dry state in orthodox seeds might be the change in the H1-histone:nucleosome ratio to 2:1 from the 1:1 ratio that typifies the hydrated condition (Ivanov and Zlatanova 1989).

Nuclear architecture is a further factor that is probably involved in chromatin stability. The structural framework of the nucleus has been convincingly demonstrated for plant cells and is based on intermediate-type filaments called lamins (Moreno Díaz de la Espina 1995). The nucleoskeleton, organized into the lamina (underlying and connected to the inner surface of the nuclear envelope) and matrix (ramifying throughout the nucleus) is suggested to support and localize the chromatin in discrete domains, imposing the topological organization and coordination of intranuclear processes (Moreno Díaz de la Espina 1995). It is implicit that during dehydration and in the desiccated state of orthodox seeds, orderly reorganization of the nucleoskeleton should occur with its restitution as a functional framework upon rehydration.

While little is known about the effects of dehydration on the DNA, chromatin, and nuclear architecture in desiccation-sensitive seeds, their stability in the dehydrated state clearly must be a prerequisite for desiccation tolerance. Maintenance of the integrity of the nucleus as a whole, and the genome in particular, may be imperfectly expressed, or the ability for this may even be totally lacking, in recalcitrant seeds. (For a fuller account of some of these aspects, see Leprince and others (1995) and Pammenter and Berjak (1999)). What is equally likely is that DNA repair mechanisms themselves are inadequate to restitute damage caused by dehydration of desiccation-sensitive seeds (see below).

INTRACELLULAR DE-DIFFERENTIATION

De-differentiation, a characteristic of maturing desiccation-tolerant seeds, is essentially a means by which intracellular structures are simplified and minimized (reviewed by Vertucci and Farrant 1995), which strongly suggests that membranes and cytoskeletal elements are vulnerable to dehydration. This phenomenon is reversed in orthodox seeds when water is taken up early during germination (Bewley 1979, Dasgupta and others 1982, Galau and others 1991, Klein and Pollock 1968, Long and others 1981).

An examination of the quantitative and qualitative status of mitochondria in seeds of *Avicennia marina*, *Aesculus hippocastanum*, and *Phaseolus vulgaris* showed that the proportion of cell volume occupied by these organelles was highest in *A. marina*, which is very desiccation sensitive, and substantially less for *A. hippocastanum*, which is in keeping with its less recalcitrant nature. In *P. vulgaris*, mitochondria occupied a significantly smaller proportion of the cell volume, even preceding the onset of maturation drying (Farrant and others 1997). Also, the mitochondria occupied a far greater proportion of the cell volume in the axis meristems of the two recalcitrant species than in the orthodox species, *P. vulgaris*. There were also marked differences in the structural complexity of the mitochondria among these three species: *A. marina* and *A. hippocastanum*, had well-developed cristae and a structure that was generally typical of an active, hydrated plant tissue; while in *P. vulgaris*, the mitochondria were almost completely de-differentiated even at tissue water contents comparable to those of the recalcitrant species at shedding (Farrant and others 1997). It thus seems that retention of organelles in the highly differentiated state is a major factor in the desiccation sensitivity of recalcitrant species, whereas the ability for ordered de-differentiation is, in fact, a prerequisite for seed survival in the dehydrated state.

There has long been uncertainty as to whether dehydration *causes* de-differentiation, or this intracellular minimization actually *precedes* the initiation of maturation drying (e.g. Vertucci and Farrant 1995). However, the observations on *P. vulgaris* reported by Farrant and others (1997), indicating that mitochondrial de-differentiation occurs, and that respiratory rate declines markedly (see also below) before maturation drying, support the idea that substantial qualitative and quantitative change actually occurs in advance of water loss.

“SWITCHING OFF” OF METABOLISM

Electron transport, albeit at a low level, has been recorded for dehydrated plant tissues, and respiration is measurable even at seed water contents as low as 0.25 g g^{-1} [20 percent, wmb] (Vertucci 1989, Vertucci and Farrant 1995). However, in the water content range 0.45 to 0.25 g g^{-1} (30 to 20 percent [wmb]), unbalanced metabolism may lead to the generation, and essentially uncontrolled activity, of free radicals (Finch-Savage and others 1994a, Hendry 1993, Hendry and others 1992, Leprince and others 1990b, Vertucci and Farrant 1995). It is therefore imperative that, during maturation drying, desiccation-tolerant seeds be able to pass through this water content range with the minimum of damage. The efficient operation of antioxidant systems (Leprince and others 1993, Puntarulo and others 1991), as well as the “switching off” of metabolism, would reduce such damage. Rogerson and Matthews (1977) recorded that a sharp decline in respiratory substrates precedes, and presumably causes, the fall in respiratory rate which, they suggested, is an essential event enabling an orthodox seed to withstand rapid loss of water. The observations of Farrant and others (1997), indicating that a decline in respiratory rate occurs while mitochondria become substantially de-differentiated *prior* to maturation drying in the orthodox seeds of *Phaseolus vulgaris*, support the data and suggestions of Rogerson and Matthews (1977).

In desiccation-sensitive seeds, lethal damage occurs in the water content range 0.45 to 0.25 g g^{1} (Vertucci and Farrant 1995) and, in some species, at considerably higher levels (Pammenter and others 1993). Death of relatively hydrated recalcitrant seeds (at *c.* 0.7 g g^{-1}, or higher [40 percent, wmb]) occurs when water is lost slowly. However, rapid dehydration rates allow survival to lower water contents (Farrant and others 1985). This observation led initially to the use of relatively rapid air-drying of excised embryonic axes to facilitate cryostorage (Normah and others 1986, Pritchard and Prendergast 1986) and later to the development of the flash-drying technique (Berjak and others 1990), by which the axes are dehydrated much more rapidly.

Flash-dried axes are *not* desiccation tolerant; on the contrary, they will not survive for longer than a day or two at best, under ambient conditions (Walters and others 2001) although they may be cryostored successfully (Wesley-Smith and others 1992). The desiccation sensitivity of recalcitrant material is the outcome of the fact that the axes (seeds) are actively metabolic, and the success of very rapid dehydration is that it minimizes the effects of this metabolism. This important point about drying rate is discussed in detail later.

Damage occurring in conjunction with unbalanced metabolism at these relatively high water contents should not be confused with desiccation damage in the strict sense. The latter describes the damage that occurs when water that is required to maintain the integrity of intracellular structures is removed (Walters and others 2001). Desiccation damage *sensu* *stricto* is the consequence of removing (any, or some, depending on the species) structure-bound, nonfreezable water (Pammenter and others 1991, Walters and others 2001). Lethal damage occurs upon loss of this water, even if flash-drying has successfully maintained axis viability to, or close to, this level of hydration (Pammenter and others 1991).

Another critical aspect of ongoing metabolism is cell cycling. The cell cycle describes the nuclear DNA content as 2C in cells that are not preparing for nuclear division, and as 4C in cells in which DNA replication has occurred, where the constant, C, denotes the DNA content of the haploid condition. During the cell cycle four distinct phases can be identified, *viz.* the G_1 phase (2C), which is followed by the S phase, during which DNA replication occurs; after this the cells enter the G_2 phase, during which the amount of DNA remains doubled (i.e. 4C) as a result of events in the S phase, and this is followed by the phase known as G_2M, when mitosis reduces the DNA content to the 2C level typical of somatic cells in the next G_1 phase. Brunori (1967) found that in orthodox *Vicia faba* seeds, most of the cells were arrested in G_1, and that DNA replication was one of the first events to be curtailed as the embryo cells lost water. S-phase replication is resumed only after several hours of imbibition, when water again becomes available to postharvest, orthodox seeds, as shown by Sen and Osborne (1974) for *Secale cereale* (rye): as soon as replication to 4C values occurs and the cells enter G_2M, desiccation tolerance is lost.

In the the highly recalcitrant seeds of *Avicennia marina*, there is only the most transient arrest of DNA replication in root primordia (meristems) of *Avicennia marina* lasting no more than 24 hours around shedding. This is the time when the seeds (although highly desiccation sensitive) are *relatively* most tolerant of water loss and least active. Ongoing cell cycling is associated with marked desiccation sensitivity of the DNA. When only 16 to 18 percent of the total water is lost from the *A. marina* material, there is a reduction of 70 to 80 percent in the nuclei that will incorporate thymidine, and after a 22-percent water loss, damage of the DNA cannot be repaired even when water is made freely available. Ongoing cell cycling, therefore, is another manifestation of the fact that metabolism is not "switched off," at least in these highly recalcitrant seeds, which is considered to be a major factor accounting for their desiccation sensitivity. In related work on the temperate recalcitrant species *Acer pseudoplatanus*, however, cell cycling was found to be arrested, with over 60 percent of the cells in the 2C state (Finch-Savage and others 1998). However, seeds of *A. marina* are poised for immediate germination, while those of *A. pseudoplatanus* are dormant, requiring cold stratification before they will germinate. For seeds of *Azadirachta indica,* recorded as showing intermediate behavior, the 2C DNA level has been reported as occurring to the virtual exclusion of 4C (Sacandé and others 1997). These disparate results on the status of the cell cycle in three nonorthodox seed species serve to highlight the fact that different factors may contribute to the nature, and differing degrees, of desiccation sensitivity.

PRESENCE AND EFFICIENT OPERATION OF ANTIOXIDANT SYSTEMS

A range of antioxidant processes operate in orthodox seeds (e.g. Hendry 1993, Leprince and others 1993), and the role of such processes under conditions of water deficit and desiccation stress in plants has been reviewed by McKersie (1991) and Smirnoff (1993). As discussed above, it is particularly in the water content range from 0.45 to 0.25 g g^{-1} (30 to 20 percent, wmb), that unregulated metabolic events resulting in the first wave of free-radical generation are likely to occur (Vertucci and Farrant 1995). This implies that antioxidant systems (i.e. free-radical scavenging systems) should be maximally effective during maturation drying of orthodox seeds, and again when seeds take up water upon imbibition.

Reviews of metabolic damage associated with dehydration of recalcitrant seeds highlight the idea that free-radical generation may well be a major injurious factor (Berjak and Pammenter 1997; Côme and Corbineau 1996a, 1996b; Smith and Berjak 1995), particularly because protective mechanisms appear to become impaired under conditions of water stress (Senaratna and McKersie 1986, Smith and Berjak 1995). Rapid formation of free radicals and decreasing activity of antioxidant systems have been reported as occurring during dehydration of the seeds of the temperate recalcitrant species *Quercus robur* (Finch-Savage and others 1993). Lipid peroxidation, which is a major consequence of uncontrolled free-radical generation, with the ultimate accumulation of a stable free radical in the embryonic axes, has been shown to accompany dehydration of the seeds of three temperate, recalcitrant species—-*Q. robur*, *Castanea sativa,* and *Aesculus hippocastanum* (Finch-Savage and others 1994a)–and free radical formation has been reported to accompany viability loss in seeds of the highly recalcitrant, tropical species *Shorea robusta* (Chaitanya and Naithani 1994). While hydroperoxide formation has been shown to accompany dehydration at a range of temperatures of the recalcitrant seeds of *Zizania palustris*, significantly more was produced at 37 °C than at 25 °C, and tetrazolium tests revealed that viability was severely affected by water loss at the higher temperature (Ntuli and others 1997).

From the evidence reviewed above, there is no doubt that damage ascribable to uncontrolled free-radical generation occurs during dehydration in the recalcitrant seeds of a range of species that show differing degrees and manifestations of nonorthodox behavior. This implies not only that free radicals are produced as a consequence of water stress in these desiccation-sensitive seeds, but also that antioxidant systems are ineffective at curbing them. Together, then, these factors must be seriously considered as constituting one of the major causes of desiccation sensitivity.

ACCUMULATION AND ROLES OF PUTATIVELY PROTECTIVE MOLECULES

Late Embryogenic Accumulating/Abundant Proteins (LEA's)

LEA's (Galau and others 1986) comprise a set of hydrophilic, heat-resistant proteins associated with the acquisition of desiccation tolerance in developing orthodox seeds (Galau and others 1991 reviewed by Bewley and Oliver 1992, Kermode 1990, Ried and Walker-Simmons 1993). Their synthesis appears to be associated with the high ABA levels that peak during the later stages of seed development (Kermode 1990). The characteristics of LEA's and the conditions under which they appear have led to suggestions that they function as protectants, perhaps stabilizing subcellular structures in the desiccated condition (Close and others 1989, Dure 1993, Lane 1991).

The position of LEA's (or dehydrin-like proteins, as they may be termed) in nonorthodox seeds appears at first sight to be anomalous, as some species do not express these proteins while others express them to variable extents. Seeds of *Avicennia marina*, which are extremely desiccation sensitive, appear not to express LEA's at all (Farrant and others 1992a). In contrast, seeds of *Zizania palustris* (North American wild rice), which are recalcitrant (Vertucci and others 1994) but show differential responses to dehydration depending on temperature (Kovach and Bradford 1992a, Ntuli and others 1997), do express this type of protein (Bradford and Chandler 1992, Still and others 1994). Dehydrin-like proteins were shown to be expressed in a range of temperate, recalcitrant species (Finch-Savage and others 1994b, Gee and others 1994), but the absence of such proteins correlated with low ABA levels was found to characterize the mature, recalcitrant seeds of 10 tropical, wetland species (Farrant and others 1996). Those authors showed the presence of dehydrin-like proteins in other temperate and tropical recalcitrant (nonwetland) species, and suggested that their occurrence may be habitat-related, perhaps also providing protection against low-temperature stress. In a comparative study on mature seeds of two tropical tree species, neither of which occurs in wetlands, dehydrin-type proteins were absent in *Trichilia dregeana*, while accumulating in *Castanospermum australe* (Han and others 1997). The immature seeds and the seedlings of these two species were shown to differ in terms of production of such proteins in response to stresses imposed by dehydration, application of ABA, or exposure to cold, with *T. dregeana* not responding by the production of these putatively protective proteins (Han and others 1997).

Thus, it seems that the ability to express LEA's or dehydrin-type proteins cannot be taken as an indication that the seeds of a particular species will or will not withstand dehydration. This indicates clearly that desiccation tolerance must be the outcome of the interplay of more than one (and probably many) mechanisms or processes. Details of this, particularly pertaining to LEA's/dehydrins, sugars, and various stresses, have been reviewed by Kermode (1997). However, the variable expression of LEA's/dehydrins in recalcitrant seeds on a species basis may, in association with the presence or absence of other factors, account for the *degree* of nonorthodox behavior exhibited under a particular set of circumstances.

Sucrose, Oligosaccharides, or Galactosyl Cyclitols

The possible role(s) of nonreducing sugars in relation to desiccation tolerance in seeds has been extensively reviewed (e.g. by Berjak and Pammenter 1997, Horbowicz and Obendorf 1994, Obendorf 1997, Vertucci and Farrant 1995). Accumulation of nonreducing sugars, particularly of the raffinose series (Blackman and others 1992, Koster and Leopold 1988, Leprince and others 1990a) and/or galactosyl cyclitols (Horbowicz and Obendorf 1994, Obendorf 1997) has been implicated in the acquisition and maintenance of the desiccated state in orthodox seeds, generally in two major ways. These are in terms of the "Water Replacement Hypothesis" (Clegg 1986, Crowe and others 1992) and vitrification, otherwise referred to as glassy state formation (Koster and Leopold 1988, Leopold and others 1994, Williams and Leopold 1989).

Orthodox seed maturation invariably seems to be accompanied by the accumulation of nonreducing oligosaccharides which coincides with the reduction of monosaccharides, and maintenance of the desiccated state is associated with high levels of sucrose and other oligosaccharides. Evidence for the replacement of membrane-associated water (the Water Replacement Hypothesis, i.e. the replacement of water by sucrose to maintain lipid head-group spacing, thereby preventing gel-state transformation) is equivocal, and a recent critique questions its relevance in the desiccated state of orthodox seeds (Hoekstra and others 1997). However, the role of sucrose in the formation of intracellular glasses (i.e. vitrification) is more convincing. The metastable, glassy state occurs *at low water contents* in seeds, when sucrose and certain oligosaccharides or galactosyl cyclitols form high-viscosity, amorphous, super-saturated solutions (Obendorf 1997). The occurrence of glasses is held to impose a stasis on intracellular reactivity, protecting macromolecules against denaturation and possibly preventing or minimizing liquid crystalline gel phase transformations of the lipid bilayer of membranes (e.g. Leopold and others 1994).

Walters and others (1997) have suggested that a significant proportion of the sugars may be tightly associated with LEA's–these complexes acting to control and optimize the rate of water loss during dehydration of orthodox seeds. It should be noted, however, that this should not obviate the participation of either the LEA's or the sugars in the maintenance of orthodox seed viability in the desiccated state.

The formation of intracellular oligosaccharides occurs at the expense of monosaccharides, and confers the advantage that immediately available respiratory substrates are removed (Koster and Leopold 1988, Leprince and others 1992, Rogerson and Matthews 1977). This would serve to reduce the spectrum of damaging reactions that can occur as orthodox seeds pass through critical water content ranges favoring unbalanced metabolism, during maturation drying (see *"Switching off" of metabolism*, above).

Whatever the role(s) of sucrose and oligosaccharides or galactosyl cyclitols may be in orthodox seeds, *seeking parallels for desiccation-sensitive seeds is entirely inappropriate*. While sucrose and other oligosaccharides are produced in some of the few recalcitrant seed species that have been assayed (Farrant and others 1993, Finch-Savage and Blake 1994), glass formation will occur only at water contents *well below* the lethal limit. When recalcitrant seeds are dehydrated under ambient conditions (which is what would occur in the natural habitat), they lose viability at relatively high water contents–in the region of 0.7 g (or more) water per g dry mass [40 percent, wmb] (Pammenter and others 1991), which are *far* higher that those required for glass formation to occur (Bruni and Leopold 1992, Leopold and others 1994, Sun and others 1994, Williams and Leopold 1989). The same argument holds if water replacement by sugars is an operative phenomenon in orthodox seeds; this too would occur only at water contents of 0.3 g per g dry material (Hoekstra and Van Roekel 1988), which is well below the lethal limit for slowly drying recalcitrant seeds.

The one involvement of sugars in the variable desiccation sensitivity of recalcitrant seeds might be via the mechanism suggested by Walters and others (1997) for maturing orthodox seeds, *viz.* the modulating effect of sugar/LEA complexes on dehydration rate. Very marked variability occurs in the rate at which recalcitrant seeds of different species lose water under the same conditions (Berjak and Pammenter 1997, Farrant and others 1989) and it is possible that the significance of sugars and LEA's in embryos of recalcitrant seeds of some species lies in the modulation of the drying rate by complex formation. Walters and others (1997) have also suggested that LEA proteins in temperate recalcitrant seeds may play a role in their survival during overwintering.

DEPLOYMENT OF CERTAIN AMPHIPATHIC MOLECULES

It has been suggested that partitioning of endogenous amphipathic molecules (amphipaths) into membranes upon water loss may be a prerequisite for desiccation tolerance (Golovina and others 1998). Those authors have presented evidence of the movement during dehydration of both introduced, apolar spin probes and endogenous amphipaths into the bilayer of desiccation-tolerant pollen. This process, which was complete after dehydration to the relatively high water content of 0.6 g per g dry mass (37 percent, wmb), was reversed during rehydration, when the amphipaths repartitioned to the cytomatrix (aqueous cytoplasm). This reverse movement was suggested to account for the transient leakage that is invariably observed when desiccation-tolerant material (pollen and seeds) is imbibed from the dry state (Golovina and others 1998).

The partitioning of amphipathic molecules into the bilayer was suggested by those authors as serving to maintain the integrity of membranes in the dry state in desiccation-tolerant organisms, by substantially lowering the water content at which the phase change of membrane lipids occurs. Liquid crystalline to gel phase changes in membranes are well documented in response to dehydration, but the essential property for desiccation tolerance is that they must be reversible, reestablishing the membranes in a functional condition upon rehydration (Hoekstra and others 1992). This demands that integral membrane proteins retain their position in the desiccated state, a role that might also be ascribed to the amphipathic molecules.

If the partitioning of amphipaths into membranes is established as a universal phenomenon occurring during dehydration of orthodox seeds, it is possible that they are absent or, if present, incompletely functional or nonfunctional in desiccation-sensitive seeds. Dehydration of the embryos from recalcitrant *Camellia sinensis* seeds was found to induce a phase change in membrane lipids, which was reversible, but the proteins were irreversibly affected (Sowa and others 1991). It may be significant that at a water content of 0.6 g g^{-1}, when amphipath partitioning has been observed to be complete (Golovina and others 1998), slowly dried recalcitrant seeds, and even the flash-dried axes of certain species, will have lost viability (Pammenter and others 1991, 1993; also see below). In highly desiccation-sensitive recalcitrant seeds, it is possible that phase changes of the membrane bilayers might not be reversible, for example, if nonbilayer structures or hexagonal phases result (reviewed by Vertucci and Farrant 1995). Partitioning of endogenous amphipaths into the bilayer upon dehydration is unlikely to act in isolation; thus, even if such molecules are present in cells of recalcitrant seeds, they may well depend on another mechanism or process to achieve their reversible migration.

THE POSSIBLE ROLE OF OLEOSINS

The term *oleosin* refers to a unique protein type that surrounds the lipid (oil) droplets in plant cells (Huang 1992). Oleosins have a central, hydrophobic domain that interacts with the periphery of the lipid, and an amphipathic N-terminal domain that, with the C-terminal domain, facilitates interaction with the aqueous cytomatrix. The oleosin boundary of lipid bodies allows these hydrophobic masses to be accommodated as discrete entities in the aqueous cytomatrix under hydrated conditions, and it has been suggested that their role during dehydration prevents the bodies from coalescing in desiccation-tolerant seeds (Leprince and others 1997).

Leprince and others (1997) recorded a lack (or inadequate amount) of oleosins in desiccation-sensitive seeds of some species, and although little obvious change in the integrity of the bodies as a consequence of dehydration was observed, rehydration appeared to have deleterious effects on their stability. Coalescence of lipid bodies is a common abnormality accompanying deterioration, even in cells of stored, orthodox seeds (Smith and Berjak 1995). Although the effects of fungi associated with both stored orthodox and recalcitrant seeds in bringing about lipid body coalescence cannot be ruled out, the occurrence of this phenomenon could well be, at least partly, a consequence of some deficiency in desiccation-sensitive seeds. In view of the findings of Leprince and others (1997), the deficiency of an adequate oleosin sheath around the lipid bodies may underlie the inherent instability of these organelles during rehydration following damaging levels of desiccation of some recalcitrant seeds. However, it must be stressed that the presence of fully functional oleosins cannot, in itself, account for desiccation tolerance. Rather, it must be viewed as one of the mechanisms contributing to the spectrum of properties necessary if orthodox seeds are to survive extreme dehydration.

THE PRESENCE AND OPERATION OF REPAIR MECHANISMS DURING REHYDRATION

There is both indirect and direct evidence that repair mechanisms do come into play when dry orthodox seeds are rehydrated. For example, seeds that have been stored under adverse conditions, but are still 100-percent viable, typically show a lag before there are visible signs of germination, during which it is commonly accepted that repair processes are taking place. Ultrastructural studies on maize seeds have provided evidence supporting this contention, where mitochondrial repair was observed during the lag period (Berjak and Villiers 1972). Studies on rye seeds have shown that even in the dry state there is progressive deterioration of the DNA as a result of endo- and exonuclease activity during storage (Elder and others 1987), which cannot be repaired until the seeds are rehydrated (Boubriak and others 1997).

Much of the evidence for the operation of repair processes during rehydration comes from osmopriming experiments on low-vigor seeds. This process involves controlled rehydration to the end of phase II, which achieves a hydration level that facilitates repair but precludes germination proper (Bray 1995, Bray and others 1993). Those authors have shown that replacement of damaged rRNA occurs, and lesions in the DNA and protein-synthesizing systems are repaired, during priming.

It is generally agreed that free radical generation (see above) continues in air-dried orthodox seeds during storage (reviewed by Smith and Berjak 1995) and the ensuing damage obviously must be repaired on rehydration, arguing strongly for the presence and efficient operation of antioxidant systems at this stage. During dehydration of desiccation-sensitive seeds and seedlings, however, such systems have been shown to fail (Hendry and others 1992, Leprince and others 1992) and are assumed to remain ineffective when water is once again provided (Côme and Corbineau 1996a, 1996b).

When recalcitrant seeds or axes excised from such seeds are subjected to nonlethal dehydration, it is generally observed that there is an increase in the time taken for the onward growth of germination, which might be interpreted as facilitating repair. However, this is likely to be strictly limited; present studies have shown that after 22 percent of the water is lost from hypocotyl tips of *Avicennia marina*, dehydration-associated DNA damage can no longer be repaired when water is once again provided. DNA instability to dehydration is also shown by seedlings produced from orthodox seeds, once they have reached the stage when desiccation tolerance has been lost (Boubriak and others 1997).

Very little work that targets the aspect of possible repair of mature, dehydration-damaged recalcitrant seeds has yet been done. It is presently tacitly assumed that the necessary repair systems are present, but are themselves damaged by dehydration beyond certain limits–limits that might vary among seed species of markedly differing desiccation sensitivity. However, this aspect requires considerable investigation to obtain both qualitative and quantitative data to clarify the situation.

DRYING RATE - A VITAL FACTOR IN DETERMINING THE DEGREE OF DEHYDRATION THAT WILL BE TOLERATED

We now know that much confusion has occurred in comparative work on individual species of recalcitrant seeds because of conflicting data regarding "critical water contents," below which viability will be lost. This is because the dimensions of the *time* taken for water to be lost, or the temperature at which the drying experiments were carried out, have been ignored. While the effects of temperature will not presently be discussed, there are several publications focused on the seeds of *Zizania* spp. which show that this parameter can have very marked effects on the outcome of drying regimes and/or optimal storage water contents (Kovach and Bradford 1992b; Ntuli and others 1997; Vertucci and others 1994, 1995). The effect of the maturity status of the seeds–which is often extremely difficult to ascertain for recalcitrant types–also has significant effects on the degree of dehydration that will be tolerated (reviewed by Berjak and Pammenter 1997, Finch-Savage 1996) but also will not be taken further.

The aspect of the *time* taken for water to be lost is a variable that has been identified as having profound effects on the degree of dehydration that desiccation-sensitive seed material will tolerate. The more rapidly dehydration can be achieved, the lower is the water content to which the seeds or axes can be dried without damage accumulation that culminates in viability loss. This is particularly marked when excised axes are dried (Berjak and others 1993; Normah and others 1986; Pammenter and others 1991, 1993). Very rapid drying of excised recalcitrant axes (flash-drying) facilitates nonlethal dehydration to water contents in the region of 0.4 to 0.25 g g^{-1} dm, which is close to the hydration level where all the water is nonfreezable (generally structure-associated), although tolerance to such low water contents is not invariably the case (Pammenter and others 1993). It must be noted, however, that such rapid drying does *not* mean that the seed tissues are potentially desiccation tolerant; rather, the faster dehydration can be achieved, the less the time during which the axes are in the water content range that permits damaging, potentially lethal, aqueous-based reactions to occur. As discussed below, these are the processes that, given sufficient time, will cause viability loss at relatively high water contents when the tissues are dehydrated slowly (Berjak and others 1989, 1993; Pammenter and others 1998; Pritchard 1991). Far from actually being desiccation tolerant, axes from recalcitrant seeds will survive only for very short periods (hours to a day or two), at the lowest water contents attainable (Walters and others 2001).

Marked effects of drying rate on whole seeds are generally harder to attain, because seed size often prevents the achievement of suitably rapid dehydration. However, not all recalcitrant seeds are too large, or lose water too slowly, to facilitate the achievement of very different drying rates. The ability to achieve lower water contents while retaining viability has been recorded for whole seeds of *Avicennia marina* (Farrant and others 1985) and *Quercus rubra* (Pritchard 1991). We have recently carried out studies to ascertain the effects of drying rate on whole seeds of *Ekebergia capensis*, a tropical, meliaceous, recalcitrant species) for which markedly different drying rates can be achieved (Pammenter and others 1998). The results obtained illustrated the effects of drying rate dramatically: viability loss was already apparent in slowly dried seeds at high axis water contents [1.25 g water per g dry material (55 percent, wmb)] while those that were dehydrated rapidly showed unimpaired vigor and full germinability at an axis water content of 0.7 g g^{-1} (40 percent, wmb). Seeds dried at an intermediate rate retained viability to the intermediate axis water content level of *c.* 1.0 g g^{-1} (50 percent, wmb). Ultrastructural observations suggested that different damaging mechanisms bring about intracellular damage, depending on the drying rate. Advanced degradation of membranes, particularly of the plastids, and an abnormality of the lipid bodies occurred in axes from slowly dried seeds at water contents in the region of 1.1 g g^{-1} (52 percent, wmb) when viability had declined to 37 percent. The damage became steadily worse with slow drying to lower water contents, until, at 0.6 g g^{-1} (37 percent, wmb), only fragments of intracellular components remained. At a water content of 0.57 g g^{-1} (36 percent, wmb), axes from rapidly dried seeds (viability 80 percent) showed little signs of intracellular damage; it was only at considerably lower axis water contents that signs of deterioration were noted, which coincided with declining viability. At no stage did the extensive degradation that characterized axis cells from slowly dried seeds occur, supporting the proposal that if desiccation-sensitive material can pass quickly enough through water content ranges at which lethal reactions are prevalent, then it is possible to dry the material down to a far lower hydration level (see Vertucci and Farrant 1995 for discussion of the various hydration levels).

There will be a water content at which *rapidly dried* material that is desiccation sensitive will sustain injury, and, while the value varies from species to species, it is usually near the range where only structure-associated (nonfreezable) water remains (Pammenter and others 1991, 1993; Pritchard 1991). Damage occurring at such relatively low water contents is defined as desiccation damage in the strict sense (Pammenter and others 1998; Walters and others 2001) and is suggested to coincide with the perturbation of the nonfreezable water (Pammenter and others 1991). In contrast, desiccation-tolerant material can withstand the removal of a considerable proportion of this water (Pammenter and others 1991, Vertucci and Farrant 1995).

Slowly dried desiccation-sensitive material sustains damage at relatively high water contents, certainly those where solution (i.e. freezable) water prevails. This damage is suggested to result from aqueous-based, degradative reactions that are the result of unbalanced metabolism (Pammenter and others 2001; Walters and others 2001). Recalcitrant seeds (and, indeed, probably all nonorthodox types) are hydrated and metabolically active when shed (Berjak and others 1989, Berjak and Pammenter 1997). As water is slowly lost, metabolism will continue, but when the seeds are still at relatively high water contents, metabolism will become unbalanced or out-of-phase as a result of internal water stresses (Senaratna and McKersie 1986, Smith and Berjak 1995, Vertucci and Farrant 1995). A likely consequence of this unregulated metabolism will be the generation of free radicals and accompanying oxidative damage (Finch-Savage and others 1994a, Hendry 1993, Hendry and others 1992, Leprince and others 1990b). The severity of this type of damage, which is being termed metabolic damage (Walters and others 2001), is predicted to increase in inverse proportion to the drying rate, with viability loss occurring at increasingly high water contents.

CONCLUDING COMMENTS

It is proposed that nonorthodox seed behavior is a consequence of the lack of some, or perhaps all, of the suite of protective mechanisms or processes that together confer desiccation tolerance on orthodox seeds. There is likely to be a gradation in the presence and/or efficacy of the proposed processes/mechanisms among seeds of nonorthodox species, accounting for the variability of the responses to stresses, particularly that imposed by dehydration. The most desiccation-sensitive recalcitrant seeds are probably those that lack virtually all the protective and restitutional factors that facilitate the acquisition and maintenance of desiccation tolerance in orthodox seeds.

Two major factors are proposed to contribute to the loss of viability of recalcitrant seeds: (1) the consequences of unbalanced metabolism during dehydration [and possibly also when such seeds are stored in the hydrated condition (Smith and Berjak 1995)]; (2) desiccation damage in the strict sense, which occurs when water that is essential for the integrity of intracellular structures is removed; in recalcitrant seeds, this equates with nonfreezable water (Pammenter and others 1991).

We will probably be unable to account satisfactorily for nonorthodox seed behavior, particularly that of truly recalcitrant seeds, until complete understanding is gained of the apparently numerous interacting factors that enable desiccation-tolerance to be achieved.

CHAPTER 5

Dormancy and Germination

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DORMANCY, GERMINATION, AND ADAPTATION

The seed phase is the most important stage in the life cycle of higher plants as regards survival; dormancy and germination are natural mechanisms to ensure this. The seed is often well equipped to survive extended periods of unfavorable conditions, and the embryo is protected by one or several layers of other tissues. These include endosperm, perisperm, seedcoats, and fruit tissues, which protect the embryo from physical damage and nourish it (in the case of the endosperm); all contribute to spreading the seeds after abscission. As we shall see, these surrounding layers play an important part in the regulation of dormancy and germination. For many tree species native to the northern hemisphere, with seed maturing and dispersing in late fall to early spring, dormancy is an acquired trait to carry them over the winter conditions ready for germination next spring. Similarly, for seeds of tropical tree species maturing and dispersing during the dry, hot season, dormancy prevents germination until the arrival of the rainy season.

However, most tropical tree seeds have no dormancy and can germinate readily after seed fall, provided there is moisture available. Most recalcitrant seeds, because of the absence of maturational drying and the fact that embryo growth and germination processes constitute a continuous process, show no developmental arrest. In some species, such as *Hopea ferrea*, the radicle emerges with a mucilage-like coating, thereby protecting the radicle from drying out. However, seeds of some tropical and subtropical species have a seedcoat-imposed dormancy, for example, legumes. Additional types of dormancy in the seeds of tropical and subtropical tree species include combined seedcoat and embryo dormancy in *Podocarpus falcatus* (Wolf and Kamondo 1993); the mechanical restriction of seedcoat in *Podocarpus usambarensis*, and embryo dormancy in *Warburgia salutaris* (Msanga 1998); and morphophysiological dormancy in *Taxus mairei* and *Myrica rubra* (Chien 1997, Chien and others 1998). According to Msanga (1998), of the seeds of 122 indigenous tree species in Tanzania, 70 percent are known to be nondormant, 29 percent show seedcoat-related dormancy, and less than 1 percent display a double dormancy. In southeast Asia, seed dormancy has been attributed primarily to seedcoat problems (Hor 1993).

In the moist tropics, there is often no requirement for seed dormancy since the microclimate is always favorable to seed germination and seedling establishment immediately following seed dispersal (Wolf and Kamondo 1993). However, seedcoat dormancy is commonly found in the species growing in semiarid and arid areas of the Tropics. The degree of dor-

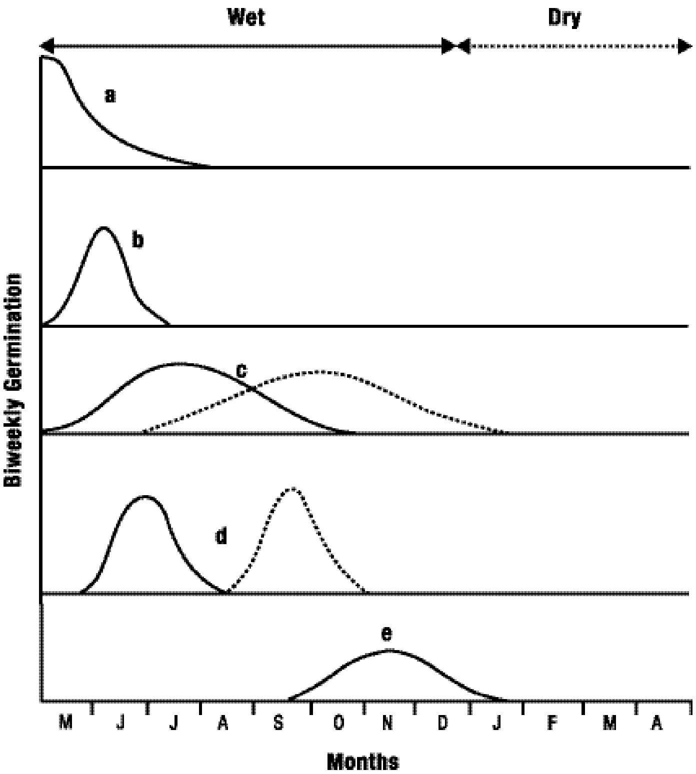

Fig. 1. Some seed germination strategies shown by tropical trees (adapted from Garwood 1986). The duration of the wet and dry seasons, and the timing of germination, are entirely arbitrary and may vary considerably between different forest types.

mancy among, and within, seedlots of the same species varies with provenance, crop year, and individual trees (Poulsen 1996, Wolf and Kamondo 1993). Although seeds of many tropical species have no dormancy, germination of some tree species is delayed as if they were dormant (i.e. *Diospyros kirkii, Moringa oleifera* Lam.) (Albrecht 1993, Msanga 1998). It is especially interesting to note that even seeds of many of the recalcitrant species exhibit delayed germination (i.e. *Allanblackia stuhlmannii, Strychnos cocculoides, Xymalos monospora, Ocotea usambarensis*) (Msanga 1998).

Apart from the rather clear-cut examples of coat-imposed dormancy as typified by many legumes, it is important to realize the great diversity seen in the synchrony of germination and the often wide range over which it can occur, even in the wet Tropics. This is illustrated diagrammatically in fig. 1. In the example illustrated there is a relatively long, wet period and a somewhat shorter dry period of 4 months. The shapes of the biweekly germination data (adapted from Garwood 1986) and their duration are somewhat arbitrary, but nevertheless illustrate five strategies.

What might be regarded as a recalcitrant strategy is seen in (a), where germination is almost immediate, high, and declines rapidly. It is evident that many pregermination events must have been taking place during development on the mother plant, as there is an absence of a lag phase in germination (seen in (b), however). The more typical pattern of dry dispersal, followed by imbibition and a single peak of synchronous germination in (b), might be considered representative of seeds without any significant coat-imposed dormancy. Such a sharply synchronous pattern might be seen in rapidly establishing forest species. The germination strategy illustrated in (c) represents the approach of maximizing germination in time, so as to widen the range of circumstances or locations for germination. The bimodal pattern may be seen as an “add on” benefit to maximize this strategy still further. The bimodal pattern shown in (d) achieves essentially the same temporal distribution as the unimodal pattern in (c), but with a greater element of synchrony. A cautious “failsafe” model is shown in (e), where germination timing is programmed to occur only after a number of quantal units of favorable hydrotime have been allowed to pass (Bradford 1996).

THE TROPICAL FORESTS OF THE WORLD

Tropical forests have been classified as moist evergreen, moist deciduous, and dry deciduous types, and account for, respectively, 20 percent, 10 percent, and 20 percent of the world’s 2950 million hectares of forest (Borota 1991). Some of the principal trees of economic importance are presented in table 1, but the ecological value of other species should not be forgotten. Unfortunately these two objectives are often in conflict, although sustainable forestry requires integration of conservation and economic objectives.

Table 1

Important Tropical Trees, Listed Alphabetically by Geographical Region

(adapted from Borota 1991)

Africa	America	Australasia
Burkea	*Anacardium*	*Acacia*
Ceiba	*Andira*	*Afzelia*
Celtis	*Bombacopsis*	*Dalbergia*
Entandrophragma	*Caesalpinia*	*Dipterocarpus*
Khaya	*Carapa*	*Dryobalanops*
Maclura	*Cedrela*	*Eucalyptus*
Ocotea	*Guarea*	*Gonostylus*
Peltophorum	*Ocotea*	*Melaleuca*
Podocarpus	*Swietenia*	*Pterocarpus*
Triplochiton	*Virola*	*Shorea*
		Tectona

FACTORS AFFECTING GERMINATION AND SEED QUALITY

THE SCOPE AND OTHER REGIONAL DATA

As is perhaps evident from table 2, the topic is vast and scattered in many publications. Some tree seed manuals have appeared (Kamra 1989, Ng 1996, Poulsen and others 1998). Other reports are available on a regional basis for Australia, Brazil, Colombia, Costa Rica, Cuba, The Solomon Islands, and Thailand (Cavanagh 1987, Chaplin 1988, Figliolia 1985, Ortiz 1995, Pêna and Montalvo 1986, Quirrós and Chavarría 1990, Trivino and others 1990, Turnbull and Doran 1987, Uetsuki 1988). A manual presenting a practical framework for conducting field research on the reproductive biology of Asian forest trees has recently appeared (Ghazoul 1997), and in chapter 1 of this volume, Flores discusses aspects of tree seed biology.

Table 2

Flower, Fruit, and Seed Characteristics of Some Tropical Seeds by Family and Genus

R Denotes Recalcitrant Genera

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Anacardiaceae	*Spondias*[1]	Small, 4-5 united carpels;	Usually drupe; solitary seed		Yes:
		1 ovule;	with thin endosperm or		fleshy inhibitors?
	Schinus[2]	3 united	none; fleshy cotyledons		Woody inner coat?
	Schinopsis	carpels; 1 ovule	[1](3800) [2](30)		[2](10-30 days)
	Sclerocarya[R]				
	Lannea[R]				
Apocynaceae	*Aspidosperma cruenata*[1]	Large,	[1]Seed, undulator (871)		No?
	Hancornia[R]	2 united or free carpels,	follicarium, follicle,		
		paired fruits; fresh non	lomentarium		
		dehiscent fruit or dry,			
		splitting			
Bignoniaceae	*Tabebuia rosea*[1]	Showy bell- or funnel-	Many seed, 2 locule capsule		No?
		shaped corolla, single	[1](35) [2](5)		
	Spathodea	superior ovary;	amphisarcum, ceratium,		
	Jacaranda[2]	numerous ovules flat,	septicidal capsule		
		winged seeds			
Bombacaceae	*Bombacopsis quintata*[1]	5 sepals and petals—	[1]Seed, floater (33)		
	Ceiba pentandra[2]	sometimes fused; epicalyx	[2]seed, floater (74); [3]seed		[1]No
	Ochroma[3]	whorl.	with cotton-like fibers		[2,3]Yes—
	Bombax[4]	Many locules.	no or reduced endosperm		malvaceous affinities?
	Pachira[R]		amphisarcum, loculicidal or		[4]<15 ÞC damaging
			septicidal capsule [3](9)		
Boraginaceae	*Cordia alliodora*[1]	Uncoiling cymes:	[1]Fruit, helicopter (6)		
	Cordia aff. *panicularis*[2]	salver or bell-shaped,	4 (rarely 2) nutlets		No?-mostly herbs/shrubs?
		5 corolla lobes	or a drupe with or without		
		2 fused carpels—	endosperm [2](275)		
		2-4 locules			

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Burseraceae	*Aucoumea*[1]	Panicles of	[1](98)		
	Bursera	small unisexual flowers;	Drupe, sometimes		No
	Commiphora	sepals fused,	capsule,		
	Dacryodes	petals free,	no endosperm		
		3-5 carpels;			
		2-5 locules			
Leguminosae-		Legume, camara, samara	Legume, camara, samara		
Caesalpionioideae		more or less irregular	[1]5 seeds in thin pods	Nodulation	Yes
	Acrocarpus[1]	lateral petals (wings)	[2]6-10 seeds, dehiscent pods,	*Rhizobium*	[2]No, 11-20 days
	Afzelia[2]	calyx 5 unequal lobes;	(4000)		
		sepals free; short-toothed			
		calyx			
	Bauhinia[3]		[3]Dehiscent pod		[3]Some
	Cassia[4]		[4]Unassisted (9-32),		[4]Yes
			indehiscent pods		
	Caesalpinia				
	Delonix				
	Hymenaea[5]		[5]Indehiscent heavy pod		[5]Yes
			10 seeds (2000-6000)		
	Oxystigma				
	Parkinsonia[6]		[6]2-6 seeds, indehiscent pods		[6]Yes, 2-10 days
	Peltogyne		(76)		
	Swartzia				
	Tamarindus[7]		[7]1-10 seeds, indehiscent		[7]Yes, 40-50 days
			pods (714)		
Canellaceae	*Warburgia*[R]	Axillary flowers; small; 4-5	Berry - 2 or more seeds; oily		No, 15 days
		sepals, 10 petals; 2-5 carpels	endosperm (100)		embryo dormancy?
		single locule			
Casuarinaceae	*Casuarina*	Highly reduced, unisexual;	Hard woody fruits enclosed	*Frankia* and mycorrhiza	No, 11-23 days
		aggregate flowers cup-like	in bracteoles;		
		and naked; 2 fused carpels	wind dispersal samaroid nut,		
			(11)		
			No endosperm		

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Combretaceae	*Terminalia amazonica*[1]	Small and clustered; toothed	[1]Fruit, rolling autogyro (4)		No, 60-90 days
	Terminalia ivorensis[2]	calyx; no petals	[2]Fruit, rolling autogyro		
	Lumnitzera[R]		(160)		
	Laguncularia[R]		No endosperm,		
	Conocarpus[R]		variable cotyledons,		
			woody endocarp		
Dipterocarpaceae	*Anisoptera*				
	Dipterocarpus	Showy in racemes;	Single-seeded nut with wing	All mycorrhizal association	No
	Dryobalanops[1][R]	3 carpels;	and membranous calyx;		
	Hopea[R]	3 locules;	no endosperm		
	Shorea[2][R]	2 ovules: only	(pseudosamara)		
	Vatica	one developing	[1](4784)		
			[2](250-1075)		
Euphorbiaceae	*Croton*[1]	Condensed inflorescence;	Shizocarp or drupe,		Coat-imposed?
	Hura[2]	5 perianth segments;	mericarps dehisce after		[1]35-45 days
	Macaranga[2]	or lacking;	separation [3](29)		
	Manihot	and petals present;	abundant endosperm		
	Omphalea	locules open lengthwise;	[1]Woody endocarp		
	Ricinodendron	3 fused carpels,	[2]Coccarium, bacca,		
		3 locules, 1-2 ovules	polospermatium		
Lauraceae	*Ocotea*[1][R]	Racemose or cymose;	Berry or drupe-like fruit,		[1]30-45 days
	Persea[R]	regular in multiples of 3;	enclosed variously by		Other genera
	Cinnamomum camphora[2]	poor petal/sepal differences;	perigynous part of flower		not recalcitrant?
	Sassafras randaiense[3]	single locule, single ovule	(cupule);		[2]Alternating temperatures
	Neolitsia ariabillima		no endosperm [1](666)		[3]Dormant - cold
					stratification
Lecythidaceae	*Barringtonia*[R]	Long spikes	Large fruits with fleshy		Coat imposed?
		showy and fluffy; 4-6 calyx	outer, hard/woody inner		
	Gustavia	and petal segments; 2-6	layer, and indehiscent;		
	Petersianthus	carpels and locules; 1 to	no endosperm		
		many ovules			

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Malvaceae	*Thespia*	Calyx of 5	Dry capsular or schizocarpic		Yes?
		sometimes joined sepals;	fruit,		
		epicalyx; 5 free petals;	hairy seed, no endosperm		
		5 or more carpels			
Meliaceae	*Azadirachta* ^{1R}	Often cymose panicles; 3-5	Capsule, fruit, berry; rarely		No: ^{1}30-40 days
		free or united sepals also	nut		
	Guarea ^{2}	petals; ovary 2-6 locules			
	Trichilia ^{3R}		Winged: *Azadirachta* and		
			Guarea; fleshy aril or		
	Carapa ^{R}		sarcotesta in others		
	Cedrela ^{4R}		^{1}(200) ^{2}(3500)		
			^{3}(100-600) ^{4}(20)		
	Entandrophragma ^{R}		^{5}(476) ^{6}(490)		
	Khaya ^{R}		^{2,3}loculicidal capsule		
			^{4,6}septifragal capsule		
	Melia ^{5}				^{5}15-75 days
	Swietenia ^{6}				^{6}4-30 days
Melastomataceae	*Astronia*	4-5 sepals,	Berry or loculicidal capsule;		No
	Memecylon	free petals,	small seeds; no endosperm		
	Tibouchina	1-14 carpels; 4-5 locules;			
		2 to many ovules			
Leguminosae-	*Acacia* ^{1}	Erect or pendulous raceme;	Dehiscent or nondehiscent	Nodulation:	Yes - ^{1}*A. nilotica*
Mimosoideae	*Inga* ^{2}	regular flowers:	pods; 1-5; 10-12 seeds per	*Rhizobium*	*A. tortilis;*
	Pithecellobium ^{R}	5 sepals and petals,	pod; ^{1}(7-169) ^{2}(200-1970)		No - ^{1}*A. senegal*
		numerous stamens;			See Tables 3 and 4
	Albizzia ^{3}	5-10 stamens	^{3}Nondehiscent pods; 8-14		^{3}Yes
			seed per pod (83)		
	Prosopsis ^{4}		^{4}Nondehiscent pods; 25		^{4}Yes, 10-30 days
			seeds per pod; sweet pulp		
			(31)		
	Pentaclethra ^{R}				

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
	Faidherbia^{5}		^{5}Nondehiscent pod;		^{5}Yes, 5-20 days
			11-19 seeds per pod (76)		
	Leucaena^{6}		^{6}Nondehiscent pod; 12-25		^{6}Yes
			seeds per pod (50)		
	Parkia^{7}		^{7}Nondehiscent pod; 19		^{7}Yes
			seeds with pulp (76)		
Moraceae	*Artocarpus*^{R}	Small solitary flower	Variable fruits;		^{1}Variable, see text
	Cecropia ^{1}	ovary with single ovule	pseudodrupe, sorosus,		^{2}No, 45-60 days
	Castilla		synconium		
	Maclura ^{2}		with or without endosperm		
			^{1}(1)		
Myrtaceae	*Eucalyptus* ^{1}	Cymose (mostly)	^{1}Unassisted (0.25-18)	^{1}Mycorrhizae	No, 3-30 days
		or racemose; 4-5 (usually)	^{2}Fleshy berry (120-6000)	^{2}?	
	Eugenia ^{2R}	free sepals or	(Rarely drupe)		
	Melaleuca	reduced/absent			
	Metrosideros ^{3}			^{3}Mycorrhizae	
		4-5 small free petals;	^{3}Unassisted (0.057)		
	Syzgium^{4R}	1-5 locules, 2-many ovules		^{4}?	
			If dry: capsule or nut		
			^{1}Capsiconium		
			^{4}Polyembryonic (333)		
			Little or no endosperm		
Myristicaea		Small inconspicuous;	At maturity fibrous fruit		No
	Cephalosphaera	incapitate, fascicled or	splits open: 2-4 valves:		
	Myristica	corymbose infloresence,	single large seed (dehiscent		
	Virola^{R}	no petals, calyx or 3 united	berry) (800-3700)		
		sepals,	small embryo, large		
		single ovule; 1 or 2 carpels	endosperm with ingrowing		
			perisperm; aril		

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Leguminosae – Papilionoideae	*Andira*	Irregular: lateral petals enclosed by standard in bud; 10 stamens			
	Calopogonium				
	Dalbergia[1]		[1]Nondehiscent flat pod; 1-4 seeds; rolling autogyro (248)		[1]No
	Gliricida[2]		[2]Dehiscent pod, 3-10 seeds (90)		[2]No
	Lonchocarpus[3]		[3]Fruit, rolling autogyro (143)		
	Milletia				
	Platylobium[4]			[4]Mycorrhizae	
	Pterocarpus macrocarpus[5]		[5]Fruit, undulator (337)		[5]Alternating temperatures best
	Swartzia polyphylla[R]				
Polygonaceae	*Triplaris*[1]	Small flowers; solitary or grouped in raceme; 3-6 sepals - enlarge in fruit. No petals; 2-4 carpels in one locule	[1]Fruit, helicopter, (77); triangular nut		No
	Coccoloba[2]		[2](150-280) (Abundant endosperm)	[2]Mycorrhizae	
Proteaceae	*Grevillea*	Raceme spike or head; ring of bracts, irregular: 4 perianth lobes; 2-4 scales (petals) alternate. Ovary with single carpel, 1 to many locules; persistent style	Wind dispersal (22) fruit a follicle with winged seed; no endosperm	Mycorrhizae	Coat imposed?
Sapotaceae	*Autranella*	Borne in fascicles, sepals free, two whorls of 2-4; 1 of 5. Equal number of petals; many fused carpels, many locules, single ovule.	[1]Berry (800-6250) 1-several seeds, oily endosperm, bony testa, large embryo		Coat-imposed?
	Pouteria[1]				
	Tieghemella				
Sterculiaceae	*Guazuma*	Regular in complex cymes; 3-5 sepals; 5 free or fused petals; ovary with 2-12 carpels; locules 2 or more ovules	Indehiscent dry capsule: 80-100 seeds or berry-like (310)		?
	Triplochiton scleroxylon				

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Verbenaceae	*Gmelina*^{1} *Petitia* *Premna* *Tectona*^{2}	Irregular in racemose, cymose inflorescence. Calyx and corolla 4 or 5 lobed. Ovary of 2 (4,5) fused carpels divided into 4 (or more) locules. 1 ovule per locule (false septa).	Stony 1-2 seeds. Drupe sometimes capsule, or schizocarp ^{1}(715) ^{2}(10000) Little or no endosperm		No, ^{2}20-50 days ^{2}Poor germination
Vochysiaceae	*Vochysia*	Irregular in compound raceme; 5 sepals; petals 1-5, unequal size; 3 fused carpels, 3 locular ovary	3-chambered capsule with winged seeds; no endosperm		No
Zygophyllaceae	*Balanites*^{1} *Bulnesia* *Guaiacum*	Regular, solitary, paired or cymes; 4-5 free sepals and petals; ovary of 5 fused carpels, 5 locules, 1 to many ovules.	Capsule slitting into 5 parts (or berry or drupe) endosperm; seed pulp ^{1}(2800)		Some, ^{1}7-30 days

Data from: Albrecht 1993, Augspurger 1986, Foster and Janson 1985, Grubb and Coomes 1997, Heywood 1978, Jurado and others 1991, Spjut 1994.

INHERITED SEED CHARACTERISTICS

There are many factors influencing seed germination in general, and often the inherited effects on tropical and subtropical seed germination show differences from those of the temperate species. The following are considered important components of tropical and subtropical tree seed germination: seed germination mode, morphological and physiological constraints, the orthodox-intermediate-recalcitrance continuum, and seed polymorphism.

Seed Germination Mode

Three distinct seed germination behaviors can be recognized: epigeal, hypogeal, and intermediate (Msanga 1998). In addition, relatively unknown cryptogeal germination behavior was found in several tree and shrub species growing in the savanna tropics (Jackson 1974). Epigeal germination is considered to be fast and synchronous in contrast to the slower cryptogeal mode (Vazquez-Yanes and Orozco-Segovia 1993), which is more prevalent in larger seeds (Bazzaz and Pickett 1980). In a study of 64 leguminous species of the Amazon forest, hypogeal germination was observed only in large seeds that were more than 3.1 cm long, whereas in small seeds of less than 1 cm in length, epigeal germination prevailed (Moreira and Moreira 1996). Hypogeal germination was also most prevalent in species associated with seasonally flooded habitats.

Figure 2 illustrates these different germination patterns with their descriptions.

Epigeal germination—This is the most common germination behavior and occurs in most coniferous and broadleaved species when cotyledons are forced above the ground by elongation of the hypocotyl, for example *Acacia, Afzelia, Diospyros, Jucbernadia, Juniperus procera, Pinus,* and *Tamarindus.*

Hypogeal germination—This type of germination occurs only in broadleaved seeds in which the cotyledons remain beneath the ground while the epicotyl elongates, as in *Agelaea heterophylla, Allanblackia stuhlmannii, Antiaris toxicaria, Khaya anthotheca, Ocotea usambarensis,* and *Quercus* spp.

Intermediate (between epigeal and hypogeal) germination—Two types may be distinguished. In the first, the seedcoat cracks and the radicle emerges through the scar end and develops into a taproot, then cotyledons unfold to release the developing shoot as typified by *Bauhinia petersiana, Clerodendrum cephalanthum,* and *Uapaca kirkiana*; in the second, the cotyledons remain inside the seedcoat but are lifted above the ground, as typified by *Dipterocarpus* and *Rhizophora*.

Cryptogeal germination—This type of seed germination, in which new shoots arise below the ground even though the seed germinated on the surface, occurs in several savanna tree and shrub species, for example *Combretum binderanum, C. molle, C. fragrans*, and *C. sericeum*. Apparently this type of germination evolved as an adaptation to an environment long subjected to annual burning, and serves to reduce water loss (Jackson 1974).

It is also interesting to note that, unlike the tree seeds in the temperate region, where the radicle always protrudes from the micropylar end of the seed unless germination is abnormal,

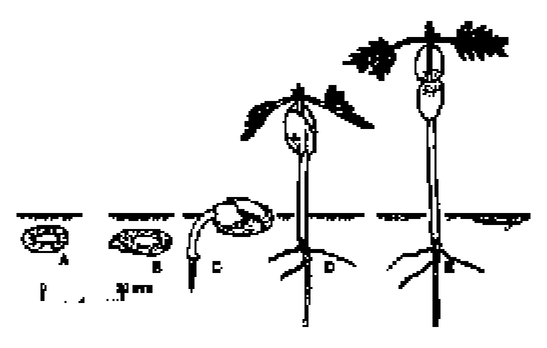

Fig. 2a. Epigeal germination (e.g. *Albizia lebbeck*) from time of sowing to full seedling development: A. at sowing; B. 5 days, C. 10 days, D. 15 day and 25 days after sowing (after Msanga, 1998).

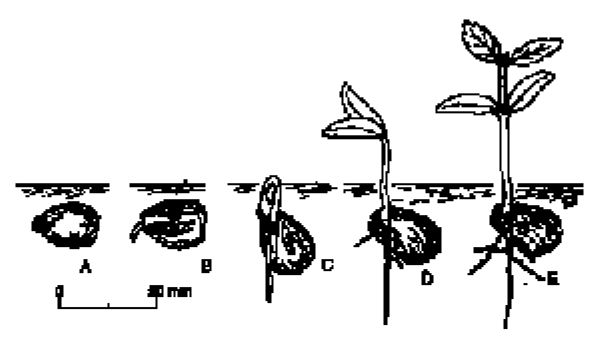

Fig. 2b. Hypogeal germination (e.g. *Vitex keniensis*) from time of sowing to full seedling development: A. at sowing; B. 14 days, C. 21 days, D. 28 days, and E. 35 days after sowing (after Msanga, 1998).

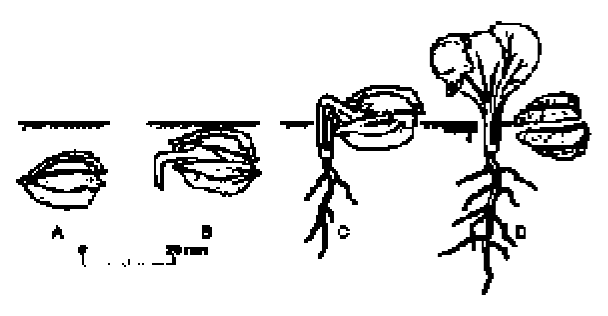

Fig. 2c. Intermediate germination (e.g. *Uapaca kirkiana*) from time of sowing to full seedling development: A. at sowing; B. 15 days, C. 20 days, and D. 30 days after sowing (after Msanga, 1998).

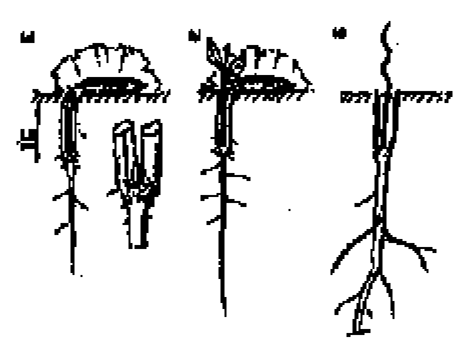

Fig. 2d. Crypotogeal germination (e.g. *Combretum sericeum*): January 4, 1969 (a); January 16, 1969 (b); June 8, 1969 (c) original plumule damaged, resulting in the growth of the cotyledonary axillary buds from the root crown. (after Jackson, 1974).

germination of some tropical tree species such as *Hopea ferrea* and *Markhamia lutea* have radicles that emerge from the middle of seeds (Msanga 1998, Pukittayacamee 1996).

Morphological and Physiological Constraints

The time of germination can be controlled not only by dormancy mechanisms (which are more strongly under genetic control) but also by timing of dispersal (which may be seen as more of a product environmental-genomic interaction). Thus, seed germination is ultimately the product of interactions such as flowering, pollination, seed development, seed dispersal, and seedling establishment. Developmentally the flower, fruit, and seeds constitute a morphological continuum and thus collectively exert a powerful influence on seed dormancy and germination. Primack (1987) has noted that the fruit wall may determine many aspects of seed germination. The fruit wall may split open at maturity in capsules, pods, and follicles, or it may persist as a hard protective layer in nuts, caryopses, and achenes. In addition, the fruit wall may envelop the seeds in soft, nutritious flesh, as seen in berries and pomes. Remnants of fruit structure that remain will determine its immediate physical and chemical environment, and have a dominant effect on germination. Finally, the seedcoat, which originated from the integuments of the ovule, also exerts an influence on germination.

In table 2 some differences are given which exist between families, genera, and even within species, as regards fruit size and type for some of the genera of tropical trees. The classification of fruit types has been taken from the recent revision by Spjut (1994), along with information from various sources of fruit weights. We accept that this table is likely to highlight the many gaps in our knowledge, but hope that it serves as an incentive for further study.

Most trees bear fruits with distinctive modifications for dispersal by explosive discharge, wind, or consumption by birds and mammals. It is noteworthy that Corner (1954) distinguished between megaspermous and microspermous seeds in the families of tropical plants, and that the megaspermous group included the families *Annonaceae, Bombacaceae, Burseraceae, Connaraceae, Dipterocarpaceae, Ebenaceae, Fagaceae, Guttiferae, Lauraceae, Lecythidaceae, Myristicaceae, Palmae*, and *Sapotaceae*, many of which are well represented in table 2.

The property of maintaining seed size reasonably constant within a species, while all other organs of the plant show high plasticity, has been attributed to the maintenance of continuity between generations (Harper and others 1970).

As can be seen in table 2, seed size varies over several orders of magnitude, with *Cocos nucifera* at one extreme (600 g) while *Eucalyptus* spp. (0.25 to 18 mg) and *Metrosideros* (0.057 mg) are at the other. It has also been noted that fleshy fruits are very common in most tropical rain forests, often in excess of 70 percent, while lower frequencies of 18 to 63 percent have been noted in the forests of Queensland, Australia (Willson and others 1989).

Dormancy and the Orthodox-Intermediate-Recalcitrant Continuum

We have refrained from defining dormancy and germination until this late stage for two reasons. First, although it is clear that these states are perhaps intuitively and morphologically evident, biochemical definitions are still lacking (Bewley 1997, Hilhorst and Torop 1997). Dormancy is generally regarded as a temporary suspension of visible growth (i.e. germination) and for many seeds the final phase of seed development involves significant water loss and entry into a metabolically inactive state. This definition, however, is framed to encompass man's important crop plants. If, when provided with suitable temperature, water, and oxygen, germination does not occur the seed is considered to be dormant. Traditionally dormancy is seen as being coat- or embryo-imposed, or a combination of the two. While coat-imposed dormancy is well researched in the legumes, and pretreatments to overcome this type of dormancy are discussed further, well-studied examples of the other dormancy imposition mechanisms are wanting for tropical tree species. Also, in view of the various syndromes mentioned in the Introduction, it might be more appropriate to consider tropical tree seeds as falling into three **germination** categories: coat-imposed germination, prompt germination, and delayed germination. These overlay, or perhaps integrate with, the three seed **storage** categories: orthodox, intermediate, and recalcitrant. Indeed, the question might be asked: to what extent in tropical tree seeds is maturational drying to low (orthodox seed) moisture contents an obligate or facultative attribute? The seeds of many tree species from the humid rain forests are recalcitrant and readily germinable upon falling on the ground as long as moisture is available (several Dipterocarps such as: *Dipterocarpus grandiflorus, Hopea ferrea, Shorea* spp.), while some of the species such as *Podocarpus macrophyllus*, and mangrove species such as *Rhizophora* germinate on the mother tree. Seeds of these species have the shortest longevity and complete their germination processes very quickly. In contrast, some recalcitrant seeds in Africa germinate very slowly (e.g. *Bersama abyssinica* attains 45 percent of its germination after 7 weeks and 70 percent after 10 weeks from sowing). The slowest recalcitrant seed germination was reported to reach 12 percent after 2 months and 70 percent after 3 months from sowing (Msanga 1998). See also figure 1, which graphically illustrates these aspects.

In the subtropical region of Taiwan, recalcitrant seeds of several tree species like *Beilschmiedia erythophloia, Cinnamomum subavenicum, Litsea acuminata, Neolitsea variabillima,* and *Podocarpus nagi* require moist chilling treatment for maximum germination (Lin 1994).

For seeds of nondormant orthodox tree species such as *Acacia drepanolobium, Albizia anthelmintica, A. tanganyicensis, Eucalyptus camaldulensis* Den, *E. globulus, E. muculata, E. paniculata, Gliricida sepium, Samanea saman,* and most recalcitrant species, germination is usually completed between 3 and 14 days. Seeds of other tropical trees such as *Faidherbia, Cassia,* and *Delonix* have seedcoat-imposed dormancy and require some physical or chemical scarification treatment to overcome their dormancy. This allows water, oxygen, or both to enter the seeds and permits the embryo to overcome the mechanical restriction of surrounding tissues. Seedcoat-imposed dormancy is the major cause of many tropical tree seed germination problems and is discussed further in the section entitled Pretreatments to Overcome Dormancy.

Seed Polymorphism

In general, the frequency distribution of seed size and shape from either single plants or populations is a continuous distribution, normal or skewed. In plants showing seed polymorphism, two or more sharply defined distribution patterns are seen (Harper and others 1970). Attributes such as seed size, shape, dormancy, or internal structures are some of the forms in which polymorphism may be manifested.

For example, three seed types are seen in the legume *Ononis sicula* of the Israeli desert, whose seeds are polymorphic in color, size, weight, and water permeability. South American species of *Ormosia* produce both red and bicolored (black and red) seeds, the production of which appears to be highly variable. While the red seeds are susceptible to bruchid attack, the bicolored seeds are highly toxic and rarely attacked by bruchids (Van Staden and others 1989).

Seedcoat color changes are often associated with the onset of impermeability during seed maturation and there is evidence that seedcoat color is controlled by a single gene (Egley 1989). The adaptive value of this polymorphism is clearly evident: orange seeds of *Platylobium formosum* were seen to be less dormant than black seeds when studied over two successive years (Morrison and others 1992).

These workers also studied the dormancy patterns of some common Australian leguminous species, and showed that seed weight and volume were significantly related to the properties of nondormant seeds. Three groups were distinguished: those with a relatively small nondormant fraction at maturity (0 to 10 percent) which was maintained through time; those with a relatively large nondormant fraction (10 to 40 percent) which maintained dormancy over time, and those that possessed a relatively small nondormant fraction whose dormancy decreased over time. To what extent the above patterns are evident in tropical tree species remains to be determined. The presence of two or more distinct seed types in fruits is well documented in herbaceous species, e.g. *Xanthium* (Harper and others 1970). Augspurger and Hogan (1983) have noted that *Lonchocarpus pentaphyllus* has mature indehiscent fruits that may contain one, two, and three (rarely four) winged seeds; while this had clear implications for dispersal, the influence on germination remains unknown. Variable numbers of seeds per fruit were also noted for *Platypodium elegans, Dalbergia retusa,* and *Pterocarpus rohrii*, but again there is no clear evidence how this polymorphism may influence germination. That different sizes of seed may show marked differences in germination is well known: large and medium-sized seeds of *Syzgium cumini* gave better germination than smaller seeds (Ponnamal and others 1992); seed size did not influence germination percentage in *Virola koschnyi*, although large seeds produced more vigorous seedlings (Gonzalez 1993).

Sometimes the pattern observed is not entirely consistent. Roy (1985) showed that although the germination index for small seeds of *Albizia lebbeck* (L.) Benth. was greater than for large seeds, the actual percentage germination and seedling vigor were greater for larger seeds. This contrasts with another study (Prem Gupta and Mukherjee 1989) where 62 percent germination was recorded for large seeds (0.1 g) of *A. lebbeck* as against 74 percent for smaller seeds (0.08 g).

The germination of three weight classes of *Acacia melanoxylon* R. Br. (ranging from 0.0099 to 0.021 g) varied from 55 percent for lighter seeds to 95 percent for the heavier cohort (Gomez Restrepo and Piedrahita Cardona 1994).

Seed Maturity and Postharvest Handling

Apart from the above inherited characteristics that may influence germination, there are environmental influences and factors within the control of the seed scientist which fall under this heading. Some of these have been identified as: ecological conditions of the mother tree, seed collection date, seed quality and treatment, seed storage (discussed in chapter 3 of this volume), and seed germination tests. All seeds, whether they are orthodox or recalcitrant, require timely collection at or near their full maturity, then careful handling from collection to storage to obtain maximum physical and physiological quality. However, a wide range of reproductive patterns is seen in tropical trees. Flowering and fruiting patterns may be continuous and predictable; show some seasonability (using environmental ones such as photoperiod, temperature, and drought); or be somewhat erratic. In dipterocarps it has been noted that flowering and fruiting may occur once every 2 to 3 years, and in some species may occur only every 11 years (Jansen 1974); sometimes only a third of the forest population may seed at any one time (Turner 1990). In addition, the number of flowers that develop into mature fruits can vary enormously, not only in a species-specific manner but also from year to year. Flower and fruit abortion can be considerable. For example, in *Ceiba pentandra* less than 0.1 percent of flowers mature into fruit, and only 10 percent of initiated fruits mature (Stevenson 1981). Immature or incompletely dried seeds have long been known to affect seed germination and vigor, and the choice of an optimal collection time is often a compromise between several factors. If flowering and fruiting are protracted, no one harvest time will provide seed of uniform maturity. Mahedevan (1991) has reported that tree-to-tree variations in fruiting and seed maturation in *Acacia nilotica*, *Albizia lebbeck*, and *Azadirachta indica* militated against a single collecting time. Marked genetic influences may also operate, as seen in the provenance trials of *Acacia mangium* from 20 localities, which yielded wide variations in seed characteristics and production (Bhumibhamon and others 1994).

Often, features such as fruit or wing color may provide useful indicators of seed maturity and germination. For *Gmelina arborea*, yellow and yellow-green fruits gave higher germination than green fruits (Mindawati and Rohayat 1994), while in *Shorea pinanga* and *S. stenoptera*, harvest of fruits with fully brown wings greatly improved final germination (Masano 1988). The narrow window for optimal harvest was shown by the study of Kosasih (1987) on *Shorea ovalis*. Harvests made at 9, 10, and 11 weeks, during which time coat changes occurred, showed 13 percent, 25 percent, and 93 percent germination, as well as more rapid germination. External signs of fruit ripeness, and suitable postharvest handling techniques, have been reported for 18 tree species from Colombia including *Bombacopsis quinata, Calophyllum mariae, Cordia allodorata, C. gerascanthus, Didymopanax morotonii, Jacaranda copaia, Tabebuia rosea, Virola* spp., and *Zanthoxyllum tachuelo* (Trivino and others 1990).

The potential for insect attack exists at any stage of seed production, and seed predation by insects causes the selective abscission of young fruits. A stand of *Cassia grandis* aborted 95 percent of initiated fruit, 81 percent of which were seen to be insect damaged (Stevenson 1981). For basic information on insect attack of orthodox seeds during storage the reader is referred to Howe (1972), while Birch and Johnson (1989) discuss seed predation specifically in the legumes. Field studies indicate that seeds may be subjected to seasonal attack, especially at the peak maturation period. Information is available on weevil attack in dipterocarps (Khatua and Chakrabati 1990, Kokubo 1987). Postfertilization weevil attack in *Syzgium cormiflorum* was reported to be as high as 70 percent (Crome and Irvine 1986). Sometimes insect attack is restricted to external pulpy tissues and does little harm (Eusebio and others 1989). Postdispersal seed mortality of 30 to 35 percent for *Virola nobilis* was accounted for by insect attack (Howe 1972), while a figure of 25 percent has been given for *Ocotea tenera* fruits on the parent tree (Wheelwright 1993).

A number of *Bruchus* spp. attack fruits in the field and are brought into storage with ripe seeds. Attacks on *Acacia* spp. have been especially well documented (Hedlin and Eungwijarnpanya 1984), while the genus *Caryedon* is prone to attack *Combretum, Cassia,* and *Acacia* spp. (Howe 1972). Eungwijarnpanya and Hedlin (1984) and Abdullah and Abulfatih (1995) have reported insect damage on species of *Acacia, Albizia, Bauhinia, Cassia, Dalbergia, Dipterocarpus, Shorea,* and *Tectona.* Johnson and Siemens (1992) have recorded bruchid attacks on *Acacia farnesiana* and *Pithecellobium saman* in Ecuador and Venezuela, while large-scale attack on seeds of *Virola surinamensis* by *Conotrachelus* weevils was observed around fruiting trees by Howe and others (1985). In some instances, toxic seed constituents may significantly limit seed predation by insects, such as *Pentaclethra*. Central American woody legumes form two natural groups by seed weight: the mean seed weight of 3 g in 23 species that have toxic seed constituents and are not attacked by bruchid beetle larvae, and the mean seed weight of 0.26 g in 13 species that are attacked by bruchid beetles (Harper and others 1970).

Interactions between insect and fungal damage may operate additively in some cases. Damage was found to range between 50 percent in November and over 70 percent in February for seeds of *Albizia lebbeck* collected in Madhya Pradesh (Harsh and Joshi 1993). A general account of seed fungi may be found in Baker (1972) and Mittal and others (1990). Both recalcitrant and orthodox seeds harbor fungi, which may have serious impact on germination. Mycock and Berjak (1990) examined seven recalcitrant crop species and found a spectrum of fungal contaminants in all; fungal proliferation was exacerbated by storage. Fungi were also evident in the orthodox seeds of the tropical tree species *Albizia, Cedrela, Entandrophragma, Gmelina, Khaya, Leucaena, Maclura, Terminalia,* and *Triplochiton* (Gyimah 1987). A diverse and abundant mycroflora were found to be associated with six species of *Eucalyptus* investigated by Donald and Lundquist (1988). Hot water treatments (50 °C), surface sterilization (10 percent sodium hypochlorite), or fungicidal treatment (captan) were effective in reducing fungi and increasing germination. Physical sieving alone, whereby fine chaff was removed from seed lots, was able to reduce fungal contamination appreciably. Under field conditions, ants were seen to exert a positive effect on seed germination in *Hymenaea courbaril* by removing pulpy and fungus-infected pulp (Oliveira and others 1995). Further details on seed pathology may be found in chapter 6, by Old and others. Recalcitrant fruits are commonly collected before they reach full maturity due to their short collecting windows. Consequently, they must be handled with great care in transporting and processing to limit fungal and insect attack and maximize germination. The effect of postharvest handling on the quality of provenances of recalcitrant seeds of *Azadirachta indica* has been reported (Poulsen 1996). Immature or improperly processed seeds have long been known to affect seed germination and vigor. Collection of fruits/seeds from the ground is convenient and economical, but usually results in poor quality seed if improperly timed (Willan 1985). In Brazil, emphasis has been placed on reducing transporting time of fruits of *Gmelina arborea* in sacks to prevent losses in germinability (Woessner and McNabb 1979). Willan (1985) suggested that critical factors for recalcitrant fruits were ventilation, temperature, moisture content, nursery practices, and careful handling in long-distance transport.

The processing of fleshy fruits requires timely extraction to avoid fermentation. All recalcitrant fruits should be dried in the shade with good ventilation. Seeds of some recalcitrant species like *Bersama abyssinica* and *Trichilia emetica* require 4-day postharvest ripening before processing (Msanga 1998). A period of postharvest ripening was also required by *Shorea siamensis* and *Shorea roxburghii* (Panochit and others 1984, 1986), as well as for *Persea kusanoi*, *Neolitsea acuminatissima*, and *Cinnamomum philippinise* (Lin 1994, Lin and others 1994). Handling is especially critical for germinating intermediate and recalcitrant fruits/seeds requiring slow drying under shade and cool temperatures (e.g.*Swietenia macrophylla*), then washing and macerating to remove pulpy tissues.

It sometimes may be difficult, particularly in smaller-seeded species, to distinguish between fully developed or incompletely filled seeds. Density separation, using solutions of either polyethylene glycol or potassium carbonate, provides a convenient means of effecting separation between “floaters,” “sinkers,” and debris (Hurley and others 1991, Tsuyuzaki 1993).

PRETREATMENTS TO OVERCOME DORMANCY

Dormancy in tropical and subtropical tree seeds is predominantly seedcoat imposed. Various effective and practical treatments have been developed to break this dormancy. Nicking, hot water soaking, and physical or acid scarification have all been used to good effect with the seeds of the many legume species of tropical and subtropical origin.

The role of the seedcoat in regulating imbibition is well known in legumes, and differences in seedcoat permeability resulting from maturational factors, mechanical damage during harvest, or scarification treatments may all impinge negatively on germination by causing imbibition injury (Powell and Matthews 1979, 1991). In the tropical forage legume *Calopogonium mucunoides*, the water absorption pattern was characteristic for each individual seed lot, and higher imbibition rates were associated with seeds of lower quality (Souza and Marcos-Filho 1993).

LEGUME SEEDCOAT STRUCTURE

The impermeable properties of the legume seedcoat to water or gases, and its property of providing a mechanical restraint to the embryo, are achieved by a combination of structural and/or chemical properties, which have been elucidated by anatomical and ultrastructural studies. While the seedcoat is seen as a hindrance to uniform and rapid germination, it should be remembered that the coat nonetheless performs the critical functions of regulating water uptake, providing a barrier to fungal invasion, and reducing leakage from the embryo during imbibition. As Hanna (1984) noted, most investigations have unfortunately concerned themselves with finding mechanisms for improving germination rather than determining mechanisms involved in the process.

Although the topic has been extensively investigated for more than four decades (Bhattacharya and Saha 1990, Dell 1980, Hyde 1954, Maumont 1993, Serrato-Valenti and others 1995), it is perhaps necessary to bring the results of these many reports together in one place. One recent useful review on this topic is that of Egley (1989).

Figure 3 illustrates some of the relevant features of the legume seedcoat. It is important to remember that while impermeability is seen in all three legume families, there are many differences, and not all legumes necessarily have a significant coat-imposed dormancy (see also table 2). Fresh seeds of *Gliricidia* and *Xylia* germinated readily (Iji and others 1993), and although seeds of *Hymenacea courbaril* showed hard coats, good germination was reported at 23 °C in soil, without any scarification treatment. Developmental events during late maturational drying are critical to the acquisition of impermeability. All sites that were open during early development, such as the hilum, micropyle, and chalazal pore, seal up during the late stages of seed drying. At 20 percent water content, and below, the epidermis of the seedcoat is considered to become markedly impermeable.

The cuticle on the seed surface is the first line of impermeability, although it is no longer considered to be the major or sole barrier to water entry. Below the cuticle lie thick-walled, tightly packed rows of columnar cells (Palisade or Malpighian cells) which completely enclose the embryo except for the hilum, micropyle, and chalazal pore; these cells are considered to play a major role in preventing water ingress. During the final stages of maturational drying, seed shrinkage intensifies the process of compression of these cells, and the occlusion of their lumen, along with impregnation of the wall by such substances as suberin. Typically the hilum is responsible for further seed drying, acting as a hygroscopic valve by closing at high atmospheric relative humidity (r.h.), thereby limiting water vapor uptake. Likewise, by opening when atmospheric r.h. is low, the hilum permits further water loss from the seed. Differential tensions between the palisade and counter-palisade cells are thought to cause hilar movement (fig. 3D). Caesalpinoid and mimusoid legumes generally lack

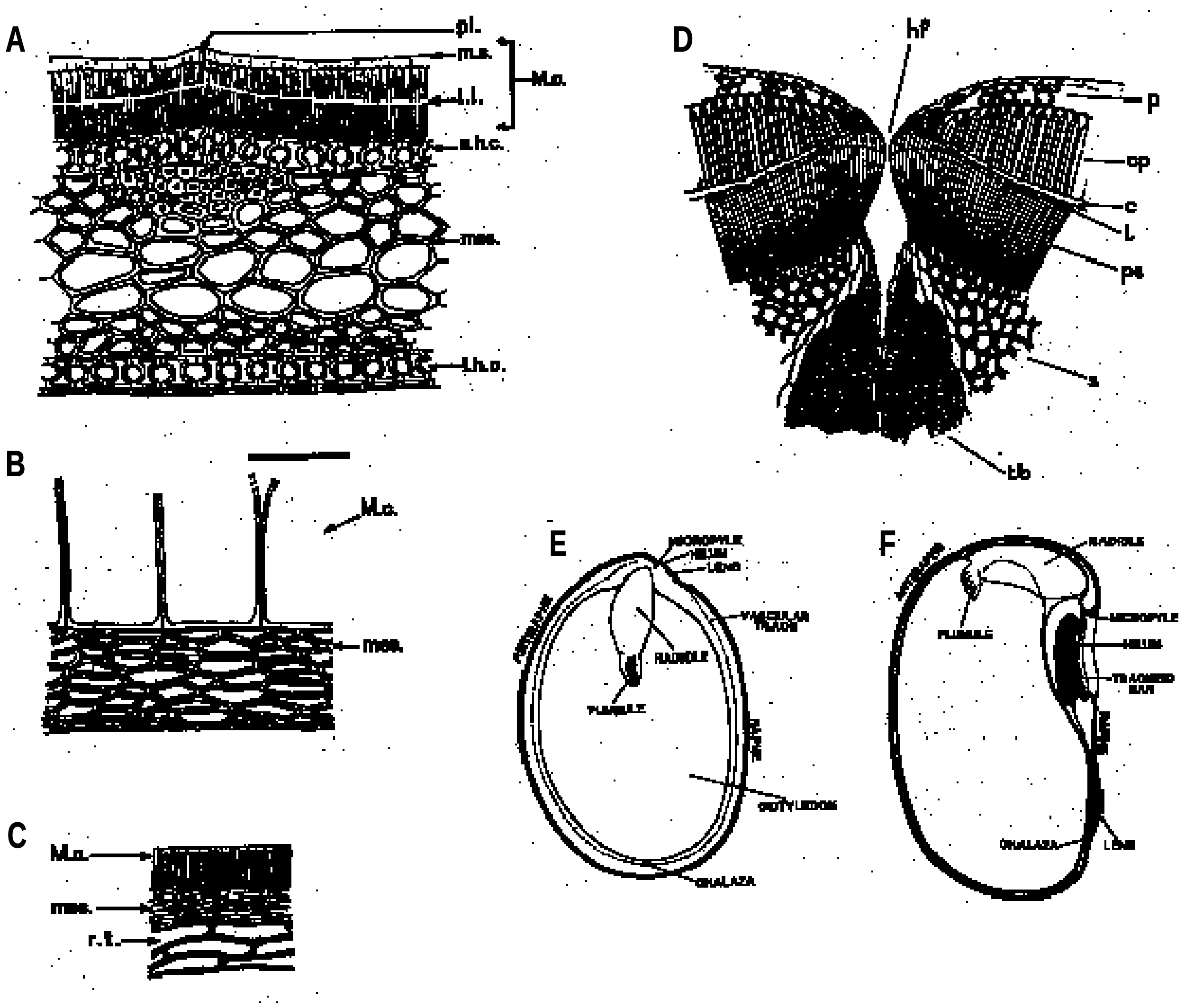

Fig. 3. Microscopic and macroscopic morphological details of some legume seeds and testae: (A) *Acacia galpinii*, (B) *Inga acreana*, and (C) *Pithecellobium cochleatum* (Reproduced from Maumont 1993); (D) Section through hilar region of *Lupinus arboreus* (Reproduced from Hyde 1954); medium longitudinal sections through raphe-antiraphe regions of (E) *Acacia farnesiana*, and (F) *Schotia brachpetala* (Reproduced from van Staden and others 1989). Abbreviations: pl. = pleurogram; m.s. = mucilage stratum; l.l. = light line; e.h.c. = external hourglass cells; M.c. = Malpighian cells; mes. = mesophyll; i.h.c. = internal hourglass cells; r.t. = resinous tissue; h.f. = hilar fissure; p = palisade; c.p. = counter-palisade layer; P.e. = palisade epidermis; s = spongy (mesophyll); t.b. = tracheid bar.

the complex hilum seen in the papilionids, and so the water regulation system needs further clarification. Below the Malpighian cells there is sometimes a squat layer of hypodermal "hourglass" cells with thickened walls (fig. 3A), but this is not universal, and sometimes compressed mesophyll cells are seen (figs. 3B and 3C).

These cells, which may have thick or hard pectic layers, have also been implicated in restricting water uptake or movement. Inner "hourglass" cells are the last cell type in "typical" legume coats (fig. 3A), but in other genera other cells may be seen, e.g. resinoid tissue *Pithecellobium* (fig. 3C).

The "hourglass" cells do not develop below the strophiolar plug region (also called the lens), and sometimes thin-walled parenchyma cells create a natural point of weakness (e.g. *Albizia* and *Acacia*). Other cell types have been reported here, such as the "white cells" of *Leucaena leucocephala* (Serrato-Valenti and others 1995), and these may be important in the early aspects of water movement into the seed. The long, narrow Malpighian cells in the strophiolar (lens) region have a greater tendency to split when subjected to heating, physical, or chemical treatments, but the exact manner of lens rupture may seem to be legume-specific. Irreversible lens rupture seems common in mimusoid legumes, but not in the papilionids; the vascular bundle below the lens and its association with coat rupture needs to be considered in the overall process. The "ejection" of lens cells is characteristic of *Albizia* given heat treatment, compared to a more controlled lifting in *Acacia*. Finally, the chalazal split, which may be geographically quite distinct from the hilum, may lose its sealing deposit or it may break down naturally; subsequent water uptake may cause differential cell expansion and buckling of the wall layers of the testa.

Often, once the seedcoat has been breached and imbibition has occurred, germination may still be impaired. This has been variously attributed (but not proven) to hormonal aspects and the requirement for other germination signals (e.g. light). Frequently, darkening (tanning-type reactions), associated with maturation drying is considered to play a role in the impermeabilization process. To what extent this is a regulated developmental event occurring at a specific, particular, water content (like LEA proteins) or is purely a "last ditch" response associated with final loss of cellular integrity, is unknown. The process does seem to show striking parallels with peroxidase-initiated free-radical polymerization of lignins (and suberins) seen in xylem vessel differentiation (Fukuda 1996, McCann 1997). There is some evidence that the rates of maturational drying can influence seedcoat properties (Egley 1989), and hence coat-imposed dormancy. Nutrient status, cytokinins, and abscissic acid have also been suggested as additional elements involved in seedcoat development (Egley 1989).

TREATMENTS TO BREAK SEEDCOAT DORMANCY

Nicking

This treatment involves cutting the seed at the distal (cotyledonary) end with a sharp tool like a scalpel, a razor blade, or a large nail clipper. The treatment is practical for treating small quantities of seed for testing or research purposes, but is time consuming and laborious. It has been found effective in releasing the dormancy of *Acacia tortilis, A. seyal, Albizia gummifera, Brachystegia spiciformis, Delonix elata, Faidherbia albida, Leucaena leucocephala, Maesopsis eminii,* and *Terminalia* spp. (Msanga 1998, Wolf and Kamondo 1993).

Soaking in Water

This is the simplest treatment to give the seeds an early start in the germination process. It has effects not only on the activation of enzymes and mobilization of reserves, but also on the softening of hard seedcoats and leaching out of chemical inhibitors. Soaking in water for 2 to 48 hours has been reported to improve seed germination of many tropical tree species such as *Acacia mearnsii, A. melanoxylon, A. nilotica, Adenanthere mirosperma, Albizia amara, A. procera, Grevillea robusta, Trewia nidiflora,* and *Pinus caribaea* (Matias and others 1973). Aerated, cold-water soaking for 28 days at 1.1 °C was found to be effective in breaking moderate dormancy and enhancing germination of *Pinus taeda* seeds (Barnett and McLemore 1967). In contrast, Andressen (1965) found cold, distilled-water soaking at 3 °C for 7 to 14 days depressed the germination of *Pinus strobiformis* seeds of northern Arizona and northern New Mexico. Experience of the USDA Forest Service's Eastern Tree Seed Testing Laboratory indicated that long periods of soaking (7 to 14 days) is apparently injurious to coniferous seeds unless they are soaked in aerated water (Swofford 1965).

Alternate soaking and drying of agricultural seeds has been studied as a treatment to improve seed germinability and increase crop productivity (Basu and Pal 1980, DasGupta and others 1976). Yadav (1992) investigated the influence of various soaking-drying treatments on the subsequent performance of *Tectona grandis* in field plantings. Germination was most rapid for alternate soaking and drying treatments, while the highest total germination occurred with 6 or 8 days of uninterrupted soaking. Soaking treatments of 10 and 12 days were deleterious to germination, and seeds receiving the soaking-drying treatments gave better germination than the control. The above results are fully supported by an earlier study on *T. grandis* which showed 12-hour alternate soaking and drying for 1 month improved germination for 36 provenances of seed. Most seeds germinated in a single flush, but for five sources, two to three successive flushes were observed at 9- to 10-month intervals (Bedell 1989). Apparently, as pointed out by Berrie and Drennan (1971), this treatment was extensively reviewed earlier by Kidd and West. They suggested that soaking and drying treatments can have varying effects on germination depending on the rate of drying, the species tested, and the duration of the soaking. Berrie and Drennan (1971) found that the beneficial effect of the treatment was some advancement of the onset of germination, due probably to slight changes in the seed covering and also to the initiation of metabolic events which could withstand the drying. They claimed that there was little harmful effect from drying if it was carried out before cell division and enlargement had begun, but some of the chemical changes induced by soaking cannot be reversed to the original dry seed condition by drying. When embryo growth is apparent, some embryo damage will usually result from the drying. The physiological basis of the beneficial effects of soaking and drying treatment is not yet well understood (Basu and Pal 1980). Based on the research results on agricultural crop seeds from Basu and Pal (1980), the effect of soaking and drying was primarily prophylactic; it seemed to be able to eliminate the cause of subsequent seed deterioration rather than to repair the damage already inflicted to the bio-organelles. Nevertheless, this interesting seed treatment deserves further study.

Hot Water Soaking

This treatment involves soaking seeds in water at 40 to 100 °C depending on the species and seedcoat thickness, for a specific period of time or until the boiling water cools to room temperature. For example, *Celtis africana, Cordia sinensis* (stored seeds), and *Melia volkensii* seeds require soaking in water at 40 °C and then cooling down to room temperature. For *Acacia nilotica* and *Tamarindus indica*, pouring 80 °C water over the seeds in a container, followed by a soaking for 24 hours, was found to be effective (Albrecht 1993). Pouring 100 °C water over the seeds of *Adansonia digitata*, *Calliandra calothyrus,* and *Sesbania sesban,* with continued soaking as the water cooled off for 24 hours, was reported effective in breaking seedcoat dormancy (Albrecht 1993). In contrast, a brief soak in 90 °C water for 1 minute resulted in good germination of *Acacia mearnsii* and *A. melanoxylon* seeds (Albrecht 1993), while 30 seconds of soaking in boiling water overcame seedcoat dormancy of *Acacia mangium* seeds (Bowen and Eusebio 1981). This treatment is the quickest, cheapest, and simplest method for releasing seedcoat dormancy of many tropical species in operational applications.

Acid Scarification

This treatment is effective and practical for breaking seedcoat dormancy of many tropical species, but it is not commonly used due to its cost, the risk, and safety precautions involved. The treatment requires soaking seeds in 95-percent pure (1.84 specific gravity) sulphuric acid in an acid-resistant container such as thick plastic, for various periods depending on the species, draining the acid over a screen, then washing and drying the seeds. The drained acid can be re-used. The effectiveness of the treatment can be judged by the high percentage of swollen seeds and their dull, pitted appearance (Bonner and others 1974). According to Swofford (1965), for proper application of acid scarification the seed moisture content should be less than 10 percent because higher moisture content makes the action of sulphuric acid more violent, with possible seed injury.

The acid scarification can be applied either at room temperature or in a heated condition (70 °C) (Tietema and others 1992). The timing of this treatment is critical, as the soaking period and the postsoak washing have to be precisely controlled to avoid seed injury. Table 3 provides details of acid scarification treatment periods for some tropical tree species from the published literature.

Soaking in Hydrogen Peroxide Solution

Soaking seeds in 5 to 30 percent H_2O_2 for 30 minutes effectively reduced seed-borne microflora and stimulated germination of *Vangueria infausta* (Msanga and Maghembe 1989) and *Albizia schimperana* (Msanga and Maghembe 1986). For improved germination of camphor (*Cinnamomum camphora*) seeds, they must be soaked in 15 percent H_2O_2 for 25 minutes (Chien and Lin 1996).

Physical Scarification

This treatment can be achieved either manually, for small quantities of seed for laboratory testing or research purposes, or by mechanical equipment like the “seedgun” (Mahjoub 1993, Poulsen and Stubsgaard 1995, Msanga 1998), the Forberg mechanical scarifier (Piotto 1993), or the cement mixer (Albrecht 1993). When small quantities of seed are required, the “glow burner” or “hot wire” is an effective and efficient device for many tropical seeds (Poulsen and Stubsgaard 1995, Msanga 1998). When large quantities of seed are needed for operational sowing, use of a seedgun was also reported to be effective and efficient (Mahjoub 1993, Poulsen and Stubsgaard 1995, Msanga 1998).

A sandpaper-lined commercial mill was used by Todd-

Table 3

Some Recommended Acid Scarification Treatment Periods for Breaking Seedcoat Dormancy in Tropical Tree Species

Species	Acid condition	Treatment period (min)	Reference
Acacia auriculiformis	R	30	Pukittayacamee 1996
A. burkei	H	4	Tietema and others 1992
A. erioloba	R	3	Tietema and others 1992
A. hebeclada	R	120	Tietema and others 1992
A. karroo	H	2	Tietema and others 1992
A. nilotica	R	5-75	Zodape 1991
A. nilotica	H	9	Tietema and others 1992
A. tortilis	R	90	Tietema and others 1992
Albizia procera	R	15	Pukittayacamee 1996
A. lebbeck	R	5-75	Zodape 1991
Burkea africana	R	40	Tietema and others 1992
B. racemosa	R	5-75	Zodape 1991
Celtis africana	R	5	Tietema and others 1992
Cassia siamea	R	15	Kobmoo and Hellum 1984
C. nodosa	R	20	
C. fistula	R	20	
Leucaena leucocephala	R	20-60	Cruz and others 1995
Parkinsonia aculeata	R	5-75	Zodape 1991
Peltophorum africanum	R	60	Tietema and others 1992
P. lasyrachi	R	15	
P. pterocarpum	R	30	Pukittayacamee and others 1996
Terminalia brownii	R	60	Specht and Schaefer 1990

R = room temperature; H = heated to 70 °C.

Bockarie and others (1993) to uniformly scarify seeds of *Cassia sieberiana* and produce a uniformly high germination, equal to that of sulphuric acid treatment. Significant differences were noted among parent trees as regards the best pretreatments employed (table 4). As Gosling and others (1995) have noted, there is no real consensus on what constitutes the "best" method of pretreatment; intrinsic biological variation between species, seedlots, and individual seeds is doubtless responsible for much of this. Sulphuric acid treatments were successful in improving the germination of all 20 leguminous species tested including *Acacia albida*, *Albizia lebbeck*, *Caesalpinia decapetala*, *Delonix regia*, *Leucaena leucocephala,* and *Parkinsonia aculeata*. Dry heat (60 to 100 °C), a little-used method in general, was effective in 68 percent of species tests, whereas mechanical scarification was effective for 90 percent of the tested species.

An especially promising advantage from the use of the acid scarification technique has recently been suggested (Duguma and others 1988, Some and others 1990, Todd-Bockarie and others 1993). This involves acid scarification, washing and drying at a central facility, followed by distribution to nurseries and storage for later use. Storage for up to a year may be possible for prescarified seeds of *Acacia albida*, *A. nilotica*, *Bauhinia refescens*, *Parkia biglobosa*, *Faidherbia albida*, *Leucaena leucocephala,* and possibly *Cassia sieberiana*.

Sometimes the choice of method may be a compromise between labor intensiveness and seed quality/quantity. For instance, Gosling and others (1995) concluded that while chipping was labor intensive it nonetheless yielded the fastest germination rate over the widest range of temperatures tested

Table 4

Some Comparative Studies of Different Scarification Methods Applied to Tropical Tree Seeds

Species	Treatment conditions	Comment/response	Reference
Acacia auriculiformis A. holosericea	Nicking, H_2SO_4 15 or 30 min, hot water 1-5 min	Higher germination with nicking but seedling growth poorer than with other treatments.	Marunda 1990
A. farnesiana	Sandpaper scarification:	98% germination	Gill and others 1986
	HNO_3 or H_2SO_4:	65-66% germination	
	Soaking and drying:	64% germination	
	Control, untreated:	30-40% germination.	
A. tortilis, A. craspedocarpa, A. pachyacra, A. farnesiana, A. saligna	None (control). Mechanical scarification, hot water treatment, mechanical + hot water.	All treatments gave 103-186% germination increase over control; mechanical + hot water best overall. Benlate used; 15 °C best.	Omari 1993
Albizzia lebbeck	Hot water 75-100 °C, 3 s + 24 h water soak at room temperature + 24 h high RH hold + direct soil sowing.	100% germination	Millat-E-Mustafa 1989
Cassia fistula, C. glauca, C. javanica, C. nodosa, C. sienna	Mechanical, H_2SO_4, and sheep rumen scarification compared.	Mechanical most effective overall; H_2SO_4 best for C. javanica	Todaria and Negim 1992
C. bicapsularis, C. javanica, C. speciosa	H_2SO_4 1, 2, 3 h:	54-90% germination	Rodrigus and others 1990
	Boiling water + 8, 12, 24 h soak:	2-12% germination	
	Manual scarification:	69-79% germination	
C. sieberiana	Wide range of heating, organic solvents, mechanical and combinations –		Todd-Bockarie and others 1993
	Nicking:	93% germination	
	98% H_2SO_4, 45 min:	93% germination	
	95% EtoH, 9 h:	40% germination	
	Hot or boiling water, 2, 4, 6 min:	0-12% germination	
	Commercial mill:	85% germination	
	Control:	2% germination	
	Coffee grinder:	45% germination	
Leucaena leucocephala, L. greggii, Pithecellobium pallens, P. flexicaulis, Propsis laevigata	File and sandpaper + H_2SO_4 10-20 min	Better response than mechanical only	Foroughbakhch 1989

Table 4 (continued)

Species	Treatment conditions	Comment/response	Reference
Leucaena leucocephala	95% H_2SO_4, 7 min:	98% germination	
	95% H_2SO_4, 4 min:	99% germination	
	Bag impaction:	64% germination	Passos and others 1988 (Further details in fig. 4; Gosling and others 1995)
	Hot water 100 °C, 2 s:	76% germination	
	Hot water 100 °C, 4 s:	82% germination	
	Control:	73% germination	
	H_2SO_4, 1 h:	77% germination	
Terminalia brownii	Control	66% germination	Specht and Shaefer 1990
	V-shaped nick at radicle end:	81% germination	
T. spinosa	No treatment	Weaker endocarp: easy to germinate	
T. ivorensis	H_2SO_4 3 h + cellulase 24 h + GA_3 5 d	Most effective treatment for lignified coat	Corbineau and Côme 1993

for *Leucaena leucocephala*. Hot or boiling water treatments, although easier to apply in bulk, did compromise germination, especially when conducted at higher temperatures. Figure 4, reproduced from Gosling and others (1995), shows clearly the "narrow island" for optimal dormancy-breaking, and strongly emphasizes the interaction of longer times and higher temperatures in producing a larger "sea" of deleterious seed treatments. Indeed, any heat treatment should be regarded as a form of accelerated aging, no matter how short the duration.

Stratification

This is a simple, inexpensive, and effective technique for overcoming seed dormancy of temperate tree species depending upon the type of dormancy involved: warm stratification is applied for seeds that have immature embryos; cold stratification is used to break physiological dormancy; and a combined warm and cold stratification is effective for seeds that have both immature embryos and physiological dormancy. Warm stratification involves placing seeds in a moist medium such as sand, sawdust, vermiculite, peatmoss, or a mixture of two media in a loosely covered container at 20 to 25 °C for various periods of time depending on the species. In the Tropics, warm stratification is not commonly used for releasing dormancy of the tropical tree species although Msanga (1998) has suggested this treatment for *Warbugia salutaris*, which is suspected of having an embryo dormancy with delayed germination.

Cold Stratification

Also known as moist chilling, this involves placing seeds in a moist medium of sand, sawdust, peatmoss, vermiculite, or any other porous material in a loosely covered container (e.g. plastic bag) at 1 to 5 °C for various periods depending on the species. The most commonly practiced method of cold stratification in North America is so-called "naked stratification" which requires soaking seeds in tap water for 24 to 48 hours, draining the water, surface-drying the seeds, and placing them in a loosely tied plastic bag at 2 to 5 °C for various periods. Recently, the cold stratification treatment was modified by drying back the seed moisture content to 10 to 15 percent lower after soaking (i.e. *Abies*) (Edwards 1989, Leadem 1989, Tanaka and Edwards 1986), or surface-drying the seeds in the midstratification period then continuing the stratification period (Tanaka and Edwards 1986). Albrecht (1993) found that seed dormancy of *Juniperus procera* was effectively broken by moist chilling in sand at 3 °C for 60 days. It is interesting to note that seeds of many subtropical orthodox as well as recalcitrant species exhibit deep dormancy and require cold stratification to enhance seed germination (e.g. *Phellodendron wilsonii*, *Sassafras randaiense*, *Castanopsis carlesii*, *Quercus gilva*, *Quercus glauca*, *Quercus spinosa*, *Elaeocarpus japonica*, *Neolitsea ariabillima*, and *Neolitsea parvigemma*) (Lin and oth-

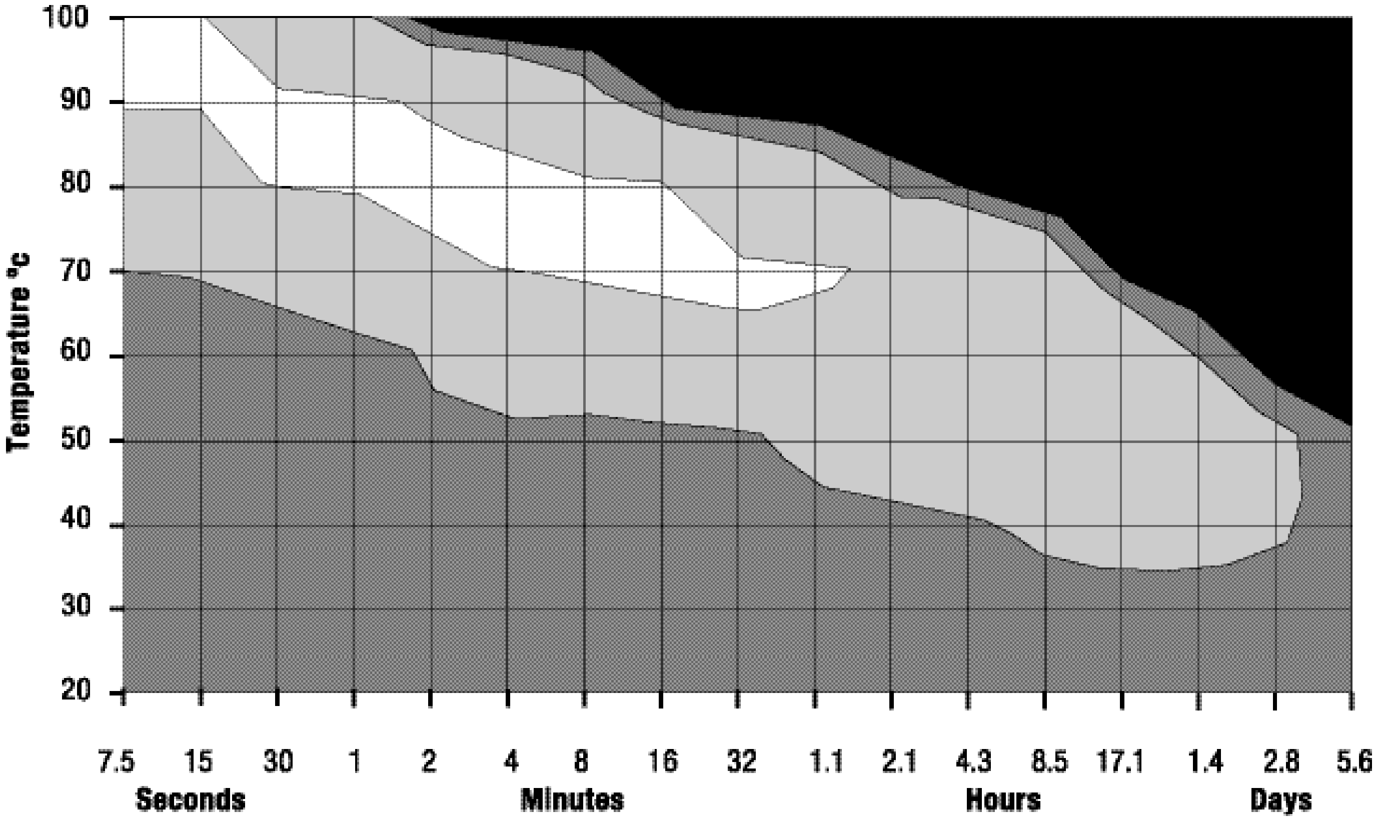

Fig. 4. Germination contours produced from temperature and time treatments of *Leucaena leucocephala* seeds (Reproduced from Gosling and others 1995).

ers 1994, Lin 1994). Chien and others (1998) reported that *Taxus mairei* seeds require not only 6 months of warm stratification at alternating temperatures of 25 °/15 °C or 23 °/11 °C, but also 3 months of cold stratification at 5 °C to overcome the combined morphological and physiological dormancy. Apparently, the warm stratification caused the underdeveloped embryo and ABA concentration to decline, whereas the cold stratification induced the accumulation of GAs and/or increased the sensitivity of seeds to GA's, thus resulting in the release of physiological dormancy and enhancing seed germination (Chien and others 1998). It should be realized that the beneficial effects of cold stratification are not limited to breaking seed dormancy and promoting the percentage and rate of germination; it also minimizes the effects of seed handling and adverse germination environments (Wang 1987).

Chilling for 56 days was recommended for seeds of *Celtis africana, C. sinensis,* and *Pteroceltis tartarinowii* (Browse 1990). In Cuba, seeds of *Quercus oleoides* subsp. *sagraena* responded well to chilling at 4 °C in moist sand at 20 percent moisture content (mc), and 60 percent germination was recorded after 7 months (Figueroa and others 1989). Obviously in species that are known to be recalcitrant, or where ecotypes may exist, the chilling injury limit should be avoided. For instance, Mori and others (1990b) showed that temperatures below 15 °C were deleterious to four species of Malaysian dipterocarp, *Bombax valetonii,* and *Acacia auriculiformis.*

GERMINATION CONDITIONS

Several conditions need to be fulfilled to ensure germination; these include moisture, temperature, aeration (oxygen), light, and an appropriate medium (or substrate), plus a suitable container.

Moisture

The requirement for water as a medium for biochemical processes leading to germination, such as weakening the seedcoat, activating enzymes, and breaking down food reserves, scarcely requires emphasis. It is generally recognized that seed

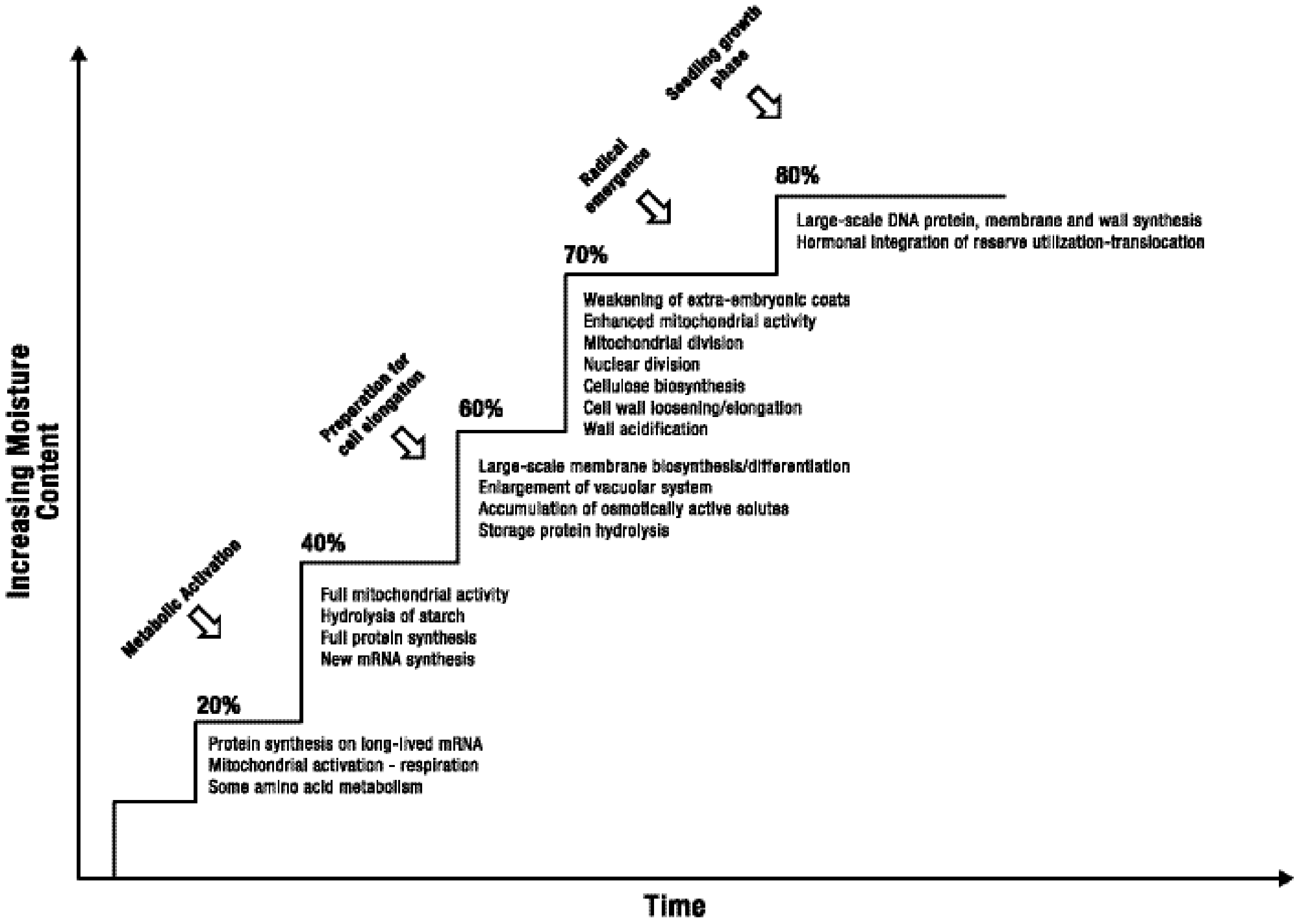

Fig. 5. Some proposed relationships between the major biochemical/structural events and increases in seed water content, which lead to germination and seedling establishment (Adapted from Obroucheva and Antipova 1997). In this model, loss of coat impermeability is associated with hard-coated legumes; nuclear division and cell wall elongation may be synchronous, and precede radicle emergence, or separated in time by the process of radicle emergence. The lack of "milestone" molecular events is a reflection of a paucity of knowledge, rather than a deliberate omission.

germination is more sensitive to moisture stress than is subsequent seedling development (Mayer and Poljakoff-Mayber 1989). In normal germination, the germination medium is sufficiently moistened throughout the course of germination. While inadequate moisture in the medium will result in delayed and poor germination, excessive moisture will hinder germination due to decreased aeration. It is therefore important that the germination medium be not so wet that a film of water forms around the seeds, or, when pressing the medium, a film of water forms on the finger (Bonner and others 1974). Seeds of some tropical species such as *Paraserianthes falcataria* were found to be sensitive to excessive medium moisture in germination (Wang and Nurhasybi 1993).

Some steps associated with water uptake are illustrated graphically in figure 5 and show, in a generalized way, some metabolic and other events which take place at particular hydration levels. It shows four stages associated with the germination process: (1) metabolic activation, (2) preparation for cell elongation, (3) radicle emergence, and (4) seedling growth (Obroucheva and Antipova 1997). A critical event is the requirement for the embryo to overcome the resistance of encompassing tissues. This is achieved by embryos lowering their water potential, by lowering either the osmotic potential or their turgor. That the concept of seed water potential is a crucial event in germination has now been embodied in a model using the concept of hydrotime (Bradford 1996). While not necessarily explaining what germination is biochemically, this model reveals underlying patterns and simple relationships that result in the germination time courses observed for seeds under given conditions. More detailed biochemical aspects of respiratory events, in dormancy and germination, may be found in Côme and Corbineau (1989) and Botha and others (1992), which are beyond the scope of the present chapter. Although the latter are concerned with cultivated crops it would seem reasonable to assume that some of the patterns seen, say, in cultivated legumes such as peas and beans, share much in common with their arborescent tropical relatives.

The relationship between water and germination (seed survival) for three Panamanian species of the Rubiaceae is illustrated in figure 6 (adapted from Garwood 1986). Seven watering trials were employed, during which buried seeds were watered over a 4-month period by: watering daily for a month; four combinations of not watering for 1 or 2 months; and watering only for 3 days on each of four successive months. Thereafter, all treatments were watered daily for a further 5 months and germination evaluated. What is clear from these results is that species (c) shows a requirement for at least 3 successive months of water availability during early planting (histograms 3 and 5). An extended absence, or intermittent pattern, of water availability for 4 months is essentially lethal (histograms 6 and 7). On the other hand, while species (b) shows some sensitivity in response to an absence of water in the first and third months (histogram 5), withholding water for 4 successive months was not as damaging (histogram 6); this was clearly so for species (a). Although species (a) was not greatly affected by an intermittent water supply over 4 months (histogram 7), species (b) showed only a marginal improvement over the previous treatment. Thus, species (a) appears capable of slowed development (underdeveloped embryo?) when water is limited, whereas species (b) cannot adjust greatly and in (c) there is no adjustment at all. This illustration is used to indicate that while species (a), (b), and (c) "climb the steps" to germination as indicated in figure 4, their requirements for moisture may differ greatly over time with the possibility of "pausing" at certain steps along the progression. Recalcitrant seeds, on the other hand, show little potential for "pausing" and none for reversal of the steps, being "committed" to a continuous water content increase, and germination. Metabolic events associated with recalcitrant seeds were discussed by Berjak and Pammenter in chapter 4. The observation that a 10-percent increase in water content by the excised embryonic axes of dormant seeds was sufficient to ensure germination, and that there are differential patterns of water localization between dormant and nondormant seeds (Hou and others 1997), serves to further stress the importance of water to the germination process. Some further details on water availability, oxygen supply, and synchronization of germination may be found in the upcoming section on oxygen.

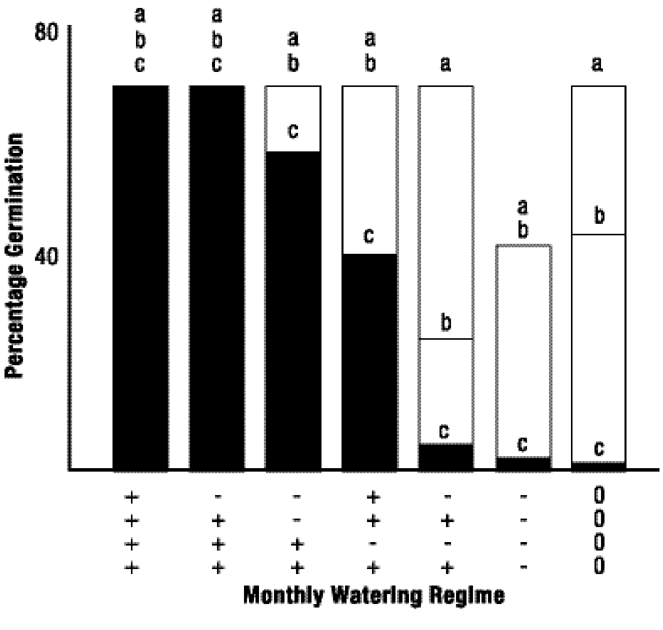

Fig. 6. Relationship between watering regimes and seed survival for three rubiaceous species a, b, and c. += watering daily; -=watering for three days only of each month; 0=no watering for each month (Adapted from Garwood 1989).

Temperature

Because temperature influences both the percentage and rate of germination of seeds, it is one of the most critical factors affecting seed germination. Although seeds of each species have optimal temperatures for attaining maximum germination, most species can reach their maximum germination at an alternating temperature regime of an 8-hour day at 30 °C with light and a 16-hour night in darkness at 20 °C (AOSA 1992, International Seed Testing Association 1996). Alternating temperatures are preferred to constant temperatures because they can overcome shallow seed dormancy and enhance uniform germination. Some of the subtropical tree seeds like *Taxus mairei* and *Cinnamomum camphora* require an alternating temperature regime for releasing dormancy as well as for germination (Chien and Lin 1996, Chien 1997). When alternating temperatures of 30 °/20 °C, which are prescribed for most tree seed germination (AOSA 1992, International Seed Testing Association 1996), are not available, a constant temperature of 25 °C can substitute for them. For most tropical tree seeds, room temperature of 25 to 30 °C in the Tropics will be quite suitable for maximum germination. The temperature effect can be modified by light as well as by moist chilling treatment (Wang 1987).

Liengsiri and Hellum (1988) noted that while six different provenances of *Pterocarpus macrocarpus* showed different germination characteristics, maximum final germination could be attained for all sources using alternating temperatures of 30 °/25 °C (8:16 hr). Corbineau and Côme (1986) reported that the optimal temperature for the germination of the recalcitrant species *Shorea roxburghii* and *Hopea odorata* was 30 to 35 °C. Differences were also noted between the lower temperature limits for seed germination in the two species, and these were different from those of seedlings.

When the germination of isolated embryos of seven species of *Inga* was investigated by Pritchard and others (1995), it was found that radicle elongation was possible at temperatures of 11 °C, but no epicotyls were produced. This further supports the idea that radicle emergence may not accurately reflect the ability of the embryo to produce a seedling.

Optimum germination temperatures for *Prosopsis argentina* and *P. alpataco* were shown to be 35 °C, with the minimum temperature being 15 °C and the maximum 40 °C (Villagra 1995); other studies have indicated somewhat lower temperature optima (e.g. 25 °C for *P. flexuosa* and *P. chilensis*) although the lower temperature limit of 15 °C seems to be common throughout (Catalan 1992). Seeds of *Ochroma lagopus* are stimulated by very high temperatures, possibly attributed to an association with fire in the natural habitat. The presence of a suberized light line in the palisade cells of the sclerenchymatous seedcoat, suggested parallels with the coat-imposed dormancy of legumes (Vazquez-Yanes and Orozco-Segovia 1993).

Seed germination and seedling growth were investigated for several Malaysian species by Mori and others (1990b), including *Shorea assamica, S. parviflora, Dryobalanops aromatica, Neobalanocarpus heimii, Bombax valetonii, Duabanga grandiflora,* and the exotic *Acacia auriculiformis*. Not surprisingly, performance was linked to the day/night temperature regimes of their respective ecotypes.

Seeds of *Manihot glaziovii* are known to be deeply dormant, possibly as a result of coat-imposed dormancy. Drennan and Van Staden (1992) found that, while incubation of seeds at 25 °C gave 70 percent germination after 14 days, temperatures of 35 °C resulted in 98 percent germination, but only if seeds were subjected to a temperature shift to 25 °C after 21 days. Exposure to the ethylene-producing compound, ethrel, resulted in over 90 percent germination within 14 days, over the temperature range 20 to 30 °C. Temperatures of 35 °C and 40 °C were inhibitory to germination and, unless seeds were subjected to a temperature shift, no improvement in germination was seen in the presence of ethrel.

Oxygen

Seeds of many species will not germinate well at an oxygen level considerably lower than that normally present in the atmosphere (Mayer and Poljakoff-Mayber 1989). In laboratory germination tests, seeds of most tree species germinate well with the air available in the germination medium and with exchange through loosely fitting germination containers. Germination will be inhibited by depressed oxygen supply when there is excessive moisture in the medium. As a general rule, oxygen availability should not be a concern in the Tropics since germination usually takes place in the open at room temperatures.

While the above generalizations may be entirely appropriate for most tropical tree species, the situation may be quite different for some seeds of the flood plain forests of Amazonia. Kubitzki and Ziburski (1994) have noted that (under field conditions) *Swartzia polyphylla* seeds are dispersed after peak inundation and germination begins almost immediately (b, in fig. 8), whereas in *Pithecellobium inaequale* fruiting occurs between May and June, coincident with near-peak flooding (*Pithecellobium* and *Pachira* were regarded as showing precocious germination), and germination commenced within 2 months. Interestingly, *Pithecellobium adiantifolium* shows a more “failsafe” strategy; germination starts after the majority of forest species had already begun germinating (third horizontal line from bottom of fig. 8 representing fruiting duration, and the dot at S indicating start of germination). By way of contrast, *Laetia corymbulosa* and *Simaba orinocensis* have peak fruiting early in the inundation cycle (third horizontal line from top of fig. 8) and “mark time” for some 5 months until commencement of germination. *Pseudobombax munguba* was identified as an obligate light-requiring species with minimal time between fruiting, dispersal, and germination (second from bottom, fig. 8). *Triplaris weigeltiana* showed an extremely compressed and “tail-end” synchronization (c, in fig. 8). Germination was nonetheless rapid, within 2 months of peak

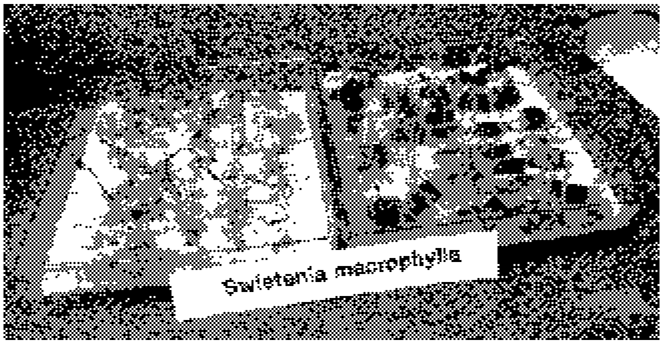

Fig. 7a.

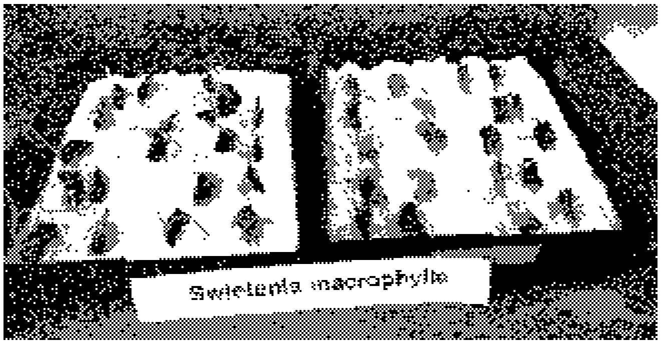

Fig. 7b.

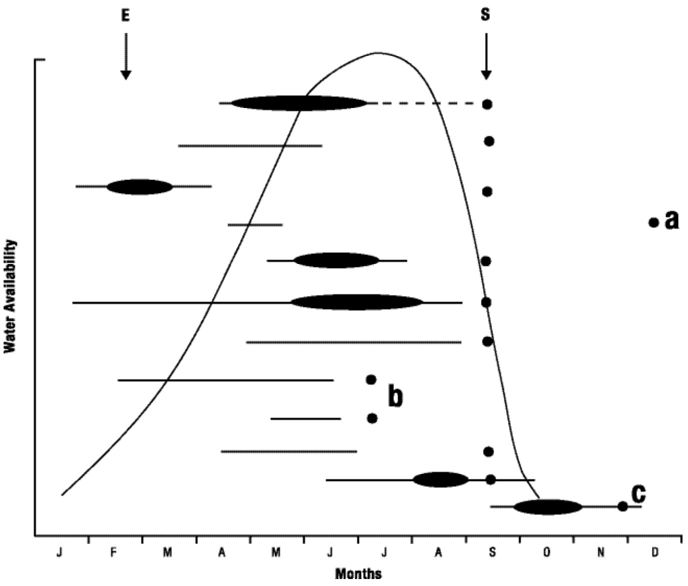

Fig. 8. Illustrates relationship between water availability on Amazonian floodplain (bell-shaped curve) and duration of fruiting period for several tree species. In some, peak fruiting is illustrated by the dilated parts on the horizontal lines. Although these are temporally very diverse (duration and length), the start of germination is mostly synchronoous at (•); the start and end of germination are indicated by the arrows at S and E. See text for further details (Adapted from Kubitski and Ziburski 1994).

fruiting. This latter species appears to be a standard, orthodox species with a wind-dispersed fruit and no dormancy mechanism. What is perhaps most striking about the information presented in figure 8 is the predominant initiation of germination in August-September of 85 percent of the 33 species studied; only 15 percent were outliers (as represented by species a, b, and c). This synchronous start to germination occurred irrespective of the duration of the fruiting period. What mechanism can act to produce such a remarkable synchrony? Kubitzki and Ziburski (1994) suggest that for many species the low oxygen tensions associated with immersion provide a dormancy-breaking cue. Strong experimental support for such a proposal was obtained for *Simaba orinocensis, Pouteria cuprea,* and some other species; only 30 percent of species studied showed no positive response to annoxia. It is important to realize that while the germination data given above do not all represent tree species, they strongly suggest that germination cues used by some tropical trees may well differ to a significant degree from those used by domesticated crops.

Light

Light is an important factor for seed germination, with both positive and negative effects. The promotional effect of light is through a single photoreaction controlled by the blue pigment phytochrome. The phytochrome is known to exist in two photoconvertible forms: P_2, which absorbs light @ 660 nm; and P_{fr}, the far red light which absorbs light @ 730 nm. Seeds of many temperate tree species are known to be light sensitive, and their germination is promoted by red light and inhibited by far red light (Toole 1973). For light to be effective, seed moisture has to reach a threshold level. For North American jack pine (*Pinus banksiana*) seeds, the threshold moisture content is 17 percent of fresh weight (Ackerman and Farrar 1965). The effectiveness of light on germination is temperature dependent (Ackerman and Farrar 1965) and interacts with moist chilling treatment (Pons 1992). Unfortunately, there is little information on the requirement of light for optimum germination of tropical tree seeds. Judging from their natural habitats, seeds of some species in the Tropics may require little or no light for germination. Therefore, daylight should meet the requirement for tropical seed germination. Surprisingly, it was found in one case that the *Swietenia macrophylla* seeds germinated well, without fungal infection, in the dark, in comparison to those germinated under light (fig. 7) (Wang and Nurhasybi 1993). No obvious explanation is available for these results.

It is generally held that the requirement for light (quantitative and qualitative) is associated with smaller seeds and dormancy mechanisms. Germination is triggered by increases in light as well as by the ratio of red to far-red light and temperature (Denslow 1987). Except for the well-documented case of *Cecropia obtusifolia*, evidence for classical red light responses are lacking (Vazquez-Yanes and Smith 1982). The light requirements for four species of *Cecropia* from the Amazonian flood plains were investigated by Kubitzki and Ziburski (1994). Two showed no obligate requirements for light, and germinated equally well in darkness (*C. latiloba, C. membranacea*) whereas *C. concolor* was unable to germinate in the dark, and *C. ulei* germinated poorly (17 percent) in the light. Significantly, the latter two species were typically associated with drier, noninundated habitats. Molofsky and Augspurger (1992) have provided evidence from field studies that the small-seeded *Luehea seemanni* is strongly light requiring, whereas the large-seeded *Gustavia superba* showed a minimal light requirement for germination.

Perhaps until more precise information on the light responses of tropical trees is forthcoming, it may be more appropriate to adopt the four categories recognized by Schultz (1960). The first were light-requiring, short-lived species such as *Cecropia*; the second, longer-lived, strongly light-demanding "nomads" such as *Simarouba amara,* which gives 60 to 80 percent germination in full light; the third, those which germinate better in light than in darkness such as *Jacaranda copaia*; and finally a large group of primary forest species which germinate naturally under closed forest canopies or maybe even in darkness (during later development, however, light requirements may be evident). It may seem reasonable to assume that the category "prompt germinators," frequently used to describe seeds of tropical tree species, may well reflect an absence of light (and perhaps other particular) requirements. Vazquez-Yanes and Orozco-Segovia (1984) cite studies by several other authors from different tropical forests of the world which show a high incidence of rapid germinators: 65 percent of the woody flora of Malaysian forests, 79 percent of species studied in the Ivory Coast, and 9 out of 10 species examined in Zaire.

Light-regulated germination is commonly reported in many ecological studies in relation to primary tree species, secondary invaders, and weedy species for tropical forests. *Macaranga, Musanga, Trema, Melastoma,* and *Maclura* seem to fall into this generalist category (Bazzaz and Pickett 1980). Light-temperature interactions also exist, but evidence is available only for *Schefflera* and *Ochroma* (Vazquez-Yanes and Orozco-Segovia 1984). The paucity of knowledge in this area probably reflects the fact that the majority of tropical tree species may show only minimal light requirements (their generally larger seed size may militate against this also), as well as the fact that the "rapid" germination strategy appears to minimize its importance; this does not mean that quite exquisite, qualitative and quantitative mechanisms await discovery.

For example, Drake (1993a) has shown that for *Metrosideros polymorpha* germination was greater under white, red, or far-red light (all ≤62 percent) compared to dark treatments. The light requirement could not be overcome by fluctuating temperature treatments (5/15 °C or 15/25 °C). Far-red responses of seeds of *M. polymorpha* var *polymorpha* were greater than those of *M. polymorpha* var *macrophylla*, which differ primarily in having pubescent and glabrous leaves.

Germination Media (Substrates)

The media generally used for germination are sand and/or soil. However, for seed germination testing, filter papers, blotters, agar, or sand are recommended (AOSA 1992, ISTA 1996). Each germination medium has its own property and suitability for different species. In the Tropics the cost and availability of certain media are also important factors. In the National Tree Seed Centre of Petawawa National Forestry Institute, Chalk River, ON, Canada, Kimpak (cellulose cotton) was commonly used for germination tests of most tree species, but it has become expensive and difficult to procure in recent years. A wide range of seed germination papers are available from Anchor Paper Company, St. Paul, MN, U.S.A. (Internet site: www.anchorpaper.com). In the Tropics, paper towels and sand are used for small and large seed germination tests, respectively, in the ASEAN Forest Tree Seed Centre, Thailand. Sand is the standard germination medium used for germination tests of all species in the National Tree Seed Program in Tanzania (Msanga 1998). Sand is probably the most suitable medium for tropical tree seed germination due to its availability, low cost, capacity to hold moisture, and suitability for large seeds.

Media should not only be adapted to suit availability under local conditions, but the approach of "one substrate suits all" should be cautioned against. For example, with recalcitrant seeds of *Podocarpus milanjianus*, Schaefer (1990) compared the effects of cold storage in perforated polyethylene bags without medium against those of damp sawdust or peat. Although the exact extent of hydration of the latter media was not recorded, seeds in peat lost moisture compared with those kept in polyethylene bags (ca. 43 percent m.c.), while sawdust-stored seeds increased to 58 percent m.c., and gave 72 percent germination.

Over the last few years evidence has been accumulating to suggest that the germination medium has importance beyond merely being a medium for water retention and transmission of light. When the seeds of eight weedy species were placed on the surface of an agar substrate, or 2 mm below the surface, in a variety of orientations, some surprising results were observed. Five of the eight species showed less germination when planted with radicle ends pointing downward, two showed no differential response to orientation, while one species responded poorly to burial and germinated best when on the agar surface (Bosy and Aarssen 1995). These authors speculated that uneven exposure to gravity, oxygen, or light may have been responsible for these effects. No significant effect of different soil types (loamy soil; washed, sterile river sand; or nonsterile river sand) was seen on the emergence of *Ceiba pentandra, Leucaena leucocephala, Gmelina arborea,* and *Tectona grandis*, although *T. grandis* germination was orientation sensitive (Agboola and others 1993). Seeds of *Bauhinia retusa* germinated best if sown with the radicle end upward, while performance was poorest if the radicle end was directed downward (Prasad and Nautiyal 1995). These authors interpreted the greater success of the root-upward orientation to the fact that as soon as the radicle emerges, it turns downward under the influence of geotropism, thereby facilitating a "hook" for easier shoot emergence.

Where seeds are very small, e.g. *Metrosideros polymorpha* (seed mass ca. 57µg), depth of burial can have serious impact on germination. Seedling emergence for seeds buried at a depth of 2 mm in sand was half that of surface-sown seed and minimal at 5 mm depths; 6 to 10 percent germination was recorded in continuous darkness (Drake 1993a).

GERMINATION BOXES OR TRAYS

There are no specifications for germination boxes and trays

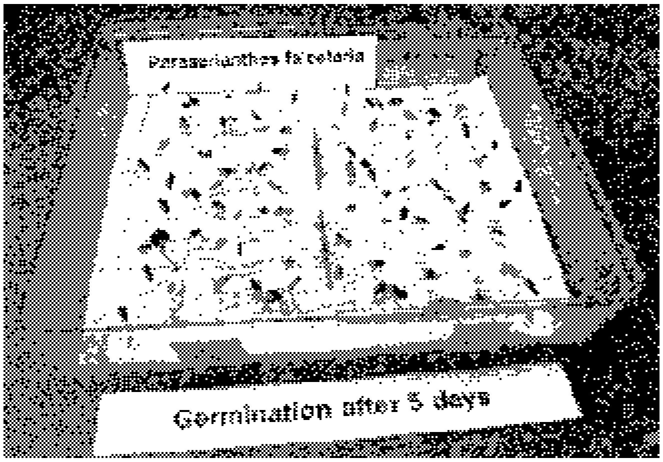

Fig. 9-1.

Fig. 9-2.

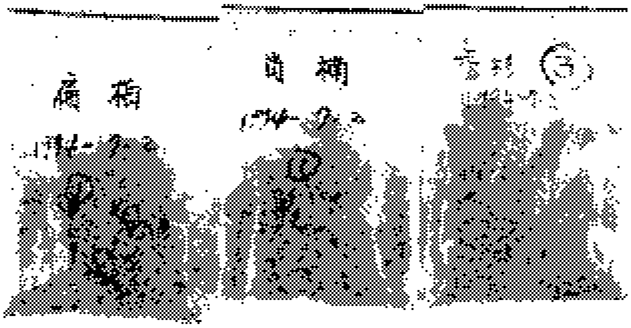

Fig. 9-3A.

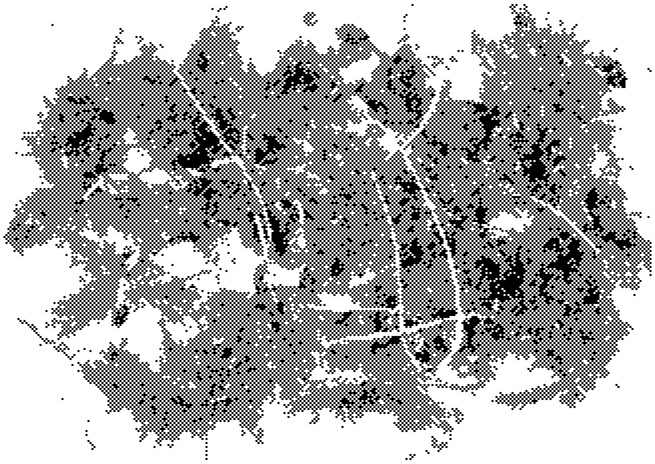

Fig. 9-3B.

for standard germination tests in the international rules for seed testing. Petri dishes or plastic boxes of various sizes are commonly used for germination tests or research on tree seeds. However, these boxes and dishes are usually too small for proper tropical tree seed germination tests and often promote a serious fungal growth problem. The lids of some of the boxes may be too tightly fitting and suppress air circulation. More recently, a specially designed germination box has been tested and considered ideal for germination tests or research (Wang and Ackerman 1983). The germination boxes are commercially available and widely used in many countries of the world (fig. 9-1). In Tanzania, an aluminum bowl is used in conjunction with washed river sand as a medium for germination tests (Msanga 1998) (fig. 9-2). For tropical seed germination, it is important that the capacity of the germination box or tray be large enough to avoid crowding and fungal contamination.

In the Seed Laboratory of Taiwan Forestry Research Institute, sealable polyethylene bags are used with sphagnum medium for all seed germination tests and research (Chien and Lin 1996, Chien and others 1998) (figs. 9-3A and 9-3B).

ASSESSMENT OF GERMINATION

Although there are many indirect, rapid tests for evaluating seed quality, they are not always reliable for assessing seed viability. For evaluating the germinability of seeds, the only dependable technique is the direct growth method or germination tests. The laboratory standard germination tests for seeds of tree species in international trade have been well described and documented (AOSA 1992, International Seed Testing Association 1996). Unfortunately, such well-established germination test protocols are not available for tropical tree seeds, although those rules are often applied for tropical tree seed germination and germination testing. Because of the nature of tropical tree seeds, there have been some research attempts to establish standards for tropical tree seed germination tests. Williams and others (1992) recommended four 25-seed replications for *Acacia* seed germination tests and compared the maximum tolerated range of variation with the ISTA prescription of four 100-seed replications. The authors also recommended a reduction in the number of seeds used for large-seed germination tests due to the amount of space required for such large seeds as *Syzygium suborbiculare* and *Castanopspermum australe*.

In Malaysia, Krishnapillay and others (1991) established a test standard for determining the moisture content for *Hopea odorata* seeds. They suggest that a sample size of 20 to 25 seeds would be sufficient for accurate seed moisture content determination where the seeds can be oven-dried at either 103 °C for 20 hours of 90 °C for 24 hours.

Our understanding of tropical tree seeds has advanced considerably over the last 20 years, and is perhaps moving from a stage of collection of information to one of consolidation and more goal-directed work on specific physiology. However, as Bewley (1997) has noted, we still cannot answer the two fundamental questions: how does the embryo emerge from the seed and how is emergence blocked in dormancy? Evidence is now accumulating from the cultivated crop species to suggest that ABA prevents radicle extension and maintains dormancy, whereas GA's seem to be involved in the promotion and maintenance of germination after ABA-mediated events are overcome. For tropical tree species such basic information is lacking, in spite of the greater ease and sophistication of the analytical techniques available. Geographical distance and lack of funding are partly to blame for this anomaly, as is perhaps the fact that seed physiology and biochemistry can more safely (and profitably, because of funding) be conducted on cultivated crops.

While the above goals may be seen to have highlighted the shortcomings of short-term research, the prospects for the longer-term activities appear much brighter. International symposia on genetic conservation and the production of tropical tree seed provide proof that there is much to be proud of, although it admittedly is heavily biased in favor of *Acacia*, *Casuarina*, and *Eucalyptus* spp. Some of the noteworthy publications in this regard are by Arisman and Havmoller (1994), Boland (1989), Harwood and others (1991), Midgley (1990), and Thomson and Cole (1987).

Breeding programs, recurrent selection, along with identification of genetic diversity and its maintenance, are receiving increasing attention, even if the rewards appear to be long term (Bangarwa and others 1995, Bumatay and others 1994, Chamberlain and Galwey 1993, Harwood 1990, Harwood and others 1994, Namkoong and others 1988, Plumptre 1995, Singh and Deori 1988, Wood 1976).

A greater awareness now exists of the effects of afforestation by "alien" species on stream flows, and the long-term nature of recovery to preplantation levels (Scott and Lesch 1997); attempts at the restoration of degraded natural forests (Alexander and others 1992, Ray and Brown 1995) strongly underscore the role of seed optimization and seedling establishment in the process. The role of rhizobia, vesicular-arbuscular mycorrhizal fungi, nodulation by the actinomycete *Frankia*, as well as suitable phosphate or liming applications are now recognized as important elements of seedling growth. In this regard some valuable studies have emerged for *Albizia, Casuarina, Parkia, Dalbergia, Enterolobium, Gliricidia, Intsia, Leucaena, Sesbania,* and *Shorea* (Diem 1996, Dommergues 1996, Lang and others 1995, Osundina 1998, Sayed and others 1997, Surange and others 1997).

Tropical tree seeds will continue to provide mankind with much-needed resources only if researchers remain challenged by the need to understand the many aspects of seed biology, and if governments and international agencies continue to provide the necessary funding and platforms for research, collaboration, and international exchange. The world's 2950 million hectares of forest will shrink further if economic gain is allowed to override sound management practices.

CHAPTER 6

Pathology

PART I. PRINCIPLES
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PART I. PRINCIPLES

Seeds and seedlings are frequently affected by physical and physiological disorders and the diseases caused by fungi, bacteria, and viruses. Young plants or seedlings are particularly susceptible to a number of diseases because of their tender tissues and because they often have difficulty in establishing themselves. Health and vigor of seedlings and their further growth are to a considerable extent dependent on the quality of seeds. Since seedlings grown from the seeds are the primary source of planting stock and the improved seeds are expensive, it is necessary to investigate the seed and seedling pathogens and, if necessary, apply some control measures either before sowing the seeds or at seedling stage.

In the past, damping-off fungi, cone rust, a number of cone and seed insects in pines, and fungal damages to oak acorns, hazelnuts, chestnuts, walnuts, and seeds of birch and elm were considered the only major problems in seed and seedling production. Many fungi have now been isolated and studied for their effects on seeds of both conifer and hardwood tree species (Mittal and others 1990) and some have caused considerable losses of seeds and seedlings. Loss of several kilograms of seed of *Pterocarpus indicus, Acacia auriculiformis,* and *Leucaena leucocephala*, at the Pantabangan Dam Watershed in the Philippines during 1979, has been reported by the National Irrigation Administration (Quiniones 1987). According to Chalermpongse and others (1984), in Thailand, the loss of seeds due to infection of *Botryodiplodia theobromae* on *Swietenia macrophylla* was 92 percent, *Colletotrichum gloeosporoides* on *Dalbergia cochinensis* was 4 percent, *Alternaria longissima* on *Bauhinia* sp. was 2 percent, *Pestalotiopsis* sp. on *Cassia bakeriana* was 6 percent, *Macrophoma* sp. on *Eucalyptus camaldulensis* was 1 percent, and *Fusarium* sp. on *Shorea obtusa* was 2 percent.

Deterioration of tree seeds by fungi involves problems differing in many aspects from those of grains. For example, tree seeds are exposed to many conditions before storage that permit the development of mold fungi. Cones are often collected in sacks and kept at collection points or processing plants for varying periods under conditions that favor fungal development prior to seed extraction. After extraction, the seeds are dried and stored for varied periods until used in field or nursery. Hence, it is important to know the characteristics of fungi associated with important species, what damage they cause, where and when and under what circumstances the damage occurs, and what can be done to prevent the damage.

The science of tree seed pathology is still very young. The occurrence and distribution of most of the tree seed pathogens is well realized but there is very little understanding of their impact on seed production, seed quality, and seed viability. Interest in these problems has been growing steadily in the past few decades, but recently this interest has changed into serious concern mostly because of the problems encountered in the renewal and management of the forests, which are a major resource worldwide. Some information about the characteristics of seed-borne fungi is now available but is mostly related to temperate tree species. Therefore, in discussing the tropical tree seeds this information will also be briefly discussed at times for reference.

FUNGI OF FOREST TREE SEEDS

Fungi associated with tree seeds vary in different host species, in different regions, and in different years. Many of them are molds and develop on the seed surface only; some cause internal infections too. Nearly all seeds carry spores of various microscopic fungi either on the surface or within the seed. A superficial mycoflora is almost always found because of the ready adhesion of spores to the uneven surface of the seeds. Although the number of spores occurring varies considerably, as in Norway spruce and Scotch pine, it can be as high as 50 to 150,000 spores, and, in some seedlots, several hundred thousand spores per 1 g seed (Urosevic 1961). Under favorable conditions, some spores germinate, the mycelium penetrating into the cotyledons of the seed and feeding on the embryo.

Several kinds of fungi can be associated with tree seeds. Thus, there are species causing decay and reducing the germination of stored seeds, species attacking germinating seeds and seedlings, and other species that are more or less harmless, or at least appear to be so. Present knowledge does not permit precise separation of individual species of fungi occurring on seeds. However, it is clear that many species usually considered as unimportant and harmless can cause considerable damage under certain conditions, for example: unsuitable storage conditions, seeds of poor quality (immature, low vigor, or heavily molded), unsuitable growing conditions (involving moisture, temperature, or aeration), etc. Therefore, while evaluating the importance of these fungi, it is essential to consider the biology of the individual species of fungi.

Depending upon their location, the seed-borne fungi can, in general, be classified in two groups: externally seed-borne and internally seed-borne. The first group includes species of *Botryosphaeria, Botrytis, Fusarium, Mucor, Phialophora, Rhizopus*, and *Trichothecium*. They are not usually host specific and may involve more than one species. Some of the well-known internally seed-borne fungi include species of *Alternaria, Aspergillus, Botrytis, Botryodiplodia, Caloscypha, Cephalosporium, Fusarium, Phoma, Schizophyllum*, and *Sirococcus*. These may cause deterioration of seed quality and pre- or post emergence mortality of seedlings (Singh and Mathur 1993).

Urosevic (1961) provided instructions for health testing of oak acorns, including a key for distinguishing fungi from acorns, and divided the acorn mycoflora into two groups: (i) parasites and semiparasites such as *Ciboria batschiana, Ophiostoma spp., Gloeosporium quercinum, Phomopsis quercella, Cytospora intermedia, Botrytis cinerea,* and *Pestalotia* sp.; and (ii) sparophytes including *Alternaria, Aspergillus, Fusarium, Penicillium, Trichoderma,* and others.

Based upon their pathogenicity, Sutherland (1995) classified the seed-borne fungi of conifers as (i) saprophytes or weak pathogens; (ii) pathogens such as the cold fungus *Caloscypha fulgens* which consistently kills seeds; (iii) pathogens mainly important as seedling pathogens, e.g. *Sirococcus conigenus;* and (iv) fungi, e.g. *Fusarium* spp., whose pathogenicity depends upon factors including fungus species and pathogenic strain, and host and host stress.

DISEASES AND DAMAGES BY SEED-BORNE FUNGI

Symptoms of seed-borne diseases are usually divided into pre- and post emergence damping-off. The former consists of reduced emergence and decay of the radicle just emerged from the seedcoat; the latter is subdivided into root rot, cotyledon rot, and basal stem rot after the seedlings emerge from the soil. Reduction in seed germination, decay and loss of viability of seeds during storage, and the diseases of seedlings are among the major problems wrought by fungal pathogens.

GERMINATION REDUCTION

Inhibition of coniferous seed germination by widespread contaminators (Garbowski 1936, Rathbun-Gravatt 1931, Ten Houten 1939) and through artificially inoculated fungi (Fisher 1941, Timonin 1964) has been reported. Huss (1956) observed that the molding had virtually no effect on pine seeds of high viability, but poor quality seeds suffered a substantial reduction of germination. It has also been observed that the destruction of seeds largely depended on their growth rate, and as germination progressed, the resistance to destruction increased (Gibson 1957). The extremely common and numerous species of mold fungi, viz. species of *Mucor, Rhizopus, Trichothecium, Botrytis, Penicillium*, and others, which colonized the surface of *Quercus* acorns or got into the surface tissues, were found of secondary importance in the loss of germinability of acorns (Potlaichuk 1953). Gibson (1957), however, reported that the saprophytic fungi, viz. *Aspergillus* spp., *Mucor* spp., *Rhizopus* sp., *Trichoderma* sp., and *Cladosporium* sp., of the seedcoat microflora could, under favorable conditions, invade tissues of the germinating seeds and kill the seedlings of *Pinus patula*. The seedcoat microflora could thus be directly responsible for the weakening of seed vigor, predisposing it to the attack of soil-borne pathogenic fungi. Shea (1957) supported the view and mentioned that the influence of molds on seeds could vary considerably and their mere presence did not mean that they were harmful. However, Prisyazhnyuk (1960) mentioned that the greater the infection by fungi of seeds, the lower the germinability of seeds of *Pinus sylvestris, Larix sibirica, Picea abies,* and *Abies sibirica*. Rowan and De Barr (1974) observed extensive molding of three seed lots of slash pine during germination tests. Following the standard testing procedures, the seeds were cracked individually and almost 90 percent of them were found full, although the germination ranged from 31 to 79 percent only. *Fusarium solani* was obtained from the ungerminated seeds.

Out of the 12 *Fusarium* isolates tested through inoculation on *Pinus patula* seeds (Pawuk 1978), 3 reduced germination, whereas 9 increased percent damping-off but did not affect seed germination or seedling growth. *Leucaena* seeds infected by *Colletotrichum graminicola* failed to germinate, and if the infection was carried to the nursery, seedlings under moisture stress succumbed to the damping-off disease (Quiniones 1987). *Botryodiplodia theobromae,* which causes black dry rot in mahagony (*Swietania macrophylla*) and caused 92 percent seed deterioration in Thailand (Chalermpongse and others 1984), did not affect germination but, after potting in the nursery, the rot developed during the hardening-off period of seedlings (Quiniones 1987).

Stratification, also known as moist cold prechilling of seeds, is commonly used to break dormancy in seeds, and to attain vigorous, speedy, maximum, and uniform germination for laboratory testing and green house and nursery sowing (Wang 1986). It is a common practice for most conifer and several hardwood seeds. Sutherland (1979) reported spread of *Caloscypha fulgens* on seeds of several conifer species at low (3 to 5 °C) temperatures of stratification. The fungus mummifies the seeds, resulting in poor germination. Mittal and others (1987) observed the development and spread of fungi on *Pinus strobus* seeds during stratification. These fungi, generally, did not lower seed germination but diseased the germinants.

DECAY AND LOSS OF VIABILITY DURING STORAGE

Large quantities of high-quality seeds are required annually for artifical regeneration. In view of the lack of uniformity and predictability of cone and seed crops, bulk quantities of seeds are collected in good seed years and stored for use in intervening years to ensure a continuous supply of seeds for annual production of planting stock and for direct seeding. Storability of seeds is dependent upon temperature, time, relative humidity, and method of storage, as well as the moisture content of, and initial fungal inoculum on, seeds to be stored. Improper storage of cones, as reported by Shea (1960), caused heating of cones as a result of biological activity and these cones suffered more damage by fungi. Sixty percent of the *Pinus sylvestris* seeds stored in sacks; about 30 percent of seeds stored in boxes, bins, and tin drums; and only 10 percent stored in hermetically sealed vessels were infected with various fungi (Prisyazhnyuk 1960).

Quercus acorns lost up to 70 percent of their germination capacity during storage due to fungal infections (Potlaichuk 1953). Achenes of *Platanus occidentalis* stored at 2°C showed no loss in germinability even after 7 months at 20 and 30 °C; however, germinability decreased and most fungi on achenes increased with increasing temperature, relative humidity, and time of storage (Fakir and others 1971).

In conifers, Lavender (1958)) found no loss in germination capacity of *Pseudotsuga menziesii* seeds stored in cones up to 4 months at normal fall temperatures in an unheated warehouse. Bloomberg (1969) reported that seeds in *Pseudotsuga menziesii* cones stored for 225 days under operational conditions were free of diseases but, during germination tests after extraction, up to 56 percent of them became diseased. Rediske and Shea (1965) observed significant reduction in the same seed viability when freshly picked cones of high moisture content (60 percent) were sacked and stored in outside bins in the fall. However, full viability of these seeds could be retained for 3 years when stored in sealed cones at 0 °F (Barton 1954). When the same seeds were stored in canvas bags, germination was somewhat reduced within 6 months, and severely reduced after 12 months of storage. Gordon (1967) advised refrigeration of extracted seeds of *Pseudotsuga menziesii* immediately after their removal from the cone, to inhibit further fungal activity within the seed. However, Rediske and Shea (1965) supported Schubert's (1960) observation on *Pinus monticola* seeds: that fungi remained active in pine seed at temperatures below the freezing point.

There have been suggestions for storing tree seeds at subfreezing temperatures to maintain their germinability (Willan 1985). Cryopreservation of seed germplasm at or near the temperature of liquid nitrogen has the potential for reducing deterioration of seed to such a low level that essentially perpetual preservation can be achieved (Stanwood 1985). However, based on artificial inoculations of *Fusarium sporotrichioides* and *Mucor hiemalis* on water-soaked *Pinus strobus* seeds before storing at -18, -80, -145, and -197 °C for 35 days, Mittal and Wang (1989) inferred that storing tree seeds at ultra-low temperatures will not eliminate contaminating fungal pathogens.

SEEDLING DISEASES

Damping-Off

Pre- and post emergence damping-off caused by various fungi are the most dangerous diseases affecting conifers as well as hardwood species. Quiniones (1987) reported establishment of *Fusarium solani*, a soil inhabitant, in the seeds of *Leucaena* and *Agathis* which caused post emergence damping off in the nursery and in the outplanted seedlings.

Seedling Blight

Sirococcus blight caused by a seed-borne fungus *Sirococcus strobilinus* is an important disease of seedlings of several spruce and pine species, and of *Pseudotsuga menziesii* throughout the northern Temperate Zone (Sutherland 1985). In this case, the pathogen attacked very young seedlings, killing the primary needles from the base upward. Dead seedlings remained upright, and small, black pycnidia usually formed at the base of infected needles. Diseased seedlings usually occurred randomly, characteristic of seed-borne diseases.

Seedling Wilt

Another important disease transferred by seeds is the tracheomycosis wilting of plants (Urosevic 1964). This symptom can be elucidated as a reaction of the host to the irritation by the parasite wherein the typical blocking of trachae by thalli, and a yellowish brown, rubber-like substance filling the adjacent parenchymatous cells, are produced.

Others

Reduced seedling height and leaf symptoms (chlorotic and necrotic lesions and malformed leaves) are also sometimes observed in seedlings raised from the fungus-inoculated seeds of *Acer saccharum* (Janerette 1979), *Picea glauca*, and *Pinus strobus* (Mittal and Wang 1986, 1993).

TESTING OF SEED-BORNE FUNGI

Seed-borne fungi testing includes isolation and study of fungi during cone collection and processing, seed extraction, processing, storage, germination, and seedling growth. Unlike with agricultural crops, methods for health testing of most forest tree seeds have not been standardized, and the testing is usually done using normal procedures of moist blotter and agar plates. Singh and Mathur (1993) have elaborated on the seed-health testing methods including direct observation, washing test and incubation methods (blotter and agar plate) for seeds, and seedling symptom test and growing-on test for seedlings. Some special methods like dilution plate method, ultrasound technique, isozyme patterns, seed tissue excision, seed sectioning, radiography, and ELISA technique have also been discussed. The ISTA recommendations for germination testing, which are more clearly available for agricultural crop seeds, are usually followed as standard practice. Seed size and, sometimes, unavailability of tree seeds in large quantities, makes it difficult to use large numbers of seeds in testing. Therefore, it is important to find out how many seeds of a tree species should be tested in how many replicates.

For many years it has been difficult to secure accurate, maximum germination of all viable seeds or achieve the true planting value of forest tree seeds. For example, the dormant nature of the seeds of *Abies balsamea*, *A.fraseri*, and other *Abies* species, which required a moist prechill treatment of 21 to 28 days or more at 3 to 5 °C, together with fungal contamination and growth during the 2-month overall test duration, have been responsible for sometimes erroneous, erratic, or negative germination results. Another problem generally encountered in seed testing involves seed pretreatment. For this purpose, Wall (1974) and several others used 0.1-percent mercuric chloride solution for 2 minutes, following the ISTA recommendations for seed-health testing of agricultural crop seeds. Wall (1974) also used 0.5-percent sodium hypochorite solution for 2 to 3 minutes for surface sterilization of diseased red pine seedlings. Mittal (1995) recommended treatment with 2-percent sodium hypochlorite solution for 10 minutes for

Picea glauca and *Pinus strobus* seeds for greenhouse sowing as well as for laboratory testing. Thus, there existed different opinions on the type and duration of treatment that seeds should receive before testing.

For testing pathogenicity through artificial inoculation of seeds with some seed-borne fungi, different methods for seed inoculations are employed. Several workers have attempted rolling of seeds on fresh fungal cultures, whereas others used spore suspensions. At several platforms, a controversy existed over the method of inoculation and the testing environment, which need to be standardized for different types of seeds.

The reduction of germination under conditions of artificial infection does not correspond exactly to the reduction of germination that occurs under conditions of natural infection. Under natural conditions, the various microorganisms on seeds interact within themselves and with the microorganisms present in the soil or growing media. Such an interaction is often even antagonistic, which affects the ability of individual microorganisms to develop rapidly and to infect seeds. Often, in artificial inoculation studies, the conditions for facilitating microbial growth are provided. This suggests a need for testing the pathogenicity of various fungi in natural soils or growing media under greenhouse or field conditions (Mittal and Wang 1990).

FACTORS AFFECTING DEVELOPMENT AND SPREAD OF SEED-BORNE FUNGI

ABIOTIC FACTORS

Collection, Extraction, and Processing

The time, place, and method of collection of cones or seeds, and their subsequent handling during transport, extraction, and processing, affect the development and spread of mycoflora on tree seeds. It is generally presumed that cones and seeds acquire various fungi, including molds, while they are still on trees. *Pinus pinea* cones contained discolored, powdery seeds, in some of which the kernel was still sound but in others was blackened and completely destroyed by the grayish mycelial growth of *Alternaria alternata* (Sibilia 1927). Similarly, a pathogen *Coniothyrium* sp., established itself in and on the *Betula aleghanensis* seed before it fell to the ground (Shigo and Yelenosky 1963). However, Salisbury (1955) and Prisyazhnyuk (1960) reported that most of the individual seeds from tightly closed cones of conifers were completely free from molds. Seeds should be extracted from the cones immediately after harvest to minimize seed infection from the microbial population already present on cones.

The later the oak acorns were collected from the fields, the more infected they were with fungi (Potlaichuk 1953). *Penicillium, Fusarium, Alternaria,* and *Trichothecium roseum* were found to be the most common fungi during acorn development. Development of *Cladosporium herbarum,* which was frequently encountered on the acorns in the first and last samples during their development, depended on the amount of rainfall; the highest occurrence was during the period of heavy rainfall.

Dewinging of the seeds can lead to considerable reduction in germination, presumably through damage to the testa and subsequent fungal invasion (Gordon 1967, Harding 1952, Huss 1956, James and Genz 1981). While studying the fungi associated with seeds of *Picea glauca* and *Pinus strobus* during cone processing and seed extraction, Mittal and Wang (1987) observed that the contamination occurred and spread during air drying and seed extraction processes, and that considerably more fungi occurred on both types of seeds after they were left on the forest floor for 15 days. Mojtahedi and others (1978) found that the wash water was a source of fungus contamination when fresh, uncracked pistachio nuts were tested for *Aspergillus flavus* and aflatoxin before and after a commercial washing treatment.

Storage Conditions

The moisture content of seeds, initial fungal inoculum on seeds, and the method of storage, all affect the spread of fungi on seeds during storage. Full viability of extracted Douglas fir seeds was retained for 3 years when stored in sealed cans at 0 °F. However, when stored in canvas bags, germination was somewhat reduced within 6 months and seriously reduced after 12 months (Barton 1954). Significant reduction in Douglas fir seed viability when freshly picked cones of high moisture content (60 percent) were sacked or stored in outside bins in the fall, was observed by Rediske and Shea (1965). Immediate gentle drying or refrigeration maintained viability.

While orthodox seeds, which can tolerate low moisture content and low storage temperatures and, therefore, can be stored successfully for often longer periods, the recalcitrant tree seeds are fast-perishable. Their high moisture content and storage often at ambient or relatively higher temperatures help in establishing several storage fungi. Fast deterioration of the recalcitrant seeds by these storage fungi is expected to be due to the debilitation of seeds caused by internal moisture stress generated within the cells or tissues, primarily as a result of the water-requiring process of vacuolation (Berjak 1996). This debilitation impaired phytoalexin synthesis by the seeds, facilitating proliferation of associated fungi or bacteria. Prevention of fungal activity during storage can be more easily achieved by controlling the moisture content of the seeds than by controlling the storage temperature, because fungal activity is possible between –8 °C and +80 °C when the seed moisture content and the relative humidity of storage are high enough (Roberts 1972b). It is therefore important to find out the optimum moisture content and the storage temperature requirements for individual forest tree species.

Stratification

The killing of viable seeds of some conifer species has been particularly serious during the long, cold, prechill treatment at 3 to 5 °C (Sutherland 1979). Mittal and others (1987) studied the development and spread of fungi on *Pinus strobus* seeds during stratification, though the former did not, usually, lower the seed germination in further testing. The prechilled seeds germinated vigorously and speedily, and therefore probably escaped the damages, supporting the views of Gibson (1957). However, some germinants failed to emerge completely from the seedcoat and others were damaged by top decays caused by *Alternaria alternata*, *Fusarium oxysporum*, and *Penicillium variabile* in the laboratory, possibly due to the high moisture content of the prechilled seeds and the high environmental temperature: the two important factors contributing to fungal development, spread, and infection (Mittal and Wang 1986). This suggested a need for treatment by some surface cleaning or sterilizing agent before stratifying the seeds, especially the highly dormant seeds.

Cultural Practices

Surface-sterilized seeds with pierced testa sowed in normal moist soil completely failed to germinate, presumably due to invasion by soil saprophytes (Gibson 1957). It seems possible that the destruction of seeds was facilitated by the proximity of a relatively large food base, the seed reserves adjoining the small volume of living tissue.

Sitka spruce seeds incubated at 10 °C were highly susceptible to fungal attack because they remained dormant while the pathogen was growing at near its maximum rate (Salt 1967). Losses in nurseries are not necessarily related to the time taken for seedlings to emerge, but they are likely to be greater in places where fluctuations in temperatures over 10 °C are usually less prevalent. Losses are expected to increase with earlier dates of sowing. Autumn sowing is most unreliable because in warm soil, the seeds germinate early and escape damage, whereas in cold soil they do not germinate until the following spring, and suffer maximum loss.

Most soil mixes for containerized conifers contain vermiculite or perlite incorporated with sphagnum peat. This type of mix is usually well drained and acidic, the two factors that help reduce diseases (James 1985). Major groups of pathogens associated with nursery diseases are species of *Fusarium* and watermolds, such as *Pythium* and *Phytophthora*. Although watermolds may be seed-borne, they are more often introduced into container nurseries through contaminated irrigation water. These fungi cause disease on very young seedlings, and are favored by poorly drained soil mixes and prolonged wet conditions in the greenhouse.

BIOTIC FACTORS

Fungal colonization of conifer seeds is facilitated by insects like seedbugs, and by squirrel damages to seeds (James 1985, Rowan and De Barr 1974, Sutherland 1979). Elaborating on the insect-fungal interaction during infection of oak acorns, Urosevic (1959) reported that at the time of oviposition, various fungi were introduced by the insects into the acorns. These fungi then penetrated into the mature acorn tissues. Death of the acorns was thus brought about not only by the damage caused by the larvae of the weevil, but also by fungi accompanying the weevil. The penetration of the acorn by the fungal mycelium entailed negative effects more rapidly and more injurious than did the maturation feeding of the larvae. Acorns thus affected might represent a dangerous focus of infectivity during both initial storage and long-term storage of the acorns.

MANAGEMENT OF SEED PATHOGENS

SEED COLLECTION, PROCESSING, AND STORAGE

Collection of seeds from healthy, disease-free areas or orchards; collection from healthy trees, healthy cones or acorns at the appropriate time; collection from tree and not from ground or from squirrel caches, etc.; transport of cones or seeds in well-aerated, clean, dry containers or bags; avoiding damage to seeds during extraction and processing; and use of optimum seed extraction and storage conditions, all need be studied for different forest tree species and considered for prevention of fungal infections on seeds.

SURFACE TREATMENT

Although adverse effects on seed germination have sometimes been reported, seed treatment with sterilants to reduce or eliminate fungal contamination has been considered necessary for production of healthy seedlings at several nurseries. For sterilizing conifer seeds with minimal stimulation or retardation to them, an immersion of the seeds in a commercial detergent followed by treatment with 30-percent hydrogen peroxide has been recommended (Gordon 1967). Hydrogen peroxide treatment (30 percent for 45 minutes) improved the total germination from 47 to 80 percent and from 25 to 61 percent in the 2, poor-quality, unstratified seeds of *Pinus taeda* (Mason and Van Arsdel 1978). Water treatment at 57 °C for 10 minutes was found quite effective in eliminating large numbers of seed-borne fungi of *Pinus roxburghii* and *P. wallichiana* (Munjal and Sharma 1976). Delatour and others (1980) also suggested hot water (44 °C for 8 hours) soak treatment for killing *Ciboria batschiana* in *Quercus* acorns.

CHEMICAL CONTROL

Coating seeds with a repellent against birds and small rodents, and a fungicide against damping-off has been a common practice in forest tree nurseries at several places. Although a lot of literature on chemical seed treatment control of seed-fungi has accumulated, most studies were made on conifers. The sulphuric acid treatment to *Araucaria excelsa* seeds, which has been prescribed by quarantine regulations against *Cryptospora longispora,* was found effective in eradicating the seed-borne fungi but the acid was detrimental to seed germination (Khan and others 1965). A 70 to 75 percent dust of PCNB applied to the seed of balsam, Fraser, and grand firs gave excellent control (100 percent) of *Rhizoctonia solani* without any injury to the germinating seedlings. Mittal and Sharma (1981), based on their observations with different tree species (*Cedrus deodara, Eucalyptus citriodora, E. hybrid, Pinus roxburghii, P. wallichiana*, and *Shorea robusta*), suggested that Brassicol, Bavistin SD, and Dithane M-45, as seed dressers, could be used to effectively control most of the common seed-borne fungi of these tree species. For control of a common fungus, *Aspergillus niger,* on the seeds of *Shorea robusta*, seed treatment with Bavistin SD or Brassicol was most effective (Mittal and Sharma 1982).

Effective control of several fungi, such as *Botryodiplodia theobromae, Colletotrichum gloeosporoides, Fusarium* spp., *Macrophomina phaseolina, Pestalotia* sp., *Phoma* sp., and *Phomopsis* sp., on the seeds of *Acacia auriculiformis, Albizzia* spp., *Gmellia arborea, Leucaena leucocephala*, several *Pinus* spp., *Pithecelobium dulce, Pterocarpus indicus, Cedrella odorata*, and *Grevillea robusta,* has been successfully achieved through the combined use of Benlate (0.15 percent) and Dithane M 45 (0.15 percent) (Cortiguerra 1985, Pacho 1985).

Seed treatments with oil, talc, and dye have also been found beneficial but much less so than treatment with Thiram (a fungicide) for Sitka spruce (*Picea sitchensis*) (Salt 1967).

Since detrimental effects of chemical seed treatment on seed germination and seedling quality have also been reported (James 1983), it is desirable that lower concentrations, which should not be phytotoxic, be tried. Kozlowski (1986) reported that Captan at concentrations up to 2500 ppm did not affect seed germination of *Pinus resinosa;* however, concentrations of 500 ppm or higher injured roots, stems, and cotyledons within 13 days. Root injury consisted of collapse of root hair cells, epidermal cells, and cortical cells, and the cotyledon injury included the collapse of epidermal and mesophyll cells. Similar observations were made earlier by Cram and Vaartaja (1956) and Vaartaja (1964).

LEGISLATION

Vigorous implementation of the seed laws, such as the Seed Acts and Seed Certification Programmes for quality evaluation and management, and the standards for seed collection, extraction, storage, and movement, is needed to avoid the seed problems.

CONCLUSION

There is an increasing awareness worldwide that unless we intensify efforts at gene conservation, reforestation, and intensive forest management, serious depletion of the world's forests will result. Although reforestation is recognized as an essential activity, an adequate supply of seeds of high quality and high genetic potential is often a limiting factor in many countries. This emphasizes the need for organized seed production and seed research to resolve many problems related to reforestation.

Several fungi have been studied on tree seeds; they vary in different host species, in different regions, and in different years. Even the detrimental effects to seeds during germination and storage, and to seedlings in nurseries, vary in different host species and environments. With the favorable environment in the Tropics, viz. high atmospheric temperatures coupled with high humidity, damage to seeds and seedlings is greater there. Biotic factors like squirrel and seedbug damages, and abiotic factors like time and method of collection, shipment, extraction, processing, testing, and storage of seeds, all affect the occurrence of fungi in seeds. Improvement in these practices, use of surface sterilants and/or fungicides, and following legislated practices like quarantine will help in the worldwide management of seeds.

PART II. PRACTICE

Australia is the origin of a unique and extensive resource of tree and shrub species which have proven to be of great value for the establishment of plantations in many parts of the world. Examples include approximately 5 million ha fast-growing eucalypt plantations in Brazil; the *Acacia mangium* resource, almost 1 million ha, recently established in Indonesia; *Acacia saligna,* planted extensively in north Africa and the Middle East as a fodder tree; *Acacia colei*, planted around villages in semiarid Niger to provide edible seed to supplement inadequate diets (Harwood 1994), and the extensive plantings of *Casuarina equisetifolia* on sandy shorelines of southern China and Vietnam for typhoon protection and a wide range of timber and nonwood benefits (Nguyen 1996).

Although Australian native trees, especially eucalypts, have been grown as exotics for more than a century, the area of plantations has expanded rapidly during the last 30 years. This expansion has been driven by the development of hardwood pulp as a major international commodity to meet the increasing demand for paper, and the widespread adoption of Australian trees for community forestry in Asia and parts of Africa. Having evolved in a continent characterized by climatic extremes and infertile soils, Australian native trees have proved to be well adapted to cultivation as multipurpose trees on degraded soils and provide a wide range of products including timber, poles, fuel, and oils.

The Australian Tree Seed Centre (ATSC), part of CSIRO Forestry and Forest Products, has acted for 35 years as a national seed bank, supplying seed to researchers in Australia and over 100 other countries. The seed originates in natural forests but over the last decade ATSC has been complementing these collections with seed-orchard seed. Seed orchards have been established in tropical and temperate Australia, and in several overseas countries in southern and Southeast Asia and Oceania, in collaboration with a wide range of agencies.

In 1987 research was initiated by ATSC to investigate the presence of fungal pathogens in stored seed. Although seed dispatched overseas by ATSC is routinely treated to meet the phytosanitary requirements of the recipient country, there was little information on the seed pathology of the three most important Australian native genera grown in plantations, domestically and overseas, namely *Eucalyptus*, *Acacia*, and *Casuarina.*

This contribution to the chapter on seed pathology reviews the world literature on the seed pathology of those eucalypts, acacias, and casuarinas which are grown on a significant scale as plantation species in the tropics, and highlights some issues related to quarantine and the movement of pathogens internationally.

STORAGE FUNGI AND SEED-BORNE PATHOGENS

Most seeds carry spores of various fungi, either on the surface or within the tissues, and counts as high as 150,000 spores per tree seed have been reported (Anderson 1986). Some seed-borne fungi can cause the death of seeds and seedlings whereas other fungi, for example species of *Aspergillus, Penicillium, Chaetomium, Rhizopus,* and *Trichoderma,* which are the genera most often isolated from seed samples of a wide range of species (Mohanan and Sharma 1991, Yuan and others 1990), are saprophytes. If improperly stored, the growth of saprophytic fungi on seed can drastically reduce viability, but with a few exceptions, e.g. *A. niger* (Yuan and others 1997), they are rarely implicated in causing the death of seedlings.

Much of the literature on seed-borne fungi of these three tree genera consists of lists of fungal species with little information as to their pathogenic status. There are relatively few reports in the literature where isolation of putative pathogens from seed of eucalypts, acacias, and casuarinas has been complemented by inoculation tests to establish their pathogenicity. Some examples where this has been carried out include Bhawani and Jamaluddin (1995) who tested the pathogenicity of *Curvularia lunata* to *Acacia nilotica*; Harsh and others (1992) who found that a *Verticillium* sp. present in seed samples caused a post-emergence damping-off of seedlings; Saxena (1985) who investigated seedling mortality of *Eucalyptus* sp.; and Yuan and others (1990) who isolated 25 fungal genera representing at least 38 species from seed lots of *Acacia* spp., *Casuarina* spp., and *Eucalyptus* spp. and tested the pathogenicity of 14 fungal species by inoculating *A. auriculiformis*, *C. cunninghamiana*, and *E. camaldulensis*. A similar study was subsequently carried out on 10 seedlots of *E. pellita,* a tree species of increasing importance for plantations in the humid Tropics (Yuan and others 1997).

EUCALYPTUS SEED MYCOFLORA AND SEED-BORNE PATHOGENS

Lists of fungi isolated from samples of eucalyptus seed are often included with records from a range of other tropical tree species (table 1). Examples include Mohanan and Sharma

Table 1

Pathogenic Fungi Associated with Tropical Eucalypt Seeds

Fungus	Host	Country	Reference(s)
Botryodiplodia sp.	*E. grandis*	Uruguay	Mittal and others, 1990
Botrytis cinerea	*E. grandis*	India	Mohanan and Sharma, 1991
Colletotrichum sp.	*E. citriodora*	India	Mohanan and Sharma, 1991
Coniella australiensis	*E. pellita*	Australia	Yuan and others, 1997
Curvularia eragrostidis	*E. alba*	Thailand	Pongpanich, 1990
	E. pellita	Australia	Yuan and others, 1997
Curvularia fallax	*E. pellita*	Australia	Yuan and others, 1997
Curvularia geniculata	*E. tereticornis*	India	Reddy and others, 1982
Curvularia inequalis	*E. citriodora*	India	Mittal and others, 1990
Curvularia lunata	*E. camaldulensis*	Thailand	Pongpanich, 1990
	E. grandis	Thailand	Pongpanich, 1990
	E. tereticornis	Thailand	Pongpanich, 1990
	E. globulus	India	Mohanan and Sharma, 1991
	E. grandis	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
	E. camaldulensiss	Australia	Yuan and others, 1990
	E. grandis	Australia	Yuan and others, 1997
	E. pellita	Australia	Yuan and others, 1997
Curvularia pallescens	*E. alba*	Thailand	Pongpanich, 1990
	E. camaldulensis	Thailand	Pongpanich, 1990
	E. robusta	Thailand	Pongpanich, 1990
	E. globulus	India	Mohanan and Sharma, 1991
	E. grandis	India	Mohanan and Sharma, 1991
Curvularia pubescens	*E. citriodora*	India	Mittal and others, 1990
Curvularia senegalensis	*E. camaldulensis*	Australia	Yuan and others, 1990
	E. nitens	Australia	Yuan and others, 1990
	E. pellita	Australia	Yuan and others, 1997
Curvularia verruculosa	*E. grandis*	India	Mohanan and Sharma, 1991
Cylindrocladium clavatum	*E. tereticornis*	India	Mohanan and Sharma, 1991
Drechslera australiensis	*E. grandis*	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
	E. pellita	Australia	Yuan and others, 1997
Drechslera halodes	*E. saligna*	India	Reddy and others, 1982
	E. tereticornis	India	Reddy and others, 1982
Drechslera rostrata	*E. grandis*	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
Fusarium equiseti	*E. grandis*	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
	E. deglupta	Philippines	Mittal and others, 1990
Fusarium moniliforme	*E. camaldulensis*	Thailand	Pongpanich, 1990
	E. grandis	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
	E. grandis	Uruguay	Mittal and others, 1990

Table 1 (continued)

Fungus	Host	Country	Reference(s)
Fusarium oxysporum	*E. deglupta*	Thailand	Mittal and others, 1990
Fusarium poae	*E. alba*	India	Mohanan and Sharma, 1991
Fusarium semitectum	*E. camaldulensis*	India	Mohanan and Sharma, 1991
	E. camaldulensis	Egypt	Mittal and others, 1990
Fusarium solani	*E. citriodora*	India	Mittal and others, 1990
Fusarium sp.	*E. camaldulensis*	Australia	Yuan and others, 1990
	E. pellita	Australia	Yuan and others, 1997
Harknessia fumaginea	*E. pellita*	Australia	Yuan and others, 1997
Harknessia hawaiiensis	*E. pellita*	Australia	Yuan and others, 1997
Macrophomina phaseolina	*E. grandis*	India	Mohanan and Sharma, 1991
	E. tereticornis	India	Mohanan and Sharma, 1991
Macrophomina sp.	*E. camaldulensis*	Thailand	Pongpanich, 1990
Pestalotiopsis disseminata	*E. pellita*	Australia	Yuan and others, 1997
Pestalotiopsis funerea	*E. alba*	India	Mittal and others, 1990
	E. grandis	Uruguay	Mittal and others, 1990
Pestalotiopsis mangiferae	*E. tereticornis*	India	Reddy and others, 1982
Pestalotiopsis neglecta	*E. pellita*	Australia	Yuan and others, 1997
Phomopsis sp.	*E. citriodora*	India	Mohanan and others, 1991
Ramularia sp	*E. crebra*	Australia	Drake, 1974
	E. melanophloia	Australia	Drake, 1974
Verticillium albo-atrum	*E. grandis*	India	Mohanan and others, 1991
Verticillium sp.	*E. grandis*	Uruguay	Mittal and others, 1990
	E. hybrid	India	Harsh and others, 1992

(1991), who also highlighted issues of seed collection processing, storage, seed health testing, treatment and certification and indicated where improvement was needed; Agmata (1979), who provided the first list of tree seed-borne fungi in the Philippines; Mittal and others (1990), who compiled a world checklist of microorganisms associated with tree seed; and Richardson (1983) who provided an annotated list of seed-borne diseases. Lists of seed mycoflora for *Eucalyptus spp*. alone are provided by Sharma and Mohanan (1980), Tiwari and Sharma (1981), and Reddy and others (1982).

Several authors have demonstrated pathogenesis of seed-borne fungi, either by isolation of putative pathogens from both seed and blighted seedlings, or by inoculation studies. Mittal (1986) and Mittal and Sharma (1982) studied the mycoflora of *Eucalyptus* hybrid (predominantly *E. tereticornis*) and *E. citriodora* (syn. *Corymbia citriodora*) and also the means of controlling pathogenic fungal species. Saxena (1985) detected 30 species of fungi on seed of *E. grandis* and related seedling mortality to seed mycoflora, and Michail and others (1986) reported on fusarium postemergence damping-off of *Eucalyptus* spp. and its control. Four potentially pathogenic species, *A. niger*, *Fusarium* sp., *Penicillium canadense*, and *Rhizopus oryzae*, were found on seed of *E. citriodora* (Mittal and Sharma 1982). Drake (1974) found that a species of *Ramularia* infected unopened capsules of *E. crebra* and *E. melanophloia* while still borne on the tree, and caused up to 50-percent sterility.

Yuan and others (1990) inoculated *E. camaldulensis* seed with 14 putative pathogens isolated from seed and recorded seedling emergence compared to controls. All fungi except *Botrytis cinerea and Cytospora* sp. reduced emergence, with *Fusarium*, *Curvularia*, and *Pestalotiopsis* spp. being the most pathogenic. In a later study with *E. pellita* (Yuan and others 1997), *A. niger*, *Dreschlera australiensis*, *Harknessia fumaginea*, and *Pestalotiopsis disseminata* all reduced germination and/or caused seedling mortality postemergence compared to controls. *Coniella australiensis*, a widespread leaf pathogen of eucalypts, was also isolated for the first time from seed. It was suggested that these fungi may have originated from leaf debris within the samples and that such tissue offers a possible means for dissemination of foliar and stem pathogens with seed.

RISKS FROM THE DISSEMINATION OF PATHOGENS WITH EUCALYPT GERMPLASM

In a publication outlining technical guidelines for the safe movement of germplasm of *Eucalyptus* (Ciesla and others 1996), 32 pathogenic fungi were listed as being associated with eucalyptus seed. A revised list is given as table 1. All these fungi are generally regarded as being widely distributed geographically, and the presence of such pathogens in seed lots represents little in the way of quarantine hazard. Foliar pathogens, such as *Mycosphaerella* spp., *Kirramyces* spp., and *Aulographina* sp. (which are specialized pathogens found in most parts of the world where eucalypts are grown) were either absent from seed lots or escaped detection. It can be reasonably assumed that these pathogens have originated in Australia and have been disseminated internationally with seed or vegetative plant material, perhaps many decades ago. Another possibility is that fungal pathogens of Myrtaceae, which are widely grown as crop plants, e.g. guava and cloves; or form part of the indigenous flora, e.g. in Southeast Asia, South America, and Africa; could adapt as pathogens of eucalypts and may pose a threat to a wide spectrum of native vegetation if introduced in Australia. The occurrence of guava rust, *Puccinia psidii,* on eucalypts in South and Central America (Ferreira 1983) has created a particular risk as the fungus is damaging to eucalypt plantations. Stringent controls are in place governing the importation of eucalypt seed to Australia from South America.

ACACIA SEED MYCOFLORA AND SEEDBORNE PATHOGENS

As noted above for eucalyptus, records of the mycoflora of seeds of *Acacia* spp. are commonly combined with lists for other tree species (Dayan 1986). In a recent report on surveys of tropical acacia diseases by Old and others (1997b) some reference is made to seedling diseases, notably those recorded in Thailand (Pongpanich 1997), but the emphasis of the report is on diseases of plantations and native stands.

There are very few reports in the literature of seed-borne fungi causing diseases of acacia seedlings. *Curvularia lunata* has been recorded by Bhawani and Jamaluddin (1995) as causing shoot dieback of seedlings of *A. nilotica.* This fungus has been recorded previously from seed of *A. auriculiformis* and recently from *A. crassicarpa* and *A. aulacocarpa*. Several of the pathogens recorded by Mohanan and Sharma (1988) as causing diseases of exotic acacias in India are putative seed-borne organisms. Table 2 lists plant pathogenic species recorded on seed lots of tropical acacias.

Yuan and others (1990) inoculated *A. auriculiformis* with the same 14 seed-borne fungi used to inoculate eucalypt seed, with similar results. *Fusarium* spp., *Dreschlera* sp., *Curvularia* spp., and *Pestalotiopis* spp. caused the most severe pre-emergence blight of inoculated seedlings. An unpublished study of the mycoflora of *A. aulacocarpa*, *A. auriculiformis*, *A. crassicarpa*, and *A. mangium* seed by Yuan and others (1997) has indicated the presence of *Botryodiplodia* (syn. *Lasiodiplodia*) spp., *Curvularia* spp., *Dreschlera* spp., *Fusarium* spp., and *Pestalotiopsis* spp.

The lists of pathogenic fungi on acacia trees in native stands and plantations in northern Australia and in India presented by Old and others (1997a) and Sharma and Maria Florence (1997) include species of *Pestalotiopsis, Phoma, Phomopsis, Lasiodiplodia,* and *Curvularia,* which can be seed-borne. The detailed etiology, however, of the diseases of acacias recorded in both reports is largely unknown. Old and others (1997a) gave a brief account of a severe disease outbreak on *A. mangium* in 1992 in northern Australia caused by a *Cercospora* spp. The pattern of disease incidence suggested that the origin of the outbreak was in the nursery where seedlings were raised, and plants grown from seed imported from Papua New Guinea initially showed the highest level of disease. Although severe damage occurred in several plantations, the disease was present at very low levels during the following year and was undetectable subsequently. Detailed analysis of all seed lots used in the plantings failed to isolate *Cercospora* sp. (Old and others 1993). In view of several well-known examples of seed-borne *Cercospora* spp., this could have been the origin of the disease. Alternatively, the pathogen is indigenous and occurring undetected on native *Acacia* species in the region.

RISK FROM THE DISSEMINATION OF ACACIA PATHOGENS WITH GERMPLASM

As with eucalypts, the species recorded so far on the seed of tropical acacias are regarded as being already widely distributed throughout the regions where tropical acacias are grown. Also, they are generally pathogens with a broad spectrum of hosts. Unlike eucalypts, the seed of many acacia species are relatively large (10 mg to 1 g) and the presence of retained floral parts such as the aril offers niches for the carriage of saprophytic growth of facultative pathogens. (Table 2)

The recent report of an international workshop on diseases of tropical acacias (Old and others 1997b) gave an account of the status of a range of pathogens and the diseases they cause in Australia, India, and Southeast Asia. The stimulus for the workshop was the rapid expansion of plantations of tropical acacias, especially in Indonesia, Malaysia, and Thailand. Every year several tons of seed of *A. mangium*, the most widely grown species, are collected from native stands or seed orchards and dispatched between countries of the region. There seems little doubt that this practice carries significant risk of transporting pathogens on seed or associated plant debris. The practice of immersing seeds in boiling water prior to sowing to break dormancy may reduce the likelihood of chance contaminants being spread, but there is an urgent need for more information on the diseases of these species and the possibilities of seed-borne spread.

CASUARINA SEED MYCOFLORA AND PATHOGENS

There is very little information in the literature on seed-borne diseases of tropical *Casuarina* spp. Mittal and others (1990) listed 18 fungi associated with *C. equisetifolia*, 10 of these being putative pathogens (table 3). Sahai and Mehrotra (1982) examined the mycoflora of forest tree seeds including *Casuarina* (species not stated) but only one of those recorded (*Fusarium semitectum*) can be regarded as a putative pathogen. Yuan and others (1990) sampled the mycoflora of *C. equisetifolia* seed but recorded only four recognized pathogens including *A. niger, Botrytis cinerea, Curvularia senegalensis,* and *Pestalotiopsis* spp. *Alternaria alternata, B. cinerea, Pestalotiopsis spp.*, and a *Phoma spp.* were isolated from *C. cunninghamiana*. The most useful summaries of diseases of *Casuarina* are those of Mohanan and Sharma (1989, 1993). In the latter publication they noted that information on seedling diseases in India is meager despite the raising of casuarina seedlings in that country for nearly a century. They reported that the soil-borne pathogens *Rhizoctonia solani* and *Macrophomina phaseolina* are the main pathogens of seedlings. Of these, *M. phaseolina* has been listed as seed borne but is actually a very common soil-borne fungus with a very wide geographical distribution, causing the well-known charcoal root rot of a broad range of tree species (Srivastava and Kalyani 1990).

Of more interest to seed pathology is the record by Mittal and others (1990) of *Phomopsis casuarinae* as being seed borne. This is a well-known pathogen, recorded in Portugal (Dos Santos 1966) and in India (Mohanan and Sharma 1993). The fungus causes stem cankers and foliar lesions, and is probably more severe on stressed trees, sharing this characteristic with *Botryosphaeria* spp (Pongpanich and others 1996) and *Trichosporum vesiculosum* (Mohanan and Sharma 1993, Narayanan and others 1996). Table 3 presents a list of diseases of Casuarina for which an association with seed has been established or may be inferred.

RISKS FROM THE DISSEMINATION OF PATHOGENS WITH CASUARINA GERMPLASM

One of the more significant diseases of *Casuarina equisetifolia* is the blister-bark pathogen *Trichosporum vesiculosum (nom. illegit.).* The status of this organism as a pathogen has been questioned (Boa and Ritchie 1995). However, Narayanan and Sharma (1996) and Narayanan and others (1996) summarized the available information which strongly points to the fungus being a damaging pathogen of stressed trees. The fungus spreads by production of very large quantities of sooty spores within blisters under the outer bark, which rupture to release spores. The etiology of the disease is imperfectly understood, but it is likely that wound infection is the major means of spread with further movement within an affected stand by root-to-root contact (Narayanan and others 1996).

Until 1994 the fungus was known as a pathogen of casuarina only in India (Bakshi 1951) and in Mauritius (Orian 1961). However, blister-bark disease has been found in central Vietnam (Sharma 1994) and was identified at two locations in Thailand in 1995 in replicate plantings of an international *Casuarina* provenance trial (Pongpanich and others 1996). The seed for this trial had originated in many countries, including India, and although there is no information as to the origin of the outbreak, it is possible that the fungus was seed borne. *T. vesiculosum* would not be detected by standard seed testing methods; however, its fecundity suggests that chance contamination of seed could have been the origin of the simultaneous appearance of this disease in two locations in Thailand separated by approximately 200 km. There is a need for further

Table 2

Pathogenic Fungi Associated with Tropical Acacia Seeds

Fungus	Host	Country	Reference(s)
Botryodiplodia theobromae	*A. confusa*	Philippines	Agmata, 1979
(syn. Lasiodiplodia theobromae)	*A. auriculiformis*	Thailand	Chalermpongse and others, 1984
Botryodiplodia sp.	*A. auriculiformis*	Australia	Yuan and others, 1997
Colletotrichum gloeosporioides	*A. auriculiformis*	India	Mohanan and Sharma, 1988
Colletotrichum sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
Curvularia brachyspora	*A. auriculiformis*	Thailand	Chalermpongse and others, 1984
Curvularia eragrostidis	*A. auriculiformis*	Australia	Yuan and others, 1997
Curvularia lunata	*A. auriculiformis*	Australia	Yuan and others, 1990
	A. catechu	India	Vijayan, 1988
	A. confusa	Philippines	Agmata, 1979
	A. crassicarpa	Australia	Yuan and others, 1997
Curvularia pallescens	*A. auriculiformis*	Philippines	Mittal and others, 1990
Curvularia senegalensis	*A. auriculiformis*	Australia	Yuan and others, 1990
Curvularia sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
Cylindrocladium sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
Diplodia sp.	*A. crassicarpa*	Australia	Yuan and others, 1997
Drechslera spp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
	A. crassicarpa	Australia	Yuan and others, 1997
Fusarium equiseti	*A. catechu*	India	Vijayan, 1988
Fusarium moniliforme	*A. raddiana*	Israel	Mittal and others, 1990
Fusarium oxysporum	*A. catechu*	India	Vijayan, 1988
Fusarium semitectum	*A. auriculiformis*	Philippines	Mittal and others, 1990
	A. auriculiformis	India	Mohanan and Sharma, 1988
	A. modesta	India	Mittal and others, 1990
Fusarium solani	*A. catechu*	India	Vijayan, 1988
	A. holosericea	Australia	Yuan and others, 1990
Fusarium sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
	A. auriculiformis	Australia	Yuan and others, 1990
	A. auriculiformis	Australia	Yuan and others, 1997
Hansfordia sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
Helminthosporium sp.	*A. mearnsii*	Australia	Yuan and others, 1990
Lasiodiplodia sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997
Pestalotia sp.	*A. mearnsii*	China	Liu, 1988
Pestalotiopsis disseminata	*A. auriculiformis*	Australia	Yuan and others, 1997
Pestalotiopsis neglecta	*A. auriculiformis*	Australia	Yuan and others, 1997
Pestalotiopsis phoenicis	*A. auriculiformis*	Australia	Yuan and others, 1997
Pestalotiopsis sp.	*A. auriculiformis*	Australia	Yuan and others, 1990
Phoma sp.	*A. auriculiformis*	India	Mathur, 1974
	A. auriculiformis	India	Mohanan and Sharma., 1988
	A. confusa	Philippines	Agmata, 1979
	A. modesta	India	Mittal and others, 1990
	A. raddiana	Israel	Mittal and others, 1990
	Acacia sp.	Egypt	Mittal and others, 1990
Phomopsis sp.	*A. auriculiformis*	Thailand	Pongpanich, 1997

Table 3

Pathogenic Fungi Associated with Tropical Casuarina Seeds

Fungus	Host	Country	Reference(s)
Botryodiplodia theobromae	*C. equisetifolia*	Philippines	Mittal and others, 1990
Botryodiplodia sp.	*C. equisetifolia*	Philippines	Mittal and others, 1990
Curvularia brachyspora	*C. equisetifolia*	Philippines	Mittal and others, 1990
Curvularia lunata	*C. equisetifolia*	Philippines	Mittal and others, 1990
	C. equisetifolia	Thailand	Mittal and others, 1990
Curvularia pallescens	*C. equisetifolia*	Philippines	Mittal and others, 1990
Curvularia senegalensis	*C. equisetifolia*	Australia	Yuan and others, 1990
Fusarium moniliforme	*C. equisetifolia*	Philippines	Mittal and others, 1990
Fusarium semitectum	*Casuarina* sp.	India	Sahai, 1982
Macrophomina phaseolina	*C. equisetifolia*	Philippines	Mittal and others, 1990
Pestalotia sp.	*C. equisetifolia*	Philippines	Mittal and others, 1990
Pestalotiopsis sp.	*C. equisetifolia*	Australia	Yuan and others, 1990
	C. cunninghamiana	Australia	Yuan and others, 1990
Phoma sp.	*C. equisetifolia*	Philippines	Mittal and others, 1990
	C. cunninghamiana	Australia	Yuan and others, 1990
Phomopsis casuarinae	*C. equisetifolia*	India/Australia	Bose, 1947

research on this pathogen to determine its taxonomic affinities, its pathogenic status, and the etiology of blister-bark disease. Until further information is available it would be imprudent to disregard the possibility that the disease may be seed borne. (Table 3)

CHAPTER 7

Ecological Life Histories

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Research on the ecological life history (or life cycle) of tropical trees has lagged behind that of other plants, particularly trees of the Temperate Zone. In the Tropics, life-history research has followed two lines of inquiry: demography and succession. Compared to temperate trees, tropical trees (*sensu latus*) appear to have both a shorter timespan to first reproduction and shorter lifespans. Elucidating life-history strategies in species-rich tropical forests is daunting because the traditional dependence on seed and seedling behavior is inadequate, and a complete life-history analysis is required for each species to define appropriate groupings. Analysis of the behavior of seeds, seedlings, and saplings of lowland tropical moist, wet, and rain forest trees suggests two groups of species: pioneer and nonpioneer (or climax). For most trees (nonpioneers), the survival of adults contributes most to fitness, not the number of seeds or seedlings they produce or how fast they grow. For pioneers, the seed bank and the growth of juveniles affects fitness most. More research is needed to validate these trends, however, because the tree species and environmental conditions in the Tropics are diverse. Further division of nonpioneer life histories by functional grouping has proved difficult because a continuum of traits appears to exist among all species.

Formation of tree-fall gaps has been emphasized as the main disturbance event in the life cycle of tropical moist to rain forest trees, and gaps are where most tree life histories experience their critical stages of development. Incident light and, to a lesser extent, nutrients are the factors most responsible for the growth of individuals through gaps or inside a closed canopy. In dry forests, water is more important than light as the factor that determines the success of individuals. Some life-history traits in dry forest trees are small seeds, moisture-related seed dormancy, reliance on root or stem sprouts for regeneration, synchronous growth and reproduction processes, low abundance of seedlings, reduced seed banks, and high density of stems.

Large and infrequent disturbances such as hurricanes instantaneously introduce extreme conditions that significantly alter the stages of the lifecycles of some tropical trees. Sprouting, formation of tree unions, small individuals, short life spans, rapid changes in sun and shade adaptation, explosive establishment of seedling populations, accelerated rates of primary productivity and nutrient cycling, and increased abundance of gap-dependent canopy species, are examples of life-history traits in frequently disturbed areas. In degraded sites, such as those with frequent landslides or human-affected systems, different groups of species—including different life forms and a greater fraction of alient species—achieve success in regeneration. These differences suggest that another set of life-history characteristics is required to overcome these extreme environments. Much research is needed before a clear picture of the diversity of life-history strategies of tropical trees emerges.

INTRODUCTION

> Most plant communities are successional and each species is doomed to local extinction; the two strategies of "escape to somewhere else" or "wait until the right habitat reappears" are alternative ways of meeting the deterioration of the local habitat (Harper 1977).

Harper's words articulate the options available to most plants, including trees in tropical forests. The challenge for scientists is to determine which plants follow which strategy, describe variations of plant response to changing conditions, and examine life-history phenomena in search of patterns of response that can be used to categorize species and improve the capacity to manage tropical forests. Unfortunately, ecological understanding of tropical forests is poor, in part because they are so complex. The complexity of tropical forests comes from the high concentration of tree species per unit area and the wide diversity of ecological conditions that characterize tropical latitudes. On average, tropical trees face more diverse biotic competition and a more varied climate than do temperate and boreal trees. How to address the ecological life histories (or life cycles) of so many tree species growing under so many climatic and edaphic conditions challenges tropical forest ecologists and foresters.

Quantitative analysis of the ecological life history of plants was formalized by Pelton (1953). Before this synthesis, the focus on plants from a population or demographic point of view lagged behind the study of animal populations or that of plant communities (Harper 1967, Hubbell and Werner 1979, McCormick 1995). Moreover, the study of life histories of tropical trees has lagged behind that of temperate trees. In Harper's (1977) 892-page review, fewer than 30 pages contain any reference to tropical tree species, and most of the information is about seed dispersal and predation. Since 1977, many studies have focused on tree regeneration in canopy gaps of tropical-lowland moist and wet forests, but few studies have addressed complete life histories of trees in tropical forests as a whole and dry forests in particular (Alvarez-Buylla and others 1996; Clark and Clark 1992; Garwood 1989; Gómez-Pompa and Vázquez-Yanes 1974; McCormick 1995; Putz and Brokaw 1989; Swaine and Lieberman 1987; Whitmore 1984a, 1984b; Zimmerman and others 1994).

Swaine and others (1987b) observed that most tropical studies do not last long enough to account for the longevity of trees. In Puerto Rico, with some of the longest tree-growth plots in the Neotropics, records now exist covering almost 60 years—the recurrence interval of catastrophic hurricanes (Lugo and others 2000). The situation is compounded by the difficulty in aging tropical trees (Bormann and Berlyn 1981). Wyattt-Smith (1987) regretted the shortage of information on the dynamics of tropical tree populations and added that many long-term tropical studies focused on trees >10 cm d.b.h. Regeneration and establishment through the seedling and sapling phases as well as to flowering and fruiting phases received less attention. He emphasized that understanding the dynamics of large trees of any species requires study of the regeneration and establishment phases. This need exists even though characterizing ecological life histories of tropical trees has usually focused on the short-term responses of seeds and seedlings (e.g., Swaine and Whitmore 1988).

Our review of the literature uncovered two complementary lines of life-history research in tropical forests. One approach is demographic, with a strict focus on individual species (Alvarez-Buylla and others 1996, Hubbell and Foster 1990, McCormick 1995, Silvertown and others 1993). This research can either be comprehensive, based on a population; or fragmented, focused on one or several aspects of the life cycle of a single tree. A second line of research is successional; it focuses on community function and aims to understand the role of tree populations in succession (Bazzaz and Pickett 1980, Clark and Clark 1992, Ewel 1980, Gómez-Pompa and Vázquez-Yanes 1974, Richards 1964). Although demographic techniques are used, this research selects groupings of species with the objective of cataloging functional groups according to their role in succession. In our review, we first place ecological life-history research on tropical trees in context with life-history studies in other plant groups, and then present life-history information according to various lines of research. We end with a review of ecological life- history research in forests that are subjected to large and infrequent disturbances, water limitation, and other ecological stressors. Our objective is to present the paradigms of ecological life-history research for tropical trees and, where possible, propose improvements to these paradigms based on experience in the Caribbean. Throughout the review, we highlight research needs to support improved life-history models for tropical trees.

PARAMETERS OF THIS REVIEW

CAVEATS AND DEFINITIONS

The literature tends to generalize about the Tropics, particularly through comparisons with temperate conditions (Lugo and Brown 1991). Generalizations are useful, but they can lead to pitfalls and myths for two reasons. First, consistency is lacking in the use of such terminology as tropical, tropical forests, rain forests, primary forests, and secondary forests (cf. Brown and Lugo 1990, Lugo and Brown 1991). Readers cannot be sure what environmental conditions or forest states are being referred to without precise definitions. Second, the high richness of species and diversity of life forms that typify the Tropics assure that exceptions to most generalizations will be found. In this review, we retain the terminology on forest types used in the original articles when referring to their findings, and we use those of Holdridge (1967) when expressing our views.

The term "large and infrequent disturbance" is used here *sensu* Romme and others (1998):

> large and infrequent disturbances are defined as those whose intensity exceeds the intensity at which a threshold occurs in the response curve [of ecosystem parameters], and that are statistically infrequent.

Examples are hurricanes above certain intensity scales, large floods, large and intense fires, landslides that exceed certain volume thresholds, and extreme droughts.

METHODS FOR STUDYING ECOLOGICAL LIFE HISTORIES

A life history is defined as the combined changes in expectations for further life and reproduction in an organism as it ages or grows. Life histories are assumed to evolve in response to the organism's environment; life-history tactics are the individual traits of the life history that are selected for or against. The way in which selection and life-history tactics evolve depends on species-specific tradeoffs among tactics (i.e., reproduction vs. survival). How life cycles evolve was shown by Lewontin (1965) using a simple graphical model which was incorporated in Harper's (1977) idealized life cycle of a higher plant (shaded portion of fig. 1). Harper's life cycle diagram showed the reproductive periods of the life cycle that are critical to the demographic success of plants: time of first reproduction, capacity to change the time of onset of the fecundity period, time of peak fecundity, capacity to change the peak period of fecundity, time when fecundity ceases, capacity to change the time when fecundity ceases, and total number of offspring produced.

The fecundity period begins at the age of first reproduction and continues until reproduction ceases because of senescence or death. Age of first reproduction is the most critical aspect of a life history because population growth is a com-

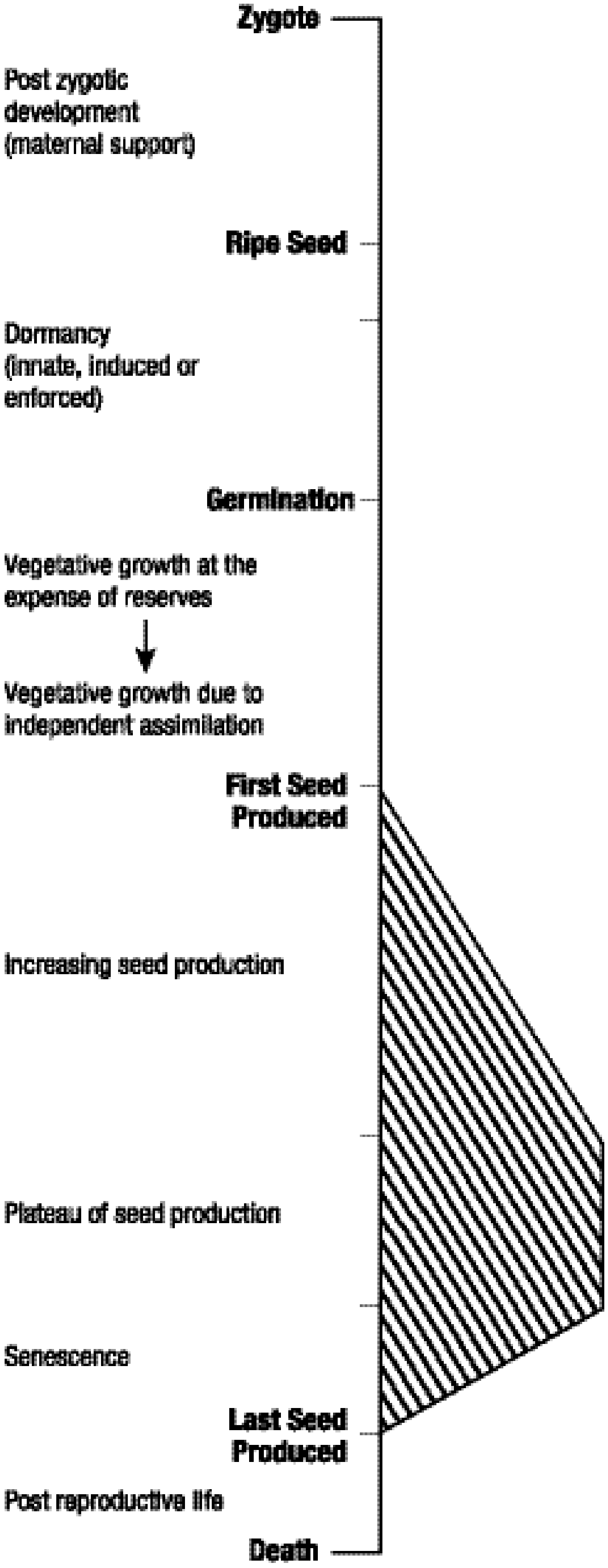


Fig. 1. Idealized life cycle of a higher plant. The shaded portion represents the pattern of production and total amount of seeds produced. From Harper (1977).

pounded variable: the earlier organisms reproduce, the earlier a new generation will be positioned to reproduce themselves and add more individuals to the population. Trees reproduce late relative to other plants as a tradeoff with early growth (Stearns 1992). Reproduction is impossible or difficult until a minimum size is achieved; thus, early growth allows trees to reach the canopy where reproduction is maximized.

A life history can be best analyzed as a life table, a square matrix providing the age- (or size-) specific probabilities of death and amount of reproduction in each age (or size) class. Age-based matrices are termed Leslie matrices (Leslie 1948) in which the only nonzero entries are on the first row (fecundities) and along the diagonal (survivorship). Nonzero entries reflect impossible transitions such as going from age 7 to 9 in a single time step. Stage-based (population transition) matrices are called Lefkovitch matrices (Lefkovitch 1965) in which any element of the matrix may be nonzero because any class could contribute to any other class in the next time interval.

A life cycle graph (fig. 2a) includes all relevant demographic data for a tree, which is readily translated into a population transition matrix (fig. 2b). The transition matrix provides quantitative data on a yearly time step for transition probabilities from one stage to another (Caswell 1989). For tropical trees, a stage-based or Lefkovitch matrix rather than an age-based matrix is most appropriate because tropical trees are difficult to age and, more importantly, except in senescent trees, the size of a tree rather than its age best determines its future behavior.

Columns in the transition matrix indicate, for each stage, the combined probability of surviving and of growing, of declining in size, or of remaining in the same stage by the next time step (usually a year). Seed production (F = fecundity) is depicted in the top row (number of seed produced by the average small or large adult tree). The probability of remaining a seed in the seed bank, a seedling, a sapling, and so on, is provided by the diagonal (L). The chances of surviving and growing to the next stage are below the diagonal (G), and the chances of declining in size because of catastrophe (D) appear above the diagonal. Each row looks backward, defining each stage in terms of the fecundity, survival, and growth of the contributing stages during the previous year. The matrix has great flexibility in terms of the type of life-history information available. For example, clonal growth would be indicated by arrows from any of the adult classes to the juvenile class and would appear in the transition matrix above the diagonal position (combined with D). With a seed pool, or if a seed pool does not exist in the population for more than a year, then the seed stage should be omitted (Caswell 1989, Silvertown and others 1993); reproduction is then described as the average seedling production by each adult stage. This procedure is used in cases when the time step of the transition matrix is a year.

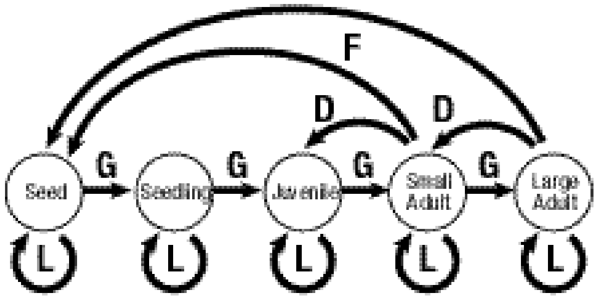
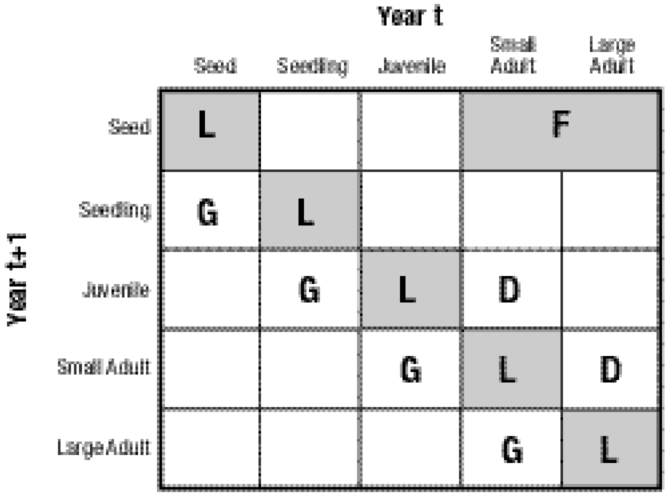


Fig. 2a. A five stage (seed to large adult) model of a life cycle of a tree showing critical demographic processes (a). Survival is L, growth is G, size reduction due to catastrophe is D, and fecundity by seed production is F.



Year t

Year t+1	Seed	Seedling	Juvenile	Small Adult	Large Adult
Seed	L			F	
Seedling	G	L			
Juvenile		G	L	D	
Small Adult			G	L	D
LargeAdult				G	L

Fig. 2b. The same diagram in matrix form (b) suitable for analysis by the power method of Caswell (1989). From Hubbell and Werner (1979).

In mathematical terms, the transition or projection matrix **A** provides the average contributions of an individual in a particular stage (*j*) to another stage (*i*) in a predefined time interval. Each element is termed a*ij*; these values are whole numbers in terms of fecundity, and range from 0 to 1 in the remainder of the matrix. A variety of population measures can be derived from **A** (Caswell 1989). The most important of these is lambda (l), the population growth rate or the change in the number of individuals at each stage over time (assuming the relative number of individuals at each stage is the same over time). The value l is important because it also provides a definition of fitness in evolutionary studies–the expected number of offspring to be produced by an organism with a particular set of traits in a particular environment. One set of indices that are frequently derived from **A** are the elasticities. Elasticity (e*ij*) is a measure of the proportional sensitivity of l to small changes in the a*ij*’s, and it thus provides a clear measure of the relative importance of different life stages to the organism’s fitness. Because of bottlenecks between life stages, a 10-percent increase in seedling survivorship will not have the same effect as a 10-percent increase in adult survivorship or a 10-percent increase in fecundity.

SEED LONGEVITY IN TROPICAL FORESTS

To show how recent research is modifying early pantropical generalizations, we use information on seed longevity. The accepted generalization is that tropical tree seeds have short spans of viability (Harper 1977, Mabberley 1983, Ng 1983). Many species conform to the accepted generality, particularly in true rain forests, but many seeds do not have short spans of viability and others have some kind of dormancy (Gómez-Pompa and others 1976, Smith 1970, Whitmore 1984b). Ng (1980) found an exponential decline in the relation between number of species and time required for germination in Malaysian rain forests, with 50 percent of 335 species completing their germination in 6 weeks. About 15 percent of the species exceeded 20 weeks before they began germination.

Vázquez-Yanes and Orozco-Segovia (1993) found that seed crop, seasonality of production, and number of seeds per fruit vary greatly, due to the enormous diversity of plant taxa and life forms in tropical rain forests. They also observed that the seeds are remarkably diverse in size, shape, morphology, anatomy, moisture content, nature of reserves, and presence of secondary compounds. They reported that the mean longevity of seeds in tropical rain forests, where the forest floor is wet, dark, and hot, may be one of the shortest of any plant community because seeds tend to germinate soon after dispersal. Seeds of pioneer species in rain forests, however, show long longevity, reaching turnover times of more than 1 year. In seasonal tropical forests, some seeds may be released with low moisture (wind-dispersed seeds such as those of *Swietenia macrophylla*) and can remain quiescent until moisture becomes available. A large data set on seed production, size, and dispersal mechanisms is available for Amazonian forests in Knowles and Parrotta (1995, 1997).

The factors that independently or in combination may extend the ecological longevity of seeds are: dormancy mechanisms, delayed germination, metabolic interruption, presence of a hard or impermeable coat that prevents fast rehydration and diminishes predation, abundant seed production that allows many seeds to survive predators and parasites, and strong chemical defenses against parasitism and predation. Vázquez-Yanes and Orozco-Segovia (1993) suggested that plants that become established in the undisturbed forest floor have less complex, environmentally regulated dormancy mechanisms than those established in scattered gaps. Garwood (1989) gave examples of the diversity of seed germination and seed-dispersal patterns along gradients of regeneration strategies in the lowland Tropics (table 1). Unfortunately, the amount of information available on the physiology of dormancy of rain forest seeds is too limited to allow generalizations on the mechanisms for different ecological groups of plants.

Table 1

The expected distribution of tropical seed-bank strategies among regeneration strategies, based on the distribution of germination behaviors and frequency of dispersal

(Source: Garwood 1989)

	Regeneration Strategy[a]			
Seed-bank Strategy	Weedy Species	Short-lived Pioneers	Long-lived Pioneers	Primary species
Transient	R + A	R + A	R + A/I	R + A/I
Transient with seedling bank	—	—	—	R + A/I
Pseudo-persistent	R + C	R + C	—	—
Delayed-transient	—	—	D + A/I	D + A/I
Seasonal-transient	S + C/A	S + C/A	S + A/I	S + A/I
Persistent	F + C/A	F + C/A	—	—

[a] Germination behavior + dispersal frequency. Germination behavior denoted by: R, rapid germination and short-term viability; S, seasonal dormancy and intermediate-term viability; D, delayed germination and intermediate-term viability; and F, facultative dormancy and long-term viability. Dispersal frequency denoted by: C, continuous; A, annual; and I supra-annual (intermittent).

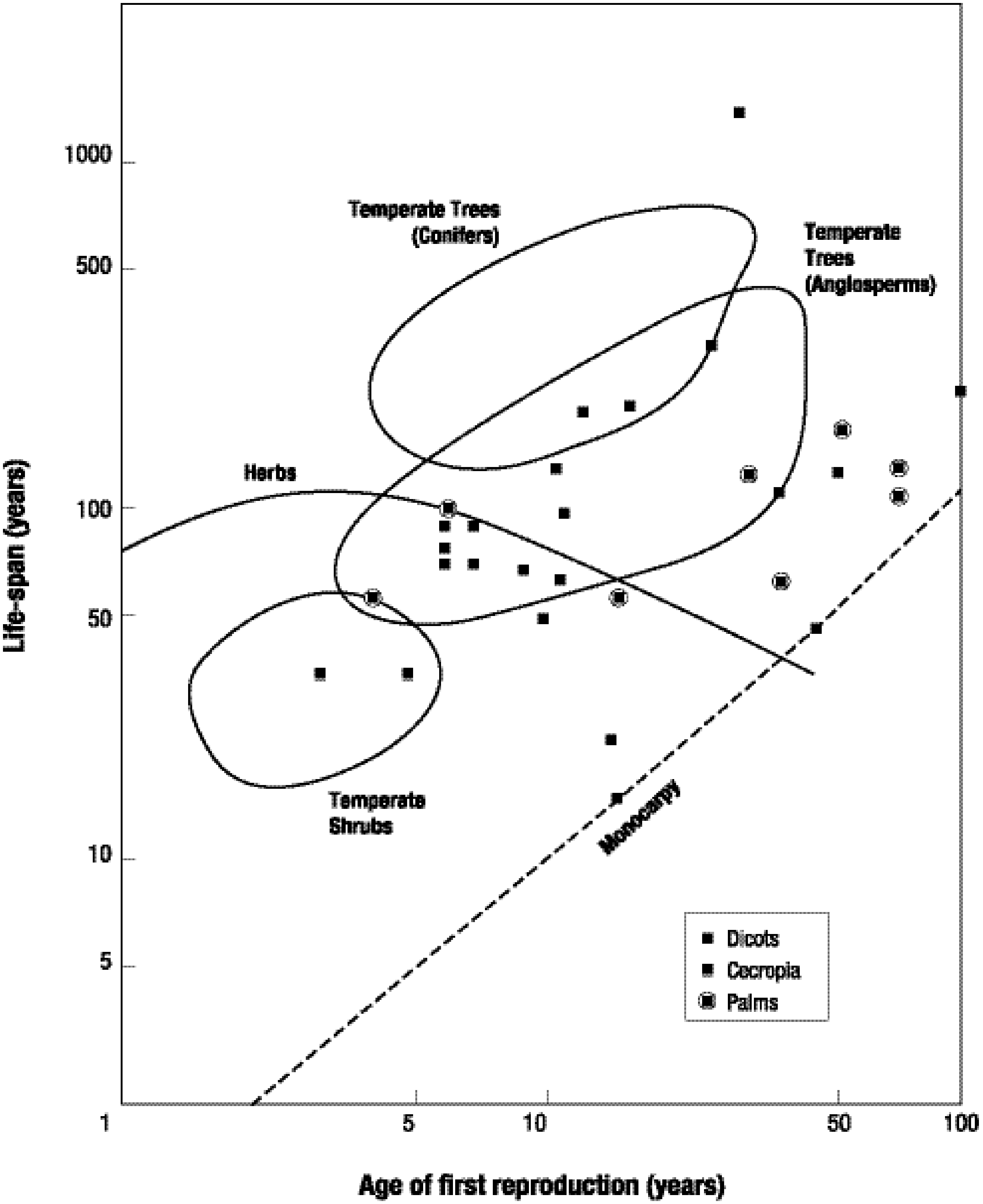


Fig. 3. Relationship between juvenile period (age of first reproduction) and total life span for perennial plants. Modified from Harper (1977). Original data are from Harper and White (1974) with additional data for tropical trees obtained from Alvarez-Buylla and Martínez Ramos (1992), Bullock (1980), Francis (1989), Francis (1991), Hartshorn (1972 and personal communication), Muñiz Meléndez (1978), Olmstead and Alvarez-Buylla (1995), Piñero and others. (1984), Sastre de Jesús (1979), Silander (1979), Van Valen (1975), You (1991), [two from silvics manual: *Mammea americana* and *Swietenia mahogoni*]

LIFE HISTORIES OF TROPICAL TREES COMPARED TO OTHER PLANTS AND TREES

Harper and White (1974) compiled data on the age of first reproduction of seed plants. They differentiate between semelparous plants (those that reproduce once and die, i.e., age of reproduction is the same as lifespan), herbs, shrubs, and trees–both angiosperms and gymnosperms (fig. 3). Compared with other plants, trees have long lifespans and tend to reach the age of first reproduction late. We added new data on tropical trees (Dicots, *Cecropia,* and palms) to Harper and White's figure and included them with those in their original diagram. The results suggest that tropical trees (*sensu latus*) tend to reproduce at younger ages and have shorter lifespans than temperate trees. In addition, some understory tropical palms appear to have long juvenile periods relative to their lifespan (Bullock 1980, Olmstead and Alvarez-Buylla 1995, Van Valen 1975). The only tropical pioneers in the figure (*Cecropia*) behaved like temperate shrubs: they had very short lifespans and early ages of first reproduction. More research is needed to verify these tendencies.

Grime (1979) identified the environmental extremes of evolutionary specialization in plants in terms of stress, competition, and disturbance. From these extremes, he described three main strategies of plant response: stress tolerators (S), competitors (C), and ruderals (R). Stress tolerators grow in competition-free environments where resource availability is low. Competitors grow in areas where resource availability is high and where competition from established vegetation is also high. Ruderals are weeds that grow in competition-free environments where resource availability is high. Grime identified secondary strategies that develop from a combination of these three strategies and placed various plant groups in the context of these response strategies (fig. 4).

Most trees occupy the range of conditions largely defined as stress-tolerance competitors, which adapt to relatively undisturbed conditions with moderate intensities of stress. From these determinations, we can generalize regeneration strategies that best adapt trees to the conditions they face. For example, as stress increases, trees rely more on persistent seedling banks than on seed banks (Garwood 1989). Mangrove trees are tropical trees without a seed bank; their viviparous seedlings form a seedling bank (Tomlinson 1986). In this view, pioneer trees exist near the ruderal corner of the triangle where resources (light) are relatively high and competition relatively low. Unfortunately, Grime developed his scheme primarily for herbaceous plants in the temperate zone; the utility of this scheme for discriminating among life histories of trees remains untested, as does the distinction between temperate and tropical trees.

The demographic approach to tree life histories has been more fruitful and produced a scheme similar to Grime's. Silvertown and others (1993) analyzed Lefkovitch matrices for 66 species of plants, calculating the summed elasticities for fecundity (F), survival (L), and growth (G) for each species. The results were depicted on triangular diagrams similar to Grime's habitat classification scheme. Species differed in their demographic parameters in a manner that would meet expectations. Elasticities for semelparous (biennial) herbs were highest on the F and G axes and those for perennial herbs appeared in the middle of the diagram. Understory herbs were intermediate for L and G, and low on the F axis. Woody plants, including a few tropical trees, were almost entirely restricted to one corner of the triangle, where F and G were both near 0 and L was near 1. Thus, for most trees, the survival of adults contributes most to fitness, not the number of seeds or seedlings they produce or how fast the trees grow. The few exceptions to this pattern were shrub species in the fire-prone habitats where F and G were intermediate.

With the same approach, Alvarez-Buylla and others (1996) focused on 13 tropical tree and palm species; they found that the highest elasticities in 12 of these species were found in the survival of adults or preadults, a finding similar to the global analysis of Silvertown and others (1993). The one exception was *Cecropia obtusifolia*, the only pioneer species on the list, for which the survival of seeds in the seed bank and the growth of juveniles showed the highest elasticities. This finding agrees with the accepted expectation that pioneer and nonpioneer species would differ. *Cecropia obtusifolia* would occur toward the center of the G-L-F space (Silvertown and others 1993), with temperate shrubs in fire-dominated habitats. Therefore, the life histories of the temperate and tropical

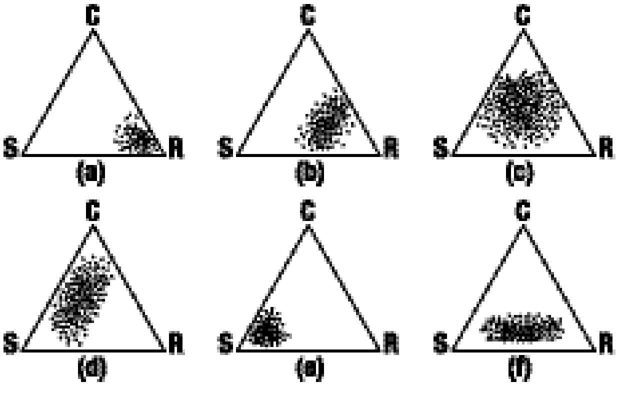


Fig. 4. Diagram describing the range of strategies encompassed by (a) annual herbs, (b) biennial herbs, (c) perennial herbs and ferns, (d) trees and shrubs, (e) lichens, and (f) bryophytes. From Grime (1979).

angiosperm trees studied tend to be similar, except for fast-growing tropical pioneers. However, a large sample of matrices is needed to confirm this pattern. This approach could also be used to determine whether nonpioneer species show any distinctive pattern of change in their elasticities.

THE ECOLOGICAL LIFE HISTORY OF TROPICAL TREES

Schimper (1903) distinguished between sun- and shade-adapted plants, and Richards (1964) contrasted species that grew in open areas or gaps in rain forests (light demanding or intolerant [of shade]) with those that regenerated inside the forest (shade bearing, tolerant, or primary forest dominants). These observations formed the basis for a variety of ecophysiological studies at leaf, seedling, and whole-tree scales (Bazzaz and Pickett 1980, Fetcher and others 1987, Kitajima 1994, Lugo 1970, Medina in press, Odum and others 1970). Sun-adapted plants are distinguished by photosynthetic light-response curves that saturate at high light intensities; photosynthesis rates of shade-adapted plants saturate at low light intensities. Respiration rates in shade-adapted plants are low, allowing them to persist for long periods in the shade.

Fetcher and others (1987) found that the metabolism of early successional species is less affected by the previous environment after being moved to a new environment than are late-successional species. Therefore, they surmised that early successional species are able to acclimate to new environments more rapidly than are late-successional species. When response variables were considered separately, however, Fetcher and others (1987) found that species with apparently similar ecological roles do not necessarily have similar acclimation responses. Kitajima (1994) found that traits that maximize carbon gain in seedlings do not necessarily lead to a higher survival in shade, and that acclimation responses of individual photosynthetic traits do not necessarily differ between shade-tolerant and shade-intolerant species. Instead, she found that morphological traits were negatively correlated with the survival of individuals in shade. The explanation is that faster growth rates are achieved at the expense of defense or storage allocation. Morphological traits achieve a degree of protection and storage allocation that assures shade survival even at slow rates of growth.

The dichotomy in light response (sun-adapted or heliophytic vs. shade-adapted or non-heliophytic) is the basis of the quotation from Harper (1977) at the beginning of this review. The dichotomy has led to the many name pairs critically reviewed by Swaine and Whitmore (1988), such as pioneer vs. nonpioneer, colonizing vs. climax, secondary vs. primary, shade bearers vs. light demanders, nonequilibrium vs. equilibrium, r-selected vs. k-selected, weeds vs. species of closed vegetation, ephemerals vs. persistents, nomad vs. dryad. Swaine and Whitmore (1988) used seed germination and seedling establishment as the basis for proposing two ecological groups to substitute for all the commonly used name pairs. Their proposed nomenclature was pioneers vs. nonpioneers (or climax).

We agree with Swaine and Whitmore (1988) and Clark and Clark (1992) that the only classification scheme for tropical tree life histories that is supported by data is the contrast between pioneer and nonpioneer species. Whether these two types of species form distinct groups (Clark and Clark 1992, Swaine and Whitmore 1988, Zimmerman and others 1994) or are the end points in a continuum of life-history types (Alvarez-Buylla and others 1996, Gómez-Pompa and others 1976) is presently unclear and deserves further research. The distinguishing characteristics of these two life-history types were summarized by Swaine and Whitmore (1988) but a different listing of characteristics was provided earlier by Gómez-Pompa and Vázquez-Yanes (1974) (fig. 5). The character syndrome of pioneer tree species in tropical rain forests as proposed by Swaine and Whitmore is tabulated below.

- Seeds germinate only in canopy gaps that are open to the sky and receive some full sunlight.
- Plants cannot survive in shade–young plants never found under a closed forest canopy.
- Seeds small and produced copiously and more-or-less continuously.
- Seeds produced from early in life.
- Seeds dispersed by animals or wind.
- Dormant seeds usually abundant in forest soil (especially fleshy-fruited species); seeds orthodox (no recalcitrant species known).
- Seedling carbon-fixation rate high; compensation point high.
- Height growth rapid.
- Growth indeterminate with no resting buds.
- Branching relatively sparse.
- Leaves short-lived.
- Rooting superficial.
- Wood usually pale, low density, not siliceous.
- Leaves susceptible to herbivory; sometimes with little chemical defense.
- Wide ecological range; phenotypically plastic.
- Often short-lived.

All pioneers are expected to have the first two characteristics but not all pioneers have all the others in the list.

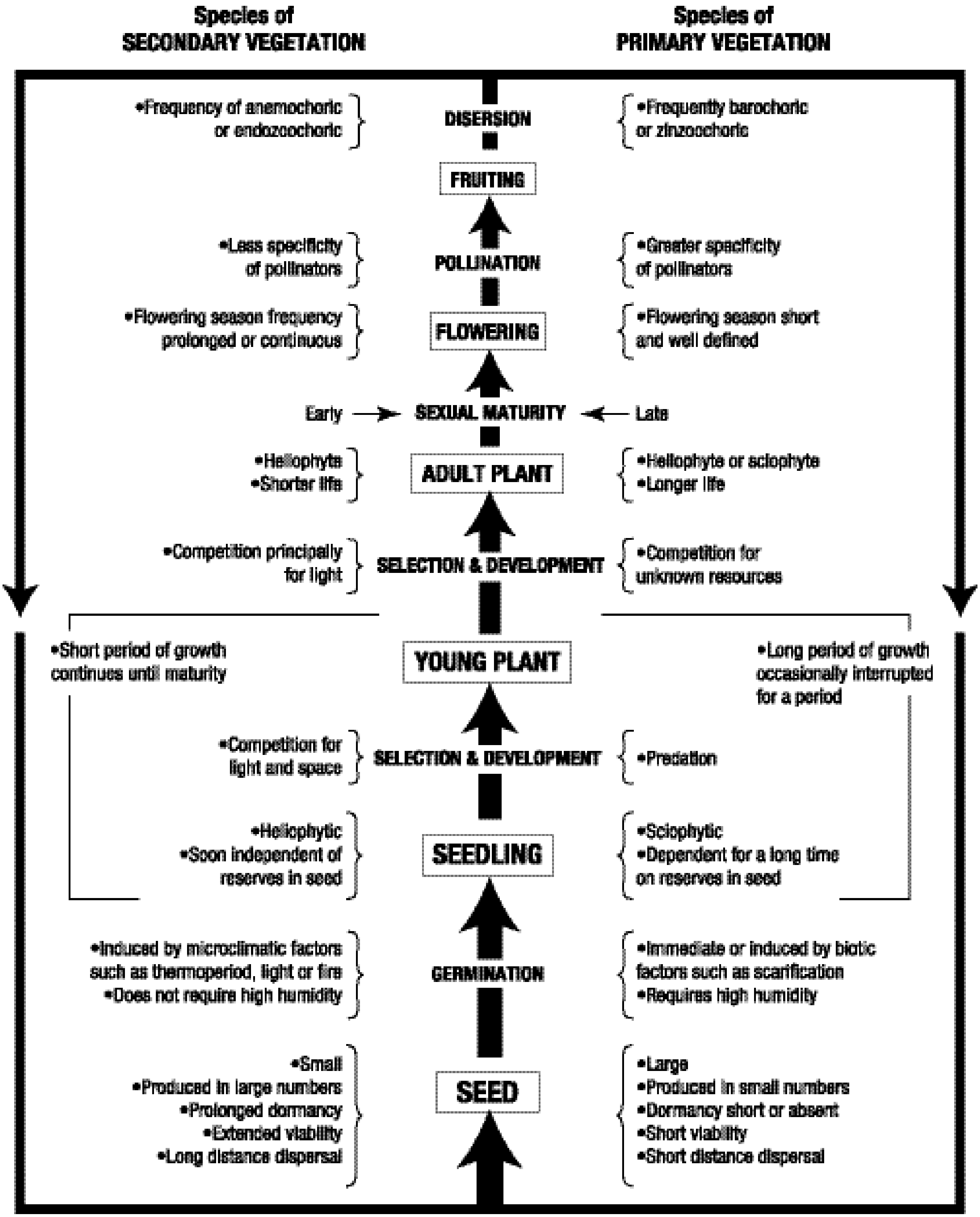


Fig. 5. Life cycle of secondary and primary plant species of tropical forests. Each step of the diagram can be isolated for research purposes. From Gómez-Pompa and Vázquez-Yanes (1974).

Successional viewpoints of tree life cycles consider the role of the species in the recovery from disturbance. Historically, this recovery has been viewed primarily in the context of gap-phase regeneration in tropical moist, wet, and rain forests. Secondary species respond to disturbance (light gaps) by increasing local numbers. Secondary species are ephemeral in space and time. Populations of primary or climax species become predominant long after a disturbance event or persist through a disturbance, recovering after the disturbance through direct regeneration (Yih and others 1991, Zimmerman and others 1994). We present a guide (fig. 6) for some of the schemes used to classify tropical trees according to successional functional groups for the variety of tropical tree life histories discussed in the following pages.

Whitmore (1984b) formalized the description of the life cycle of tropical trees in the Far East by describing the development of trees from seeds to senescence. He described growth after formation of a gap as going through gap, building, and mature phases. This sequence summarizes the model of gap phase dynamics from beginning to end. However, Whitmore cautioned against the generalization that gap-phase and mature-phase species can be identified, because a tropical rain forest has a suite of species that can complete their life cycles along a gradient of conditions from closed forest to very large gaps. Gap size is critical in determining the microclimatic conditions that seedlings face in developing into trees. Species can be categorized by their light demand or shade tolerance and their capacity to growth through the tangle of competing vegetation that invades forest gaps. Whitmore identified two types of pioneer species: short-lived, which mature in 10 to 30 years, and long-lived, which mature after 80 years. However, no sharp distinction exists between these two groups.

Whitmore (1984b) arranged 12 tree species in the Solomon Islands into four groups according to their response to gaps: seedlings that establish and grow inside the canopy shade; seedlings that establish and grow inside the canopy but show

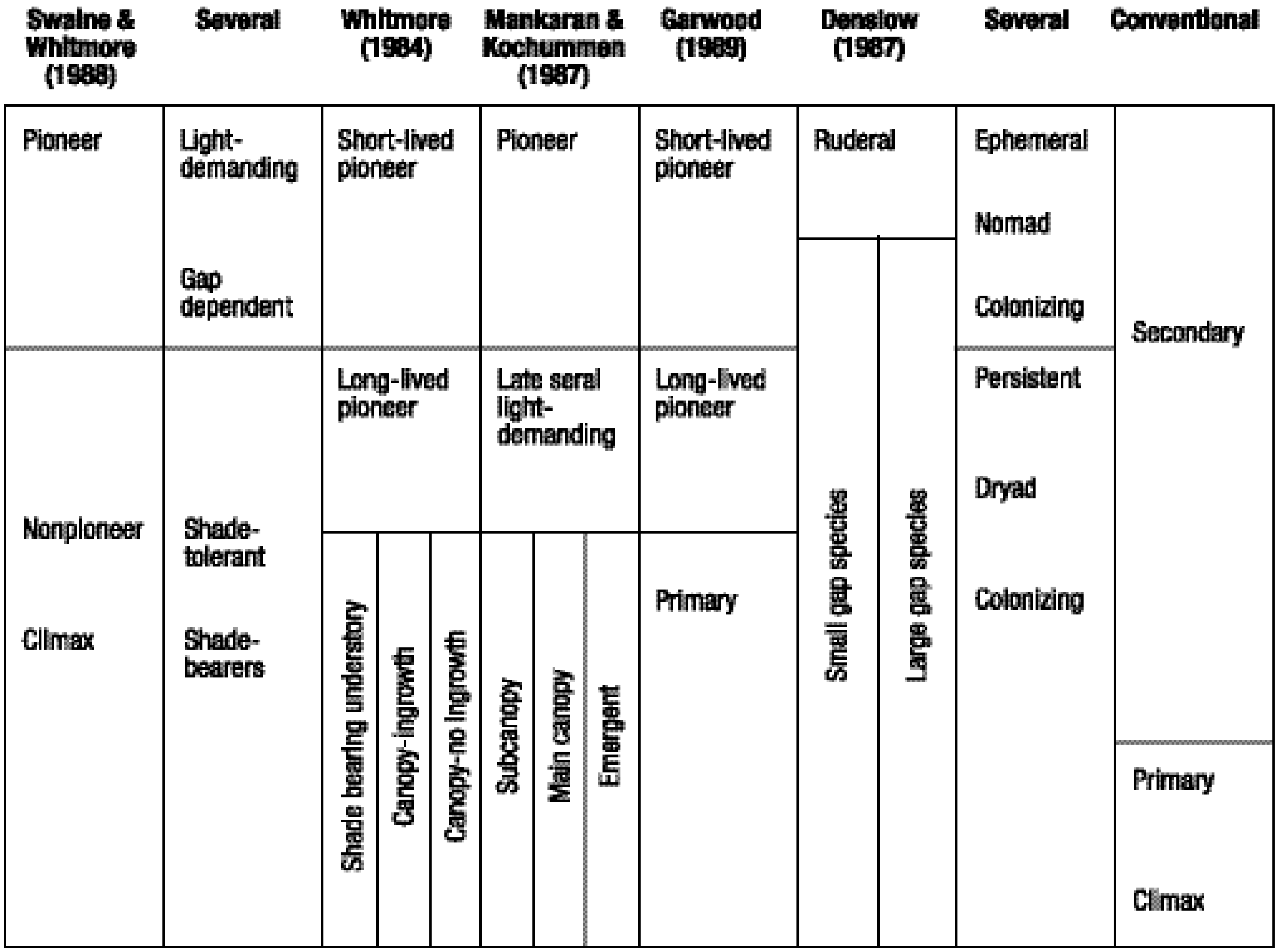


Fig. 6. Some common schemes used to classify tropical forest trees. Cross comparisons among schemes are only approximate and numerous exceptions exist (see text).

some signs of benefiting from gaps; seedlings that establish mainly inside the canopy, but definitely require gaps to grow; and seedlings that establish mainly or entirely in gaps and grow only in gaps (the pioneer species). This arrangement illustrates the continuity of response to environmental gradients.

Using tree mortality and recruitment data collected in Malaysia by Wyatt-Smith, Whitmore (1984b) grouped the trees of a mature forest into five groups according to life-history strategy: short-lived pioneer and long-lived pioneer species without recruitment under a closed canopy, shade-bearing or shade-tolerant understory species not reaching the canopy, canopy species without ingrowth, and canopy species with ingrowth (fig. 6). Ingrowth means that the seedlings of the population were able to develop into trees inside the canopy. This analysis showed that emergent trees were light demanding, and the main canopy species were strongly so. Shade bearers failed to reach the canopy. Periodic gap formations or large-scale disturbances create conditions for the regeneration of crown-dominant species.

A similar categorization was used by Manokaran and Kochummen (1987) for trees in long-term plots in a dipterocarp forest in Peninsular Malaysia (fig. 6). They placed species in five groups according to their characteristics: pioneer–short-lived tree species requiring a gap to germinate and establish, showing rapid growth, extremely light demanding, and intolerant of shade; late-seral–light demanding tree species but relatively tolerant of shade and prominent during the late stages of succession (can persist into the mature forest); emergents–mature phase, light demanding, long-lived species growing above the main canopy of primary forests to more than 30 m, usually with spreading crowns; main canopy–mature phase, light demanding, relatively long-lived species that form the main canopy of primary forest, growing to heights between 20 and 30 m; and understory–mature phase, shade-tolerant tree species forming the lower strata of the primary forest, with maximum heights below 20 m.

Garwood (1989) grouped life-history strategies into four regeneration groups to analyze the role of seed and seedling banks, advanced regeneration, and sprouting in lowland tropical forests (fig. 6). The four groups follow: (1) primary species–germinate and establish in the shaded understory of undisturbed forest; (2) long-lived pioneer species or late secondary species–germinate in shade or sun but grow only in forest gaps, are intermediate between short-lived pioneers and primary species, and dominate secondary forests but are also components of primary forests; (3) short-lived pioneer species–germinate and establish only in large forest gaps or human-produced clearings and are small-seeded, shade intolerant, and fast growing; and (4) weedy species (*sensu* Gómez-Pompa and Vázquez-Yanes 1974). Weedy species are not shown in fig. 6. These regeneration groupings were matched to six seed-bank strategies (transient, transient with seedling bank, pseudo-persistent, delayed-transient, seasonal-transient, and persistent (fig. 7), and the resulting matrix is shown in table 1. Rapid germination and short-term viability are found in all regeneration strategies, as are seasonal dormancy and annual dispersal frequency. Primary species are the only species with transient seedling banks. Long-lived pioneers and primary species are the only species with delayed seed germination, intermediate-term viability, and intermittent dispersal frequency. The diversity of regeneration and seed-bank strategy combinations is obvious, and the seed bank changes in density and composition through succession.

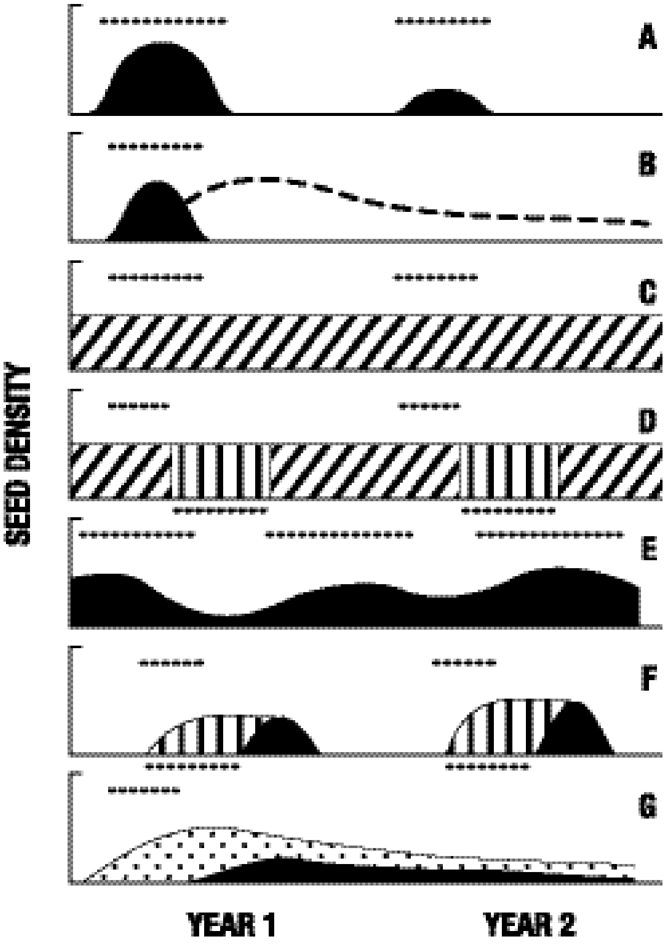


Fig. 7. Tropical soil seed bank strategies. (A) transient. (B) Transient replaced by seedling bank. (C) Persistent. (D) Persistent with periodic seasonal dormancy. (E) Pseudopersistent of fluctuating size. (F) Seasonal-transient. (G) Delayed-transient. Fruiting periods are denoted by asterisks, dry season by small open circles, seedling banks by dashes, germinable seeds without dormancy that must germinate or die, by black areas, seeds with seasonal dormancy by vertical lines, seeds with facultative dormancy under forest canopy by slanted lines, and seeds with delayed germination by stippling. From Garwood (1989).

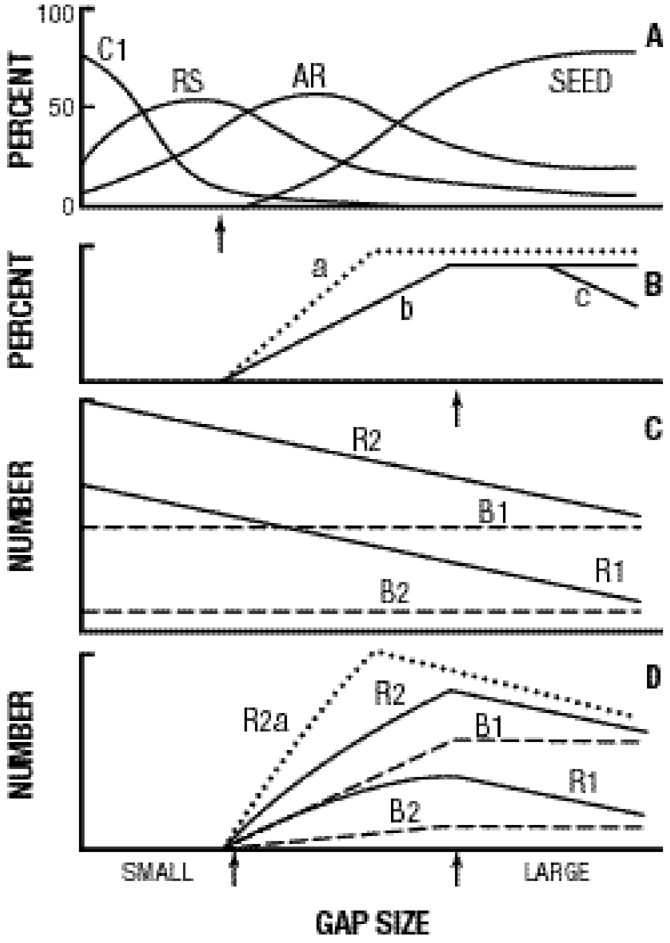


Fig. 8. Relationship of gap size to changing roles of different regeneration pathways in lowland tropical forests. (A) percentage contribution to regeneration from different pathways: canopy ingrowth (CI), root and shoot sprouts (RS), seedling bank and advance regeneration (AR), and seed bank and seed rain combined (SEED). The arrow indicates the minimum gap size for establishment of pioneers from seed. (B) Percentage of available pioneer seeds from the seed bank or seed rain that will germinate, successfully establish, and contribute to regeneration. The arrow indicates the gap size at which the maximum contribution to regeneration first occurs. The maximum contribution and gap size at which this occurs may differ among taxa (a vs. b). If mortality is greater in larger, more environmentally stressful gaps, the percentage of seeds contributing to regeneration will decrease (c). (C) Number of seeds available for regeneration at the time of gap creation. The number arriving in the seed rain (R1 or R2) will decrease as gap size increases because distance from forest edge and seed sources increases. The number of seeds in the seed bank (B1 or B2) will be independent of size of the gap just created. (D) Number of seeds contributing to regeneration from seed rain and the seed bank. Number contributing at each gap size is the product of number available (Fig. 8 C) and percentage contributing (Fig. 8 B: b for R1, R2, B1, B2; a for R2a). In B-D, percentage and number increase in arbitrary units along the axes. From Garwood (1989)

Gap size influences regeneration pathways in lowland tropical forests (fig. 8). Garwood (1989) proposed an increased dependence on seed rain and seed bank, and a sharp reduction in the role of root and stem sprouts as gap size increases. Advanced regeneration (AR) peaks at intermediate gap sizes (fig. 8a). Pioneer seeds are increasingly capable of germinating and completing their life cycles with increased gap size, unless environmentally stressful conditions develop in the large gaps (fig. 8b). Seed rain decreases with increased gap size as dispersal mechanisms limit seed rain in the very large gaps (Greene and Johnson 1995, 1996), but the number of seeds that can germinate in the seed bank is independent of gap size at the time of gap formation (fig. 8c). As a result of the previous two trends (figs. 8a and 8b), the number of seeds contributing to regeneration peaks toward large gaps and diminishes in the very large or small ones (fig. 8d).

Denslow (1980, 1987) suggested that most tropical tree species have different regeneration properties keyed to particular gap sizes, and that gap-size frequency distribution influences the types and richness of species in tropical forests. Life-history strategies for tropical forest trees could then be grouped according to light responses. She arrayed species in a continuum of light availability from high light requiring, shade intolerant, ruderal species; through light-requiring species with some shade tolerance; to highly shade-tolerant, slow-growing species. These categories conform to Grime’s ruderal, competitive, and stress-tolerant types, but Denslow noted that the resource (incident light) that regulates the response is always related to disturbance.

The light response of tropical trees is complex because light requirements change over the life cycle of individuals. These changes in turn have implications for life history groupings of trees (Augspurger 1984). In a study of gap-phase regeneration, Brokaw (1985, 1987) found evidence of gap-size specialization in only three of the many pioneer species he studied. Moreover, Clark and Clark (1992) showed that grouping of species according to the response of seeds and seedlings to light can differ when all stages of the life cycle are considered.

Gómez-Pompa and Vázquez-Yanes (1974) focused attention on secondary species, especially those with short lifespans which they termed nomads. Their life cycle model (fig. 5) contrasts secondary and primary tropical trees in life-history attributes such as periods of growth, lifespan, dispersal, pollination, flowering, time to reach sexual maturity, selection and development, germination, and seed characteristics. Although Gómez-Pompa and Vázquez-Yanes were using a dichotomy to contrast tree life histories, they segregated 21 life-history groups along an axis of successional time (fig. 9). A subsequent summary of demographic data for species in Mexico underscored the absence of a dichotomy between climax and pioneer species. Instead, a

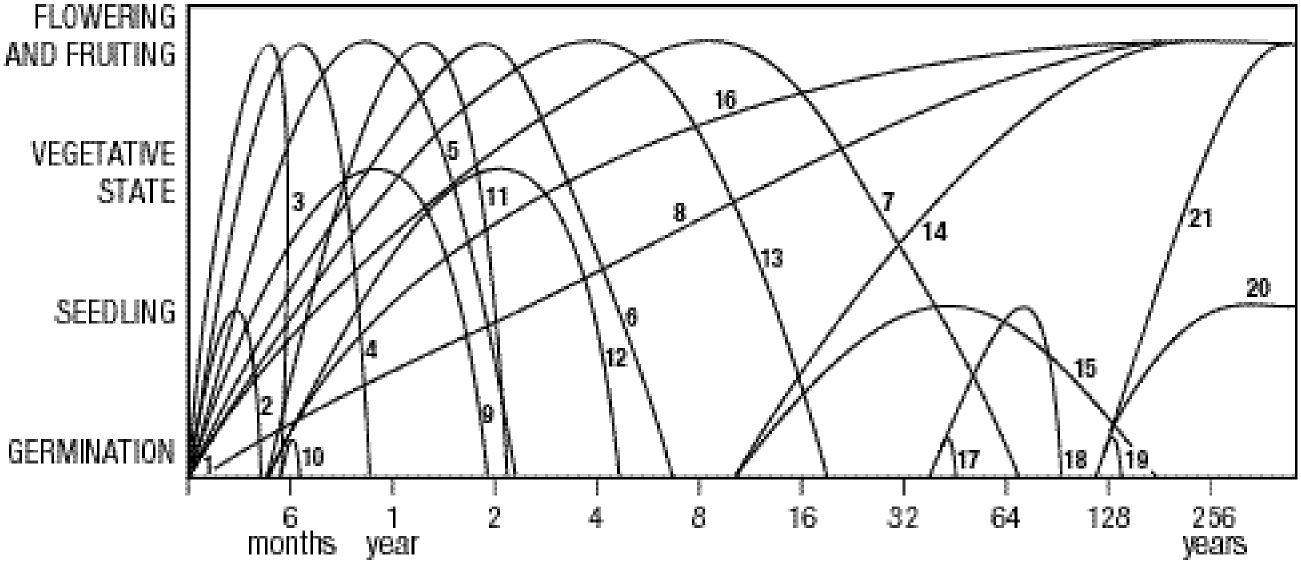


Fig. 9. A model of life-cycle patterns along a time gradient in the successional process. Each one represents a complete or an incomplete life cycle. (1) Species that germinate and die. (2) Species that germinate, produce a few leaves, and die. (3) Species that complete their life cycle in a few months. (4) Annual species. (5) Biennial species. (6) Species with life cycles of few years (<10 yr). (7) Species with a long life span, several decades, but eventually dying (species from old secondary forests). (8) Primary species with life spans of hundreds of years that have lived since the beginning of the succession. (9) Species that never reach the stage of sexual reproduction. (10) Species that germinate a few months after the succession begins and soon die. (11) Annual species that germinate after the succession begins. (12) Species that germinate after the succession begins but do not reach the stage of sexual reproduction. (13) Species with a short life cycle (<30 yr). (14) Species with a long life cycle that germinate when the succession is well advanced. (15) Species that germinate when the succession is well advanced and remain in the seedling or "young" plant stage for a few years. (16) Species that germinate a few months after succession begins and then have a life cycle hundreds of years long (primary species). (17) Species that germinate and die in old successional stages. (18) Species that germinate and live at the seedling or "young" plant stage in old successional stages, and then die. (19) Species that germinate and die in the primary forest.(20) Species that germinate and grow to a seedling or young plant stage inside the primary forest and remain there waiting for suitable conditions for continuing growth. (21) Species that germinate and grow in the primary rain forest and may reach reproductive stage after having long life cycles (primary species). From Gómez-Pompa and Vázquez-Yanes (1974).

continuum of tree life histories between these two extremes was found (Alvarez-Buylla and Martínez-Rámos 1992).

Gap processes appear to be a major determinant controlling which trees reach the canopy and form the mature stages of tropical moist, wet, and rain forests. Swaine and others (1987a) gathered evidence to show that fast-growing trees are more likely to reach the canopy and to have lower rates of tree mortality than slower-growing trees. They also found that large-diameter trees had faster growth rates than small-diameter trees. Hartshorn (1980) found that more than two-thirds of the tree species at La Selva, Costa Rica are shade intolerant and almost half of 320 tree species depend on gaps for their regeneration.

Clark and Clark (1992) observed that, for tropical wet forests, only one group of species has been clearly identified as sharing a common life history: short-lived pioneers *sensu* Whitmore (1984b). These species are characterized by high fecundity, small seeds, dependence on large openings for germination and establishment, high growth rates, short life spans, and high mortality in the shade (table 2). Representative genera are *Trema*, *Ochroma*, and *Macaranga*. Clark and Clark (1992) noted that the data are not sufficient to justify classifying the remaining tropical trees as shade tolerant or gap dependent, as if these categories were as well established as short-lived pioneer. The absence of documented operational criteria to justify the groupings limits grouping species by life-history characteristics. Clark and Clark list the following steps as needed to understand tropical tree regeneration: (1) evaluating requirements for germination and seedling establishment; (2) studying all juvenile size classes; (3) assessing performance in measured microsite conditions over the range of sites occupied by the species; (4) observing over a long term, particularly for analysis of suppression, survival, and microhabitat dynamics; and, preferably, (5) comparison of species in the same forest.

When Clark and Clark (1992) applied their criteria for 6 years to nine species in a wet forest of La Selva, they found that juveniles were associated with four patterns of microsite

Table 2

Character syndrome of pioneer tree species in tropical rain forest. Not all pioneer possess all the characters below the second listing.

From Swaine and Whitmore (1988).

1. Seeds only germinate in canopy gaps open to the sky and which receive some full sunlight.
2. Plants cannot survive in shade—young plants never found under a closed forest canopy.
3. Seeds small and produced copiously and more-or-less continuously.
4. Seeds produced from early in life.
5. Seeds dispersed by animals or wind.
6. Dormant seeds usually abundant in forest soil (especially fleshy-fruited species).
   Seeds orthodox (no recalcitrant species known).
7. Seedling carbon-fixation rate high; compensation point high.
8. Height growth rapid.
9. Growth indeterminate with no resting buds.
10. Branching relatively sparse.
11. Leaves short-lived.
12. Rooting superficial.
13. Wood usually pale, low density, not siliceous.
14. Leaves susceptible to herbivory; sometimes with little chemical defense.
15. Wide ecological range; phenotypically plastic.
16. Often short-lived.

occupancy. Among the six nonpioneer species that reached the canopy and lived as emergent trees when mature, two species were associated with low crown illumination and mature-phase forest in all juvenile stages. The two species with the smallest saplings were in predominantly low-light mature sites, but crown illumination and association with gap or building phases increased with juvenile size. Two species were strongly associated with gap or building phases as small juveniles and again as subcanopy trees, but were predominantly in mature-phase sites at intermediate sizes. Juveniles of two pioneer species showed the highest crown illumination and association with gap or building phases.

Clark and Clark (1992) concluded that life-history classification based on generalized concepts such as gap dependence and shade tolerance is inadequate to describe the complex size-dependent patterns of life-history differences and similarities among nonpioneer tropical tree species (*sensu* Swaine and Whitmore 1988). The task of elucidating the number of life-history strategies in tropical forests is daunting because the traditional dependence on seed and seedling behavior to make these determinations is inadequate; whole-life history and analysis are required to reach appropriate groupings.

Clark and Clark (1992) also observed that the regeneration of some emergent canopy trees was not gap dependent. Others have proposed (Denslow 1980, 1987) or found (Hartshorn 1978, 1980; Whitmore 1984b) that gap-dependent regeneration is common in tropical forests of the Neotropics and the Far East. These observations question the relative importance of high light adaptation (heliophytes) in the life history of mature and emergent trees in tropical forests. For emergent canopy trees at La Selva (Clark and Clark 1992), gap-dependent regeneration is not always as important as it is for other functional groups of species, such as pioneers or too many mature forest and emergent canopy trees in the wet forests of Puerto Rico (Zimmerman and others 1994). This difference brings attention to the importance of large-scale disturbances in the life histories of tropical trees.

ECOLOGICAL LIFE HISTORY IN RELATION TO LARGE AND INFREQUENT DISTURBANCES

Describing the life cycle of tropical trees commonly involves three phases (Hallé and Oldeman 1975). Phase I begins with germination, perhaps inside a gap, and continues until definitive morphological mechanisms and rhythms appear in the vegetative apparatus. Phase II begins when the specific vegetative architecture is qualitatively acquired; it proceeds as long as the young tree remains in the constant ecological conditions, often nearly optimal, that characterize tropical undergrowth. This phase can be called the microclimatic phase; the young tree can expand freely, sheltered from ecological traumas and directed by its genetic constitution. Phase III (influenced by macroclimate) begins when the tree, having acquired comparatively large dimensions, penetrates the canopy of the forest and, in full sun, develops a large, hemispherical crown of foliage. This narrative of tree development occurs in tropical moist, wet, and rain forests not subjected to large and infrequent disturbances. The absence of large and infrequent disturbances provides trees with ample time to reach and dominate canopy space.

Large and infrequent disturbances can significantly modify the chain of events implied by Hallé and Oldeman. Storms and hurricanes increase the area of canopy openings and can lessen the time the developing tree is protected from the macroclimate of the site. Vandermeer and others (1996) found that a hurricane in Nicaragua acted as a density-independent factor that eliminated competitive dominance of species, thus preserving species diversity by retarding competitive exclusion. In the following discussion we examine how large and infrequent disturbances affect ecological life histories of trees, and ask what effects they might have as agents of evolution.

HURRICANES, LANDSLIDES, AND OTHER LARGE AND INFREQUENT DISTURBANCES

Hurricanes, landslides, and other large and infrequent disturbances are significant because they can change the landscape or spatial matrix on which trees must complete their life cycles. Under the model of gap-phase dynamics, gaps are part of a large matrix of closed forests. Typically, about 0.7 to 1.2 percent of the forest area is converted to gaps annually (Denslow 1987), and gaps may cover no more than 10 percent of the landscape at any one time (Brokaw 1982, Hartshorn 1978, Lang and Knight 1983). Compared to sites subject to hurricanes or landslides, conditions for regeneration in gaps are fairly predictable (Denslow 1987). With the passage of a high-intensity hurricane, however, the landscape matrix is inverted, and gaps become the rule rather than the exception (Boose and others 1994, Brokaw and Grear 1991). Closed forest fragments can now cover less than half of the landscape. After these disturbances, microclimate and seed sources differ from those in normal forest gaps (Fernández and Fetcher 1991, You and Petty 1991). As a consequence, tree regeneration may take a different trajectory and involve species substitutions, especially if site conditions change significantly (Dittus 1985, Lugo and Scatena 1996, Walker and others 1996a). Processes are much faster. For example, tree mortality increases from 1 to 5 percent per year to 5 to 40 percent instantaneously (Lugo and Scatena 1996). Seedling abundance and temporal dynamics also change dramatically (fig. 10). Before the hurricane, seedling density in the forest as a whole averaged about 540 seedlings per ha (Smith 1970). Seedlings could reach densities of up to 1600 per ha, but they covered only 2 percent of the forest floor. After experimental disturbances, Smith (1970) counted as many as 3,000 seedlings per ha. Variability was high, with standard deviations ranging from 400 to 8,000 seedlings per ha. After the hurricane, seedling densities increased to about 55,000 per ha in highly affected areas (fig. 10a, b), and they covered the forest floor.

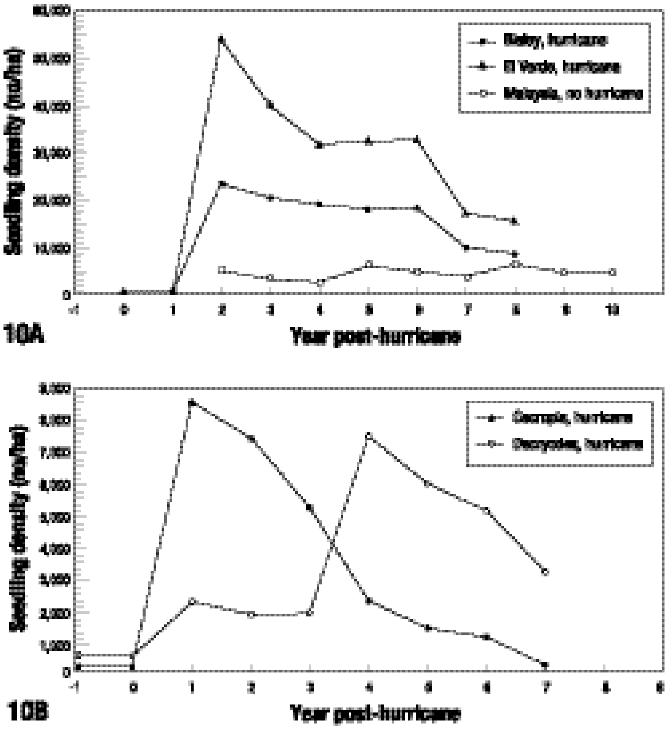


Fig. 10. A. Fluctuation of seedling populations of *Parashorea tomentellas* in Sepilok, Sabah and of seedlings after Hurricane Hugo in Puerto Rico. From Whitmore (1984) for Sabah from Brokaw, Haines, Walker, and Lodge, (unpublished) for El Verde, and from Scatena and others (1996) and Scatena (unpublished) for Bisley. The minimum seedling height for El Verde was 10 cm; for Bisley, it was 23 cm. **B.** Fluctuation of seedling populations of two species at El Verde, Luquillo Experimental Forest, Puerto Rico. *Cecropia peltata* is a pioneer species and *Dacryodes excelsa* is a primary forest species. **A and B.** Posthurricane data are from Brokaw, Haines, Walker, and Lodge (unpublished). Prehurricane data are from Lugo (1970) and Smith (1970).

Landslides occupy a small fraction of the landscape (<3 percent of a subtropical lower montane wet forest) (Walker and others 1996a), but they change soil and light conditions so

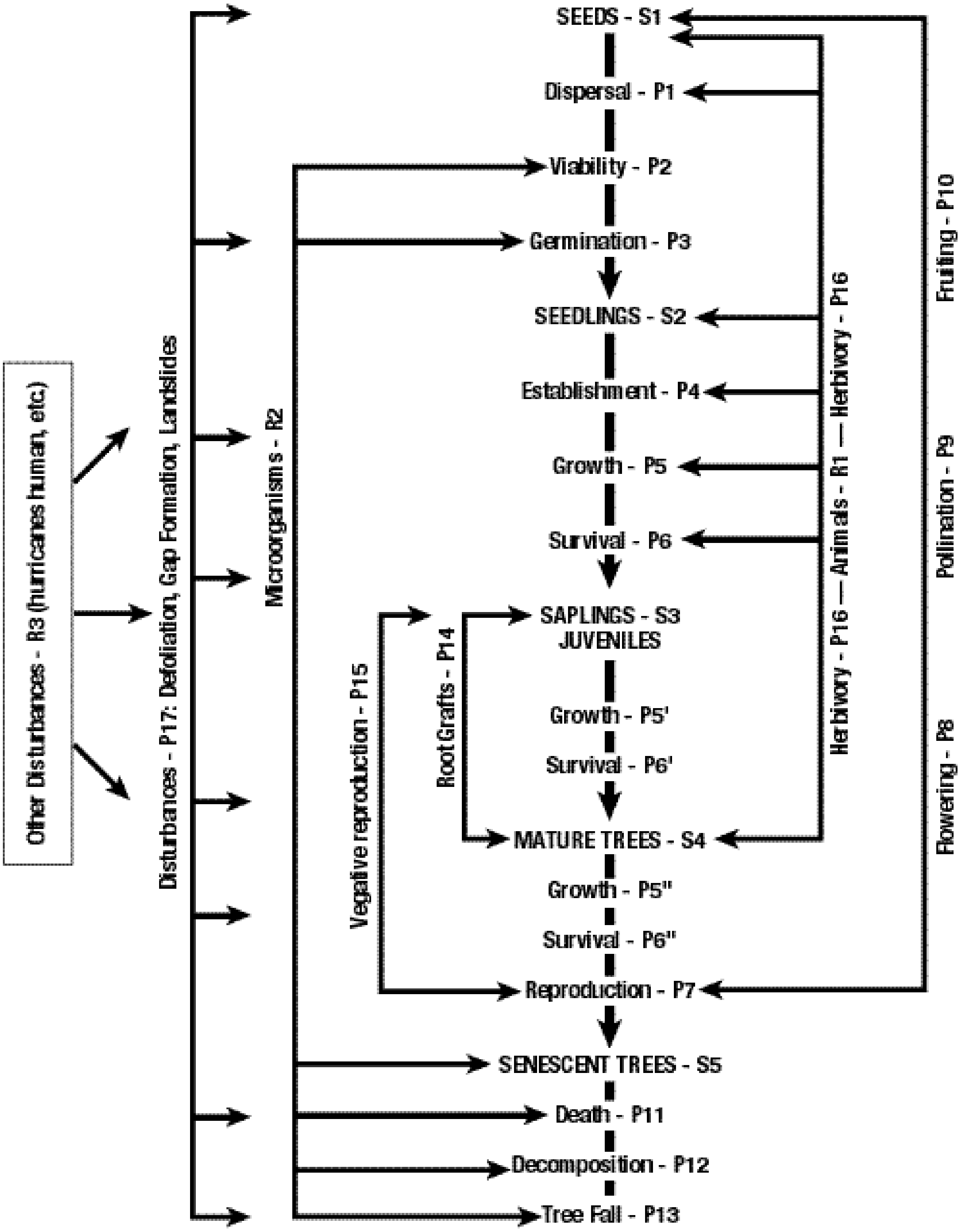


Fig. 11. Conceptual model of the ecological life-cycle of tree species in a subtropical wet forest in Puerto Rico. Life-cycle stages are S, processes are P, and population regulators are R. The number of each stage, process, or population regulator is shown after each letter code. From McCormick (1996).

much that different flora become established at the site (Walker and others 1996a). Succession can be arrested on landslides (Walker 1994), and tree establishment can be delayed, depending on the conditions of the substrate (Walker and others 1996a).

Human-caused disturbances associated with deforestation and site degradation also influence successional trajectory (Thomlinson and others 1996). Conditions for establishing species can be extreme, and, again, different species can invade as a result of human disturbances. When site degradation accompanies the disturbance, the possibility of invasion by alien species increases in both the seed bank (Garwood 1989) and the aboveground vegetation (Aide and others 1996). The reasons alien species tend to invade highly degraded sites but seldom invade undegraded natural areas are not clearly understood, but they have been the subject of much analysis (cf. Williamson 1996).

The Caribbean experience with its large, infrequent disturbances and degraded landscapes (Lugo 1996) provides a new dimension to the analysis of life histories of tropical trees because the classic work in the Far East (Whitmore 1984b) and Central America (Clark and Clark 1992, Gómez-Pompa and Vázquez-Yanes 1974) was conducted outside the hurricane belt in mature forests long removed in time from major disturbances. In the Caribbean and other parts of the Tropics, abiotic disturbances change conditions so much and so frequently that individuals must somehow complete a life cycle without the benefit of long periods of environmental stability. Life-history traits approaching those of pioneer species (*sensu* Swaine and Whitmore 1988) should be more common than those similar to shade-tolerant climax species. Similarly, the importance of heliophyte species and other life forms, such as vines, should increase. Differences between the climax and pioneer species may not be as wide ranging as those in tropical climates that do not experience large and infrequent disturbances.

RESULTS FROM WET FORESTS IN THE LUQUILLO MOUNTAINS

The tree species of the Luquillo Mountains have been classified as successional or primary according to their seed size, wood density, ratio of understory relative density to canopy relative density, and ratio of seedling relative density to canopy relative density (Smith 1970, Weaver 1995). Seed size and wood density indicators failed to produce a clear-cut dichotomy among species and yield; instead, the characteristics form a continuum, with pioneer and primary species characteristics at each end of the spectrum. The relative-density ratios of the understory and seedlings had some discontinuities that allowed three groupings of species among the 29 studied by Smith (1970). Weaver (1995) found similar results in his analysis of 20 species in a *Cyrilla racemiflora* forest. Weaver's results were notable because the dominant species in the forest (*Cyrilla*) was classified as a successional or gap species. When examining the response of tree species to Hurricane Hugo, Zimmerman and others (1994) found some evidence of a distinction between pioneer and nonpioneer species. Detailed study of the demography of more species as well as their role in succession might help explain why classifying species as pioneer or nonpioneer in the Luquillo Mountains is so difficult.

Building on the work of Pelton, McCormick (1995) developed a model of the ecological life history of trees in subtropical wet forests in the Caribbean (fig. 11). McCormick's life-cycle model was used explicitly to gather demographic data on a variety of tree species (Bannister 1967, Lebrón 1977, Muñíz Meléndez 1978, Sastre de Jesús 1979, Silander 1979, You 1991) to understand the role of tree populations in the plant community. The model includes five life-cycle stages from seeds to senescent trees, 17 processes (three associated with seeds, three with seedlings, two with saplings, three with mature trees, three with senescent trees, and six that feed back from one stage to a previous stage of development), and three classes of population regulators such as animals, microorganisms, and disturbances.

This model, like that of Gómez-Pompa and Vázquez-Yanes (fig. 5), is useful as a checklist for the kinds of measurements needed to evaluate the parameters of the life cycle of a species. In addition, McCormick's model includes disturbances as a regulatory process in the life history of tropical trees. Similarly, even though the importance and consequences of the three processes of tree senescence in the Tropics are poorly understood, they provide valuable insight into forest development and functioning (Lugo and Scatena 1996, Scatena and Lugo 1995).

Each of the six species studied (table 3) exhibits complex life-history traits with strategies that are considered pioneer in one stage of development and nonpioneer in another. *Manilkara bidentata* has deep-shade-bearing seedlings that survive for decades under a closed canopy and exhibit slow growth, but mature individuals dominate in the canopy. These traits suggest a nonpioneer strategy. However, *Manilkara bidentata* grows explosively after a disturbance, much like pioneers (You and Petty 1991). Even more notable are species that behave as primary species in some locations and as pioneer species in others (e.g., *Prestoea montana*) (Bannister 1967, Lugo and others 1995). The establishment of *Buchenavia capitata* (Sastre de Jesús 1979), a late-successional species, is furthered by hurricanes. The species thrives in riparian areas where continuous disturbances cause high turnover rates of individuals of all species (Scatena and Lugo 1995). *Palicourea*

Table 3

Summary of Ecological Life Cycles of Six Tree Species in the Luquillo Experimental Forest

	Cecropia peltata	*Prestoea montana*	*Buchenavia capitata*	*Palicourea riparia*	*Inga vera*	*Manilkara bidentata*
Stages						
Seed	Numerous (6.7 x 10^6 per individual), small (2 mm length), long viability (2 to 6 mo.). Germination favored by forest disturbance (76% vs. 0.3%)	Large (fruit approx. 1 cm, wt 0.07 g), numerous (mean = 1.4/m^2 throughout forest). Short viability. Long maturation (>3 mo). High predation.	Large fruit, high production (22.4 x 10^6/ha/yr), but high predation (>20% eaten by rodents).	Prolonged dormancy and viability.	Large, few survivors, and poorly dispersed. Poor viability (1 week of "dry days" = no germination).	Large and few (0.3/m^2); no dormancy.
Seedling	High survival in gaps (80% vs. closed forest 0%). Rapid height growth.	Relatively long-lived (3 x longer than mean for all species). Slow growth (mean height growth = 0.1 mm/mo in forest.	High mortality (86%).	Acclimate quickly to new light conditions.	Shade adapted but respond to increased light. Sixfold increase growth in gaps.	Very long lived (35 to 50 yr), shade adapted, and strong (survive burial by litter).
Juvenile	Rapid growth in gaps (max. 2.2 m/yr height and 3.0 cm/yr diameter.	High mortality (sapling survival is no greater than seedling).	High survival to maturity (59%).	Shade adapted.	Growth is light limited. High mortality (>99% from seedling to juvenile).	Low mortality. Very shade tolerant.
Mature tree	Growth shifts more to radial increase (mean = 0.6 cm/yr, max. = 1.5 cm/yr. Short-lived (<30 yr).	Intermediate life span (mean 61 yr). Intermediate reproductive maturity (25 yr). Long time to reach canopy (50 yr).	Apparent high survival (87%) once trees reach subcanopy (10 m or more, 30 to 50 yr).	Reproductive maturity within 2.5 yr.	Early senescence (35 yr).	Long lived: 50 yr to canopy >100 yr life span.
Process						
Germination	Requires light or disturbance (76% in gaps, 0.3 in closed forest).	Intermediate success (53%). Slow (3 to 6 mo).	During dry season, mesocarp removal requires 45 days.	Very low and limited by light (14% in gaps vs. 6% in forest).	Initially high (83%) but diminishes rapidly (20% after 3 mo). Restricted to gaps.	No dormancy, 42% germination of viable seed.
Growth	Explosive (trees ≥2 m/yr). Reach canopy <10 yr.	Shade-adapted, light- limited (10-fold greater in light, 10- fold greater growth).	Light limited. Seedling growth 3.7 cm/mo in gaps vs. 0.7 cm/mo in closed forest.	Rapid and extreme response to light. High photosynthetic rates but low quantum yield.	Light limited.	Shade adapted. Seedling growth >40-fold in gaps vs. forest.
Reproduction	Prolific (>10^6 seeds/yr/ tree). Wind pollinated. Early maturity (<4 yr).	Bee and fly pollination. High seed production (>5000/individual/yr).	Prolific seed production (448,000/tree/yr). Wind damage to flowers.	Pollination by bees and hummingbirds. Light-limited (95% fewer seeds produced in forest vs. gaps).	Vivipary results in high seed loss to predators. Prolific flowering but few seeds (one seed per 255 flowers). Damage by pollinators. Very inefficient.	Late maturation. Bee pollination. Few seeds/fruit. Few seeds produced.

Table 3 (continued)

	Cecropia peltata	*Prestoea montana*	*Buchenavia capitata*	*Palicourea riparia*	*Inga vera*	*Manilkara bidentata*
Dispersal	Widely in forest (mean 300/m^2 throughout forest). Birds and bats.	Poor; birds and rats (density under parent tree 5.5m^2 vs. 1.4m^2 throughout forest).	Nearly nonexistent (5.2 seeds/m^2 under parent tree vs. 0.6/m^2 in forest.	Birds, well-dispersed.	Birds, rodents, and water. Very poor. No seed in forest except under parent tree.	Bat-dispersed seed (95% of eventual seedlings). High mortality under parent (70% over 3 yr).
Survival	Short-lived (30 yr). Gaps only.	Intermediate life span (mean 61.1 yr). Seed to seedling 53%. Seedling to juvenile 32%. Seed to mature tree 0.05%.	Furthered by hurricanes.	Light limited (77% in gaps vs. 53% in forest).	Seed and seedling survival very poor.	Long-term seedling survival >35 yr. High post-hurricane survival of seedlings provides recruitment to tree size class.
Phenology	Flower all year. Max. Jan. to Mar. Dry season.	Flower all year. Max. June to Sept. Max. fruit Oct. to Jan.	Flowering at leaf fall during dry season.	Reproduction all year but not prolific.	Max. fruit Mar.-June.	Extremely sporadic flowering, tree to tree, branch to branch.
Special Adaptations	Rapid growth. High reproduction. Good dispersal.	Prop. roots, shade-adapted.	Pollination benefits from leaf fall. Excellent wood quality.	Reversible acclimation to light. No ecotypes.	Vivipary and pollination very inefficient. Suspect loss of original pollinators and dispersal species	Bat dispersal to favorable sites. Long- lived seedlings and acclimation to increased light contribute to hurricane resistance. Benefits from hurricanes and bat dispersal.
Habitat Preference	Obligate gaps.	Boulder fields, ravines.	Throughout forest.	Gaps.	Mesic sites.	Excellent wood. Mesic plateaus and slopes.

riparia (Lebrón 1977) is a gap species that thrives after hurricanes and other disturbances, such as exposure to ionizing radiation, but grows as a small tree under the canopy of the mature forest. *Palicourea* reaches reproductive maturity in 2.5 years. *Inga vera* is a nitrogen fixer with vivipary, gap dependency in its early stages of regeneration and shade tolerance in the seedling stage (Muñíz Meléndez 1978). *Cecropia peltata* (now *C. schreberiana*) is a typical pioneer species throughout moist and wet forests in Puerto Rico (Silander 1979), but not in rain or floodplain forests or in pastures (Aide and others 1996, Frangi and Lugo 1998, Walker and others 1996b).

The following short summaries of the life-history traits of two species in the wet forests of the Luquillo Mountains illustrate some of the previous generalizations, show the complexity of life-history strategies, and highlight characteristics that could be construed as responses to a high-disturbance regime. The canopy tree *Manilkara bidentata* is considered a primary forest species based on its shade tolerance in the seedling stage, slow growth inside the forest canopy, high-density wood, large seeds, and few seeds (You 1991, table 2). Seeds have a short period of viability and no dormancy mechanism. Seedlings of this species are large, woody, and can live >40 years in the forest understory. Mature trees are also long lived. Saplings are shade tolerant, have a low mortality rate, and are considered the critical point of the life cycle (You 1991, You and Petty 1991). In spite of these characteristics, transplanted seedlings can grow up to 24 times faster in tree fall gaps than they grow in the shade (You 1991).

Table 4

Effects of Hurricane Hugo on the Life Cycle of *Manilkara bidentata*, a Primary Forest Tree Species

	From young to old seedling		From old seedling to sapling	
Parameter	Pre-hurricane	Post-hurricane	Pre-hurricane	Post-hurricane
Recruitment cost[a]	168.3	7.5	4.0	0.3
Transition period (months)	140	28	292	16

[a] Number dead/number recruited to next size class.

Source: You and Petty (1991); data from El Verde.

Hurricane Hugo caused a pulse in the mortality of large *Manilkara* trees (4 percent), young seedlings (61 percent), and old seedlings (30 percent) (You and Petty 1991). Mortality below the canopy was the result of crushing by wood fall and burial by litter. No flowers, fruits, or seeds were found for 9 months after the hurricane. As a result, new recruitment was expected to be delayed for at least 2 years after the hurricane. Those individuals that survived the hurricane, however, adjusted to new light conditions, grew faster, and moved into larger size classes with greater efficiency in less time than before the hurricane (table 4). Given the low mortality of the advanced life stages in this species, the hurricane actually increased the presence of *Manilkara bidentata* in the forest. Hurricane disturbance also boosted the number of saplings in the forest to higher values than before the hurricane. The result was that a single hurricane was sufficient to overcome both its own instantaneous effects and those of past selective logging on the populations. To take advantage of this disturbance event, the individuals involved changed from deep-shade tolerance to a strong, sun-adapted growth pattern, which required discarding old leaves and forming new ones (You and Petty 1991).

Dacryodes excelsa (tabonuco) is another primary forest species (Smith 1970). Its seedlings are shade adapted and incapable of adjusting to full sunlight (Lugo 1970). The seedlings depend on mychorrhizae for their establishment (Guzmán Grajales and Walker 1991) and respond positively to the presence of litter on the ground and negatively to its absence. During the 1960's and 1970's, finding saplings and poles of the species was difficult when the forest canopy at El Verde was closed and the forest was in an apparent steady state (Lugo and others 2000; Odum 1970). Many fruit crops were sterile year after year. Periodically, however, large seedling explosions occurred, with average seedling densities of 481 per ha (Lugo 1970). Seedlings were more common in ridges where densities reached 8,776 per ha ±1,240 in high years and 728 per ha ±307 in low years. In valleys, seedling densities reached 4,304 per ha ±1010 in good years and 2,334 per ha ±118 in low years (Lugo 1970). Without significant disturbances, tabonuco seedling populations have a half-life of 6 months and their growth is limited to increasing leaf numbers and some stem thickening (Lugo 1970). With canopy opening by Hurricane Hugo and closure 5 years later, seedlings, saplings, and poles became common (fig. 10b), although the peak densities lagged the hurricane by 4 years. In contrast, the pioneer *Cecropia peltata* peaked in seedling density less than 1 year after the hurricane (fig. 10b).

Seedlings of *Dacryodes excelsa* had more and larger leaves than before the hurricane, and height growth was explosive (authors' personal observations). We estimate that for the *Dacryodes excelsa* population at El Verde, seedling explosions occur at about 60-year intervals after major hurricanes. In the regeneration strategy of *Dacryodes excelsa*, seedlings are constantly turning over until a hurricane event creates the conditions under which a particular seedling crop will successfully reach the canopy, while in the *Manilkara bidentata* strategy seedlings survive the interhurricane interval in the forest as advanced regeneration.

Seedling populations of *Dacryodes excelsa* tend to concentrate on ridges (Lugo 1970) where adults dominate and form tree unions by interconnecting all individuals through root grafts (Basnet and others 1993). These tree unions effectively exclude competitors from these locations, which have the best aerated soils in the forest (Silver and others 1999). Tree unions provide effective resistance to wind storms because trees on ridges survive the highest winds observed in Puerto Rico (Basnet and others 1992, Scatena and Lugo 1995, Wadsworth and Englerth 1959). Another mechanism of wind tolerance is the disposal of branches during the storm, followed by vigorous resprouting after the event (Zimmerman and others 1994). As a result, many species in the tabonuco forest have low ratios of canopy area to stem area (Pérez 1970). Because the root connections of the tree union allow materials to interchange among trees, suppressed and dead trees and stumps resprout after the disturbance event (Basnet and others 1992, 1993; Scatena and Lugo 1995). This resprouting assures that the tree union will continue to exert dominance over ridge sites regardless of the fate of particular individuals within the union.

After hurricanes in Nicaragua and Puerto Rico, many species resprouted new branches from delimbed trunks within a few months of the disturbance, and this was an important component of post-hurricane recovery (Yih and others 1991, Zimmerman and others 1994). Yih and others (1991) called this resprouting direct regeneration, and Zimmerman and others (1994) showed how it was tied to plant life histories. Trees showed clear tradeoffs in hurricane damage and recovery. Many species had low mortality in the hurricane, lost many branches, and resprouted at high frequency after the hurricane. Pioneers suffered high mortality (30 to 60 percent of the trees >10 cm d.b.h.) due to high frequencies of broken stems; survivors exhibited low frequencies of sprouting. These frequencies, summarized using principal components analysis, suggested that the responses of pioneers were separate from those of the remaining nonpioneers. The primary differences, reflecting the tradeoffs mentioned above, fell along the first principal axis. This axis correlated with an index of shade tolerance for these same species, developed from data in Smith (1970), which indicates a connection between seedling and adult life-history traits.

RESULTS FROM LANDSLIDES IN THE LUQUILLO MOUNTAINS

Landslides expose large areas of mineral soil, depositing the organic surface soil at the bottom of the landslide. These two regions of the landslide often have differing successional trajectories because of different nutrient availability (Walker and others 1996a). Fetcher and others (1996) studied the growth and physiological responses of two pioneer and two nonpioneer species to fertilization in the exposed mineral soils of a landslide. The two nonpioneer species (*Manilkara bidentata* and *Palicourea riparia*) (table 2) responded to increased phosphorus availability but not to increased nitrogen, but the two pioneer species (*Cecropia schreberiana* and *Phytolacca rivinoides*) responded to both phosphorus and nitrogen. Pioneer species appear to be highly nutrient demanding, which might help explain why they do not successfully invade degraded sites. Landslides also pose conditions–hot and organic matter-free substrates with little soil structure–that are extreme for tree seed germination, but benefit from the establishment of ferns and other herbaceous species. These latter species can dominate the site for long periods while soils rehabilitate, resulting in periods of arrested succession (Walker 1994).

RESULTS FROM RAIN FORESTS IN THE LUQUILLO MOUNTAINS

In elfin and *Cyrilla* forests in the subtropical rain forest and subtropical lower montane rain forest life zones, excessive moisture and poor dispersal conditions create difficulties for plant regeneration (Brown and others 1983). Cloning, a regeneration strategy observed under these conditions, is seen in *Tabebuia rigida* at high elevations in the Luquillo Mountains. After observing a plane-crash scar in an elfin forest for 23 years, Weaver (1990b) suggested that these forests lacked pioneer tree species. The grasses that invaded the site were slowly being replaced by the previously common tree species without an intervening stage of highly abundant pioneer trees. Walker and others (1996b) found evidence to support the hypothesis that pioneer species do not grow in the elfin forest. After Hurricane Hugo, fertilized plots in low-elevation forests were dominated by *Cecropia schreberiana*, but the only species available to respond to increased nutrient availability in the hurricane-damaged elfin forest were grasses, which grew in great abundance. No pioneer tree species invaded after the hurricane. Lugo and Scatena (1995) interpreted this as allogenic autosuccession resulting from the wetland conditions of forests, such as elfin, palm, *Cyrilla*, and mangroves. Under these wetland conditions, species like *Prestoea montana*, *Tabebuia rigida*, *Cyrilla racemiflora*, and *Rhizophora mangle* can be interpreted as successional or climax species depending on where they grow (Lugo 1980, Lugo and others 1995, Weaver 1995).

RESULTS FROM DRY FORESTS IN PUERTO RICO AND CENTRAL AMERICA

Dry forest plants face conditions that are very different from those in moist, wet, and rain forests. In dry forests, plants do not appear to compete for light, but they must secure a reliable water supply under conditions of high air temperature, high atmospheric saturation deficit, and irregular and low amounts of rainfall. Seedling establishment and tree growth under these conditions require life-history strategies different from those that are successful in moist to rain forests (Bullock 1995; Castilleja 1991; Gerhardt 1994; Lugo and others 1978; Medina, in press; Molina Colón 1998; Murphy and Lugo 1986a, 1986b; Murphy and others 1995). The concentration of sap in dry forest species, which is high compared to that of species from moist to rain forests, tends to increase with aridity (Medina 1995). This concentration allows dry-forest trees to secure water from soils with low water content. Succulent tree species like *Clusia* sp. maintain lower osmotic pressures in their sap and survive dry forest conditions by storing water and conducting crassulacean acid metabolism (CAM) (Medina 1995). Bullock (1995) noted that, contrary to the situation in wetter forests, trunk size is a mediocre predictor of reproduction in dry forests. He also suggested that greater density of individuals may favor outcrossing in dry forests.

In spite of the water limitation in dry forests, plants there face a highly heterogeneous environment. The basis for environmental heterogeneity rests on edaphic gradients such as soil depth, fertility, and moisture, as well as seasonal variation in most environmental factors including rainfall. Medina (1995) has shown that dry forests harbor more plant life forms than do moist to rain forests. Each of these different life forms has different metabolic strategies (from evergreen to deciduous to succulent), different functional attributes (Ewel and Bigelow 1996), and different life-history characteristics. Unfortunately, this diversity of ecological life histories has not been documented in detail. Molina Colón (1998) classified dry forest species into pioneer or primary based on propagule size, fruiting periods, soil conditions required for germination, shade tolerance, gap size preferences, growth rates, and length of vegetative period. With these criteria, she placed *Leucanena leucocephala, Croton astroites, C. rigidus, Guazuma ulmifolia,* and *Lantana arida* as pioneer species, and *Bursera simaruba, Bucida buceras, Machaonia portoricensis,* and *Eugenia fortida* as primary species.

Seeds in the Guánica Forest, Puerto Rico, are dispersed primarily by birds and ants and germinate only when adequate moisture is available (Castilleja 1991). The seed bank is low in number of seeds and species represented (Castilleja 1991, Molina Colón 1998, Murphy and others 1995). Seedlings are uncommon on the forest floor and limited to shaded sites. Seedling recruitment is an infrequent event and most trees can coppice by either roots or stems (Dunevitz 1985, Dunphy 1996, Ewel 1971, Molina Colón 1998, Murphy and others 1995). Most life-history events in the Guánica Forest (such as flowering, fruiting, leaf fall, leaf growth, tree growth, and seed germination) are synchronized with the cycles of rain and drought (Murphy and Lugo 1986a, 1986b; Murphy and others 1995). However, because access to water differs in these areas, some trees may have a complete complement of green foliage, flower in the midst of extended drought, and be completely deciduous.

Castilleja (1991) compared the seeds from the Guánica Forest with those from Luquillo (dry vs. wet forest) and found that dry-forest seeds tend to be remarkably small. Although fruiting seasons occur, they do not appear to be timed as a moisture avoidance mechanism, as they are in Costa Rica (Frankie and others 1974). Seeds are dispersed by birds year round, which represents a positive adjustment to highly variable rain. In other tropical dry forests, seeds are predominantly wind dispersed (Frankie and others 1974). Seeds in Guánica Forest have impermeable coats and delayed hypogeal germination; they germinate in response to adequate moisture supply. Seedling density varies according to forest cover, increasing in closed-canopy deciduous forests and decreasing toward the cactus scrub. Seedling banks, like seed banks, are sparse and reflect the canopy dominants. Seedling recruitment is very infrequent and responds to moisture availability. One species, *Bursera simaruba*, showed higher recruitment rates and growth rates when emerging from crevices on exposed limestone; it grew faster in exposed areas than in shaded locations where other species tended to grow better. Most species in Guánica Forest avoid drought, and both the seedling and seed banks fail to exhibit the abundance and diversity of trees in the overstory (Castilleja 1991, Molina Colón 1998). These findings highlight the importance of resprouting as an important regeneration strategy in this forest (Dunevitz 1985; Dunphy 1996; Ewel 1971; Molina Colón 1998; Murphy and Lugo 1986a, 1986b; Murphy and others 1995).

In dry forests with greater rainfall and deeper soils than in the Guánica Forest, the forest is taller (Murphy and Lugo 1995), and seedlings are larger and represent a more diverse group of species. More moisture, shade, and nutrients are available, which allows for a more diverse set of strategies for seedling establishment and growth. Gerhardt (1994) studied seedling development strategies for four tree species (*Hymenaea courbaril, Swietenia macrophylla, Manilkara chicle*, and *Cedrela odorata*) and found significant differences in their response to light and moisture. Drought was the main cause of mortality, and some species invested in developing deep root systems before elongating. Root competition increased the effect of drought and when it was reduced by trenching, seedling development was improved. Some evergreen cover reduced mortality during the dry season. Thinning the canopy benefited *Hymenaea courbaril* and *Swietenia macrophylla* but lowered the survival of *Manilkara chicle* and *Cedrela odorata*. Attaining large seedling size before the onset of the dry season improved the chances of survival. *Hymenaea courbaril* and *Swietenia macrophylla* established well in pastures and young secondary forests. *Manilkara chicle* had low survival in these environments, and *Cedrela odorata* failed in most environments, limiting its recruitment to wet years.

CONCLUDING REMARKS

Available results suggest notable differences when species from contrasting forest types are compared (i.e dry forests with moist to rain forests, or wetland forests with nonwetland forests) as well as differences of degree between forests with similar climate but different disturbance regimes (i.e. wet forests having only tree-fall gaps, with wet forests subjected to hurricanes). These differences are presented below as generalizations, but they actually represent hypotheses to be tested through further research.

The major difference between dry and moist forests is the overwhelming role of water in dry forests versus that of light in moist, wet, and rain forests. Tree life histories in tropical dry forests are thus more responsive to water than they are to light, and the opposite is true in moist to rain forests. Timing and rate of life-history processes are synchronized to intensity, timing, and variability of rainfall in dry forests; but in moist to rain forests, the life histories are synchronized to intensity and duration of incident light.

In wetland tropical forests, low soil oxygen is a factor that influences seed germination and, as a result, life-history traits include vivipary, seedling banks, absence of seed banks, cloning, adventitious tissues, pulsed regeneration tied to favorable periods, frequent sprouting, and short successions culminating in autosuccession.

Life histories of trees influenced by hurricanes are characterized by short life spans, early age of first reproduction, leaf heterophylly, ability to change quickly from shade tolerance to shade intolerance, advanced regeneration, conspicuous sprouting, tree unions, and low crown-area to stem-area ratios. As stressors increase (from moister forests without hurricanes, to forests of the same climates with hurricanes, to wetland forests), the number of species capable of completing their life cycles decreases.

The sequences described in figure 8 for gap dynamics do not apply to sites with hurricane regeneration, in part because the conditions after a hurricane differ from those predicted for large gap size. In large gaps, advanced regeneration and resprouting are supposed to be at minimal values, but after a hurricane, these two mechanisms of regeneration achieve predominance. Moreover, compared to sites with gap-phase dynamics as the main disturbance regime, the time available for uninterrupted growth is dramatically reduced in sites with large and infrequent disturbances. Interruption of growth conditions may act as a selective force for life-history traits that include shorter life spans, earlier reproductive age, smaller biomass accumulation, sprouting, and morphological and physiological plasticity in early stages of the life cycle. Similarly, the observed changes in species and life-form composition in landslides and sites degraded by human-caused factors signal the limits of adaptation of the life histories of normal tree species. These changes also suggest the selection of more extreme biotic adaptations for establishment and survival in these disturbed environments, perhaps analogous to the concept of the supertramp in birds (Arendt 1993).

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CHAPTER 8

Ethnobotany

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American botanist J. W. Harshberger first defined the term "ethnobotany" in 1896 as "the studies of plants used by primitive and aboriginal people" (Balick and Cox 1996). Since then, many attempts have been made to provide a descriptive definition (Bennett 1997). In broad terms, ethnobotany is the study of the relationship and interactions between plants and people (Balick and Cox 1996). This field of study analyzes the results of indigenous manipulations of plant material together with the cultural context in which plants are used (Balick and Cox 1996). It includes collaboration with disciplines such as ecology, chemistry, anthropology, economics, and linguistics (Prance 1991). However, the amount of interdisciplinary work done in ethnobotany needs to be increased in the future (Martin 1995, Prance 1991).

HISTORY OF THE USES OF PLANTS IN TROPICAL AMERICA

The use of plants by indigenous Americans dates back more than 10,000 years (Hoyt 1992, Porter 1981). Man was largely a predator of the fauna and a gatherer of the surrounding flora: grains for food, bark for clothing, and probably herbs for medicine. The first deliberate planting of seeds was probably the logical consequence of a simple series of events (Raven and others 1992). People who gathered grains (fast-growing weeds) probably spilled some of them accidentally near their campsites or maybe planted them deliberately and created a more dependable source of food (Raven and others 1992). Domestication, selection of parent material, and irrigation played a major role in the development of agriculture (Smith 1967), which in any form implies favoring useful plants over nonuseful within a particular culture. From the time he first conceived agriculture, man began important changes in his relationship with plants and engaged in ethnobotany.

FOODS

The region we now know as Mesoamerica (which includes central and southern Mexico, Guatemala, Belize, El Salvador, Honduras, and northern Nicaragua) has been the source of genetic resources in modern agriculture for many fruits and vegetables (Hoyt 1992). Seeds of many species of gourds and squashes from 6000 B.C. have been found in ancient Mesoamerican settlements. These well-preserved seeds record in some measure the history of agriculture and development of cultures in the New World (Cutler and Whitaker 1967). For example, it has been shown that seeds of *Cucurbita pepo* (Cucurbitaceae) were eaten with sugar obtained by the action of an enzyme. This food, called "pepitoria," is still eaten by natives of Mexico and Guatemala with the only difference being that now the sugar is obtained from sugar cane (*Saccharum officinarum*), a well-known plant introduced from New Guinea (Davidse and others 1994) by the Spanish colonists.

Another important plant of American origin is maize (*Zea mays*, Poaceae), one of the world's most productive plants, which accounts for a large percentage of the global food production. This cereal was planted in Mexico as early as 3000 B.C., although ancestral forms dating back to 5000 B.C. have been found in Puebla (Mangelsdorf and others 1967). Maize formed the agricultural basis of all the major New World civilizations: the Maya, Aztec, Inca, and Anasazi. This crop was also used as a main source of food by all the European explorers and conquerors who came to America. Mangelsdorf and Reeves (1943) suggest that without maize the colonization would not have been a success. It was and still is cultivated in association with beans and squash. Preparation methods for food made from maize vary, but one still finds handmade tortillas (maize patties made with limestone-treated grains) and stone-grinding slabs (metates) like those used by ancient Mayas (Sahagún 1582). A hot beverage called atole is made from mashed corn grains and is also probably of pre-Columbian origin. Maize was not only an important food crop but had religious significance as well; as the Mayan bible (Popol Vuh) tells, humans were formed from corn flour, and maize was represented too by many gods like Centlotl (Saenz 1988).

As many authors have stated, cacao (*Theobroma cacao*, Sterculiaceae) is America's contribution to the world as an important stimulating beverage (Coe and Coe 1996, Thompson 1956, Young 1994). The origin of the cacao tree is still debated. While some consider it as being from the Amazon (Smith and others 1992, Young 1994), others have stated that it is probably of Mesoamerican origin (Coe and Coe 1996). In any case, this "food of gods" (from *Theo broma*, the name Linnaeus gave to this species) was domesticated in Central America and was a valuable plant used as food and currency, as well as being a religious symbol for Olmecs and Mayas. A fossil record from an Olmec site in San Lorenzo, Mexico, dates its use to 1000 B.C., while the Dresden Codex has pictures depicting offerings of cacao fruit celebrating a new calendar year (Coe and Coe 1996). The Aztecs of Mexico and Mayans of northern Central America prepared a chocolate drink by pounding cacao beans with maize kernels, then adding boiling water with hot pepper chile. In the 1920's Wilson Popenoe reported that this traditional beverage was still served in San Cristobal Verapaz, Guatemala (Smith and others 1992). Cacao was not well received at first in Europe after the conquest, but as traditional spices were replaced by sugar, its popularity increased dramatically. Various techniques have developed to create chocolate liquor, cocoa, and chocolate as we now know it. One of the most famous is *dutching*, which uses pressure to extract the fat of the cotyledons, or *nibs*, yielding darker, milder flavored, and more soluble cocoa. About 90 percent of all cocoa used today is dutched (Simpson and Conner-Ogorzaly 1986).

MEDICINES

Long before Europeans came to America, native Americans, including Mayas, Aztecs, and Incas, had a well-developed understanding of plants, especially those used for medicine. The Badianus Manuscript (Emmart 1940), written by Martin de la Cruz in 1552, includes more than 200 species of plants used by Aztecs as medicine. Many of these plants are still in use today throughout America and some have even been naturalized in most tropical areas. Such is the case of *Psidium guajava*, a member of the Myrtle family (Myrtaceae) and mostly known as guava. This tree is most esteemed for its sweet-sour fruits used to make thick jelly or paste for desserts, but Aztecs and Mayas long ago prepared a decoction of leaves and bark of guayaba to treat gastrointestinal problems such as diarrhea (Emmart 1940). Today guayaba is known in every Mesoamerican and Caribbean country as a medicinal plant (Gupta 1995).

"Many American indigenous cultures lived, and still do, in tropical areas which are rich not only in plant diversity but fauna as well (Groombridge, 1992), and are threatened by encounters with a variety of dangerous animals such as poisonous snakes. Old manuscripts as well as current ethnobotanical information reveal that the use of *Dorstenia contrajerva*, of the mulberry family, (Moraceae) was and continues to be popular among tropical settlements (MacVean, 1995; Emmart, 1940) as an antidote to snake bites. Malaria, a disease caused by a mosquito-borne of the protozoan *Plasmodium* spp., is another example. Early in the 1600's during the conquest of the Inca empire many Spanish soldiers suffered from horrible fevers and Jesuits learned from the Incas that the bitter bark of a native tree was given as a beverage to treat fevers. Since then, the world has been indebted to the Incas that used the alkaloid, quinine, obtained from *Cinchona* spp. Today synthetic antimalarial drugs such as Fansidar (sulphadoxine perymethadine) and Aralen (cloroquinine) replace the need for quinine. Cinchona is still important in treating heart arrhythmias (Balick & Cox, 1996)."

OTHER USES

Narcotics

Coca leaves from the South American bush *Erythroxylum coca* (Erythroxylaceae) are valued by the people of the Andes region as a source of stimulatory alkaloids. From the Spanish conquest to the present, leaves have been collected, then dried for fermentation and chewed with lime, an agent that aids the absorption of alkaloids (Simpson and Conner-Ogorzaly 1986). These are taken to maintain blood sugar levels and alertness, to help travelers adjust to high altitude, and to reduce hunger pangs. Coca too was domesticated in pre-Columbian times. Archaeological findings show utensils and coca bags more than 3,000 years old (Furst 1972). Spanish conquerors tried to prohibit coca use until they realized that the Indian slaves would work harder if allowed to chew it. This plant was taken back to Europe and acquired fame with Angelo Mariani's wine, which contained extracts of the leaves. The Coca Cola Company originally used both *Erythroxylum coca* and *Cola nitida* (Sterculiaceae) to make its caffeine-rich, stimulating beverage, whereas today coca leaves, with the cocaine removed, are used to flavor the syrup from which this soda is made (Balick and Cox 1996, Plowman 1984, Simpson and Conner-Ogorzaly 1986). Due to cocaine-induced violence, the Harrison Narcotics Act was passed in 1900 in which the drug was declared illegal. Nevertheless, the abuse of cocaine has escalated to the point at which its legal use in medicine has become difficult (Balick and Cox 1996).

Materials

Since plant material does not preserve well in humid and tropical conditions it can only be speculated that ancient peoples used plants for shelter. The descendants of the Maya, for example, use palms as a source of construction material (Balick and Cox 1996). When visiting the Yucatán Peninsula, México, or Petén, Guatemala, the traveler can see that most of the small houses are still built with poles made from different native tree species. These poles are lashed with tough vines (most of them from the Bignoniaceae). The roof is usually thatched with palms such as *Sabal* spp. which currently suffers from great harvesting pressure as a resource for thatching (Caballero 1994), not only for small village housing but also for resort hotels and chalets.

CONSERVATION AND THE INVOLVEMENT OF INDIGENOUS PEOPLE

The examples above illustrate the richness of traditional knowledge about plants. This knowledge, inherited through many generations, can still be gathered in many regions, especially throughout Mesoamerica and South America, but the need to record it before it disappears is urgent. As biological diversity diminishes so does the cultural heritage of indigenous groups, where the elders are the ones with the most knowledge of the uses of plants (MacVean 1995). Finding new, nontimber alternatives and encouraging agroforestry practices to diminish the pressure on traditional agriculture is critical in developing neotropical conservation efforts (Martin 1995), which are essential if people are to continue to depend on the forest for sustenance.

For example, traditional practitioners provide up to 75 percent of the primary health care needs of rural people in Belize (Balick and Mendelsohn 1991). Setting an example for conservation through nontimber alternatives, the Association of Traditional Healers in Belize established a reserve for medicinal plants, located in the Yalbak region of Belize. Local healers gather medicinal plants from the reserve while scientists carry out ecological inventories as well as studies of regeneration of plants after harvest. To prevent habitat destruction and overharvesting of the supply of medicinal plants, the Ix Chel Tropical Research foundation has started a program to develop horticultural nurseries (Arvigo and Balick 1995, Balick and Cox 1996).

QUANTITATIVE ETHNOBOTANY

Historically, rain forests have been very profitable as sources of timber, whose harvest was a quick and simple way to obtain cash. The remains of the rain forest were burned. Today another form of forest destruction is slash and burn, a consequence of demographic pressure and the conversion of forested land to annual crops. However, ethnobotanists have pointed out that there are other viable and profitable alternatives to clearcutting. An interdisciplinary team from the New York Botanical Gardens led by Charles Peters did a 1-ha plot inventory of useful plants and estimated the net present value of harvesting fruits and latex at $6,330 (Peters and others 1989). Tree farming in countries such as Brazil gave yields of $3,184 per ha, while cattle pasture gave a net present value of $2,960. The yield from nontimber products is higher and provides a method of integrating the use and conservation of South American forests. Botanist Brian Boom has done similar quantitative ethnobotany with the Chacobo Indians in Bolivia and has found that 82 percent of the species on a hectare (75 of 91) were useful (Boom 1989, Prance 1991). In order to suggest a sustainable use of tropical forests, quantitative ethnobotany and density studies that include regeneration rates are necessary. To date, few studies of this sort exist for the Neotropics (Balée 1987, Balick and Mendelsohn 1991, Boom 1989, Di Stefano and Morales 1993, MacVean 1995, Peters and others 1989, Phillips and others 1994, Phillips and Gentry 1993).

PLANTS OF THE FUTURE

Plants for Food

Of the several thousand species of plants known to be edible, only about 150 have ever become important enough to enter into modern agriculture and commercial trade (Plotkin 1988). Foods used by natives since pre-Columbian times are mostly unknown, undervalued, and underutilized, which illustrates how developing countries are both biologically and culturally rich but are cash poor. Problems such as overpopulation and malnutrition are rampant. However, combining ethnobotanical, nutritional, and biochemical research efforts, scientists have found that the nutritional status of the rural poor can be improved by native plants. Such is the case for amaranth and a variety of pot herbs.

Amaranth

Amaranth (*Amaranthus* spp., Amaranthaceae) was a very important cereal during pre-Columbian times. Its decline can be attributed in part to the fact that early Spaniards forbade its use because the Mayans and Aztecs used it in religious services as well as for food (Balick and Cox 1996, Simpson and Conner-Ogorzaly 1986). Even though prohibited, amaranth flourished because of its hardiness and easy cultivation. Natives were nutritionally dependent on this plant mainly because it was a grain with high lysine content (Plotkin 1988). Central American grain amaranth species are not true grains but the fruit of the species, though their flavor and cooking procedures are similar to that of grains. This beautiful plant is still used by Indians throughout the Mexican and Guatemalan highlands. Amaranth has several features that make it appealing as a crop for developing countries: it is a plant that can flourish in arid environments, it can be easily harvested, and it has high protein content. The works of Ricardo Bressani, editor of the Amaranth Newsletter (Universidad del Valle de Guatemala) show that amaranth pasta, for example, has 30 percent higher protein value than regular pasta. The protein quality of amaranth is higher than that of any other cereal grain currently used in the human diet (Bressani 1997) (see table 1). Amaranth is currently being marketed in the United States as breakfast cereal and is now being sold in health food stores (Plotkin 1988).

Table 1

Protein Quality of Amaranth and Other Common Cereal Grains

Grain	Protein quality (% of Casein)	Reference
Amaranthus caudatus		
Raw	74.8*	Pedersen [and others] 1987
Popped	74.4*	
Drum dried	89.1	Bressani [and others] 1987
A. cruentus		
Drum dried	86.1	Bressani [and others] 1987
A. hypochondriacus		
Drum dried	85.0	Bressani [and others] 1987
Maize, lime cooked	45.0	Bressani and Marenco 1963
High protein grain		
Raw	72.6	Bressani [and others] 1990
Lime cooked	82.6	Bressani [and others] 1990
Sorghum, raw	30.6**	
Rice	60.0	Howe [and others] 1965
Wheat flour	26.0	Howe [and others] 1965
Oats	73.6	Howe [and others] 1965
Rye	52.0	Howe [and others] 1965

*Net protein utilization

**Relation nutritive value

Source: Bressani 1997, unpublished data.

Table 2

Composition Per 100 g of Fresh Edible Leaves in Mesoamerica

	Protein	CHO*	Fiber	Calcium	P	Iron	Vit A**	Vit B1	Vit B2	Niacin	Vit C	Energy
	(g)	(g)	(g)	(mg)	(mg)	(mg)	(mg)	(mg)	mg)	(mg)	(mg)	kcal
Chaya	5.2	10.7	2.4	244	71	2.2	2.5	0.2	0.4	1.6	350	64
Bledo	3.7	7.4	1.5	313	74	5.6	1.6	0.05	0.24	1.2	65	42
Chipilín	7.0	9	2	287	72	4.7	3	0.33	0.49	2	100	56
Macuy	5.0	7	1.4	199	60	9.9	0.2	0.18	0.35	1	61	45
Calabash	4.2	3.4	1.5	127	96	5.8	0.8	0.14	0.17	1.8	58	26
Spinach	2.8	5	0.7	60	30	3.2	1.2	0.06	0.17	0.6	46	30
Lettuce	1.0	3	0.5	16	23	0.4		0.05	0.03	0.3	7	13

Chaya = *Cnidosculus aconitifolius*
Bledo = *Amaranthus* sp.
Chipilín = *Crotalaria longirostrata*
Macuy = *Solanum americanum*
Calabash = *Cucurbita* sp.
Spinach = *Spinacea oleracea*
Lettuce = *Lactuca sativa*

*Carbohydrates
**Vitamin A activity
Source: Molina-Cruz [and others] 1997

Pot Herbs

Pot herbs such as chipilín (*Crotalaria longirostrata*), macuy (*Solanum americanum*), and Chaya (*Cnidosculus aconitifolius*) are underutilized in all of Mesoamerica. These native plants need special attention since they are highly nutritional alternatives to conventional vegetables in the human diet (table 2). They all have a high content of protein, vitamin B2, and vitamin C. They are also fast growing and well adapted to a wide range of altitudes. Both chipilín and macuy can be planted from seeds and chaya sprouts very easily from cuttings. It seems contradictory and ironic that plants such as lettuce and spinach, with much lower nutritional content, have been commercialized throughout the world while hardly anyone has ever heard of the much more nutritious and tasty chaya (Molina-Cruz and others 1997) (table 2).

Plants for Fiber

Fiber plants are second to food plants in terms of usefulness to humans (Plotkin 1988). People of the Tropics still use plant fiber for housing, hammocks, netting, baskets, and furniture (Balick and Cox 1996, MacVean 1995, Plotkin 1988). Promising American species include palms such as *Desmoncus* spp. (Arecaceae), the rattan of the New World. Many natives, including the Maya Itzá and Peruvian peasants, have started using this climbing palm, called bayal in Guatemala, to make artisanal products that include furniture and baskets. The stem from this palm is cleaned (de-barked), left to dry, and then shaped into beautiful handwork (MacVean 1995).

Ethnobotanists face many challenges in the future, especially because of biological and cultural loss. There is urgent need to document thoroughly, analyze, and sustainably use our biodiversity—involving local people, giving them credit and intellectual property rights to discoveries that result from information provided. Indigenous cultures, granted equal partnership with modern societies, are capable of leading their own future, helping us continue to discover the gifts of the relationships between plants and man.

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CHAPTER 9

Notes on Tropical Dendrology

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What is dendrology? The term dendrology (dendrología in Spanish) is a scientific and artificial word. It is derived from two Greek words meaning trees and discourse or study, or the study of trees. A review of the history of usage of the term has been made by William A. Dayton (Dayton 1945). Perhaps the first use of the word was in the year 1668 as the title of a book or encyclopedia on trees by Ulisse Aldrovandi, Italian physician and naturalist. The limits of the science of dendrology are controversial. Originally, dendrology included all aspects of trees, and in that time there was no science of forestry. Now, and especially in Europe, dendrology includes also the shrubs, but in the United States of America it is restricted frequently to trees.

In actual use, dendrology is limited to the *botany of trees* or precisely to the *taxonomy of trees*. It can be considered as a division of forestry or botany that treats of the taxonomy of trees. In some universities of the United States the subject matter of dendrology is taught by a professor of forestry, and in others by a professor of botany who is a specialist in taxonomy or systematic botany.

Dendrology, then, is a division of forestry or botany that treats of the taxonomy of trees and other woody plants, including *nomenclature, classification, identification,* and *distribution*. The subject matter in tropical countries should be called *tropical dendrology*, or the taxonomy of tropical trees, in order to distinguish it from a course in dendrology as taught in a university of the United States or Europe. Those countries and continents of the Temperate Zone have trees very different from those of tropical regions. A forester who has studied dendrology only in a forestry school in the United States knows very little about tropical trees, for example.

WHY STUDY DENDROLOGY?

The study of tropical dendrology has five principal objectives:

Nomenclature of trees—To learn how trees are named, including scientific names, common names, and the code of botanical nomenclature.

Classification of trees—To learn how trees are classified into families, genera, and other groups according to their arrangements. To learn the names and characteristics of the common and important botanical families of trees.

Identification of trees—To be able to place an unknown tree in its family. To learn how to find the name of unknown trees or to identify trees by means of keys, manuals, and floras. To know the reference books for identification of the trees of your country. To learn how to collect botanical specimens. To learn how to maintain and use a herbarium.

Distribution of trees—To learn how trees are distributed into climatic zones and forest types. To know the geographic distribution of important forest trees.

Important forest trees—To know the important forest trees of your country, including scientific names, common names, family, distribution and abundance, and uses.

REFERENCE BOOKS ON DENDROLOGY

There are very few textbooks on dendrology. In the United States of America there are a few, such as the Textbook of Dendrology by William M. Harlow and Ellwood S. Harrar (Harlow and Harrar 1950). Various manuals and floras of regions and States are used also. However, the books do not include tropical trees and are not useful in the tropical countries.

As *there are no texts on tropical dendrology* for the tropical American countries, these notes may serve as an introduction to the subject. References and texts on plant taxonomy have much material that relates to dendrology. Many of these are published in English and other languages, rather than in Spanish. Various books, pamphlets, and articles on the trees, woods, and plants of a country or locality are useful to foresters in that country.

WHAT IS A TREE?

Everybody knows what a tree is, but it is not easy to prepare a precise definition. It is possible to classify seed plants, or flowering plants, into four artificial groups on the *basis of size and habit of the stems*: *trees, shrubs, herbs,* and *vines*. The ancient Greek Theophrastus (372 to 287 B.C.), disciple of Aristotle and called the Father of Botany, distinguished trees, shrubs, and herbs. These artificial groups are not related to the natural classification of botany into the botanical families.

The definitions in *Forest Terminology* (Society of American Foresters 1944), translated into Spanish by M. A. González Vale as *Terminología Forestal* (González Vale 1950), are modified slightly here.

- *Tree* (árbol): A woody plant that has a well-defined, erect, perennial trunk and a more or less definitely formed crown and that generally attains a height of at least 12 to 15 feet (or 4 to 5 m) and a trunk d.b.h. of 7 to 10 cm (1.3 m).

- *Shrub* (arbusto): A perennial woody plant smaller than a tree, usually with several perennial stems branched from the base.

- *Herb* (hierba): A plant with an herbaceous or soft stem, annual or perennial, but not woody. (An herb can be annual or perennial or, in cold climates, have a stem that dies to the ground each year.)

- *Vine* (bejuco): A woody or herbaceous plant with the stems not erect but depending on other plants or objects for support.

PRACTICAL APPLICATIONS OF DENDROLOGY

Dendrology is like a tool or an instrument for becoming acquainted with and studying the trees. The names serve as a guide for referring to the trees. *Before making a survey of the forest resources of a tropical country, it is necessary to know the names of the species*. Always, foresters need to know the names of the important trees with which they work.

THE NOMENCLATURE OF TREES

Nomenclature is a division of taxonomy that treats of the names of plants, including the correct names, synonyms, and rules of nomenclature.

Trees, like other plants, have two kinds of names, common names and scientific names. Both are important and necessary, and both have their advantages and disadvantages.

Common names are in the *language of the country*. Their origin is an interesting subject. Some Spanish names of trees in tropical America are words used before by the American Indians. Others are the same as those of different trees in Spain. Perhaps the Spanish colonists gave these names to unknown trees of the New World that resembled trees of the Old World. Some common names are of other kinds, such as descriptive—from the use, from the environment, or from the region or place where the species is found. In the United States, other English common names are translations of the scientific name or given in honor of the discoverer or another person.

ADVANTAGES OF COMMON NAMES

(1) They are in the language known by the people.
(2) They are used by the country persons, woodsmen, people in general, and in commerce.

DISADVANTAGES OF COMMON NAMES

(1) They change in different places, countries, and languages.
(2) The same common names can be used for different species in different places, countries, etc.
(3) Many species do not have their own distinct common names. There are still unknown species without names.
(4) Many common names are not exact. Some species have

indefinite common names that correspond only to a genus or to a botanical family.

(5) There is no definite authority or code of rules governing common names and for making them uniform.

As they are in modern languages, common names are useful only in one language and change from one country to another. A useful tree species of extensive distribution can have 5 to 10 or more names in various localities and in commerce. For example, a tree of the West Indies can have an English name in Jamaica, a Spanish name in Cuba, and a French name in Haiti. And perhaps in the other islands, such as Puerto Rico and the Lesser Antilles, it has other names. If it extends to South America or Central America, the names can change more. Also, there is confusion because the same common name can be used for different species in various parts of its natural range.

Therefore, for exactness and clarity and to avoid confusion, the botanists and also the foresters are obliged to use the scientific names of trees.

ADVANTAGES OF SCIENTIFIC NAMES

(1) They are uniform in a universal system in use throughout the world.

(2) They are in the Latin language, which is the language of no country and, being a dead language, does not change through the years.

(3) They show the classification and relationships of the species.

(4) There is an International Code of Botanical Nomenclature with rules for scientific names and for naming new species.

DISADVANTAGES OF SCIENTIFIC NAMES

(1) They are strange and long.

(2) They are not used by the people.

The Latin language that was used by the scholars of past centuries was continued by the biologists for the scientific names of plants and animals. A few centuries ago the botanists were studying medicinal plants or herbs and wrote books with the descriptions and text in Latin. The Latin description of a phrase served as the name.

Carolus Linnaeus (1707-1778), the distinguished Swedish naturalist, established the binomial system of nomenclature in the year 1753. In that year he published in Latin his book *Species Plantarum* (Species of Plants), which is the beginning of modern botanical nomenclature (Linnaeus 1753).

The binomial system of nomenclature, or system of two names, means that the name of each species of plants consists of two Latin words, the genus and the specific epithet. (The same system is used for animals.)

For example, the scientific name of the species of mahogany of Central America and South America is *Swietania macrophylla*. To these two words the systematic botanists add the name of the author, the botanist who first gave this name to the species and published a botanical description of it. Thus, *Swietenia macrophylla* King. Botanical works should include the author's name. However, generally it is unnecessary to write or remember the author, and foresters seldom need to mention the author.

Scientific names are subject to definite rules. These rules are adopted and revised by the systematic botanists in international botanical congresses. The last congresses were at Stockholm, Sweden, in 1950, and at Paris, France, in 1954. The most recent edition of the rules is called *International Code of Botanical Nomenclature* (Lanjouw and others 1952). Minor changes or amendments were made in 1954 and will be incorporated in a revised edition.

Under the Code, the scientific names are in Latin or, if from other languages or of artificial origin, they have Latin endings. The generic name is a noun and begins with a capital letter. The specific epithet commences with a small letter and can be: (1) an adjective that agrees with the generic name in gender (masculine, feminine, or neuter), (2) a noun in the Latin genitive case such as the name of a person, or (3) the name of another genus or another plant in apposition. The two words are underlined in manuscripts or on the typewriter and are in italics in publications. In origin and derivation the scientific names are descriptive or otherwise, like the common names.

There are three very important rules in the Code. The *rule of types* states that a scientific name is based upon a specimen called the type. The identity is fixed with this specimen, which is kept in a large herbarium. According to the *rule of priority*, the correct name of a group is the oldest that is in accord with the Code. For example, in the past many species have been given more than one scientific name by different botanists working independently. Thus, there is only one valid name, the oldest, and the others are called synonyms. The *rule of homonyms* treats of homonyms or identical names. The same name cannot be used for two different groups, and if a name was used earlier for one group, it never can be employed for another.

From these rules it may be seen that scientific names are not perfect. Among the botanists there is no complete agreement in the names, their application, or their limits. Some species still have two scientific names in use in different books. However, the scientific names are much more distinct and clear than the common names.

PRONUNCIATION OF SCIENTIFIC NAMES

Being in Latin, the scientific names are pronounced like Latin words. The Latin language is pronounced almost like Spanish, and the vowels are similar in both languages. Then, it is simple and easy in Spanish-speaking countries to treat the scientific names as if they were written in Spanish. However, there are some names derived from foreign words, such as modern languages. These names are pronounced as in the original language, often with accent different from Spanish. The British and other Europeans pronounce scientific names correctly according to Latin, but in the United States these words generally are spoken as if English.

ABBREVIATION OF NAMES OF AUTHORS

The names of some authors are written in abbreviated form after the scientific names. Generally these are botanists who have named many species or who have long names.

Complete names of these persons can be found in glossaries of some botanical references. Usually the abbreviation stops just before the second vowel. An exception is that of Carolus Linnaeus, which is only “L.” For example, *Rhizophora mangle* L., mangrove or mangle. Also, there is seen H. B. K., for Humboldt, Boupland, and Kunth, as in *Byrsonima crassifolia* H. B. K., chaperro.

DOUBLE CITATION OF NAMES OF AUTHORS

Some scientific names of plants are followed by names of two authors, the first in parenthesis. For example, *Delonix regia* (Bojer) Raf., flamboyant-tree or flamboyán. This means that the first author gave the name of the specific epithet but in another genus or as a variety. Afterwards, the second author changed the name and put the specific epithet in this arrangement. In this case the earlier name, which also is now in use, is *Poinciana regia* Bojer. Some botanists regard *Delonix* as a genus distinct from *Poinciana* and others do not.

THE CLASSIFICATION OF TREES

Classification is a division of taxonomy that treats of the botanical arrangement of plants into groups, such as families and genera, in accord with the relationships.

This is the problem. There are approximately 350,000 known species of living plants. It is not possible to study and know them all one by one. How can they be arranged into groups for study, for compilation of data on the characteristics, and for organization of all this information? There are two kinds of classifications: artificial and natural.

ARTIFICIAL CLASSIFICATIONS

An *artificial classification* is a simple and convenient arrangement but is not done according to the relationships. It is like compartments or pigeonholes in a box or cabinet, one compartment for each species. The ancient Greek Theophrastus proposed the artificial classification previously mentioned. This arrangement of plants on the basis of stem habit as trees, shrubs, or herbs is useful and convenient. Foresters study mainly the trees, which form an artificial group.

Another artificial classification was the sexual system of Carolus Linnaeus, published in 1732. All plants were placed in 24 classes based upon the stamens: their number, union, and length. The classes were divided into orders, based upon the number of styles in each flower. This system served to identify specimens and was very useful in its time.

NATURAL CLASSIFICATIONS

A *natural classification* attempts to group together similar plants according to their relationships. After Linnaeus, other botanists proposed natural systems of classification of plants. In these works the species were arranged in natural groups such as families. The French botanist Antoine de Jussieu devised one of the first natural systems in the year 1789.

The modern classification of plants and animals is based upon the principle or theory of organic evolution. In 1859 the British naturalist Charles Darwin published his famous work, The Origin of Species (Darwin 1955). The principle of organic evolution means simply that the higher forms of plants and animals have developed from the simple or lower forms over millions and millions of years. Specialized plants have originated from primitive species. In other words, plant life has changed slowly during long periods of time.

Natural classification is based upon relationships through descent. Evolution can be compared with a tree. In theory, plant life began as a seed. Through millions of years it grew into a tree with many branches representing the plant kingdom. The buds correspond to the species that exist now, and the branches to the extinct or fossil species. Then, all the twigs on one branch belong to the same family and are related. But as the branches do not exist now, the relationships are not well known and are subject to differences of opinion among botanists.

There are many evidences and proofs to support the principle of organic evolution. Morphology, or the study and comparison of the form and parts of plants, is important. For example, those species with similar form or structure are thought to be related. Other evidences can be found in other subdivisions of biology such as anatomy, embryology, genetics, cytology, paleontology, and geographical distribution.

The methods of organic evolution are not so well understood. Among the theories is the theory of mutation (or of sudden changes in the hereditary variations) and the theory of natural selection (or survival of the fittest) by Darwin.

Probably the natural system of classification of plants most generally adopted by botanists at present is that of Engler and Prantl (1887), two German botanists, in their important work of 20 volumes entitled Die Naturlichen Pflanzenfamilien (The Natural Plant Families), which covers the entire plant kingdom. The most recent evidence indicates that perhaps this system could be improved. Nevertheless, it is the most detailed and convenient and is used in many large herbaria of the world.

Another important natural system also in use is that of Bentham and Hooker (1862-63), two British botanists, in their Latin work of three volumes, Genera Plantarum (The Genera of Plants).

THE CATEGORIES OF THE PLANT KINGDOM

In the natural classification, the species of trees and other plants are arranged into groups of small and large rank in a hierarchy. These groups of the plant kingdom are placed in categories. The categories are in Latin and also in modern languages. They are listed below in Latin, English, and Spanish, with examples.

Latin	**English**	**Spanish**
Regnum Vegetable	Plant Kingdom	Reino Vegetal
Divisio	Division	División
Classis	Class	Clase
Ordo	Order	Orden
Familia	Family	Familia
Genus	Genus	Génera
Species	Species	Especia
(Varietas)	(Variety)	(Variedad)

Latin Example	**English Example**	**Spanish Example**
Spermatophyta (Divisio)	Spermatophytes (Division)	Espermatofitas
(Subdivisio Angiospermae)	(Subdivision Angiosperms)	(Angiospermas)
Dicotyledoneae	Dicotyledons	Dicotiledóneas
Geraniales	Gereniales	Geraniales
Meliaceae	Mahogany family	Meliáceas
Swietenia	Mahogany	Caoba
Macrophylla	Central American	de Honduras

At the end, but not a category, is the individual (individuum in Latin and individuo in Spanish). Also, subgroups for other categories can be added in large groups as needed, such as the subdivision in the example above: subfamily, subgenus, etc.

The plant kingdom now consists of approximately 350,000 known species of living plants grouped into 19,000 genera. The division of Spermatophytes (phanerogams or seed plants) now contains 2 subdivisions, 7 classes, 45 or more orders, more than 300 families, more than 10,000 genera, and more than 250,000 species.

Then, the most important unit in the botanical classification is the species. Each individual, tree or other plant, belongs to a species and only to one particular species. It is difficult to define a species and also the other categories. It can be said that the *species* is composed of individual plants (or animals) that are similar in appearance and that can reproduce or breed among themselves and produce other individuals resembling the parents.

A *genus* is a *group of related species*. A *family* also is composed of a group of *related genera.* An *order* consists of a group of *related families*, etc.

The *variety* is a division or minor variation of a species or a group of individuals that differ slightly from the others. The majority of species have no varieties or are not divided into varieties. *Varieties are named, particularly in cultivated species*.

Scientific names of families and higher categories are plural, while names of genera, species, and varieties are singular.

The name of an *order ends in ales* and is derived from its type family. For example, geraniales is from the family geraniaceae, which is derived from the genus *Geranium*.

The termination of names of the botanical *families is -aceae*. However, the Code permits the use of eight exceptions with endings in *-ae*. For example, Palmae, Fabaceae, and Gutiferae. The name of a family is derived *from its type genus* or from a synonym. For example, Melisceae comes from *Melia*.

The subject matter of tropical dendrology includes the study of families of the important forest trees with distinguishing characteristics and examples.

THE IDENTIFICATION OF TREES

The identification of a tree consists of determining the correct scientific name, generally by means of manuals, floras, keys, etc.; or of determining that the plant or specimen is the same as a previously known plant with a scientific name. In these references a special botanical terminology is used for describing the differences in morphology or in the parts of the trees. For this reason, in the laboratory we study the terminology of the leaf, flower, fruit, etc.

METHODS OF IDENTIFICATION OF TREES

The question is: How to learn the name of a tree? There are several methods; in each case we should use the easiest, simplest, and most rapid method that also arrives at the correct name.

The Question

The simplest method of learning the name of a tree is to ask someone who knows the name. This method can be used anywhere. Whenever there is the opportunity, we should go to the forests with other foresters or botanists who know the species well. This method is very useful, particularly in a new region where many trees are strange. In the university and in the herbarium, as in the field, the question aids identification.

This method is especially important for learning common names, because many common names are not found in the books. The rural people who know well the trees of their locality have learned the names from other persons and not from botanical books. When in doubt, one should ask two persons, to see if both give the same name. Also, when the common name is known, it is frequently easy to obtain the scientific name of the genus or species in references on plants or woods.

However, there are limitations and disadvantages to the question method. (1) Other persons, including specialists, can be mistaken in the names and in the identifications. (2) In some localities there are no persons who know all the trees, especially the scientific names. (3) Many times foresters have to work alone and where there is no help in making the identifications. Therefore, foresters need to know how to identify trees and botanical specimens as well.

Books, Manuals, Floras, Catalogs, Keys, Monographs

Wherever there is a good illustrated manual of the region, as there is in various parts of the United States, one can look through the illustrations. This method, useful though not scientific, can waste time and cannot be employed where there are many tree species; an illustrated manual could not illustrate many species of minor importance.

These books generally are written by botanists for botanists and with the technical terminology of systematic botany. Thus, foresters in the study of dendrology should learn to read and understand these botanical books, which have numerous—perhaps too many—technical terms. There is a need for more popular illustrated manuals containing a minimum of technical terms and written for foresters and the public.

Therefore, we shall study in the laboratory the botanical terminology of the *leaf*, the *flower*, the *fruit*, and other parts of the trees, such as the *stem* and the *bark*.

A *flora* of a region generally contains botanical descriptions and keys. However, some tropical countries lack descriptive floras.

A *catalog* has a list of the species of a region, often with other notes. The Catalogo de la Flora Venezuela also has keys to genera.

A *monograph* is a study of a genus or family in a country or larger region. For example, Rubiaceae of Venezuela by Standley, and *Podocarpus* in the New World by Buchholz and Gray.

A *key*, like a key to a door, is a simple device for opening the way to the name, or an artificial device for finding rapidly the scientific name of a plant. This is much easier than reading many descriptions. The old botanical references of one or two centuries ago had no keys. In order to identify an unknown plant with a botanical book without a key, it is necessary to read the descriptions until reaching one that agrees with the plant. Thus, it is necessary to read half the book on average in the identification of a specimen.

The key is dichotomous, or with forks or branches two by two. It divides the plants of a book into groups of two or by halves until it arrives at the name that corresponds to the specimen. In a key there are pairs of contrasting short phrases, generally of a single line each. It is necessary to determine which of the two phrases agrees with the specimen. If the phrase contains two or more parts, all characters should agree with the specimen. Below the correct phrase is found another pair of contradictory phrases. The selection of a correct phrase is repeated until one arrives at the name. If there is a description, one should read it in order to check whether it fits the specimen. If it does not agree, probably there is an error and use of the key should be repeated by hunting another fork which leads to the correct identification.

There are keys to families and to genera within a family and to species within a genus. But unfortunately, in some tropical regions there are few keys to species. When there are two or more keys for use, it is simplest to use the shortest or that of the smallest region or with the smallest number of parts.

The *two kinds of keys are the indented key and the parallel key*. The indented key begins with the contrasting phrases of the pair at the left of the page, usually not together but separated by other pairs following a little more to the right. Generally there are number or letters to facilitate the comparison, but not in some short keys. Below each line the next pair is indented.

The parallel key always has the two contrasting phrases of the pair together, one directly below the other, and the position of the pairs that follow is indicated by numbers.

We should know how to use both kinds of keys, because both are found in reference books. Each has its advantages and disadvantages. The long keys of many pages usually are parallel and do not lose space as in an indented key with many short lines. The indented key generally is preferred because it is easier to follow, and if an error is made the correct branch can be found more rapidly.

The Herbarium

An herbarium is a collection of plant specimens, dried, pressed, mounted on cardboards, identified, and arranged according to a botanical classification. The specimens are placed in large cases or cabinets of steel or wood. Special ones are preserved by other methods such as large fruits in boxes and succulent plants or small plants in liquid.

The herbarium serves for the identification of botanical specimens and also for reference and teaching. Type specimens are the base of botanical nomenclature, and all the specimens together show the geographic distribution. The herbarium is the basis of many investigations and publications on taxonomy.

How is the herbarium used in the identification of trees? There are two principal methods:

(1) To verify the identification made by a key or a description in a botanical reference. It is much easier to compare a specimen with a named specimen than with a description.

(2) For comparison with specimens of various species. When there are no botanical references adequate for identification, the herbarium is very useful. For example, in a country that lacks a descriptive flora or keys to species, it is necessary to take the botanical specimens to an herbarium that has collections from the country or the region in order to find identified specimens of the same species.

Whenever the herbarium is used in identification, first the botanical references should be consulted. It saves time to identify the specimen as completely as possible with keys and floras beforehand. Time is lost in using the herbarium before eliminating many similar species with the books. The genus of most plants can be determined with the books of other regions.

If the specimen is poor or is not complete with flowers and fruits, it is difficult to follow a key. Then the herbarium can be examined by trial and error in search for identical specimens, but this method is slow.

In the identification of a dried specimen in the herbarium, frequently it is necessary to dissect the flower in order to study the parts. The dried flower can be soaked in hot or boiling water before examination. Then it will become soft and can be examined without breaking and nearly as well as when fresh.

Shipment of Specimens to a Large Herbarium

Instead of making his own determinations, the forester can send botanical specimens to a large herbarium for identification.

In order to facilitate the determinations and also to prepare specimens that will be preserved permanently in a large herbarium, foresters should know how to collect and prepare good specimens.

The principal advantage of sending specimens to a large herbarium is that the identifications by the specialists will be correct and in accord with the most recent studies.

The disadvantages are that it is necessary to collect and prepare botanical specimens, and that frequently there is a delay of some months or more than a year until the determinations are received. (Generally small collections are named faster than large ones.)

Before shipping the specimens for identification, one should always write and mention the number of specimens and the region or State where they were collected. Some herbaria do not have specialists in plants of certain parts of the world and are not interested in specimens from those countries. The service of identification is free, but in place of payment the herbarium keeps the specimens.

When there is a specialist working on a particular group, such as a family, and writing monographs on its genera, this botanist is the best authority on that group and can make the best identifications.

Many countries have national herbaria which vary greatly in size. The largest herbaria in the world are principally in Europe and North America. Extensive collections from tropical America are deposited in three herbaria in the United States: Chicago Natural History Museum, Chicago, IL; New York Botanical Garden, Bronx Park, New York City, NY; and United States National Museum, Washington 25, DC. Specialists from these and other herbaria in the United States have made extensive botanical explorations and collected many thousands of specimens in tropical America

THE COLLECTION OF BOTANICAL SPECIMENS

THE NECESSITY OF COLLECTING BOTANICAL SPECIMENS

In the identification of an unknown tree, a specimen is worth more than many words or notes. It is difficult to identify a tree solely from the notes written in the forest.

From time to time foresters need to collect some botanical specimens of the trees with which they work. If they do not know the trees in the forest, then they should preserve specimens for identification later or for shipment to a large herbarium or to a specialist for determination.

For example, on making an inventory of the forest resources of a region, numbers or common names can be used for the unknown trees. Then, specimens should be collected for later identification.

Systematic botanists have various methods of collecting specimens. However, foresters generally collect only a few specimens and can employ the simple methods. In an emergency a twig can be broken from a tree and pressed in a notebook, in the pocket, or in a book. But it is worth the trouble to collect good specimens and in the end the identifications will be better.

INSTRUCTIONS FOR MAKING COLLECTIONS

Collect Sufficient Material of Good Specimens with Flowers or Fruits

This is the first rule. Frequently, botanists are interested in collecting incomplete specimens of rare plants, but foresters are not. *A rare tree generally is unimportant in forestry.*

It is very difficult to identify correctly and completely a sterile specimen of a tree from only the leaves and twigs. Trees in various families have very similar leaves. Nevertheless, often unknown trees are found with neither flowers nor fruits, and it is necessary to collect sterile specimens. Possibly there can be found a tree flowering outside the regular season. If not, it is very useful to collect a wood sample from the same tree. Perhaps specialists in wood anatomy can identify the genus or family of the wood, and then botanists can continue the identification.

Collect at Least Two Sets

Two specimens should be collected from the same tree, one to keep and the other to send to the herbarium or specialist for identification. Also, a few additional flowers for dissection will be helpful. Whenever convenient, it would be useful to collect more sets. However, more time is spent and more equipment is needed in preparing the additional sets. In order to avoid a mixture of two species, all sets should be from the same tree.

Write Useful Notes in the Forest for the Label

A specimen without notes is not worth much either to the forester or to the herbarium. In the herbarium the notes on the label probably are worth more than the specimen. These notes include:

(1) **Name of the collector.**

(2) **Number of the specimen.** Each collector should use a series of numbers for convenience in his notes, in identification, and in the herbarium when later reference is made to the specimens.

(3) **Date.**

(4) **Locality.** The country, State, municipality, exact locality, or distance and direction from a city or from a point on the map.

(5) **Elevation above sea level.**

(6) **Forest type.** Associated species. Soil. Whether planted or wild.

(7) **Common name.**

(8) **Size and habit.** Height and diameter of the tree, or whether the plant is a shrub, vine, or herb.

(9) **Uses.**

(10) **Other notes.** Abundance. Color of the flower. Fruit. Bark and latex. Wood. Roots.

Naturally all these notes cannot be obtained for all specimens.

COLLECTING EQUIPMENT

It is difficult to collect botanical specimens of trees because the branches usually are high. In a search there may be located a small tree of the same species or a tree with low limbs on the edge of the forest. Sometimes the tree can be climbed or felled. Or leaves, flowers, and fruits fallen on the ground beneath can be found.

In obtaining specimens, tools such as knives, machetes, and axes are indispensable. Also, pruning shears and a pruning hook or pole may be used.

A notebook with pencil or pen, a hand lens, and a ruler or measuring tape are useful. So are field glasses and a camera.

It is important to carry the specimens from the forest to the office or base without losing parts, without damage, and without drying. Probably the best method is to carry a light press with old newspapers directly to the forest. Or the specimens can be placed in a canvas bag or wrapped in newspapers. Also, there are the large cans that are used with moist newspapers inside. For large fruits and seeds, paper sacks are useful.

PRESSING EQUIPMENT

Botanical specimens in the herbarium are dried and pressed, in order to preserve them better and save space. The challenge in drying the specimens is to remove the moisture with pressure, and rapidly. If it is not pressed, the specimen does not stay flat but wrinkles and folds. Then it is fragile and breaks or becomes damaged easily. If it is not dried rapidly and completely, mold damages it. Also, when dried rapidly the specimens retain their natural color better and do not lose leaves or other parts.

In an emergency, specimens can be pressed with only some newspapers and a weight, such as books, boards, bricks, or stones.

The Press

Generally a wood press, size 12 by 17 or 18 inches, with two straps of leather or canvas is used.

The old newspapers or newsprint that are folded for the specimens should be the same size as the press. Also, 50 to 100 or more sheets of blotting paper or driers such as felt are needed.

The sample is arranged within the newspaper. It should not be larger than the cardboard mounting sheets, which measure 16-1/2 by 11-1/2 inches. A large specimen can be folded in the form of V, N, or M. Since the mounting sheet and pressed specimen have only two dimensions instead of three, some leaves and twigs should be removed, leaving the base of the petioles to indicate the leaf arrangement. Generally one should not arrange a leaf directly on top of another. If too many leaves are left, the specimen does not dry well and the leaves underneath cannot be seen.

Outside, on the corner of the newspaper sheet, can be placed the number of the specimen that corresponds to the number of the collector in his notebook. Between each two folded papers containing specimens is inserted a drier. When all the specimens are arranged in papers, the press is tightened and fastened.

The press should be put in a warm dry place. Daily, or twice daily, the driers are changed until the specimens within the papers become completely dry and break when they are bent. The first time that the driers are changed the specimens should be examined and rearranged as needed; those that have become folded should be straightened. The moist driers are dried in the sun, near a stove, or placed one by one against the walls and on the floor of a room. If driers are lacking, newspapers can be utilized. The time for drying varies from a few days up to a week, depending upon the size of the specimens, thickness of the leaves, etc. This method is rather slow, consumes much time, and does not prepare good specimens of trees with thick leaves. However, it serves well enough for foresters who do not collect many specimens and do not wish to carry much equipment.

Heat

Botanists who collect botanical specimens in quantities in tropical regions always use heat to dry the specimens rapidly. In the laboratory, electric ovens with ventilators or fans, or an apparatus of electric heaters or electric lightbulbs, can be used under the press.

In the field, a portable stove of gasoline or kerosene or kerosene lanterns can be employed.

Corrugated Driers

With heat, corrugated sheets or ventilators of cardboard or metal are needed in order that the hot air can pass within the press and remove the water from the specimens. The corrugated sheets have the same size as the press. Those of cardboard can be flat on one or both sides. The metal sheets are made of aluminum or iron and last longer. They fit together in less space and dry the specimens in half the time required with cardboard. After 12 hours or more in an ordinary press with driers, the corrugated sheets are inserted in place of every second drier, and the press is mounted above the stove. A cloth is placed around the stove and fastened tightly around the bottom of the press, but opened near the bottom or on one side to permit entrance of air. With metal sheets the majority of the specimens will dry within 12 to 24 hours. At about the middle of this time the straps should be tightened and the press turned over. As there is danger of fire, *the stove never should be left unattended*.

After being dried the specimens should be arranged in order by number and kept in cardboard boxes or packages in a dry place. If they are stored for much time, insecticides should be applied.

THE HERBARIUM

From time to time, foresters collect botanical specimens for large herbaria and also use the herbaria in identification. Perhaps with the duplicate specimens they may make small herbaria of the regions where they work. Therefore, they should know something of the arrangement and care of the herbarium. How to identify specimens in the herbarium was discussed earlier.

THE MOUNTING OF SPECIMENS

After being identified and before being placed in the steel or wood cabinets, the specimens are mounted on mounting sheets of white cardboard. These cardboards, which measure 16-1/2 by 11-1/2 inches, should be of good, durable quality. In some herbaria the specimens are mounted with glue or paste. In others, narrow pieces of gummed cloth tape are used. With both methods the thick parts, such as stout twigs and large fruits, can be sewed with needle and thread. Loose parts, such as additional flowers and fruits, are placed in pockets or envelopes glued to the mounting sheet.

The Label

The label is glued or pasted on the lower right corner of the mounting sheet. Generally labels are printed in part. The notes by the collector should be added with a typewriter. In addition there are added the scientific name with author, the name of the person who made the identification, and preferably also the year of the identification.

Genus Folders

The mounted specimens of a genus, or of a species if there are many, are placed in a folded cardboard sheet 12 by 17-1/4 inches after folding. The generic name is placed on the lower left corner outside.

ARRANGEMENT OF THE HERBARIUM

Large herbaria generally follow a natural system of classification in their arrangement. The most popular is that of Dalla Torre and Harms, based upon that of Engler and Prantl (1887), with numbers for the families and genera. Each genus of seed plants has a number, and the specimens are arranged and may be found in this numerical order.

In a small herbarium of a region, or in a personal herbarium, it is simpler to follow the order of the botanical flora of the country. Generally the order of the families in botanical references is that of Engler and Prantl (1887). Within a family, it is simplest to arrange the genera and species alphabetically.

PROTECTION AGAINST INSECTS AND MOLD

It is always necessary to protect the herbarium against insects and, in humid climates, also from mold. No method is perfect. Perhaps the simplest is to place repellents, such as paradichlorobenzene or naphthaline, in small cloth sacks or pockets within each cabinet, at the top. From time to time, every few months during the year, it is necessary to add more chemicals.

Mercuric chloride (bichloride of mercury) in solution is employed for killing insects on botanical specimens. Before mounting, the specimen is dipped into this solution and then dried. Fumigation with carbon disulfide or a poisonous gas is another method. Or the specimens can be placed in a special cabinet or in an oven, where insects may be killed with heat.

BOTANICAL TERMS

In order to use botanical references in the identification of trees, it is necessary to understand the botanical terminology. The botanical descriptions for identification and also the natural classifications are based principally upon morphology and anatomy. In distinguishing the species of trees, differences in parts are used, such as presence or absence, number, arrangement, shape, size, etc. Thus, foresters should know the names of the important parts of a tree.

Flowering plants (Angiosperms), those with both flowers and seeds, and particularly the trees, are composed of parts or organs. The principal organs are the *root*, *stem*, *leaf*, *flower*, and *fruit*. The first three—root, stem and leaf—are vegetative in function and serve in the development and growth of the plant from the seed:

The *root*, composed usually of a vertical axis and branches, grows downward, anchors the plant in the soil, and absorbs the nutritive substances, but never bears leaves.

The *stem*, composed generally of a vertical axis and branches, grows upward (or opposite to the root), and supports the leaves and flowers.

The *leaf*, or foliar organ, generally is flat and green and functions to manufacture the food for the plant.

The other two organs, the flower and the fruit, are reproductive in function and serve in the production of seeds to propagate the species:

The *flower*, usually colored, is the organ of reproduction and consists of an axis or stem with modified leaves of four kinds: the calyx, corolla, the stamens with pollen, and the pistil with the feminine elements or ovules.

The *fruit* is the mature ovary developed from the pistil and containing the mature seeds.

In the botanical classification of trees and also in their identification, the most important and most useful organs are the reproductive organs. The flower and fruit show the natural relations and botanical families much better than the other organs. The vegetative organs respond more easily and more rapidly to differences in the environment, such as climate and soil, and consequently are less constant and more variable. However, when a tree has neither flowers nor fruits, it is necessary to make use of these organs, such as leaves, bark, and wood, in the identification.

Systematic botanists have a special terminology of many words for describing the differences among the many thousands of species of plants. These words are derived from the ancient languages Latin and Greek. Many are similar to Spanish words and not difficult to remember. In the past centuries, botanists wrote their books and descriptions in Latin, and for this reason there now remains for us a very rich botanical terminology. Actually there are more terms in plant taxonomy than are needed, and some are rarely used.

Foresters do not need as many terms as do botanists. In the study of dendrology we shall learn the common terms that are used in descriptions of tropical trees. Other new or unfamiliar terms that are found in publications can be sought in botanical glossaries or other botanical references.

THE ROOT

The root generally is not important in classification of trees. As they are within the ground, roots are not seen or easily examined. Also, they probably have very few characteristics useful in identification. However, a few species of trees have *aerial roots* that are useful in the forest for recognition.

Characters of the bark utilized in identification include external and internal color; the surface, the texture—whether smooth, rough, or furrowed; whether thin or thick; and if there is latex (colored juice or sap) or odor.

The trunks of some species have the base enlarged into buttresses, especially in the wet tropical forests.

It is difficult to describe the characteristics of bark and its differences. However, with experience in the forest one can recognize and distinguish various tree species by the bark.

THE STEM

The stem bears the branches and leaves. The *node* is the point on the stem where one or more leaves are inserted. Sometimes it is enlarged or marked with a ring. The *internode* is the space on the stem extending between two consecutive nodes.

The *bud* is a short growing point of a stem, composed of young leaves or flowers and frequently also of some scales. In tropical regions generally there are no scales. However, in temperate regions with cold winters there are dormant buds covered with scales. There are two principal types of buds. The *terminal bud* is in the apex of the stem or a branch. The *lateral bud* (or axillary bud) is located at the base of a leaf and can grow into a branch. (Branches, or lateral stems, are formed only at the nodes and from lateral buds.)

THE LEAF

A tree that has leaves in all seasons of the year is *evergreen*. If it remains without leaves during part of the year, such as in the dry or cold season, a tree is *deciduous*.

The *parts of the leaf* are the *blade* and the *petiole*. In some species there are also two (or one) *stipules*, or scales, usually deciduous, at the base. Also, in some species the petiole is lacking, and the leaf is said to be sessile. Upon falling, the leaf leaves a scar at the node.

In *number of blades* the leaves are simple or compound. The *simple* leaf consists of a single blade. The compound leaf is composed of usually several blades (two or more), which are called *leaflets*. Leaflets may have petioles or not, but never have buds at the base. This character, the absence of the bud at the base, distinguishes a leaflet from a simple leaf. Compound leaves are divided into *pinnate* and *digitate* leaves. Leaves are *pinnate* when the leaflets are inserted along a common axis. If the axis is divided, the leaf can be twice pinnate (*bipinnate* or three times pinnate (*tripinnate*). Leaflets are alternate in some species and opposite in others. If a pinnate leaf ends in a single leaflet it is *odd pinnate* (*imparipinnate*). If it has paired leaflets and ends in two leaflets it is *even pinnate* (*paripinnate*). Leaves are *digitate* (or palmate) when the leaflets are inserted together at the apex of the petiole.

Shapes of Leaf Blades

The shape or form of leaf blades generally is characteristic of a species and is used in identification. Many terms are employed for describing the shape, but it is sufficient here to mention only the commonest types. A *linear* leaf has the blade long and narrow with margins parallel, for example in grasses or the grass family. A *lanceolate* leaf has the blade in the shape of a lance, several times longer than broad, broadest near the base, and pointed at the apex. (The reverse shape is called oblanceolate.) An *ovate* leaf has the blade oval but broadest toward the base, more or less as in the longitudinal shape of an egg. (The reverse shape is called obovate.) An *elliptic* leaf has the blade oval but broadest at the middle. An *oblong* leaf has the blade several times longer than broad and with margins parallel. A *circular* leaf (or orbicular) has the blade more or less in a circle.

Margins of Leaf Blades

The margin or border of the leaf blade can be: *entire,* when the margin is smooth, or straight or curved, but without teeth or lobes; *toothed,* when it has pointed teeth, such as on a saw; or *lobed,* when it has deep indentations or lobes, which are larger than teeth but not deep enough to divide the blade into separate blades.

Apexes of Leaf Blades

The apex of the leaf blade can be: *acuminate*, gradually narrowed to the point in the shape of a wedge; *acute*, with short point; *obtuse*, with blunt point; or *rounded*, circular and without a point.

Bases of Leaf Blades

The base of a leaf can be: *acute*, with short point; *rounded*, or circular and without a point; or *heart-shaped*, with a deep indentation as in the heart.

Venation of Leaf Blades

According to the venation or network of veins, the leaf blade can be: *parallel-veined* when the veins are parallel; *pinnate-veined* or *not-veined*, when there is a single principal vein or midrib with other, lateral veins on the sides; or *palmately-veined*, when there are several principal veins which arise at the base and spread like fingers of the hand.

THE FLOWER

A complete flower consists of four concentric parts, spirals or circles (whorls), called: the *calyx*, the *corolla*, the *stamens* (the androecium), and the *pistil*. However, some flowers lack one or more of these parts. The *calyx* is composed of modified small leaves, generally green, and called *sepals*. The *corolla* is composed of modified small leaves, generally colored, and called *petals.*

The *stamens* are the masculine organs of the flower and provide the pollen, which is the male element. A *stamen* consists of two parts: the *filament* or stalk, generally thin, and the *anther* or enlarged part at the apex, composed of pollen sacs with the pollen grains.

The *pistil* is the feminine organ of the flower and is composed of one or more modified small leaves called *carpels*. The *carpels* form the ovary which is the feminine element and which is transformed into the fruit. The ovary contains one or more ovules which develop into the seeds. Other parts of the pistil are: the *style*, a small column above the ovary which supports the stigma; and the *stigma*, the uppermost enlarged part of the pistil, which receives the pollen grains. The stigma can have different shapes, such as rounded, lobed, or feathery.

The *receptacle* is the enlarged base of the flower where the floral parts are inserted. The *peduncle* is the stalk of the flower. If there are several flowers together, the stalk or secondary peduncle of each one is called a *pedicel*.

In the different families there are many differences in the shape of the flower and in the number, size, and arrangement of the parts. The parts of a circle or whorl can be separate (free) or united into a tube, or united with other parts. The *gamopetalous* corolla has the petals united. The *regular corolla* has petals of equal size and symmetrically arranged. The *irregular* corolla has the petals unequal.

The carpel can be compared with a leaf on whose borders have developed the ovules. Also, the leaf has become incurved until the ovules are within a cavity of the ovary. The ovary encloses one or several small cavities called *cells* or *locules*, which contain the *ovules*. An ovary formed from one carpel has necessarily a single cell. An ovary formed by two or more carpels has a single cell if the carpels are joined by their borders. If the carpels are folded toward the interior, they form as many cavities or cells as there are carpels. According to the number of cells the ovary can be: unilocular, bilocular, trilocular, or multilocular.

In position with respect to the other floral whorls, the ovary can be *superior* (free), or *inferior* (adhering). The *superior ovary* is free or separate in the middle of the flower and is inserted above the other whorls. The *inferior ovary* is united with other parts of whorls which appear to be inserted above.

Pollination is the transport of the pollen from the anther to the stigma. The pollen grain germinates and forms the pollen tube, which carries the male element to the ovule. Fertilization is the union of the nucleus of the male element with the nucleus of the female element in the ovule to form the fertilized egg. The fertilized egg divides to form the embryo, and the ovule is transformed into the seed. The *seed* is the mature ovule and consists of the embryo with stored food and one or two seedcoats.

The *inflorescence* is the arrangement or disposition of the flowers on the stem. It is *terminal* when it is at the apex of the stem, or *lateral* (or axillary) when it is at the base of a leaf, on the side of the stem.

There are many types of inflorescences, but it is sufficient here to mention only some of the commonest. The *soli-*

tary inflorescence (or simple) has the flowers isolated or one by one, separated by the leaves.

The *spike* has an elongated axis and flowers without pedicels. The *racine* has an elongated axis and flowers with pedicals. The *panicle* is a compound racine with the axis branched.

The *umbel* has the flowers together at the apex of the peduncle, terminating in spreading pedicels of equal length. (Also, there is the compound umbel.) The *head* has the apex of the axis broadened as a disk and the flowers without pedicels. The *cyme* is a definite or determinate inflorescence with the principal axis ending in the first flower, and below it arising other secondary axes with flowers.

THE FRUIT

The *fruit* develops from the mature ovary, contains the seeds, and sometimes bears other flower parts which persist. A *simple fruit* comes from a single pistil. An *aggregate fruit* develops from several pistils of a single flower (annona, strawberry, etc.). A *multiple fruit* comes from several flowers united (fig, pineapple, etc.).

Simple fruits are classified as *dry* and *fleshy* (juicy); the dry fruits are *indehiscent,* if they do not open to discharge the seeds, or *dehiscent,* if they open.

There are several types of simple fruits. The *achene* is a dry indehiscent fruit with a single seed that does not adhere to the wall of the fruit. The *nut* is a dry indehiscent fruit with a single seed and with the wall of the fruit thick, hard, and woody. The *pod* (or legume) is a dry dehiscent fruit of one carpel which opens on two lines, while a *follicle* opens on one line. The *capsule* is a dry dehiscent fruit of two or more cells that opens on as many lines as there are cells.

The berry is a fleshy indehiscent fruit with several seeds. The *drupe* is a fleshy indehiscent fruit generally of one carpel (or more) and with a single seed (or more) enclosed in a stone or hard wall.

THE DISTRIBUTION OF TREES

Distribution of trees includes the geographic area where they occur, the climatic zone, the forest type, and the altitude or elevation above sea level.

In the study of plant geography there are two kinds of geographic distribution, that of the flora and that of the vegetation. The *flora* of a region is a list of the species of plants. The units of the flora are the species, genera, etc. The *vegetation* of a region is the appearance or the physiognomy of the plants or the growth form or habit of the commonest species. The units of vegetation are the plant communities, such as formations, associations, and forest types.

For example, let us suppose that two areas have only two species of plants: a tree species and a grass species. In one there is a single example of a tree and many individuals of the grass—it is a grassland. In the other there are many trees and few plants of the grass—it is a forest. Both areas have the *same flora* or list of species but have *different vegetation.* One is a grassland and the other a forest.

Thus, the distribution of the trees of a region can be studied from the viewpoint either of the flora, or of the geographic range of each species. Distribution maps of each tree species can be made. Or, from the viewpoint of vegetation, vegetation types can be studied in relation to climate. *Maps of vegetation types*, such as forests, grasslands, etc., can be made. In dendrology both types of geographic distribution of plants are studied. Maps of the distribution of individual tree species and likewise of forest types are prepared.

Many tree species of tropical America are not sufficiently known for compiling maps of geographic distribution or for analyzing the origin, the migrations, and the distribution. Some species have a broad range, while others are rare and local.

For example, some tree species have a very large distribution in tropical America, from Central America or Mexico to Brazil. Those of ocean shores, such as the mangroves, have a wide range up to Florida in the southeastern United States. Other trees are confined to high mountains, still others to grassy plains, or to deserts, etc. Few are local or endemic. A job for the future is to prepare more detailed distribution maps.

The study of vegetation and distribution of vegetation types is often included in a subdivision of biology known as ecology. Much of the following material treated under ecology might equally well be considered as forestry or dendrology.

ECOLOGY

The name ecology (originally spelled oecology) was first used in 1869 by the German zoologist E. Haeckel. It is derived from two Greek roots meaning home and discourse or study, or, literally, the study of homes. *Ecology* is defined as the study of organisms in relation to their environment. Opinions differ as to whether ecology really is a subject-matter branch of biology or whether it is merely a point of view for studying biology. Thus, ecology might be biology with emphasis on the surroundings of animals and plants.

Ecology is often subdivided into autecology and synecology. The former prefix is a Greek root meaning self, while the latter means together. *Autecology* is the ecology of the individual, or study of an individual organism or species in relation to its environment. By some authors, autecology is considered as physiology—for example, an investigation of a single tree species in relation to its surroundings. In contrast, *synecology* is the ecology of the group, or study of groups of organisms, or communities, in relation to their environment.

Since the subject matter or viewpoint of ecology is so large that it embraces biology, ecology is usually divided into *animal ecology*, which treats of animals in relation to their environment, and *plant ecology*, which deals with plants in relation to their environment. By some authors, plant ecology is restricted to synecology, the study of plant communities or vegetation.

Plant ecology was established by the Danish botanist E. Warming (1895) in his classic book, Oecology of Plants, first published in Danish. Another important early reference was Plant Geography upon a Physiological Basis, by the German botanist A. F. W. Schimper (1898).

The *environment*, or surroundings, includes everything that may affect an organism or group of organisms in any way. In plant ecology, one classification divides the environment into factors, or environmental factors, as follows: (1) *climate factors*, or climate, which include temperature, rainfall, and other widely distributed elements chiefly from the atmosphere; (2) *physiographic or edaphic factors*, such as topography and soil; (3) *biotic factors*, or other organisms. Because modern man has had such a profound influence, mostly destructive, on other organisms, man has often been separated from the third group as a fourth group of factors called *anthropeic factors*. As fire has become widespread and has had serious effects upon vegetation, it is often listed as a fifth group, known as *pyric factors*.

One of the principles of ecology is often called *balance of life*, or *web of life*. This means that organisms living together in a group or community are more or less balanced, or at equilibrium, interrelated by their mutual requirements for food for energy, the original source of which is the sun. The activities within the group, and particularly the number of individuals, are in balance with the available supply of energy. A simple relationship of several kinds of organisms, each dependent upon a surplus of another for food, is called a *food chain*. For example, in a pond the green algae or pond scums make food with energy received from the sun and are eaten by microscopic animals. These in turn are consumed by less-minute aquatic animals later eaten by small fish. The latter are devoured by larger fish, which are prey of birds, mammals, and man. The relationship of foods generally is more complex, with branches, and is a network or web rather than a chain.

Adaptation, or the adjustment of organisms to their environment, is another principle of ecology. Each species fits a set of external conditions, sometimes within very narrow limits, where it is in equilibrium or in balance.

An important principle of ecology is that of *change*, also known as the *dynamic viewpoint*. The whole universe, or rather the universes about us, from the giant galaxies of stars to the minute particles within the atom, are changing or in motion all the time. Specifically, the climate of a region is slowly changing and the soil is changing. Therefore, the vegetation, which is dependent upon climatic and soil factors, is slowly changing at a particular place too.

CLASSIFICATION BASED ON WATER RELATIONS

Tree species as well as other plants, and also vegetation, can be classified on the basis of water relations or distribution based upon rainfall or water. There are three or more principal groups: a *hydrophyte* is a plant of wet places with adequate water, such as one growing along river banks; a *xerophyte* is a plant of dry places with very little water, as in deserts; a *mesophyte* is a plant of places with average amounts of water, such as forests neither very humid nor very dry—most trees and most other plants belong here.

A *tropophyte*, literally change plant, is a plant that grows under conditions that change markedly during the year, such as plants of places where the quantity of water changes during the year from much to little in seasons from humid to dry; for example, a deciduous tree in a tropical savanna. The term *tropophyte* also is applied in the temperate zones, where the temperature changes during the year, to a tree that is deciduous in the cold or winter season.

A *halophyte* is a plant of places with concentrations of salt, such as sea shores and alkali deserts; for example, the mangroves.

Also for vegetation the adjective terms hydrophilous, xerophilous, mesophilous, tropophilous, and halophilous are used. However, this Greek suffix means loving and suggests teleology, an old idea that there is a cause or reason for everything. Trees do not have intelligence and cannot love water. In biology generally, and particularly in ecology, one must be careful not to seek a purpose underlying each adaptation or peculiar structure.

PLANT COMMUNITIES

In the vegetation the plants arrange themselves in groups or communities. Any group of plants in a place or common habitat can be called a *plant community*. This term has no restrictions in size.

A *plant formation* is a plant community of the highest rank, characterized by a definite appearance or physiognomy and composed of plants with a definite growth form; for example, the rain forest or the paramo.

The formation is composed of smaller units, the associations. A *plant association* is a division of a formation with a definite floristic composition and with certain dominant species. The forest types of the foresters correspond to the plant associations of the ecologists; for example, a forest of *Podocarpus*. Some associations are limited in extent by climatic factors and others, the edaphic associations, by the factors of the soil.

Plant communities are constantly changing though sometimes very slowly. Great changes in the composition of a community follow changes in the environment, which in turn may be caused by the organisms living there. The term *succession*, or *plant succession*, is given to the changes in the plant communities, one following another, at the same place. The succession leads to the *climax association*, which is the highest, most complex, and most nearly stable community existing in the climate of that area. Where the highest vegetation of the succession is limited by edaphic factors rather than climate, the climax association, such as on a particular soil type, is called an *edaphic climax*. The mangrove swamp forest is an example.

Plant successions are of two main kinds: primary and secondary. A *primary succession* begins on a bare area previously without vegetation, such as a new island, a new volcano, or a landslide area. A *xerarch succession*, or *xerosere*, is one beginning with a dry, bare habitat and leading to a climax. A *hydrarch succession*, or *hydrosere*, starts with a wet habitat and continues to a climax. The climax has medium moisture conditions, rather than extreme. Virgin forests represent climaxes or normal developmental stages.

A *secondary succession* is that following a disturbance in the normal, primary succession; for example, after cultivation, cutting of forests, fire, overgrazing, or wind damage. In densely settled regions most of the vegetation has been disturbed by man's activities. Few areas of virgin forest remain and the forests are largely secondary. Ultimately the secondary succession leads to the same climax as the primary succession, but the rate depends upon the degree of disturbance. If great, such as when soil formed during thousands of years is eroded away, the recovery is very slow.

GROUPS OF PLANT FORMATIONS OF THE WORLD

The plant formations of the world can be arranged into four or five large groups:

1. *Forests*, characterized by trees.
2. *Grasslands*, characterized by grasses.
3. *Deserts*, characterized by shrubs, spiny trees, cacti, etc., and by scarcity of water.
4. *Tundras*, characterized by lichens, mosses, etc., and by very low temperatures.
5. *Oceans*, characterized by seaweeds or algae.

Some botanists place mountains in a distinct group, but they have a mixture of the formation groups.

The vegetation is a result of the climate of a region and also of the soil and other factors, such as the plants and animals, mankind, and fire. Thus, the plant formations are indicators of the climate. A map of the vegetation serves equally to show the climate.

There are some studies on the vegetation of the world that attempt to classify it on the basis of temperature and rainfall. A good classification of the climates of the world is that of C. Warren Thornthwaite (1933). His map is useful also for the plant formations of the world. Another system of classification of the plant formations of the world was proposed by L. R. Holdridge (1946).

THE CLIMATE OF FORESTS

In dendrology we are particularly interested in the forests. The climate of forests is characterized by four essentials: (1) a vegetative season sufficiently long; (2) a vegetative season sufficiently *warm*; (3) sufficient *water all the year*, or soil and subsoil both humid; and (4) humid winters (in temperate zones). It is unimportant to the forest (1) when the rain falls or whether it is in the growing season or not; (2) whether the precipitation is uniform in distribution or not; and (3) where the soil water originates, whether it be from rainfall or from rivers or from subterranean sources. Damaging or injurious to the forest are (1) dry and windy winters (in the temperate zones) and (2) a short growing season.

VEGETATION OF LATIN AMERICA

Among the classifications of the vegetation of tropical America may be mentioned the illustrated articles by A. C. Smith and I. M. Johnston (1945) and by J. S. Beard (1944).

The general scheme of classification used by Smith and Johnston (1945) is as follows:

I. Forests or wooded regions
  1. Tropical and subtropical rainforest
  2. Tropical deciduous forest
  3. South Brazilian forest and savanna zone
  4. Palm forest
  5. Subantarctic beech forest
  6. Thorn forest
II. Grasslands and savannas
  1. Savanna regions
    a. True savannas

        b. Uruguayan savannas
        c. Cargo
    2. Pampean grassland
III. Deserts or semidesert regions
    1. Coastal deserts of Pacific South America
    2. Patagonian-Fuegian steppe
    3. Desert scrub
    4. Transitional vegetation of central Chile
    5. California chaparral
IV. Montane zone
    1. Mexico, Central America, and the larger West Indies
    2. Northern Andes
    3. Southern Andes
V. Maritime or littoral zone

Beard's (1944) summary of formations of climax vegetation in tropical America, grouped into five formation series, in both English and Spanish, is listed below. The first, rain forest, is a formation not divided into series.

ENGLISH	SPANISH
1. **Rain Forest**	**Selva pluvial**
2. **Seasonal Formations**	**Formaciones estacionales**
Evergreen seasonal forest	Selva varanera siempreverde
Semievergreen seasonal forest	Selva varanera semideciduo
Semideciduous seasonal forest	Selva varanera semideciduo
Deciduous seasonal forest	Selva varanera deciduo
Thorn woodland	Espinar
Cactus scrub	Caronal
Desert	Desierto
3. **Dry Evergreen Formations**	**Formaciones siempreverdes aecas**
Xerophytic rain forest	Selva pluvial xerofítica
Littoral woodland	Bosque de playa
4. **Montane Formations**	**Formaciones de montañe**
Lower montane rain forest	Selva pluvial intermedia
Montane rain forest	Selva nublada
Palm brake	Matorral de palmeras, Manecal
Elfin woodland	Bosque ensno
Frost woodland	Bosque de helada
Mountain pine forest	Pinar de montañe
Bamboo brake	Bamboal
Paramo	Péramo
Tundra	Tundra
5. **Swamp Formation**	**Formaciones de pantano**
Swamp forest	Selva de pantano
Palm swamp	Pantano de palmeras
Herbaceous swamp	Pantano herbáceo
Mangrove woodland	Manglar
6. **Marsh or Seasonal Swamp Formations**	**Formaciones de lodasal o de pantano estacional**
Marsh forest	Selva de lodezal
Marsh woodland	Bosque de lodezal
Palm marsh	Lodezal con palmeras, Morichal
Savanna	Sabana

PART II

SPECIES DESCRIPTIONS

The significance of Part Two is that it compiles gathered materials to serve those with a broad interest in tropical tree seeds. Much of this material had never been published, or perhaps had only limited or regional distribution. Please note that some species are not as completely described as others. These incomplete descriptions represent neither omissions nor a lack of understanding by the describing author, but gaps in the data available at printing time. Also, there is an inconsistency for species descriptions and their botanical drawings. First, not all species had completely available herbarium specimens to illustrate seedling, leaf, flower, fruit, and seed. Omissions for any species indicate the artist did not have that material. Second, there are additional botanical drawings that have no species descriptions. This material was available for illustrations but was not described. Perhaps these gaps are valuable, because they give researchers some perspective on what we know and what we do not know about a given species.

Nomenclature is current as of August 4, 2000, from Missouri Botanical Garden, TROPICOS.

This section is offered as a practical guide intended to provide useful information to collectors, handlers, seedsmen, and nursery managers. The reported data is always in the following order:

scientific name
author name(s) and affiliation(s)
family name
synonyms
common names
occurrence
growth habits
geographic race and hybridization
use
flowering and fruiting
collection of fruits, cones, seeds
extraction and cleaning
storage
pregermination treatments
germination tests
nursery practices
seedling care
additional information

Abies guatemalensis Rehder

ANA LUCRECIA E. DE MACVEAN
Herbario, Instituto de Investigaciones
Universidad del Valle de Guatemala

PINACEAE (PINE FAMILY)

Abies tacanensis Lundell, *A. guatemalensis* var. *tacanensis* (Lundell) Martínez

Abeto de Guatemala, Guatemalan fir, pacachaque, parchac, pashaque fir (Asociación Becaria Guatemalteca 1995), pinabete (Williams 1981), romerillo (Asociación Becaria Guatemalteca 1995)

Abies guatemalensis is native to the highlands of Mexico, Guatemala, the Santa Barbara Mountains in Honduras, and has also been reported by A. Molina (Escuela Panamericana El Zamorano) from El Salvador (Williams 1981). This species has the southernmost range for its genus (Donahue and others 1985). It grows in wet, high forests in the Guatemalan provinces of Quiché, Chichicastenango, Totonicapán, Sololá, Huehuetenango, Quetzaltenango, San Marcos, Jalapa; and in the Mexican states of Chiapas, Oaxaca, and Guerrero (Asociación Becaria Guatemalteca 1995) associated primarily with *Pinus ayacahuite* C. Ehrenb. ex Schltdl., *P. rudis* Endl., and *Cupressus lusitanica* (Perry 1991). Its distribution is limited by altitudinal requirements and human predation.

This fir is an evergreen tree reaching heights up to 45 m with a grayish trunk almost 1 m d.b.h. or larger. Leaves are linear, spirally arranged, solitary, lustrous light green above, and usually silvery beneath. In general, *Abies* forests in Mexico and Guatemala require a mean annual rainfall above 1000 mm in deep, well-drained soils of volcanic origin (Rzedowski 1981) with a moderate pH of 5.4 to 5.7 (Donahue and others 1985).

This handsome fir has been used for decades as a Christmas tree. Since 1973, *A. guatemalensis* has been listed in Appendix I of the Convention of International Trade of Endangered Species (CITES), and data obtained from the U.S. Department of the Interior (1979) lists *A. guatemalensis* as a threatened gymnosperm. Remaining stands are now protected, and cutting for any purpose is prohibited. Its timber is soft with a specific gravity of about 0.32 to 0.37. Despite protective legislation, the wood is still used for construction, firewood, and charcoal (Donahue and others 1985).

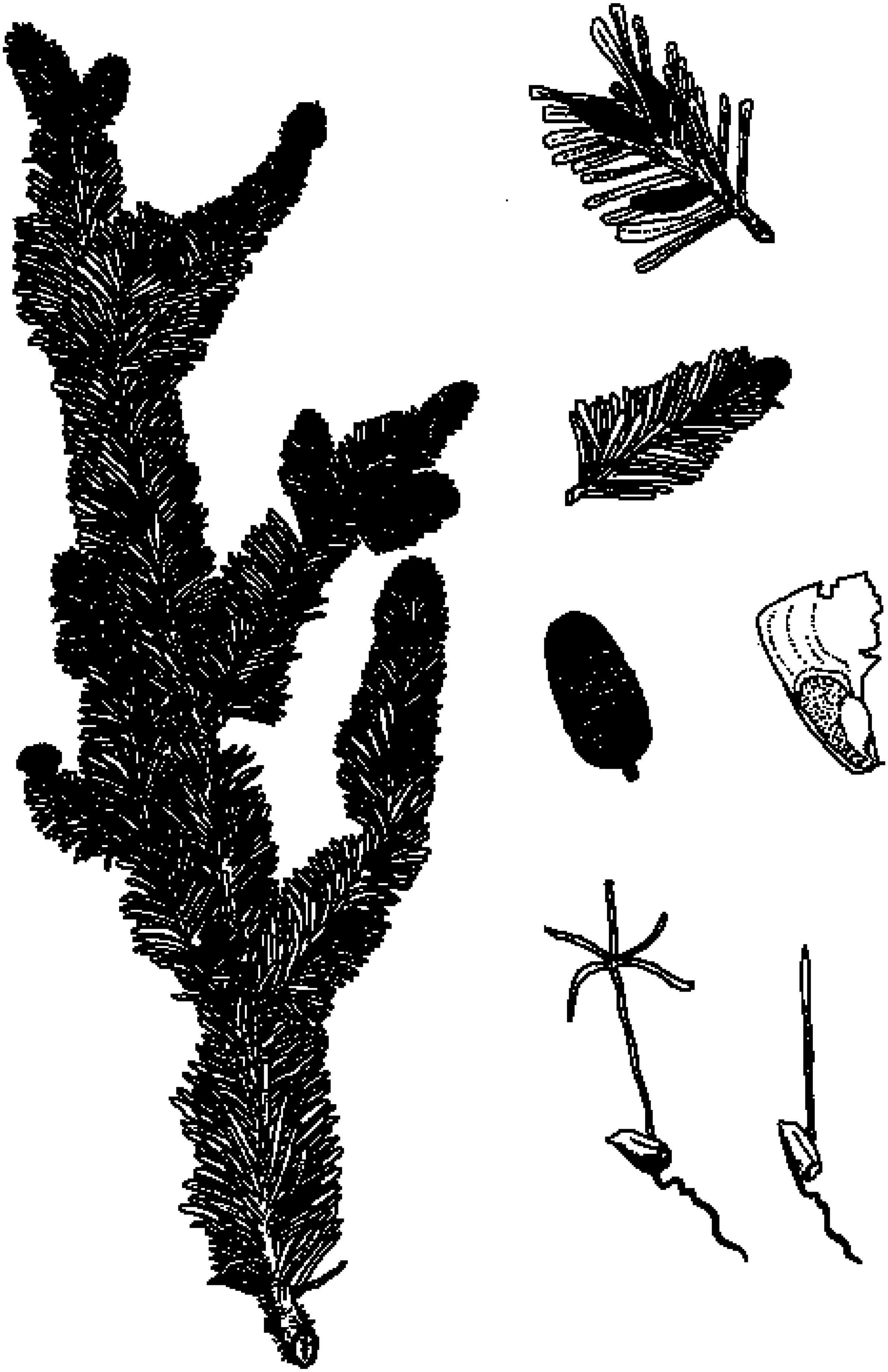
Although not well documented, the solitary flowers appear in May and June. The staminate strobili appear from buds of the previous season and are borne on the undersides of the lower crown branches in the axils of the leaves. Ovulate cones are erect and composed of many bracts, each subtending a large scale with two inverted basal ovules (Harlow and Harrar 1969). All species of *Abies* are monoecious (Dallimore and Jackson 1974). The erect cones are subsessile, cylindrical, and up to 12 cm long and 5 cm wide. The bracts are cuneate obovate, shorter than the cone scales, and concealed by them. The scales are broader than they are long, with external puberulous margins (Dallimore and Jackson 1974). The seeds are light brown, up to 8 or 10 mm long; the wings are 15 mm long and 1.5 mm wide (Dallimore and Jackson 1974).

Closed cones are collected from November through January (Donahue and others 1985). Due to cone disintegration, the best time to collect is when the cone scales are maturing, which can be noted in the field as a change of color from green to deep green or purplish green and the appearance of resin drops, easily seen with binoculars (Donahue and others 1985). Because the cones are collected before maturation, they should be kept shaded for 8 weeks in burlap bags to maximize percentage viability. After treatment, the seeds are extracted carefully. Seed collection is good in alternate years. Resin pocket breakage may lead to fungal attack, reducing percentage viability. After wing removal, seeds are exposed to direct sunlight for 6 hours to reduce water content to 8 percent, which improves long-term storage (Donahue and others 1985). *Abies guatemalensis* seeds collected from Mexico average about 42,000 per kg while those from Guatemala average 35,000 per kg.

Like most *Abies*, the germination rate is poor (Donahue and others 1985, Dvorak and Donahue 1992, U.S. Department of Agriculture 1974). Percentage germination of fresh seeds is

15 percent, and after 1 year of cold storage (3 to 5 °C) drops to 2 percent. Cold and humid stratification improves the viability to 30 percent (Donahue and others 1985). Seed stratification on moist blotter paper at 4 °C for 40 days and application of gibberellic acid at 200 ppm (mg per L) proved to be the most effective treatment of *A. guatemalensis* to improve germination from 17 percent (no treatment) to 37 percent (Salazar 1991). A 40-day stratification period alone produced a higher total germination than 0, 20, or 60 days (Dvorak and Donahue 1992).

The seeds are planted in April and May in shallow trays containing rich organic soil. Seedlings may be grown in either full sun or 50-percent shade and should be protected from heavy rains. Transplants to individual bags should be made 4 to 6 weeks after sowing. After 2 years, *A. guatemalensis* is ready for outplanting. Trees can be severely infested by bark beetles (*Dendroctonus* spp.) (Donahue and others 1985) and seeds can be attacked by seed wasps (*Megastigmus* spp.) (Donahue and others 1985, Hiratsuka and others 1995).



Acacia auriculiformis A. Cunn. ex Benth

JOHN K. FRANCIS
International Institute of Tropical Forestry,
USDA Forest Service

FABACEAE (BEAN FAMILY)

No synonyms

Ear form acacia, ear leaf wattle, kasia, northern black wattle

Acacia auriculiformis is native to the savannas of Papua New Guinea and Irian Jaya, the islands of the Torres Strait, and northern Australia (National Academy of Sciences 1980, Turnbull 1986). The tree has been extensively planted in moist habitats throughout the tropics and in many subtropical areas.

Acacia auriculiformis is a fast-growing, medium-sized tree that has phyllodes—modified petioles that look like simple, lanceolate, parallel-veined leaves. The tree may reach 30 m in height and 60 cm d.b.h. in the most favorable environments and has a crooked trunk that is often forked and has reddish brown or gray-brown bark (National Academy of Sciences 1980). The crown is formed of relatively few robust limbs and does not cast a dense shade. In its native habitat, *A. auriculiformis* grows between sea level and 400 m where mean annual rainfall varies from 900 to 2000 mm in a monsoonal pattern (Turnbull 1986) and mean annual temperatures range from 26 °C to more than 30 °C (National Academy of Sciences 1980). The tree will grow in a wide variety of soils including oxisols, soils with sand or clay texture, salty soils, and soils with pH ranging from 3.0 to 9.5 (National Academy of Sciences 1980). *Acacia auriculiformis* grows best in humid, deep, medium-textured, alluvial soils.

Genetic variation among provenances of *A. auriculiformis* is probably high with considerable potential for genetic improvement, stem form being the major selection criterion (Gavinlertvatana and others 1987). Hybrids of *A. auriculiformis* and *A. mangium* frequently arise when the two species grow adjacent in plantations or natural stands (Turnbull 1986). *Acacia auriculiformis* is a diploid species with 26 chromosomes (Brewbaker and others 1983).

Acacia auriculiformis is cultivated widely for fuelwood and charcoal. It has a relatively high specific gravity (0.60 to 0.75) and caloric value (4,800 to 4,900 kcal per kg), and the wood burns well (National Academy of Sciences 1980). The species is favored for revegetating mine spoils and other degraded lands (Turnbull 1986) and is planted extensively as a shade and ornamental tree (Barrett 1956). The wood is used to a limited extent for pulp (National Academy of Sciences 1980).

Tiny, 3-mm flowers, with both male and female parts (Little 1983), appear June through July in Australia (Turnbull 1986) and February through April in Puerto Rico (Parrotta 1997). They are borne on spikes up to 8 cm long in pairs on the leaf axils (Turnbull 1986). Seed pods are flat, twisted, and undulating when ripe, 2 to 4 months after flowering. The small black seeds, 4 to 6 mm long and 3 to 4 mm wide, are encircled by a long red or orange funicle (string) from which they are suspended after the pods open. Each pod contains up to 15 seeds (Parrotta 1997).

Pods can be clipped from the trees with pruning poles after they turn dark brown or after they open. After air drying, small quantities of seed can be separated by hand. Larger seed lots should be hammermilled and separated by shaking and blowing. The process is difficult because the funicle tangles with debris and screens. The seeds, numbering about 30,000 to 62,000 per kg (Turnbull 1986, Wiersum and Ramlan 1982), may be stored at ambient temperatures in air-tight containers for 18 months (Wiersum and Ramlan 1982).

Pregermination treatments are required for good germination. At least two methods have given good results: immersing in boiling water followed by cooling and soaking for 24 hours (National Academy of Sciences 1980) and soaking in warm water for 24 hours, then sowing in full light (Wiersum and Ramlan 1982). In tests conducted in Puerto Rico, germination of fresh seeds without pretreatment was 4 percent, while hot water pretreatment increased germination to between 47 and 65 percent (Parrotta 1997). Germination starts in about 6 days (Wiersum and Ramlan 1982).

Seeds should be sowed under full light in germination trays or beds filled with loose, well-drained soil at depths of 0.6 to 1.2 cm (Parrotta 1997). Seeds can also be sowed directly into containers and thinned later. Seedlings first develop true pinnately compound leaves. When the narrow phyllodes develop, the seedlings can be pricked into pots or nursery bags. Seedlings can be outplanted into prepared sites in about 3 months, when they reach 15 to 30 cm in height; larger seedlings should be used where severe competition from weeds or grass is expected (Turnbull 1986). Seedlings 1 to 2 m in height grown in 4- to 12-liter pots are used for shade or ornamental trees. On most sites, periodic control of weeds, grass, and vines will be necessary for 1 to 2 years after planting.

Acacia farnesiana (L.) Willd.

JOHN K. FRANCIS
International Institute of Tropical Forestry,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Acacia cavenia Bert., *A. leptophylla* DC., *Vachellia farnesiana* (L.) Wight & Arn.

Acacia odorant, amarilla, aroma, aromo, biorama, cachito de aromo, cachito do aromo, cambrón, casha, cashaw, cassia, cassie, cimarróespinal, cují casha, cuntich, espinillo, espino blanco, espino ruco, esponjeira, huisache, palú, paují, pelquisache, subín, subinche, sweet acacia, uña de cabra (Little and Wadsworth 1964)

Acacia farnesiana is probably native only to southern France and Italy (Parrotta 1992a). However, today it can be found naturalized throughout the tropics and the warmer subtropics.

Acacia farnesiana is a multiple-stemmed shrub or small tree with short to long spines, feathery foliage, and fragrant flowers that rarely exceeds 5 m in height and 15 cm d.b.h. It has smooth, gray bark with many lenticels. The species grows and reproduces aggressively in areas annually receiving about 500 to 1000 mm of rainfall where mean annual temperatures vary from 15 to 28 °C. *Acacia farnesiana* grows on a wide variety of soils including sands and clays; disturbed, nutrient depleted, and saline soils; very rocky sites; and in a wide range of pH levels (Parrotta 1992a).

The species is systematically complex. It has been described as an assemblage of microspecies (Parrotta 1992a). Three species have been split out of the parent taxa: *A. smallii*, *A. pinetorum*, and *A. caven* (Clarke and others 1989, Seigler and others 1979). *Acacia farnesiana* is a tetraploid species with 2n=52 chromosomes (Seigler and others 1979).

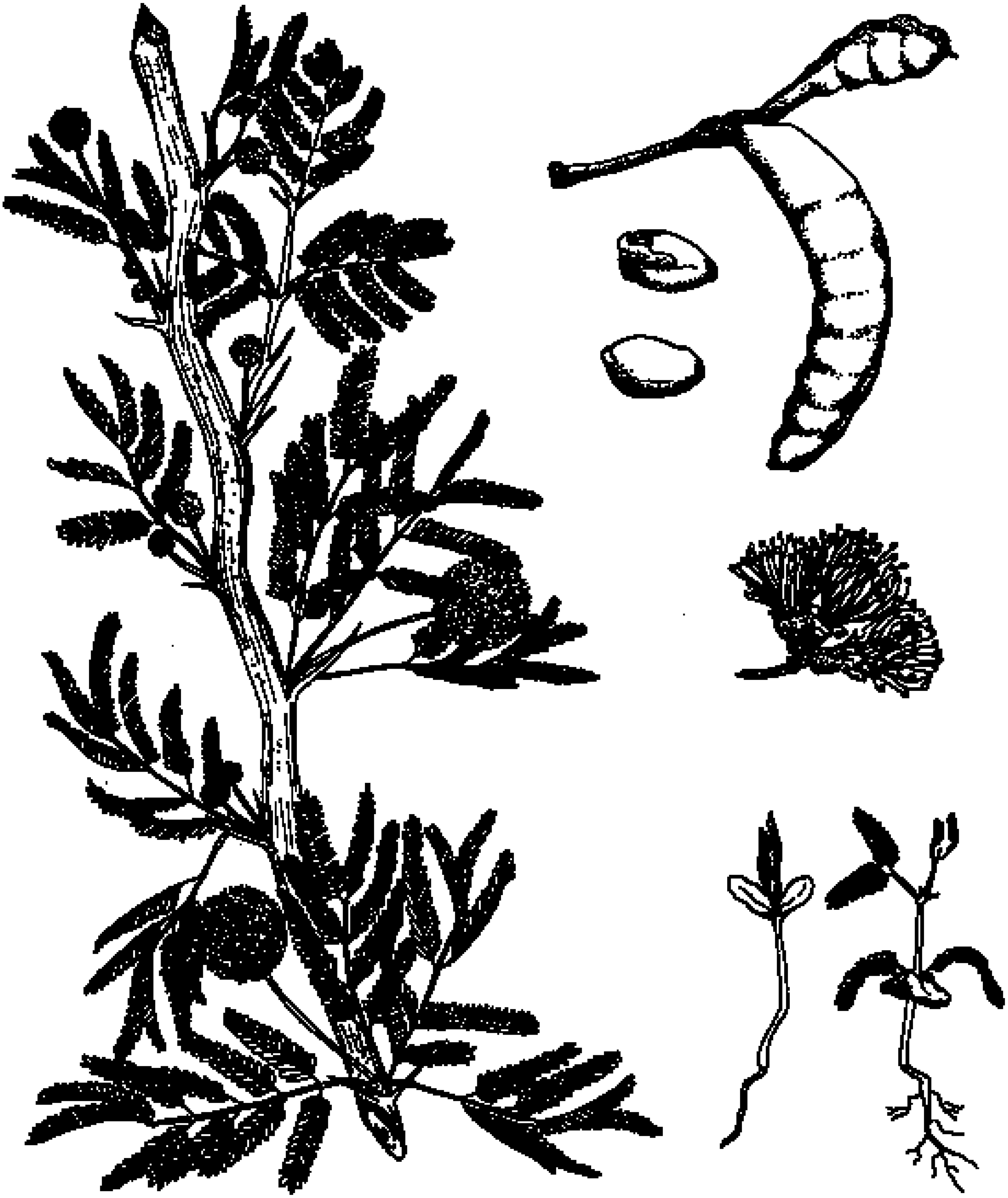
Acacia farnesiana has many minor uses. It is one of the most important forage plants in vast areas of degraded pasture. The foliage and pods are browsed heavily by goats, sheep, and wild ungulates (Little and Wadsworth 1964). The wood is used primarily for fuel. Air-dried wood has a fuel value of 4,600 kcal per kg (Webb and others 1980). The heartwood is hard and heavy with a specific gravity of 0.79 to 0.84 (Joshi 1983, Little and Wadsworth 1964). The sapwood is yellowish and the heartwood is red-brown. The trunks may occasionally get big enough to fashion into tool handles and small implements. The flowers, leaves, fruits, bark, and roots are used in herbal medicine (Little and Wadsworth 1964). The species is also planted to rehabilitate degraded soils and shifting sands (Parrotta 1992a).

Flowering begins when the tree is 2 or 3 years of age (Parrotta 1992a). Although flowering of *A. farnesiana* occurs annually, it is timed to coincide with the moist seasons: November through February in Puerto Rico, December through March in Central America, January through April in northeastern India, and September through February in eastern India (Parrotta 1992a). Round flower heads are borne singly on stalks, one to three of which arise from leaf axils. The tiny yellow flowers, with both male and female parts (Little and Wadsworth 1964), are pollinated by honey bees and other insects. The rounded or slightly flattened, small (3.6 to 7.6 cm) seed pods are dark brown to almost black when ripe. They contain a sweetish pulp that makes them attractive to animals, particularly ungulates, which are the principal dispersers. The pods ripen in 4 to 6 months and remain attached to the shrub or tree. Seeds fall to the ground after the pods decay or are destroyed by insects. A sample of pods collected in Puerto Rico contained an average of 14.4 ± 1.2 seeds per pod (Parrotta 1992a).

The pods can usually be collected by hand from the trees or shrubs. A pruning pole is used on the occasional tall tree. After air drying, the pods can be crushed and the seeds separated by screening and blowing. Another method of cleaning (and scarifying) is to feed the pods to cattle and separate the seeds from the manure. A sample of *A. farnesiana* seeds collected in Puerto Rico averaged 7,600 per kg (Francis and Rodríguez 1993). Others report seed averages of 11,000 to 13,000 per kg (Joshi 1983, Webb and others 1980). Dry seeds stored at ambient temperatures in sealed containers retain their viability for 30 or more years (Joshi 1983).

Some form of pretreatment is required for good germination. Fresh seeds commonly give 10- to 40-percent germination (Gill and others 1986, Marrero 1949). Methods reported to increase germination include soaking in cold water for 48 hours (Joshi 1983), soaking in hot water for 10 to 20 minutes (Kumar and Purkayastha 1972), and incubation at temperatures between 60 and 70 °C for 6 to 12 hours (Gill and others 1986). Scarification in concentrated sulfuric acid for 20 to 60 minutes or in concentrated nitric acid resulted in 65- to 70-percent germination (Gill and others 1986, Scifres 1974). Abrasion with sandpaper enabled germination as high as 98 percent (Gill and others 1986).

Seeds should be sowed in well-drained media. Optimal sowing depth is 2 to 4 cm (Gill and others 1986). Germination begins in about 6 days (Francis and Rodríguez 1993). Plantations may be established by direct seeding or by planting bare-root or containerized seedlings (Joshi 1983). Broadcasting seed in a Texas pasture resulted in the establishment of seedlings for only 1 to 2 percent of the seeds (Mayer and Bovey 1982). Using prepared seed spots can improve the results of direct seeding. For nursery-grown seedlings, the seed is sowed in germination trays or beds, and the seedlings are transplanted to growing beds, nursery bags, or pots when they reach about 5 to 8 cm in height. Seedlings reach plantable height of 30 to 50 cm in 6 to 12 months. Outplanting should begin after the first rains of the wet season have soaked the soil. *Acacia farnesiana* is very shade-intolerant. Newly established seedlings can withstand competition at or below their height, but do not tolerate shading by taller vegetation. Spoiled and eroded areas may not require weeding, but grassy and brushy areas will. Once established, *A. farnesiana* are not harmed by cattle grazing, but may be severely browsed by goats and sheep.



Acacia hybrid *(mangium x auriculiformis)*

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Forest Tree Seed Centre, Thailand

FABACEAE (BEAN FAMILY)

No synonyms

Krathin tepnarong

The *Acacia* hybrid, a cross between *A. mangium* and *A. auriculiformis,* grows in Indonesia, Malaysia, Thailand, Vietnam, and China (Kha 1996; Kijkar 1992; Rufelds 1987, 1988).

The *Acacia* hybrid is a medium-sized tree that looks similar to *A. mangium*. In 2 years, the tree can reach 8 to 10 m and 7.5 to 9.0 cm d.b.h. The species grows on sandy loam or sandy clay loam soils; however, it also thrives on lateritic crude soils. *Acacia* hybrid is found where temperatures range from 12 to 35 °C, annual precipitation is 1200 to 1850 mm, and elevation is 50 to 350 m.

The wood properties of *Acacia* hybrid are similar to those of *A. mangium*, although the hybrid has a slightly higher wood density (0.455 g per cm^3) (Kha 1996). Its straw-colored softwood is good for chipwood, pulp, paper production, medium density fiber board, and oriented-strand board. Its dark-colored heartwood is used in general construction and for furniture, small hand tools, small construction beams, housing tools, and parquet flooring (Kha 1996, Pinso and Nasi 1991).

Flowers appear in July and August and again in November and December. *Acacia* hybrid begins to set flowers at about 3 years. The flowers are creamy to whitish and arranged in a straight or slightly bent, 8- to 10-cm-long spike. Because male flowers in the hybrid are usually located toward the bottom of the spike, less than 3 percent of the inflorescences produce fruits (Kijkar 1992). The pod (fruit) is usually very curly and twists like pods of all *Acacia* species. The pods mature in about 3 months (Ibrahim 1993). A pod holds 5 to 9 seeds. The seed is about 0.3 x 0.4 cm and about half of it is attached to the pod by a yellowish-red funicle. After collection by cutting small twigs where matured pods are found, seeds are extracted by threshing and winnowing. Seeds average approximately 75,500 to 80,000 per kg .

Because the seedcoat is plastic-like and very hard, pretreatment is recommended. Seeds can be scarified by soaking them in concentrated sulfuric acid for 15 minutes and rinsing thoroughly in water, or soaking them in hot water overnight. With presowing treatments, seeds of *Acacia* hybrid will germinate in 7 to 10 days. However, *A.* hybrid seeds are not commonly used in regeneration programs because they may produce *A. auriculiformis* (52 percent) or *A. mangium* (2 to 3 percent) (Kijkar 1992, 1997). The species should be propagated vegetatively by rooting cuttings or by tissue culture. Both methods have proven very successful (Darus 1993, Kijkar 1992).

Cuttings of rejuvenile materials of *Acacia* hybrid usually root well (more than 92 percent). Coppicing shoots from the stumps or rejuvenile shoots from the hedge orchard should be treated with rooting hormone (Indole Butyric Acid—IBA 100 ppm or commercial powdered hormone—Seradix No. 3) and kept under controlled conditions. Relative humidity should remain above 80 percent and temperature below 30 °C.

Tissue culture techniques have also been successfully developed using aseptic emerging seedlings as multiplication materials (Darus 1993).

Young stecklings should be kept under 50-percent shade for 3 to 4 weeks before hardening; plantlets from tissue-cultured hybrids must be acclimatized before outplanting to open areas.

ADDITIONAL INFORMATION

The *A.* hybrid differs from *A. auriculiformis* and *A. mangium* in several ways. When *A.* hybrid is young, the bark is greenish white, similar to the bark of *A. auriculiformis*. As it ages, the bark turns greenish brown or brown. It is as smooth as the bark of *A. auriculiformis,* with slightly scalely and shallow furrows at the foot of the tree (Kha 1996, Kijkar 1992, Lapongan 1987, Pinso and Nasi 1991, Rufelds 1988). The hybrid's branching behavior differs from *A. mangium* and *A. auriculiformis*. The tree has many small and light branches that can be easily pruned. Its main stem, though not as straight as that of *A. mangium*, is much straighter than the main stem of *A. auriculiformis*. Unlike the stem of *A. mangium*, that of *Acacia* hybrid has no angles or ribs (Darus and Ghani 1989, Kijkar 1992). Its phyllode is about 4 to 6 cm wide and 15 to 20 cm long with four veins similar to those of *A. mangium*, but the vein on the outer edge of the crescent is not easy to see. Its seeds are similar in appearance to those of *A. auriculiformis* except that the funicles of the hybrid are lighter and are only partly attached to the seeds (Kijkar 1992).

Acacia koa A. Gray

JAMES A. ALLEN
Paul Smiths College,
Paul Smiths, NY

FABACEAE (BEAN FAMILY)

Acacia hawaiiensis (Rock) Degener & I. Degener; *A. heterophylla* Willd. var. *latifolia* Benth.; *A. kauaiensis* Hillebr.; *A. koa* var. *hawaiiensis* Rock; *A. koa* var. *lanaiensis* Rock; *A. koa* var. *latifolia* (Benth.) St. John; *A. koa* var. *waianaeensis* St. John; *A. koa* var. *waimeae* Hochr.; *A. koaia* Hillebrand.; *Racosperma kauaiense* (Hillebr.) Pedley; *R. koa* (A. Gray) Pedley (Wagner and others 1990)

Koa, koai’e, koai’o, koa’ohā

Acacia koa is one of three closely related species native to the Hawaiian Islands, where it is found on all the main islands except Niihau and Kahoolawe. It grows in almost pure stands, in mixed koa-ohia (*Metrosideros polymorpha* Gaudich.) stands, and in association with a variety of other tree species (Whitesell 1990).

Acacia koa is a moderately fast-growing tree capable of attaining a height of approximately 35 m and 1.5 m or more d.b.h. In its native range, it is found on volcanic soils of a wide range of ages, from the ash and a’a lava rock soils on the slopes of still-active volcanoes to oxisols. The largest and best-formed trees are found on sites with moderately well-drained to well-drained, medium to strongly acid soils, and annual rainfall in the range of 1900 to 5100 mm. Koa grows on a range of other soil types and in areas with much lower rainfall, but its growth is slower and its form often poorer than on more optimal sites (Whitesell 1990). It occurs over a wide elevational range, from about 50 to 2100 m. Little is known of the tolerance limits of mature trees to heat and cold, but significant mortality occurs when *A. koa* seedlings are exposed to temperatures below about –4 °C for more than a few hours (Scowcroft 1998).

There is considerable ecotypic and geographic variation within the species (Brewbaker 1997, Whitesell 1990) but no published information on specific hybrids or geographic races. Isozyme analyses have shown that trees from Kauai, Oahu, and Maui appear to be closely related (Conkle 1997). Trees from these three islands also differ morphologically (e.g., they have smaller phyllodes) than trees on the island of Hawaii (Dudley 1997).

The wood of *A. koa* has a specific gravity of about 0.55, and reportedly is nearly identical to walnut (*Juglans nigra* L.) in weight and strength (Skolmen 1968). It is variable in color, frequently has a curly, highly attractive grain, has very good working properties, and takes a high polish. However, it is not resistant to decay and is quite susceptible to drywood termites (Little and Skolmen 1989). Native Hawaiians traditionally used the wood for house construction, canoes, paddles, surfboards, and other products. The wood is currently used for furniture, cabinets, paneling, bowls, and carving. It is featured in Hawaii’s state capitol offices, many corporate offices, and private homes throughout Hawaii.

Flowers are borne on the outer parts of the crown in axillary racemes with spherical, pale yellow heads averaging about 8.5 to 10 mm in diameter. Flowering generally peaks in mid- to late winter, but may extend into early summer at low elevations (Whitesell 1990). Some flowering may occur throughout the year. Trees as young as 2 to 3 years old have been known to flower and produce fruit, but most production seems to occur between the ages of about 5 and 30 years. Mature seed pods are flattened, 7.5 to 15 cm long, and 1.5 to 2.5 cm wide. Each pod contains about 12 seeds, which are ellipsoidal, laterally flattened, 6 to 12 mm long and 4 to 7 mm wide, dark brown to black in color, and slightly shiny (Little and Skolmen 1989, Wagner and others 1990, Whitesell 1990). Pods may dehisce while on the tree or fall to the ground unopened.

Seeds are generally obtained by collecting pods directly from trees in the fall and early winter, either by hand or by using a pruning pole. Pods are easily broken open by hand for seed extraction. Yield of viable seeds per pod is often low due to poor seed setting and infestations of seed weevils and other insects. Cleaned seeds average from 5,300 per kg to more than 37,000 per kg (Allen 1997, Whitesell 1990). Seed size depends to some degree on source, with seeds from Oahu and Kauai often smaller than seeds from the island of Hawaii. The seeds of this species are easy to store, not needing to be kept in sealed containers. Seeds will remain viable for many years if stored in a cool, dry place; they may remain viable for 25 years or more on the forest floor (Judd 1920, Whitesell 1990).

The seeds have a hard seed coat which retards germination without pretreatment. Mechanical scarification, a brief treatment with sulfuric acid, or a hot water soak all work well. The hot water treatment is safe and reasonably practical for large batches of seeds; seeds are placed in almost boiling water that has been removed from the heat source, then left to soak for 24 hours. There is some evidence that damage can occur if the volume of hot water compared to that of seeds is too high—a ratio of 5:1 or less is recommended. For small volumes of seeds, one end of the seedcoats can be easily clipped with a pair of scissors or shears.

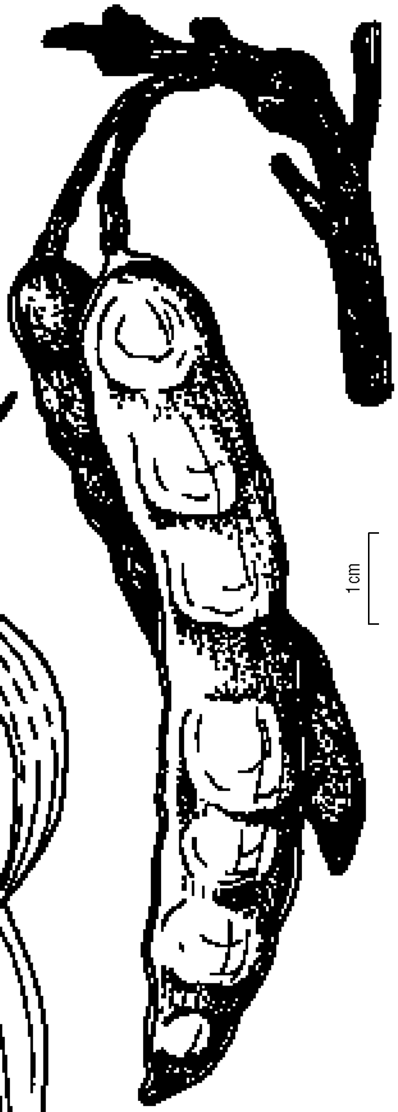
Acacia koa seedlings are almost always grown as containerized stock. Often grown in tin cans or plastic bags in the past, seedlings today are more commonly grown in small dibble tubes. Seedlings can be grown to a plantable size of 20 cm in about 10 to 14 weeks. If seedlings are grown in sterile soil media, rhizobial application at the time of sowing will ensure good survival and growth of the seedlings. The soil media should not be too wet, because seedlings are prone to damping off. Insect pests, especially white flies, may also present problems. Survival and growth of outplanted seedlings are best on clean, well-prepared sites with follow-up weed control during the first year. Koa can also be direct-seeded with at least moderate success (Bryan 1929, Fujii 1997).

Several planting trials have demonstrated that seed source should be an important consideration in any *A. koa* planting program. Variation among sources has been reported in form, growth rate, apparent resistance to volcanic fume damage, and level of susceptibility to insects and disease (Conrad and others 1995, Dudley 1997, Skolmen 1990). In general, seed sources from the same island as the planting site and from similar elevations and site conditions should be used. *Acacia koa* can regenerate extensively from root suckers and is capable of vigorous natural regeneration on sites with exposed soil and adequate protection from herbivores (Whitesell 1990).

ADDITIONAL INFORMATION

Acacia koa is also closely related to *A. heterophylla* Willd., a species found on the Mascarene Islands in the Indian Ocean. The relationship and the distinguishing differences between koa and *A. heterophylla* are described in Carlquist (1965), Vassal (1969), and Pedley (1975), and briefly summarized in Wagner and others (1990). *Acacia koa* is in the *Acacia* subgenus Heterophyllum, members of which are generally thornless and have leaves that initially may be bipinnately compound, but on trees larger than saplings tend to be reduced to phyllodes (modified petioles).


2cm


1 cm

Acacia mangium Willd.

JOHN K. FRANCIS
International Institute of Tropical Forestry,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Mangium montanum Rumph.

Black wattle, hickory wattle, mangge hutan, mangium, Sabah salwood,
tongke hutan (Turnbull 1986)

Acacia mangium is native to northern Queensland in Australia, Papua New Guinea, Irian Jaya, and the Moluccas Islands in Indonesia (Turnbull 1986). The species has been planted throughout the humid tropics (Centro Agronómico Tropical de Investigación y Enseñanza 1992, Szott 1995, Turnbull 1986). It has naturalized in Puerto Rico (Francis and Liogier 1991), Brazil, and many other areas.

Acacia mangium is a fast-growing, medium-sized, evergreen tree with phyllodes that serve as leaves (Nitrogen Fixing Tree Association 1987a). Trees reach 30 m in height and 60 cm in diameter in their native range (Turnbull 1986). The bole is usually straight and topped with a symmetrical crown of relatively light limbs; the lower bole is often fluted. The bark is reddish brown and lightly furrowed. *Acacia mangium* grows best in warm climates with 1500 to 3000 mm of mean annual rainfall (Turnbull 1986). The species grows in a wide variety of soil types. These soils are acid with medium-to-low fertility and can be poorly drained. Soils with high pH are not tolerated (Turnbull 1986).

Acacia mangium forms hybrids with *A. auriculiformis* in natural stands in Papua New Guinea and hybrids have been reported in cultivation in Sabah (Turnbull 1986). *Acacia mangium* is closely related to *A.auriculiformis* and *S. holosericea*.

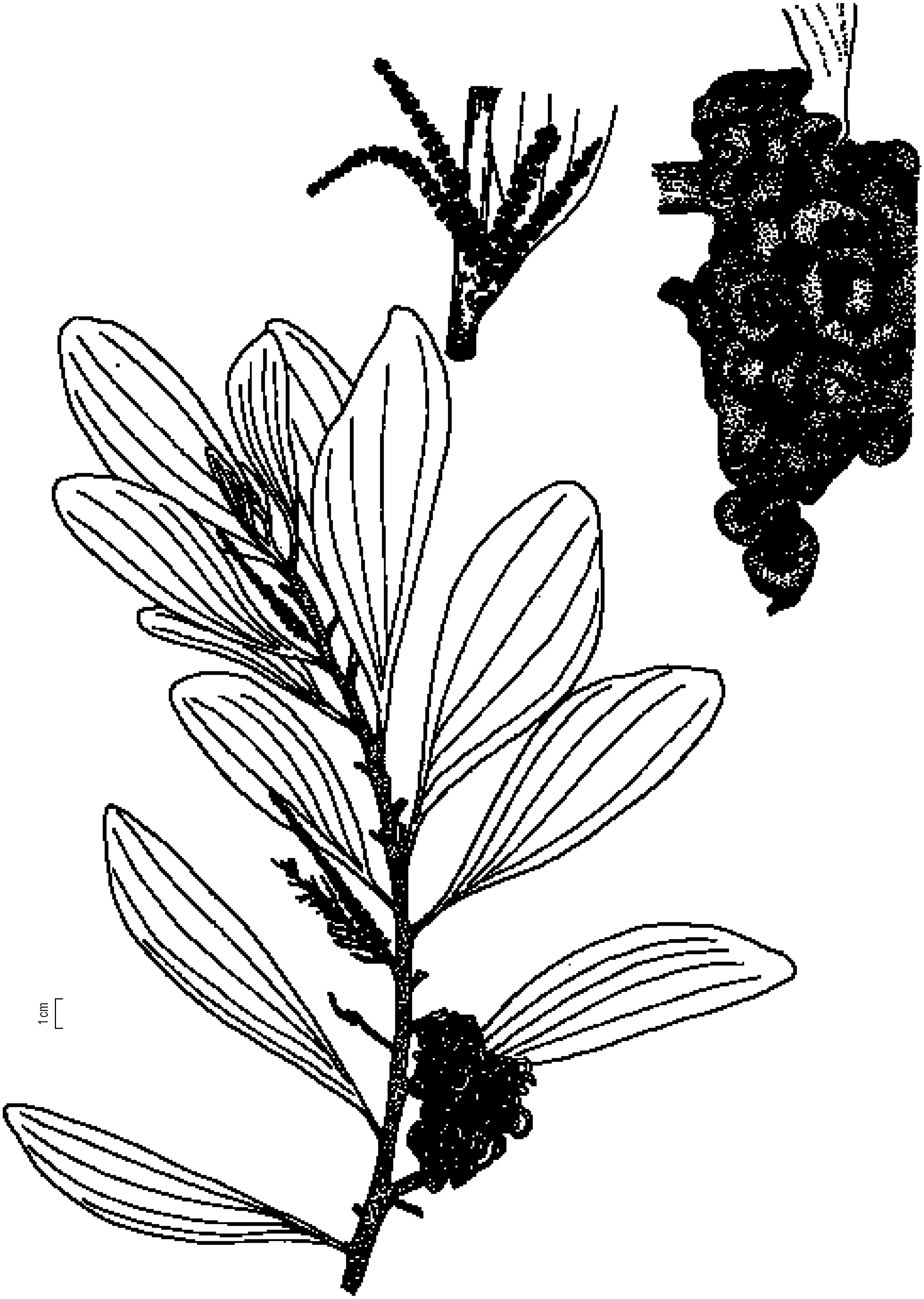
Acacia mangium is planted primarily for site rehabilitation. Its quick growth and dense shade make it an effective tool in reforesting *Imperata* grass swards and reducing fire risk (Nitrogen Fixing Tree Association 1987a). Its ability to grow well on infertile soils, especially those low in phosphorus, make it a favorite for rehabilitation of mine spoils and eroded sites. The tree also produces a usable wood. It is hard and has an air-dry specific gravity of 0.69. The sapwood is cream colored; the heartwood is yellow-brown. The wood is suitable for particleboard, plywood, veneer, pulp, fenceposts, firewood, and charcoal (Nitrogen Fixing Tree Association 1987a). The leaves can be used as livestock fodder (Turnbull 1986).

The small flowers are grouped in spikes up to 10 cm long, singly or in pairs in the leaf axils near the branch tips. The trees flower annually, usually at the end of the rainy season or the early part of the dry season. Fruits ripen 5 to 7 months after flowering (Centro Agronómico Tropical de Investigación y Enseñanza 1992). Flowering occurs in May in Australia with fruits maturing from late October to December. Fruits ripen in July in Indonesia, September in Papua New Guinea (Turnbull 1986), and February to April in Central America (Centro Agronómico Tropical de Investigación y Enseñanza 1992). The dark brown, crinkled, and coiled ripe pods partially open, and the small (2.5 by 4 mm), black seeds hang by orange, fleshy funicles. The seeds are dispersed when small birds consume the oily funicle or they eventually fall to the ground under the mother trees. Individual trees in an *A. mangium* plantation produced 1 kg of seed per year (National Academy of Sciences 1980).

The fruits may be harvested by clipping them from trees with pruning poles when they change to the dark brown color and begin to crack open. Although they are best harvested before the fruits are fully open (Bowen 1981), the pods with hanging seeds remain available on the trees for several weeks. The viability of *A. mangium* seeds tends to increase over the course of the fruiting season while the seed size decreases (Bowen 1981). After air drying, small amounts of seed may be separated by hand. Mechanical separation involves hammer-milling the pods followed by shaking, blowing, and screening. Seed cleaning is difficult because the stringy funicles tangle with debris and screens. Cleaned seeds average 80,000 to 110,000 per kg (National Research Council 1980). Storage with moisture content of 4 to 12 percent at 3 to 5 °C in sealed containers is recommended, but seed stored at ambient temperatures will retain its viability for up to 2 years (Bowen 1981).

Pregermination treatments promote prompt, uniform, and high levels of germination. Seeds should be placed in boiling water for 30 seconds, then cooled by soaking in cold water for 2 hours before planting (Centro Agronómico Tropical de Investigación y Enseñanza 1992). Germination, reported at 60 to 80 percent (after pregermination treatments), may begin after 1 day and continue for 10 to 15 days (Centro Agronómico Tropical de Investigación y Enseñanza 1992, Newman 1989).

Seeds are sowed in germination trays or beds. When seedlings have about three leaves (Turnbull 1986), they are pricked into plastic nursery bags where they grow to plantable size. Seeds are sometimes sowed directly into 1- to 2-liter nursery bags; this method requires thinning to one plant per bag after seedlings emerge. Although *A. mangium* seedlings usually autoinoculate with *Rhizobium* symbiotic nitrogen fixers, artificial inoculation in the nursery is recommended (von Carlowitz 1991). Bare-root planting and direct seeding into prepared seed spots have been used, but because they give low survival, these methods are generally not favored. Seedlings are ready to outplant in about 16 weeks (Turnbull 1986). Plantation spacing affects growth, and individual trees respond with greater diameter increments in spacings from 2.5 by 2.5 m to 4.0 by 4.0 m (Szott 1995). Site preparation may include felling residual woody vegetation, burning grass and slash, and sometimes cultivating. On some sites, weeding may be unnecessary, but planted *Imperata* swards require weeding at 1.5, 3, and 5 months (Nitrogen Fixing Tree Association 1987a). Height growth between 1.5 and 5.0 m for each of the first 3 years, decreasing thereafter, has been observed in some plantations (Szott 1995). In other plantations, 1 to 2 m or more of height growth and 1 to 3 cm of diameter growth per year are usually obtained (Centro Agronómico Tropical de Investigación y Enseñanza 1992, National Research Council 1983b).


1cm

Acacia mearnsii De Wild.

V.M. NIETO and J. RODRIGUEZ
Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

FABACEAE (BEAN FAMILY)

Acacia decurrens Wendl, *Acacia mollisima* De Willd.

Acacia

The *Acacia mearnsii* is a fast-growing but short-lived tree that can reach 25 m in height and 30 cm d.b.h. The crown is wide when the tree is isolated. In closed plantations, *A. mearnsii* grows straight. It has a dark green foliage of persistent nature and compound leaves. The folioles are tightly packed, small, and less whitish in the inferior part. The species requires deep soils with good drainage. It grows in soils with a clayey, loose clayey, loose sandy, or sandy texture. The tree tolerates slightly acid soils with a tendency toward neutrality. It tolerates poor soils but not stagnant waters; the schists and ferruginous subsoils must be avoided. Excessively sandy or lateritic soils must also be avoided. In Colombia, *A. mearnsii* grows between 1800 and 3000 m, where average temperature ranges between 12 and 17 ^{o}C and annual precipitation ranges between 500 and 2000 mm. It is a heliophyte species that does not tolerate prolonged droughts (Montana and others 1974). According to the classification of life zones by Holdridge (1978), *A. mearnsii* grows in the vegetal formations of the Low Mountainous dry forest (bs-MB), Low Mountainous wet forest (bh-MB), and Low Mountainous very wet forest (bmh-MB).

Because *A. mearnsii* has limited uses, its physicomechanical properties have not been obtained. The wood has been used as round wood, props for mines, spikes, firewood, and charcoal and in construction. Additionally, it has been used for short fiber pulp and in tannins. The species fixes nitrogen in the soil, making it useful in soil recovery. The shape and anchoring of its radicle system make it useful in controlling erosion. Occasionally, it has been used as forage, especially in zones and seasons of shortage (Serrato Patiño 1985).

The flowers are light yellow and the fruits are legumes. The seed is rounded, black, shiny, hard, and smooth with a yellow funiculus, 5 cm long, 4 mm wide, and 1 to 2 mm thick. Seeds average 65,053 per kg.

When seeds are stored at a temperature of 4 ^{o}C in hermetic containers, their viability can be maintained for several years. The seeds require a post-ripening period of 2 to 4 months in dry storage before good germination can be obtained. Appropriate pregermination treatment involves mechanical scarification with sandpaper until the seeds lose their shine and appear completely porous. Secondary pregermination treatment consists of submerging the seeds in boiling water for 1 minute, leaving them in the same water for 24 hours, and washing the mucilaginous pulp thoroughly. They may also be immersed in nitric acid at 4 percent for 24 hours.

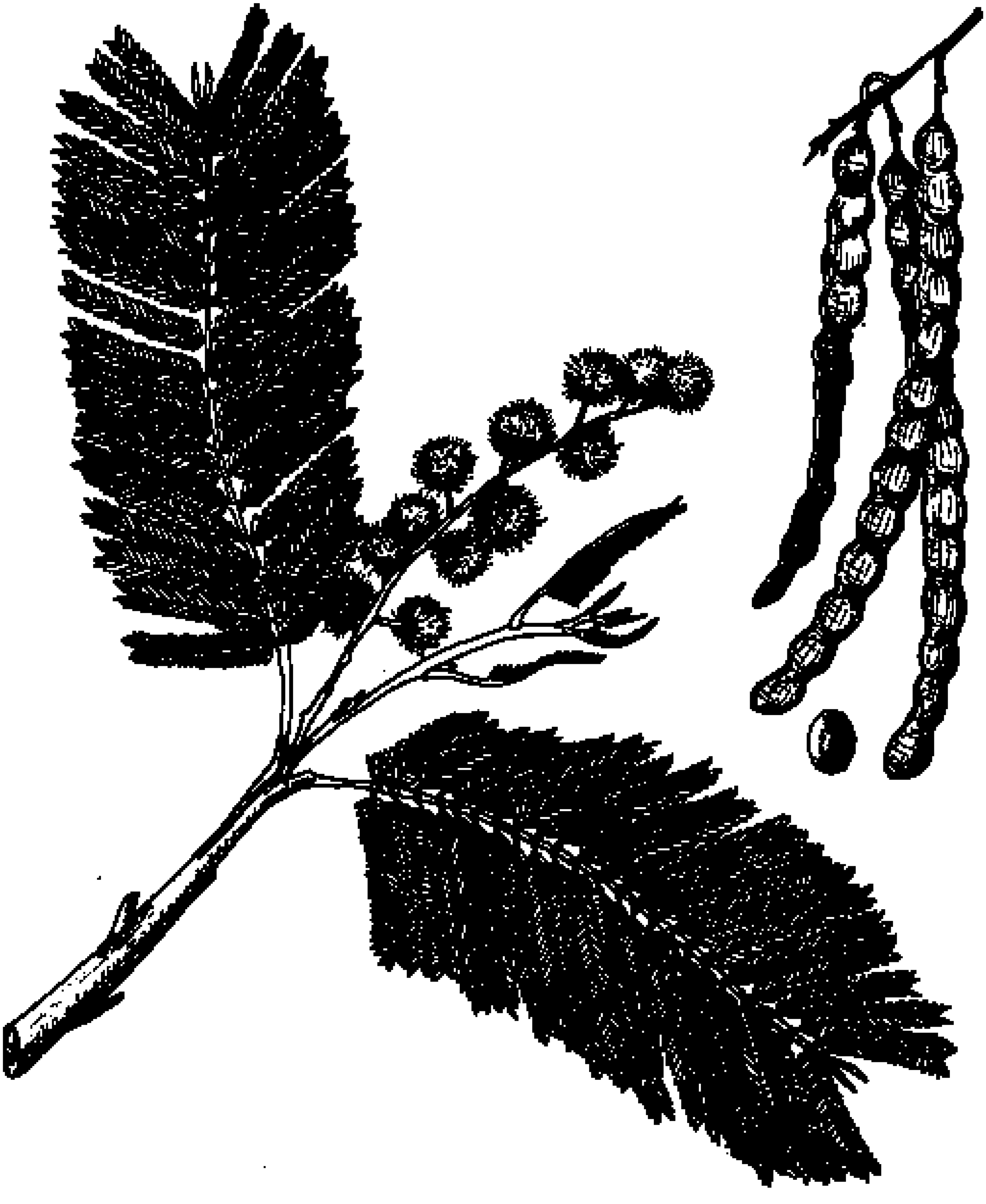
Germination in a laboratory occurs in 2 to 19 days. In the nursery, germination occurs on the 16th day. About 20,000 plantules are obtained per kg of seeds in nurseries (Trujillo 1996).

Because the species is difficult to propagate by stem cuttings, reforestation by using seeds from trees (in groups larger than 30) with desirable phenotypic traits is recommended. Seeds must be sowed in a substrate consisting of two parts sand and one part soil, previously disinfected with a commercial product, such as formol or Basamid, or simply with hot water. They should be sowed deep enough to prevent uncovering when watered. Seeds may be sowed in rows 10 cm apart to obtain 500 plantules per m, or by scattering, using 20 g of seeds per m^2 (Trujillo 1996).

Plantules are lifted when they are 3 to 5 cm in height at approximately 3 months of age. To reduce mortality during transplantation, plantules must be lifted in the shade, avoiding heat and excessive wind. All existing vegetation should be removed from the site. If the soil is very compact, it should be scarified to a depth of 25 cm in a radius of 0.5 cm around the plantule. The initial planting distance between trees is usually 2.5 by 2.5 cm. In agroforestry systems, distances of 6 to 10 m between trees must be used. When the plantules are 30 to 40 cm they can be transplanted to the field.

ADDITIONAL INFORMATION

Acacia mearnsii does not withstand floods and strong winds, which can bend or overturn it. Fungal attacks by *Corticium salmonicolor* occur, and ants can cause serious damage. The tree is susceptible to physiological disorders that manifest themselves as gummosis.



Acacia melanoxylon R. Br.

V.M. NIETO and J. RODRIGUEZ
Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

FABACEAE (BEAN FAMILY)

No synonyms

Acacia japonesa, acacia negra

Acacia melanoxylon is a fast-growing tree that can reach 15 m in height and 20 cm d.b.h. The species grows in loose clayey, loose sandy, or sandy textured soils. It endures slightly acid soils with a tendency toward neutrality and requires good drainage and deep soils. It grows at elevations of 1800 to 3000 m with a minimum temperature of 3 ^{o}C, a maximum temperature of 22 ^{o}C, and an annual average of 15 ^{o}C, with annual precipitation ranging from 900 to 2700 mm. The tree is moderately resistant to frost and tolerates shade during its first years. It grows in the vegetal formations of the Low Mountainous dry forest (bs-MB), Low Mountainous wet forest (bh-MB), and Low Mountainous very wet forest (bmh-MB) (Bartholomaus and others 1990).

Because *A. melanoxylon* is not considered a timber-yielding species, its physical and mechanical properties are unknown. In Colombia, it is used for round wood such as fence posts and firewood, and in the manufacturing of charcoal. It has also been used for furniture and drawers, and occasionally for tool handles, veneer, and plywood. The fruits and especially the wax they produce have been used industrially. As a nitrogen-fixing species, it is fit for the recovery of soils. Its physical traits make it useful as an ornamental or shade tree or in hedges. It can also be used as forage.

The fruits are gathered when they become yellow. When the fruits have dried in the sun for 1 day, the seeds are extracted. Seeds average 56,805 per kg. Seeds are stored at 4 ^{o}C in hermetic containers and can be kept for up to 7 years.

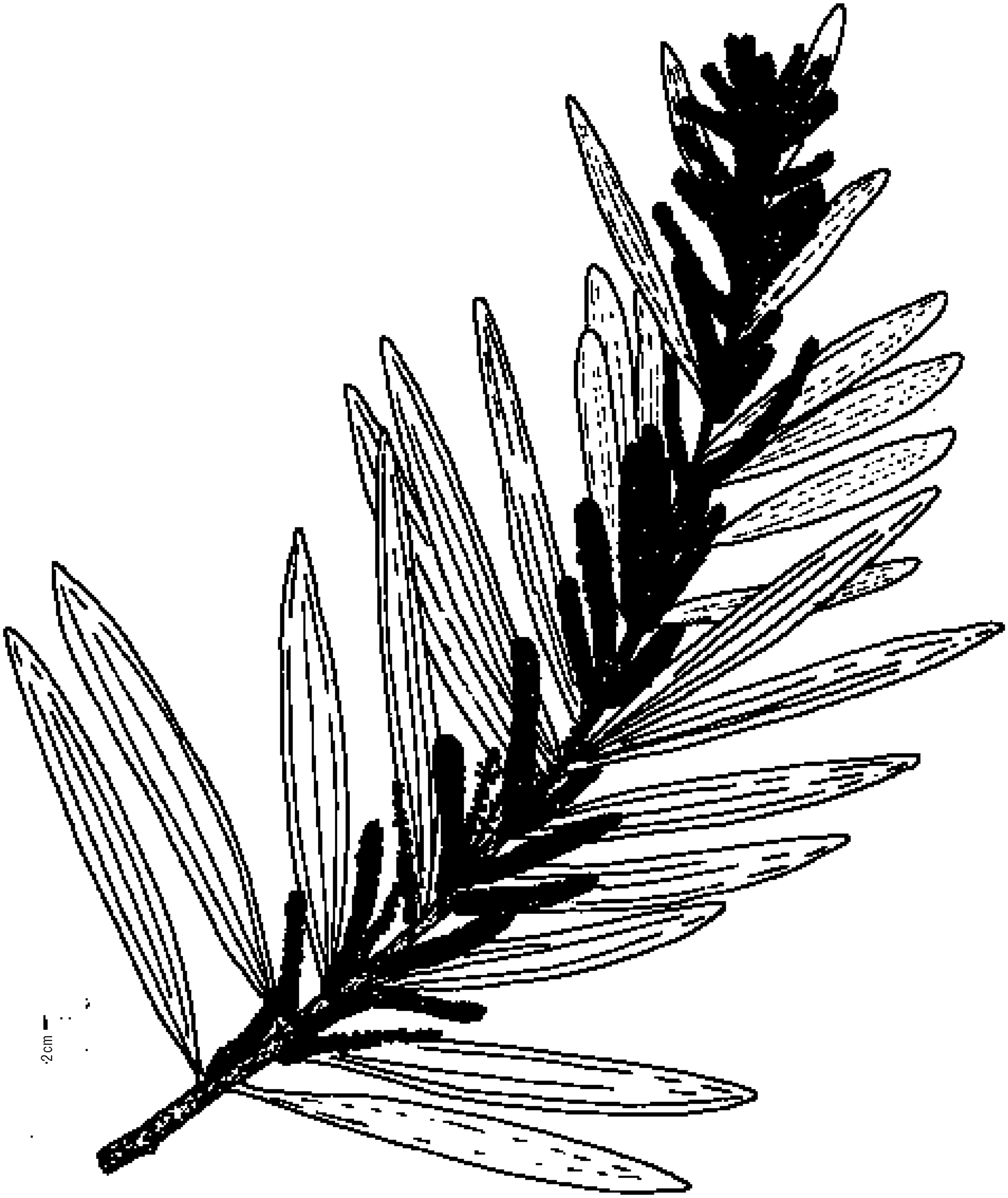
The appropriate pregermination treatment involves mechanical scarification with sandpaper until the seeds lose their shine and appear completely porous. A secondary pregermination treatment consists of submerging the seeds in boiling water for 1 minute and leaving them in the same water for 24 hours. Another pregermination treatment consists of submerging the seeds in concentrated sulfuric acid for 20 minutes. Germination in the laboratory occurs in 6 to 25 days.

About 25,000 plantules are obtained from 1 kg of seed in nurseries (Montero and Estevez 1983). The seeds can be sowed in a definitive place or in seedbeds at 1 cm deep and 1 cm apart from each other, in rows 10 cm apart. The plantules are transplanted when they reach 20 cm. The recommended substrate consists of two parts sand and one part soil, which must be disinfected before planting the seeds. Seeds should be sown deep enough to prevent uncovering when watered, but they should not be embedded. The plantules are lifted when they are 3 to 5 cm tall (Trujillo 1983).

If planting is used to recover soils, the vegetation must be removed in a 50 cm diameter circle around the planting hole. When planting for the production of wood or fruits, the ground must be clear of underbrush. Generally, the trees are planted at minimum distances of 2 by 2 m, with clods of soil. Direct planting can also be used. The species is often planted with the *Pinus radiata* C. Don species to improve the soil. During the first stages of development the trees need to be free from vegetative competition, which requires clearing of the ground at least once or twice a year (Paloma Lozano 1994).

ADDITIONAL INFORMATION

Ants cause great damage to *A. melanoxylon*. The species is also susceptible to damage caused by fungal attacks by *Armillaria* sp. In very wet soils, the roots rot. The trees are easily uprooted by strong winds. These trees should not be planted on avenues or foregardens because they send up shoots and their roots spread.


2cm

Acosmium panamense (Benth.) Yakovlev

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FABACEAE (BEAN FAMILY)

No synonyms

Bálsamo amarillo, cencerro, chakté, chichipate, corteza de Honduras, guayacán, huesillo, quina silvestre, yacti

Native to the tropical regions of America, *Acosmium panamense* is naturally distributed in southern Mexico and all of Central America. The species is part of the evergreen tropical forests (Standley and Steyermark 1946a).

Acosmium panamense is an evergreen tree that grows up to 40 m in height and 95 cm d.b.h. Its rate of growth is unknown. The trunk is straight and may have small spurs. Composed of rising branches, the crown is spread out, pyramidal, and sometimes flattened. Leaves are imparipinnate, 9 to 22 cm long, with 9 to 13 ovate to oblong-lanceolate leaflets 5 to 7 cm long. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an annual average temperature of 26 °C with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May, and the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging from 900 to 1800 mm.

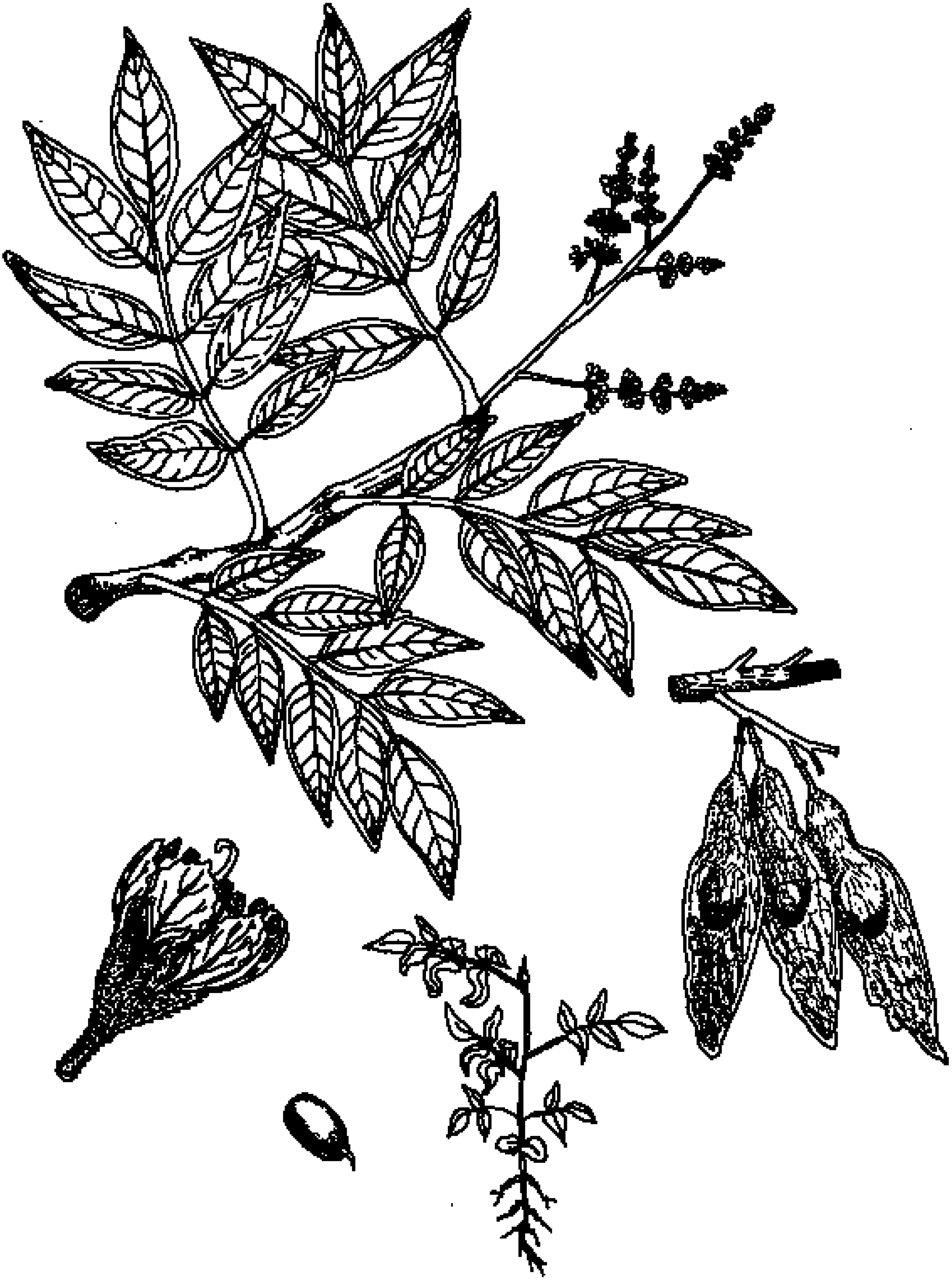
The wood has a specific gravity of 1.10 and a specific weight of 1.260. The wood is hard, heavy, strong, and resistant. It is used in rural areas for construction. In El Salvador, the bark is used to treat malaria (Dillon 1980, Pennington and Sarukhan 1968).

Acosmium panamense blooms September through November. The fragrant flowers are white, cream, or yellow; 6 mm long; and arranged in panicles. The fruits (legumes) ripen November through March. The legumes are oblong to elliptic oblong, narrowly alate, indehiscent, 5 to 9 cm long by 2 cm wide, laterally flattened, obtuse, mucronate, and acute at the base and have reticulate nervation. Each fruit contains one to four seeds (Pennington and Sarukhan 1968, Standley and Steyermark 1946a).

The fruits are collected January through April. They are gathered when their pericarp is dry and they are brown in color. The fruits are cut from the tree by using long, wood poles with metallic hooks. The gathered fruits are dried in the sun for 1 or 2 days to facilitate breaking. The fruits are placed in the sun inside boxes to prevent the wind from scattering them. The seeds are extracted by breaking the fruits by hand. Impurities are removed from the seeds in several ways. One method involves using sieves. Another involves using the air current of a fan. In this latter method, the seeds are placed in a vertical column separator of impurities through which a stream of air is passed. The materials that are lighter than the seeds are quickly removed. Clean seeds average 12,640 (Vega and others 1981) per kg. Seeds will remain viable naturally for 12 months. Seeds germinate 12 days after sowing, with germination at 7 percent (Vega and others 1981).

ADDITIONAL INFORMATION

The seed hilum is subbasal, elliptic, split, 1 mm long, and surrounded by a whitish hilar aril. The micropyle is puntiform and discernible under the microscope. The lens is elevated like a small protuberance, black, rhomboid, located near the hilum, on the trajectory of the vascular bundle, and opposite the micropyle. The endosperm is abundant, whole, located on the lateral surfaces of the embryo, vitreous, whitish, translucent, and gelatinous when it comes in contact with water. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are shaped like the seed; they are whole, expanded, flat, pulpy, and independent of one another and have a cordate base. The plumule is rudimentary. The radicle is conical and partially covered by the cotyledons (Dillon 1980; Hutchinson 1964; Niembro 1982, 1983; Rudd 1972).



Acrocarpus fraxinifolius Wight. & Arn.

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FABACEAE (BEAN FAMILY)

No synonyms

Acrocarpo, árbol guijarra, cedro rojo, decro rosado, fresno, fresno hindú, Kenya shade tree, lazcar, mundani, pink cedar, shingle tree

Acrocarpus fraxinifolius is native to the tropical regions of Asia. Distributed naturally in India, China, Burma, Borneo, Sumatra, Indonesia, Vietnam, and Bangladesh, the species is part of tropical evergreen and subevergreen forests.

Acrocarpus fraxinifolius is a fast-growing tree, which annually can grow 1.3 to 3 m. The tree can reach 60 m in height and 2.4 m d.b.h However, 90 cm is the most frequent d.b.h. The straight trunk has spurs and the round crown is composed of rising branches. The leaves are bipinnate, with five to six pairs of pennae. The species grows in acid and calcareous soils, at elevations between sea level and 2000 m (Troup 1921). In Mexico, it prospers from sea level to 1700 m elevation, in places with annual precipitation between 500 and 3000 mm and temperatures between 15 and 26 °C.

The wood of *A. fraxinifolius* is hard and strong. Because it physically resembles ash and walnut woods, it is used as a substitute for these two species. The wood is used in the construction of houses and in the manufacture of furniture and packing cases. In Africa the tree is planted to provide shade in coffee plantations. *Acrocarpus fraxinifolius* is also cultivated as an ornamental (National Academy of Sciences 1979, Whitmore and Otarola 1976).

The flowers are scarlet red and arranged in axillary racemes. In its natural habitat *A. fraxinifolius* blooms during the dry season, and the fruits ripen 1 month after the bloom. Introduced in the Yucatan Peninsula (Mexico), the species flowers March through May, and the fruits ripen May through August. The fruits remain on the tree for 5 to 6 weeks. The dark brown legumes are 8 to 16 cm long, 1 to 2 cm wide, laterally flattened, narrowly alate on one side and belatedly dehiscent. Each fruit contains 5 to 7 seeds (Holdridge and Poveda 1975, National Academy of Sciences 1979). The seeds are ovate to oval, laterally flattened, 4.6 to 6.8 mm long, 3.4 to 4.2 mm wide, and 1.4 to 1.6 mm thick. The seedcoat is brown to dark brown, smooth, opaque, and cartaceous, and very hard with small fracture lines.

Fruits are collected from the ground or from the trees. A long pole with metal hooks is used to collect fruit from trees. The fruits are placed inside wood boxes with metallic mesh bottoms; the boxes are placed in covered, ventilated areas. When the fruits are dry, they are macerated by hand. The seeds are easily extracted by banging the fruits with a stick. Impurities are removed from the seeds in several ways. One method involves using sieves. The other method involves using the air current of a fan. In this later method, the seeds are placed in a vertical column separator of impurities through which flows a stream of air. The materials that are lighter than the seeds are quickly removed. Clean seeds average 31,600 per kg. The seeds can be stored in polyethylene bags at room temperature for more than 1 year without losing viability (Chavelas and Devall 1988a).

Because the seed teguments are hard and impermeable, pretreatment is required. Two forms of treatment are used: scarifying with concentrated sulfuric acid for 10 minutes or submerging the seeds for 1 minute in water at a temperature of 90 °C. They then are left soaking in cool water for 5 to 6 hours. The treated seeds are planted 2 cm deep in seedbeds, and germination occurs within 15 to 30 days. Germination is epigeal (Chavelas and Devall 1988a).

ADDITIONAL INFORMATION

The hilum is subbasal, circular, and generally covered by a small funicular aril. The micropyle and lens are indiscernible. The endosperm is abundant, whole, located on the lateral surfaces of the embryo, cornaceous, whitish, translucent, and gelatinous when it comes in contact with water. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are shaped like the seed, whole, expanded, flat, foliaceous, and independent of one another. The plumule is partially developed in pinnae. The radicle is conical, prominent, and slightly oblique (Hutchinson 1964; Watson and Dallwitz 1983a, 1983b).


2cm

Adenanthera pavonina L.

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FABACEAE (BEAN FAMILY)

No synonyms

Arbre a réglisse, circassian bean, corail végétal, coral, coralillo, coralín, coralitos, jumbie-bead, mato colorado, palo de mato, peonia, peronias, peronias chatas, red sandalwood, réglisse, sandal beadtree

Adenanthera pavonina is found naturally in India. In America, it has been introduced in Puerto Rico, Cuba, Jamaica, Trinidad, Tobago, Venezuela, Brazil, Costa Rica, Honduras, and southern Florida.

Adenanthera pavonina is a deciduous tree that reaches 60 m in height and up to 45 cm d.b.h. The trunk is basically straight with smooth bark and many fissures. The spreading crown has relatively few leaves. The leaves are bipinnate and 30 to 60 cm long with numerous oblong leaflets that are rounded on both ends and have a small point at the apex.

Adenanthera pavonina has been planted as a shade and ornamental tree in urban centers and gardens (Food and Agriculture Organization 1957). The wood has a specific gravity of 0.60 to 0.80 and is strong and durable; it is used for firewood and in rural construction, carpentry, and cabinet making. It is also used to make red dye. The seeds are ground and mixed with water and borax to manufacture a type of cement. The seeds are also used as beads in necklaces and bracelets (Hoyos 1979, Kostermans 1980, Little and others 1967). The pulp of the fruit is used for medicinal purposes.

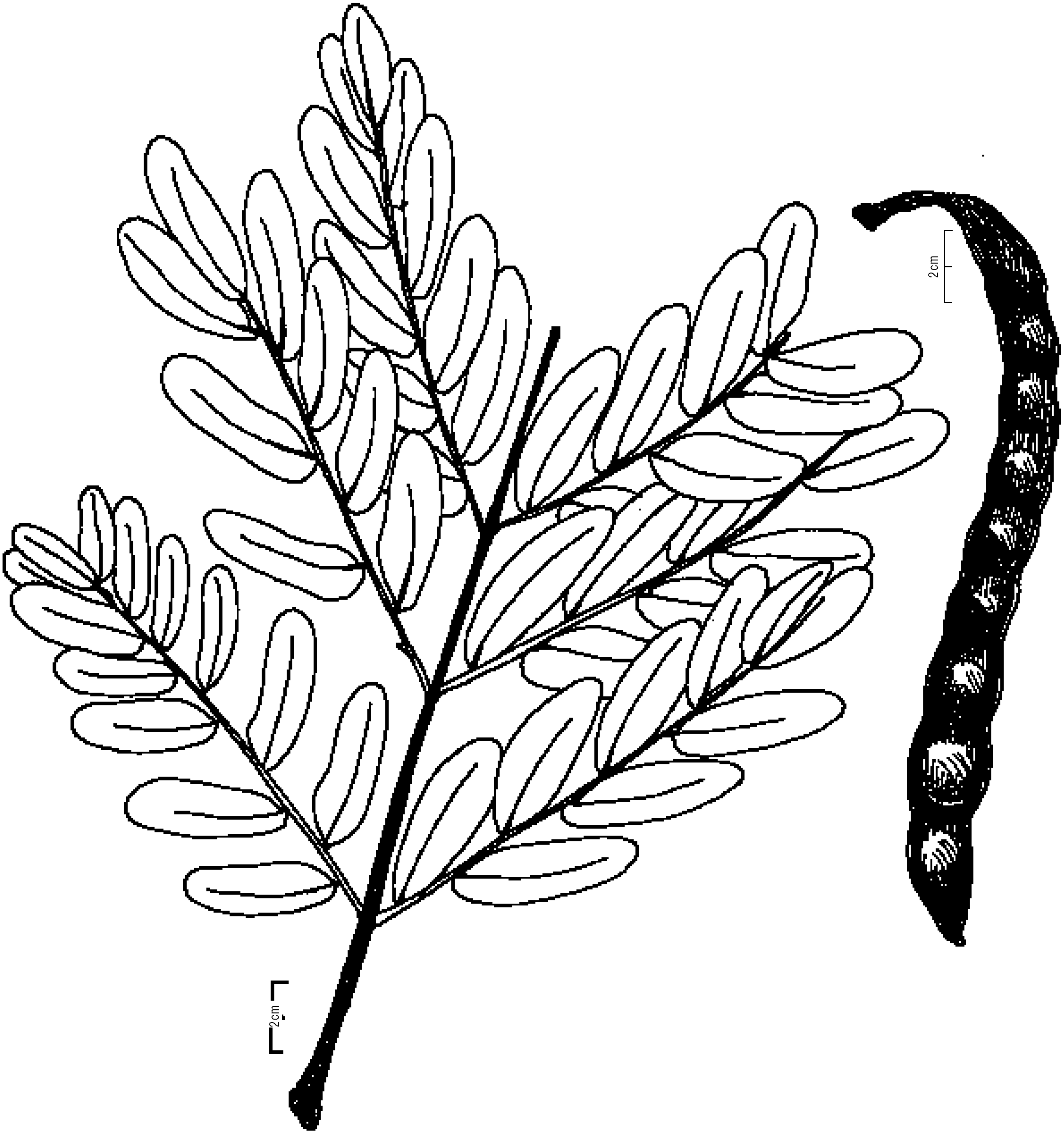
The tree blooms from the end of summer until winter. The flowers are pale yellow to orange and arranged in racemose inflorescences. The fruits (legumes) ripen in the fall or winter of the same year (Little and Wadsworth 1964). The dark brown legumes are straight or curved, narrowly oblong, laterally flattened, about 25 cm long and 1 cm wide and have dehiscent valves that twist as they open on ripe fruit (Isely 1973, Little and others 1967). The seeds are ovate to elliptic-lenticular, laterally flattened, biconvex in cross section, 9.0 to 9.4 mm long, 8.0 to 9.0 mm wide, and 5.8 to 6.2 mm thick. The seedcoat is scarlet red to coral red, smooth, shiny, bony, and very hard and generally has no fracture lines.

Because the fruits are dehiscent, collection is determined by the presence of warm, dry winds. Under these conditions, the fruits open quickly, releasing the seeds. Collectors watch for the change in coloring of the pericarp, which goes from green to brown and finally to dark brown. The fruits must be collected shortly before they open up and release the seeds. Seed collectors climb the trees and use poles with metal hooks to cut fruits from the trees. The fruits are placed in wooden boxes with metallic mesh bottoms and stored in sheds with good ventilation. As the fruits dry, the valves twist open, releasing seeds. The seeds are gathered by hand and passing them through sieves removes the impurities resulting from seed extraction. Small impurities and dust are removed using a vertical column blower. Clean seeds average 3,250 per kg (Food and Agriculture Organization 1957).

The seeds are stored in hermetically sealed plastic, glass, or metal containers at room temperature or in cold chambers with temperatures of 5 to 6 °C. The seeds of this species show a high capacity for germination (Food and Agriculture Organization 1957).

ADDITIONAL INFORMATION

The seeds have pleurogram or fissural line lateral surfaces that follow the contour of the seed and open up on the hilar end. The rose hilum is elliptic or puntiform, sometimes covered by a small funicular aril and pulp, and lobed. The micropyle is indiscernible. The lens is oblong at the opposite end from the micropyle. The endosperm is abundant, whole, located on the lateral surfaces of the embryo, cornaceoous, whitish, translucent, and gelatinous when it comes in contact with water. The yellow embryo has a straight axis and is almost laterally symmetrical. The cotyledons are shaped like the seed; they are whole, expanded, plano-convex, and independent of one another. The plumule is moderately developed in pinnae. The radicle is conical and partially covered by the cotyledons (Bravato 1974; Corner 1951, 1976; Gunn 1984).


2cm
2cm

Albizia adinocephala (Donn. Sm.) Britton & Rose

L.A. FOURNIER
Escuela de Biología, Universidad de Costa Rica

FABACEAE (BEAN FAMILY)

Pithecelobium adinocephalum Donn. Sm., *P. discolor* Pitt.

Chaperno blanco, gavilán, gavilana

Albizia adinocephala grows on the Atlantic and Pacific coasts of Central America from Belize to Panama.

Albizia adinocephala is a fast-growing, medium-sized tree reaching 6 to 18 m in height and 30 to 45 cm d.b.h. The tree has a straight trunk, dense crown, and gray, smooth bark. The leaves are alternate and bipinnate, with stipules; the pinnae are 1 to 3 jugate; the leaflets are 2 to 5 jugate, lanceolate or ovate (sometimes ovate-elliptic), 2 to 6 cm long, 1 to 2 cm wide, glabrous, pale beneath, with an extrafloral nectary at the petiole base. The tree grows from sea level to 1200 m in a wide range of soil types, rainfall, and temperatures.

The tree is used for firewood. Because the species can grow in a wide range of environmental conditions, this author thinks it has potential for forest recovery and planting in agroforestry systems.

Albizia adinocephala flowers most of the year; however, in the seasonal climate of the low and middle lands, it flowers primarily from July through August. The small white flowers have paniculate heads and white stamens. The fruit is a flat, glabrous legume, 10 to 17 cm long and 1.5 to 2 cm wide. The fruit matures 7 to 8 months after flowering, most frequently from September to April.


1cm
1cm
1cm

Albizia lebbeck (L.) Benth.

JOHN A. PARROTTA
International Institute of Tropical Forestry, USDA Forest Service

FABACEAE (BEAN FAMILY)

Albizia lebbeck (L.) Benth.

Acacia, acacia amarilla, algarrobo de olor, amor platónico, aroma, aroma francesa, barba de caballero, barba di junkuman, black ebony, bois noir, cabellos de ángel, canjuro, carbonero de sombr'o, casia amarilla, chachá, coracáo de negro, dormilón, East Indian walnut, forestina, guarmuche, koko, lebbek, lebbek albizia, lengua de mujer, lengua viperina, muche, músico, pisqu'n, samán, shack-shack, singer-tree, siris-tree, tcha-tcha, tibet-tree, vieille fille, West Indies-ebony, whistling-bean, woman's-tongue (Little and Wadsworth 1964)

The genus *Albizia* comprises approximately 150 species, mostly trees and shrubs native to tropical and subtropical regions of Asia and Africa (Allen and Allen 1981, National Research Council 1979). *Albizia lebbeck* is native to deciduous and semideciduous forests in Asia from eastern Pakistan through India and Sri Lanka to Burma. The tree has been introduced as an ornamental and plantation tree throughout the tropics and northern subtropics, including the Greater and Lesser Antilles, Central America, Colombia, Venezuela, and Brazil (Adams 1972, Grisebach 1864, Hutchinson and Dalziel 1958, Little and Wadsworth 1964).

Albizia lebbeck is a fast-growing, medium-sized deciduous tree with a spreading umbrella-shaped crown of thin foliage and smoothish, finely fissured, grayish-brown bark. Depending on site conditions, annual height growth ranges from 0.5 to 2.0 m; on good sites, individual trees attain an average maximum height of 18 to 25 m and 50 to 80 cm d.b.h. (Parrotta 1988a, Troup 1921). The species grows well from sea level to 1500 m on sites receiving between 500 and 2500 mm annual rainfall and tolerates both light frosts and drought (Troup 1921, Venkataramany 1968). While it grows poorly on heavy clay soils, it tolerates saline, sodic, and lateritic sites. The tree grows best on moist, well-drained soils (Bangash 1977, Troup 1921).

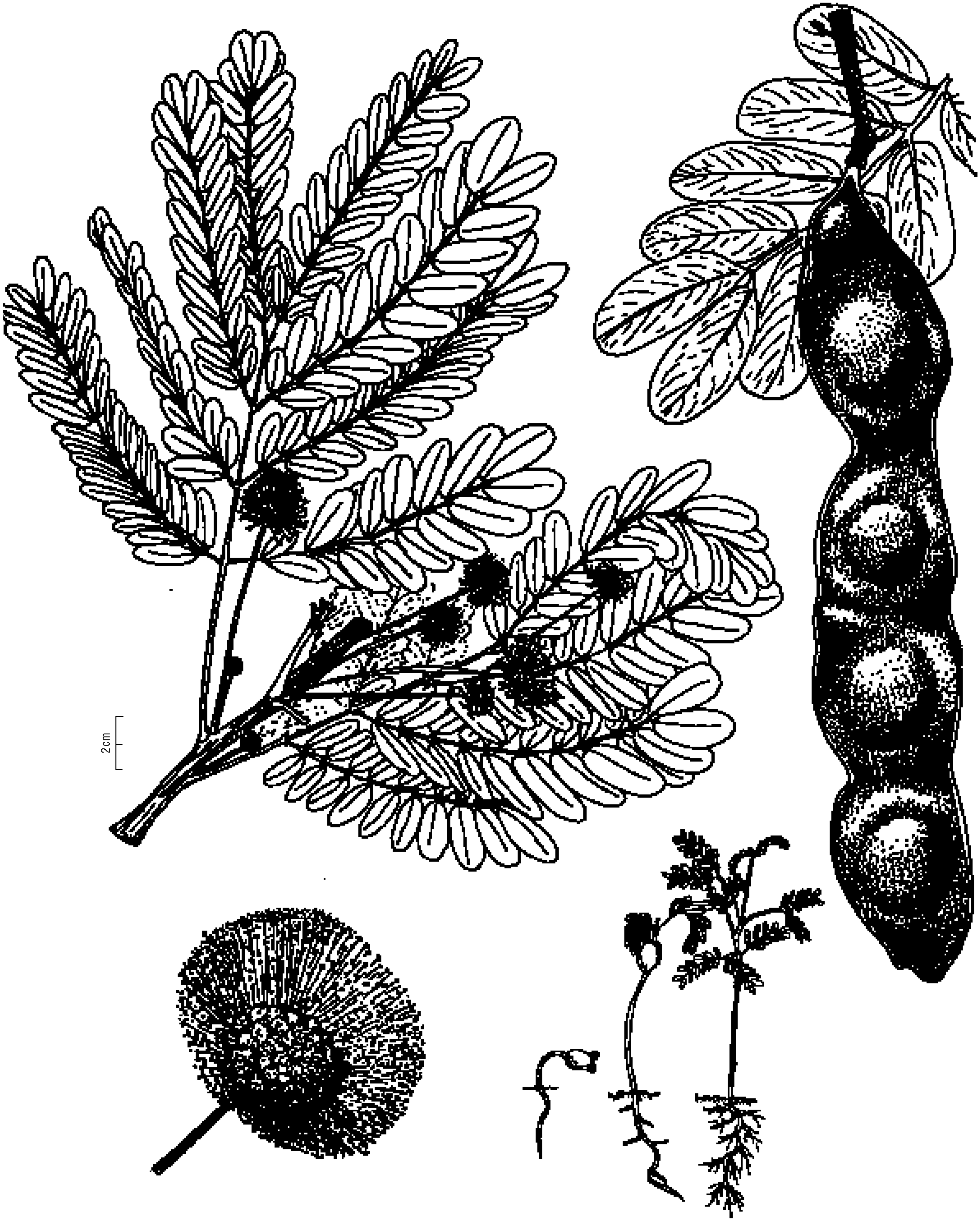
Albizia lebbeck, a valued timber species within its native Asian range, was previously exported to Europe under the trade name East Indian walnut (Allen and Allen 1981, Troup 1921). Its light yellowish-brown to light brown heartwood has a specific gravity of about 0.55 to 0.90 and is coarse-grained, strong, and relatively durable. It seasons and works well and is used for furniture, flooring, veneer, paneling, carving, posts, and a variety of agricultural implements. The cut bark yields a reddish-brown gum that is used as a substitute for gum arabic obtained from *Acacia senegal* Willd. (Farooqi and Kapoor 1968, National Research Council 1979). Its leaves, seeds, bark, and roots are all used in traditional Indian medicine (Chopra and others 1956, Kirtikar and others 1935). In its native range, the species is sometimes planted as a shade tree in coffee, tea, cardamom, and cacao plantations. It is also pollarded to use as a host for the lac insect (Macmillan 1962, Venkataramany 1968).

Flowers usually appear with new leaves over an extended period beginning at the end of the dry season; in the Caribbean region this season occurs between April and September (Little and Wadsworth 1964). Flowering can occur on trees as young as 10 months (Parrotta 1988a). The fragrant, cream-colored flowers develop on lateral stalks in rounded clusters 5 to 7.5 cm across the many threadlike, spreading, whitish-to-yellow stamens tipped with light green, borne at the ends of lateral stalks 4 to 10 cm long. The fruits, flattened pods 10 to 20 cm long and 2.5 to 3.8 cm broad, are produced in large numbers and each contains several seeds. Immature pods are green, turning straw-colored on maturity, usually 6 to 8 months after flowering. The dry pods remain on the tree well into the following flowering season. Seeds are released from the mature, dehiscent pods while still attached to the tree or from windblown pods that later split open or decompose. Under natural conditions, insect attack is responsible for high seed predation (Parrotta 1988a).

The mature pods may be collected by hand from the ground or low branches or clipped with pruning poles. Seeds are easily extracted from the pods by hand or by crushing the pods and winnowing. *Albizia lebbeck* seeds are small, oblong, approximately 9 by 7 mm long and broad, compressed, and light brown in color with a smooth, hard testa. Seeds average from 7,000 to 11,000 per kg (Parrotta 1988a).

Seeds may be sowed without pregermination treatment, although soaking the seeds in boiling water for 1 minute, followed by cool water for 24 hours, increases germination rate and uniformity. Germination of freshly extracted seeds in Puerto Rico was 60 to 90 percent; after 1 year of cold storage at 5 to 10 °C, percentage germination dropped to 12 percent (Parrotta 1988a). However, seeds can be stored for up to 5 years in sealed containers at room temperature with only moderate reduction in percentage viability (Troup 1921, Venkataramany 1968).

Germination is epigeal, and generally occurs between 4 to 20 days after sowing, with peak germination a 12 to 18 days (Parrotta 1988a). Germination and early seedling development are favored by sowing seeds just below the soil surface in a loose, moist medium under light shade or full sun (Troup 1921, Venkataramany 1968). If inoculated with *Rhizobium* or sowed in soils that contain these nitrogen-fixing bacteria, lateral roots quickly develop large, branched nodules. In Puerto Rico, seedlings raised in plastic sleeves under light shade reached plantable size (20 to 30 cm) in 3 months (Parrotta 1988a). Seedlings develop a long, stout taproot at an early age, are drought-tolerant, and require only minimal weeding during the first months after outplanting.


2cm

Albizia niopoides (Spruce ex Benth.) Burkart

E.M. FLORES
Academia Nacional de Ciencias de Costa Rica, Costa Rica

FABACEAE (BEAN FAMILY)

Feuilleea niopoides (Spruce ex Benth.) Kuntze (Revisio Generum Plantarum 1: 188; 1891); *Pithecellobium caribaeum* Urb. (Symbolae Antillanum 2[2]: 260; 1900); *Pithecolobium hassleri* Chodat (Bulletin de l'Herbier Boissier, sér. 2, 4: 483; 1904); *Albizzia caribaea* (Urb.) Britton & Rose (North American Flora 23[1]: 44; 1928); *Acacia guacamayo* (Britton & Killip) Standl. (Tropical Woods 52: 26; 1937); *Albizia hassleri* (Chodat) Burkart (Darwiniana 7: 517; 1947); *Albizia richardiana* King & Prain (Annals of the Royal Botanic Garden, Calcutta 9: 32; 1940); *Pithecellobium niopoides* Spruce ex Benth. (Transactions of the Linnean Society of London 30[3]: 591; 1875); *Senegalia guacamayo* Britton & Killip (Annals of the New York Academy of Sciences 35[3]: 142; 1936); *Senegalia liebrmannii* Britton & Rose (North American Flora 23[2]: 116; 1928)

Gallinazo, gavilana, guanacaste blanco, silk tree (Barneby and Grimes 1996, Brako and Zarucchi 1993 Burkart 1979)

The genus *Albizia* has about 150 species of unarmed, small to large trees widely spread in the tropical and subtropical zones of Asia, Africa, Australia, Mascarene islands, and America (Nilsen 1981, Zamora 1991). It reaches the greatest diversity in Africa, Madagascar, and Central and South America (Nilsen 1981). The species extends from southern Mexico throughout Central America to eastern Peru and the Amazon region to the Brazilian coast. It is also found in the Antilles (Barneby and Grimes 1996, Brako and Zarucchi 1993, Burkart 1979).

Albizia niopoides is a medium-to-tall tree, 10 to 30 m in height and 35 to 100 cm d.b.h.(Laboratorio de Productos Forestales 1981). The tree has a straight bole and glabrous young twigs which are greenish or yellowish with scarce lenticels (Zamora 1991). The crown is wide, round, extended, resembling that of *Enterolobium cyclocarpum* (Jacq.) Griseb. The bark is light gray or yellowish with exfoliating, thick scales in a concentric pattern; the scales leave crateriform scars which seem excavated with a chisel (Holdridge and Poveda 1975, Salas Estrada 1993, Zamora 1991). Leaves are alternate, bipinnate, paripinnate; with 5 to 10 pairs of opposite pinnae, each with 30 to 55 pairs of pinnules (foliolules). The tree grows well in the dry tropical forests of the lowlands in Central and South America at elevations from 0 to 500 m, temperatures of 24 to 32 °C, and annual rainfall of 1000 to 2500 mm. The soils are alluvial, floodable but with good drainage, on plateaus and flatlands with slopes of 5 percent and moderate drainage (Hartshorn and Poveda 1983). The species can reach higher elevations (up to 1200 m) and can be found in humid forests (Holdridge and Poveda 1975, Salas Estrada 1993). Frequently, the tree is emergent in the canopy of primary dry forests (Hartshorn and Poveda 1983).

The tree's attractive form makes it suitable for shade and as an ornamental. The heartwood is light reddish-brown and the sapwood is yellow; the wood is heavy (green weight = 1000 kg per m^3, with 58 to 60 percent moisture and specific gravity of 0.60 to 0.65), with a medium texture, homogeneous, straight or interlocked grain, and medium luster and has a golden glare in the radial surface. It exudes a light, rancid, vanilla odor, and the taste is not characteristic (Creemers and Lemckert 1981, Herrera and Morales 1993). Volumetric contraction is low (9.8). The mechanical properties are medium (Herrera and Morales 1993). The air-dried wood shows small splits on the sides and ends. It is moderately easy to work and saw and it polishes well. Natural durability is low but the wood can be preserved and impregnates well. It can be used in heavy construction (treated wood), general interior and exterior construction, mine posts, railroad foundations (treated wood), fences (treated wood), sticks, carts, floors, furniture, match boxes, and handles. It is also used as firewood (Herrera and Morales 1993, Salas Estrada 1993) and in papermaking (Runkel Factor = 0.44 to 0.46; Peteri's Coefficient = 78 to 80) (Laboratorio de Productos Forestales 1981). The species has been used in the native pharmacopoeia. South American natives used the saponin-rich roots to heal contusions and anginas, and the boiled bark is used to heal scorpion bites. The species has been planted primarily in grasslands and areas undergoing early natural regeneration because its nitrogen-fixing capacity improves the soil.

Albizia niopoides flowers in March and April. The fragrant, white flowers are grouped in pedunculate heads and are pentamerous, synsepalous and synpetalous. The calyx is tubular, distally toothed, and 1 mm long. The corolla is funnelform, valvate, and 2 to 3 mm long. The numerous stamens are basally united forming a tube. The anthers are small (Woodson and Schery 1950b). Fruits are found mainly in August and September. The pod is laterally compressed (6 to 14 by 1 to 2.5 cm), straight, glabrous, thin, chartaceous, and longitudinally dehiscent (Zamora 1991). The pericarp is brown or yellowish brown and dull with an inconspicuous mesocarp. The endocarp is dull, whitish, and slightly septate, with many seeds, transverse, not overlapping, in one series (Gunn 1984, Holdrige and Poveda 1975). The seeds are ovate or oblong, laterally compressed, and without aril; the testa is thick, glossy, creamy or light brown, monochrome, hard, and osseous, with pleurogram, linea fissura open at the hilar end, and fracture lines. The funiculus is long, filiform, and whitish or light brown.

Pods must be collected before dehiscence by shaking the tree's branches or by gathering those on the ground. Seeds average about 22,500 per kg. The seeds are hard and have orthodox behavior. They have acceptable germination after storage for 1 to 2 years. Seeds should be soaked in hot water (80 ^{O}C) for 1 minute followed by a bath in lukewarm water (30 to 40 ^{O}C) for 24 hours. This pretreatment contributes to uniform germination, and floating seeds can and must be removed. After imbibition the seeds must be sown in greenhouse beds filled with potting mix or sand at ambient temperature (24 to 32 ^{O}C). The percentage of germination is 85 percent if damaged seeds are discarded.

Germination is epigeal, and the seedling is phanerocotylar. The root protrudes in 2 to 4 days. The taproot may or may not have nitrogen-fixing nodules. The first eophyll is pinnate. The seedling must be transplanted to plastic bags before the first eophyll completes its extension. In some experiments, the seeds have been sown directly in the soil, and outplanted as pseudosticks. If seedlings develop in plastic bags they can be transferred to the field in 4 months. Four-month-old seedlings are 35 to 40 cm tall.

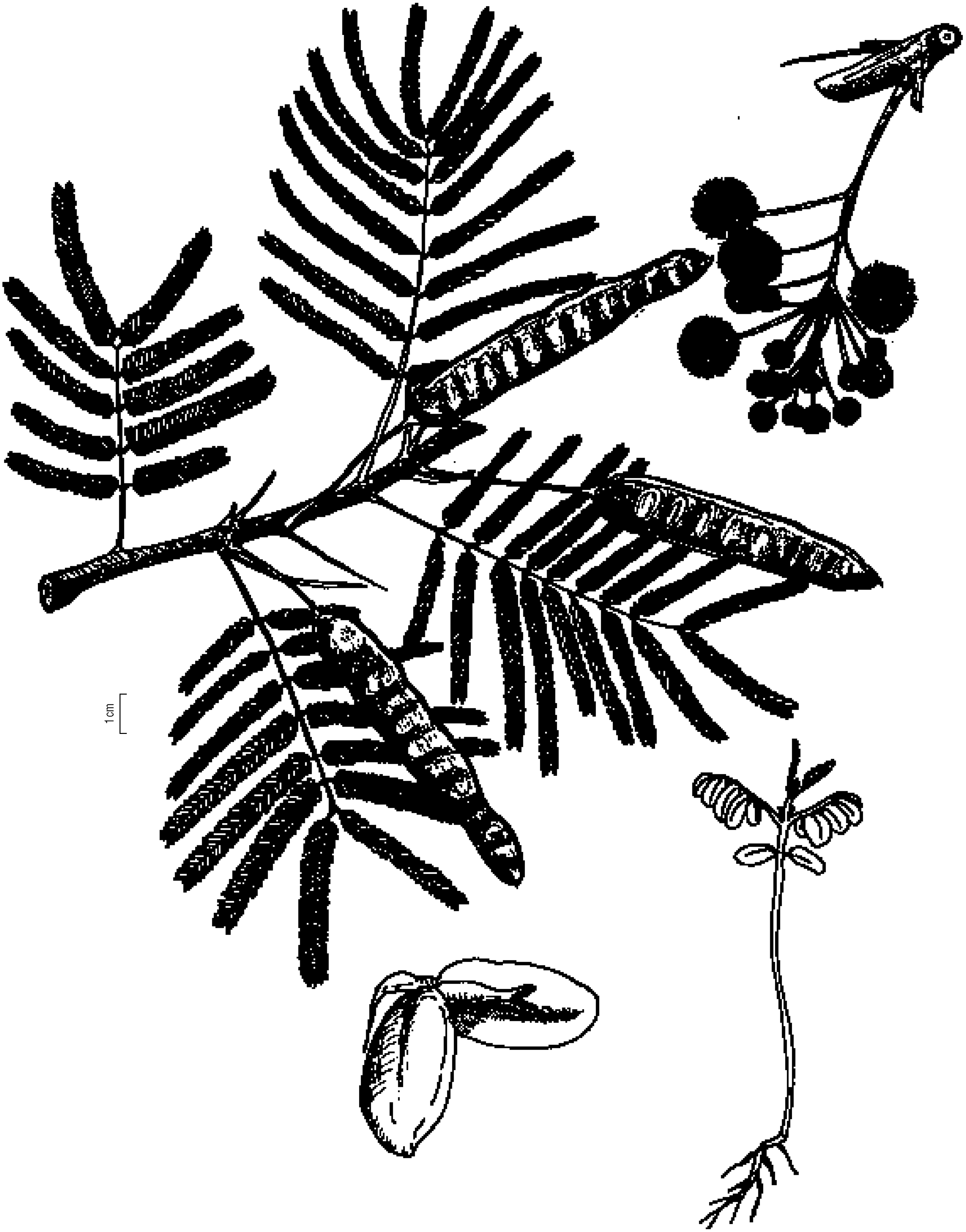
ADDITIONAL INFORMATION

The leaf pinnules are (5-) 7-9 (-11) by 1 (-2) mm, linear, apex obtuse or acute, and glabrous. The petiole has a short pubescence and is pulvinate. The pulvinus is adaxial, basal, concave, and longitudinally oblong. The rachis is adaxially channeled, bearing an extrafloral nectary toward the distal end. The petiolules bear basal and adaxial pulvinuli. Stipules are 6 to 7 mm long, setiform, and deciduous (Zamora 1991). The flowers are sometimes heteromorphic in the same head, and the central flowers have thicker staminal tubes and dimensions different than those in the marginal (Nilsen 1981). The gynoecium is monocarpellar, and placentation is laminar. The numerous ovules are anatropous, bitegmic, and crassinucellate.

Primarily pollinated by moths, the flowers are also visited by other insects, hummingbirds, and passerine birds; whether birds are visitors or pollinators is unknown. Pollen is partially heteromorphic, with internal pores, occurrence of two supplementary sets of pores, nonequatorial apertures of the simple porate type, exine areolate, and tectum sometimes perforate (Guinet 1981).

The hilum of the seed is small, exposed, and sometimes concealed by funicular remnants. The vascular bundle extends around the seed from the hilum to the micropyle in the raphe-antiraphe line. The endosperm and perisperm are absent. The embryo is large and investing; the embryo axis is straight and the radicle is short and thick. The plumule is well developed with several foliar primordia and the cotyledons are large, thick, and ovate, enclosing the embryo axis.

Many seeds are damaged by bruchids and weevils while inside the pod.


1 cm

Albizia odoratissima (L.f.) Benth.

M.K. HOSSAIN and T.K. NATH
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Chittagong University, Bangladesh

FABACEAE (BEAN FAMILY)

Mimosa odoratissima Roxb.

Bansa, bilkumbi, bilwara, cham koroi, chichola, chichunda, chichwa, chinduga, jatikoroi, kala siris, kalia siris, karmaru, karu vagai siris, tentua koroi, tetua koroi, thitmagyi, thitpyu (Alam and others 1985, Brandis 1906, Gamble 1922, Hasan 1963, Kamaluddin 1984, Sana 1989, Troup 1921)

The genus contains 14 Indian species. *Albizia odoratissima* is widely distributed as a common constituent of many types of mixed deciduous forests, where it grows sporadically. It is frequently found on hill slopes of sub-Himalayan tracts from the Indus eastward; Bangladesh; Myanmar; central, western, and southern India; and the low-lying country of Ceylon. In northern India, *A. odoratissima* is common in the outer Himalaya and in the Siwalik hills. It extends throughout the greater part of the Indian Peninsula in dry and moist deciduous forests. In Ajmer-Merwara, India it is one of the most important species, growing in dry forests on hill slopes with *Anogeissus pendula* Edgew., *Acacia catechu* (L.f.) Brandis, *Boswellia serrata* Roxb., and other trees. In Myanmar, *A. odoratissima* is common in the upper mixed forests with teak (*Tectona grandis* L.f.) and its associates, extending into the dryer types. In Bangladesh, the tree is common in the mixed deciduous forests of Chittagong and Sylhet and is also planted in villages.

Albizia odoratissima is a large, woody, fast-growing, deciduous, multipurpose tree reaching 15 to 25 m in height. The tree grows about 87 cm in height annually. *Albizia odoratissima* grows in a wide variety of soils, but prefers moist, well-drained, loamy soils. Found from sea level to about 1667 m, *A. odoratissima* grows best in areas with 635 to 3048 mm of annual rainfall.

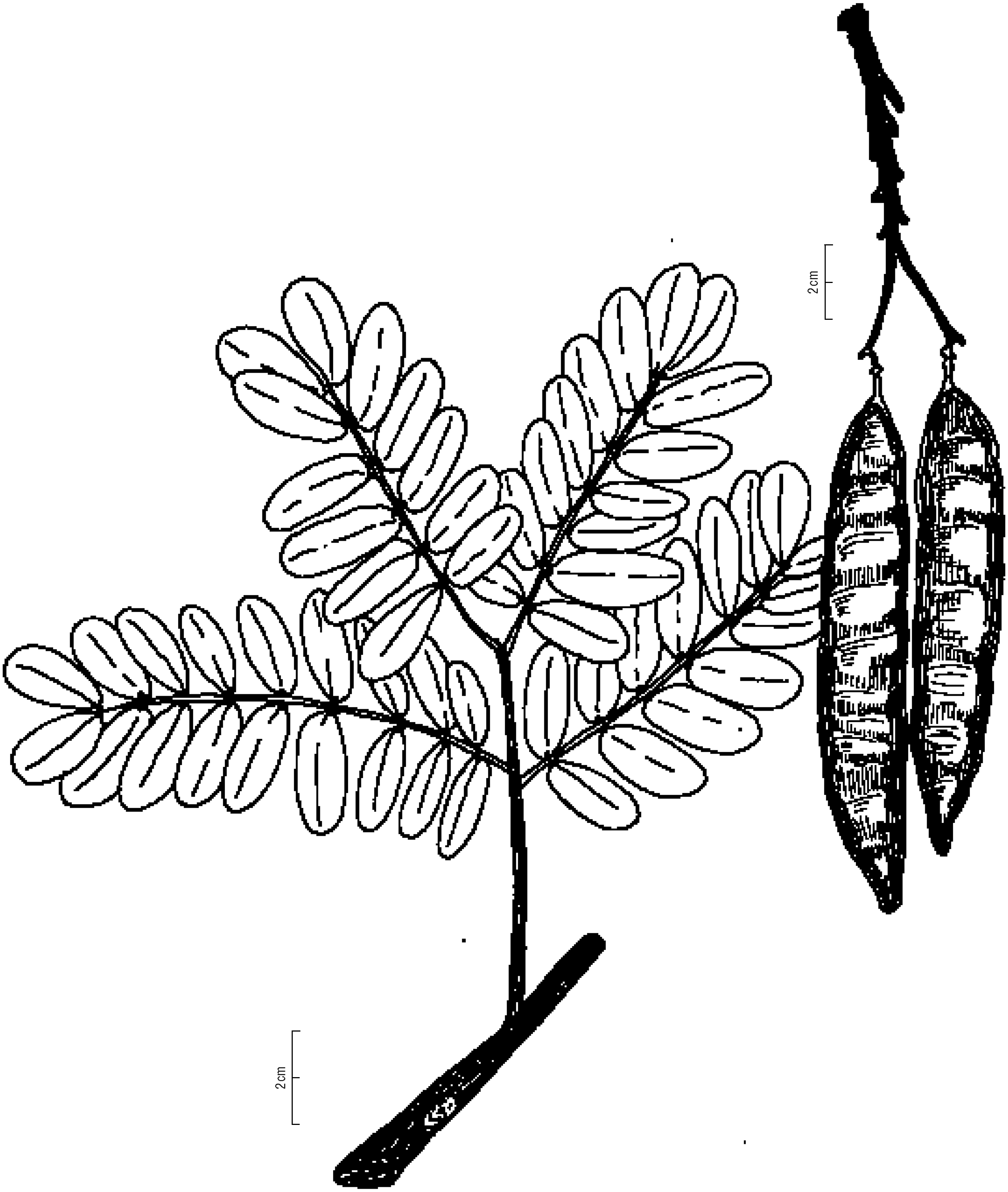
Basically a hardwood species, *A. odoratissima* has a dark brown heartwood and a specific gravity of 0.73 (Gamble 1922). The wood seasons, works, and polishes well and is fairly durable. The heartwood is used in buildings, wheels, furniture, agricultural implements, and house posts. In Bangladesh, about 75 percent of the total area planted in tea is shaded by this species (Sana 1989). Its leaves and twigs are good cattle feed (Brandis 1874, Laurie 1945, Mukherjee 1884). The bark of *A. odoratissima* and *Flacourtia ramontchi* L'Hér. is applied daily to the bodies of persons with intermittent fevers (Cauis 1986).

The pale yellowish white, fragrant, sessile flower heads appear in large terminal panicles from April through June. Pods ripen February through April in the following year. Ripened pods are 13 to 30 cm long by 2.54 to 3.3 cm wide and are reddish brown or purplish green with darker markings over the seeds. The pods contain 8 to 12 reddish brown, obovate seeds.

Mature pods are collected from selected mother trees by lopping branch tops. The pods are dried in the sun until they open, and the seeds are extracted by hand. Seeds are dried in thin layers under cover. *Albizia odoratissima* seeds average about 22,000 per kg (Chowdhury 1975, Matin and Rashid 1992). Seeds stored in gunny-bags or air-tight containers will remain viable for 1 year.

Seeds should be soaked in cold water during the night before sowing as a germination pretreatment (Hossain 1993). Seeds sowed in seed trays, polybags, and seed beds filled with soil and cow dung (3:1) showed 69 percent, 69 percent, and 47 percent germination, respectively, within 2 to 10 days without pretreatment (Matin and Rashid 1992).

Albizia odoratissima is easily propagated by seeds and coppices (Alam and others 1985). Containerized stock may be grown in either partial shade or full sun. Thirty days after transplanting, seedlings in partial shade showed 100 percent survival; those in full sun showed about 94.5 percent survival (Matin and Rashid 1992). The roots are primarily superficial, and numerous root suckers are produced. Young plants are susceptible to frost, causing plantations in Ajmer-Merwara, India to fail (Troup 1921).


2cm
2cm

Albizia procera (Roxb.) Benth.

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International Institute of Tropical Forestry, USDA Forest Service

FABACEAE (BEAN FAMILY)

Acacia procera Willd., *Mimosa elata* Roxb., *Mimosa procera* Willd. (Benthall 1933, Gamble 1922)

Acacia blanca, albizia, tall albizia, white siris (Little and Wadsworth 1964)

Albizia procera is native to moist deciduous and semievergreen hill forests, swamp forests, and lowland savanna woodlands in Asia from northern India through southeast Asia to the Philippines, Indonesia, Melanesia, and northern Australia (Nielsen 1979, Parrotta 1988b, Venkataramany 1968). It was introduced as an ornamental and fuelwood species into the U.S. Virgin Islands at least 100 years ago and into Puerto Rico in 1924 (Little and Wadsworth 1964). It has naturalized in Puerto Rico, where it is an aggressive colonizer of abandoned farmlands, pastures, roadsides, and other highly disturbed, moist sites at elevations below 600 m where annual rainfall exceeds 800 mm (Parrotta 1988b). It is occasionally planted in southern Florida (Little and Wadsworth 1964).

Albizia procera is a fast-growing deciduous tree that generally reaches 10 to 20 m in height and 30 to 60 cm d.b.h. and has a straight to somewhat curved stem, smoothish light brown to light greenish gray bark, and a spreading thin crown (Little and Wadsworth 1964, Troup 1921). Depending on site conditions, annual height growth ranges from 1 to 2 m and annual diameter growth from 1.5 to 2 cm during the first 15 years (Parrotta 1988b, Venkataramany 1968). In natural forests in northern India, the species can reach 36 m in height and 90 cm d.b.h. (Troup 1921). It grows best on very moist, alluvial sites of well-drained loams or clays but can tolerate shallow, dry, stony, and sandy soils (National Research Council 1979, Troup 1921, Venkataramany 1968). The tree grows well in tropical and subtropical environments with an annual rainfall between 1000 and 5000 mm and elevations from sea level to about 900 m. Relatively drought resistant, *A. procera* is susceptible to frost (Troup 1921).

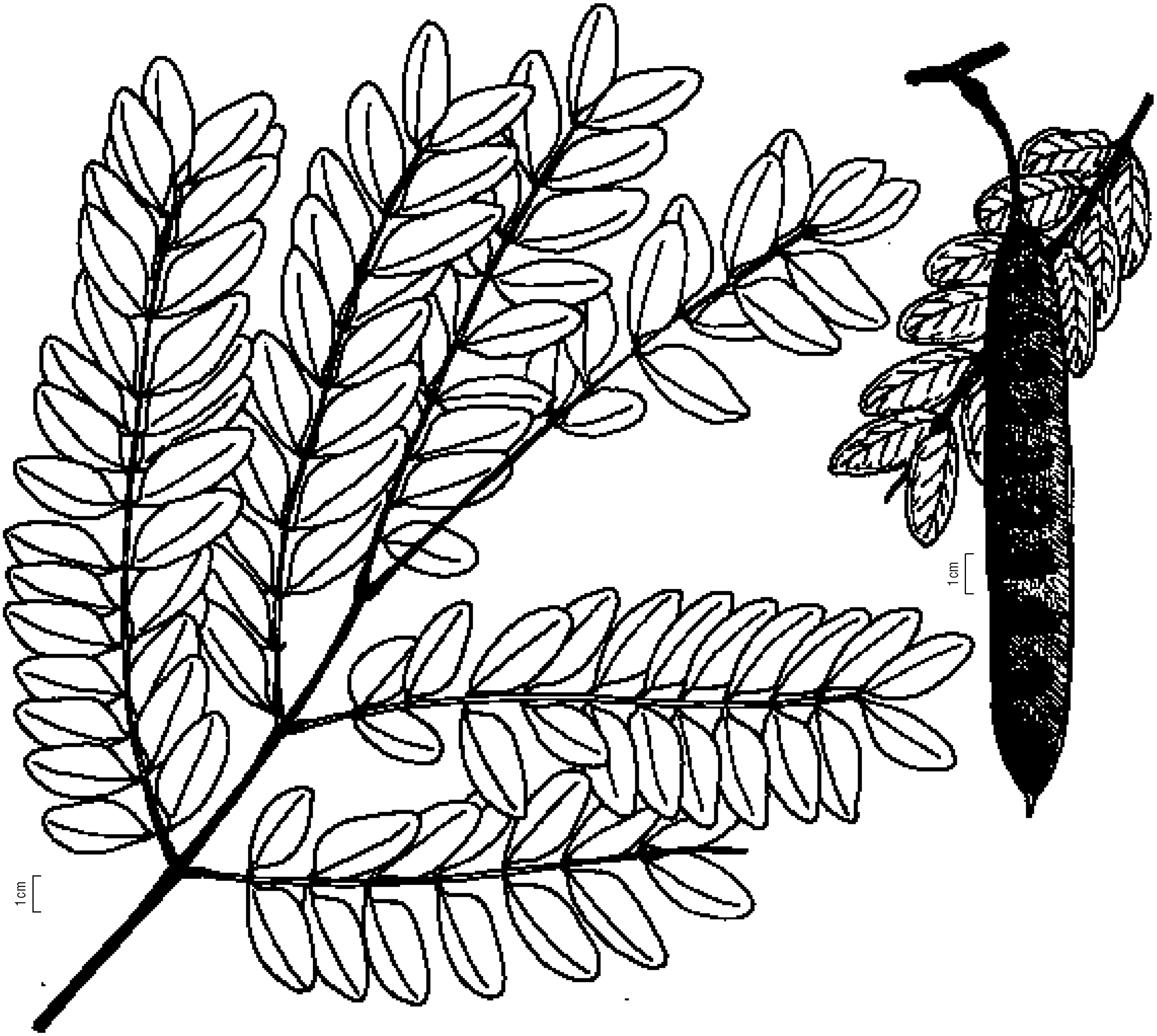
Albizia procera is considered a useful timber species in its native Asian range, where it is used for a variety of purposes. The soft sapwood is whitish to light yellow and of little value; the light brown to light chocolate-brown heartwood is moderately hard (specific gravity: 0.6 to 0.9), straight-grained, strong, durable, and resistant to attack by dry-wood termites (Little and Wadsworth 1964, Venkataramany 1968). It is difficult to saw because the grain is broadly interlocked, though with care it works to a smooth surface and polishes well (Brown 1978). The cut bark yields a reddish brown gum that is used as a substitute for gum arabic obtained from *Acacia senegal* Willd. (Farooqi and Kapoor 1968). Its leaves are valued as livestock fodder (George and Kohli 1957) and are also used in traditional Indian medicine (Chopra and others 1956, Kirtikar and others 1935). The bark is reported to be a strong poison, and the leaves are known to have insecticidal and piscicidal properties (Benthall 1933, Chopra and others 1941). In its native range, *A. procera* is sometimes planted as a shade tree in tea gardens (Parrotta 1988b; Skoupy and Vaclav 1976) and used for afforestation of degraded lands (Venkataramany 1968).

Flowering generally occurs during the rainy season; in Puerto Rico this season is between August and October. In Puerto Rico, flowering begins at 3 to 4 years of age, when trees reach a height of approximately 4 m (Francis 1998). The distinctly fragrant (suggesting molasses) flowers form whitish globose heads 20 to 24 mm in diameter, borne on racemes 8 to 25 cm long near the ends of twigs (Little and Wadsworth 1964). The fruits are flattened pods 10 to 20 cm long and 1.8 to 2.5 cm broad, changing from green to deep red or reddish brown on maturity; each contains 6 to 12 seeds. The fruits ripen 6 to 9 months after flowering, during the dry season, and usually remain on the tree until the whole twig bearing the pods is shed. The seeds are small, approximately 5 by 6 mm, flat, elliptical to nearly orbicular, with a hard, smooth, greenish-brown, leathery testa. They are released from the mature, dehiscent pods while still attached to the tree or from wind-blown pods that split open or decompose. The seeds are less subject to insect predation than those of *A. lebbeck* (Parrotta 1988a, 1988b).

The mature pods may be collected from the ground beneath parent trees or clipped from branches with pruning poles. The seeds are readily extracted by splitting or crushing the pods by hand and separating them by winnowing. Seeds average 17,600 to 25,300 per kg (Francis and Rodríguez 1993, Troup 1921). They can be stored for several years in sealed containers at room temperature with only moderate reduction in percentage viability (Troup 1921, Venkataramany 1968). In India, seeds stored in this way for 15 years showed 20-percent germination (Venkataramany 1968).

Seeds may be sowed without pregermination treatment, although placing the seeds in boiling water for 1 minute, followed by soaking them in cool water for 24 hours, increases germination rate and uniformity. Germination of freshly extracted seeds collected from various locations in India ranged from 50 to 95 percent (Venkataramany 1968). Mechanical scarification of fresh seeds is also very effective, yielding 99-percent germination in one test conducted in Puerto Rico (Francis and Rodríguez 1993).

Germination is epigeal, and occurs from 2 to 21 days after sowing, provided soil moisture is sufficient (Troup 1921). Germination and early seedling development is best if seeds are sowed just below the soil surface in a loose, moist medium under full sun or light shade (Troup 1921, Venkataramany 1968). Vigorous seedlings produce a long, stout taproot, and lateral roots soon form *Rhizobium* nodules if nursery soils naturally contain or are inoculated with appropriate strains of these beneficial nitrogen-fixing bacteria (Parrotta 1988b). In the nursery, seedlings reach plantable size (20 to 30 cm) within 2 to 3 months. Seedlings are capable of withstanding moderate suppression, but growth rates are usually very slow until seedlings overtop competing vegetation. In plantations established on grass-dominated sites, weeding is recommended during the first 2 years.


1cm
1cm

Alchornea latifolia Sw.

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Jefe Departamento de Investigación Forestal, Escuela Nacional
de Ciencias Forestales, Siguatepeque, Honduras; and
Gerenta General Semillas Tropicales, Siguatepeque, Honduras

EUPHORBIACEAE (SPURGE FAMILY)

No synonyms

Achiotillo, amargoso, envuelve cera, quesillo, sombra, tapatamal, ternera

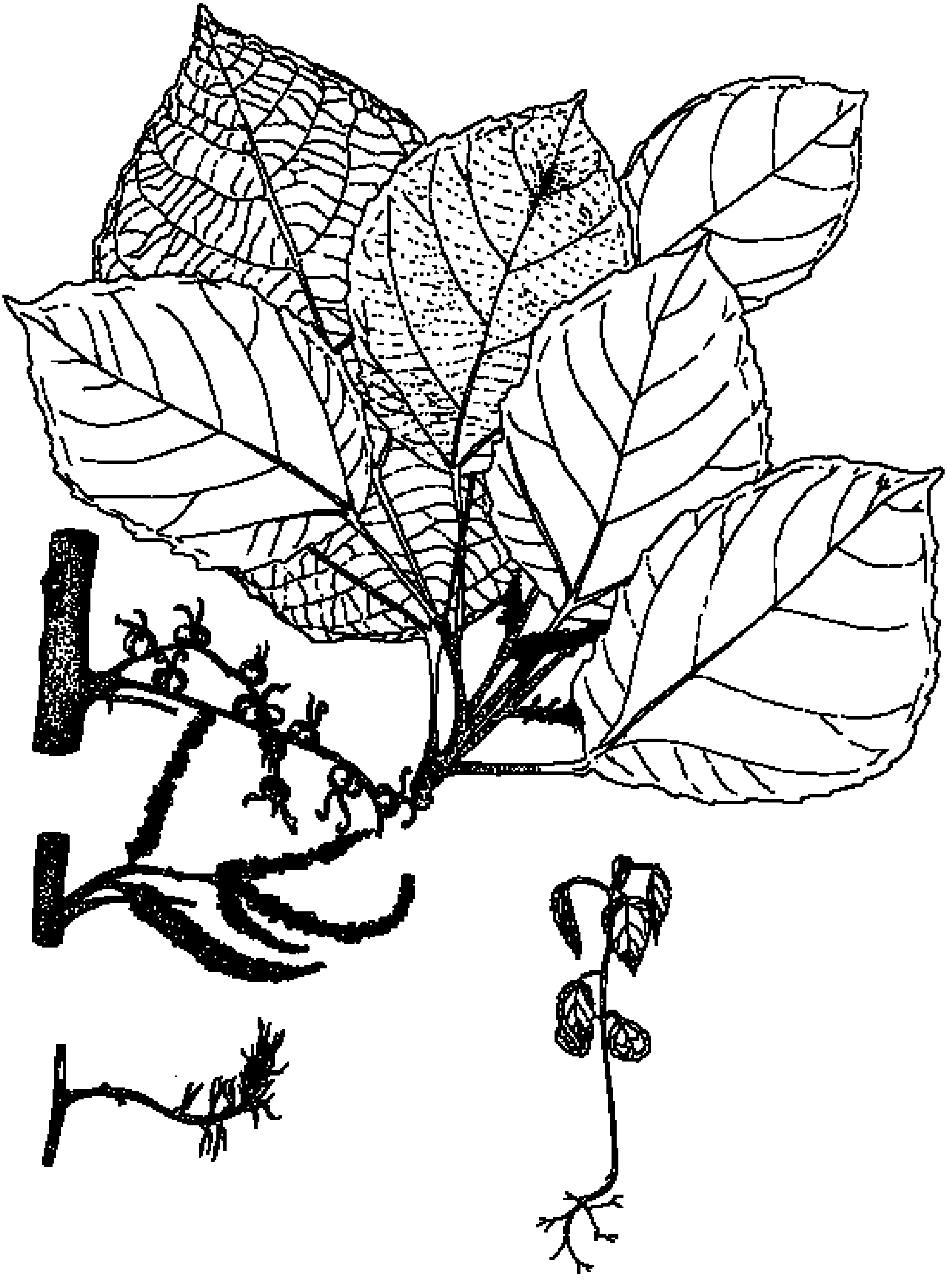
Alchornea latifolia is found from southern Mexico to Panama and the West Indies, where it forms part of the middle stratum of high forests (Benitez and Montesinos 1988). In Honduras it is found in wet and semideciduous forests, in the departments of Cortes, Santa Barbara, Atlantida, Comayagua, Colon, and Olancho.

Alchornea latifolia is an evergreen, medium-sized tree, reaching 15 to 20 m in height and 60 cm in diameter. It has a liberally umbellated crown with dense and heavy foliage (Standley 1931). The interior bark is whitish and slightly bitter; the exterior bark is smooth or finely fissured and reddish brown with whitish spots. The branches are oblique and spread out fully, generally dropping down at the end (Little and Wadsworth 1964). The small branches are thin and cylindrical with numerous orange lenticels. The big, elliptic-oval leaves are arranged in spirals; they are simple, trinervate, with two to four base glands, and grouped at the end of the small branches. In Honduras the tree grows abundantly from sea level to elevations of 1500 m.

The leaf has a long petiole, 4 to 6 cm, cylindrical to elliptic, glabrous, with scattered hairs. It has an ovate or elliptic limb, rounded or briefly acuminate around the apex, 3 to 8 cm by 8 to 20 cm. It has an obtuse or slightly rounded base, more or less serrated around the edge, more or less pulpy, with young leaves becoming subcoriaceous later. The right side is shiny and dark green, and the back is light green. It has scattered stellate hairs on both sides and hairs around the axils of the nervation. The main vein is greatly prominent underneath; a pair of strong basal veins run toward the center of the leaf; and five to six pairs of secondary veins set deep on the right side are prominent on the back. Acrodrome secondary veins have extensions on the teeth (Jiménez 1997).

The wood of *A. latifolia* has a light-brown duramen and whitish alburnum, no characteristic odor or taste, straight hilum, medium texture, low shine, and soft streak. It is soft with a medium grain, is neither durable nor very resistant to attacks by fungi that cause rotting, and is very susceptible to attacks by termites. It dries at moderate speed in the open air, with no severe defects. It is moderately easy to preserve by the hot-cold method. Specific gravity is 0.39. Total radial shrinkage is 2.69 percent, intermediate 1.08 percent. Total tangential shrinkage is 8.51 percent, intermediate 4.96 percent, and volumetric shrinkage 8.8 percent. The tangential/radial shrinkage ratio is 3.160. The saturation point of the fiber is 24.50 percent. The wood is used in light construction, columns, beams, floors, frames, furniture, poles, fence posts, handicrafts, veneer, matches, boxes, crates, barrels, mesh floats, cores for veneer, and firewood (Benitez and Montesinos 1988).

The small, yellowish or greenish-white flowers are in axillary shoots approximately 5 to 15 cm long. The fruits are subglobulous capsules, 8 to 10 mm in diameter, with the style persisting at the apex, opening up in two valves. They are coffee-color when ripe. Each fruit contains two to three red, flattened seeds (Jiménez 1997).



Alfaroa costaricensis Standl.

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JUGLANDACEAE (WALNUT FAMILY)

No synonyms

Campano chile, chiciscua, gaulín, gavilancillo (Burger 1977)

All seven species of the genus *Alfaroa* in America grow primarily in the mountainous tropical regions from Mexico to Colombia. Because species within the genus have not been reported farther north, Veracruz is probably the latitudinal northern limit of the genus (Navare 1983). Costa Rica is the center of diversity because three of the four species reported (*A. costaricensis, A. maningii* León, and *A. williamsii* A. Molina R.) are found within a 50-km radius of San Jose. *Alfaroa costaricensis* grows in temperate woodlands in the central region of Colombia.

Alfaroa costaricensis is a slow-growing, medium-sized tree that can reach 15 to 27 m in height and 30 to 60 cm d.b.h. Its bark is flat with small scarifications. It regenerates easily in lawns (Arnáez and Moreira 1992). Although it normally grows in cloudy areas, *A. costaricensis* requires light when it grows deep in the canopy of the forest. The species grows in well-drained soils on slopes of 5 percent or more. It grows at elevations between 600 and 2220 m in areas that annually receive 1500 to 2500 mm of precipitation and sustain temperatures of 15 to 20 °C (Moreira and others 1992).

Considered a timber tree, *A. costaricensis* has attractive wood with a fine pink fiber. It has smooth tension and is difficult to saw and finish. It is used for furniture, posts, coal, and building lumber (Arnáez and Moreira 1992, Burger 1977, Janzen 1983).

The species flowers from November through February. The male inflorescences are widespread in alternate aments 16 cm long. Ten aments on a branch form a paniculate terminal. The female flowers are 5 to 6 mm long and 1 to 1.5 mm wide. The fruits measure 1.6 to 2.5 cm long and 1.4 to 1.6 cm in diameter. The pericarp is hard, thick, and brown and it protects the seed. Even though rodents consume many nuts, natural regeneration does not appear to suffer.

January through April, the fruits are collected directly from the ground or from the trees. Collectors use a pruner with an extension to remove the fruits from the tree or climb the tree. The fruits are placed in sacks for transport. In Costa Rica, fruits average 274 per kg and the weight of 1,000 fruits is 3.65 kg. Seed storage is not recommended, and seeds should be planted immediately. Seeds are not viable 3 months after harvest (Arnáez and Moreira 1992). During maturation, the pericarp adheres to the cover of the seed.

The fruits are given a preemergent treatment by soaking in water at 22 °C for 24 hours. Seeds sown in different substrates of sand, moss, and humid soils germinate in 12 days; 50 to 70 percent of them germinate (Moreira and others 1992). Germination is hypogeal. Seeds will germinate in trays or bags kept at room temperature if they are planted in a loose substrate of organic matter and soil that is kept wet (Moreira and others 1992).

Initial growth is slow, and shade is recommended in the first stages. Plantules may be transplanted 7 weeks after sowing and grow best in the sun. When the seedlings reach 20 cm in height, they may be outplanted. Seedling development is slow in height and diameter (Moreira and others 1992), but plagues and diseases have not been detected.


1 cm
1 cm

Alnus acuminata Kunth in H.B.K.

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Escuela de Biología, Universidad de Costa Rica

BETULACEAE (BIRCH FAMILY)

Alnus jorullensis Kunth in H.B.K., *A. arguta* (Schlecht) Spach, *A. ferruginea* HBK,
A. mirbellii Spach., *A. spachii* (Reg.) Call.

Aile, aliso, cerezo, ilamo, jaúl, jaulillo, palo de lana, saino

Alnus acuminata occurs naturally from Mexico to Peru, Bolivia, and Argentina. It is widely cultivated in its natural range in plantations and in agroforestry systems combined with pastures of *Axonopus scoparius* (Flüggé) Kuhlm. and *Pennisetum clandestinum* Hochst. ex Chiov. (primarily in dairy farms). It has been introduced successfully to southern Chile and New Zealand (South Island).

Alnus acuminata is a fast-growing, medium-sized tree up to 25 m in height and 50 to 60 cm d.b.h. The trunk is cylindrical and straight with a slightly swollen base, and the pyramidal crown has few well-developed branches. The bark is gray-brown and smooth; the branches are terete and more or less glabrous. The buds are sparsely ferruginous-velutinous. Leaves are 5 to 17 cm long, 3 to 7 cm wide, acute to acuminate at the apex, and obtuse to rounded at the base. The leaf margin is serrate, peltate glandular above when young, and peltate glandular and ferruginous-velutinous below. Secondary veins are parallel and prominent in the lower surface of the blade. The leaves are usually deciduous. The tree thrives in poor and degraded soils because it is capable of fixing nitrogen in root nodules (a symbiotic relationship with *Actinmices allenii*), and develops a symbiotic relationship with a mycorrhizal symbiont *Alnicola* sp. (*Basidiomycetes, Agaricales*). However, *A. acuminata* requires high atmospheric humidity and humid soils with good drainage. It grows over a wide elevational range from 1300 to 3000 m as a pioneer species in almost pure stands. The tree has adapted to a wide range of rainfall (1500 to 3000 mm per year) and an annual average temperature of 16 to 18 °C. It can also survive temperatures below 0 °C for short periods of time (Camacho 1981).

Alnus acuminata is a variable species, and three subspecies are recognized (Centro Agronómico Tropical de Investigación y Enseñza 1986a): (1) *Alnus acuminata* subsp. *acuminata* has a natural range limited to South America, elliptic leaves, and is pubescent with serrate margin. (2) *Alnus acuminata* subsp. *arguta* (Schlecht.) Furlow is from Mexico and Central America, has ovate leaves, and is marginally double serrate. (3) *Alnus acuminata* subsp. *glabrata* (Fern) Furlow is from the central and southern parts of Mexico, has narrow-ovate leaves, is glabrous, and has a double serrated margin. *Alnus jorullensis* Kunth in H.B.K., a native of Mexico and Guatemala, is considered a closely related species.

With a specific gravity of 0.36 to 0.41, the wood of *A. acuminata* is considered moderately light. Both the sapwood and the heartwood of *A. acuminata* are reddish yellow with good luster when dry (Carpio 1992). The wood dries fast and easily without defects. It has excellent workability and preserves well, but is not durable when exposed to the weather. The wood is used for furniture, window parts, doors, poles (preserved), veneer, paper pulp, boxes, cement forms, pencils, matches, posts, musical instruments, broomsticks, and shoe parts (Camacho 1981, Carpio 1992, Centro Agronómico Tropical de Investigación y Enseñza 1986a). The species is widely used for firewood in the mountains of Guatemala (Centro Agronómico Tropical de Investigación y Enseñza 1986a). The wood of 20- to 50-year-old trees in Guatemala has a caloric content of 19,250 kJ per kg and a very low content of ashes (0.34 percent). In Costa Rica, charcoal is produced from the hardwood of 20- to 50-year-old trees, which have a caloric power of 29,220 kJ per kg with a 0.65 percent of ash. The charcoal produced from young trees (2 to 3.5 years old) has a caloric power of 32,400 kJ per kg with 0.28 percent of ash. In Guatemala, the litter from natural stands of the species is used as organic fertilizer in corn orchards.

Flowering occurs more than once during the year but is very abundant from March to May. The trees begin to flower and set fruit at the age of 7 to 8 years. The staminate, pendulous catkins (immature) are 2.5 mm long and 4 mm wide, with small pistillate flowers in erect or pendulous aments, 1.5 to 2 cm long. Pistillate inflorescences develop into a woody, cone-like structure that contains 80 to 100 minute winged nuts. These cones mature from June through February depending on the country.

Seeds should be collected when the mature female catkins (cones) turn dark brown and are close to dehiscence. The cones are collected from the trees and are placed on blankets until they open and the seeds are gathered. Seeds average 2.5 million per kg. The seeds should be stored in glass containers in refrigerators and kept at 4 °C to maintain viability. Even under these conditions seeds lose their viability in 1 year or less (CATIE 1986).

Seeds are usually germinated in flat boxes filled with sterilized sand. Seedlings are transferred to nursery banks or plastic bags. When transferred as bare roots to nursery banks, seedlings must be kept moist. The seedlings can be outplanted in about 6 to 8 months, when they are 30 to 40 cm in height. Saplings collected from areas of natural regeneration are outplanted or kept in the nursery for 2 to 3 months. Leaf cutting ants (*Atta* sp.), fungi, and weeds should be kept under control.

ADDITIONAL INFORMATION

Arguedas and others (1993) report the attack of 14 species of insects that produce damage to different parts of the tree, leaves, bark, and stems. Squirrels (*Sciurus granatensis*) feed on the bark; wild rabbits (*Sylvilagus brasiliensis*) destroy many seedlings that grow naturally; and six genera of fungi (*Collectotrichum*, *Fusarium*, *Melampsoridum*, *Phomopsis*, *Rosellinia*, and *Trichoderma* affect different parts of the tree species (Arguedas and others 1993).


2cm
1cm
1cm

Alnus jorullensis Kunth in H.B.K.

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BETULACEAE (BIRCH FAMILY)

Alnus acuminata

Aliso, cerezo, chaquiro

Alnus jorullensis is a tree that grows at a medium rate, reaching approximately 30 m in height and 40 cm d.b.h. The trunk is straight with a smooth bark, and branching starts at 2 m. The crown is oval; foliage is shiny, light green; leaves are 8 cm, alternate, with a serrated edge and a light green backside. *Alnus jorullensis* prospers naturally in soils of volcanic origin and on sandy layers with volcanic ashes. The species requires soils with a constant and very high humidity content and prefers soils with light textures that are acid and humiferous. It prefers deep, well-drained soils that are muddy or muddy-clayey with an alluvial or volcanic origin, although it can grow in poor soils, from gravel or sand to clay. The species grows naturally at average annual temperatures of 7 to 18 °C, and it will endure short frosts. It grows naturally near streams and brooks, along paths with adequate light and humidity (Lamprecht 1990, Venegas 1971). Annual precipitation ranges between 1000 and 2500 mm with 2 to 5 dry months. In Colombia, *A. jorullensis* grows at elevations between 1000 and 3500 m. It is found in vegetal formations of Low Mountainous dry forest (bs-MB), Mountainous wet forest (bh-M), very wet Mountainous forest (bmh-M), and pluvial Mountainous forest (bp-M) (Falla and Cia 1973).

The wood is moderately resistant to bending and compression. It has excellent workability and good finish and is used for furniture, drawers, cabinets, doors, windows, pencils, toothpicks, and matches. Because it has a high volume in relation to a low weight, the wood is used in the wood-shaving board industry. Traditionally, it has been used as firewood and charcoal. It can be used potentially as the core of lath boards, for casting molds, and as round arches for concrete; in light boxes for packing and molded products not exposed to excessive wear and tear; and for tri-ply veneer. If treated it could be used for large stakes, posts, and pilings. It is used in construction for structural elements only subjected to small loads. The bark is used as a source of tannins for tanning and of yellow and beige dyes. Yellow and green dyes are obtained from the leaves. Finally, the tree is useful in agroforestry (Lamprecht 1990).

The flowers are cream colored. The masculine (7 cm) and feminine (1 cm) flowers are separate but on the same tree. The fruit is small and gray and shaped like a cone or pineapple 1.5 cm in diameter. Each fruit contains several seeds. Viable seeds average 457,599 per kg. Seeds can be stored at 4 °C in hermetic containers for short periods.

Pregermination treatments are not required. However, seeds can be placed in a container of humid sand and the humidity increased to 5 percent while in a refrigerator or cold room for 10 days. Germination in the laboratory occurs between 6 and 29 days. It is slower in the field.

Between 20 and 70,000 plantules are obtained from 1 kg of seeds in nurseries. The recommended substrate is made up of two parts sand and one part soil, which must be disinfected before planting the seeds. Seeds should be sowed deep enough to prevent uncovering when watered, but they should not be too embedded. They must be well protected from wind and changes in temperature, preferably with a plastic protective cover or polyshade. The plantules are lifted when they are 5 cm high (Trujillo 1983, Velez 1971).

Propagation may be done by seeding or by stem cutting. The seeds must be planted in seedbeds at 5 mm deep and 2 cm apart from each other, in rows 10 cm apart. They are then covered with a very thin layer of straw and watered twice a day. The plantule is transplanted when it reaches 20 cm. The substrate must be mycorrhizal, through inoculation of the fungus *Actinomices alhil.* The recommended substrate is very fine organic soil or moss to cover the seed; as a substrate, soil and sand are used in a 1:1 proportion, very well sifted. The density of the sowing is 1,000 to 2,000 plantules per m^2. Transplantation must be done 1 month after germination has started, when the first pair of true leaves is completely developed. Shade should be provided for the transplanted material. When vegetative propagation is used, the stem cuttings—cut beveled at both ends and placed in a rather wet medium—produce a high rate of root taking. The species is also easily propagated through root cuttings and through aerial shoots (Venegas 1971).

The planting site must be prepared appropriately (loosened soil) and aggressive underbrush and defoliating ants must be controlled. The plantules should be field planted 6 to 9 months after germination when they are 15 to 40 cm. The site can be planted with pseudostem cuttings, where the stem is cut 10 cm and the roots are pruned 25 cm from the neck of the root, leaving vegetal material more resistant to drought. Planting densities range from 4,400 trees per ha to fewer than 500 trees per ha when associated with pastures. The main factors limiting growth are underbrush, defoliating ants, and fungal attacks at the nursery stage. The most limiting factor for its establishment is low humidity, both in the soil and in the atmosphere.

Anacardium excelsum (Bertero & Balb. ex Kunth) Skeels

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ANACARDIACEAE (CASHEW FAMILY)

Anacardium rhinocarpus D.C., *Rhinocarpus excelsa* Bert. & Balb.

Espavé, espavé acanju, espavel, espavel amarillo, espavel rosado, rabito wild cashew

Anacardium excelsum is very common in both the Atlantic and Pacific watersheds, from Guatemala to northern South America, including the Guyanas. The tree often dominates on the flood plains and in gallery forests (Zamora 1993).

Anacardium excelsum grows at a medium rate (González 1980) to 45 m in height and 3 m d.b.h. This large tree has a straight trunk, a rounded and dense crown, and brown-gray bark that is scaly or smooth and shows leaf scars. *Anacardium excelsum* leaves are simple, alternative, relatively large, without stipules, obovate-oblong in outline, and rounded at the apex. They are 15 to 35 cm long, 5 to 15 cm wide, glabrous, and coriaceous in texture. Secondary veins are prominent in the lower surface, and usually located at the end of the branches. Many of the trees drop their leaves for a short period of time during late November and December and green flushes of new foliage appear in early January (Allen 1956). *Anacardium excelsum* grows in a wide range of soils and climatic conditions. It grows from the lowlands of both coasts up to 900 m, and well-developed trees have been found as high as 1200 m.

The wood of this species is moderately light with a specific gravity of 0.38. Carpio (1992) reported that in air-dry conditions the sapwood is pink and the heartwood varies from dark brown to red-brown. The wood has a fine grain, a rough texture, and a persistent leather-like odor. The wood dries well without major defects, works easily, and is naturally durable. The wood easily accepts preservatives that protect against termites and fungi. The wood is used in general construction and carpentry and for wood tools, furniture, veneer, trays, boxes, and concrete forms. However, sawmills complain that the wood tends to saw woolly and is hard to finish smoothly (Allen 1956). The raw nuts are toxic but are reportedly edible when roasted, and the macerated bark is sometimes used in Panama as bait for catching fish (Allen 1956).

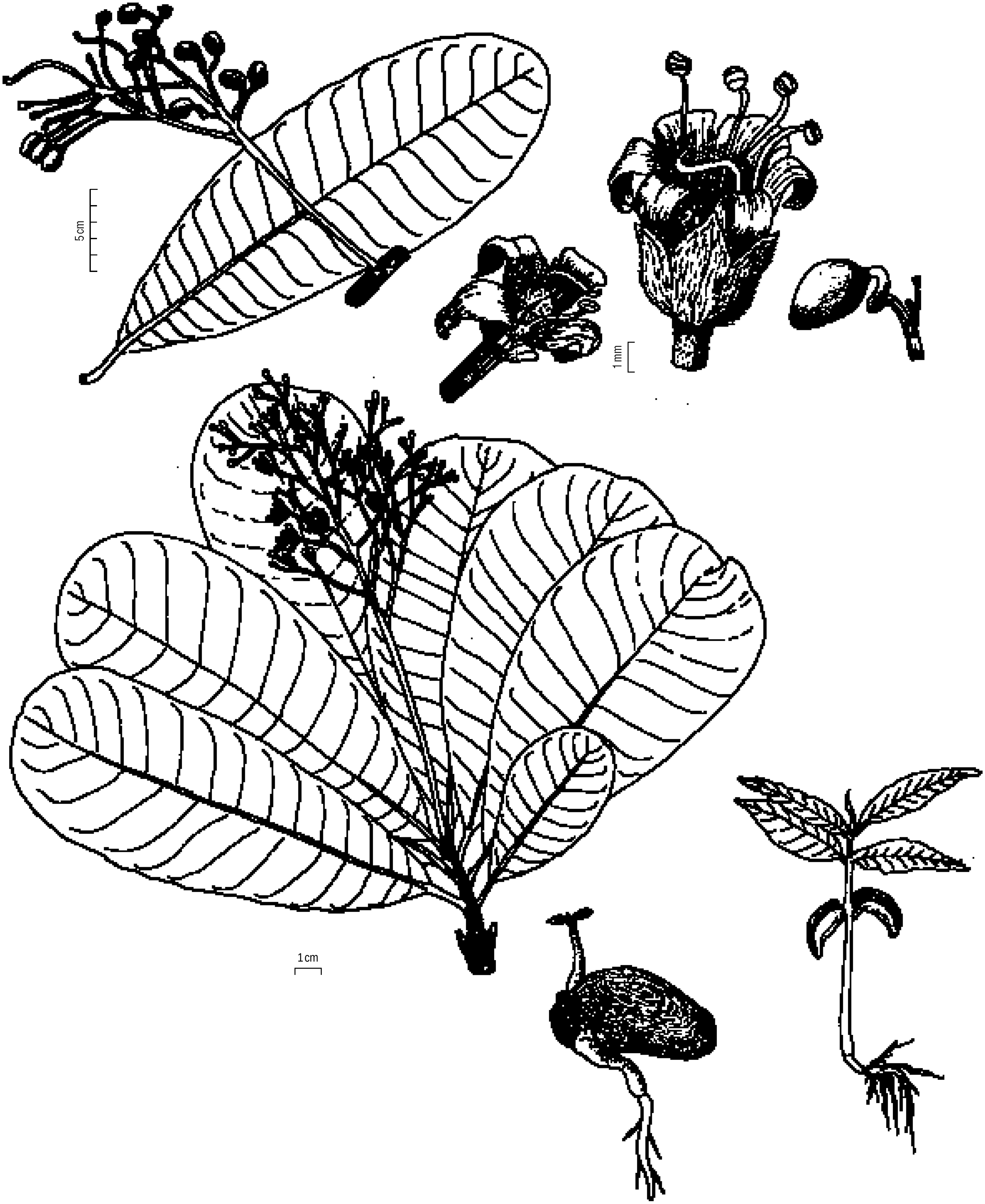
After the flushes of new foliage in January, small white flowers appear through April in pale green or white, large, terminal panicles (Jiménez and others 1996). As the flowers age, they turn pink and develop a strong, clove-like fragrance, which permeates the forest (Allen 1956). The fruit is a kidney-shaped drupe, 2.5 to 3.5 cm long, 1 to 2 cm wide, which matures from March through May. The fruits are usually fully mature 3 months after flowering (personal observation). Once the fruits drop to the ground the seeds germinate almost immediately, provided the soil remains at a good moisture level. The fleshy part of the fruits of this species is carried by bats to their feeding sites where they drop the entire seed (Janzen 1991). Parrots that feed on mature fruits similarly disperse the seed (personal observation).

The fruits gathered from the ground contain just one seed each which cannot be separated from the pericarp. Although the seeds of this species have a very low viability, some tests reveal that viability can be extended to at least 60 days by storing seeds in plastic bags in a refrigerator at about 6 °C (Trujillo 1996a).

Pretreating seeds in boiling water for 10 minutes or immersing in water at room temperature for 12 hours enhances germination. Germination apparently occurs within 20 days (personal observation). Seedlings, shade tolerant during early stages of development, need more light for survival and further growth in later stages. Due to insect predation, fungal diseases, and poor environmental conditions, seedling survival is very low.

ADDITIONAL INFORMATION

Little and Wadsworth (1964) indicate that the flowers of *A. occidentale* L. “Cashew,” a species closely related to *A. excelsa* (Jack) Jacobs, are attractive to bees; therefore, it is possible the same is true for this species. The small, inconspicuous flowers of *A. excelsum* are a type common to a great many tropical trees of almost unknown reproductive biology (Janzen 1991). The tree produces a resinous sap that may cause allergic reactions in some people.


5cm
1mm
1cm

Andira inermis (W.Wright) Kunth ex DC.

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FABACEAE (BEAN FAMILY)

Andira jamaicensis (W. Wright) Urb. (Symbolae Antillarum 4(2): 298; 1905); *Geoffraea inermis* (W. Wright) W. Wright (London Medical Journal 8: 256; 1787); *Geoffroea jamaicensis* W. Wright (Philosophical Transactions of the Royal Society of London 62: 512; 1777); *Geoffroea jamaicensis* var. *inermis* W. Wright (Philosophical Transactions of the Royal Society of London 67: 512; 1778)

Acapúrana, acatrus, akoelie kiererie, akoelie tjerere, almendro de montaña, almendro del río, almendro macho, almendro montés, almendro real, andirá jareua, andirá uchy, angelica, angelim, angelim do igapo, angelim morcegueira, angelim rana, angelin, angelino, aracuhy, arenillo, avineira, barbosquillo, bastard cabbage, bat seed, black blossom berry, bois palmiste, cabbage-bark, carbón, carne asada, chaperno, chigo, chirai, cocú, congo, cornwood, cuartololoti, cuilimbuca, cujía, cumaru-rana, gallina, iximche, jacarandá morcega, kabbes, koeraroe, koeraroe talaboe, koraro, kuraru, lombricero, lombrigueira, maats, macallo, macayo, majagua, moca, moca colorada, morcegueira, pacay, palo de seca, partridge wood, peloto, pheasant wood, pilón, purga, quinillo dorado, quira, red cabbage tree, redietjabesi, rere erepare, rode kabbes, Saint Martin, Saint Martin rouge, Sapupira da varzea, uchy-rana, vreemoesoehoedoe, wild olive, wormwood, yaba, yaba amarilla, yaba colorada, yabo, yava, zwarte kabbes (Record and Hess 1949)

Andira inermis is found in the lowland forests of southern Mexico, Belize, Central America, the West Indies, northern South America, and Brazil. The species was introduced and cultivated in West Africa (Adams 1972, Brako and Zarucchi 1993, Croat 1978, Howard 1988, Whitmore and Hartshorn 1969).

Andira inermis is a fast-growing, evergreen, medium-to-large tree that reaches 10 to 35 m in height and 1.70 m d.b.h. It has a straight bole, mostly unbuttressed (Salas 1993). The tree has a spreading or rounded dense crown; branchlets are sparsely pilose or glabrate. Young twigs are round, brownish, and puberulous. The outer bark is ragged and dark gray or medium brown, while the inner bark is light pinkish-brown; it has a coarse texture with longitudinally deep fissures. The bark exfoliates in large plates and has an unpleasant odor (Croat 1978, Whitmore and Hartshorn 1969). Leaves are alternate, imparipinnate, and generally glabrate; with 7 to 17 pairs of opposite leaflets with oblong or rounded base; leaflets are subcoriaceous with petiolules 5 mm long and dark veins. The leaflet blade is shiny green adaxially and dull green abaxially; midvein is swollen, and protuberant abaxially. Stipules are free, prominent, slender, linear-subulate, 1 to 2 cm long, and caducous (Whitmore and Hartshorn 1969). The species is riparian and grows best in lowlands that are periodically inundated. It grows at elevations ranging from 0 to 400 m where temperature varies from 28 to 35 °C and annual rainfall from 2500 to 6500 mm. It may be found in primary and secondary forests with alluvial, acid-clayey, or sandy soils.

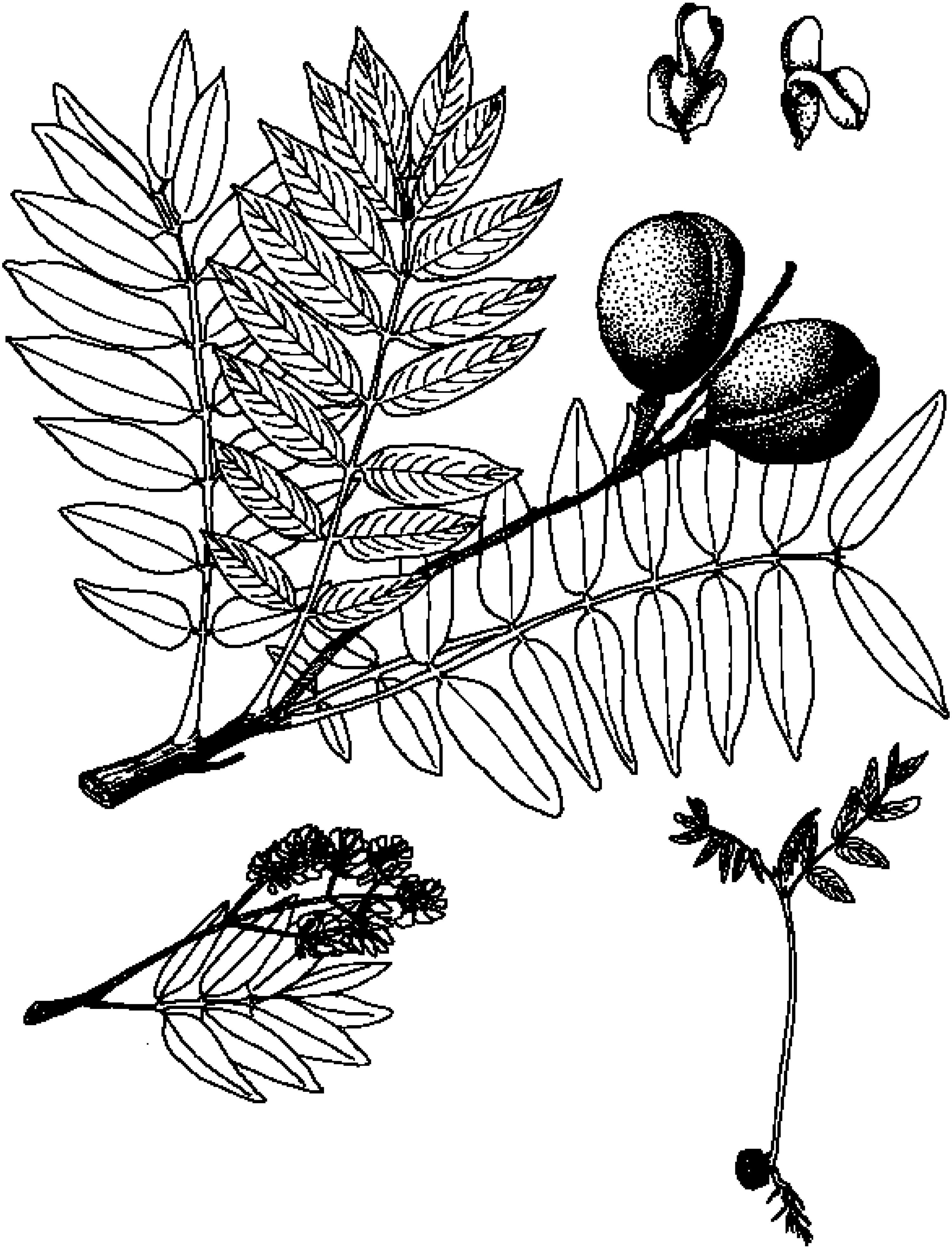
The timber is strong, hard, and heavy. The narrow sapwood is pale brown to grayish yellow and usually clearly demarcated from the yellowish-brown to dark reddish-brown heartwood (Chudnoff 1984). The average specific gravity (green volume/dry weight) is 0.64. The green weight is 1140 kg per m^3 (76 percent moisture content) (Llach 1971b). Wood texture is coarse, with a moderately irregular grain and a rather low luster and without distinctive odor or taste when dry. Bands of light-colored parenchyma tissue give this wood a distinctive figure. The sapwood is susceptible to discoloration by sap-stain fungi during the early stages of drying. Radial shrinkage (green to oven-dry) is 4.6 percent and tangential shrinkage is 9.8 percent; volumetric shrinkage is 12.5 percent. *Andira inermis* has superior values in the rupture module (1470 kg per cm^2), elasticity module (186 kg per cm^2 by 1000), maximum load (13.4 m kg per cm^3), and hardness (655 to 822 kg) (Llach 1971b). It is easy to work, saw, and cut; but it is difficult to obtain a smooth surface because of the alternating bands of hard and soft parenchyma. The wood polishes and varnishes well after filling. Heartwood is resistant to decay fungi and moderately resistant to dry-wood termites. The wood is used for heavy construction, house framing, exterior siding, turnery, furniture, cabinetwork, parquet flooring, and decorative veneer (Chudnoff 1984). The seeds and bark are rich in the alkaloid andirin (García 1974). The bark is used in the Brazilian Amazon as a purgative and vermifuge; it is poisonous in large doses (Schultes and Raffauf 1990). Fresh seeds are toxic and cannot be eaten. They are used as an antihelmintic to induce vomiting (Schultes and Raffauf 1990). The tree has a good shape and beautiful flowers and has been used as an ornamental.

Flowers and fruits may be seen throughout the year. Flowering occurs from February to May, with most fruits maturing in September and October. A second flush of blooms may occur in October, with fruits maturing in January and February (Croat 1978). The flowers are grouped in terminal panicles 15 to 30 cm long, each with numerous pink or purple flowers. The calyx is campanulate, shortly five-toothed, and 3 mm long. The corolla is long and has a suborbicular standard; wings are almost straight, oblong, obtuse, and free; the keel is similar to the wings. The vexillar stamen is free or rarely connate with the others to form a sheath; the anthers are versatile. The ovary is stipitate or rarely subsessile with one ovule. The style is short and curved, and the stigma is small. The species is an obligate outcrosser because it is self-incompatible (Croat 1978). The fruit is a green, short-stipitate camara that is oval or subglobose, 2 to 4 cm long, with one seed. The fruit has a leathery exocarp, fleshy mesocarp, and a ligneous endocarp (Polak 1992). The seed is approximately 2 cm in diameter. Fruit and seed dispersal is synzoochorous. Bats and scatter-hoarding rodents have been reported as dispersers (Mabberley 1997, Van Roosmalen 1985).

Fruits are collected from the ground under the trees. The seeds are separated from the fleshy mesocarp. Tissue separation is done with a sharp knife as soon as the fruit is collected to avoid damage by Curculionids (*Cleogonus* sp.) and fungi. Surrounded by the woody endocarp, the seeds are soaked in running water for 24 hours and sown in greenhouse beds. The seeds show recalcitrant behavior and cannot be stored.

Germination is hypogeal and the seedling is cryptocotylar. Seeds germinate in 20 to 25 days. Germination is approximately 60 to 70 percent.

The seeds are sown directly in the soil or in plastic bags filled with soil and sand. Once established, seedlings grow vigorously. They are not susceptible to insect attacks. Bare-root seedlings can be transferred to the field 3 to 5 months after seed sowing. *Andira inermis* has been planted in experimental plots with a planting distance of 3 by 3 m. Outplanted saplings grow slowly during the first year; their leaves do not wither.



Anthocephalus chinensis (Lam.) Rich. ex Walp.

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RUBIACEAE (MADDER FAMILY)

Anthocephalus indicus A. Rich.; *Nauclea cadamba* Roxb.; *Saarocephalus cademba* Kurz;
Anthocephaus cadamba Miq.

Atta vanji, kadaga, kadam, kadambe, kadambo, kaddavailo, kadwal, kalem pagem,
kalempajan, katoam bangkal, lurambo, manlettan-she, maw, roghu, sanko,
velli kadambu (Troup 1921, Gamble 1922, Chudnoff 1984)

Anthocephalus chinensis grows in the sub-Himalayan tract at latitudes from 9 ° S to 27 ° N. The species is found from Nepal eastward to Bangladesh, India (Assam province and Chotanagpur district at Bihar Province, Myanmar (Burma), Sri Lanka, the Philippines, Indonesia, and Papua New Guinea (Whitmore 1984).

Anthocephalus chinensis is a large, deciduous (or sometimes evergreen), and fast-growing species with spreading branches (Troup 1921, Zabala 1990a). Under normal conditions, it reaches 17.67 m in height and 25.3 cm d.b.h. within 9 years. A mature tree can attain 20 to 30 m in height and 50 to 100 cm d.b.h. The crown is open and round and bears drooping branches. The stem is straight, more or less cylindrical, and unbuttressed, with a somewhat regular bole. The bark is thin, slightly rough, grayish to light brown (Zabala 1990a), and smooth in young trees. It becomes darker and longitudinally fissured in older trees and exfoliates in small rectangular plates that are yellowish brown inside (Troup 1921). The leaves are simple, opposite, 12 to 25 cm by 5 to 10 cm, ovate, elliptic-oblong, shining, coriaceous and glabrous above, and pubescent beneath (Brandis 1921, Zabala 1990a). The tree becomes leafless or nearly leafless during the hot season.

Anthocephalus chinensis grows in moist, warm regions, often on alluvial ground, along rivers, and in swampy areas (Troup 1921). In Bangladesh it is a tree of the moist, deciduous and evergreen forests of Sylhet and Chittagong, and also occurs along channels and in marshy places. This broad-leaved species has high fertility requirements and does not grow well on leached soils even when soil physical conditions are good and rooting is not impeded (Evans 1982). It grows best on deep, moist, alluvial sites, often in secondary forests along river banks (Chudnoff 1984). *Anthocephalus chinensis* can be planted along river and canal banks and the lower part of roadsides (Alam and others 1991). In stiff, badly drained areas growth is very poor, and the species does not thrive in dry areas (Zabala 1990a). High to medium texture with neutral to acidic soil is suitable for *A. chinensis.* Free and moist draining conditions are necessary. *Anthocephalus chinensis* grows at elevations of 0 to 1300 m where mean annual rainfall is 1300 to 1400 mm. The tree tolerates a 3-month dry season where the mean maximum temperature is 24 to 34 °C, mean minimum temperature is 16 to 26 °C, and mean annual temperature is 20 to 32 °C. It is sensitive to frost. In its natural conditions, the species grows in temperatures from 25 to 35 °C and grows well where annual rainfall is 1440 to 5080 mm (Zabala 1990a).

The wood is white to yellowish-white or cream-white with a yellowish cast on a longitudinal surface, often with grayish sap stain of fungi. It is moderately hard and heavy (specific gravity 0.40 and calorific value 4,800), straight grained, somewhat lustrous, and medium-coarse in texture. Pores are large, oval, elongated, subdivided (sometimes in short radial lines), and scanty. Medullary rays are fine, numerous, close together, and bent outward where they touch the pores (Gamble 1922). The wood is used in matchsticks boxes, tea boxes, bobbins, veneer, plywood, crates, and furniture (Chudnoff 1984, Zabala 1990a). The logs are used for dugout canoes, roof structures, and light construction (Alam and others 1991). It can also be used for joinery work (Gamble 1922). The sapwood of *A. chinensis* rates fair for wood wool or cement boards (Kamil and Serwandi 1975).

The tree flowers May through July. The yellow flower is terminal, 3.80 to 5.10 cm in diameter and has a single head, 2.54 to 3.80 cm peduncles, a glabrous corolla, erect lobes, and oblong persistent calyx-lobes. The small fruits of individual flowers are inserted in a central fleshy mass which forms a composite fruit and turns brownish or yellowish when ripe (Evans 1982). The fleshy fruits ripen and fall in January and February (Zabala 1990a). Cattle, birds, and other animals consume the fruits and subsequently disperse the seeds. With the early showers preceding the monsoon, the seeds are washed into heaps along with silt and germinate in dense masses at the beginning of the rainy season.

Fruits are collected in August and September (Choudhury 1975). They are collected manually from the plant or the ground. Safety belts, ladders, extension pruners, pruning shears, pruning saw, and bags are used in fruit collection. After collection, fruits are left to ripen (Pollard 1969). They are placed in protected areas, not left under the trees because they may be partially consumed by white ants. The fruits are either dried in the sun so the fleshy part can be removed manually or mechanically, or soaked to separate the seeds (Venator and Zambrana 1975). These methods are equally effective. In another method, ripened fruits are soaked in water until they rot, pulped or macerated on newspapers, and dried in a warm place (Zabala 1990a). The seeds are carefully separated from the dried pulp by slightly blowing the mass (Evans 1982, Zabala 1990a). Seeds average 18,000,000 to 26,000,000 per kg (Whitmore 1984). Seeds have several years of dormancy (Fox 1972) and can be stored satisfactorily if they are kept in air-tight or almost air-tight containers in a dark room under dry conditions (Zabala 1990a).

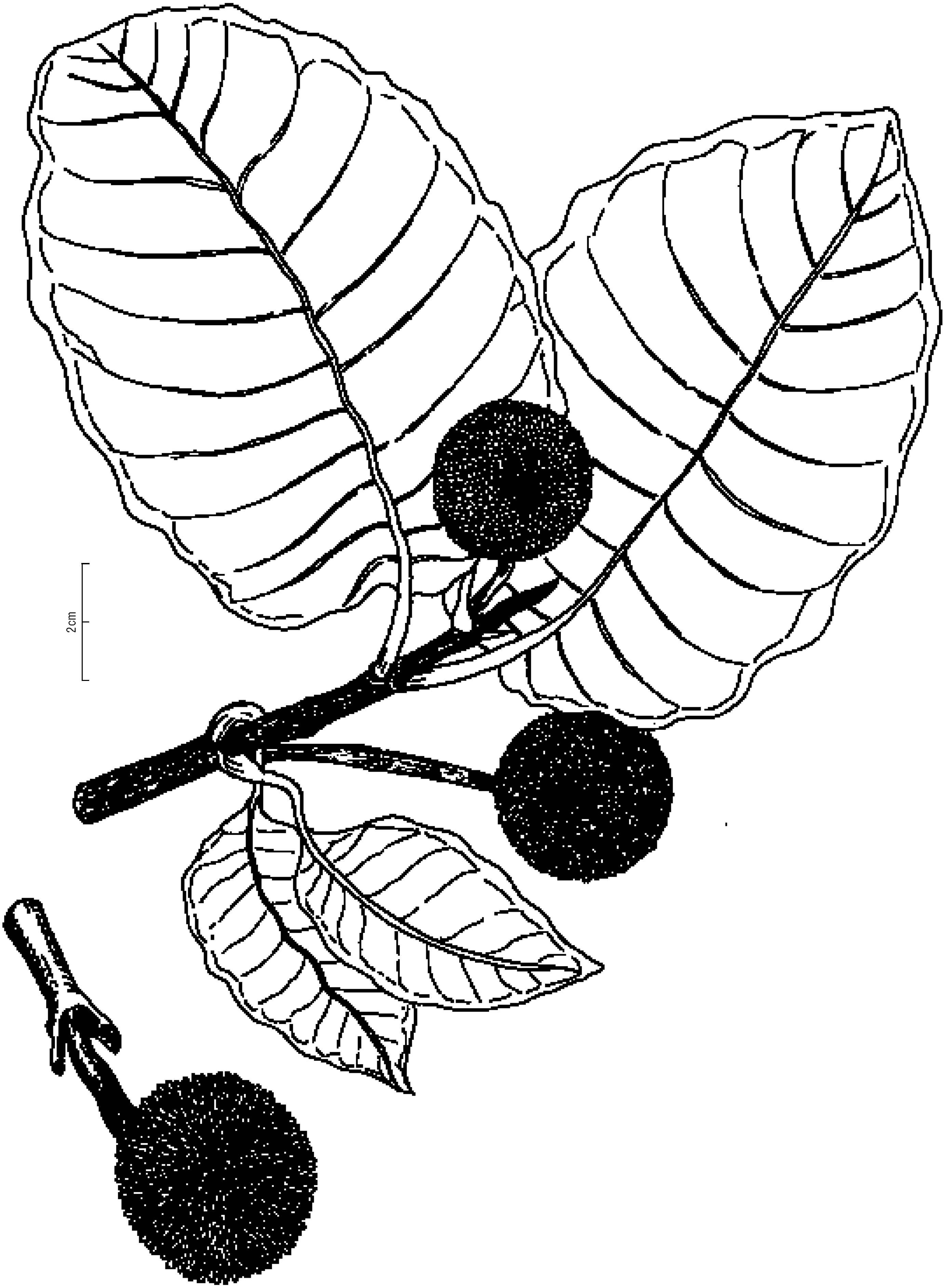
Germination is epigeous. Seeds germinate in 8 to 22 days. Fresh seeds germinate at 90 percent, diminishing to 5 percent at 13 months (Zabala 1990a). Old seeds germinate best in full sun, and fresh ones in shade (Whitmore 1984). Seed boxes are placed in the shade. The seedlings are 2.5 cm tall and have 2 or 3 pairs of true leaves after 3 to 4 weeks. They are pricked out with a small ball of earth surrounding the roots into plastic pots and hardened off in 30 percent shade (Zabala 1990a). During this early stage, the plants require light shade and protection from the sun; they require more light as they grow older (Zabala 1990a). Seedlings grown in shade become spindly trying to reach the light. If heavy rain is expected, the seedlings should be protected. After pricking out, 95 percent survival is likely (Pollard 1969). Young transplanted seedlings receive intensive silvicultural care. After 6 months, when the seedlings are about 30 cm tall, they are outplanted at the onset of the rainy season with 2 by 2 m spacing (Zabala 1990a). Mechanical thinning may be required at 8 years. In Bangladesh, four, three, and two weedings are carried out in the first, second, and third years respectively (Choudhury and Choudhury 1983). Young saplings are subject to damage from browsing by cattle and deer (Troup 1921).

As a plantation tree, *A. chinensis* can be planted with leguminous species such as *Paraserianthes falcataria* (L.) I.C. Nielsen, *Albizia chinensis* (Osbeck) Merr., and *A. lebbeck* (Zabala 1990a). Coppice-with-standard or clearfelling followed by artificial regeneration is used for this species. It is a good natural pruner and rarely needs artificial pruning (Evans 1982). It is a fast-growing, shade intolerant plantation species in the tropics (Evans 1982). In the Philippines, growth of *A. chinensis* is improved when it is interplanted with the legume *Leucaena leucocephala* (Lam.) de Wit (Evans 1982).

ADDITIONAL INFORMATION

In germination, the radicle emerges and the hypocotyl elongates, carrying the cotyledons enclosed in the testa aboveground. The testa usually adheres to one cotyledon for some time before falling to the ground (Troup 1921).

Sudden death is a severe problem in Costa Rica. It often occurs in sethes and the symptoms are typical of a root infection. Affected trees show cambial and sapwood staining spreading upward from the roots (Gibson and Nyland 1977). Wild populations in Sabah have very low pest populations (Thapa 1971), but dense stands are prone to attack by caterpillars of the moth *Arthroschista hilaralis* (Pyralidae) (Mastan 1969). *Margaronia hilaralis* is a common leaf-rolling insect pest of *A. chinensis* in Malaysia. This insect can be checked by spraying with 0.051 B.H.C. in water (Thapa 1970). The larva of *Mecistocerus* sp. eats out an elliptical-shaped depression, of which half is in the sapwood and the inner bark. The grub eats or irregularly winds longitudinal galleries in the bast and sapwood (Stebbling 1914).


2cm

Apeiba aspera Aubl.

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Santafé de Bogotá, Colombia

TILIACEAE (LINDEN FAMILY)

No synonyms

Corcho, guásimo blanco, peinemico, peinemono

Apeiba aspera is a fast-growing tree that can reach 20 m in height and 30 cm d.b.h. It has an angular, gray, slightly greenish shaft. The bark is thin or of medium thickness and detaches irregularly during the year. The leaves are simple and alternate with stipules; the back side is a much lighter green than the right side; both surfaces are glabrescent when young. The tree requires deep soils with moderate drainage. Although it tolerates wet places, it prefers clayey or loose clayey soils and can endure acid soils with low fertility and a flat or hilly topography. It grows at elevations between sea level and 500 m, with annual precipitation ranging between 2000 and 8000 mm. *Apeiba aspera* tolerates a range of 24 °C minimum temperature and 30 °C maximum temperature, with an annual average of 28 °C (Rodriquez 1988). It is found in the following vegetal formations: very wet Tropical forest (bmh-T), wet Tropical forest (bh-T), and pluvial Tropical forest (bp-T) (Venegas 1978). It cannot endure attacks by parasites (Lorantaceae). It is susceptible to prolonged droughts and to soils with excess drainage.

The wood is light and soft, and hardens after drying in the air. It is pale cream to grayish in color, with occasional pink hues. Its low density makes it appropriate for divisions, acoustic veneering, and wings on lath boards for doors. It is used primarily for decorative finishing of home and building interiors. Additionally, it has been used in the manufacture of doors, windows, socles, and ceilings, and in light construction.

The medium size flowers are yellow and borne on inflorescences opposite the leaves. The fruits are in flattened capsules, black when ripe, with stiff, slightly sharp thorns. The seeds are black, small, and abundant. Viable seeds average 37,018 per kg. Seeds can be stored for 1 year in hermetic containers at a humidity content less than 10 percent and 4 °C.

The appropriate pregermination treatment involves sandpapering the seeds until they lose their natural shine and appear completely porous. A secondary pregermination treatment consists of immersing the seeds in sulfuric acid at 95 percent concentration for 40 to 70 minutes (Montero and Estevez 1983, Trujillo 1996). Germination occurs in laboratories at 7 to 28 days.

About 20,000 plantules are obtained from 1 kg of seeds in a nursery. *Apeiba aspera* produces abundant seeds and is easily handled in nurseries. The substrate must be made up of two parts sand and one part soil, which must be disinfected before seeds are planted. Seeds must be sowed deep enough to prevent uncovering when watered, but they must not be too embedded. The species can reproduce asexually (through stem cuttings), but the technical standards for implementation have not been researched.

All underbrush should be removed from the planting site. The species does tolerate shade but grows more in full sun. At planting, each tree should be fertilized with 40 g of NPK in a triple 15 formulation. This treatment will result in a higher survival rate and better initial growth. The planting distance must be appropriate to allow the diametrical development of trees and to decrease embranchment. Distances of 3 by 3 m or 4 by 4 m are recommended.


3cm
2cm

Araucaria angustifolia (Bertol.) Kuntze

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ARAUCARIACEAE (NORFOLK PINE)

Araucaria brasiliensis, Columba angustifolia

Araucaria, curiy, pinheiro do Brasil, pino del Paraguay, pino Misionero, pino Paraná

Araucaria angustifolia lives in the subtropical forest in association with evergreen and deciduous broadleaves. In natural stands the species grows between 19°15' S and 31°30' S; 41°20' W and 54° W. In Brazil it covers the states of Rio Grande Do Sul, Santa Catarina, Minas Gerais, and Paraná; in Argentina, the northeastern province of Misones. The species rarely grows in Paraguay.

Araucaria angustifolia is a fast-growing evergreen tree reaching 35 to 50 m in height and 1.5 to 2 m d.b.h. in natural stands. Young trees have a pyramidal crown, resembling a closed umbrella. In adult trees the lower branches abscise and the tree looks like an open umbrella with the tips of the branches bending upward. The species grows in a variety of soils: poor soils derived from sandstone and rich ones derived from basalt. The latter are lateritic, deep, and permeable, with an acidic pH. Found at elevations from 300 to 2000 m, the trees grow where the annual rainfall is 1250 to 2450 mm. In natural stands the climate is mild with temperatures between 10 and 21 °C, and frosts occur on 10 to 25 days annually. *Araucaria angustifolia* lives up to 300 years.

Seeds collected from different population origins and geographic sites have produced significant growth variability in plantations. Ecotypes or geographic races may be identified (Fahler 1981, Gurgel 1973). Laboratory assays of hybridization of *A. angustifolia* and *A. araucana* (Mol.) Koch have been tested with no practical commercial results (Tesdorff 1969).

The wood is soft, with a creamy yellowish color; the corewood becomes darker when cut and has no resinous canals. It is used for plywood, studs, structural beams, mouldings, and pulpwood. The seeds are edible, and local inhabitants collect them as a food source. Commercial afforestation of pure stands has given very good growth results up to 35 m^3 per ha per year in the deep red soils of Misiones, Argentina.

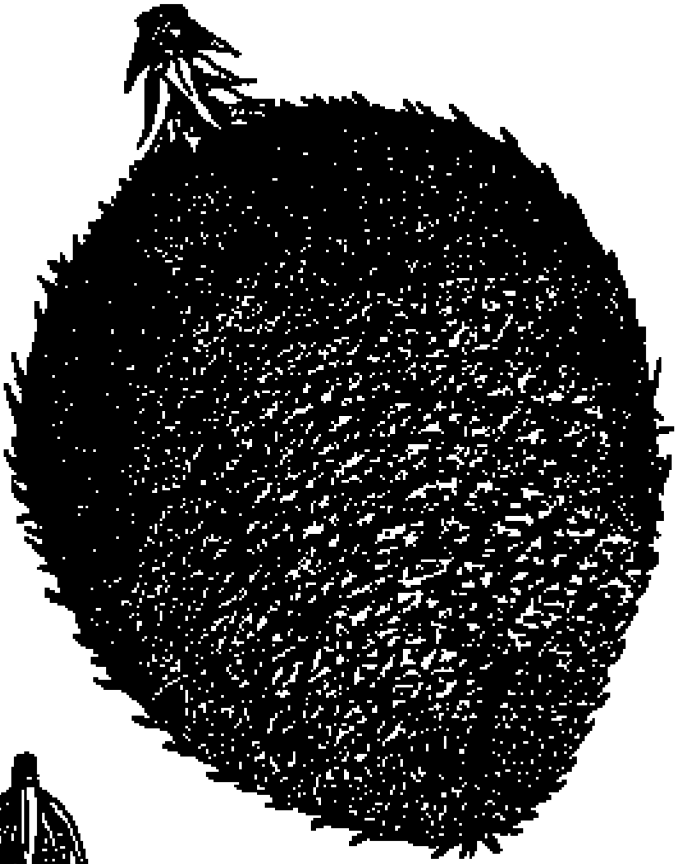
Flowering generally occurs in August and September. The cones ripen 20 to 22 months later during May and June and fall in June and July. Male and female strobili are usually borne on different trees, but sometimes they appear on separate branches of the same tree. The male strobili is dense, cylindrical, 8 to 20 cm long, and 3 cm wide. The cones are broader than long with a circumference of 30 to 50 cm; each seed weighs 6 to 7 g. An isolated tree may produce 50 to 80 kg of seeds. Seeds average 190 per kg.

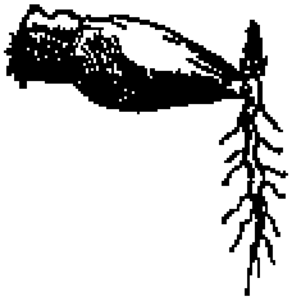
Araucaria angustifolia seeds are currently classified by flotation in water. The lighter seeds float and are discarded. However, the floating seeds may have been collected from young trees or heavily shaded stands. These seeds may be viable, but generally would have germination rates lower than those of heavy seeds. The average rate of germination is 80 percent, with a viability of 6 to 7 months. Viability decreases after harvest, but seeds refrigerated at 3 to 4 °C may maintain their viability for more than 1 year. Seeds may also be classified by their size (length of the embryo without the bract): big seeds more than 45 mm, medium seeds 45 to 35 mm, and small seeds less than 35 mm. Two hundred days after germination, the seedlings of big seeds were 30 percent taller than those of small seeds, and the germination rate of the big seeds during the first 30 days was 50 percent higher.

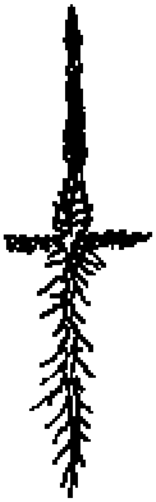
Seeds can be pregerminated by placing them in layers with a shade screen. Within 20 to 30 days, emerging sprouts should be potted. The seedlings can be outplanted in 1 year. *Araucaria angustifolia* may be direct-seeded on previously harrowed terrain. Various sowing positions have been tested: vertical, slanted, and horizontal; the latter is the most favorable to germination. The sprouting seedlings must be protected against sunscald with a screen. In recent years, nursery seedlings raised in containers have been used extensively for afforestation.

ADDITIONAL INFORMATION

Araucaria angustifolia may be planted outside its natural distribution area, provided the soil is deep and the water table is not shallow. At higher latitudes, such as 38° S, *A. angustifolia* flowers and fruits prolifically at 15 years. Cone production is almost constant, and understory regeneration is abundant. However, the species grows more slowly outside its areas of origin. Plantations should be considered only for shade or landscape, not for timber production.







Artocarpus heterophyllus Lam.

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MORACEAE (MULBERRY FAMILY)

Artocarpus philippensis, A. brasilliensis, A. maxima

Apushpa, ashaya, banun, chakki, champa, herali, jack, jackfruit, kanthal, khanon, khnor, kos, langka, makmi, miij, miijhnang, mit, nangka, pagal, pala, palasu, palavu, panas, panasa, panasam, peignai, pila, waraka, wela (Alam and others 1985, Brandis 1906, Gamble 1922, Gunasena 1993, Jensen 1995)

Artocarpus heterophyllus is the most widespread species of the genus. It forms forest associations with homesteads (Leuschner and Khaleque 1987, Topark-Ngarm 1990), tropical rain forests, dry evergreen forests, and the montane vegetation of mountain groups (Gunasena 1993). *Artocarpus heterophyllus* grows in the evergreen forests of the western hills of India, Sri Lanka, and the Deccan plain of Bangladesh (Alam and others 1985, Chopra and others 1963). It is normally found in association with permanent human settlement throughout the Indian subcontinent, Bangladesh, the coast of east Africa, Myanmar, northern Brazil, Jamaica, and Surinam (Alam and others 1985, Chopra and others 1963, Jarret 1959, Morton 1965, Purseglove 1968).

Artocarpus heterophyllus is a fairly fast-growing, large evergreen tree with a large, dense crown; it reaches 20 m in height and 30 to 60 cm d.b.h. It grows in a variety of soils including well-drained alluvial, sandy, or clay loam, and in soils with a pH range of 6 to 7.5 (Jensen 1995, Purseglove 1968). The species is sensitive to frost in its early life and cannot tolerate drought or wet (Singh 1960). If the root touches water, the tree will not bear fruit and might even die (Drury 1873). Occurring at elevations from 400 to 1200 m (Jensen 1995), it grows best where annual rainfall is 1250 mm (Gamble 1922) and the range of normal temperature is 16 to 35 °C.

The species is the national fruit tree of Bangladesh and a special class of timber tree in Sri Lanka. The heartwood is bright yellow; the density at 12 percent moisture content is about 0.69 g per cm^3. The wood is strong, hard, durable, and easy to saw, machine, or carve. It is used in high-quality furniture, house construction (doors, windows, roof rafters), masts, oars, implements, and musical instruments such as violins and tambooras (Gunasena 1993). *Artocarpus heterophyllus* is in many ways superior to teak (*Tectona grandis*) (Howard 1951). However, its strength is 75 to 80 percent that of teak (Wealth of India 1985). Roots of old trees are greatly prized for wood carving and picture framing (Morton 1965). Though heartwood is resistant to borer and termite attack, sapwood is highly susceptible to borer attack and perishes easily. Penetration of preservative is difficult but the wood seasons quickly. The fruit of *A. heterophyllus* is popular among the rural people of the Indian subcontinent. It enjoys special favor in some home gardens because it has numerous culinary uses and is abundant during the heavy monsoon rains. The seeds are eaten boiled or roasted or after soaking in syrup. The leaves and rind of the fruit are excellent sources of fodder (Jayawardena and Perera 1991). Parts of the tree are used to treat physical ailments. The unripe fruit is acrid, astringent, and carminative. The ripe fruit is laxative, cooling, and fattening and is useful in treating biliousness. The seeds are diuretic. Ash of the leaves is used to heal ulcers (Burkill 1935). An extract of the roots is used in treating skin diseases, asthma, and diarrhea. Mixed with vinegar, the latex promotes the healing of abscesses and snake bites and reduces glandular swelling (Jayaweera 1982). An infusion of mature leaves and bark is used to treat diabetes and gallstones (Gunaratne 1992). Finally, the heartwood yields a yellow dye when chips are boiled.

The tree begins to flower and fruit after about 5 years. However, grafted trees fruit earlier. Inflorescence is solitary, axillary, and cauliforous, with ramiflorous, short, leafy shoots. Inflorescence occurs from November through January. Male heads are sessile or on short peduncled receptacles, sometimes borne on the ultimate twigs; female heads are on oblong ovoid receptacles with simple spatulate styles exserted to 1.5 mm, syncarpous, 30 to 100 cm by 25 to 30 cm, cylindrical or somewhat clavate. The fruits are borne on the trunk and on the main branches. They are oval or oblong, 30 to 60 cm in length and 15 to 30 cm in diameter, and sometimes weigh as much as 10 to 50 kg. The skin is studded with short spikes, is pale green when immature, and becomes greenish-yellow to brown when ripe. The ripened fruit is sweet, fleshy, and has a crisp pericarp (Wealth of India 1985). Each fruit can contain between 100 and 500 seeds (Morton 1965), and each seed is enclosed in a yellowish, juicy sheath with a strong flavor. The seed is kidney-shaped and has thin, white, coriaceous, smooth testa. The seed is 25 to 30 by 15 to 20 mm with unequal cotyledons (Gunasena 1993).

Ripened fruits are collected April through September. Collectors climb the trees and remove the ripened fruits with a knife or scythe. The yellowish, juicy sheaths enclosing the seeds are separated by hand. In some cases, fruits are heaped for some days to rot the juicy sheath and pericarp. Then they are washed in water to separate the seeds from the sheath. Seeds are dried in partial shade on the ground and can be stored no longer than 1 month before planting. Seeds average 45 to 90 per kg.

Germination requires 3 to 8 weeks but is expedited by soaking in water for 24 hours (Hayes 1953). Panggabean (1979) reported that seeds stored in light or darkness at ambient temperatures or at 6 °C germinated 1 to 4 days after storage. After 22 days, germination ranged from 80 to 86 percent, and at 38 days none of the seeds germinated. The seeds germinate satisfactorily on coconut husks containing enough soil to cover the seed, and are outplanted with the husks.

Artocarpus heterophyllus propagates from seeds and cuttings. Direct sowing is preferred to transplanting because the taproot can sustain damage during transplantation (Gunasena 1993). High germination rate, early establishment, ease of method, and reduced cost favor direct sowing. Two or more seeds are sown at 3 by 3 m spacing. If properly established, the species grows rapidly in the first 5 years. At the end of the third year, *Swietenia macrophylla* King may be underplanted as a soil cover. By the end of the fifth year, the soil should be well protected and the forest floor kept very clean (McNeill 1937).

For rapid clonal propagation through tissue culture, using half MS salts and 2 mg per L IBA and NAA, juvenile shoots show 60 to 80 percent success in rooting (Jaiswal and Amin 1990). But Kamaluddin and others (1996) found more than 80 percent rooting success using a low-cost, nonmist polythene propagator when cuttings were taken from 3-month-old seedlings and treated with 0.2, 0.4, or 0.8 percent IBA. The growth of seedlings is slow to moderate during the first season, but fairly rapid in later years.

ADDITIONAL INFORMATION

A brown weevil, *Ochyromera artocarpi* Marshall, bores into tender buds and fruit resulting in fruit drop. A number of fungi have been observed attacking different parts of *A. heterophyllus*. *Ganoderma lucidum* causes root rot, *Corticium salmonicolor* causes twig blight and stem canker, and *Fomes durissimus* causes heart rot (Wealth of India 1985).


1cm
1cm

Astronium graveolens Jacq.

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ANACARDIACEAE (CASHEW FAMILY)

Astronium fraxinifolium Schott ex Spreng. [Systema Vegetabilium ed. 16 4(2): 404. 1827]; *Astronium fraxinifolium* var. *glabrum* Engl. (Monographiae Phanerogamarum 4:456. 1883); *Astronium graveolens* var. *brasiliense* Engl. [Flora Brasiliensis 12(2):399. 1876]; *Astronium graveolens* var. *inodorum* Triana & Planch. (Annales des Sciences Naturalles; Botanique, sér.5, 14: 268. 1872); *Astronium graveolens* var. *planchoniana* Engl. (Monographiae Phanerogamarum 4: 455. 1883); *Astronium planchonianum* Engl. [Flora Brasiliensis 12 (2): 399. 1876]

Algarrobo, almendro macho, arantha, barcino, bauwana, bolaquivo, cero, ciruelillo, ciruelo, ciruelo de montaña, copaiva, cuchi blanco, culebra, diomate, foncotín, gateado, gateado barcino, glassy wood, gomavel, gonçaleiro, gonçalo, gonçalo alves, gonçalo do matto, guacamaya, guaritá, guasango, gusanero, jejuira, jocote de fraile, jovillo, kulimche, masicarán, muira-catiara, muira-coatiara, muria-quatiara, palo de cera, palo de cruz, palo de culebra, palo mulato, palo obrero, pau gonçalo, pimientillo, potro, quebracho, quiebrahacha, quitacalzón roble gateado, ronron, sangolica, sangualica, sangue-sugueira, sirguelillo, tibigaro, tirigaro, urunday-ibá, urunday-para, urunday-pytá, yaga-biche, yoke, yomate, zongolica, zorro (Jiménez 1993, Record and Hess 1949, Salas 1993)

Astronium graveolens grows in southern Mexico, Central America, Colombia, Venezuela, Trinidad, Guyana, Ecuador, Bolivia, Paraguay, and Brazil (Croat 1978, Pennington and Sarukhan 1968, San Roman and others 1981).

Astronium graveolens is a medium-to-large tree that reaches 8 to 35 m in height and 35 to 100 cm d.b.h. The tree is symmetrical with a straight bole, small narrow buttress flanges 1 to 2 m tall, and a spreading or round dense crown. Young twigs are gray, green, or grayish brown with dark and protruding punctiform lenticels (Blackwell and Dodson 1968, Record and Hess 1949). The bark is 8 to 20 cm thick, with an outer pinkish layer underlined by a yellow layer. The bark is ragged and light or dark gray; it exfoliates in plates leaving light yellow or white areas, which exudate very sticky and transparent resins. The resin has a trementine odor and flavor (similar to vinegar); it is astringent and slightly sweet. Lenticels are numerous. Leaves are alternate, imparipinnate, spirally arranged, and 11 to 36 cm long including the petiole, with 5 to 15 pairs of leaflets, opposite or subopposite, sometimes alternate and lanceolate or oblong-lanceolate, with entire or slightly serrate margin. The leaflet apex is acuminate; the base is asymmetrical, obtuse or rounded, with reticulate venation, pinnate-eucamptodromous. The secondary veins have an acute-wide divergence angle of 65 to 80°. The leaflet blade is shiny dark green adaxially and dull light green abaxially. There are numerous dark spots throughout the leaflet blade and frequent ovoid galls at the margin. The old leaflets turn yellow before abscission. The tree is deciduous and sheds its leaves before flowering; the new leaves appear together with the flowers at the end of the dry season.

The species grows well in poorly drained limestone soils or rocky and alluvial soils. *Astronium graveolens* grows on moderate mountain slopes at elevations ranging from 150 to 1000 m. In Central America, the species is most abundant along the Pacific coast, at elevations between 500 and 600 m (Centro Agrónomico Tropical de Investigación y Enseñanza 1998b). It is a subcanopy or canopy species in the tropical dry premontane or low montane forest with temperatures of 20 to 32 °C and annual rainfall from 750 to 3000 mm (Salas 1993).

The timber color varies from light to dark brown or reddish, is more or less conspicuously marked with vertical blackish bands of variable spacing, and often produces a very striking and beautiful figure. There is a considerable range of density among different specimens and also within the same sample, the dark zones being the heavier (Record and Hess 1949). When fresh, the sapwood is light brown-grayish or dark brown-yellow, while the heartwood is gray-orange or reddish brown to bright red with narrow to wide irregular stripes of medium to very dark brown. After exposure to air and light the wood becomes brown, red, or dark reddish with nearly black stripes. The grayish or brownish-white sapwood is 4 to 9 cm wide and sharply demarcated (Chudnoff 1984). The timber has some resemblance in figure and texture to golden ebony or coromandel (*Diospyros quaesita* Thw.), although it has a warmer tone. Sometimes the wood exhibits a mottled figure that resembles Brazilian rosewood (*Dalbergia nigra* (Vell.) Allemao ex Benth.) (Record and Hess 1949). Growth rings are visible to the naked eye, with an average of 12 rings per 5 cm. The grain varies from straight to intercrossed; the texture is fine and homogenous; and the luster is regular or high.

The wood is very heavy, with a basic specific gravity of 0.75 to 0.78 (Creemers and Lemckert 1981, San Roman and others 1981). The green weight is 1120 kg per m^3 with 50.2 percent moisture content and 1228 to 1230 kg per m^3 with 46 to 47 percent moisture content. The dry weight is 850 to 860 kg per m^3. The rupture module is 1511 kg per cm^2 when dry and 955 kg per cm^2 when green (Chichignoud and others 1990, Herrera and Morales 1993, San Roman and others 1981, Simpson and Sagoe 1991, Wangaard and Muschler 1952). The wood is fairly easy to rather difficult to work, turns readily, finishes very smoothly, and takes a high natural polish; it is noteworthy for its durability. The wood is moderately difficult to season. There is some crook and bow accompanied by a slight tendency to twist; checking is slight. Wood air-drying occurs at a moderate rate. Shrinkage in green to oven-dry wood is quite normal for this type of wood (radial 4 percent, tangential 7.6 percent, volumetric 10 percent) (Chudnoff 1984). Air-drying takes approximately 29 weeks (San Roman and others 1981). There are slight drying defects, such as cracking at the ends and small lateral cracks, in less than 5 percent of the material (Herrera and Morales 1993, San Roman and others 1981). The wood weathers well and is highly resistant to moisture absorption. It is difficult to glue (Chudnoff 1984). The timber is very resistant to insect attack. The wood is very resistant if it is not in contact with the soil (Bultman and Southwell 1976); however, it is susceptible to white and brown-rot fungi when left at the forest floor, with slight damage after 12 months. When in use, the wood can be damaged by *Brasilianus mexicanus* (Cerambycidae) or by termites after 2 years (Jiménez 1993). *Astronium graveolens* is among the most outstanding for heavy, durable, construction timbers, and it is also highly favored as a wood for fine furniture, cabinets, and decorative veneers. It is used for specific items, such as knife handles, brush backs, archery bows, and billiard cue butts, and in turnery and carving (Chudnoff 1984).

Flowering occurs during the dry season (in Mexico it flowers March through May; in Honduras, February through April; and in Costa Rica, December through February), with most fruits maturing February to May (Brenes 1994, Jiménez 1993, Nichols and González 1992, Pennington and Sarhukán 1968). The species is dioecious, with flowers grouped in glabrous axilar or terminal panicles up to 20 cm long; the inflorescence has small, deciduous, pink bracts. The staminate flowers are small, actinomorphic, and pentamerous. The calyx has ovate orbicular sepals, with a round apex; the sepals are imbricate and glabrous. The corolla has green petals, glabrous, elliptic or ovate, with a round apex. The androecium has 5 to 7 stamens with compressed subulate filaments and oblong anthers. The flowers have a small, central, nectariferous disc, pentalobed, patelliform , and glabrous. The pistillate flowers are actinomorphic and have articulated pedicels. The calyx has ovate or elliptical sepals, imbricate, glabrous, and rounded at the apex. The petals are yellow-green, glabrous, elliptic, imbricate, and round at the apex. The androecium has five staminoids, separated from the gynoecium by a glabrous, patelliform, lobed, and nectariferous disc. The ovary is superior and unilocular with a single anatropous ovule. There are three curved, short styles, which end in a disciform and a papillary stigma.

After fertilization the sepals enlarge and surround the fruit, masking the petals, which are persistent but do not grow. In the unit of dispersal (diaspore), the petals are shiny brown-yellow, papyrus-like, and acrescent. They open and extend in a star-like shape when the fruit is maturing and contribute to its wind dispersal, acting in a samara-like fashion. The fruit is ellipsoid; 10 to 15 mm long; brown, bluish, or blackish when mature; with a single seed. It is often crowned by the styles. The fruit has a chartaceous exocarp and a yellow resinous mesocarp. The hard brown endocarp surrounds the membranous seedcoat. The seed is oblong or ellipsoid, 9 to 10 mm long, and 4 to 6 mm wide. The embryo is fleshy and ellipsoidal.

Fruits (seeds) must be collected directly from the tree before wind dispersal. Once collected, the fruits are placed on the floor and dried for 3 to 4 hours. A kilogram of diaspores contains about 18,000 seeds (Centro Agronómico Tropical de Investigación y Enseñanza 1998b).

The seeds keep their viability for 3 months if they are stored at 15 °C with an average moisture content of 15 to 25 percent. However, there is no germination (0 percent) after 1 year of storage (Centro Agronómico Tropical de Investigación y Enseñanza 1998b). The seeds lose viability in less than 1 month if stored at ambient temperature and humidity. The seed is suspected to be recalcitrant, as are other members of the family such as mango (*Mangifera indica* L.). Fresh seeds have shown 80 to 90 percent germination without any special treatment (Brenes 1994).

Germination is epigeal, and the seedling is cryptocotylar. Germination starts 4 to 8 days after sowing and is complete after 15 to 18 days. The seedlings grow slowly in the nursery (20 cm in 3 to 4 months) and they require moderate shade and humidity during the first weeks. The seedlings are ready for outplanting 5 months after sowing, when they reach a height of 35 to 40 cm. *Astronium graveolens* is grown in plantations at a planting distance of 2 by 2 m or 2.5 by 2.5 m) to prevent branching. The sapling grows best under full light.


2cm
2cm
1cm
1cm

Avicennia germinans (L.) L.

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VERBENACEAE (VERBENA FAMILY)

Avicennia nitida Jacq.

Mangle de sal, mangle negro, mangle prieto, mangle puyeque, mangle salado
(Centro Agronómico Tropical de Investigación y Enseñanza 1984a, 1984b;
Markley and others 1992; Pennington and Sarukhan 1968

This family has only one genus, *Avicennia,* which includes 11 species of trees and shrubs characteristic of mangrove forests. The genus is distributed in the wetlands of tropical and subtropical regions of Central and South America. It grows on both coasts, from Florida and the minor Antilles, through Mexico and Central America, to the coasts of Brazil and Peru, including the Galápagos Islands and other tropical and subtropical islands in America (Gentry 1993, Moldenke 1973). Species in the genus associate with *Rhizophora mangle* L., *Conocarpus erectus* L., and *Laguncularia racemosa* (L.) C.F. Gaertna. (Pennington and Sarukhan 1968, Salas 1993).

Avicennia germinans is an evergreen tree that averages 14 to 15 m in height; some trees may reach 20 m in height and 40 cm d.b.h. The trees are easy to distinguish because they have opposite decussate leaves growing on young, square, rising branches with leaf scars; they have ring-shaped joints or swollen nodes (Pennington and Sarukhan 1968) that are simple, grayish green, and opaque on the back side; the petioles form a hollow structure at the base, leaving a line similar to a stipule scar (Gentry 1993); and both surfaces of the leaves frequently show abundant salt crystals. The thick bark is gray, with a slightly salty taste (Salas 1993). The small crown is rounded (Pennington and Sarukhan 1968).

Avicennia germinans is a marine halophyte species (Bálsamo and Thomson 1995) and is physiologically adapted to grow in soils flooded with seawater. The trees can grow and develop in flooded soils with scarce dissolved gases because they have a great number of verticolor, erect pneumatophores. These spongy roots develop from the subterranean roots and push through the mud toward the surface. They absorb oxygen from the atmosphere, passing it on to the radicle system (Centro Agronómico Tropical de Investigación y Enseñanza 1984a, 1984b; McKee and others 1988). In the Caribbean region, *A. germinans* typically is located inland, in mangrove swamp areas away from the coast; apparently the species can provide differing levels of oxygenation to the anaerobic substratum. McKee and others (1988) report low concentrations of sulphur in areas where the density of aerial roots is higher.

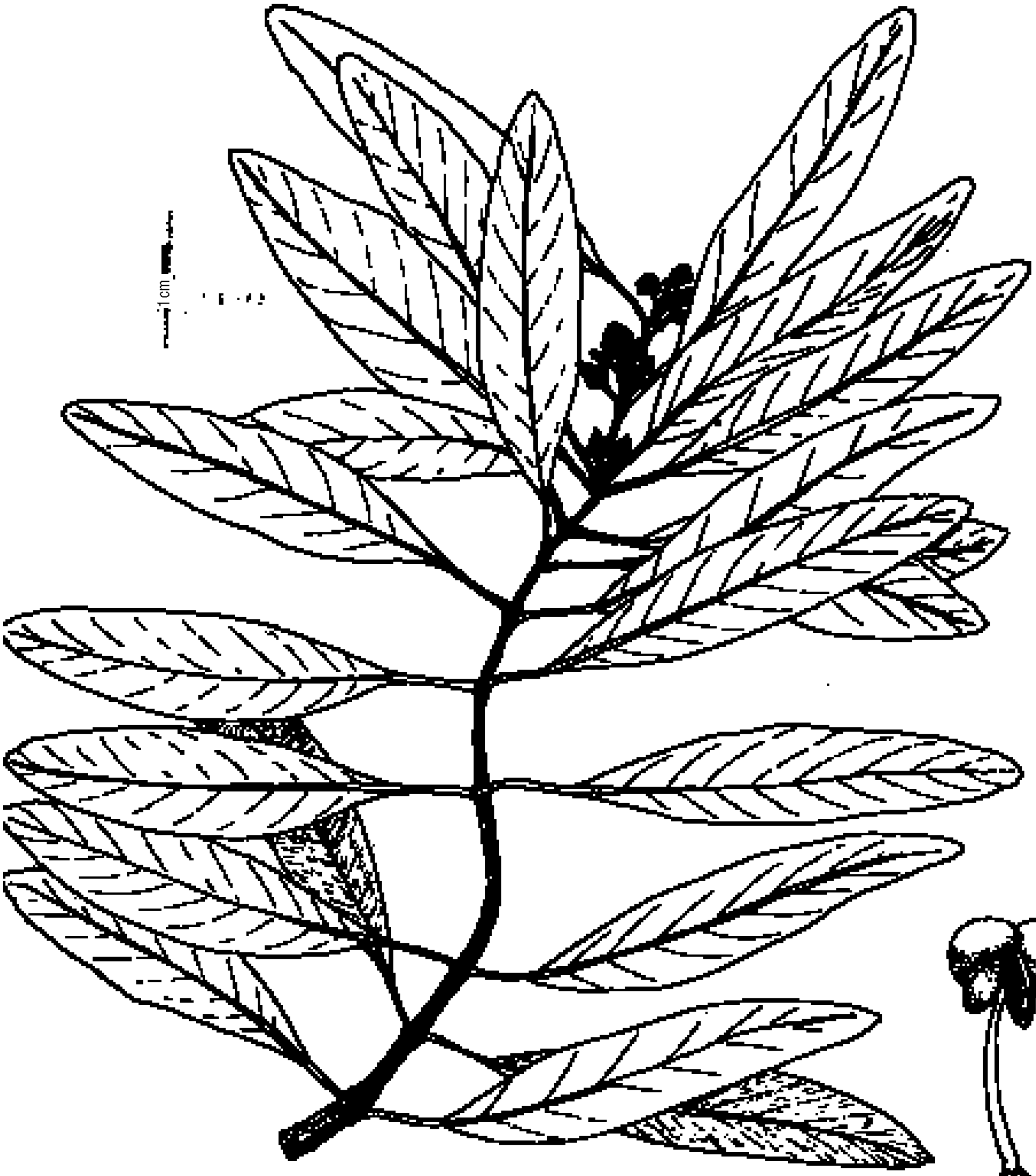
There are no known industrial uses for the wood of *A. germinans*, but where it grows it is used locally for poles in rural construction and for charcoal. The perfect, fragrant flowers remain open for several days and produce plenty of nectar, with which bees make excellent honey (Tomlinson 1980).

The tree flowers from May through July. The flowers are dense, gathered in terminal or lateral panicles; erect, in peduncles with four angles; zylomorphic, with a white corolla, yellow in color at the base; the five-lobed calyx contains three small bracts; white corolla, yellowish at the base. The fruits are two-valved flattened capsules, with a persistent calyx; they contain a big, ovoid, flattened seed, covered with silky yellowish hairs. The embryos of the seeds frequently germinate while the fruit is attached to the tree, causing its dehiscence (Pennington and Sarukhan 1968, Salas 1993). When the fruits fall, their walls open almost immediately, showing a plantule which consists of two folded cotyledons enclosing a thick radicle covered with dense radical hairs; its growth is fast and it adapts well to saline habitats (Tomlinson 1980). The production of plantules is high in September and October.

The fleshy green seed capsule germinates on the tree before falling and can survive floating in seawater for over 4 months, longer in fresh water. Seedlings tolerate some salinity but not more than that of seawater; they must be exposed at low tide for early development. Water temperatures over 40 °C are lethal to young seedlings. The seeds sprout and grow when placed on edge in moist, soft media. The tree sends up strong new sprouts from cut stumps. Both transplanted trees and planted seedlings benefit from a high-nitrogen fertilizer and a mulch of seagrass. Under good growing conditions, young trees may add 60 cm in height per year (Nellis 1994).

ADDITIONAL INFORMATION

Unlike *Rhizophora*, *A. germinans* does not colonize open habitats above the high tide line. The species can grow in fresh water and does not require salt, but it tolerates high salt concentrations (Tomlinson 1980). The plantules tolerate salt concentrations equal to or lower than salt water, but not high salinity. The excess is exuded through microscopic glands in the leaves, giving them a salty taste. Generally, the morning exudate of salt dehydrates during the day, and salt crystals accumulate on the surface of the leaf. The concentration of salt during the rainy season can decrease to less than half that of salt water, while during the dry season it can increase to more than double that of salt water. The hypodermis may be where the salt is accumulated and stored. (Smith and others, cited by Bálsamo and Thomson 1995).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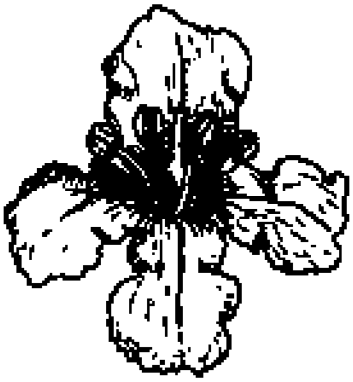
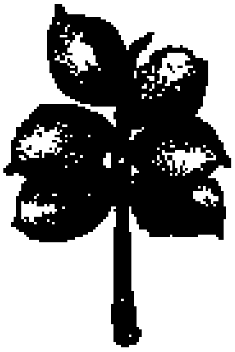
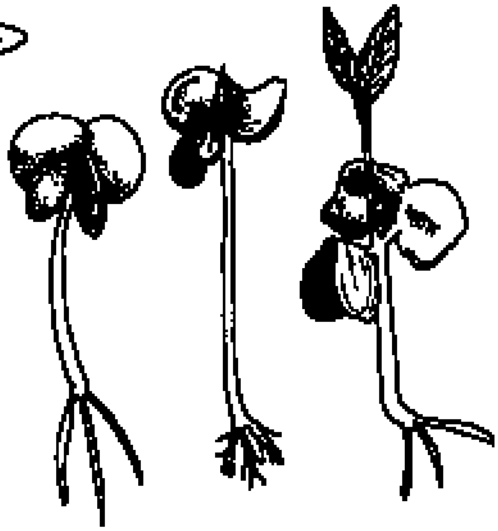






Azadirachta excelsa (Jack) Jacobs

SOMYOS KIJKAR
Association of South-East Asian Nations (ASEAN)
Forest Tree Seed Centre, Thailand

MELIACEAE/MELIOIDEAE (MAHOGANY FAMILY)

Melia excelsa, Azadirachta integrifolia

Kelantas, limpaga, marango, ranggu, sadao tiam, sentang, tiam

Originating in Borneo, *Azadirachta excelsa* grows naturally in southern Thailand, peninsular Malaysia, and Palawan Island of the Philippines. It was recently introduced to many other tropical countries, including Taiwan, Guatemala, and the State of Hawaii (Appannah and Weinland 1993, Kijkar 1995).

Azadirachta excelsa is a medium- to fast-growing tree that may reach 45 m in height (with a clear bole up to 20 m) and about 2 m d.b.h. *Azadirachta excelsa* leaves are usually pinnately compound, 30 to 75 cm long with 7 to 11 pairs of leaflets. Leaflets are 3 to 5 cm long and 2 to 3 cm wide, normally elliptic, rather bluntly pointed, and asymmetric; the base is uneven and thin with 6 to 11 pairs of side veins. Young leaves are usually serrated and become even-edged when mature (Chungpongse and Buranatham 1991, Corner 1988, Kijkar 1995). The first two leaves are opposite with three to five foliated; subsequent leaves are alternate and spiral, with leaflets opposite or subopposite and serrated. The bark of young trees is pink or brownish grey and smooth. Mature trees are brownish or grayish buff and have fissured and shaggy bark with grey, fibrous, oblong flakes. Inner bark is orange-red. Old trees in partial shade will have more greyish bark and fewer shaggy flakes than those grown in the open (Chungpongse and Buranatham 1991, Corner 1988, Kijkar 1995). Normally the trees are harvested at about 15 years when they are about 20 to 30 m high, 35 to 45 cm d.b.h., with clear boles 6 to 10 m. On very fertile sites, the trees reach these dimensions in 8 to 10 years (Kijkar 1995).

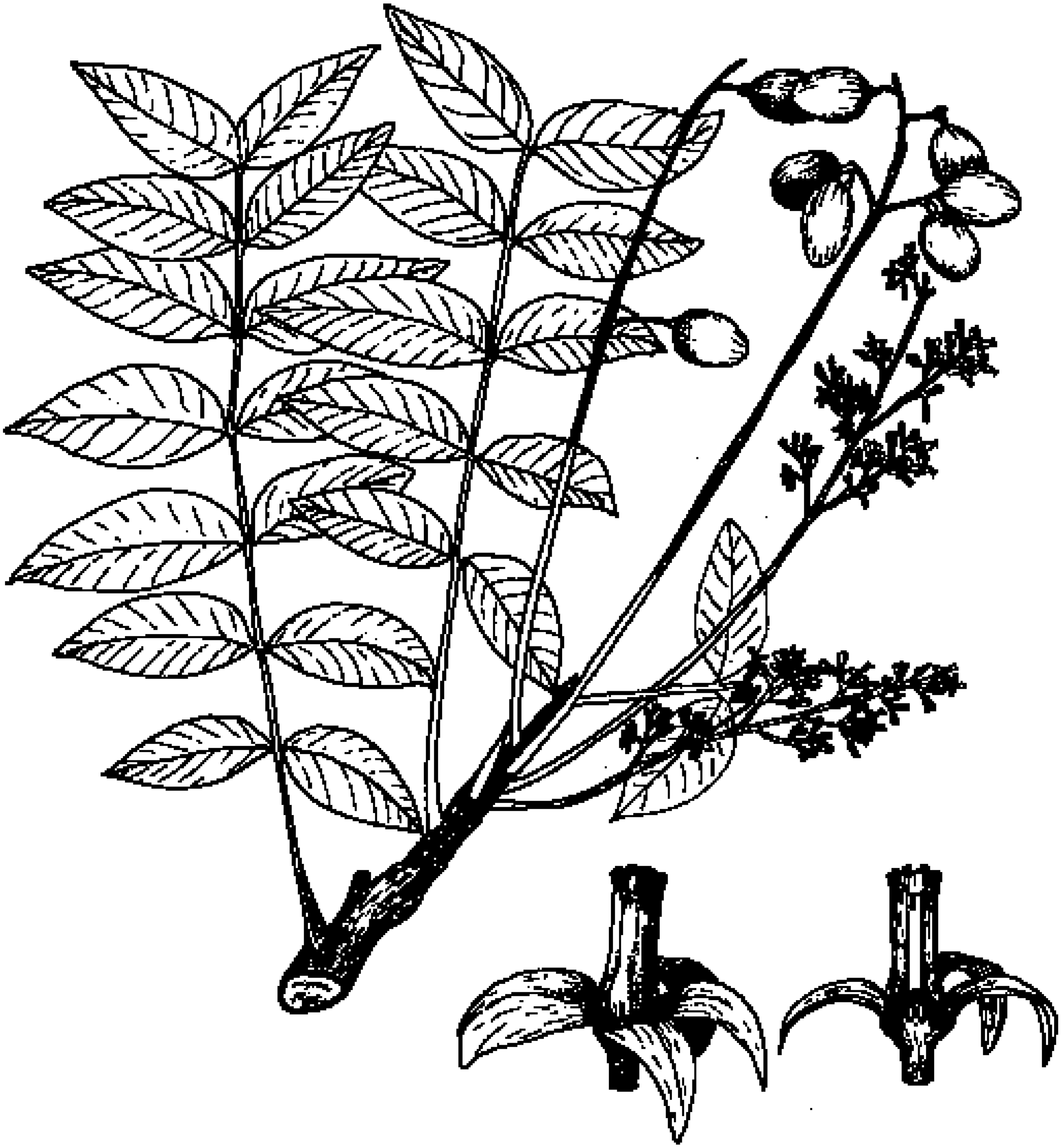
Commonly found along roadsides and farm boundaries and scattered on exposed areas, the species may attain a height of 15 to 20 m with a d.b.h. of 30 cm in 7 to 8 years (Kijkar 1995). *Azadirachta excelsa* is a lowland species that will grow up to an elevation of 600 m (Burgess 1966). It thrives on well-drained, fertile, sandy loams to loamy soils with a pH of 5.0 to 6.5, especially alluvial soils along creeks. However, *A.excelsa* cannot tolerate waterlogging or frequent flooding. The tree grows fast when annual rainfall is more than 1600 mm and mean annual temperature is 22 to 25 ÞC (Chungpongse and Buranatham 1991, Kijkar 1995).

The brown to golden brown wood is used in general construction and for furniture and carving. In addition, bioinsecticides are extracted from its seeds and leaves, and the edible young shoots and flowers are used in salads and in medicine to treat stomach diseases and nasal problems (Chungpongse and Buranatham 1991, Mungkorndin 1993).

Flowering and fruit setting start when *A.excelsa* is about 6 to 7 years old. In Thailand, the trees shed their leaves in January and February, and new leaves emerge immediately. When the new leaves turn green, the tree starts to flower, usually from late February through March. Flowers are greenish white, fragrant, and in panicles as long as the leaves. Flowers have five white petals, each measuring 5.0 to 6.5 mm long and 1.5 to 2.5 mm wide. Anthers are usually 4 mm long. The ovary divides into three carpels, each with two locules and one stigma (Corner 1988, Kijkar 1995). Fruit is usually 2.5 to 3.5 cm long and oblong, often with a constriction near one end. Initially green, the ripe yellow fruit contains one large seed with a rather leathery rind that gives a garlic scent when bruised or cut. Fruits usually mature in mid-June (Thailand) to August and September (Borneo). The seedcoat is membranous, and the seed has a straight embryo and thick cotyledons.

Because *A.excelsa* is usually a big tree with a long, straight, clear bole, seed collection from its crown canopy is very difficult. Fruit collection from the ground is commonly practiced by clearing directly beneath the canopy, removing debris and other organic materials from the site, and collecting only the freshly fallen fruits. After collection, immediate seed extraction is essential. The fruits are soaked in cold water for 1 day, and the seeds are extracted by hand or by Dybvig scarifier, then dried in shade for 1 to 2 days before sowing. Seeds average approximately 500 to 520 per kg (Kijkar 1995).

Because *A.excelsa* seeds are recalcitrant, they should be sowed immediately. *Azadirachta excelsa* seeds germinate in 6 to 23 days (Ng 1992). Direct dibbling of seeds into a prepared container to the same depth as the seed dimension (about 1 cm deep) and covering with soil is the recommended sowing method. Seeds may also be broadcast into seedbeds at scattered spacing, covered with thin layers—0.5 to 1.0 cm—of soil or sand, mulched with straw, and watered. After about 1 week, seeds will germinate well. Because crickets may damage or destroy seedlings during this stage, seedlings should be sprayed weekly with insecticides. When seedlings reach 30 to 40 cm tall (usually in 3 or 4 months), they are ready for outplanting (Chungpongse and Buranatham 1991, Kijkar 1995). The species also can be propagated vegetatively by rooting cuttings using juvenile seedlings or rejuvenile materials from root reservoirs (Kijkar 1995).



Azadirachta indica A. Juss

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Department of Forestry and Natural Resources
Punjab Agricultural University, India

MELIACEAE (MAHOGANY FAMILY)

Melia azadirachta Linn., *Melia indica* (A. Juss). Brand, *Melia parviflora* Moon.

Amargoseira Arishta, Azadirac de I'Inde, baypay, bevu, dawoon-nambu, grossblaettiger zedrach, Indian lilac, kaybevu, margosa tree, margosier, margousier, neem, nim, nimba, nimmi, nimuri, sado, tamaka

Of the two species in the genus, *A. indica* is native to India. Normally found in the Indian subcontinent (Pakistan, India, Bangladesh, Myanamar), the tree is cultivated throughout Southeast Asia, Australia, Africa, many countries in Central and South America, the Caribbean, Puerto Rico, Virgin Islands, Haiti, and the Plains of Arafat (Hegde 1992).

Azadirachta indica is a moderate-to-large tree that grows 80 cm in the first year. With its stout, short stem, the tree reaches 12 to 15 m in height (rarely 25 m) and 1.8 to 2.5 m d.b.h. It grows on dry, stony, clayey, and shallow soils having a pH range of 5.0 to 8.5. Although it can grow on calcareous soils (pH 8.5), the species develops best on soils with a pH of 6.2. Found at elevations from 50 m to 1500 m, *A. indica* grows best where annual rainfall averages 450 to 1150 mm.

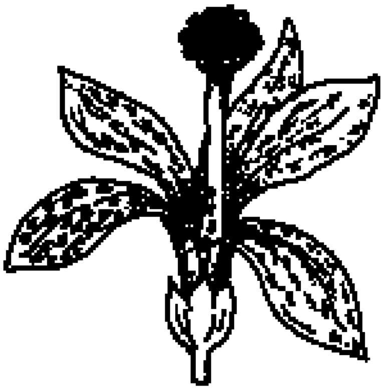
A highly esteemed tree, *A. indica* oil derivatives are used in agriculture, public health, medicine, toiletries, cosmetics, and livestock production and health. The timber seasons well even when sawed wet and has a specific gravity of 0.83. Wood is medium-to-coarse in texture, easy to work by hand or machine, and durable; but it does not take polish well. It is used for furniture, carts, axles, yokes, naves, fellos, boards, panels, cabinets, bottoms of drawers, packing cases, ornamental ceilings, oars, oil-mills, cigar boxes, carved images, toys, drums, and agricultural implements as well as in ship and boat building. Chests made of this wood are pest proof (Anonymous 1993). The species has limited ornamental use.

Flowering occurs January through May, depending on the latitude. Maximum flowering during April and May is related to high temperatures and low rainfall (Anonymous 1993). The floral parts rise acropetally (Guardamma 1956). Inflorescence is long, slender, axillary or terminal panicles with abundant white, or pale-yellow, fragrant flowers that are 0.3 to 0.4 cm across. Fruits are smooth, green, ellipsoidal drupes, 1.2 to 1.8 cm long, and 1.0 cm wide that turn yellow to brown when ripe. The seeds ripen June through August (Dwivedi 1980). A single tree of 10 to 12 years may produce 5 to 8 kg of seeds annually, while fully grown trees 20 years or older produce 30 kg of seeds. *Azadirachta indica* seeds are ovoid or spherically pointed apically with a thin testa. The seed is exarillate with a small adaxial sacrotesta (Pennington and Styles 1975). The hilum is not well marked. Seeds generally fall during rainy season and lose viability within 2 to 3 weeks (not truly recalcitrant seeds). The brown seeds are 1 cm in length and 4 to 5 mm wide. Larvae bore into seeds and certain thrips attack the flowers; the seeds are usually avoided by the desert locust (Joshi 1980).

Fruits should be collected when the drupes turn yellowish green on the trees. They may be collected by hand or machine. Collected fruits should be processed as soon as possible to ensure viability (Suri and Mehrotra 1996). Once the fleshy part of the drupe is removed, the stone is washed (not soaked) in clean water, spread in one layer, and dried in shade for 5 to 10 days. Seeds average 3,330 per kg (Singh 1994). Seeds should be stored in well-aerated containers at room temperature. Seeds stored at 15 °C retain viability up to 6 months, with germination falling from an initial 60 percent to 15 percent. Seeds with endocarps show 42 percent germination after 5 years of storage at 4 °C (Suri and Mehrotra 1996). Germination differs for ovoid or spherical (Aiyadurai 1959) seeds.

Direct sowing includes dibbling in bushes, broadcast sowing, and sowing in lines, mounds, ridges, trenches, sunken beds, or circular saucers (Chaturvedi 1993). Seeds should be sowed in nursery beds in drills 15 cm apart; the seeds should be placed 2.5 cm apart in the lines and lightly covered with soil. Germinating seedlings are vulnerable to moisture stress and bird and insect damage. Seedlings may be pricked out to 15 by 15 cm when about 2 months old (Chaturvedi 1993). Beds should be watered sparingly, weeded, hoed, and protected against frost (Kadambi 1959). Containerized stock should be grown in full sun. Polyethylene bags filled with F.Y.M. and soil in a 1:1 ratio are used for raising planting stock. Each bag is seeded with two seeds or one germinated seedling pricked out from a seedling bed. Whether seeds are sowed directly or transplanted, success is relative to nursery protection.


1cm



Bauhinia monandra Kurz

K.F. CONNOR
Southern Research Station,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Buahinia káppleri Sagot, *Bauhinia krugii* Urban, *Caspareopsis monandra* (Kurz) Britton & Rose

Alas de ángel, baujinia, butterfly bauhinia, butterfly-flower, caractére des hommes, casco de mulo, deux jumelles, flamboyán blanco, flamboyán cubano, flamboyán extranjero, Jerusalem-date, mariposa, Napoleon's plume, pata de vaca, pink bauhinia, pink orchidtree, poor man's orchid, seplina, St. Thomas tree, urape, varital variable, vlinderbloem

About 600 species of *Bauhinia* grow in the tropical regions of the world (Larson 1974). The genus includes trees, vines, and shrubs that are frequently planted for their showy flowers and ornamental foliage (Bailey 1941, Neal 1965). A native of southeastern Asia, *B. monandra* is found in the tropical regions of the world. Cultivated in the West Indies, it has naturalized throughout the islands.

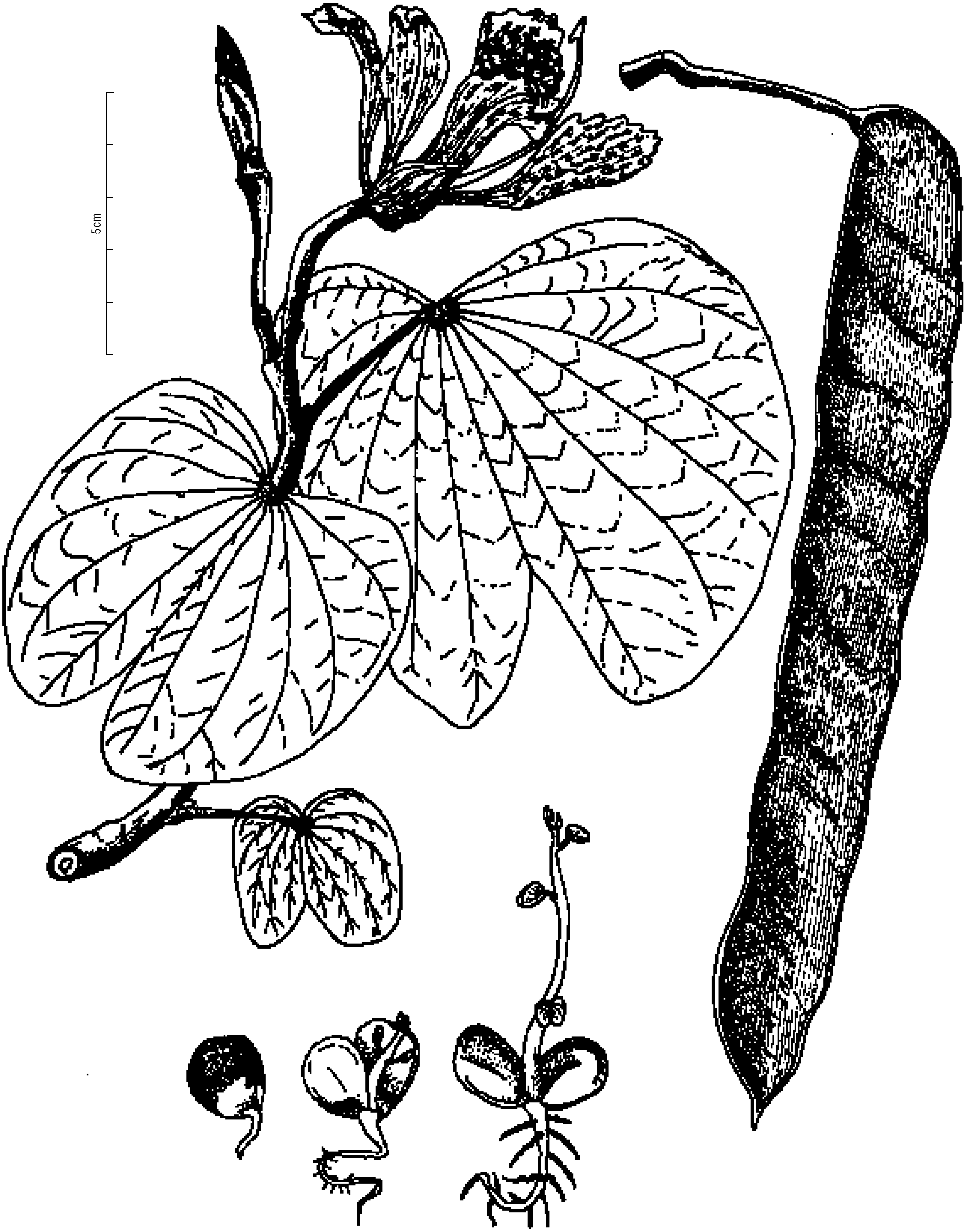
Bauhinia monandra is a small, fast-growing, evergreen tree or shrub that commonly reaches 3 to 15.2 m in height and 0.5 m in diameter. Its smooth, gray bark can become scaly and reddish brown on older trees (Little and Wadsworth 1964). The leaves of *B. monandra* are shaped like butterfly wings, rounded, and split one-third to one-half their length, forming two equal lobes. They are dissected by 11 or 13 main veins. The petioles extends into short awns between the leaf lobes. In Puerto Rico, it grows in areas that receive 900 to 2000 mm of rainfall annually and that have moist, well-drained soils (Francis and Liogier 1991). The species does not grow well on nutrient-poor sites.

Planted for its showy flowers and ornamental foliage, *B. monandra* is also used for fuelwood in Puerto Rico and for fences in Jamaica (Little and Wadsworth 1964); it is considered a weed in Guam (McConnell and Muniappan 1991). The seeds are a useful source of vitamin A (Essien and Fetuga 1989). In general, *Bauhinia* seeds contain high amounts of linoleic and oleic fatty acids and low amounts of myristic and linolenic fatty acids (Balogun and Fetuga 1985, Ramasastri and Shenolikar 1974, Sherwani and others 1982, Zaka and others 1983).

Bauhinia monandra blooms in 3 to 4 years (Bailey 1941); it flowers and fruits throughout most of the year (Little and Wadsworth 1964). The large, five-petaled, orchid-like flowers of *B. monandra* occur in short racemes; four of the spoon-shaped petals are pink and dotted with red or purple markings, while the fifth petal is mostly red or purple. The flowers range from 6.4 to 10.2 cm in diameter, have only one fertile stamen per flower and a calyx splitting along one side (Little and Wadsworth 1964, Neal 1965). The fruits are dark, dehiscent pods, 2.5 cm wide, 15.2 to 30.5 cm long, and pointed at the apex. While still on the tree, they split open with force, scattering the seeds (Little and Wadsworth 1964, Neal 1965). The black seeds are elliptic, flat, and 1 cm long. *Bauhinia monandra* seeds average 5,680 per kg (Francis and Rodriguez 1993).

Although published reports on the handling of *B. monandra* pods and seeds are not available, in most hard-seeded, temperate Fabaceae, pod ripeness is determined by a color change from green to light or dark brown (U.S. Department of Agriculture 1974). Ripe pods are picked by hand or shaken/flailed from the trees and then spread to air-dry. Seeds are threshed or mascerated from the dry pods and separated from the chaff by screening, fanning, or water flotation. Once dried (moisture content less than 12 percent; Roberts 1973), seeds are placed in sealed containers and stored between 2 and 4 °C. Dry seeds should store well for at least 3 years. *Bauhinia monandra* seeds can begin germinating 4 days after being placed on moist filter paper, and the final germination can be 100 percent (Francis and Rodriguez 1993).

The following information about related species of *Bauhinia* may be useful when preparing *B. monandra* seeds for germination. Satisfactory germination can occur after 52 weeks when *B. rufescens* seeds are scarified using 97 percent H_2SO_4, washed, dried, sealed into containers, and stored at 4 °C (Some and others 1990). However, excellent germination of *Bauhinia spp.* can be achieved without scarification (Francis and Rodríguez 1993). Orientation of the seed in the soil may be an important germination factor (Prasad and Nautiyal 1995); *B. retusa* seeds sowed with the micropylar end up had the earliest onset of germination and the highest seedling survival rate after 2 months. Those with horizontal orientation or micropylar-end-down in the soil had lower survival rates. Some species can be propagated from suckers but rarely from cuttings.


5cm

Bauhinia multinervia (Kunth) DC.

K.F. CONNOR and J.K. FRANCIS
Southern Research Station
and International Institute of Tropical Forestry
USDA Forest Service

FABACEAE (BEAN FAMILY)

Bauhinia megalandra Griseb., *Bauhinia multinervia* (H.B.K.) D.C., *Pauletia multinervia* Kunth

bauhinia, mountain ebony, pata de cabra, pata de vaca, petit flamboyant, urape

About 600 species of *Bauhinia* grow in the tropical regions of the world (Larson 1974). The genus includes trees, vines, and shrubs that are frequently planted for their showy flowers and ornamental foliage (Bailey 1941, Neal 1965). In Puerto Rico, *B. multinervia* is a naturalized, commonly occurring tree.

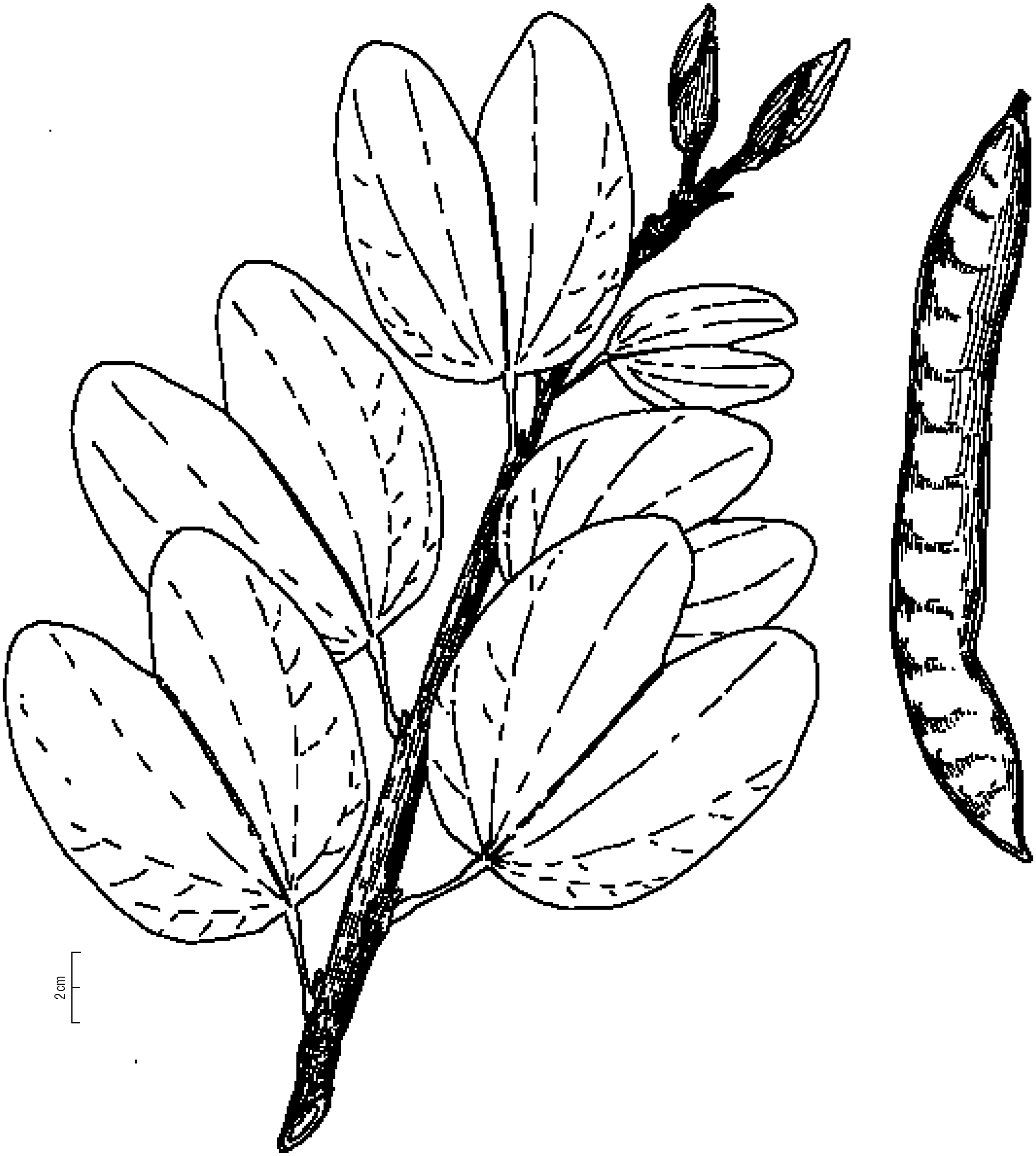
Bauhinia multinervia is a small tree that can reach 6 to 12 m in height and at least 30 cm in diameter (Pittier 1926, Howard 1988). The trees are not long-lived but can annually grow 1 m or more. Stems are primarily straight, and the crown of the tree is of medium density. The bark is gray-brown and fibrous. *Bauhinia multinervia* leaves are elliptical in shape, rounded at the base, and split one-third to one-half their length. Each leaf has 11 prominent veins (Pittier 1926). Leaf petioles are 1.2 to 4.5 cm long. Leaves, petioles, stipules, and young branches are all pubescent. Found in areas receiving between 1500 and 2500 mm annual rainfall (Francis and Liogier 1991), *B. multinervia* is an aggressive reproducer that is probably, like some of its relatives, moderately intolerant. It prefers medium-fertility soils ranging from 5.0 to 7.0 in pH. It does not tolerate poor sites, and trees usually require disturbance to become established.

The wood is reddish in color, finely grained, and easy to finish; however, the tree rarely reaches commercial size (Pittier 1926).

Bauhinia spp. bloom within 3 or 4 years (Bailey 1941). *Bauhinia multinervia* flowers grow in terminal racemes or panicles and have 10 stamens (Pittier 1926, Howard 1988). The five linear, clawed, somewhat elongated petals are white and 8 to 12 cm long by 0.5 to 1.0 cm wide. The 8- to 12-cm-long calyx is roughly pubescence and splits into five lobes. The fruits are flat, dark pods that tend to split and curl upon drying. Pods range in length from 22 to 31 cm long and are 2.3 to 2.8 cm wide. *Bauhinia multinervia* can produce seeds within 4 years of establishment. Seeds average 4,240 per kg (Francis and Rodriguez 1993).

Although published reports on the handling of *B. multinervia* pods and seeds are not available, in most hard-seeded, temperate Fabaceae, pod ripeness is determined by a color change from green to light or dark brown (U.S. Department of Agriculture 1974). Ripe pods are picked by hand or shaken/flailed from the trees and then spread to air-dry. Seeds are threshed or mascerated from the dry pods and separated from the chaff by screening, fanning, or water flotation. Once dried (moisture content less than 12 percent; Roberts 1973), seeds are placed in sealed containers and stored between 2 and 4 ^{o}C. *Bauhinia multinervia* seeds can begin germinating without scarification 6 days after placement on moist filter paper, and then final germination can be 90 percent.

The following information about related species of *Bauhinia* may be useful when preparing *B. multinervia* seeds for germination. Satisfactory germination can occur after 52 weeks when *B. rufescens* seeds are scarified using 97 percent H_2SO_4, washed, dried, sealed into containers, and stored at 4 ^{o}C (Some and others 1990). However, excellent germination of *Bauhinia spp*. can be achieved without scarification (Francis and Rodríguez 1993). Orientation of the seed in the soil may be an important germination factor (Prasad and Nautiyal 1995); *B. retusa* seeds sowed with the micropylar end up had the earliest onset of germination and the highest seedling survival rate after 2 months. Those with horizontal orientation or micropylar-end-down in the soil had lower survival rates. Some species can be propagated from suckers but rarely from cuttings.


2cm

Bauhinia purpurea DC. ex Walp.

K.F. CONNOR
Southern Research Station,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Bauhinia triándra Roxb., *Caspareopsis purpurea* (L.) Pittier, *Phanera purpurea* (L.) Benth.

orchidtree, pata de vaca, pie de cabra, purple bauhinia, ramo de orquídea

About 600 species of *Bauhinia* grow in the tropical regions of the world (Larson 1974). The genus includes trees, vines, and shrubs that are frequently planted for their showy flowers and ornamental foliage (Bailey 1941, Neal 1965). *Bauhinia purpurea* is a native of southeastern Asia from India to China and is planted in Florida, Hawaii, Puerto Rico, the Virgin Islands, and elsewhere in tropical America. The species is rare in Puerto Rico where it spreads slowly and reproduces infrequently (Francis and Liogier 1991).

Bauhinia purpurea is a fast-growing, small to medium-sized evergreen tree, reaching 7.6 m in height and 17.8 cm in diameter. It can reach a height of 4.6 m in less than 2 years (Bailey 1941). The bark is light gray and can be either smooth or finely fissured. The leaves of *B. purpurea* are smooth and elliptic in shape, have rounded lobes, and are divided one-third to one-half their length, forming a heart-shaped base; 9 to 13 main veins radiate from this base (Bailey 1941, Little and others 1974). Leaf blades vary in size from 3.8 to 12.7 cm in length, and the 2.5 to 5.1 cm petioles are enlarged at both ends (Little and others 1974). In Puerto Rico, *B. purpurea* grows in areas that annually receive at least 1500 to 2500 mm of rainfall and that have well-drained, moist soils. The species does not grow well on nutrient-poor or droughty sites.

It is primarily cultivated as an amenity tree, planted for its flowering attributes (Jim 1991). The leaves are edible (Biswas and Bhuyan 1983).

Bauhinia spp. bloom within 3 or 4 years (Bailey 1941). The flowers of *B. purpurea* are borne on unbranched axillary or terminal corymbs in autumn and winter months (Bailey 1941, Little and others 1974); only a few flowers are borne on each corymb. The calyx opens by splitting into two nearly equal parts. There are three to four fertile and six to seven sterile stamens per flower. When fully open, the large, fragrant, five-petaled flowers are 8.9 to 10.2 cm across. The petals are 5.1 cm long and 1.6 cm wide. Flower color is variable. Bailey (1941) reports that the petals are red in color, with one streaked with white on the claw; however, individual trees may have flowers that range in color from almost white to a rich purple. Little and others (1974) state that the petals are pink or purple in color, with one petal dark red toward the base. The fruits are flat, dark, dehiscent pods ranging from 20.3 to 30.5 cm in length and from 1.9 to 2.5 cm in width (Bailey 1941, Little and others 1974). Fruits twist as they open, expelling the seeds. *Bauhinia purpurea* seeds are shiny-brown, rounded, flat, and 1.3 to 1.6 cm long. Seeds average 4,670 seeds per kg.

Although published reports on the handling of *B. purpurea* pods and seeds are not available, in most hard-seeded, temperate Fabaceae, pod ripeness is determined by a color change from green to light or dark brown (U.S. Department of Agriculture 1974). Ripe pods are picked by hand or shaken/flailed from the trees and then spread to air-dry. Seeds are threshed or mascerated from the dry pods and separated from the chaff by screening, fanning, or water flotation. Once dried (moisture content less than 12 percent; Roberts 1973), seeds are placed in sealed containers and stored between 2 and 4 °C. Francis and Rodríguez (1993) report excellent germination of *Bauhinia spp*. without scarification; 99 percent of the *B. purpurea* seeds tested germinated when placed on moist blotting paper, and germination began within 4 days.

The following information about related species of *Bauhinia* may be useful when preparing *B. purpurea* seeds for planting. Orientation of the seeds in the soil may be important (Prasad and Nautiyal 1995); *B. retusa* seeds sowed with the micropylar end up had the earliest onset of germination and the highest seedling survival rate after 2 months. Those sowed horizontally, or with the mycropylar end down in the soil, had lower seedling survival rates and shorter roots. Some species can be propagated from suckers but rarely from cuttings.

ADDITIONAL INFORMATION

Pollen viability can be tested using a sucrose medium containing 20 ppm GA_3 (Kumar and others 1982).

Microscopic examination of the fruits reveals the presence of raised stomata with conspicuous subsidiary cells (Rugenstein and Lersten 1981).


1cm
1cm
1cm

Bauhinia variegata L.

K. F. CONNOR
Southern Research Station,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Phanera variegata (L.) Benth.

Buddhist bauhinia, flamboyán orquídea, mountain-ebony, orchidtree, palo de orquídeas, patabuey, poor-man's orchid

About 600 species of *Bauhinia* grow in the tropical regions of the world (Larson 1974). The genus includes trees, vines, and shrubs that are frequently planted for their showy flowers and ornamental foliage (Bailey 1941, Neal 1965). *Bauhinia variegata* is native to southeastern Asia and grows from India to China. It is one of the most commonly cultivated small trees in India and is a reliable greenhouse species (Bailey 1941). A popular planting in Florida and Hawaii, the species has escaped and naturalized in the southern foothills of Puerto Rico and throughout the West Indies.

Bauhinia variegata is a small to medium-sized evergreen or deciduous tree (Little and others 1974) that reaches 1.8 to 7.6 m in height and up to 20.3 cm in diameter. In Puerto Rico, it grows in areas that annually receive between 750 and 2000 mm of rainfall (Francis and Liogier 1991). *Bauhinia variegata* twigs are hairless, or nearly so (Bailey 1949). The leaves are variable in size, ranging from 5.1 to 12.7 cm in diameter. They are somewhat broader than they are long and are divided one-fourth to one-third in length (Bailey 1941, 1949; Little and others 1974). The resulting lobes are rounded and dissected by 9 to 13 main veins that radiate from the heart-shaped base. The species grows well in soils of medium fertility that are either droughty or moist; it is not tolerant of nutrient-poor sites. Although reproduction is abundant, *B. variegata* spreads slowly and is confined to a limited habitat.

Bailey (1941) reports that the wood is ebony in color, while Little and others (1974) state that the wood is whitish and soft. While the species is most frequently planted for its ornamental qualities, other properties are utilized: the bark is used as an astrigent in tanning and dyeing and the leaves and flower buds as a vegetable (Bailey 1941). Seeds yield 16 percent oil, which is made up of 55 percent linolenic, 36.8 percent linoleic, 26.1 percent oleic, 19.5 percent palmitic, 16.95 percent stearic, and traces of myristic fatty acids (Zaka and others 1983). The residual meal contains 41 percent protein.

Bauhinia spp. bloom within 3 to 4 years (Bailey 1941). In Puerto Rico, *B. variegata* flowers occur from autumn to spring (Little and others 1974). The five-petaled, showy flowers appear on short racemes, about seven to each shoot. They are 7.6 to 10.2 cm across and range in color from white (in the variety *candida* Buch.-Ham.) to rose or lavender-purple (Bailey 1941, Little and others 1974). Bailey (1941) and Neal (1965) report that the petals are variegated with red and yellow, and that the lowest petal is larger and marked with crimson. Bailey (1949) notes that the petal lips are often attractively marked or mottled with purple. Little and others (1974) state that one petal is streaked and that the petals have wavy margins. Petals are 5.1 to 6.4 cm long and 2.5 to 3.2 cm wide. The calyx splits along one side when opening and remains attached. There are five to six fertile stamens per flower. Fruits are dark, dehiscent pods that curve and twist when splitting open. They are long, thin, and pointed on both ends. Little and others (1974) note that pods reach lengths of 12.7 to 22.9 cm. Bailey (1941) reports pod lengths of 30.5 to 61 cm, but, in 1949, reduces pod length to "1 ft. or less." Fruits mature in late spring or early summer. Stomata are present on both the seeds and the pods (Rugenstein and Lersten 1981); the seeds are light brown, rounded, and flat.

Although published reports on the handling of *B. variegat*a pods and seeds are not available, in most hard-seeded temperate Fabaceae, pod ripeness is determined by a color change from green to light or dark brown (U.S. Department of Agriculture 1974). Ripe pods are picked by hand or shaken/flailed from the trees and then spread to air-dry. Seeds are threshed or mascerated from the dry pods and separated from the chaff by screening, fanning, or water flotation. Relatively large at 1.3 cm in diameter, the seeds average 4,950 per kg in Puerto Rico (Francis and Rodríguez 1993). Once dried (moisture content less than 12 percent; Roberts 1973), seeds are placed in sealed containers and stored between 2 and 4 °C.

Athaya (1985) reports that *B. variegata* seeds have a higher germination percent when stored after cleaning; however, viability is lost within 3 years. This viability loss may be attributable to high moisture content or mechanical damage, because hard-seeded Leguminosae should store well for longer periods of time. Germination studies of *B. variegata* using excised embryos produced results comparable to experiments using intact seeds (Babeley and Kandya 1986). Francis and Rodríguez (1993) report excellent germination of *Bauhinia spp*. without scarification, and they record a 77 percent germination for *B. variegata* seeds placed on moist blotting paper.

The following information about related species of *Bauhinia* may be useful when preparing *B. purpurea* seeds for planting. Seed orientation in the soil may be an important factor in seedling survival. Prasad and Nautiyal (1995) report that *B. retusa* seeds sowed with the micropylar end up had the earliest onset of germination and the highest seedling survival rate after 2 months. Those sowed horizontally, or with the mycropylar end down in the soil, had lower seedling survival rates and shorter roots. Some species can be propagated from suckers but rarely from cuttings.


1cm

Brosimum alicastrum Sw.

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MORACEAE (MULBERRY FAMILY)

No synonyms

Bread nut, maseco, mo, ojite, ojoche, ox, ramón, ramón blanco, talcoíte, tillo, tzoltzax, ujushe blanco

Brosimum alicastrum is native to America. It is distributed naturally from Mexico across Central America to northern South America and in the West Indies. The plant is an important component of hot-humid and subhumid tropical forests, where it forms groupings of different sizes (Little and Dixon 1983).

Brosimum alicastrum is a fast-growing, evergreen, monoecious tree with latex, of up to 40 m in height and 150 cm d.b.h. The trunk is straight, cylindrical, and grooved with well-developed spurs and a pyramidal crown made up of rising, and then hanging, branches with a dense foliage. The leaves are simple, alternate, ovate-lanceolate, elliptic to ovate, and 4 to 18 cm long by 2 to 7.5 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum ones to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm. The tree grows from sea level to 1000 m.

Brosimum alicastrum has multiple uses, although its potential is unknown outside its perimeter of natural distribution. Anthropological research indicates that *B. alicastrum* was one of the main means of support of the ancient Mayas, who cultivated it intensely. One of the most outstanding characteristics of this plant is that it remains green during the dry season, thus being the only existing source of forage in many places. The branches, leaves, fruits, and seeds are used to feed cattle. They also serve as a nutritional supplement for pigs and chickens. From 7 to 8 tons of fruits and from 35 to 40 tons of foliage can be harvested from 125 trees per hectare (Pardo-Tejeda and others 1976). The seeds are rich in starch, proteins, and vitamins A and C. In some places, they are eaten boiled and are said to taste like chestnuts. Toasted and ground, they are used as a coffee substitute. Specific gravity of the wood is 0.69. The wood is white or yellowish, and it is used for firewood, railroad ties, veneer, floors, tool handles, packing boxes, inexpensive furniture and cabinets, and bee honeycombs, as well as rural construction and handicrafts. The tree is cultivated in numerous backyards, and it is planted as a shade and ornamental tree in streets, parks, and gardens (Barrera 1981, Cabrera and others 1982, Chavelas and González 1985, Chudnoff 1979, Echenique-Manrique 1970, Flores 1993a, Lozano and others 1978, Miranda 1976, National Academy of Sciences 1975, Pardo-Tejeda and Sánchez 1980, Pardo-Tejeda and others 1976, Rico-Gray and others 1991).

The tree begins to yield flowers and fruits at 4 or 5 years of age. Because its geographic distribution is extensive, *B. alicastrum* blooms at different times, but especially January to June. Its fruits ripen between April and September, depending on geographic locations (Chavelas and Duvall 1988b). In southeastern Mexico, the plant blooms precociously and abundantly from April to July, and fruits from June to October (Juárez and others 1989). The flowers are cream in color and arranged in a capitula. In July through August the abundant fruits ripen and begin to fall to the ground. The fruits are globose berries, 2 to 2.5 cm in diameter, pulpy, sweet, and yellow or orange when ripe. Each fruit contains one seed (Cabrera and others 1982, Pennington and Sarukhan 1968). Seeds range in shape from globose to subglobose, are slightly depressed, and are 1 to 2 cm in diameter. The seedcoat is yellowish-brown, smooth, opaque, and membranous-papyritious. A vascularized thickening in the hilar region is strongly attached to the embryo in fresh seeds, but is brittle and easily released in old seeds.

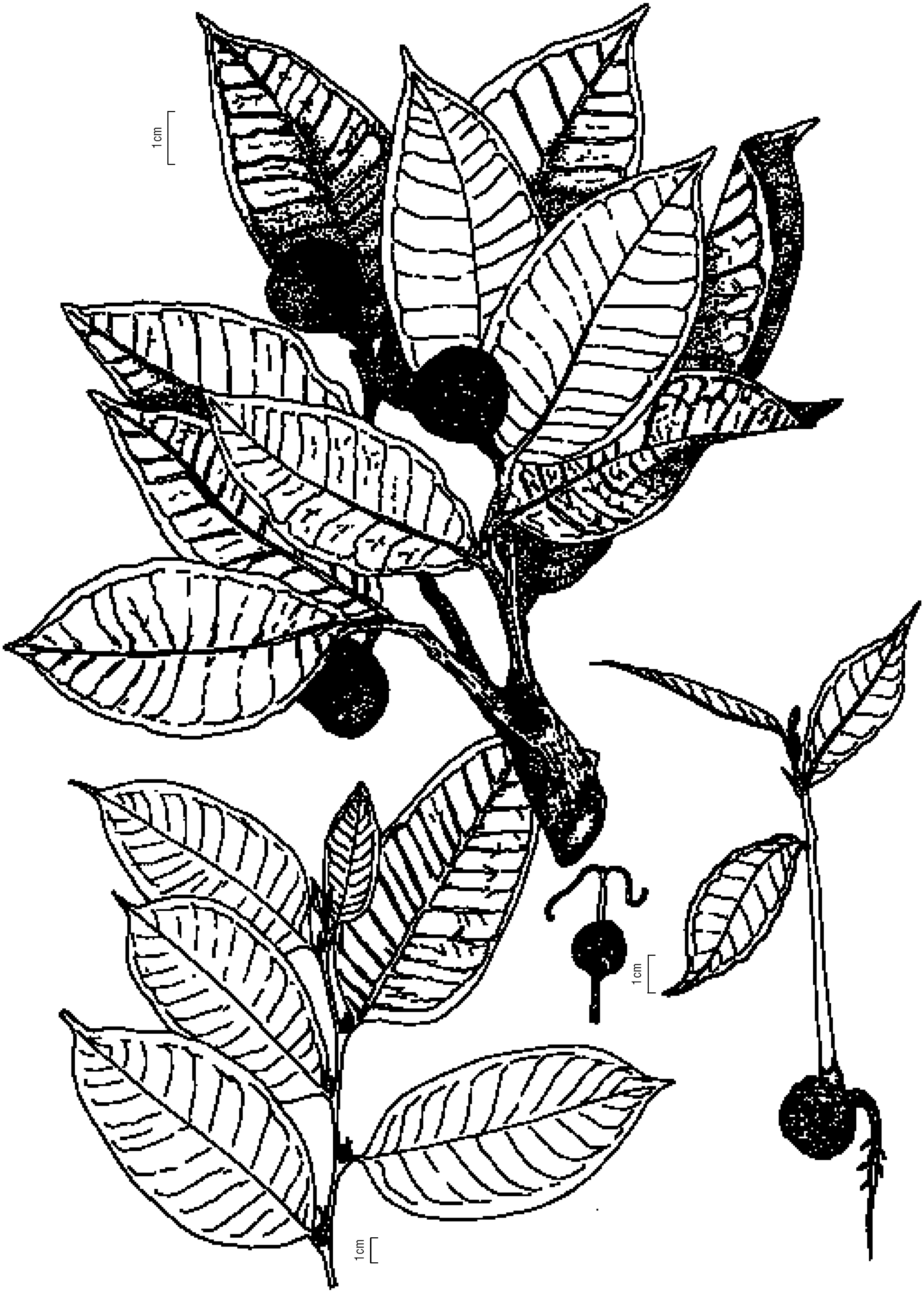
The fruits are easily collected from the ground due to their size. They also can be gathered from trees using poles with metal hooks. The peel is removed by hand, and the seeds are washed vigorously with cool water to clean off mucilage and impurities. The seeds are dried where it is cool and well ventilated. One tree can yield approximately 29 kg of seeds; seeds average 300 to 350 per kg. Seeds remain viable for approximately 3 months when stored under ambient conditions (24 to 30 °C). With longer storage, seed viability diminishes quickly because of loss of moisture (Vega and others 1981).

The germination of the seeds is cryptocotylar (del Amo 1979). Under humid conditions the fresh seeds germinate at 88 percent without pretreatment. Big seeds germinate more quickly than small seeds, and they produce bigger and more vigorous plantules (Niembro 1996). A heterogeneous sample of seeds germinated approximately 28 days after sowing (Vega and others 1981).

The growth medium used in the containers is a mixture of soil and sand, with proportions varying among nurseries. In nurseries, seeds are usually planted in black polyethylene containers, 10 cm wide by 20 cm long. They are watered every 1 to 3 days, depending on the permeability of the substrate used. Two or three months after sowing, the plantules are 30 to 50 cm tall and can be outplanted (Chavelas and Duvall 1988).

ADDITIONAL INFORMATION

The seed hilum is basal, puntiform, pale, and surrounded by a pale, vaguely circular spot. The micropyle is indiscernible. The embryo has a curved, asymmetric, green axis, with latex. Two massive, pulpy, unequal cotyledons are sinuous on their contact surfaces, one on top of the other. The plumule is undifferentiated. The radicle is curved, elongated, and partially visible, with a yellowish apex (Berg 1972, Berg and Dewolf 1975, Burger 1977, Hutchinson 1967, Pennington and Sarukhan 1968, Standley and Steyermark 1946c).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Brunellia costaricensis Standl.

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BRUNELLIACEAE (CEDRILLO)

No synonyms

Cedrillo, cedrillo macho, yerbabuena (Hartshorn and Poveda 1983)

About 15 species of the genus *Brunellia* grow in the mountains of tropical America (Standley and Steyermark 1946). Most grow in Colombia, some grow in the wet forests of the Andes, and a small number grow in Central America and the Antilles. In some countries, only one species grows (Nee 1985, Orozco 1986). *Brunellia costaricensis* is native to Costa Rica and grows in secondary forests at elevations between 1500 and 2800 m (Carpio 1992, Torres and others 1992b) in areas with 200 to 4000 mm annual precipitation and temperatures of 3 to 25 °C.

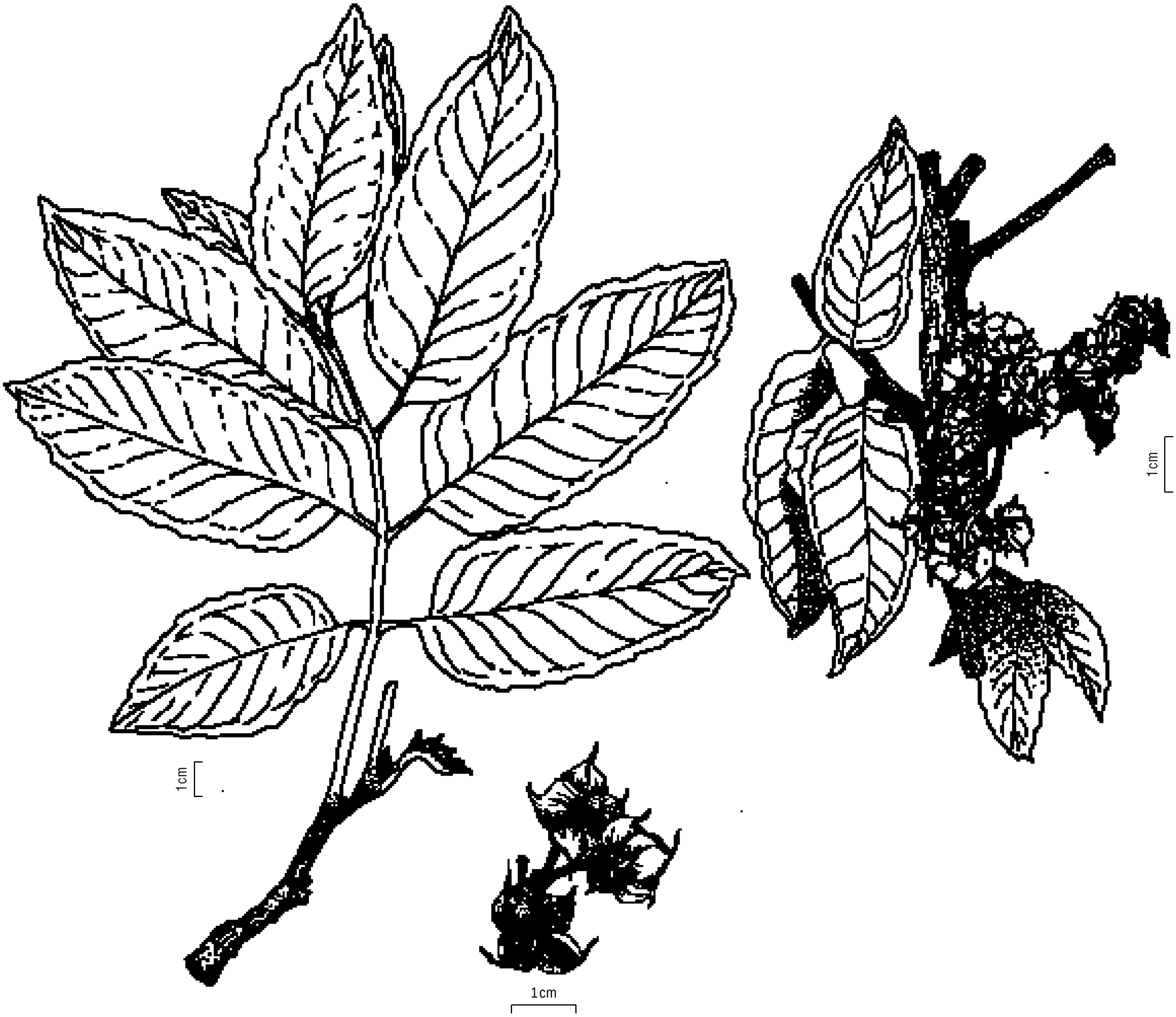
Brunellia costaricensis is a well-formed, medium-to-large tree with a cylindrical trunk. It can reach 27 m in height and 57 cm d.b.h. The species grows on slopes and in soils with good drainage. It can invade naked soil and adapt to soils left by landslides. Because it grows on bare sites, *B. costaricensis* must survive high light intensities (Hartshorn and Poveda 1983).

Considered a timber tree, *B. costaricensis* wood is light, with a specific gravity of 0.35. The sapwood is light pink and the heartwood is chestnut gray. The wood dries moderately fast and easily with no serious flaws. It is easy to work and finishes well. Its resistance to biodegrading organisms is low (Carpio 1992). Now used as a source of firewood and coal, it could be used for paper, toys, rustic handicrafts, and economical furniture (Holdridge and Poveda 1975). The wood is also used in the construction of boxes to carry fruit and for coffins and indoor construction (Carpio 1992).

The flowers appear in terminal inflorescenses (Arnáez and Moreira 1992, Cuatrecasas 1970, Nee 1985). The species blooms throughout the year; however, during some periods female flowers outnumber male flowers, and vice versa. In the high areas of the Central Valley of Costa Rica, abundant numbers of female flowers appear April through June. The sepals are green, and the petals are a tinny color. The fruit is aggregated polyfolicular with one to five fruits for every flower. Each branch bears about 331 fruits, each containing 2 seeds. Each seed is 0.20 cm wide, 0.35 cm long, and 0.193 cm thick (Arnáez and Moreira 1992, Torres and others 1992b). The species produces frequent and plentiful amounts of seeds. Birds spread the seeds, and banks of seeds on the ground are plentiful (Torres and others 1992b). *Brunellia* spreads both by seed and by resprouting (Torres and others 1992b).

Workers collect fruits all year by climbing the trees and using extension pruners. However, the highest rate of fruit production occurs from April through June. The fruits are moved in sacks to well-ventilated areas to dry. Drying frees the seeds from the follicles. The embryos of seeds stored 1 month were in good condition; however, all observations are preliminary (Torres and others 1992b).

Twelve pregermination treatments were tested. Some involved sulphate mixtures, chemical substances, and water soaks; however, germination was not achieved in any test (Torres and others 1992b).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Bursera simaruba (L.) Sarg.

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BURSERACEAE (BURSERA FAMILY)

Bursera gummifera L., *B. ovalifolia*, (Schldl.) engl.,
Elaphrium ovalifolium, Schldl.,(L.) Rose, *Pistacia simaruba*

Almacigo, chacah, chacaj, chiboue, chinacahuite, chino, copon, ginicuite,
gomye, gomye blan, gumbolimbo, indio desnudo, jiñocuavo, jiote, jobo, palo chino,
palo de incienso, palo jiote, palo mulato, palo santo, turpentine tree
(Méndez and others 1994, Schubert 1985, Timyan 1996, Witsberger and others 1982)

Bursera simaruba is native from southern Mexico to northern South America and has been introduced to the West Indies and southern Florida. It is found from Cape Kennedy to the southern Florida Keys (Elias 1980). Although found in primary forests, the species is more abundant in secondary forests. Other species in the genus include *B. microphylla*, or the elephant tree, native to southwestern U.S. and Mexico and *B. fagaroides*, or fragrant bursera, native to Arizona in the United States and western Mexico (Elias 1980).

Bursera simaruba is a dioecious tree reaching 20 to 30 m in height and 1 m d.b.h. (Aguilar and Aguilar 1992). *Bursera simaruba* is a deciduous tree with straight trunk and succulent stems common in seasonal tropical dry forests (Holbrock and others 1995). It is easily recognized by its reddish-brown, smooth, oil-looking bark, which peels off like paper. The branches are robust but easily broken. The leaves are alternative and odd-pinnate compound with 5 to 13 leaflets. The tree grows well in poor or rich soils and tolerates saline soils. It thrives in areas with 500 to 1400 mm annual precipitation and adapts to long drought periods. Although the species grows at elevations from 0 m to 1800 m, it is most common at approximately 1000 m (Lagos 1977, Méndez and others 1994, Witsberger and others 1982).

Bursera simaruba wood is white, yellowish, or light brown and has a fine-to-medium texture, a specific gravity of 0.26 to 0.40, and poor durability. Several insects, such as beetles, wood borers, and termites, attack the wood (Timyan 1996). The wood is easy to work and is used to make coffins, canoes, agricultural tool handles; to build rural homes and living fences; and as firewood (Aguilar and Aguilar 1992, Budowski 1987, Witsberger and others 1982). The fruits and foliage can be used as forage for livestock (Alfaro and Rojas 1992). The fruits, seeds, leaves, and bark have popular medicinal value in treating wounds, gout, digestive ailments, toothache, fever, kidney stones, and lung infections (Elias 1980, Gonzalez Ayala 1994, Timyan 1996). The bark is also used as antidote for snakebites, and leaf cataplasms are used to stop gangrene infections. The resinous sap can be used to make wood varnishes or glue that may substitute for gum Arabic (Aguilar and Aguilar 1992, Méndez and others 1994). In Guatemala, after the resin is collected from the trunks, it is hardened in blocks and used as incense in churches. The tree is also planted for shade or as an ornamental (Elias 1980).

In El Salvador, *B. simaruba* is leafless April through December, flowers March through June, and fruits almost all year. In Florida, *B. simaruba* blooms in winter or spring and the fruits ripen in the summertime (Elias 1980). In Costa Rica, fruits ripen January through March (Stevens 1983). The flowers are yellowish-green, 4 to 6 mm long, and borne in clusters or spikes; the fruits are pinkish drupe-like capsules with one or two seeds 6 to 8 mm long. The seeds are dispersed by birds, spider monkeys, and squirrels (Aguilar and Aguilar 1992, Lagos 1977, Stevens 1983, Witsberger and others 1982). In Costa Rica the fruits are a major food source for white-faced monkeys.

Bursera simaruba is propagated by seeds or cuttings. Seed germination is fast, and percentage germination is between 80 and 100. Seeds do not require scarification treatments. Cuttings 1.5 to 3 m long and 5 to 20 cm in diameter are planted in a permanent location during the rainy season and root easily without growth regulators (Alfaro and Rojas 1992). *Bursera simaruba* reaches maturity in approximately 15 years when propagated from seed (Schubert 1985).

Byrsonima crassifolia (L.) Kunth

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MALPIGHIACEAE (THE BARBADOS CHERRY FAMILY)

Malpighia crassifolia L., *Byrsonima pulchra* Sessé and Mocino ex DC., *Byrsonima cumingana* Juss., *Byrsonima fendleri* Turcz., *Byrsonima panamensis* Beurl., *Malpighia pulchra* Sessé and Moç.

Maricao cimarrón, changugo, chaparro, chaparro de sabana, chaparro manteca, chaparro manteco, chi, craboo, crabo, crapoo, doncela, hori, huria, manero, manteco, manteco merey, maricao, maricao verde, nance, nance agrio, nance verde, nanche, nancite, nancito, peraleja' noro, peralejo, peralejo blanco, peralejo de sabana, sabana kwari moeleidan, sabana mango, savanna serrette, tapal, wild-cherry, wild craboo, yuco (Little and Wadsworth 1964)

The genus *Byrsonima* has approximately 130 species native to tropical America (Mabberley 1997). *Byrsonima crassifolia* is found from Veracruz in Mexico to Brazil and Paraguay; it also grows in the West Indies. The species, often used as an ornamental, has been introduced to southern Florida (Little and Wadsworth 1964). The species is amply distributed and ecologically variable. *Byrsonima crassifolia* generally grows in association with *Curatella americana* L. (chumico) and both species are resistant to fire, displaying a special habit that makes the trees appear twisted (Anderson 1983).

Byrsonima crassifolia is a small evergreen tree, 4 to 10 m in height and 15 to 30 cm d.b.h. The tree has a fissured bark, gray to dark chocolate in color, with lenticels. The interior part has pink or red grooves and a bitter taste. The stems have prominent foliar scars, and young leaves are tomentose. The leaves are opposite, obovate to elliptic or ovate, scantily acuminate, 4 to 15 cm long, and 2 to 9 cm wide with an acute to obtuse base and whole margin. Found in wet tropical, dry tropical, premountain, and very wet tropical forests, the species usually grows in barren soils of dry to very wet places and is common in savannas and pastures (Holdridge 1970). Annual precipitation in these life zones ranges between 1000 and 8000 mm; minimum average annual temperature is 17 °C and maximum is 27 °C (Holdridge and others 1971). *Byrsonima crassifolia* is found at elevations up to 1500 m and grows in acidic and poor soils (Geilfus 1994).

Byrsonima crassifolia is a most variable species, especially in leaf size, leaf shape, and indumentum density (Cuatrecasas and Croat 1980). The ovary is usually glabrous; however, in some specimens it is hairy. According to these authors, the absence of a connection in the variation of the previous characteristics does not allow the recognition of subspecies. However, Geilfus (1994) reports that Brazilians distinguish five varieties according to the color of the fruit (white, red, orange, and green) and its size (larger than usual). No hybrids or geographic races have been reported.

The wood of *B. crassifolia* is opaque, reddish chocolate in color, hard, heavy (specific gravity of 0.7), and moderately durable. Throughout its range, every part of the tree is used in a variety of ways. Due to its golden yellow flowers, the tree is used as an ornamental, especially in Florida, and in some countries it is considered a honey-bearing tree. The wood is used for charcoal and firewood. The bark is used to tan hides, poison fish, and treat gastrointestinal and pulmonary diseases and skin infections. The roots are used to treat a variety of illnesses. The fruit may be used as a cotton dye and as a major component in sweet foodstuffs such as jellies and sherbets. Information about uses specific to a given country is presented in the last section of this description.

The species flowers from November through July, primarily from March through June, for approximately 6 weeks. The numerous flowers change from yellow to red-orange as they age. The five sepals are 1.5 to 2.5 mm long, obtuse, recurvate, and internally glabrous; each has two big oblong-ovoid glands. The petals are unguiculate, 10 to 13 mm long, glabrous, suborbicular, with a concave lamina and irregular margin. Usually, one petal is erect and small while the others are divergent to reflexed. The 10 stamens are 4 to 5 mm long, the base of the filaments is hispid, the anthers are introrse and 2.5 to 3.0 mm long, and the connective is thickened. The ovary has three styles and is usually pubescent, thin, and slightly longer than or equal to the stamens. Trees begin to fruit at 1-1/2 years and maximum yield begins at 4 years. Each tree produces 15 to 20 kilos of fruit during a harvest of 4 to 6 months (Geilfus 1994). One drupe (fruit) is produced from each flower. The drupes are ovate-globose, glabrous, 0.8 to 1.5 cm in diameter, green to reddish-yellow, and acidic. The fruits ripen primarily in August and September and are dispersed by birds (Anderson 1983). The seed is big, measuring approximately 0.5 to 1.2 cm in diameter (Cuatrecasas and Croat 1980).

Fruits are collected from the ground. No special tools are used, and the job is easily done by hand. When branches are not accessible, fruits can be made to fall by throwing a lightweight object, such as a piece of wood, and hitting the branches. Fruits are tightly stuffed into previously cleaned bottles with water and sold this way. Seed can be separated from the fruit with a soft squeezing action of the hand. They can also be left to dry, causing the oily fruit to shrink and expose the seed. The seeds can be preserved for several months in plastic bags that are stored in agave fiber sacks (Vega and others 1983). *Byrsonima crassifolia* seeds collected in Mexico averaged 5,280 per kg (Vega and others 1983).

Soaking or dehydrating the fruit can be considered an unintentional pretreatment that is unnecessary for germination. The species primarily reproduces through seeds, and in Mexico 30 percent of the seeds germinated at 22 days (Vega and others 1983). In current germination studies of *B. crassifolia*, seeds germinated only when given more than 50 percent direct sunlight. Seeds that germinated represented no more than 7 percent of the total planted, and germination took place in 158 to 183 days (Center for Tropical Forest Science, unpublished).

Seeds germinate between 2 and 10 weeks when planted 2 cm deep in seed beds (Geilfus 1994). Seedlings measuring 5 cm in height can be transplanted into bags. In about 2 years, seedlings may reach between 40 and 60 cm and are outplanted. Seedlings should be outplanted with 6 m spacing, and lower branches should be pruned to obtain a uniform crown.

ADDITIONAL INFORMATION

The adaxial surface of the leaf is slightly tomentose or almost glabrous when ripe. The abaxial surface is densely pubescent with pedicellate trichomes or glabrous when mature. The arched middle vein is pubescent even when the leaf is mature. The petioles are thick and 0.5 to 1.5 cm long. Terminal pseudoracemes, which grow up to 20 cm long, are usually isolated and not ramified, sometimes with a few short branches near the base. They are densely pubescent when young and almost glabrous when mature. The bracts are ovate-lanceolate, 2 to 4 mm long, and deciduous. The bractlets are ovate, acute, and 1.0 to 1.5 mm long, and the pedicels are up to 1.5 cm long (Cuatrecasas and Croat 1980).

In a biological and phytochemical study of the leaves, 22 compounds were isolated, identified, and tested for spasmogenic activity (Bejar and others 1995). Among the major compounds identified were triterpenes, flavonoids, sterols, an aromatic ester, and common and nonprotein amino acids. Bejar and Malone (1993) studied pharmacological and chemical extracts of leaves and bark and found the extracts reduced motor activity and acted as a light analgesic in rats.

The flowers of *B. crassifolia* produce abundant lipids instead of nectar; the lipids are gathered by several bee species of the genus *Centris* (Vinson and others 1997). Bees obtain pollen and the oil from glands located over the sepals in each visit to the flower. Oil is gathered by female bees primarily from the genus *Centris*. The oil is mixed with pollen to feed the larvae. The adult bees feed on the sugary nectar obtained from other species of plants with flowers. Bees from the genus *Trigona* also take the pollen from the flower (Anderson 1983).

Throughout its range, *B. crassifolia* serves in a variety of ways. It provides heat and sustenance and is used to treat a number of human illnesses. In America, the use of this species is quite ancient. Carbonized seeds, residues of the stem, and charcoal originating from 2,000 to 1,000 B.C. have been found in the area of Cuello in northern Belize (Turner and Miksicek 1984).

In Central America, the fruits are sold in bottles filled with water and used to make cold drinks, jellies, and other sweets. These fruits contain 90 to 240 mg per 100 g of vitamin C (Rehm and Espig 1991). Sometimes, the cold drinks are frozen and eaten as ice cream or sherbet, and butter is extracted from the fruits by soaking in hot water (Duke 1986). Both domesticated and wild animals eat the fruits. In addition, the bark is used to poison fish and tan animal hides, and the wood is used for charcoal and firewood and to obtain a red coloring used to treat skin diseases (Duke 1986). The epidermis of the plant and the unripe fruits are used to dye cotton.

In Guatemala, the peel of the fruit produces a light chocolate-colored coloring, which is used to dye cotton fabrics. It has also been reported to be a honey-bearing plant and, in some countries, the bark is used in tannery processes and in household remedies. A decoction of the dry bark is used to treat asthma, bronchitis, colds, coughs, fevers, tonsillitis, and skin infections (Cáceres and others 1993). The extract in hot water is used externally to treat mucous lesions and skin diseases caused by fungi (Cáceres and others 1991).

In Honduras, an infusion of the bark is used to treat diarrhea, discharges, wounds, skin diseases, toothaches, stomach aches, and oral disease (House and others 1995). Members of the Amerindian group Jicaque, located in the center of Honduras, eat the fruits uncooked or in drinks (Lentz 1985). In Nicaragua, the leaves and bark are used to treat diarrhea and the bark is ground in water and applied directly to the skin to treat measles (Barrett 1994). In Costa Rica, an infusion of the bark is used to treat chest colds (Pittier 1957). In Panama, the fresh bark is soaked in water for 24 hours, and the extract administered to treat chronic colitis and pyorrhea; the water, after the decoction of the bark, is administered as a diuretic (Gupta and others 1979).

In the Neotropics, this species is widely used for medicinal purposes. In Mexico, a decoction of the dry bark is used to treat snake bites and fever and to expel the placenta and reduce bleeding in women during childbirth (Bejar and Malone 1993). An infusion of the bark is administered to treat diarrhea and dysentery, and water from a decoction of dry branches is administered to treat bad coughs (Zamora-Martinez and Pola 1992). The liquid obtained from the decoction of leaves and dry roots is taken to treat diarrhea, to expel the placenta, and to reduce fevers (Bejar and Malone 1993). The dry fruit is also used to treat fever (Bejar and Malone 1993). The Mixe Indians from Oaxaca, Mexico use the bark to treat gastrointestinal disorders and skin infections (Geiss and others 1995).

In Colombia, the bark is used to treat diarrhea because it contains tannins (García Barriga 1992). It is also considered a good astringent and fever reducer. A decoction of the bark is used as a snake bite antidote. In Brazil, the fresh plant in water is used to treat dysmenorrhea, aches, weakness, and intense bleeding (Elisabetsky and Posey 1989). In Venezuela, Lewis and Elvin-Lewis (1977) reported that the bark is used as a fish poison.


1cm
1cm

Caesalpina pulcherrima (L.) Sw.

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(Department of Biology, New Mexico State University)

FABACEAE/CAESALPINIOIDEAE (BEAN FAMILY)

Poincianella pulcherrima L. (Timyan 1996) and *Poinciana pulcherrima* L. (Guzmán 1980)

Flor barbona, flower crest, francillade, gallito, guacamaya, paradise flower, peacock crest,
pride of Barbados, red bird of paradise, Spanish carnation, tabachin
(Allen and Allen 1981, Croat 1978, Guzmán 1980)

Caesalpina pulcherrima is native to the West Indies and Mexico (Croat 1978) and has naturalized in El Salvador and Panama. Two similar species are the Mexican bird of paradise *C. mexicana* and bird of paradise bush *C. gilliesi*.

Caesalpina pulcherrima is a fast-growing, glabrous shrub or small tree that reaches 6 to 7 m in height and 20 cm d.b.h. *Caesalpina pulcherrima* has bipinnately compound leaves and 9 to 11 pairs of leaflets. Adult *C. pulcherrima* trees are adapted to semi drought conditions and tolerate extreme heat. *Caesalpina pulcherrima* grows in a wide range of soils, temperatures, and elevations from sea level to 1000 m or higher. It freezes at 0 °C and recovers in warm weather.

Caesalpina mexicana may hibridize with *C. pulcherrima.*

Caesalpina pulcherrima is a popular ornamental in urban areas with its showy orange flowers, rapid growth, and medium size (Timyan 1996). It is commonly used for living fences and windbreaks in tropical countries and in the United States. Tannins are found in the bark, and flavonoids in the flowers and leaves (Guzmán 1980). Different parts of the plant are used to treat several conditions such as fevers, liver infections, canker sores, wounds, and eye irritations (González Ayala 1994, Timyan 1996).

Caesalpina pulcherrima has orange-red flowers in panicles that bloom and fruit 8 months after germination under moist conditions in sunny locations (Allen and Allen 1981). Flowers and pods are observed continuously during the dry season and most of the wet season. Pods mature 30 to 40 days after pollination (Croat 1978, Quintanilla 1997). The flat woody pods are 10 to 12 cm long with up to 12 seeds. Pods are green when young and dark brown when mature. Pods mature first at the base of the flower panicle.

Mature pods are collected by hand because they remain on the plant after maturation. Special tools are not required for seed extraction. Seeds extracted from the indehiscent pod and kept at 5 °C under dry conditions in air-tight plastic bags, do not need to be cleaned before planting. Seeds average 6,300 to 6,500 per kg. Pregermination treatment is unnecessary. Germination of fresh seeds is 90 to 100 percent (Navarrete-Tindall 1996) and of 3- to 4-year-old seeds, 85 percent.

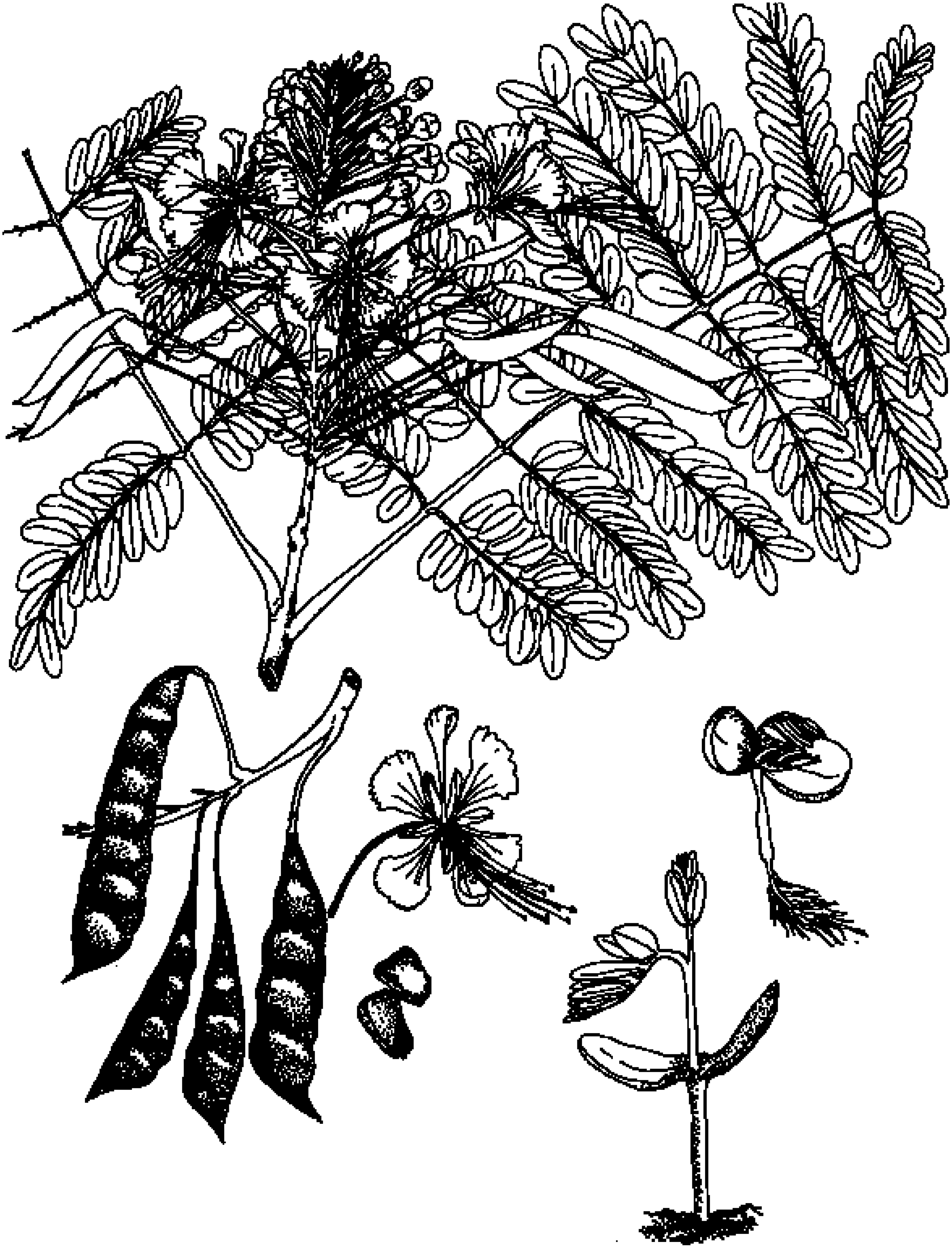
In El Salvador, seeds are planted in sunny locations in bags or pots with well-drained soils high in organic matter. In temperate regions, seeds can be germinated in Promix®, perlite, or vermiculite. Seedlings planted in the latter two media must be fertilized. Seeds germinate 4 to 7 days after planting and should be watered daily. Two- to six-month-old seedlings can be outplanted 1.5 m apart. Irrigation is required when seedlings are transplanted during the dry season. In the United States, plants are pruned in late fall or early winter to maintain a compact form.

ADDITIONAL INFORMATION

In the United States, the species is cultivated in desert areas in zone 9, with minimum average temperatures between -1.1 and -6.6 °C (Cathey 1990), and in the frost-free zone 11. In zone 9 only the root and part of the stem survive to produce new foliage the following spring.

Nodulation has not been observed on seedlings (Allen and Allen 1981), including 90-day-old seedlings inoculated with rhizobial strains from *Gliricidia sepium* (Navarrete-Tindall and Van Sambeek 1996).

Two seed sources are J.L. Hudson Seedman in the United States and Setropa in Holland (Rodale Institute 1992).



Calliandra calothyrsus Meisn.

J.R. CHAMBERLAIN
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FABACEAE (BEAN FAMILY)

Calliandra confusa Sprague & L. Riley; *Anneslia confusa* (Sprague & L. Riley) Britton & Rose;
Calliandra similis Sprague & L. Riley; *Anneslia similis* (Sprague & L. Riley) Britton & Rose;
Anneslia acapulcensis Britton & Rose; *Calliandra acapulcensis* (Britton & Rose) Standl.
(Britton and Rose 1928, Sprague and Riley 1923, Standley 1936)

Barbe jolote, barbe sol, barbillo, cabellito, cabello de angel, calliandra, clavellino,
kaliandra, pelo de angel (Macqueen and Hernández 1997)

Calliandra calothyrsus is native to the western Pacific coast of Mexico at Colima 19°04'N 103°45'W, with an outlying population in Veracruz, Mexico 19°20'N 96°20'W, through to the north coast of central Panama, 9°20'N 79°50'W. It is found in each of the following intervening countries and their states: Belize (Belize, El Cayo, Stann Creek, and Toledo); Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, and San José); El Salvador (Ahuachapán and Santa Ana); Guatemala (Alta Verapaz, El Progreso, Huehuetenango, Izabal, Petén, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, and Suchitepéquez); Honduras (Atlántida, Colón, Comayagua, Copán, Cortés, El Paraíso, Francisco Morazán, Intibuca, Ocotepeque, Olancho, and Santa Barbara); Nicaragua (Boaco, Chontales, Estelí, Grenada, Jinotega, Madriz, Managua, Matagalpa, Nueva Segovia, and Zelaya); and Panama (Chiriquí and San Blas) (Macqueen 1992, Macqueen and Hernández 1997).

Calliandra calothyrsus is a fast-growing shrub or small tree. The trees can attain a height of approximately 3 m in the first year of growth and may reach heights of 12 to 15 m, with either a single stem or many stems. In wetter environments, the species is characterized by trees of larger stature (up to 15 m tall) with red-brown to dark brown bark and angular young shoots tinged with red. In drier environments, the trees are generally smaller (between 2 and 10 m tall) and possess pale gray to light brown bark. *Calliandra calothyrsus* occurs in primary, secondary, or disturbed, lowland to premontane, dry to wet subtropical forests, especially along river and road margins, and in fallow fields. It is tolerant of medium shade, and occurs on a range of (often acid) soils (alluvial deposits, clays, and sandy loams) of various depths. *Calliandra calothyrsus* is not tolerant of frost, requiring a mean annual temperature of 22 to 28 °C, and inhabits areas with an annual rainfall of 1000 to 4000 mm at altitudes between 0 and 1850 m.

Calliandra calothyrsus is one of seven species in a subgroup of the genus, series *Racemosae,* which all typically display allopatric distributions. Sympatry does exist between *C. calothyrsus* and *C. houstoniana* (Mill.) Standl., *C. houstoniana* and *C. grandiflora* (L'Hér.) Benth., and *C. houstoniana* and *C. juzepczukii* Standl. Sympatry does not, however, always lead to hybridization, and putative hybrids have been documented only between *C. calothyrsus* and *C. houstoniana* and between *C. houstoniana* and *C. juzpeczukii* (Chamberlain 1996, Macqueen and Hernández 1997). Natural hybrids appear to be relatively uncommon, however, and are likely to have arisen through the disturbance of previously isolated habitats rather than through reproductive isolation (Chamberlain and Hubert, 2001). Interspecific hybrids between *C. calothyrsus* and *C. houstoniana,* which are predominantly infertile, have been observed, although the perfect floral structure of hybrids produced artificially castes some doubt on the occurrence of widespread hybrid infertility in the *Racemosae*.

Substantial ecotypic variation has been observed within *C. calothyrsus* (Chamberlain and others, n.d.). The analysis of isozyme and RAPD molecular markers has provided evidence for the existence of four subgroups within the species (*C. calothyrsus-1* to *-4*) (Chamberlain 1998, Hubert 1997). Distinct morphological variation was found to parallel the observed variation in molecular markers, and differences in environment (geographical location, altitude, rainfall) were, in turn, associated with particular combinations of molecular and morphological variation, lending support to the description of ecotypes within the species (Chamberlain and others, n.d.).

Calliandra calothyrsus is cultivated and used widely for fuelwood, animal fodder, green manure, shade for tea and coffee, and soil conservation in many parts of the humid tropics (Macqueen 1992, National Research Council 1983a). The species, introduced to Indonesia from Guatemala in the 1930's (Verhoef 1939), is now naturalized in many parts of Java. Until recently, these naturalized populations have been the major source of seeds for planting in southeast Asia, Australia, and east and west Africa. In Indonesia, the species has been cultivated primarily for afforestation, soil conservation, and as a bee forage in honey production, although trees are often cut or coppiced for fuelwood (Kartasubrata 1996). In other exotic environments, the species is an important source of forage for cattle and goats, in terms of both research and cultivation, e.g., in Queensland, Australia, and Embu, Kenya (Palmer and Ibrahim 1996, Paterson and others 1996b). *C. calothyrsus* is rarely used in its native range, however; possibly a combined result of relatively low population pressure on the land, the region's high diversity of other useful woody species, and poor promotion of the species through regional research establishments (Arias and Macqueen 1996).

Calliandra calothyrsus has a flowering period that can extend up to 12 months per year if sufficient soil moisture is available. Across the native range, flowering reaches a peak during October and November and ceases where a pronounced dry season is experienced (January to April). The inflorescence of *C. calothyrsus* is a paniculate raceme in which the flowers open acropetally over 60 to 90 days. The flowers are held within subumbels and the number of flowers open per subumbel ranges from 4 to 14 (Macqueen 1992). The flowers are characterized by their long, red or pink, staminal filaments, which form the brush-type floral display typical of many mimosoid legumes. From pollination to seed maturity, a period of between 90 and 120 days is required, but sequential flowering means there will almost always be a proportion of seeds on a tree that are not ripe. The fruits, flattened pods with thickened and raised margins, change color from green to golden or dark brown as the seeds reach maturity. When ripe, the pods split from the apex to the base, scattering seeds for short distances (up to 10 m) from the parent plant (Macqueen 1992).

Between-population variation for flower production, floral phenology, total pod production, number of seeds per pod, and number of aborted seeds per pod has been found in *C. calothyrsus* (Rajaselvam and others 1996). Such variation will inevitably have an impact on the timing of seed collection and the number of visits needed to acquire appropriate quantities of seed. The explosive dehiscence of pods means that accurate timing is required for efficient seed collection. According to Macqueen (1992), pods should be collected when fruit maturation is relatively constant and the majority of trees within the collection area have set seed. If there are only a few trees, or flowering and subsequent fruiting between trees has been asynchronous, seed collection may continue over several weeks.

A number of methods are used to collect fruit of *C. calothyrsus*. Collectors use long-arm pruners to cut off the inflorescence axes bearing mature fruit (Macqueen 1993b) or branches are bent down and the pods removed by hand. In seed production orchards, sacking can be placed on the ground below the *C. calothyrsus* trees, and the pods left to dehisce naturally. This method ensures that all of a tree's mature seeds are collected and labor inputs are relatively small (Hopkinson, personal communication). In natural populations, no more than 75 percent of the pods have been collected from individual trees to ensure that sufficient seeds are left to regenerate the stand (Macqueen 1992). Because pods are usually collected at the beginning of the dry season, in both the native range and exotic environments, sun-drying of both pods and seeds is often possible. The separation of seeds from pods is best achieved through slow, natural drying. Pods may be placed in wire mesh containers in the sun, and the wire mesh will then trap the seeds as the pods dehisce. The manual opening of pods has been generally avoided because the seeds may be immature and could undergo overly rapid and potentially deleterious drying on exposure to the air. Once pods are open, seeds can be thrashed out from the pod waste and cleaned manually or mechanically. At this stage, it is important to dry the seeds to between 6 and 10 percent moisture content by placing them on drying mats under warm, dry conditions without prolonged exposure to direct sun. For interim storage, the dry seeds can be placed in labeled, ventilated, canvas bags.

Seed predation by bruchid beetles (e.g. *Stator limbatus*) has been virtually nonexistent in some populations of *C. calothyrsus*, but has been found to affect 85 percent of the total seed harvest from other populations (Johnson and Lewis 1993, Macqueen 1993b). Low-temperature storage is an effective way of killing any developing beetles.

Seed moisture content and temperature are critical to successful long-term storage of *C. calothyrsus*. Seeds are orthodox and can be stored at 4 °C for periods of more than 5 years with a percentage germination of 75 to 90 percent. Airtight metal tins will protect the seeds from external changes in humidity and prevent insect and fungal attack. Problems with seed viability in *C. calothyrsus* have sometimes been reported (e.g. Roshetko and others 1996), and Macqueen (1995) emphasizes the need to collect mature seeds and reduce the time between collection in the field and storage under cool, dry conditions.

Calliandra calothyrsus germinates readily without pretreatment, especially when fresh seeds are used. Nevertheless, making an incision in the seedcoat (nicking) may improve germination. Verhoef (1939) reported that the germination rate increased from 28 to 48 percent (untreated) to 94 to 97 percent (with nicking). Halliday and Nakao (1984) also found scarification improved germination. Macqueen (2001) has suggested that situations where labor constraints make the individual nicking of seeds unjustifiable, a 10-minute soak in hot water (70 °C) followed by a 12- to 24-hour soak in cold water is the preferred pregermination treatment.

Calliandra calothyrsus is nitrogen-fixing, and the growth of the species is greatly improved by inoculation with *Rhizobium* (Lesueur and others 1996a). *Calliandra calothyrsus* was scarcely, or not at all, nodulated by strains from the genus *Bradyrhizobium* (Lesueur and others 1996a). Inoculation with a known strain of *Rhizobium* has, therefore, been recommended when introducing *C. calothyrsus* to exotic environments for the first time. Macqueen (1993a), in conjunction with the Nitrogen Fixation by Tropical Agricultural Legumes Center (NifTAL) in Hawaii, recommended and supplied strains for use in the *Calliandra* provenance trial network. Alternative strains have been identified by Lesueur and others (1996a, 1996b).

Rhizobium inoculum is stored in sterile dry peat, and must be kept sealed and refrigerated in a dark room, then used within 6 months. Inoculum can be applied as a coating to the seed using 50 g of inoculum per kg of seed. Applications of 1 ml liquid per 50 g of seed can be made using vegetable oil, a solution of 40 g gum arabic in 100 ml water, or 1 part sugar to 2 parts water (Nitrogen Fixation by Tropical Agricultural Legumes Center 1984). Alternatively, a slurry of 5 g inoculum mixed with water can be applied directly to 1,000 seedlings (Macqueen, 2001).

Another important soil association occurs between roots of *C. calothyrsus* and vesicular-arbuscular mycorrhizal fungi (VAM). Reena and Bagyaraj (1990) found that when *C. calothyrsus* was inoculated with *Glomus velum* and *Glomus merredum* (VAM fungi), the inoculated plants had greater height, leaf number, stem girth, biomass, and phosphorous and zinc content than uninoculated plants. Macqueen (2001) has recommended that when preparing land for *C. calothyrsus* cultivation, the duration of any preceding cultivation of crops without mycorrhizal associations should be minimized to avoid reduction in the land's VAM inoculation potential (Shepherd and others 1996). Direct inoculation with VAM may also provide benefits.

Calliandra calothyrsus can be propagated by seeds sowed directly at the planting site, or raised in the nursery as container seedlings or bare root seedlings. Selection of the propagation technique will depend on the planting objectives and the planting environment (e.g., soil fertility, rainfall, available resources, labor, and transport constraints). Because propagation techniques for *C. calothyrsus* have been reported in detail elsewhere (e.g., Macqueen 1993b, Roshetko and others 1997), a standard propagation method under nursery conditions is summarized. After inoculation with *Rhizobium* and VAM fungi, two seeds are sowed in a 10 cm by 20 cm standard black polyethylene container and the second seedling removed after its first adult leaves begin to show. The seedlings are then placed under 50-percent shade, which is gradually reduced before planting. The containers can be lifted occasionally to allow root pruning. When the seedlings are 20 to 50 cm tall with a root collar diameter of 0.5 to 1 cm they can be planted immediately after the first heavy rains. Young seedlings should be protected from fire, pests, weed competition, and browsing animals.

ADDITIONAL INFORMATION

Floral anthesis occurs between 1530 and 1700 hours and is followed by anther dehiscence once the flowers are fully open. The stigma are receptive from 1900 hours on, but by 0600 hours the following morning, receptivity has been lost and the flowers begin to wilt. Pollination is effected by nectivorous bats and sphingoid moths (Chamberlain and Rajaselvam 1996, Hernández 1991).

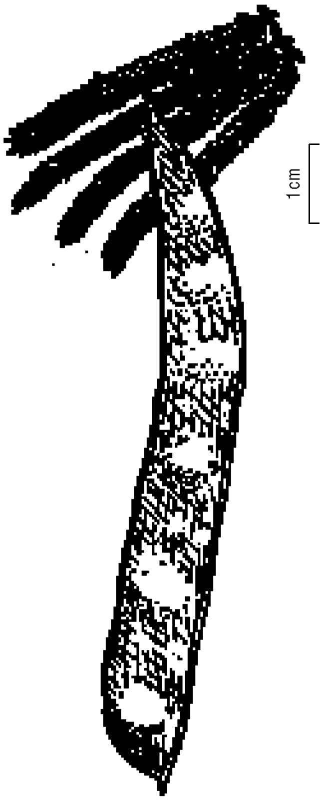
Range-wide provenance seed collections of *C. calothyrsus* have been made by the Oxford Forestry Institute with the aim of maximizing genetic diversity within the final collection (Macqueen 1991, 1993b). The seeds have been used to evaluate the diversity of the species within replicated field trials across a range of environments in terms of growth and biomass accumulation (Pottinger 1996). Based on the species' reproductive biology and ecology, Macqueen (1992) recommended the collection of seeds from at least 50 individuals within a particular provenance, spaced at distances greater than 100 m. Actual collections were from between 8 and 65 individual trees (most commonly between 20 and 50) spaced at a minimum of 50-m intervals depending on available population sizes and densities in the native range (Macqueen 1993b). The presence of root suckering in one provenance from Honduras meant that adjacent plants were genetically identical, highlighting the need to collect from well-spaced individuals. Random selection of trees for seed collection was preferred, i.e., individual trees were not selected on the basis of their phenotypic form, to ensure that a wide spectrum of genotypes was included within the seed collection and the subsequent evaluation program.

Sympatry in the *Racemosae* and the occurrence of putative *Calliandra* hybrids has important implications for the genetic integrity of seeds collected from populations of *C. calothyrsus*. Chamberlain and others (n.d.) recommend that *C.*

calothyrsus seeds always be collected from large stands that are isolated from any other *Calliandra* species. Macqueen (1995) suggests that particular care should be taken when collecting *C. calothyrsus* seeds from naturalized stands in exotic environments. As much information as possible should be gathered about the stand from which seeds will be collected, especially whether the trees were established with seeds from a single parent or from a bulk collection, etc.

Measurements from a number of populations from within the native range found that mean seed ovule ratios vary from 0.83 to 0.65 per pod per population (Chamberlain, n.d.; Hernández 1991; Macqueen 1993b). Mean ovule number varied from 9.12 to 6.70, and mean seed number per pod varied from 6.65 to 5.59. Quantities of seeds per tree are generally low (averaging about 100 g per tree, equivalent to approximately 1,400 to 1,700 seeds; Macqueen 1993a, National Research Council 1983a). Low quantities of seeds per tree are normal for the species, although such figures are often smaller than for those of comparable agroforestry trees. Therefore, such small quantities of seeds per tree should not be interpreted as a seed production problem when the species is introduced to exotic sites (Boland and Owour 1996, Chamberlain and Rajaselvam 1996).


2cm
1cm


1cm

Calophyllum brasiliense Cambess.

E.M. FLORES
Academia Nacional de Ciencias de Costa Rica, Costa Rica

CLUSIACEAE (MANGOSTEEN FAMILY)

Calophyllum lucidum Benth. (Hooker's Journal of Botany and Kew Garden Miscellany 2:370; 1843);
Calophyllum rekoi Standl. (Contributions of U.S. Natural Herbarium 20: 192; 1919);
Calophyllum antillanum Britton (Scientific Survey of Porto Rico and the Virgin Islands 5:584; 1924);
Calophyllum brasiliense var. *antilliense* (Britton) Standl. Tropical Woods 30:7; 1932);
Calophyllum chiapense Standl. (Contributions of U.S. Natural Herbarium 20: 192; 1919);
Calophyllum piaroanum A. Castillo & C. Gil (Ernstia (2nd series) 1[1]: 41, f.1; 1991)

Aca, aceite, aceito, aceito de maria, acuje, alfaro, arary, balsamaria, baré, barí, baría, barillo, Brazil beauty-leaf, cachicamo, calaba, calambuca, cascarillo, cedro cimarrón, cedro de pantano, cedro maria, chagualo, chaqualo, cojón, crabwood, cupia, dalemarie, damage, dame marie, edaballi, galopa, galpa, guanandi, guaya, jacaréuba, korakrie, kurahara, kurahura, lagarto caspi-blanco, lagarto-crespi, lech, leche, leche amarilla, leche maria, lechoso, limoncillo de Córdoba, lorahara, mangue, mani kwaha, manzano, mara, maria, maria blanco, maria colorado, mario, ocu, ocuje, ocuje macho, olandi, palo de maria, palo rey rosado, penoga, santa maria, varilla, wild cabash (Barajas and others 1979, Flores 1994b, Pennington and Sarukhán 1968, Record and Hess 1949, Salas Estrada 1993)

Calophyllum L. is a tropical genus composed of about 100 species, distributed in America, Asia, Madagascar, and Australia. *Calophyllum brasiliense* is the most important of the American species. The natural range of the species extends from Mexico throughout Central America to northern South America. The species also grows in the West Indies (Flores 1994b, Record and Hess 1949, Standley and Williams 1961).

Calophyllum brasiliense is a tree 40 to 50 m in height and 1.80 m d.b.h. The tree has a straight, cylindrical bole, sometimes with a moderate vertical torsion (on slopes); the basal two-thirds is branch free. The crown is round and dense, with ascending, thick, irregular branches. The young twigs are minutely puberulous. The bark is gray or brownish gray, coarse, thick, and vertically fissured with exfoliating small plates, a bitter taste, and many laticifers with resinous, greenish yellow or yellow latex (Cálix-Pizatti 1970, López and others 1987, Standley and Williams 1961). Leaves are decussate, simple, petiolated, exstipulated, coriaceous, and variable in size (López and others 1987, Standley and Williams 1961). Leaf blades are dorsiventral, elliptic, oblong or obovate, entire, glabrous, shiny green above, and dull and light green below. Secondary veins are closely parallel. *Calophyllum brasiliense* is a canopy tree typical of the humid tropical forests (evergreen lowlands to montane forests, gallery forests, and periodically flooded riverbanks) with an annual rainfall above 3000 mm and a temperature of 24 to 28 °C. Its elevational range is from sea level to 1500 m. The species grows well in slightly sloped areas with alluvial or clayey soils rich in silica, humid, saturated, and acid (pH 4.5 to 6.0). In Central America, the trees are commonly found in coastal areas with soils rich in iron and aluminum but poor in phosphorous and potassium, and in plains with rivers, creeks, or marshes (Chaves and Chinchilla 1994, Flores 1994b). The species is frequently found in the Amazon varzeas. *Calophyllum brasiliense* var. *rekoi* has been recorded in Central America.

The timber has excellent characteristics and is widely used. The wood is grayish red, heavy or moderately heavy; the average specific gravity (green volume/dry weight) varies from 0.45 to 0.55 and the green weight from 761 to 950 kg per m^3, along the geographical range of the species (Flores 1994b, Picado and others 1983, Simpson and Sagoe 1991). It has interlocked or sometimes straight grain, medium and quite uniform texture, and medium luster; and the figure is characterized by wide stripes in the radial surface (Creemers and Lemckert 1981, Longwood 1962, Record and Hess 1949). Odor and taste are not characteristic (Longwood 1962). It has good physical and mechanical properties; it is stable and durable and has an attractive figure (Flores 1994b, Record and Hess 1949). It is moderately stable in use and can be compared to mahogany (*Swietenia macrophylla*), Douglas fir (*Pseudotsuga meziesii* (Mirb.) Franco), and scotch pine (*Pinus sylvestris* L.), although it has superior values in rupture module, maximum load, and hardness (González and others 1990, Longwood 1962). Air drying is moderately fast and shows minor defects, mainly twisting or splitting (Instituto Nicaragüense de Recursos Naturales y del Ambiente 1993a, Longwood 1962). It is easy to saw and cut. The polishing properties are medium; 50 percent of polished pieces have a clean surface, 20 percent have irregular grain, and 30 percent show a ripped grain (Flores 1994b, González and others 1990). The wood is commonly used in internal and external construction, general carpentry, floors, furniture, posts, cabinetwork, blackboards, bridge structures, masts, railroad foundations, veneers, and canoes (Barajas and others 1979; Flores 1994b; Herrera and Morales 1993; Instituto Nicaragüense de Recursos Naturales y del Ambiente 1993a, 1993b; Kribs 1968). The Runkel Factor is approximately 0.98 (Group III), and the fibers may be used for papermaking. The timber is resistant to termites (*Captotermes niger*, *Heterotermes convexinotatus*, *H. tennuis*, and *Nasutitermes corniger*) and fungi during the first 2 years (Bultman 1976). The heartwood is difficult to impregnate; absorption is poor (58 kg per m^3), and penetration is null (Instituto Nicaragüense de Recursos Naturales y del Ambiente 1993b). The latex has been used in Central America to reduce fevers and heal cuts (Betancourt 1987, Herrera and Morales 1993). In the Brazilian Amazon, it is used to control diabetes (Van der Berg 1993). The leaves are used as an anti-inflamatory and in infusions to control asthma and digestive problems (Herrera and Morales 1993). In South America, the fruits are used to feed pigs. The seeds provide oils. The bark produces an excellent brown dye (Acuña and Rivera 1990). Xanthones and coumarin derivatives have been found in some species of the genus; triterpenes and bioflavonoids have been formed from the species (Schultes and Raffauf 1990). The species is used as an ornamental in parks and along road borders. Its high-quality timber and silvicultural characteristics have led to its use in monospecific plantations.

The tree primarily flowers in June and July with a minor bloom in November and December. Variations in the flowering pattern are found along the geographical range of the species. Blooming is usually annual. Flowers are andromonoecious, grouped in axillary panicles, pedunculated, with a subtending leaf, sometimes inconspicuous. The main axis is 3 to 9 cm long; bisexual and staminate inflorescences have 2 to 20 flowers, and flower distribution is irregular, opposed, or grouped in monochasia or dichasia. Staminate and hermaphrodite flowers are actinomorphic; the calyx is tetramerous, greenish; sepals are decussate, round, and adaxially concave; the corolla is tetramerous; the petals are decussate, ovate, glabrous with a round apex, and white, creamy, or yellowish. The staminate flowers have a soft and sweet scent; the androecium has numerous stamens centrally grouped. The filaments are filiform and narrow; the anther is oblong, basifixed, and longitudinally dehiscent. The bisexual flowers have 8 to 10 stamens. The flower is epigynous; the ovary is ovoid and unilocular. The ovary has a single pseudobasal ovule, anatropous, crassinucellate, with hypostase, massive outer integument, and thin inner integument. The style is narrow, short, and hollow; the stigma is tetralobed, obtuse, papillary; the lobes expand distally.

Fruits are globular berries, apiculate, yellow-greenish or maroon, 2.5 to 3.0 cm in length and diameter. Immature fruits are green, mature fruits yellow or yellowish brown. The exocarp is coriaceous, thin, and dull, with glandular dots. The mesocarp is fleshy, whitish turning to yellow at maturity, with a granulose texture and astringent taste. The endocarp is thin and fragmentary in the mature fruit. Bats, birds, rodents, and fish (riparian or marshy trees) disperse the fruits and seeds. Seeds are ovoid or globose; the seedcoat is brown. The testa is thick, hard, woody, and irregular; the tegmen is thin and sometimes fragmentary in the mature seed. Seed size (1.8 to 2.3 cm) is correlated to fruit size (Flores 1994b).

Fruits must be collected from the trees or gathered from the ground under trees with a d.b.h. range of 40 to 70 cm; trees with greater diameters may have physiological deterioration and usually have a hollow pith (Flores 1994b). Seed weight is 2.2 to 2.5 g and seeds average 415 to 440 per kg; 25 to 28 percent of this weight is moisture. The pericarp must be removed, and seeds must be sown directly in greenhouse beds. Seeds do not tolerate desiccation or drastic temperature fluctuations and may be considered recalcitrant.

Germination is hypogeal and the seedling is cryptocotylar (Flores 1994b). Although seeds do not require pregerminative treatments, it is convenient to soak them for 24 hours to soften the seedcoat. This soaking contributes to uniform germination and diminishes the percentage of seedlings with anomalous plumule development. Seeds planted in greenhouse beds must be transferred to plastic bags when radicles emerge (Flores 1994b). All young seedlings with anomalous development (twisted epicotyls, shoots originating from buds of the cotyledonar axils) or slow growth must be eliminated. Roots must be pruned twice using a shovel or knife (Flores 1994b). The first pruning must be done when seedlings reach a height of 20 cm; the second, 1 month before seedlings are transferred to the field (Chaves and Chinchilla 1994). Seedlings must be transferred to plantation in adobe and the extended leaves must be cut. This technique permits transplanting of seedlings at different ages, including 9 months, with very low mortality. Transferring seedlings from the greenhouse generates homogeneous plantations and trees with better boles (Flores 1994b).

ADDITIONAL INFORMATION

The leaf apex is acute, obtuse, or truncate; the leaf base is cuneiform and the margin is thick. The leaf is hypostomatic and stomata are mainly anomocytic, sometimes paracytic. Leaf venation is pinnate craspedodromous; the midrib has a straight course and projects abaxially. Secondary veins are fine, with a divergence angle of 80 to 90 degrees.

Pollination is entomophilous; the flowers are visited by numerous insects, small or medium-sized. No specific pollinator has been found.

The seed has a small hilum containing the micropyle. The endosperm is nuclear and is gradually consumed during seed development. The mature seed lacks endosperm or perisperm. The embryo is straight and massive, developing in the last stages of seed development. Cotyledons are broad, fleshy, oily, anisocotylous, gamocotylous in the distal three-quarters and concave adaxially in the basal three-quarters. The plumule is enclosed in the formed cavity. The embryo axis is poorly developed; the radicle is small and syntropous; a laticifer system extends to the whole embryo (Flores 1994b).

Calophyllum brasiliense has been planted in monospecific plots with a planting distance of 3 by 3 m. In the monospecific plots at Escuela de Agricultura de la Región Tropical Húmeda, Guácimo, Limón Province, Costa Rica, the species reached an average height of 1.36 m and an average diameter of 1.62 cm in the first year (Russo and Sandí 1993). In La Selva, Sarapiquí, Costa Rica, 3-year-old saplings in plantation reached an average increment in height of 1.4 m per year, an average increment in diameter of 1.3 cm per year, and an average increment in basal area of 0.8 m^2 per ha per year (González and others 1990). Evaluations carried out in 7-year-old plantations in Colpachí, La Virgen, Sarapiquí, Costa Rica show that juvenile trees had an average increment in height of 1.4 m per year, an average increment in diameter of 1.82 cm per year, and an average increment in basal area of 1.66 m^2 per ha per year (Chaves and Chinchilla 1994). In this location, the plantation on a slight slope (45 degrees) showed higher survival (90 percent) and higher longitudinal growth (1.47 m per year). The longitudinal growth of the species in plantation is adequate from an economic point of view and may be enhanced with appropriate silvicultural management (Chaves and Chinchilla 1994).

Applying 40 g of fertilizer (nitrogen-phosphorous-potassium) to the bottom of the hole before planting seedlings has a positive effect, increasing longitudinal growth and vigor. When planting density is high (1,100 to 1,200 seedlings per ha), the species prunes well until it reaches a height of 5 m. Clearing the ground three to four times in the first year is recommended, because the species has an adaptation period of 2 to 3 years (González and others 1990).


1cm
1cm

Calophyllum inophyllum L.

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CLUSIACEAE (MANGOSTEEN FAMILY)

No synonyms

Alexandrian laurel, beauty leaf, kamani (Little and Skolmen 1989)

Calophyllum inophyllum is in a genus of about 110 species that are pantropical in distribution but most common in tropical Asia (Gentry 1993, Liberty Hyde Bailey Hortorium 1976, Wagner and others 1990). Native from east Africa to Australia and Malesia, *C. inophyllum* has been widely planted throughout the tropics, including many south and central Pacific islands, the Hawaiian Islands, and the Caribbean islands.

Calophyllum inophyllum is a low-branching evergreen tree with a broad, spreading crown of irregular, gnarled branches. It typically attains 8 to 20 m in height and 0.5 to 1.0 m d.b.h. It is generally described as slow-growing. *Calophyllum inophyllum* is primarily a tree of the seashore and adjacent lowland forests, although it occasionally grows at higher elevations and has been successfully planted in inland areas (e.g., Uganda; Streets 1962). It grows in areas with annual rainfall ranging from about 1000 to 5000 mm. The tree grows in a wide variety of soils, from nearly pure coastal sands to clay, and is capable of growth on degraded and poorly drained sites. It can be found right at the edge of the sea, where it may be exposed to high winds, sea spray, and brackish water tables.

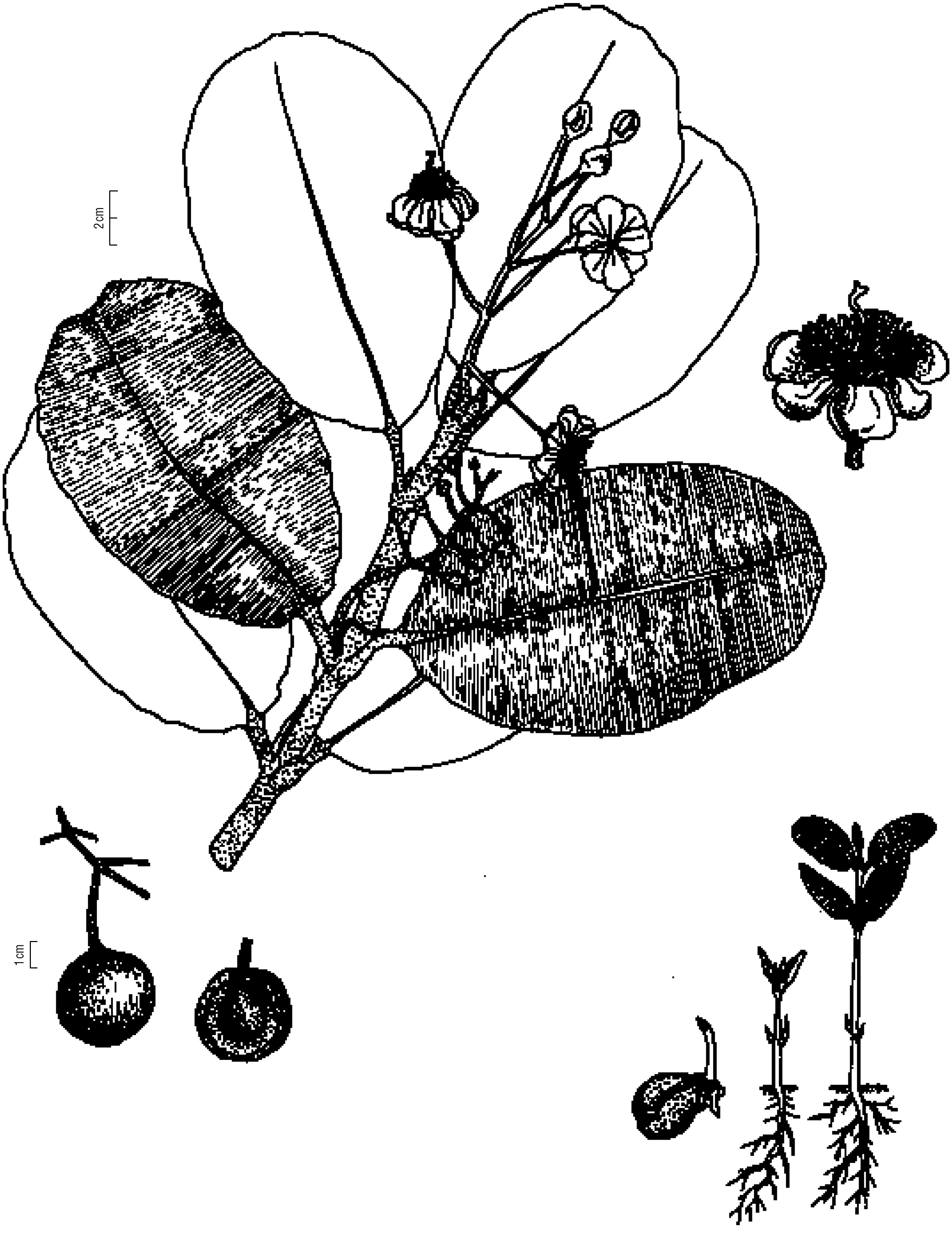
Descriptions of *C. inophyllum* often emphasize its value as an ornamental because it has attractive leaves, fragrant flowers, and a pleasing form. Indeed, it is probably planted more for ornamental purposes than for other uses. The species is commonly planted along streets and in parks in Hawaii and Puerto Rico and in urban areas throughout its native range. The wood is hard, strong, moderately durable, and often highly figured and has a specific gravity of about 0.60 to 0.64. It has been used in general construction and boatbuilding and for flooring, furniture, musical instruments, handicrafts, and a variety of other purposes (Kraemer 1951, Little and Skolmen 1989). The thick, dark green oil extracted from the seeds is used in a number of products, including oil for lighting, medicines, and body and hair grease (Little and Skolmen 1989, Neal 1965). The tree is regarded as sacred in some parts of the Pacific and is commonly featured in chants and other folklore of the region.

The white flowers are about 25 mm wide and occur in axillary, racemose, or paniculate inflorescences consisting of 4 to 15 flowers. Although some flowering may occur throughout the year (Foxworthy 1927), in most regions two distinct flowering periods occur—one in the late spring/early summer and another in late fall. The fruit (a drupe) is green, round, and typically 2 to 4 cm in diameter including a thin (3 to 5 mm) layer of pulp, the shell, and the single large seed. Fully mature fruits are yellow- or red-brown and wrinkled.

Seeds can be collected from trees by picking individual fruits or lopping off branches with pruning poles, but it is generally more practical to collect them after the fruits fall to the ground. In Hawaii, seeds are most readily available April through June and October through December.

The thick, hard shells (endocarps) of the fruit can cause long delays in germination; therefore shelling the seed before germination is recommended. The shells are relatively easy to open by tapping lightly with a piece of wood or a wooden mallet (Parras 1939) or by cracking with pliers or similar tool. In one study, seeds with intact shells germinated in an average of 57 days, compared with 38 days for seeds with cracked shells and 22 for seeds with shells completely removed (Parras 1939). Seeds of a related species (*C. calaba* L.) reportedly maintain their viability well, with fair germination occurring after seeds were stored in a dry room for 1 year (Weaver 1990); however, Foxworthy (1927, p. 134) states that *C. inophyllum* seed “does not maintain its vitality very long.” Seeds average about 100 to 210 per kg (Sastry 1990).

Shelled seeds may have a germination rate greater than 90 percent (Allen 1997, Parras 1939); therefore sowing seed directly into containers is the most efficient method. Small dibble tubes can be used when the seed is extracted from the shell; otherwise use of larger tubes (more than 6 cm diameter) or small pots or sowing in seedbeds followed by transplanting is recommended. Seedlings can be moved safely into full sunlight 1 to 2 months after germination. Seedlings should be hardened in full sunlight for 4 months before outplanting (Philippine Council for Agriculture, Forestry and Natural Resources Research and Development 1994). They develop rapidly in the nursery and may reach a height of 1 m within their first year. Direct seeding is also effective in establishing this species. Seeds should be sowed approximately 2.5 cm deep. Planting in areas with light shade may improve success.


2cm
1cm

Carapa guianensis Aubl.

L.A. FOURNIER
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MELIACEAE (MAHOGANY FAMILY)

Persoonia guareoides Willdenow, *Amapa guianensis* (Aublet) Steudel, *Xylocarpus carapa* Sprengel, *Carapa latifolia* Willdenow ex. C de Candolle, *Carapa nicaraguensis* C. de Candolle, *Granatum guianensis* (Aublet) O. Kuntze, *Granatum nicaraguensis* C.de Candolle O. Kuntze, *Guarea mucronulata* C. de Candolle, *Carapa macrocarpa* Ducke, *Carapa slateri* Standl.

Acajou, andiroba, andiroba branco, andiroba do igapó, andiroba vermelha, angiroba, bastard mahogany, bateo, bois caille, bois rouge, Brazilian mahogany, British Guiana mahogany, cabirma de Guiana, cachipou, cahoba, cahobilla, camacari, caraba, carapa, carapa blanc, carapa rouge, carapat bogamani, carapote, cedro bateo, cedro cóbano, cedro macho, cóbano, crabbaum, royal mahogany

The geographic range of *Carapa guianensis* extends from Belize, along the Atlantic coast of Central America (and the Costa Rican Pacific watershed), down to Panama. In South America, the species is found in Colombia, Brazil, Peru, Ecuador, and the overflow delta plains of the Orinoco River in Venezuela. It is abundant in the Amazon flood plains, in the states of Para and Amazonas (Brazil), and the Guianas. The tree is also found in the Antilles, from Cuba to Trinidad and Tobago.

Carapa guianensis is an evergreen or deciduous tree that may reach 60 m in height and 2 m d.b.h.; the trunk is straight and cylindrical, with buttresses of 1 to 2.5 m. Lacking branches in the basal one-half or two-thirds of its length, the crown of *C. guianensis* is wide and dense with thick, curved, ascedent, brown branches, and the young shoots are covered by conspicuous lenticels; the bark is flaky and has superficial fissures. Leaves are even-pinnate, alternative, without stipules, displayed in a helical arrangement, and crowded at ends of branchlets, usually with an apical dormant or glandular leaflet, which sometimes results in an odd pinnate leaf. The leaflets are in opposite pairs (3 to 10) and elliptic or elliptic lanceolate with entire margin; acute, obtuse, or acuminate apex; and oblique, asymmetrical, and wide base. The blades are coriaceous, deep bright green adaxially, dull green abaxially, usually reddish when older. The species can grow in pure stands in the lowlands, preferring marsh edges, swamp forests, alluvial riverbanks, and periodically flooded plains. It is a canopy species in humid and very humid tropical forests with an annual rainfall above 3000 mm and a temperature range of 20 to 35 °C. This species usually does not occur above 700 m, but in some areas of Venezuela, Ecuador, and Guadaloupe Island it can be found above 1000 m.

Ecophene existence seems evident (Flores 1994a) and the populations in the Costa Rican Atlantic and Pacific coasts could be different ecotypes.

Timber is the most valuable product of *C. guianensis* (specific gravity is 0.42 to 0.52); the wood is stable and has multiple uses. However, the wood varies because morphological and physical characteristics differ among habitats (Flores 1994a). The sapwood is pink in green conditions and reddish in dry conditions; heartwood is reddish when green and deeply bright red when dry. The wood has a fine or moderate texture and a high luster; the grain is typically straight, slightly undulated, or sometimes intercrossed. It is decorative in radial planes due to ray-gold glare and the wide longitudinal lines. It is used in cabinetwork, carpentry, turnery, general construction, flooring, boxes, packing, veneer, and masts. Shoemakers use the wood to make heelpieces. Some of the pulp can be used for papermaking. Bark tannins are used in tannery; the carapine alkaloid ($C_{10}H_{28}O_4$) is used to cure diarrhea, dysentery, rheumatism, eczema, and ulcers. The seeds provide an oil used to make soaps, candles, and insecticides.

The tree flowers primarily from January through March, but may continue through April in some zones. It may also flower in August and September. Inflorescences are large (20 to 80 cm in length), much branched, and axillary or subterminal. Flowers are unisexual and petals are white or creamy, with a light pinkish color externally. The flowers have a delicate musky fragrance; the pistillate has a round or quadrangular ovary, and the staminate has vestigial ovules. The fruit is a quadrangular, closed capsule 9 to 16 cm wide and almost the same in length.

Fruits mature in 8 months and are harvested from May through August. The dehiscence gives rise to four hard valves and opens partially or totally. The fruit possesses a thick, woody pedice that abscises at maturity, and the fruit falls to the ground. The seedcoat is hard, smooth or rough, and red-brown in color. The seeds are large and angular, and may be classified as overgrown because their development is determined by fruit size and seed number. Water seems to be an important agent in medium- or long-distance dispersal, when trees grow in swamps or near streams.

Seed-producing trees must be selected from those having a diameter over 60 cm and in good sanitary conditions. Seeds must be collected from the ground and transported in sealed, plastic bags with a small amount of water. Seeds average 30 to 35 per kg.

Seeds cannot be stored more than 2 days under normal conditions in the Tropics (temperature 24 to 30 °C; 90 perceut humidity). If seeds are dehydrated 12 to 18 percent and provided an adequate level of permanent humidity, some will germinate several months later (30 percent). Seeds are also sensitive to temperatures below 20 °C. Seed germination is hypogeal and seedlings are cryptocotylar; under natural conditions germination begins at 2 weeks. Seeds transported from the field to the greenhouse in sealed, plastic bags with adequate moisture show 92 percent germination. Once in the greenhouse, seeds must be submerged in an insecticide for 15 minutes, washed in running water twice, and kept in sealed, plastic bags with adequate moisture (no more than eight seeds per bag). They are transferred to plastic bags with substrate when radicle emergence starts. Direct sowing in plastic bags is also possible, to expedite plumule emergence. A mixture of soil and sand is an adequate substrate for seedling germination, but the humidity must be kept constant. Seedlings must be outplanted by 6 months. Under greenhouse conditions, the epicotyl suffers dieback in 20 percent of the seedlings, and the seedlings are shade tolerant during the first stages of development.

ADDITIONAL INFORMATION

This species provides food and nesting for many birds, including species of *Ara* spp., macaws, and Amazon parrots. Collared peccaries (*Tayassu tajacu*), white-lipped peccaries (*T. pecari*), and some large rodents such as agouties (*Dasyprocta punctata*) and pacas (*Agouti paca*) are the most important predators and dispersers of seeds. The roots of young seedlings are predated by the armored rat (*Hoplomys gymnurus*). The attack of some insects, such as *Hypsiphyla* moth, is strong and has a negative effect. *Hypsiphya ferrealis* destroys the seeds, *H. grandella* attacks seeds and young shoots, and *Rhizopos* sp. produces seed rotting (Arguedas and others 1993).


3cm
2cm
4cm
3cm

Caryodendron orinocense H. Karst.

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Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

EUPHORBIACEAE (SPURGE FAMILY)

Dioicia tetrandia L.

Cacay, caquetá, castaño, inchi, meta, putumayo, tacay

Caryodendron orinocense is a slow-growing tree that reaches 25 m in height and 30 cm d.b.h. The trunk is long and slightly grooved; the bark is thin and grayish, dark green, or brown. The leaves are alternate, glabrous, dark green on the right side and light green on the back side, narrowly elliptical or oval with a whole margin 12 to 15 cm long by 4 to 10 cm wide. The petiole is glabrous, grooved on the upper surface, widened at the extremes, and 1.5 to 5 cm long. The tree grows in steep topography both on the peaks and in the depressions. The phreatic level does not have a major influence on the growth and yield of *C. orinocense*. Good yields have been observed in flooded soils and in fertile lowlands, but the tree also grows to great heights on the sides of mountains. The tree grows in shallow soils with a thick texture to moderately deep soils. It also grows in loose sandy textures. The species is found in soils of low terraces with a medium to high content of interchangeable bases and a very low aluminum content. It does not endure soils with hydric deficiency. The capability of cationic exchange (CIC) ranges from 7.5 to 1.9 milliequivalents per 100 g of soil (1.9 is very high). Furthermore, the tree grows well in high terrace soils, which are very limited due to acidity, high content of interchangeable aluminum, and poor exchange bases, saturation, and phosphorus. The species is located in the transition between the wet Tropical forest (bh-T) and the very wet Tropical forest (bmh-T). The wet Tropical forest generally has an average temperature of more than 24 °C and an average annual precipitation between 2000 and 4000 mm. The very wet Tropical forest has an average temperature of more than 24 °C and an average annual precipitation between 4000 and 8000 mm (Martinez 1996). *Caryodendron orinocense* is very susceptible to fire and does not endure prolonged droughts.

The wood is used primarily as firewood and charcoal. The oil is extracted from the fruits or seeds, thus the species could be cataloged as a successor in the production of olive oil. The seeds are toasted and consumed. Although the wood is not very durable and does not finish well, it is used in interior carpentry in Putumayo and Meta, Colombia.

The tree is dioecious; the masculine flowers have a trifoliate calyx with oval sepals, pointed and membranous. The feminine flowers are sessile, forming a bracteate terminal sprig; after fertilization they lean on a somewhat elongated pedicel with small bracts in a wide triangle. The fruit is globose-oblong, 6 to 5 cm long by 4 to 5 cm wide, and dehiscent, with a green exocarp and three ligneous carpels with a small apical appendage, each one containing only one seed. One kg of fruit contains 42 to 46 seeds (without pericarp). The seeds have a large, white endosperm with a central straight embryo. The testa is hard and grayish or coffee brown in color, and is covered with a layer of wax; the tegument is membranous and wrinkled. Seeds average 275 to 325 per kg. The weight of 1,000 seeds is 3 kg.

The seed has a very short viability period, which makes sowing the species in other regions of the country difficult. It can be stored at 6 ^{o}C without significantly affecting the percentage of germination. If the seeds are dried an additional week before refrigeration the viability period of the seed tends to lengthen.

Fresh seeds germinate quickly; sometimes 75 percent have germinated by the second day and the remainder germinate in 5 days. Seeds that have been stored for several weeks and are normally much drier, take up to 15 days to germinate.

For best germination the seeds should be planted in wet sand in deep shade, because the sun dries up the projecting radicle and the cotyledons. The seeds can be extracted from the pit and planted alone, or the pit containing the three seeds can be planted. When the pit is planted, the three plantules must be separated at the moment of transplanting. Transplanting must occur approximately 4 weeks after the seeds are planted. During the 6 to 8 months in the nursery, shade must be gradually decreased (Van Dijk 1979).

The distance between trees must provide adequate space for development. The trees are usually planted at distances of 8 by 8 m or 9 by 9 m. After cutting the masculine trees, distances become 12 to 13 m. Trees that produce a lot of seeds must be pruned to prevent the branches from breaking under the weight. Attacks by large red ants can cause the death of planted trees or trees in the nursery. Coleopteran eat the medulla of the branches.


2cm

Cassia fistula L.

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FABACEAE (BEAN FAMILY)

No synonyms

Caña fistula, canafistula, canéficier, golden shower, lluvia de oro, indian laburnum, pudding pipe tree, purging cassia

Native to the tropical regions of Asia, *Cassia fistula* is naturally distributed across India, Indochina, and Malaysia. It has also been introduced to the tropical regions of Africa and America. In Africa, it is found in Kenya. In America, it has been planted in southern Florida, Cuba, Puerto Rico, Jamaica, Mexico, across Central America, Colombia, Venezuela, and Brazil. It is also found in Hawaii.

Cassia fistula is a fast-growing, deciduous tree of up to 15 m in height and 60 cm d.b.h. The trunk is straight, and the open crown consists of horizontal and extended branches with sparse foliage. The leaves are paripinnate, made up of 8 to 16 ovate to lanceolate leaflets, and 8 to 20 cm long. The tree grows in poor and thin soils. The average annual temperature where the tree develops ranges from 17.2 to 37 °C, and the average annual precipitation ranges between 500 and 3000 mm. The species usually grows in open areas subject to monsoon conditions.

Cassia fistula is used as an ornamental and shade tree around houses; on the edges of roads; and in the streets, parks, and gardens of towns. The sweet pulp is used as a mild laxative. An infusion of the fruit is used to dissolve kidney stones. The wood is used for firewood in rural areas. The wood has a specific gravity of 0.9; is hard, heavy, strong, and durable; and is used for poles and handles for farming implements and in cabinet-making and construction. The bark is used to tan hides (Little and others 1967, Lötschert and Beese 1992, Nicholson and Arzeni 1993, Rico-Gray and others 1991).

The colorful—pale yellow to golden—flowers are arranged in panicles. *Cassia fistula* blooms and fruits virtually throughout the year at a young age in most places where it is cultivated. In its natural habitat, the fruits (legumes) ripen in the months of April and May. Outside its habitat the season for ripening varies. Fruits remain hanging on the tree for 2 or 3 months after ripening. Gradually, they fall to the ground. The legumes are dangling, linear-cylindrical, 30 to 50 cm long, 1.5 to 1.7 cm in diameter, transversally septate, dark brown to black, and indehiscent when ripe; they have ligneous valves. Inside each septum, one seed is surrounded by a sweet, viscous, dark-brown pulp. Each fruit contains numerous seeds (Holdridge and Poveda 1975, Irwin and Barneby 1982, Isely 1975, Little and others 1967). The seeds are obovate-ellipsoid, biconvex in cross section, ventrally flattened, 7.5 to 10.0 mm long, 6.0 to 7.5 mm wide, and 2.5 to 3.0 mm thick. The seedcoat is light brown, smooth, shiny, and cartaceous with fracture lines.

Ripe fruits are collected from the trees and the ground. Poles with metal hooks are used to collect fruits from trees. In the first step to extract seeds, the fruits are ground in wood mortars. One of three processes can be used to separate seeds from legume residues. In one, the seeds, impurities and all, are put in containers with water. The seeds sink; the impurities float and are gathered easily with a strainer. The seeds are removed from the water and dried in the sun for 1 hour or longer, depending on lighting conditions. If the impurities are small, they can be removed using sieves. Or they can be blown away using a vertical column blower. The seeds are then washed vigorously with running water to remove remnants of pulp and pericarp that adhere to them. The cleaned seeds are placed in the sun to dry. Seeds average 5,500 per kg (Food and Agriculture Organization 1968).

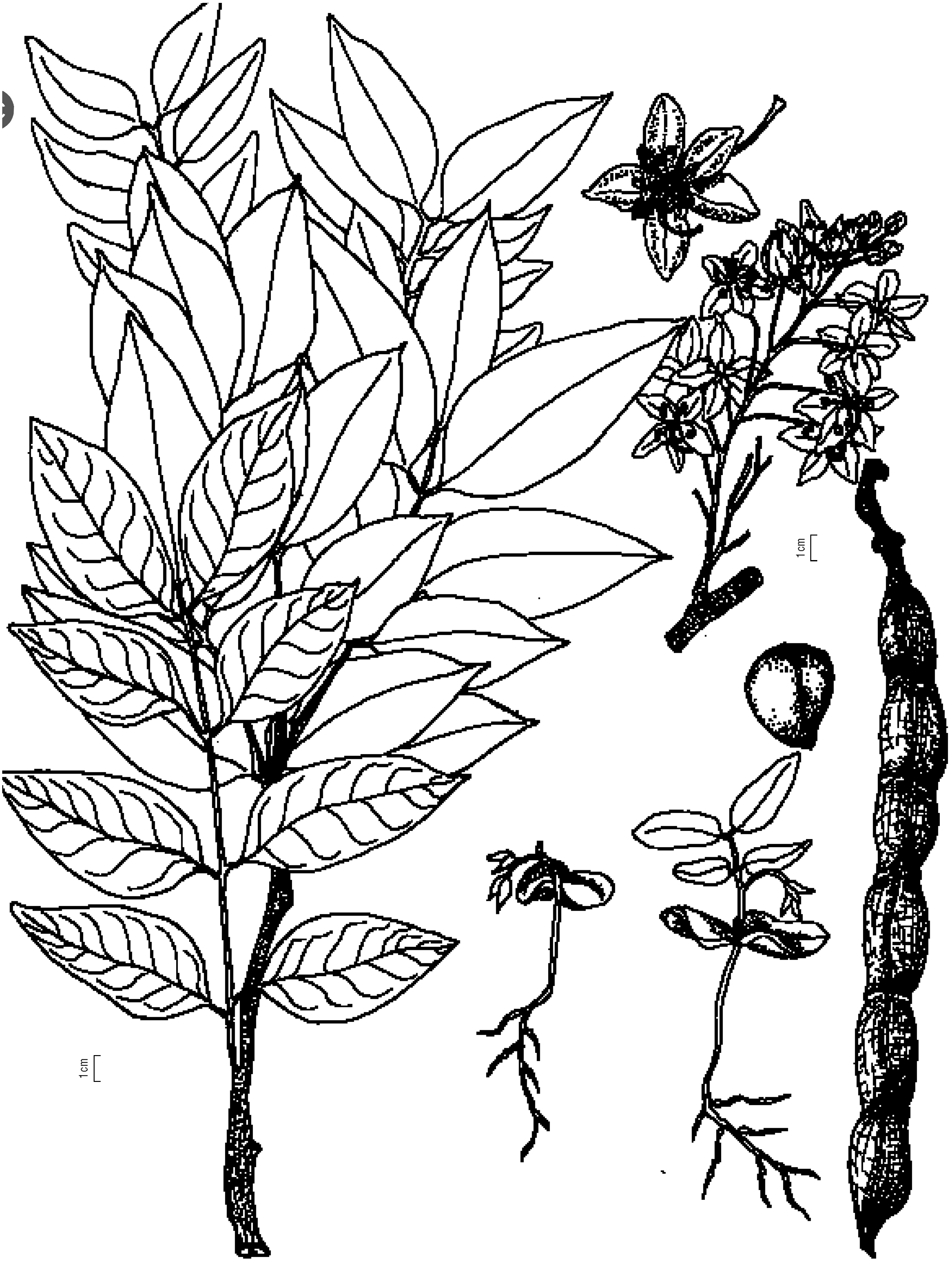
Seeds can be stored at room temperature and remain viable for 1 year. To remain viable longer, seeds must be placed in sealed plastic, glass, or metal containers in cold chambers at a temperature of 5 to 6 °C. It has been noted that after 1 year, the seeds stored in a cold chamber can still germinate. However, there have been no accurate assessments of this practice.

The seeds show a mechanical latency to germinate because the seedcoat is hard. The seeds can be soaked in boiling water for 5 minutes before planting to stimulate germination (Food and Agriculture Organization 1968).

ADDITIONAL INFORMATION

The *Cassia* genus includes some 500 species, some of which contain substances with laxative properties. These substances are found in the leaves and in the sweet and viscous pulp of the fruits (Lötschert and Beese 1992).

The vascular bundle is visible as a dark line that runs longitudinally to the seed through the middle part of its lateral surfaces. The hilum is subbasal, simple, puntiform, sometimes covered by remnants of funicular tissue, and set deep in a depression. The micropyle is indiscernible. The lens is subbasal, near the hilum, on the opposite side of the micropyle, lanceolate or oval, and set deep in a depression. The endosperm is abundant, whole, located mostly on the lateral surfaces of the embryo, cornaceous, whitish, and translucent. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are obovoid, whole, expanded, flat, thin, twisted in the shape of an S, and independent of one another. The plumule is moderately developed in pinnae. The radicle is conical and not covered by the cotyledons (Niembro 1982, Shyam and Vartak 1985).


1 cm
1 cm

Cassia grandis L.f.

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FABACEAE (BEAN FAMILY)

No synonyms

Bacul, beef-feed, bocot, cañadonga, cañafistola burrero, cañafistula, cañafistula cimarrona, cañafistula de Castilla, carago, caragua, carámano, carao, casse espangnole, chácara, coral shower, gigantón, horse cassia, liquorice tree, macut, marimari, marimari preto, pink shower cassía, quauhuayo, stinking-toe, sandal, sándalo

Cassia grandis is native to tropical regions of America. Apparently originating in the Amazon, the species' natural distribution cannot be accurately described. The tree is found in Cuba, Puerto Rico, and Jamaica. It is also found in Hawaii.

Cassia grandis is a deciduous or semideciduous tree that grows up to 18 m in height and 50 cm d.b.h. The trunk is straight and the spreading crown is high, irregular, and made up of dangling branches. The leaves are paripinnate and made up of 10 to 20 pairs of oblong leaflets that are 3 to 6 cm long and rounded or obtuse at the apex and base. The species grows well in clayey soils and generally establishes itself near river banks. It prospers in places with average annual temperatures of 22 to 26 °C and average annual precipitation of 1000 to 1300 mm. The species grows spontaneously on the banks of rivers and streams, forming gallery forests. *Cassia grandis* also grows in estuaries and soils subject to periodic flooding. Common in clearings of semideciduous tropical forests, pastures, and savannas, the tree grows at elevations between 3 and 1200 m (Hoyos 1979, Irwin and Barneby 1982, Little and others 1974, Little and others 1988, Witsberger and others 1982).

Cassia grandis is used as an ornamental to beautify streets, avenues, parks, and gardens. The sweet tasting and bad smelling pulp of the fruit is edible and is used as a laxative. The wood is hard and heavy; it is used in rural areas for home construction, sheds, and structures for roofs and in cabinet-making (Little and others 1974, Little and others 1988, Witsberger and others 1982).

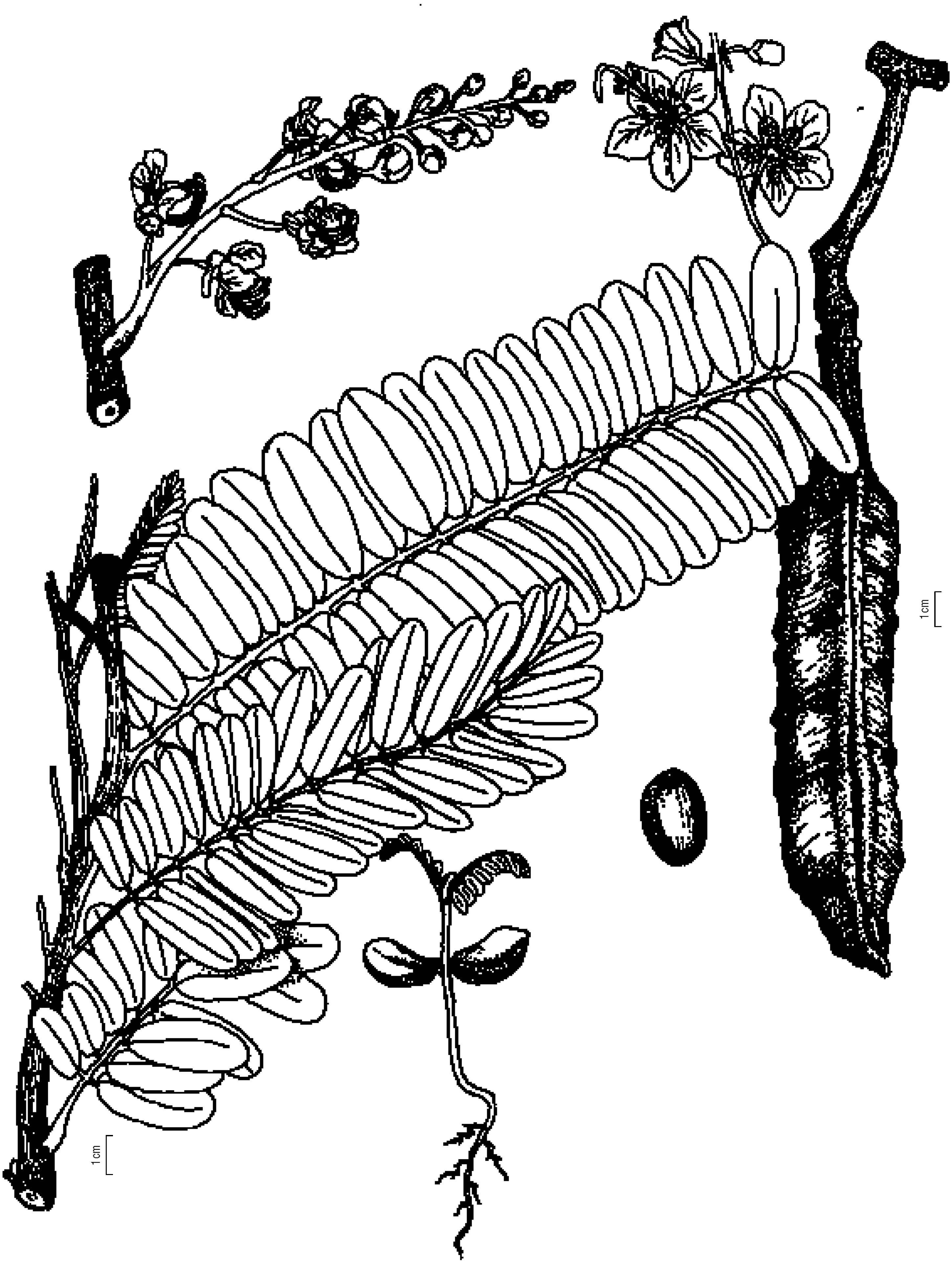
The pink to purple flowers turn salmon-color with time and are arranged in racemes. The species blooms in spring, and fruits (legumes) ripen in summer (Little and others 1988). The dark brown to black legumes are big and heavy, dangling, linear to linear-oblong, cylindrical, about 40 to 60 cm long, and 3 to 5 cm wide. Sometimes laterally flattened, the tips of the fruits are short and sharply pointed on both ends, rugose with thickened sutures, internally septate, and indehiscent when ripe. Inside each septum one seed is surrounded by pulp which is sweet tasting, liquid or viscous, and brown. Each fruit containes numerous seeds (Holdridge and Poveda 1975, Irwing and Barneby 1982, Isely 1975, Little and others 1974, Little and others 1988, Shyam and Vartak 1985, Standley and Steyermark 1946a, Witsberger and others 1982). The seeds are elliptic, obovate, obovoid-ellipsoid to oblong-obovate with the base slightly emerginate, biconvex in cross section, ventrally flattened, 13.4 to 16.6 mm long, 9.2 to 10.2 mm wide, and 4.0 to 5.0 mm thick. The seedcoat is light brown, smooth, opaque, and cartaceous, with inconspicuous fracture lines.

Poles with metal hooks are used to collect the ripe fruits from the trees. The fruits are ground in wood mortars as the first step to extracting the seeds. One of three processes can be used to separate seeds from legume residues. To remove impurites the seeds are submerged in containers of water. The good seeds will sink. On the surface, the pieces of fruit will float and can be gathered with a strainer. If the impurities are smaller, they can be separated using sieves. They can also be eliminated using a vertical column blower. The seeds are washed vigorously with running water to remove remnants of pulp and pericarp that adhere to them. The cleaned seeds are placed in the sun to dry.

Dry seeds are stored in plastic containers. Not many studies have been done on the storage of seeds of this species. Frequently, they are stored in cold chambers at a temperature of 5 to 6 °C. It has been observed that after 1 year, the seeds stored in a cold chamber still germinate. However, there have been no accurate assessments of this practice.

ADDITIONAL INFORMATION

The vascular bundle is visible as a dark line that runs longitudinally to the seed through the middle part of its lateral surfaces. The hilum is subbasal, circular, sometimes covered by remnants of funicular tissue, and set deep in a small depression. The micropyle is indiscernible. The lens is discernible, on the opposite side of the micropyle, subbasal, near the hilum, elliptic or linear, and set deep in a depression. The endosperm is abundant, whole, more abundant on the lateral surfaces of the embryo, cornaceous, whitish, translucent, and gelatinous when it comes in contact with water. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are shaped like the seed, expanded, flat and thin, twisted in the shape of an S, are independent of one another, and have an auriculate base. The plumule is moderately developed in pinnae. The radicle is conical and not covered by the cotyledons.


1cm
1cm

Cassia javanica L.

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FABACEAE (BEAN FAMILY)

No synonyms

Acacia rosada, apple-blossom cassia, apple-blossom senna, casia rosada, lluvia de rosas, nodding cassia, pink cassia, pink shower, rainbow shower, white shower

Native to the tropical regions of Asia, *Cassia javanica* is distributed naturally from India to Malaysia, Sumatra, Indonesia, southern China, and the Phillipines. In America, the species has been introduced in southern Florida, Puerto Rico, Cuba, Mexico, and across Central America.

Cassia javanica is a fast-growing, semideciduous tree up to 25 m in height and 35 cm d.b.h. The species blooms best in places with well-drained and deep soils. The trunk frequently has many shoots. The crown, consisting of descending branches with sparse foliage, is wide-open, arched, and spread out. The leaves are paripinnate, made up of 12 pairs of leaflets that are elliptic or oblong and rounded at the apex and base.

Irwin and Barneby (1982) consider *C. javanica* as a complex series of geographical varieties that are found across their areas of natural distribution. In these areas, *C. javanica* forms vary in the shape of their leaves, the color and size of their flowers, and their chromosomal number. The varieties are: *C. javanica* L. var. *javanica, C. javanica* L. var. *indochinensis* Gaghepain, *C. javanica* L. var. *pubifolia* Merrillk, and *C. javanica* L. var. *microcalyx* Irwin & Barneby.

Cassia javanica is cultivated as a shade and ornamental tree along streets and in parks and gardens.

The flowers are pale rose to crimson and arranged in racemes. *Cassia javanica* blooms during the spring, and the fruits (legumes) ripen in the fall. The legumes are hanging, thin, cylindrical, 30 to 40 cm long, 1.5 cm in diameter, dark brown to black, transversally septate, and indehiscent when ripe, with ligneous and thin valves. Inside each septum one seed is surrounded by a viscous, brown pulp. Each fruit contains numerous seeds (Holdridge and Poveda 1975, Irwin and Barneby 1982, Isely 1975, Little and others 1967). The seeds are obovate, biconvex in cross section, ventrally flattened, 6.5 to 8.9 mm long, 5.6 to 7.0 mm wide, and 2.5 to 5.5 mm thick. The seedcoat is dark brown, smooth, shiny, and cartaceous and has fracture lines.

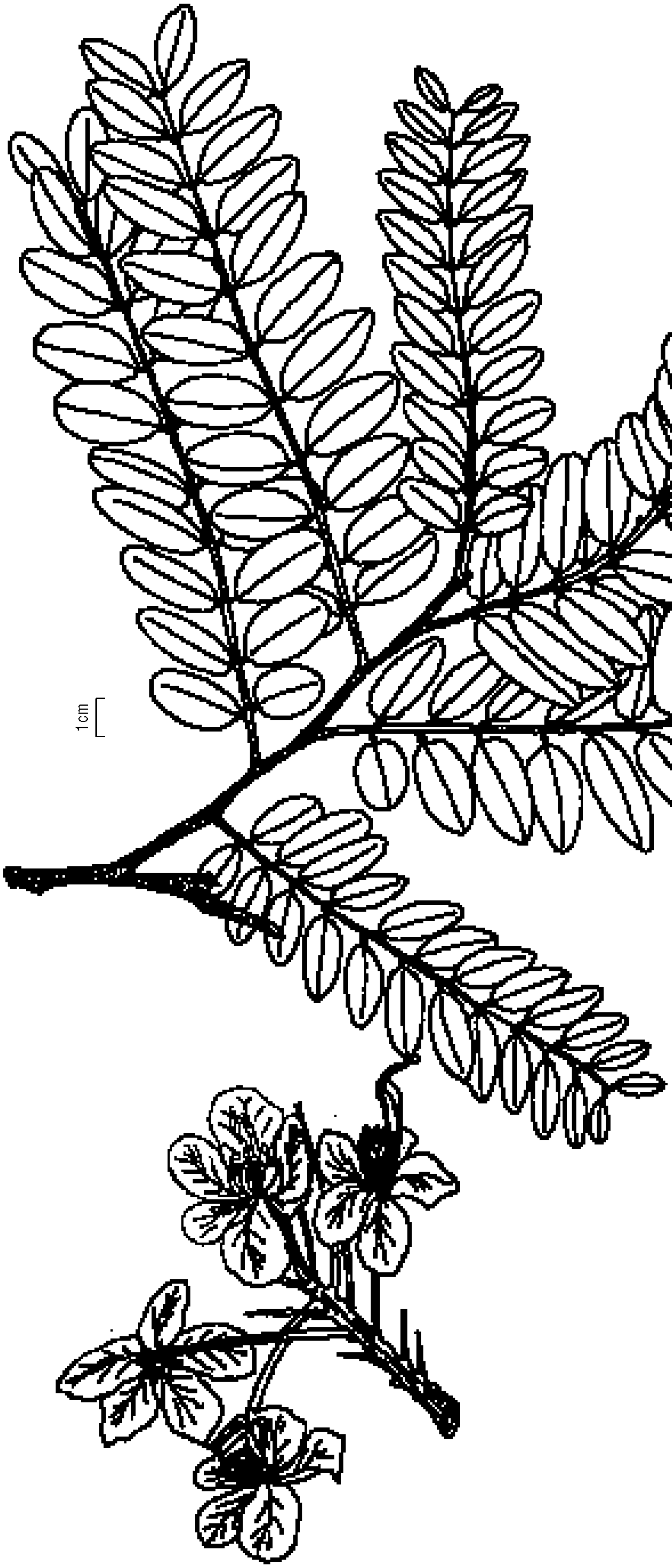
The fruits are gathered when their pericarp is dark brown or black, indicating that they are ripe. Poles with metal hooks are used to collect ripe fruits from the trees. The fruits are ground in wood mortars as the first step to extracting the seeds. One of three processes can be used to separate seeds from legume residues. To remove impurities the seeds are submerged in containers of water. The good seeds will sink. On the surface, pieces of fruit will float and can be gathered with a strainer. If the impurities are smaller, they can be separated using sieves. They can also be eliminated using a vertical column blower. The seeds are washed vigorously with running water to remove the residues of pulp and pericarp that adhere to them. The cleaned seeds are placed in the sun to dry. Seeds average 3,250 per kg (Food and Agriculture Organization 1957).

Dry seeds are stored in plastic containers. Few studies have been done on storing the seeds of this species. Frequently, they are stored in cold chambers at a temperature of 5 to 6 °C. It has been observed that after 1 year, seeds stored in cold chambers still germinate. However, there are no accurate assessments of this practice.

To stimulate germination, seeds can be placed in boiling water and soaked in the gradually cooling water for 1 day (Food and Agriculture Organization 1957).

ADDITIONAL INFORMATION

The vascular bundle is visible as a dark line that runs longitudinally to the seed through the middle part of its lateral surfaces. The hilum is subbasal, simple, puntiform, sometimes covered by a remnant of funicular tissue, and set deep in a small depression. The micropyle is indiscernible. The lens is subbasal, near the hilum, on the opposite side of the micropyle, linear, and set deep in a depression. The endosperm is whole, more abundant in the lateral surfaces of the embryo, cornaceous, whitish, translucent, and gelatinous when it comes in contact with water. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are obovoid, whole, expanded, flat, thin, twisted in the shape of an S, and independent of one another. The plumule is moderately developed in pinnae. The radicle is conical and not covered by the cotyledons (Niembro 1982, Shyam and Vartak 1985).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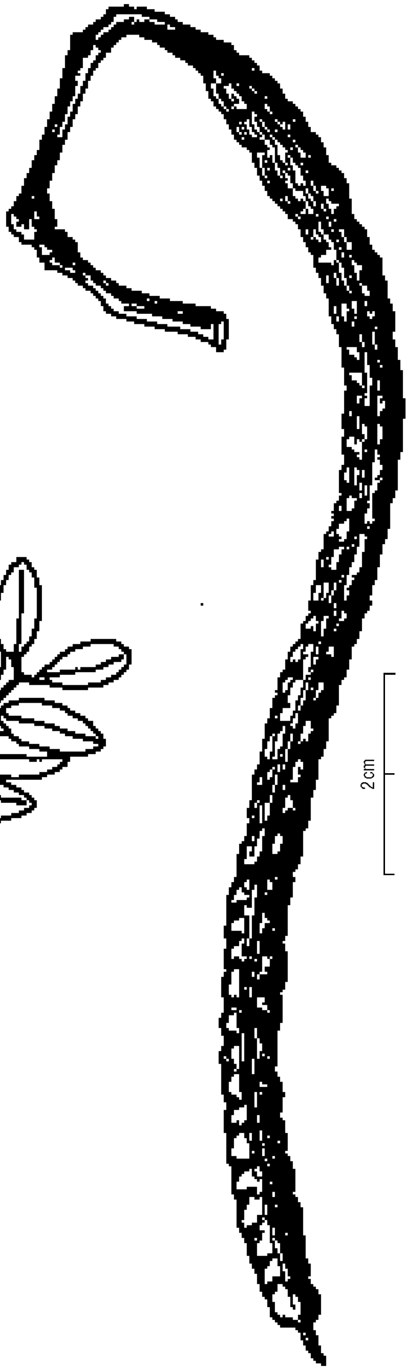
2cm

Casuarina cunninghamiana Miq.

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CASUARINACEAE (CASUARINA FAMILY)

No synonyms

Australian pine, casuarina, jan, jangli, kasa, pino australiano, pino de Australia, pino de mar, river oak, river she-oak, river sheoak, saru

Casuarina cunninghamiana is native to northeastern Australia, from Queensland to New South Wales, forming part of hot and wet subtropical forests. Because it can survive in difficult and adverse niches, the tree has been introduced as part of reforestation efforts in the tropical and subtropical countries of Africa, Asia, and America. In these countries *C. cunninghamiana* has been planted more frequently in mountainous regions than on the coasts because it is resistant to cold.

Casuarina cunnighamiana is an evergreen, fast-growing, dioecious tree, of up to 40 m in height and 65 to 100 cm d.b.h. It has a straight trunk, which is enlarged toward the base, and a pyramidal crown made up of acicular branches with sparse, hanging, grayish-green foliage. The leaves are compact and made up of 8 to 10 small scales. The tree prospers in a variety of soils, from those rich in organic matter to those sandy, poor, and eroded. In its natural habitat, the species develops at an average annual temperature of 13 to 27 °C, and an average annual precipitation of 500 to 1500 mm. The tree grows naturally from sea level to 1000 m. *Casuarina cunninghamiana* is resistant to cold and drought and endures shade, salinity, and seasonal flooding.

Because the species is fast-growing, it is used in reforestation programs to control erosion, preserve the soil, stabilize riverbeds, and stop the advance of dunes. Because it fixes nitrogen in the air, the tree thrives in places that are difficult for other species. It has been used successfully as a shade and ornamental tree in streets, parks, and gardens and as a wind-breaking hedge around rural communities. Specific gravity of the wood is 0.58. The wood is hard and dense and is used for firewood and charcoal. It is also used in rural construction and for poles, posts, furniture, particle board, veneer, parquet, pulp for paper, turned articles, and handles for tools. The bark contains tannin and is used to tan hides. The leaves and the young stems serve as forage for cattle (Little and others 1988, Nair 1993, National Academy of Sciences 1984, von Carlowitz 1991).

The tree begins to bloom and yield fruits at 4 or 5 years of age. In its native habitat, the tree blooms April through June, and the fruits ripen September to December. Outside its natural distribution area, *C. cunninghamiana* blooms and fruits at different times of the year depending on the environment. The light-brown flowers are arranged in sprigs. The fruits are multiple, gathered in an ovoid cone approximately 15 mm long by 10 mm in diameter, brown, dehiscent when ripe, with acrescent and persistent bracts. Inside each bract is a samaroid, monospermic, very small nut, which is dispersed by the wind (Little 1983, Little and others 1988, Pennington and Sarukhan 1968). These small nuts are elliptic or obovate, laterally flattened, approximately 3.4 to 4.3 mm long, 1.5 to 1.8 mm wide, and 0.9 to 1.0 mm thick, and have, at the apex, a light-brown terminal wing. The seeds are within the nuts. The seeds are elliptic, with the membranous seedcoat firmly attached to the fruit.

The abundant small cones are collected before they ripen, open their bracts, and release the small samaroid nuts. Collectors climb the trees and use poles with metal hooks to remove the cones. The small cones are placed in boxes in the sun for 2 to 3 days to accelerate the opening of the bracts. The cones are shaken inside closed containers to release the winged nuts. The nuts are separated from the small cones with sieves. For the same purpose, vertical column blowers are also used, through which flows a current of air. Nuts may average up to 1,970,000 per kg. The seeds within the nuts can remain viable for several years when stored in closed containers under ambient conditions (24 to 30 °C) (National Academy of Sciences 1984). The samaras that this tree produces are commonly called seeds. However, the real seeds, botanically speaking, are found inside them and are not removed in any way. The samaras are planted as if they were seeds because of their small size.

The germination of the seeds is phanerocotylar. Fresh seeds germinate at 55 to 90 percent without pretreatment. The seeds germinate 2 to 3 weeks after sowing.

In nurseries, the seeds are planted in seedbeds. When the shoots are 5 to 6 cm tall, they are transplanted to black polyethylene containers. The growth medium used in the containers is a mixture of soil and sand with proportions varying among nurseries. The plantules are cultivated in their containers for approximately 4 to 6 months. The plantules in the nurseries do not require any special treatment. When they are 50 cm tall and have a diameter of 6 to 8 mm at the base of the stem, the seedlings are outplanted (National Academy of Sciences 1984, Olson and Petteys 1974, von Carlowitz 1991).

ADDITIONAL INFORMATION

The embryo has a straight axis and is spatulate, almost bilaterally symmetrical, and cream in color. Two cotyledons shaped like the seed are whole, equal, expanded, flat, pulpy, and independent of each other. The plumule is rudimentary. The radicle is short and superior (Hutchinson 1967, Pennington and Sarukhan 1968, Reitz 1984, Rogers 1982, Standley and Steyermark 1952, Stoffers 1980).


1cm
2cm
2cm

Casuarina equisetifolia L.

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CASUARINACEAE (CASUARINA FAMILY)

Casuarina equisetifolia L. ex J.R. & G. Forst., Casuarina equisetifolia L.,
Casuarina litoria Rumph., Casuarina littoralis Salisb.

Australian-pine, beach she-oak, beefwood, bois de fer, casuarina, casuarine, cazuarina, cipres, coast she-oak, common ironwood, filao, filho, horsetail casuarina, horsetail-tree, pin d'Australie, pino, pino australiano, pino de Australia, sauce, she-oak, shortleaf ironwood, toa, weeping willow, whistling-pine (El-Lakany and others 1990, Little and Skolmen 1989, Little and Wadsworth 1964, National Research Council 1984a, Woodall and Geary 1985)

One of a genus of 17 species, *Casuarina equisetifolia* is native to the tropical and subtropical coastlines of Australia, Southeast Asia, Malesia, Melanesia, and Polynesia and New Caledonia. It has become pantropical as its native range expanded through introduction and naturalization (El-Lakany and others 1990, National Research Council 1984a).

Casuarina equisetifolia is a nitrogen-fixing, medium-to-large evergreen tree 15 to 30 m or more in height and up to 50 cm d.b.h. The tree has a thin crown of green, drooping branchlets that resemble pine needles. Leaves are represented as tiny teeth in whorls on the branchlets. The narrow crown of the tree becomes irregular and spreading with age. *Casuarina equisetifolia* is predominantly a coastal species and has the rare property of growing upright and symmetrical on windswept coasts. On suitable sites, *C. equisetifolia* is one of the world's fastest-growing trees. Seedlings may reach 3 m tall 1 year after planting and 8 m tall and 7 cm d.b.h. after 4 years. At age 15, plantation trees may be 17 m tall and 13 cm d.b.h. In these fast-growing plantations, mean annual increments may average 4.5 m^3 per yr (National Research Council 1984a). Occurring naturally in limestone and volcanic soils, *C. equisetifolia* thrives on loose sand a few meters from high tide as well as on infertile, red, iron-rich, leached laterite. Native stands are found along coasts at low elevations, but as an introduced species, *C. equisetifolia* grows in the tropics at elevations as high as 1500 m. Its range is restricted by freezing temperatures, although short duration, light frosts are tolerated. In the natural range of *C. equisetifolia*, annual rainfall ranges from 700 to 2000 mm, often with a dry season of 6 to 8 months. As a planted tree, it grows in areas with rainfall as little as 200 mm and as much as 5000 mm. On sand dunes in areas of low rainfall, it survives on freshwater lenses beneath the dunes (El-Lakany and others 1990, Midgley and others 1983, National Research Council 1984a).

Casuarina equisetifolia consists of two subspecies, *C. equisetifolia* spp. *equisetifolia* L. Johnson, and the smaller *C. equisetifolia* spp. *incana* (Benth.) L. Johnson. The two subspecies integrate on the Queensland coast of Australia. Genetic variation due to provenance has been demonstrated in 2- to 3-year-old trials. In China, hybrids with *C. glauca* Sieb. ex Spreng. and *C. cunninghamiana* Miq. have been produced. Also, in Florida, hybrids with *C. glauca* and possibly *C. cunninghamiana* are suspected in planted and naturalized populations. A hybrid with *C. junghuhniana* Miq. is planted in Thailand and India. (Boland and others 1984, El-Lakany and others 1990, Midgley and others 1983, Midgley and others 1986, National Research Council 1984a, Pinyopusarerk and others 1996, Woodall and Geary 1985).

The wood of *C. equisetifolia* is very dense (basic specific gravity is 0.83), difficult to saw, and splits and warps when dried. Because the wood is strong, it is used as roundwood for fencing, pilings, beams, poles, and rafters and as split wood for fencing, pilings, and roofing shingles. However, the wood is very susceptible to attack by drywood termites and is not durable in the ground. As a high-quality fuelwood that burns with great heat (5000 Kcal per kg), it has been called the best firewood in the world (Chudnoff 1984, El-Lakany and others 1990, Midgley and others 1983, National Research Council

1984a). Used extensively in windbreaks, especially in China, the trees are planted on coastal sand dunes to stabilize them. Although attractive in urban areas, *C. equisetifolia* is hazardous because it can snap or topple in hurricanes. In some regions the species is considered a nuisance because its aggressive spread disrupts native ecosystems (El-Lakany and others 1990, Midgley and others 1983, National Research Council 1984a).

Casuarina flowers are unisexual with male and female flowers that differ in appearance. Usually, male and female flowers are found on different trees, but in some regions outside its natural range *C. equisetifolia* often bears its light brown, inconspicuous, male and female flowers on the same tree. Flowering may begin as early as 2 years after seeds are sown. The wind-pollinated flowers may be borne in one or two seasonal peaks or throughout the year, depending upon the region (Boland and others 1996, Bonner 1988, Woodall and Geary 1985).

Immature fruits are greenish in color. The multiple fruits when mature are light brown, woody, warty, conelike balls 13 to 20 mm in diameter and often slightly cylindrical. Seed maturity normally occurs as the fruit turns brown. In India, seeds are mature 18 weeks after pollination. At maturity, usually September through December in the northern hemisphere, the individual fruits, each with two beak-like valves, split open to release a single, one-winged, light brown samara, 5 to 7 mm long. The species can seed prolifically at 4 years. In some tropical regions two seed crops are produced each year (Boland and others 1996, Bonner 1988).

Fruits should be brown when collected. Mature fruits can be picked by hand or shaken onto canvas sheets. In large trees, climbers collect fruits by cutting off fruiting branches and stripping the fruits later. Fruits dry and open easily in trays or on drying racks, either in the sun or in kilns. Fragments of branchlets should be removed during drying, because they are a major source of fungal infection. If dried outdoors, a thin cloth should be spread over the trays to prevent winds from blowing the seeds away. Three days of drying is adequate in India, where fruits may require insecticide treatment to repel ants (Boland and others 1996, Bonner 1988, El-Lakany and others 1990).

The mature brown seeds shake easily from open fruits and can be screened from fruit debris. Purity of 90 percent or higher is obtainable. Seed weights range from about 0.5 to 1 million or more cleaned seeds per kg. Selecting large fruits by size grading and heavy seeds by density grading gives seeds of the highest vigor. However, lack of information on the correlation between seed vigor and seedling performance suggests caution in selecting seeds solely on the basis of physical characteristics. Near-freezing or sub-freezing temperatures (-7 to 3 °C) are suitable for storage if seed moisture content is 6 to 16 percent. At ambient temperatures in the tropics, viability starts declining within 2 weeks. Low viability of freshly collected seeds has been reported in some areas (Boland and others 1996, Bonner 1988, El-Lakany and others 1990).

Seeds can be germination-tested successfully on moist media without pretreatment, but a 24-hour soak in water before testing may stimulate germination of some seed lots. Seeds treated daily to 16 hours of light at 30 °C and 8 hours of darkness at 20 °C should complete germination in 14 days. Germination tests can also be done in sand at a constant 32 °C and on filter paper at 30 °C. In addition, soaking in 1.5 percent potassium nitrate (KNO_3) and 7.5 percent calcium hypochlorite ($CaOCl_2$) for 36 hours stimulates germination (Bonner 1988, El-Lakany and others 1990, National Research Council 1984a).

Casuarina equisetifolia seedlings can be grown in containers or open beds. Bare-root seedlings can be produced in beds by broadcast sowing in the spring and covering the seeds with about 0.5 cm of soil. Watering and fertilization schedules need to be established locally, because these are dependent on the growing medium and local climate. Seedlings should be thinned to bed densities in the range of 215 to 320 seedlings per m^2. Beds may require shade in some climates. Germination should occur in 40 days and seedlings should reach plantable size of 30 to 50 cm in 3 to 4 months (Bonner 1988, National Research Council 1984a).

The success of *C. equisetifolia* as a productive plantation species depends on the roots being invaded by a variety of symbiotic organisms. Sterilized nursery soils and artificial growing media can reduce natural inoculation of roots by the symbionts. Experiments are often needed to successfully launch a new nursery. Survival and growth on nutrient-deficient sites depend on inoculation with the symbiotic filamentous bacterium, *Frankia* sp., which invades root hairs of fine roots, forming nodules. These nodules are woody and perennial and can form large masses in the root system. The atmospheric nitrogen that the *Frankia* in the nodules fixes, enables this species to grow well in soils that otherwise would be too deficient in nitrogen to sustain plant growth (El-Lakany and others 1990, Midgley and others 1983, National Research Council 1984a).

ADDITIONAL INFORMATION

The Casuarinaceae are a group of 96 species of trees and shrubs. Once all species of the family were included in a single genus, *Casuarina*. Now four genera are recognized: *Allocasuarina*, *Casuarina*, *Cuethostoma*, and *Gymnostoma*.

Casuarina equisetifolia often reproduces in dense stands from abundant self-seeding. However, in Puerto Rico natural regeneration is rare because ants eat the seeds (Little and Wadsworth 1964).

Male flower clusters form at the end of branchlets and resemble spikes or catkins. The clusters are narrow cylinders, 1 to 2 cm long and less than 3 mm wide. The tiny male flowers are crowded in rings among grayish scales and have one exposed brown stamen less than 3 mm long and 2 tiny brown sepal scales. The female flowers are in clusters or heads resembling short-stalked balls less than 3 mm in diameter and 8 mm across stigmas. The flower has a 5 mm long pistil, small ovary, very short style, and two long, threadlike, dark red stigmas (Boland and others 1984, El-Lakany and others 1990, Midgley and others 1983).

The *Frankia* species that forms a symbiotic relationship with species of *Casuarina* is found naturally in soils of native stands. When trees are planted outside their native range or sterile nursery soil is used, the *Frankia* might be missing and the seedlings must be inoculated. A number of inoculation techniques are used. A practical technique involves mixing surface soil from under *Casuarina* trees with bedding or container soils or mixes. In another procedure, root nodules are gathered from established trees and soaked in 70 percent ethanol for a few seconds to reduce the chance of contamination by pathogenic organisms. The nodules are washed and crushed in water; the coarser particles are then filtered out. The resulting suspension is applied to the roots of the seedlings or injected into the nursery soil. Fresh nodules can be dried over silica gel and stored for up to a year without losing their infective ability. Suspensions of ground nodules can also be stored in saline solution or in a polyvinylpyrrolidone solution (National Research Council 1984a).

Inoculation with pure cultures of *Frankia* may be the most effective means of inoculation, but it requires elaborate experimental procedures. The slow-growing filamentous bacterium is grown in liquid media. Whole cell cultures are infective whether used as liquid homogenates or as air-dried powders. Alginate beads and silica gel can be used as carriers for the inoculum. The very practical method of growing the *Frankia* in finely milled peat emulates a successful technique used for *Rhizobium* inoculation. The peat serves as a protective carrier for the *Frankia* and the medium remains infective for up to 2 years when stored at 4 °C (El-Lakany and others 1990, National Research Council 1984a, Reddell and others 1996).

Casuarinaceae also form symbiotic associations with ectomycorrhizal and endomycorrhizal fungi, which are needed for good growth in the field. The most common endomycorrhizal fungi associated with *Casuarina* sp. are in the genus *Glomus*.


2cm
1cm
1cm

Cecropia obtusifolia Bertol.

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CECROPIACEAE (CECROPIA FAMILY)

Cecropia schiediana Kl., *C. bicolor* Kl., *C. digitata* Ten. Ex Miq., *C. commutata* Schott, ex Miq., *C. mexicana* Hemsl., *C. panamensis* Hemsl., *C. vogeleri* Burret, *C. mexicana* var *macrostachya* Donn. Sm.

Bitâk, chancharro, chupacté, guarumbo, guarumo, hormiguillo, koochlé, trompetillo

Cecropia contains about 60 species and is one of the genera most characteristic of the American tropics. *Cecropia obtusifolia* is normally found in pioneer stages of secondary forests, sometimes forming pure stands on both coasts from Central Mexico to northern South America (Burger 1977).

Cecropia obtusifolia is a fast-growing (2 to 3 m per year) pioneer tree species. The tree reaches 10 to 20 m in height and 25 to 50 cm d.b.h. with stout, seldom-branching trunks and gray to white bark. *Cecropia obtusifolia* has few major branches and the young branches are very stout, minutely cinereous to glabrate, and hollowing, hosting nests of Azteca ants. Leaves are simple, alternative, four-ranked, with large stipules covering young leaves; petioles are very long; and blades are eccentrically peltate. Mature leaves are 30 to 50 cm wide with 9 to 13 lobes. Usually inhabited by aggressive biting ants, the tree’s tall, few-branched habit with the very large umbrella-like leaves produces a striking silhouette. It grows well in a wide range of soils, poorly or well drained. The species thrives in areas of high rainfall (2000 to 3600 mm per year) or high soil moisture and average temperatures that vary from 22 to 24 °C; it is found at elevations ranging from the lowlands to about 1300 m.

The soft, fast-decaying wood of *C. obtusifolia* is sometimes used for wood pulp. The larger trunks are sometimes split and used as water troughs, and the bark contains a tough fiber used to make coarse ropes (Allen 1956). The leaves are used in Costa Rica to prepare an infusion used to lose weight. The species has also been used in agglomerate panels and paper pulp, but the high content of gums and resins in the wood complicate industrial use.

Cecropia obtusifolia begins to flower and fruit when the trees are 5 to 6 years old. It blooms throughout most of the year (Pennington and Sarukhan 1968). In the Pacific southern region of Costa Rica, most flowering frequently occurs from August to November (Allen 1956). In the Atlantic-mid region of Turrialba, Costa Rica, flowering peaks from mid-November through July and fruiting occurs from August through October and from November through July (San Román 1987). The minute dioecious flowers appear in axillary inflorescences of spadiceous spikes in digitate clusters. Fruiting spikes are 10 mm thick and fruits are about 2 mm long and 1.2 mm wide, usually flattened, abruptly rounded at the base and apex, smooth surfaced, and surrounded by a fleshy tissue of the perianth. Species dispersal is enhanced by the production of fruit throughout much of the year. These fruits are eaten and dispersed by bats and birds. In Chiapas, Mexico, the seeds are dispersed in the excreta of *Philander opossum* and *Didelphis marsupialis* at distances of 60 m (Medellin 1994). The seeds remain viable in the substrate for 1 year, then germination drops drastically to 3 percent.

Because *C. obtusifolia* is dispersed by bats and birds that are relatively abundant in open vegetation, and because the species grows rapidly in secondary growth, the tree should be considered a good prospect for forest recovery in deforested areas (personal observations). However, *C. obtusifolia* has not been planted artificially and all the trees are regenerated naturally.

Cedrela montana Moritz ex Turcz.

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Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

MELIACEAE (MAHOGANY FAMILY)

Cedrela bogotensis Triana & planchón, *C. mexicana* Roem, *C. subandina cuatrecasa*

Cedro, cedro bogotano, cedro cebollo, cedro clavel, cedro colorado, cedro de montaña, cedro de tierra fría, cedro mondé, cedro negro, cedro rosado

Cedrela montana is a slow-growing tree that reaches 25 to 30 m in height and 30 cm d.b.h. It has a straight brown shaft that is fissured and soft, with a pink bark. The leaves are alternate, compound, and paripinnate with whole margins. The species grows in soils with good drainage, loose or loose sandy texture, a neutral or alkaline pH, and good fertility. The tree delays its growth when it is planted in low-fertility soils and soils with a clayey texture; it is also susceptible to flooded soils (Rodriquez 1988). *Cedrela montana* grows at elevations between 1600 and 2800 m, with an average annual temperature ranging between 10 and 20 ^{o}C and annual precipitation of 500 to 2000 mm. *Cedrela montana* grows in the vegetal formations of the Pre-Mountainous dry forest (bs-PM), Pre-Mountainous wet forest (bh-PM), Low Mountainous dry forest (bs-MB), and Low Mountainous wet forest (bh-MB).

Generally, the genus *Cedrela* is highly appreciated in carpentry, for exteriors and interiors and especially for furniture due to its color, grain, and workability. Characterized by its hardness and high durability, the wood is also used for plywood, cigar boxes, naval construction, racing boats, and musical instruments and as chips in construction. It is also used to make artistic carvings (Escobar and Rodriquez 1993).

The flowers are terminal and small; the calyx is regular and lobulate. The fruits are ligneous capsules, lenticellate, dehiscent, and brown. They contain winged seeds.

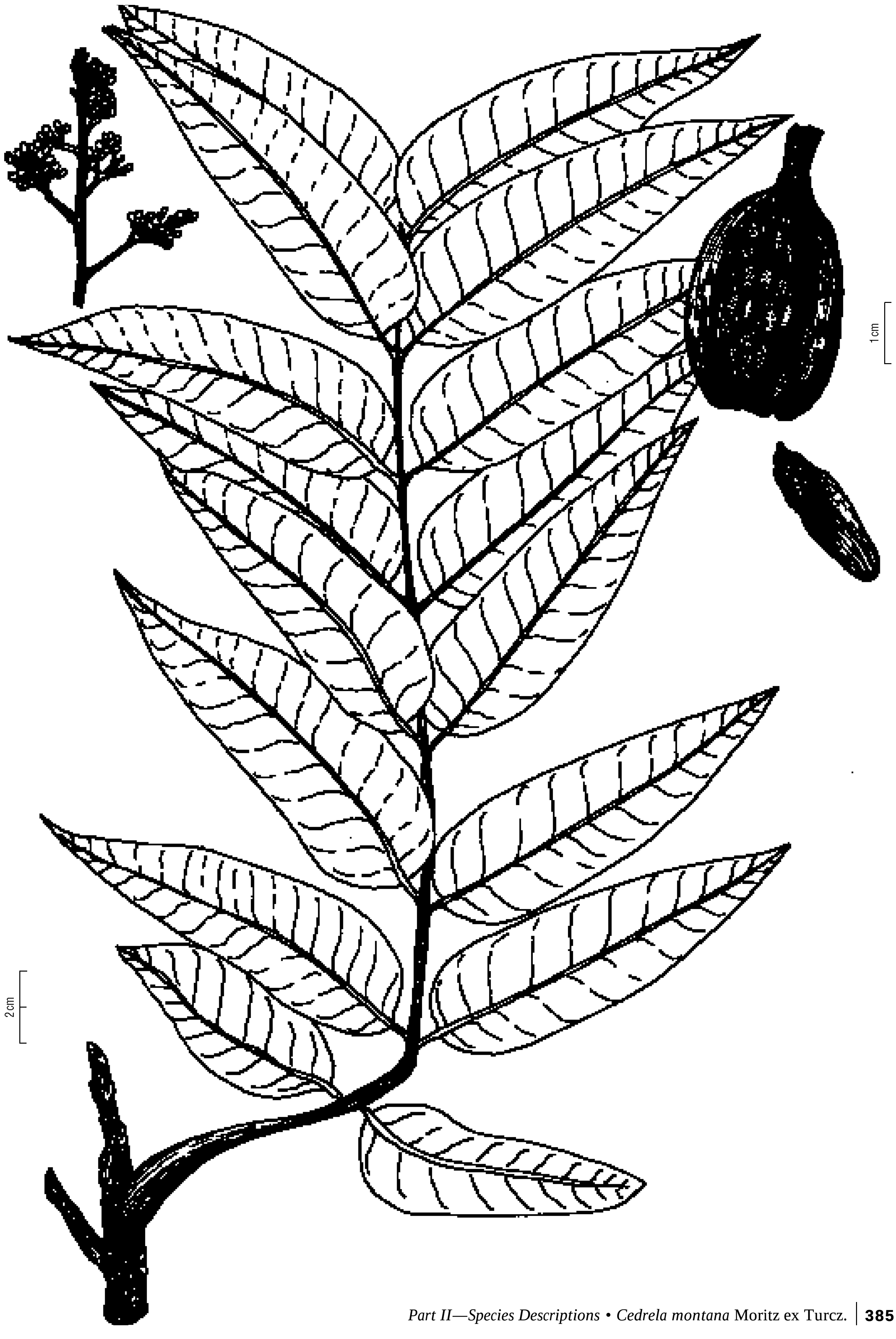
Fruits are collected from the tree, a little before they ripen and open. They are dried in the sun, and the seeds are extracted. Viable seeds average 26,254 per kg. The seeds are stored at 4 to 5 ^{o}C. Appropriate pregermination treatment involves immersing the seeds in room-temperature water for 24 hours. About 12,000 plantules are obtained from 1 kg of seed in nurseries. Purity percentage ranges between 40 and 80 percent. Germination percentage is 60 to 90 percent. Germination is epigeal and seeds germinate in 5 to 30 days.

Cedrela montana can be propagated through cuttings, shoots, or seeds if medium to high light is provided. The basal portions of stem cuttings 25 cm long and 2 to 4 cm in diameter are submerged in a solution of indolbutyric acid (0.2 mg per cc) for 24 hours before planting. The root shoots of *C. montana* can be used for forest reforestation.

When using seed to propagate the species, the recommended substrate should consist of two parts sand and one part soil, which must be disinfected before planting the seeds. Seeds must be sowed deep enough to prevent uncovering when watered, but they must not be too embedded. The plantules are lifted when they are 5 to 8 cm high. Initial shade is required, but it is gradually eliminated until the plantules are fully exposed to the sun. Plants are transplanted to the field 4 to 6 months after the initial transplant (Trujillo 1995).

The stubble at the planting site must be partially removed to prevent attacks by borers. In over-pastured soils, scarification will promote root growth. The species needs good soils; appropriate fertilization and correction of pH are recommended in poor soils.

The planting distance between trees depends on the final objectives. Homogeneous plantings are not recommended because the species is susceptible to attacks by the bud borer. It must be associated with agricultural plantings or grasses; otherwise, enough distance must be left among trees for underbrush to grow and diminish attacks by the pests. To produce a forest, distances of 8 to 15 m combined with other species are recommended. As shade for agricultural plantings, distances range from 13 to 20 m.


1cm
2cm

Cedrela odorata L.

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MELIACEAE (MAHOGANY FAMILY)

No synonyms

Acajou amer, acajou pays, acajú, cedre, cedro, cedro amargo, cedro blanco, cedro caoba, cedro colorado, cedro español, cedro hembra, cedro mexicano, cedro oloroso, cedro real, cedro rojo, cedro vermelho, Central American cedar, cóbano, Jamaican cedar, kurana, leli, Mexican cedar, red cedar, West Indies cedar

Native to the tropical region of America, *Cedrela odorata* is naturally distributed from northern Mexico through Central America to Argentina in South America, and throughout the Caribbean islands. The species has been introduced in southern Florida, Nigeria, Tanzania, Ghana, Sierra Leone, and the Fiji Islands (Betancourt 1983, Little and others 1967, Webb and others 1980).

Cedrela odorata is a deciduous tree that can reach 35 m in height and 60 cm d.b.h. In exceptional cases, specimens 40 m or more in height and 2 m in d.b.h. can be found. The trunk is straight and cylindrical, sometimes with small spurs. The leaves are paripinnate or imparipinnate, 15 to 50 cm long, made up of 10 to 22 oblong or lanceolate leaflets that are asymmetrical, 4.5 to 14 cm long and 2 to 4.5 cm wide, and have a whole margin with an acuminate apex. The tree prospers in calcareous soils as well as in soils rich in organic matter. It grows in areas with an average annual temperature of 22 to 32 °C and an average annual precipitation of 1600 to 2500 mm. It requires a 3- to 4-month dry season and grows at elevations ranging from sea level to 1200 m.

The wood from this tree is among the most sought-after in Latin America and elsewhere, primarily for its value in the manufacture of veneer and furniture. Its specific gravity ranges from 0.42 to 0.63. It is resistant to attacks by fungi and insects, and it keeps a pleasant fragrance for many years. It is used for belt rails, staves, musical instruments, and interior decoration. An infusion of its bark is used as a remedy for diarrhea, fever, vomiting, hemorrhages, dyspepsia, bronchitis, and indigestion (Niembro 1986).

As a monoecious tree, *C. odorata* has flowers of both sexes in the same inflorescence. The flowers are yellow-green and arranged in panicles. Flowering and fruiting periods vary throughout the tree's range. In Mexico, it blooms May through August, and the fruits ripen during the dry season from January through March in the following year. As the foliage begins to drop, the fruits dry and open. The fruits are capsular, oblong, or ellipsoid; 17.1 to 44.8 mm long and 14.0 to 21.1 mm in diameter; dehiscent; and green-gray to light brown with four to five valves and numerous lenticels (Little and others 1967, Pennington and Sarukhan 1968). Each fruit contains 13 to 34 developed seeds (Niembro 1995a). The seeds are samaroid, bulky at their apex, 2 to 3 cm long, and 5 mm wide (including the wing). The bulky part is oblong, slightly comose, laterally flattened, 7 to 8 mm long, 3.5 to 5 mm wide, and 1.2 to 1.5 mm thick. The seedcoat is light brown to red-brown, rugose, opaque, cartaceous, and expanded at the base on a thin and brittle lateral wing, which results from the extension of the raphe-exostome.

Cedrela odorata fruits change color as they ripen. Ripe fruits are dark coffee-colored and dehiscent. They must be gathered before they open and release the seeds. Dry and warm winds aid in ripening and dehiscence. Collectors climb the trees and cut the fruits from the trees using poles with metallic hooks. The fruits are transported in jute sacks to the processing plant, then placed in wood boxes with metallic mesh bottoms that provide air circulation and prevent the development of microorganisms. The boxes are placed in well-ventilated sheds. The fruits should not be placed in the sun to dry (a common practice in many areas), because this reduces seed viability by exposing them to high temperatures, causing irreversible damage. As the fruits dry, the valves open and release the seeds. Valves usually begin to open by the second or third day. *Cedrela odorata* seeds have a fragile and brittle wing, which is removed by rubbing the seeds by hand. Resulting impurities are eliminated using sieves or a vertical column blower. *Cedrela odorata* seeds differ in size and weight but average 40,000 to 89,047 per kg (Betancourt 1983, Patiño and Villagómez 1976, Vega and others 1981).

Vega and others (1981) note that the seeds of this tree can be stored at ambient temperatures for a period of 10 months without significantly losing viability. However, other studies (Centro Aronómico Tropical de Investigación y Enseñanza 1997b) show that the viability of the seeds stored under natural conditions diminishes quickly after 1 month. Therefore, storing seeds in polyethylene bags at a temperature of 5 °C and a moisture content of 7 percent is recommended. Stored this way, seeds maintain a viability of 50 to 60 percent for 2 years.

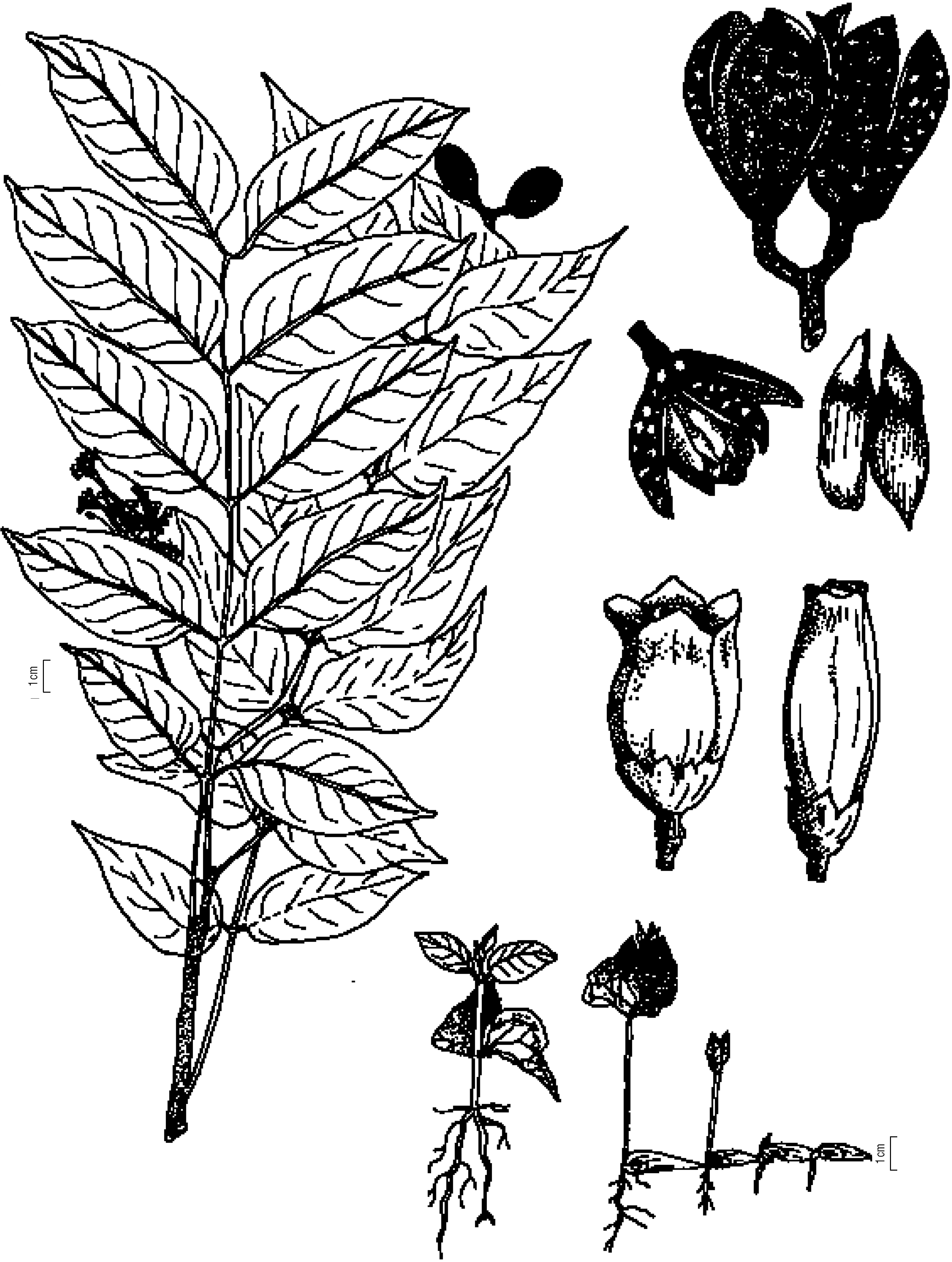
Seed germination is epigeal or phanerocotylar (Duke 1969). Because the seeds do not have a latency period, they do not require pretreatment. In the Forest Seeds Laboratory of the China Experimental Field of the National Institute of Forest, Agricultural, and Cattle Research, located in Campeche, Mexico, seeds are placed in germinators with continuous light and a constant temperature of 28 °C.

Two methods are used to propagate the species: bare root and seed. Selection of a method is driven by the cost. In southeast Mexico, *C. odorata* is propagated in nurseries primarily through the less expensive, bare root method. In some forest nurseries, the species is propagated inside polyethylene containers. Those who propagate using seeds prepare the beds by hand or by machine 4 months before planting. Seedlings that reach 30 to 40 cm in height and 1 cm in diameter at the neck of the root during the rainy season are outplanted (Patiño and others 1993b). During the first few years, *C. odorata* grows at an average annual rate of 1.3 to 1.8 m in height and 1.3 to 1.6 cm in d.b.h.

ADDITIONAL INFORMATION

The hilum is subapical, linear, and slightly deep-set; it sometimes has a remnant of funicular tissue. The micropyle is indiscernible. The endosperm is thin, pulpy, uniform, whitish, oily, and firmly attached to the embryo. The embryo has a straight axis and is almost bilaterally symmetrical, white, and located at the longitudinal axis of the seed. The cotyledons are narrowly ovoid, oblong, or elliptic; whole; flat; foliaceous; and independent of one another. The plumule is undifferentiated. The radicle is short and protrudes laterally (Corner 1976, Klein 1984, Niembro 1982, Pennington and Styles 1981, Pennington and Görts van Rijn 1984, Standley and Steyermark 1946b, Stoffers 1984, Wilson 1924).

Germination begins as the hypocotyl and radicle lengthen and the cotyledons rise above the ground. The cotyledons change from yellow to green, which indicates that photosynthetic activity has started in the plantule. Subsequently, the plumule develops. Plantules continue to grow and develop new leaves that gradually provide nutrients for the tree.


1cm
1cm

Cedrela tonduzii C. DC.

E.M. FLORES
Academia Nacional de Ciencias de Costa Rica, Costa Rica

MELIACEAE (MAHOGANY FAMILY)

Cedrela pacayana Harms (Notizblatt des Botanischen Gartens
und Museums zu Berlin-Dahlem 11: 784. 1983)

Cedar, cedrillo, cedro, cedro cebolla, cedro colorado, cedro dulce, cedro granadino,
cedro macho, cedro pochote, West Indian cedar

Cedrela tonduzii is distributed from Chiapas, Mexico to Panama in Central America. It is a canopy-emergent species in the premontane and lower montane humid and very humid tropical forests. The species is common on the slopes of the Central Volcanic Mountain Range and the Talamanca Mountain Range (Breedlove 1986, Hazlett 1979, Molina 1975).

Cedrela tonduzii is a tree that reaches 30 to 45 m in height and 80 to 100 cm d.b.h., although sometimes it may reach greater diameters (up to 180 cm). The bole is straight and symmetrical. The tree crown is open, with thick ascendant branches produced at a low height. The branchlets have sporadic small lenticels. The bark is rough; vertically fissured; and brown, reddish brown, or dark grayish brown, depending on the light intensity to which it is exposed. The bark exfoliates in small, irregular plates. The mean thickness is 1.8 to 2.0 cm. Internally it is mucilaginous and pink or reddish colored. Leaves are spirally arranged, large, compound, pinnate, light green, glaucous abaxially; petioles are greenish brown, pubescent, terete, lenticellate at the proximal end. It grows well in areas with moderate declivity and may be riparian. The species grows in fertile soils, with good or moderate drainage. Commonly, these soils have a volcanic origin and the sopes are 51. The elevational range varies from 1000 to 2800 m. In its area of distribution, the temperature range is 6 to 20 °C, and the annual rainfall is 2400 to 8000 mm.

Sapwood is yellowish gray in green condition; heartwood is bright, reddish orange. Sapwood turns grayish orange after air drying, heartwood changes to bright red. The wood oxidizes and darkens when exposed to light. Growth rings are easily seen and are demarcated by thin, regular, brown stripes. The wood is light and the basic specific gravity is 0.36 to 0.41, varying with the origin. The mean green weight is 620 kg per m^3 with 67 percent moisture content. The oven-dried wood weighs 392 kg per m^3. The wood has a straight grain, high luster, and medium texture. The wood has excellent working properties; it is easy to saw, brush, lathe, and sand (Llach 1971, Richter 1971). The rate of drying is fast; it dries without visible defects. The contraction ratio is moderate and dimensional changes are uniform. It is classified as a C-type structural wood. The natural durability of the timber is low, and its preservation is difficult (Llach 1971, Richter 1971). Chemical impregnation is recommended (Richter 1971). The Peteri's coefficient of flexibility is 42 and the Runkel factor is 0.26; the wood is very good for making paper (Llach 1971, Richter 1971). The species provides most of the wood used in the carved trays sold by the Costa Rican farmers along the South InterAmerican Highway. The wood is currently used to make high-quality furniture, cabinets, casts, and instruments. It is also used in carpentry, interior and general construction, and veneers (Llach 1971, Richter 1971). The boiled bark provides a maroon dye that may be used to stain cotton fibers (Acuña and Rivera 1990). The species is also grown as an ornamental.

The species is monoecious. The tree blooms in April and May and sometimes June. The number of flowers and inflorescences varies from one tree to another in the same area. Floral anthesis is not synchronized between inflorescences of the same tree and phenologic synchrony is moderate among individuals of a population. The species is dichogamous. Pollination is entomophilous and the probable pollination vectors are moths (palaenophily). Flowers are grouped in large, ramified, terminal or subterminal panicles, 15 to 30 cm long, generally smaller than the leaves. Terminal branchlets are usually simple dichasia, and each inflorescence may have as many as 1,000 flowers. Flowers are unisexual with vestiges of the opposite sex, actinomorphic, synsepalous, apopetalous, pentamerous, short-petiolated, and pubescent. Male flowers have long stamens and yellow, apiculate, fertile anthers; female flowers have small, brown, nonfunctional anthers. The fruit is a pendulous capsule, pentasepticide, elongated, obovoid, with conspicuous lenticels, 5 to 10 cm long. It is green during development and brown when mature. Fruits mature and dehisce, liberating the seeds, in June and July. Fruit abscission takes place several weeks after dehiscence. There are 25 to 30 fertile seeds per fruit. Seed dispersal is anemochorous; they are mobilized according to wind direction. The seed is winged, brown or reddish brown, and 3.0 to 5.5 cm long including the wing.

Seeds are collected in the tree (partially open fruits) or on the ground. Damaged or malformed seeds must be discarded. Of collected seeds, 65 to 70 percent exhibit embryo damage. A low percentage (5 to 8 percent) show developmental anomalies. In most such cases, germination is null. Seeds average 84,600 per kg. Water content in fresh seeds is approximately 32 percent. Seed viability is lost rapidly. Although the species has been studied less than *C. odorata*, seeds can probably be stored following the same procedure: storage in a dry atmosphere with a temperature range of 3 to 5 °C.

Seeds must be soaked in running water for 24 hours to obtain complete imbibition. Seeds germinate in 6 or 7 days. Selected fresh seeds have an 85 to 90 percent germination rate, which varies with seed source. Germination is epigeal and the seedling is phanerocotylar.

Seeds germinate well if sown in sand beds; 20 days later, the seedlings must be transplanted to plastic bags. The use of fertilizers rich in potassium improves seedling vigor and growth. Seedlings grow well under full light but tolerate partial shade. Three-month-old seedlings reach a height of 20 to 25 cm and bear several compound leaves, with helical distribution.

The seedling and sapling behavior in plantations is not well known; however, the species is very susceptible to *Hypsipyla*, *Sematoneura atrovenosella*, and other microlepidopters that attack the Meliaceae (Becker 1976). Several microlepidopters are associated with the genera *Cedrela*, *Carapa*, and *Swietenia*. Their larvae cause conspicuous shoot damage and drastically limit the establishment of the species in plantations. The young shoots of *Cedrela tonduzii* host *Hypsipyla grandella* (Pyralidae), *Sematoneura atrovenosella* (Pyralidae), and *Phyllocnistis meliacella* (Gracillariidae) larvae. *Hypsipyla grandella* larvae damage young shoots and fruits. Some Cerambycidae are predators of the young shoots causing stem bifurcation, and several coleopterans in the family Scotylidae may be predators of the seedlings. This susceptibility limits the tree's use in monospecific plantations. Leaf spot (*Cercospora* sp.) and powdery mildew (*Oidium* sp.) may be parasites on the leaves. *Sclerotium*, *Rhizoctonia*, and *Fusarium* may attack the seedlings. In the nursery, *C. tonduzii* has better growth than *C. odorata* during the first 6 months. Its behavior in plantations above 1000 m has not been documented.

ADDITIONAL INFORMATION

The genus *Cedrela* was described more than 250 years ago by Patrick Browne in his treatise on the natural history of Jamaica (Browne 1756). The first validated species appeared shortly thereafter in Linnaeus' book Systema Naturae (Linnaeus 1759). The aromatic odor of the wood gave rise to cedar, a name used by the Spaniards to name the genus because of its similarities to the true cedars of the Old World. The generic name is a diminutive of *Cedrus*, which means small cedar (Pennington and Styles 1975). The species name honors the naturalist Adolphe Tonduz (Type: Pittier 11945. Costa Rica, El Copey, fl., fr.).

Leaves have five to nine short-petiolulated leaflet pairs; leaflets are lanceolate or oblong-lanceolate, with entire margins; acuminate, acute or obtuse apexes; and oblique bases; leaflet blades are membranaceous or slightly coriaceous, abaxially tomentose or pilose; the upper surface is glabrous or pubescent along the midvein, hypostomatic, with stomata of the paracytic type (rubiaceous). Venation is eucamptodromous; midvein is thick, straight; secondary veins are opposite, semiopposite, and sporadically alternate.

Unisexual flowers have calyx lobes that are deltaic, puberulent; corolla is creamy; and petals have imbricate aestivation, oblong or elliptic-oblong, fleshy, adnate to the gynophore by a carina, along the proximal one-third. Androecium is pentamerous; anthers are free, filaments basally adnate to gynophore. Female flowers have a superior, syncarpic, pentalocular, glabrous, globose or ovoid ovary. Placentation is axilar, and the ovary has 8 to 14 ovules per locule; the style is short and the stigma discoid, with glandular papillae. Male flowers have a narrow ovary with locules, but ovules are vestigial; style is narrow, stigma lacks glandular papillae. Ovules are anatropous, bitegmic, and crassinucellate.

The fruit's pericarp is woody and the exocarp is brown, with lenticels. The mesocarp is slightly conspicuous and woody as is the endocarp. The latter forms the septa and surrounds the central columella. There are many transverse fibers reinforcing septa structure; at the ends and around the columella, fibers are longitudinal. In the open capsule, the columella has five conspicuous wings (corresponding to the ovary septa). It is woody and has many scars which correspond to the funicula attachment at the placental areas. The fruit valves are also woody; they open basipetally during fruit dehiscence.

The seed's funiculus is short and subapical. The seedcoat is formed by testa and tegmen; those are not lignified and are undifferentiated; the tegmen is not specialized. The wing develops from a chalazal protuberance. The endosperm is oily. The embryo is straight, fleshy, soft, and whitish or creamy. The cotyledons are extended, and the hypocotyl is conspicuous.

During germination, radicle protrusion takes place throughout the hilum. The hypocotyl completes its emergence at 8 to 9 days; the cotyledons emerge in 10 to 11 days. They are ovoid, subsessile, foliaceous, dorsiventral, with entire margin, acute or obtuse apex, base wide, oblique. Eophylls are opposite, semi-opposite, sometimes alternate, supracotyledonary, pinnately.

On the forest floor, the logs exhibit traces of damage produced by termite attack after 12 months; 2-1/2 years later the damage is severe. When wood remains above ground level, fungal attack is light at 2-1/2 years; if it is placed at ground level or underground, the damage is light at 12 months and severe after 2-1/2 years (Bultman and Southwell 1976).

Sematoneura atrovenosella larvae live inside the fruits and destroy most seeds (Becker 1976). The fruit pericarp shows circular orifices; the interior of the fruit contains insect excrements, seed remains, and white silky filaments. The young leaves are attacked by *P. meliacella* larvae established in the abaxial surface (Becker 1976). They absorb the sap and form galleries which may reach the midvein as well as the secondary veins. Before pupating, the larvae build a pupal chamber, turning the leaflet abaxially and fixing the margin to the leaflet blade with a creamy, silky glue (Becker 1976).

Different species in the Bostrychidae, Cerambycidae, Platypodidae, Curculionidae, and Brentidae are wood borers and decomposers. Adult female oviposition occurs in the wood of fallen trees; the larvae develop inside the wood, decompose it (especially the sapwood), and eventually rot it. The scale (*Pinnaspis* sp.) is a common pest, as well as leaf-cutting ants (*Acromyrmex* spp.), which defoliate seedlings, saplings, and adult trees (Flores 1996).

The species seems suitable for natural forest management (lower montane forest), mixed plantations, and agroforestal systems, and as a threatened species deserves attention as a biodiversity element. In the genus *Cedrela*, several species have compounds with biological activity (*C. odorata* L., *C. fissilis* Vell.) (Taylor 1981); the chemistry of *C. tonduzii* has been only partially explored, but leaf extracts may reduce the growth of cornborer larvae (*Ostrinia nubilalis*) (Arnason and others 1993).


1cm

Ceiba pentandra (L.) Gaertn.

C.R. ALVARADO, C.A. ALVARADO, and O.O. MENDOZA
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Gerenta General Semillas Tropicales, Siguatepeque, Honduras

BOMBACACEAE (BOMBAX FAMILY)

Bombax pentandrum Linn.

Bongo, ceiba, ceibo, fromager, kapok, pochote, silk cotton-tree

Ceiba pentandra is amply distributed in the intertropical regions of the world; its habitat is wet forests, especially secondary forests (Standley 1931). In America it grows naturally from Mexico, through Central America, to Colombia, Venezuela, and Ecuador; in the West Indies, from Cuba and Jamaica to Trinidad and Tobago (Jiménez 1997). In Honduras, it is found in the departments of Francisco Morazán, Comayagua, Yoro, Cortes, Colon, Atlantida, and Olancho.

Ceiba pentandra is a gigantic, fast-growing tree, of up to 50 m in height. It has a straight, cylindrical shaft, with commercial lengths of 20 m and diameters of up to 2 m (Benitez and Montesinos 1988, Salas 1993). Young trees have notably verticillate branches, with large conical thorns on the trunk (Standley 1931). The bark is yellowish, granulated, and smooth on the outside and pale-pinkish gray and fibrous near the alburnum. The bark turns orange and then brown and is often covered with large conical thorns. It is up to 5 cm thick. The leaves are digitate-compound and grouped alternately at the end of the sprigs (Standley 1931). In Honduras, it grows at elevations up to 1000 m, especially in wet areas. In dry regions, it is found near permanent waters.

In dry condition, the wood ranges from light brown to pale yellow, with rosy-brown streaks. It is light, with no characteristic odor or taste; it has intercrossed, and occasionally a straight hilum, thick texture, medium shine, and marked streak. There is no pronounced difference between the alburnum and the duramen. Silica content is 0.33 percent. Specific gravity is 0.24. Total radial shrinkage is 2.5 percent, intermediate 1.3 percent; total tangential shrinkage is 3.9 percent, intermediate 2.2 percent; and tangential:radial shrinkage ratio is 1.60. Total volumetric shrinkage is 6.9 percent (Benitez and Montesinos 1988). The wood is easy to saw and satisfactory to moderately difficult to plane. It accepts paint very well. It does not turn, drill, chisel, or mold well. It resists cracking caused by screws; it shows a floccose grain and regular sanding. The wood has an extremely low resistance to fungi and is susceptible to attacks by dry wood termites. It dries at a moderate speed with moderate defects. It is easy to preserve (Benitez and Montesinos 1988). The wood is used in light construction, canoes, rafts, floats, lifeboats, fillers for plywood, veneer, airplanes, model airplanes, aquaplanes, all types of thermal insulant, interior finishes, handicrafts, boxes and crates, toys, briquettes, pulp, and paper. The oil from the seed is used for lighting and in the manufacturing of soaps; the cotton from the seed is used to manufacture buoys, lifeboats, pillows, and similar articles (Aguilar 1966).

The big, whitish, hermaphroditic flowers are 2 to 5 cm long and are arranged in pendulous fascicles hanging at the end of the sprigs. The tree blooms December through January. The fruit is an ovoid, ligneous, greenish capsule, up to 14 cm long, with numerous black seeds hidden in a mass of gray silky hairs (cotton); it opens up in five valves. The tree fructifies March through April. The black seeds are round, smooth, and intermediate/recalcitrant. Seeds average 14,000 to 26,000 per kg.

Seeds cannot be stored for a long period of time (Semillas Tropicales 1998). Stored in glass or plastic containers at 4 °C with 60 percent relative humidity and 15 to 20 percent physical moisture, seeds can be preserved up to 1 year. When they are ripe and fresh, seeds have 90 to 100 percent viability. Seeds are pretreated by soaking in water for 24 hours and cutting longitudinally without damaging the embryo. Germination is good, using a substrate of sand under conditions of 20 to 30 °C alternating temperature, with 8 hours of light daily (Standley 1931).

ADDITIONAL INFORMATION

The petiole is 5 to 25 cm long, partially reddish toward the base and caniculate, thin, glabrous, and pulvinated on both ends with five to nine sessile leaflets. The lamina is lanceolate to oblanceolate, 5 to 20 cm in size, with an acuminate apex. The base is cuneiform or attenuate with whole edges; the right side is dark green and the back is pale green. Both surfaces are glabrous. The main vein is prominent on both sides and partially reddish below with 10 to 20 pairs of secondary veins that are slightly prominent on both sides; slightly acrodrome anastomosed near the edge, yellowish green, bending toward the edges, camptodrome.

Mechanical properties:

Static flexure (in green condition and at 12 percent moisture): stress at proportional limit 123 and 173 kg per cm^2, maximum stress 181 and 280 kg per cm^2, modulus of elasticity 27 x 10(3) kg per cm^2, work at proportional limit (12 percent) 0.4 kg-m per cm^3, work at maximum load (12 percent) 1.5 kg-m per cm^3.

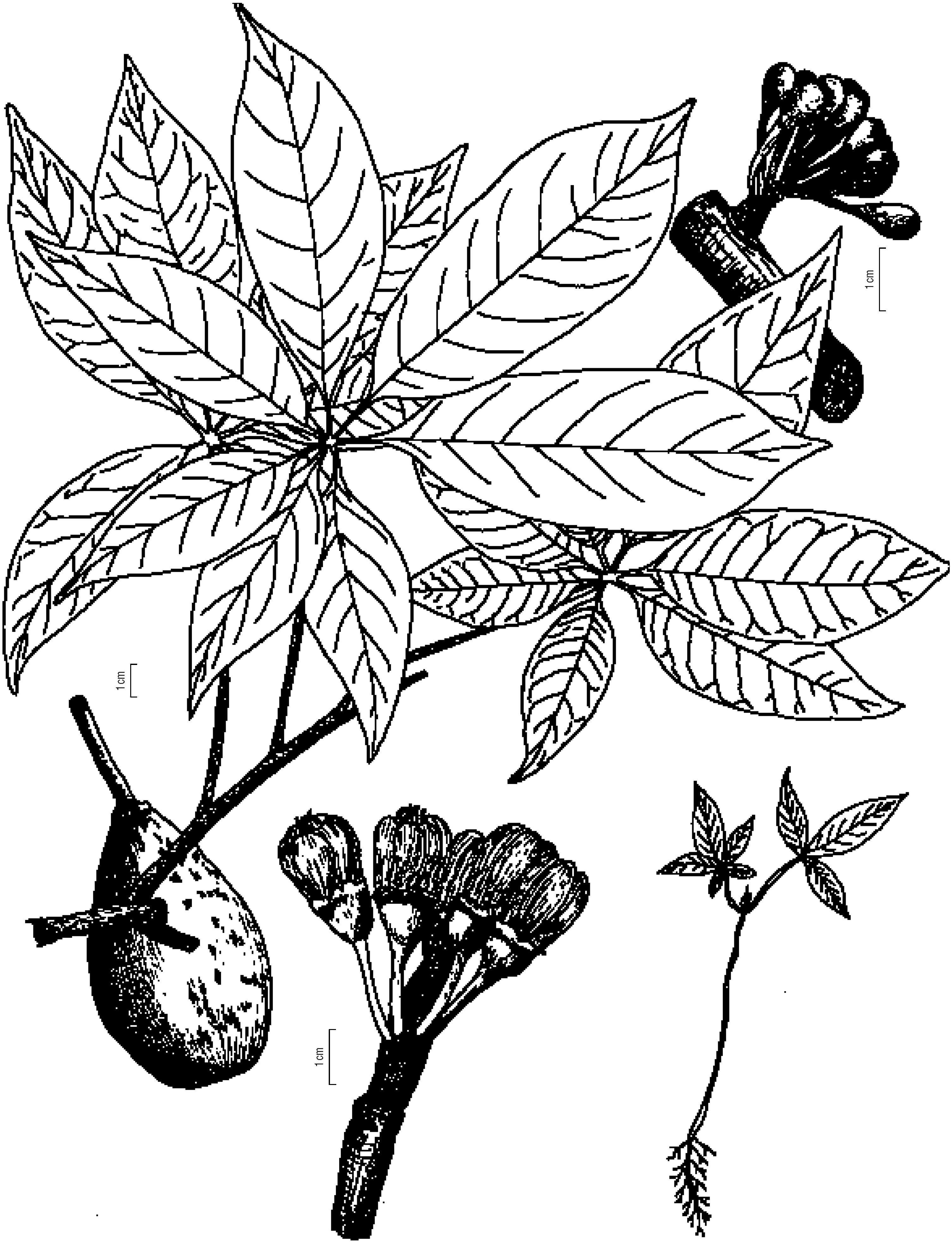
Parallel compression (in green and dry condition, respectively): stress at proportional limit 55 and 190 kg per cm^2, maximum stress in green condition 75 kg per cm^2, modulus of elasticity in green condition 32.4 x 10(3) kg per cm^2.

Specific compression (in green and dry condition, respectively): stress at proportional limit 7 and 22 kg per cm^2.

Janka hardness (in green and dry condition, respectively): tips 101 and 186 kg; lateral 74 and 108 kg.

Shear or cutting (green and dry, respectively): maximum stress 25 and 35 kg per cm^2.

Cleavage (in green condition): maximum stress 7.75 kg per cm^2 (Benitez and Montesinos 1988).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1 cm
1 cm

Coccoloba uvifera (L.) L.

ENRIQUE MAYO M.
Universidad de Panama

POLYGONACEAE (BUCKWHEAT FAMILY)

Polygonum uvifera L., *Guaiabara uvifera* House

Dreifi, dreifi di laman, druif, grape, papaturro, raisin bord-de-mer, raisin la mer, raisinier bord-de-mer seagrape, sea-side grape, una de playa, uva, uva caleta, uva de mar, uvero, zeedreifi, zeedruif (Little and Wadsworth 1964)

This species is common in the West Indies, the gulf of Mexico, Central America, and northern South America along beaches and strand locations; it is sometimes found on the Pacific coast planted as an ornamental.

Coccoloba uvifera is medium-growing and varies from being a prostrate shrub to being a small, somewhat tortuous tree 18 m in height and 30 to 60 cm d.b.h. in its best-growing sites. Sometimes the trunk is very short and branches near the soil with long, straight, and slender branches which support a wide but sparse crown.

This species naturally hybridizes with others in the genus (Liogier 1983). The results complicate the botany of the group.

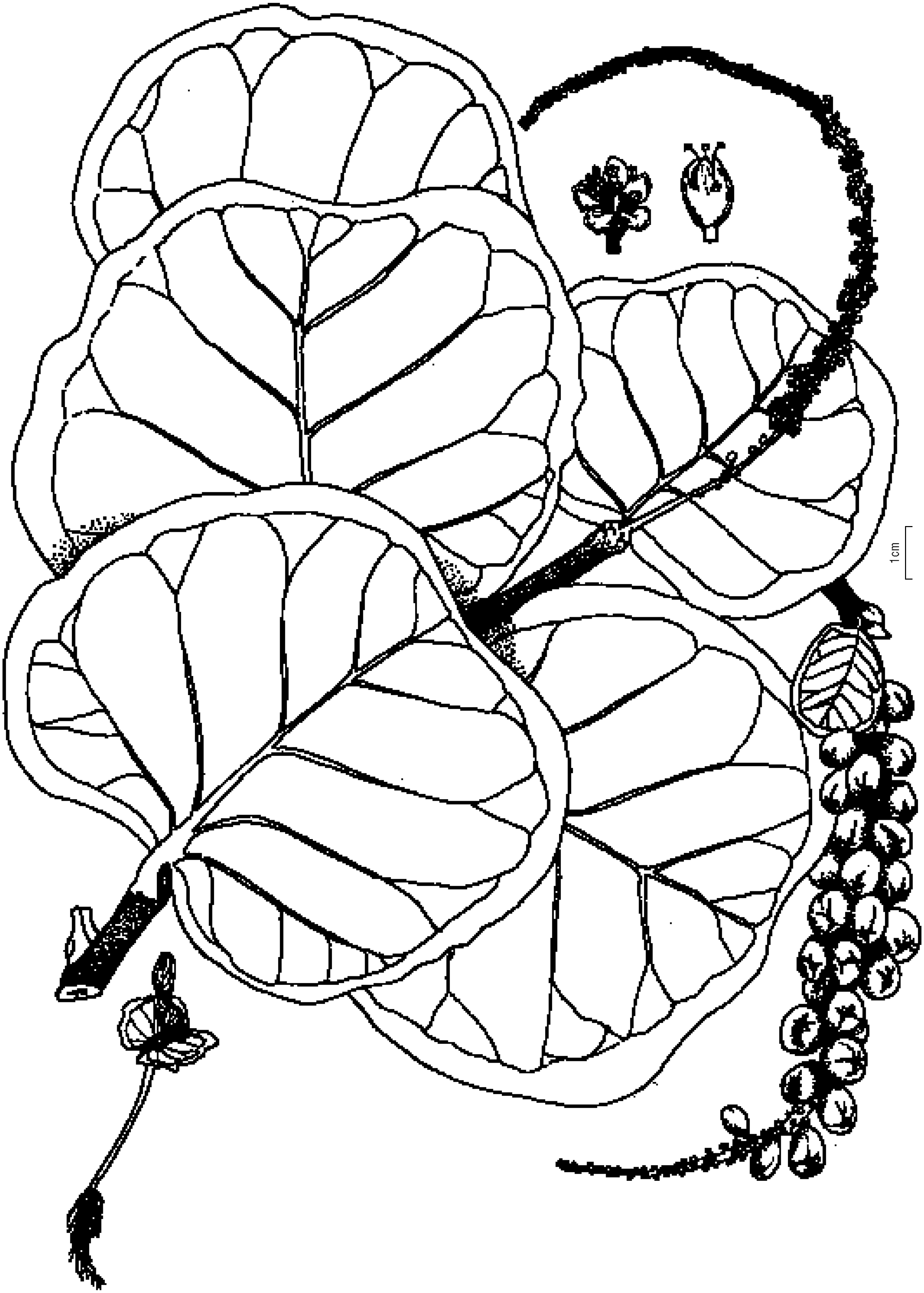
The sapwood of *C. uvifera* is light brown with heartwood somewhat darker and reddish. The wood can be worked and polished with ease, but the species' small size and susceptibility to dry wood termites limits its use to charcoal, posts, and poles. When properly preserved, the wood can be succesfully used for furniture and cabinet work. The astringent roots and bark have been used as medicines. Jamaican or West Indian Kino was once combined with the astringent red sap of *C. uvifera,* extracted from superficial cuts, to use for tanning and dyeing. The thin, fleshy covering of the small fruits has a sweet and sour taste and is eaten raw or used for the preparation of jellies and a wine-like beverage.

Flowering and fruiting occur throughout the year but the best production of fruit occurs in March and April at the end of the short dry season. The fruits hang in clusters 15 to 25 cm long. The edible hypanthium is consumed by small animals or rots in the soil, leaving one elliptic seed or achene that is dark brown with a conspicuous pointed apex. A very accurate botanical description of this species appears in the Flora of Panama (Woodson and Schery 1980), which is quoted below under Additional Information.

Dry seed of *C. uvifera* collected from under an ornamental at a Panamanian Pacific beach resort averaged about 3,500 per kg. The seed was sowed without pretreatment in regular tin pans at ambient temperature in 50 percent shade. Germination began in 25 days when 16 percent of the seeds showed a 5 to 10 mm radicle anchoring in the humid soil. The observation period was too brief to provide conclusive data.

ADDITIONAL INFORMATION

"Tree of strand areas, 2 to 15 m tall; branches stout, papillose to pilose; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3 to 8 mm long, papillose to pilose; leaves of normal shoots with stout petioles, 7 to 10 mm long, puberulent to pilose, the blades orbicular to reniform, 10x10, 11x14, 13x18, 20x27 cm long and broad, thick and minutely punctate on both surfaces, the apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe extending around the petiole, the primary veins 3 to 5 pairs usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; inflorescence stout, 15 to 30 cm long, racemose, occasionally branched at the base, the rachis puberulent, staminate flowers in clusters of one to seven, the pistillate flower solitary at each locus, the bracts ovate, 1 to 15 mm long, 2 mm broad, puberulent, the ocreolac membranaceous 1 mm long puberulent, the flowering pedicels 1 to 2 mm long. the hypanthium 2 to 3 mm long, the perianth lobes 4 mm long, 3 to 4 mm wide, the fertile stamens to 4 mm long; fruiting pedicels 3 to 4 mm long, fruit obpyriform, 1.2 to 2 cm long 8 to 10 mm in diameter, narrowed at the base, rounded truncate at the apex, the perianth rose-purple when mature; achene black."


1cm

Cocos nucifera L.

JAMES A. ALLEN
Paul Smiths College
Paul Smiths, NY

ARECACEAE (PALM FAMILY)

Palmas cocos Miller

Coco, coco de aqua, coco-palm, coconut, cocotero, niu, palma de coco (Little and Skolmen 1989)

The genus *Cocos* is monotypic. *Cocos nucifera* is believed to have originated in the Old World tropics, but the natural range is unknown and the origin of the species is the subject of considerable debate (Harries 1978, Parrotta 1993). Dispersal by humans has played a major role in the naturalization of the species on tropical and subtropical shores throughout the world.

Cocos nucifera is a medium-sized to large palm, typically ranging from 10 to 20 m tall, though sometimes reaching almost 30 m. Its trunk can reach 40 to 50 cm in diameter at the enlarged base and 20 to 30 cm d.b.h. The trunk may be straight but is often curved, probably due to the effects of storms or near constant exposure to coastal winds. The tree tolerates a wide range of site conditions, but develops best on deep, well-drained sandy loam soils with a pH between 5.5 and 8.0. Although it often grows on nutrient-poor sands and occasionally in wet, brackish sites, frequently waterlogged sites are unsuitable. Although it will grow at elevations of up to 1200 m near the equator and 900 m at higher latitudes, *C. nucifera* is primarily a coastal species and is most productive at elevations of 600 m or less (Parrotta 1993). The mean annual temperature in its native and introduced ranges is between 27 and 35 °C, with little diurnal variation (Opeke 1982, Parrotta 1993). *Cocos nucifera* grows well in areas receiving between 1000 and 5000 mm of rainfall, but excessive humidity may lead to decreased fruit production and increased incidence of disease (Parrotta 1993, Thampan 1981).

Many varieties of coconuts exist, including dwarf and tall forms and varieties with differing fruit characteristics (Thampan 1981, Woodroof 1979). Harries (1978) and Buckley and Harries (1984) describe two primary types of coconuts, a wild-type (niu kafa) with a long, angular fruit and thick husk, and a type derived by selection (niu vai) that is more spherical, with a thinner husk and a greater amount of endosperm. Both types are cultivated and intermediate types have arisen through introgressive hybridization (Buckley and Harries 1984).

Cocos nucifera ranks as one of the most useful trees in the world (Haas and Wilson 1985, Parrotta 1993, Woodroof 1979). Its large fruits are used in innumerable ways. The watery liquid of both green and mature fruits can be consumed and is nutritious and refreshing. The fleshy part of the seed (the endosperm) can be eaten raw, shredded and used for cooking, or dried. A liquid often referred to as coconut milk can be expressed from the grated endosperm (Falanruw 1997). In dried form (copra), the endosperm is processed for the manufacture of soaps, coconut oil, and other products. The endocarp of the fruit has been made into utensils, containers, small drums, handicrafts, and fuel. The trunks can be used for fenceposts and poles, although untreated wood is not very durable. It can also be processed into products such as small-dimensional lumber, flooring boards, plywood, pulp, or charcoal. Wood quality varies considerably along the length of the stem and from the interior to the exterior. Generally, only the outer part of the butt portion of the trunk is sufficiently strong to produce lumber. Specific gravity typically ranges from 0.30 to 0.90 in the outer third of the stem radius and from 0.10 to 0.35 for the inner third of the stem radius (Parrotta 1993). The wood is difficult to saw due to its high silica content but can be readily processed using saws with tungsten carbide teeth.

Flowering occurs throughout the year. New flower clusters (panicles) develop at the rate of about one per month. Clusters are approximately 90 to 120 cm long and contain both male and female flowers. The female flowers occur at the base of the inflorescence and, depending on variety, may open later or overlap with the opening of the male flowers. Cross-pollination may be predominant in tall varieties (Henderson 1988), but self-pollination is reportedly common in dwarf varieties (Thampan 1981). Flowering may begin in trees as young as 4 to 5 years in dwarf varieties and 7 to 8 years in tall varieties. The fruit is egg-shaped or elliptical, bluntly three-angled or nearly round, and about 20 to 30 cm long. It has a light brown, fibrous husk, an inner brown fruit containing a whitish layer of stored food, and a large central cavity containing watery or milky liquid (Little and Skolmen 1989). The inner fruit, or nut, has 3 round spots (eyes) on one end. About 30 to 90 nuts per tree are produced each year, depending on variety and growing conditions (Thampan 1981, Timyan 1996) and yields of up to 150 nuts are not uncommon (Parrotta 1993).

About 12 months after pollination, mature nuts can be picked by hand from the tree or collected from the ground. Harvesting can also be accomplished with harvesting hooks (Opeke 1982). Immature fruit drop is common and may reach levels of 65 to 70 percent (Opeke 1982). Solid, heavy, and almost round nuts with relatively thin husks should be selected from healthy, high-yielding trees. Fully mature nuts are usually dull brown in color. When mature nuts are shaken, it is possible to hear liquid sloshing around inside (Opeke 1982, Parrotta 1993). Freshly harvested nuts should be stored in the shade or indoors at room temperature for 3 to 4 weeks before sowing. Properly stored seeds remain viable for at least 8 months, although planting after 3 to 4 weeks is recommended.

Pretreatment of the nuts by soaking in water for 1 to 2 weeks is simple and highly effective (Thampan 1981), but the nuts can also be pretreated by other means, such as cutting the husk from the bottom end of the nut (Opeke 1982).

In sowing, the nuts are most often embedded, but not completely buried, horizontally in seedbeds of loose, friable soil. Some recommend that the eyes, which are on the side where the nut was attached to the pedicel, be raised to near the soil line (Timyan 1996, Woodroof 1979). Seedbeds should be kept moist and protected from rodents and termites. Germination typically takes about 8 to 10 weeks, and seedlings may be ready for outplanting in 6 to 8 months (Parrotta 1993, Timyan 1996). Seedlings should be outplanted in holes at least 45 cm deep and 45 cm wide, and even larger holes are recommended for hard soils or soils with deep water tables (Thampan 1981). Mixing compost or other organic matter into the planting holes is recommended. Spacing between seedlings on coconut plantations is typically about 9 m. Seedlings should receive considerable post-planting maintenance because they are vulnerable to rodents, drought, and competition from weeds during the first few years.

Cojoba arborea (L.) Britton & Rose

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FABACEAE (BEAN FAMILY)

Mimosa arborea L. (Species Plantarum 1: 519; 1753); *Mimosa filicifolia* Lam. (Encyclopédie Méthodique, Botanique 1 [1]: 13; 1783); *Mimosa divaricata* Jacq. (Plantarum Rariorum Horti Caesarei Schoenbrunnensis 3: 76; 1798); *Acacia arborea* (L.) Willd. (Species Plantarum. Editio quarta 4 [2]: 1064; 1806); *Pithecellobium filicifolium* (Lam.) Benth. (London Journal of Botany 3: 205; 1844); *Feuilleea filicifolia* (Lam.) Kuntze (Revisio Generum Plantarum 1: 187; 1891); *Pithecellobium arboreum* (L.) Urban (Symbolae Antillarum 2 [2]: 259; 1900); *Samanea arborea* (L.) Ricker (Stand. Cycl. Hort. 6: 3066; 1917); *Pithecellobium austrinum* Standl. and L.O. Williams (Ceiba 3 [2]: 114-115; 1952); *Cojoba austrina* (Standl. & L. O. Williams) L. Rico (Kew Bulletin 46 [3]: 507; 1991)

Aguijote, ardilla, ardillo, Bahama sabicú, barba de jolote, barba jolote, black tamarind, cañamazo, cojoba, cojobana, cola de marrano, cola de mico, collier, conchudo, coralillo, frijol de mico, frijolillo, iguano, John crow, John crow bead, lorito, moco de chompipe, moruro rojo, plumillo, poison lasinette, quebracho, quebracho blanco, red tamarind, sabicú, sabicú moruno, tamarindo, turkey gill, wild tamarind, zopilote (Record and Hess 1949)

The geographic range of *Cojoba arborea* extends from southern Mexico, along the East Coast of Central America, to all the West Indies except the Bahamas (Britton and Rose 1928, Record and Hess 1949, Rico-Arce 1991).

Cojoba arborea is a fast-growing tree that reaches more than 40 m in height and 50 to 80 cm in d.b.h. in the natural forest, although it is not a common constitutive element. It is an unarmed tree. The bole is usually short, thick, cylindrical, and straight (forest) or twisted (open places), with buttresses. The crown is spreading, and the foliage is shiny. In open places, the tree is usually less than 20 m tall, with a spreading top and a stout bole, sometimes more than 60 cm in diameter. The bark is brown or grayish brown and smooth or coarse and sometimes has small, longitudinal fissures; it exfoliates small, irregular scales. The inner bark is pinkish and has a bitter taste. When damaged, the bark exudes a watery, sticky, orange sap; it turns darker when exposed to air and light. The average thickness is 1.2 cm (range 1.0 to 1.8 cm). Phyllotaxy is spiral. The feathery leaves are compound, bipinnate, with 10 to 18 pairs of pinnae, opposite or semiopposite, each with 20 to 40 pairs of opposite, sessile pinnules, asymmetric, falcate-linear, acute apex, asymmetrical base, margin entire, shiny dark green adaxially and pale green abaxially. The tree is typical of the humid and very humid tropical forests of the coastal lowlands with clay or sandy alluvial soils, but it grows well at elevations up to 1200 m.

Sapwood is light orange or grayish orange in green condition, while heartwood is reddish brown with dark reddish-brown or grayish-orange stripes. The dry sapwood is light grayish brown and the heartwood is orange-gray or orange-reddish gray with conspicuous stripes. Growth rings are not well demarcated. The grain is straight or interlocked (roey), texture medium to coarse, luster medium, figure attractive radially and tangentially due to the stripes of deeper color in the heartwood (González and others 1973). The wood is odorless and tasteless. It is hard and heavy (green weight is 1100 to 1120 kg per m^3 with 86 to 90 percent moisture content; basic specific gravity is 0.58 to 0.62), similar to bur oak (*Quercus macrocarpa* Michx.) and pin oak (*Q. palustris* Münchh.), and heavier than *Samanea saman* (Jacq.) Merr. and *Balizia elegans*. The volumetric contraction is normal for its density; the radial and tangential contractions are low, and the radial-tangential shrinkage ratio is good. The mechanical properties are comparable to those of *Quercus* and superior to *S. saman* (González and others 1973, Record and Hess 1949). Working properties are good. Air-drying is moderately fast (24 weeks) and may produce undulations or small twistings. It saws and cuts well and takes a fine polish. Natural durability is high; resistance to termite and fungal attacks is moderate or high depending on the entry. Sapwood preservation is easy, complete, and uniform; heartwood impregnation is difficult, incomplete, and irregular (González and others 1973). It can be used for flooring, ceilings, ornamental work, furniture, wheel hubs, rollers, brush backs, mills, and railroad ties (Record and Hess 1949). The Runkel factor is 0.70 (group III: good for making paper), and the Peteri's coefficient of flexibility is 50. The species is also planted as an ornamental and shade tree.

Blooming occurs from October to June. Flowers are in pedunculate axillary heads in the upper leaf axils. They are uniform in size and actinomorphic. The calyx is greenish, tubular, triangular, and toothed distally; the corolla is whitish or creamy, and tubular. The stamens are numerous. Pollination is entomophilous. The floral calyx is apically expanded and has five lobules. The corolla lobes are triangular or ovate; valvate, and glabrous. The stamens are glabrous, basally fused forming a tube; the free filaments and anthers are white. The style is narrow, longer than the stamens; the stigma is small (Pennington and Sarukhán 1968). The ovary is monocarpellar, superior, and multiovular. Ovules are anatropous, bitegmic, and crasinucellate.

Fruit ripening occurs from April to October. Pods are moniliform without pulp, slightly curved, coriaceous, septate, margins constricted, round to short tapered to apex, short tapered to stipe, and terete; valves dehisce along the ventral margin and twist. The exocarp is dull, bright red outside, and glabrous; the endocarp is whitish or creamy in the inner surface. The mesocarp is missing (Gunn 1984, Nilsen 1981). The fruit contains 8 to 12 seeds in one series and is 1 to 2 cm long.

The seed is ovoid without aril; has a black, glossy thin testa; is without pleurogram; and has a long, whitish, thick funiculus. The seeds hang when the pod dehisces. Seed dispersal is ornithochorous. Parrots and parakeets are commensals and dispersers; however, gravity causes most seeds to fall. Rain helps seed removal from the pod. Seed behavior is absolutely recalcitrant. They do not resist desiccation and must be sown immediately.

Germination is 90 to 95 percent if seeds are soaked for 24 hours before sowing. Germination is hypogeal and seedlings are cryptocotylar (Flores and Mora 1984). Seed sowing must be superficial; buried seeds do not germinate well. Root protrusion starts 2 to 3 days after sowing.

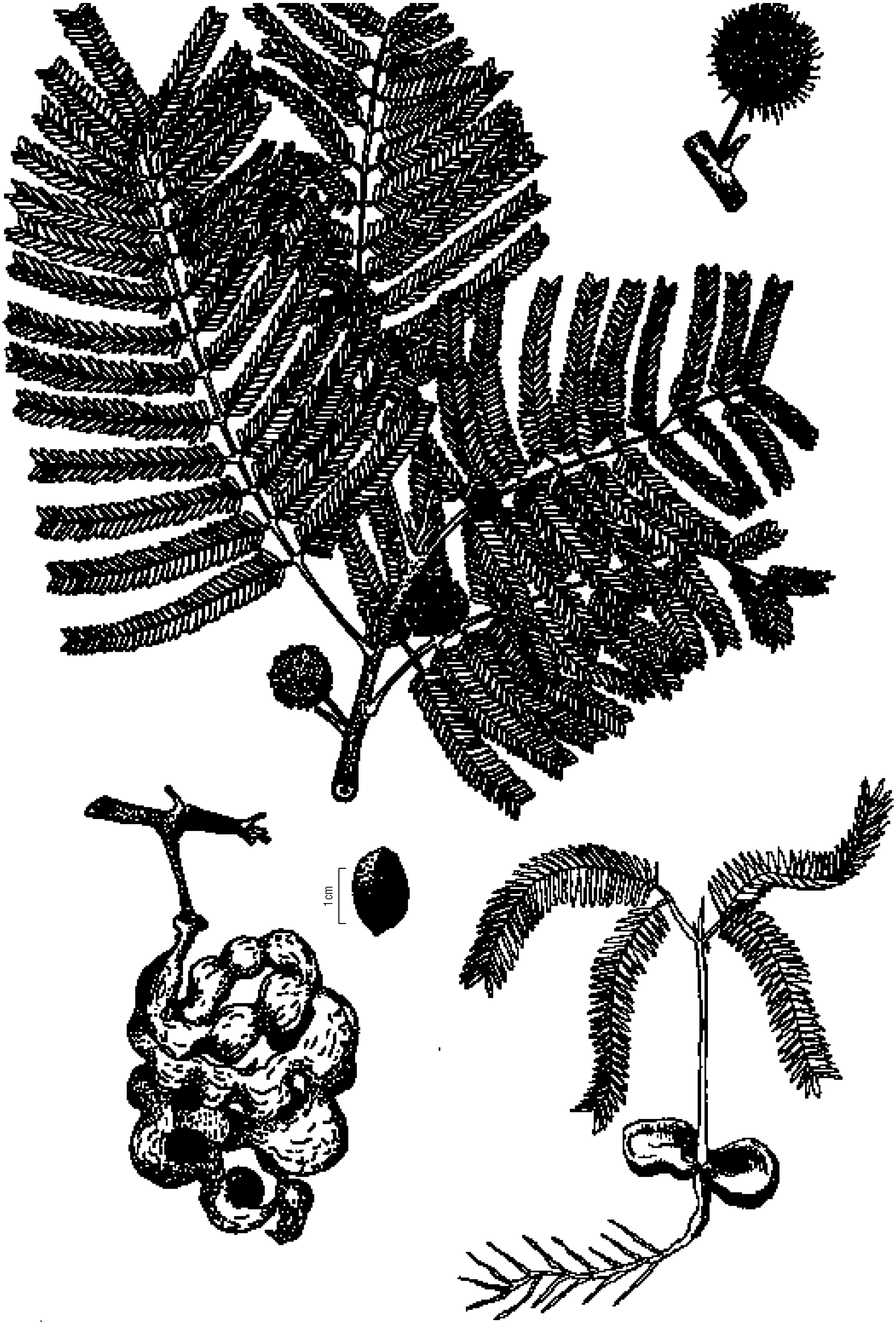
Small plantations have been established near rivers and creeks with some success. The species can be used in natural forest regeneration or planted in forest gaps and clearings. Competition with other trees intensifies longitudinal growth and produces a straight, taller bole.

ADDITIONAL INFORMATION

Leaf rachis is pubescent. A cupuliform gland is present between each pair of pinnae; a pair of glandular protuberances is in the base of each pinnule. Foliar buds are well developed.

The hilum is irregular, concealed by funicular tissues; endosperm and perisperm are lacking. Embryos are massive. The cotyledons are large, fleshy, convex outside, and slightly concave adaxially; a groined split over the radicle conceals it. Embryos are large, green, with axis straight, and have a well-developed plumule with several leaf primordia.

After root protrusion, the cotyledons open and move backward, splitting the testa along the cotyledon margins. The cotyledons grow after germination and develop small petioles, which help in cotyledon opening. The axillary buds of the cotyledons are well developed and may replace the plumule if it is damaged. The epicotyl is ferruginous.


1 cm

Copaifera aromatica Dwyer

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FABACEAE (BEAN FAMILY)

No synonyms

Camíbar, kamibar (Holdridge and Poveda 1975)

Copaifera aromatica is an endemic species in Panama, Costa Rica, and Nicaragua (Holdridge and Poveda 1975). The species grows in the canopy of pristine forests.

Copaifera aromatica is a fast-growing tree that reaches 35 m in height and 90 cm d.b.h. It has a straight and almost cylindrical bole that is covered with numerous and conspicuous lenticels. The bark is reddish brown and aromatic, and exfoliates in very thin, scaly layers (Holdridge and Poveda 1975, Jiménez, 1993, Quesada and others 1997). Leaves are alternate and paripinnate, with 8 to 12 leaflets and a thin, glabrous petiole. Leaflets are alternate, ovate-oblong, 2.5 to 9 cm long and 1.5 to 3.5 cm wide with translucid points, entire margin, small retuse apex, and obtuse base. The leaflets are usually glandular pellucid-punctate (at least when young) with a strong marginal vein. The margin often has glands or domatium-like swellings at the distal and proximal ends of the blade. Leaflets could be subsessile or petiolulate; petiolules are straight or slightly twisted (Cowan and Polhill 1981, Holdridge and Poveda 1975, Jiménez 1993, Quesada and others 1997, Van Roosmalen 1985). *Copaifera aromatica* grows in the humid and very humid evergreen forests typical of the neotropical lowlands. It grows at elevations ranging from sea level to 350 m where the temperature range is 28 to 35 °C and annual rianfall is more than 3000 mm. The species is found in fertile flat plains; however, it also has been observed in partially flooded areas.

The timber is moderately soft and heavy, and exhibits a sharp color difference between sapwood and heartwood. When fresh, the sapwood is light brown and the heartwood is dark brownish yellow. The heartwood darkens after exposure to light and air. The wood has medium texture, straight grain, low to medium luster, no distinctive odor, and a slightly bitter taste (Herrera and Morales 1993, Richter 1973). Fine, regular, light-colored bands demarcate growth rings. The figure shows silvery bands at the radial surface; these bands are inconspicuous at the tangential plane (Richter 1973). The basic specific gravity (oven-dry weight/green volume) for *Copaifera aromatica* is 0.62. The green weight is 970 kg per m^3 (56 percent moisture content). Wood drying is moderately slow, and the wood may have moderate defects such as twisting. Radial shrinkage (green to oven-dry) is 4.1 percent; tangential shrinkage, 7.4 percent; and volumetric shrinkage, 11.7 percent (Llach 1971). The wood is easy to work and its finished surface is smooth. The wood is used in general and interior construction, carpentry, and turnery and for flooring, furniture, fences, railroad ties, and tool handles (Llach 1971). The tree resin has commercial value.

The tree bark provides hard oleoresins used industrially in the manufacture of varnish and paint (Mabberley 1997). The medicinal copaiba balsam (an oily liquid obtained by tapping) has sesquiterpenes, diterpenes, and triterpenes along with phenols; presumably these compounds provide leaf resistance to fungi. Unusual condensed tannins have also been reported. The chemistry of *Copaifera* is quite similar to that of *Hymenaea*. The resins are used to relieve stomach and kidney pain (Cowan and Polhill 1981, Herrera and Morales 1993, Schultes and Raffauf 1990).

Flowering occurs August through November. The flowers are crowded in racemes or axilar panicles, with small bracts and bracteoles. Flowers are small, distichous and apetalous; they have a short hypanthium. The calyx has four imbricate sepals; the sepals are pale brown and pubescent abaxially. The androecium has numerous free stamens; anthers are introrse and anther dehiscence is longitudinal. Pollen grains are rugulose-punctate to reticulate. The ovary is stipitate, unilocular with one to two suspended ovules and surrounded at the base by a nectariferous disc. The stigma is usually capitate (Cowan and Polhill 1981).

The fruit is a pod, 1.5 to 4 cm long, 1.5 to 2.5 cm wide, and 0.8 to 2.5 cm thick. It is oblong-rounded to ovate-rounded, stipitate, laterally compressed and ligneous, with the apex bearing the stylar base. Dehiscing valves fall separately, but may remain attached to sutures in the proximal end. The nonexfoliating exocarp is dull, reddish brown to reddish, glabrous, and rugose with resin globules. The mesocarp is firm, fibrous, resinous, and ligneous; the endocarp is dull and whitish; the area around the seeds is smooth, not exfoliating, and nonseptate. If the fruit is damaged, the epicarp may exhibit resin globules (Gunn 1991). The fruits of *Copaifera aromatica* mature February to April and September to October (Quesada and others 1997).

Seeds (one to two) are parallel to fruit length and not overlapping. The funiculus is up to 5 mm long, thick to filiform, and straight. Seeds are covered by an incomplete red aril. They are 13 to 28 mm long, 9 to 17 mm wide, 3 to 12 mm thick, oblong, and laterally compressed. The testa (partially concealed by the thin aril) is brown, smooth, and hard. The embryo is large, and a basal groin, concealing the radicle, splits the cotyledons. The embryonic axis is straight and oblique to seed length. The plumule is rudimentary. The large, colorful aril surrounding the seed is edible and sugary. Seed dispersal is endozochorous; spider monkeys are the most significant dispersers (Van Roosmalen 1985). Seeds are collected from the ground from September to February.

The species is reproduced by seed. Eighty-five percent germination was obtained in tests performed with fresh seeds collected in the north zone of Costa Rica after soaking them for 24 hours in running water (Jiménez 1993). Seed behavior is orthodox, but no storage tests have been performed. Germination is epigeal, and the seedling is phanerocotylar. Cotyledons are fleshy; eophylls are opposite or alternate, often several-jugate; eophyll leaflets are generally punctate; and the marginal vein is typical in the metaphylls (Cowan and Polhill 1981).

Seeds are sown in greenhouse beds. Seeds are sown directly in the soil or in plastic bags filled with soil and sand. Natural regeneration of the species is very poor, as shown by the low number of individuals found at intermediate stages; seedlings and saplings seem to be shade tolerant (Jiménez 1993).


1cm
2cm

Copaifera camibar Poveda, Zamora & Sánchez

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FABACEAE (BEAN FAMILY)

No synonyms

Camibar (Poveda and others 1989)

Copaifera camibar was originally reported as an endemic species of Costa Rica (Poveda and others 1989); however, the species has recently been found in Venezuela (Berry and others 1997). *Copaifera camibar* grows on moderately flat plains associated with other tree species, among them *Peltogyne purpurea* Pittier, *Caryocar costarricense* Donn. Sm., *Parkia pendula* (Willd.) Benth. ex Walp., *Caryodaphnopsis burgeri* Zamora & Poveda, *Humiriastrum diguense* (Cuatrec.) Cuatrec., *Uribea tamarindoides* Dugand & Romero, and *Newtonia suaveolens* (Miq.) Brenan (Poveda and others 1989).

Copaifera camibar is a fast-growing tree that reaches 25 m in height and 75 cm d.b.h. It has a straight bole and a round crown. Young twigs are subcylindrical, with a dense ferruginous or gray-brownish pubescence. The old branches are smooth, glabrous, and gray to light brown. The outer bark is smooth, grayish, and aromatic. The sap is resinous and aromatic (Jiménez 1993, Poveda and others 1989). Leaves are alternate, paripinnate and 3.7 to 8 cm long, with 18 to 22 pairs of subsessile leaflets that turn brown when dried. The leaflet blade is glabrous, shiny olive green adaxially, and dull green abaxially; leaflets are coriaceous, alternate, sometimes opposite or subopposite, and oblong, with petiolules up to 1 mm long. Leaflets are variable in size: the basal leaflets are 4 to 9.5 mm long and 2.9 to 4 mm wide; the middle leaflets are 7.5 to 12.9 mm long and 2.8 to 4 mm wide; and the distal leaflets are 5 to 9.5 mm long and 1.5 to 3 mm wide. The leaflet has an entire margin, an asymmetrical base, and a rounded apex that is slightly emarginate with a brown gland and a prominent midvein that projects abaxially. The secondary and tertiary veins are hardly visible. Marginal veins are parallel to the margin. Stipules are green, foliaceous, and pinnate, sometimes having simple trichomes at the apex and apical gland. The stipular base is truncate; the apex is acuminate; and the stipules have translucid points (Poveda and others 1989). The tree grows in very humid, evergreen, primary forests with well-drained soils at elevations of 0 to 300 m; the temperature range is 28 to 35 °C and annual rainfall is above 4000 mm (Jiménez 1993).

The sapwood is pale brown and sharply demarcated from the dark brown or golden heartwood. The wood exhibits resinous spots in the tangential, radial, and cross sections. Wood texture is fine, with high luster and straight to slightly inclined grain. The wood is odorless and has a slightly sour and bitter taste. Growth rings are conspicuous and easily seen due to the alternating light and dark bands and annular (marginal) parenchyma. Numerous resin ducts appear as dark lines, particularly at the longitudinal planes (Canessa 1989). The timber is strong, hard, and heavy. The basic specific gravity of the wood (oven-dry weight/green volume) varies from 0.46 to 0.64. The green wood moisture content is 12 to 15 percent. The module of elasticity fluctuates from 2,270 to 2,650 at 70.3 kg per cm^2. The bending strength is 912.6 to 1490.5 kg per cm^2 and the maximum crushing strength is 426.8 to 752.3 kg per cm^2. Wood drying is slow to moderate; wood shrinkage (green to oven-dry) is normal (radial 4.4 percent; tangential 9.2 percent; volumetric 14.6 percent). The wood is easy to work and finishing is smooth. The wood is used for general construction, carpentry, turnery, furniture, and interior construction (Chudnoff 1984). The species has been exploited for many years, especially for extraction of the bark's aromatic resin. This resin is widely used in native and traditional medicines (Poveda and others 1989).

Copaifera camibar begins to flower after 5 years. It blooms in July and August and the fruits mature November to February. The flowers are grouped in axilar or terminal panicles with many branches, 1.2 to 2 cm long. The peduncle is ferruginous, 3 to 6 mm long, and up to 1 mm in diameter. The bracts are 1.9 to 3.7 mm long and 1.3 to 1.5 mm wide; they are imbricate, deltoid, concave, coriaceous, and glabrate at both surfaces. When present, the trichomes are minute and scarce at the apex, margin, and base. Floral peduncles are pilose-ferruginous and 0.3 mm long. The flower is apetalous. The calyx is pentamerous; sepals are valvate, slightly imbricate in the bud, ovate-deltoid, concave, 4.3 to 5.5 mm long, and 2 to 2.7 mm wide; the apex is acute, and the base is truncate.

The fruit is a brown-reddish legume that is monospermous, ovoid, and laterally compressed. It is slightly rugose, glabrous, coriaceous, 3 cm long, and 2.3 to 4 cm wide. The fruit is stipitate and has a rounded apex and base. The pedicel is glabrous up to 1.5 mm long. The fruit is dehiscent and opens from the apex toward the base. Fruits are collected directly from the tree before pods open. The fruit has one ovoid black seed, half covered by an orange or yellow aril; when dry, the aril turns dull red. The seeds are 1.4 to 1.5 cm long and 0.7 to 1 cm wide (Poveda and others 1989). The seeds that lie on the soil are damaged by *Rhinoceros* sp. (Curculionidae) (Jiménez 1993).

The species is reproduced through seeds. Seed behavior is orthodox; germination is epigeal; and the seedling is phanerocotylar. Seeds germinate in 20 to 34 days. Germination is approximately 50 to 65 percent after seeds have been soaked for 24 hours in running water. Seeds are sown in greenhouse beds—directly in the soil or in plastic bags filled with soil and sand.

ADDITIONAL INFORMATION

The name *Copaifera* comes from copai and the Latin verb fero (produce). The Tupi Indian tribes of the Amazon use the name copai to identify the resin of the copaiba tree (Allen and Allen 1981). In the past, *Copaifera camibar* was confused with *C. trapezifolia* Hayn; however, the collection and study of flowers and fruits led to its identification as a new species.

The sepals are glabrous abaxially and pubescent adaxially. The androecium has 10 stamens, which are free with glabrous filaments up to 1.1 cm long; anthers are oblong, glabrous, 1.6 to 2 mm long, 0.8 to 1.3 mm wide, and basifixed, with longitudinal dehiscence. The style is up to 3.2 mm long, slightly curved, and glabrous. The stigma is capitate. The ovary is unilocular, stipitate, and narrowly elliptic; with ferruginous pubescence at the margin, base, and apex; 2.4 to 3 mm long, and 1.5 to 2.3 mm wide. A glabrous, nectariferous disc basally surrounds it. Placentation is laminar. There are two ovules, which are suspended, overlapped, oblong, laterally compressed, 1 mm long, and 0.5 mm wide. The funiculus is up to 5 mm long.


2cm
2cm
2cm

Cordia alliodora (Ruiz & Pav.) Oken

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BORAGINACEAE (BORAGE FAMILY)

C. gerascanthus Jacq. (not *C. gerascanthus* L.), *C. gerascanthus* var. *domingensis* Cham., *C. velutina* Mart., *C. alliodora* var. *glabra* DC., *C. gerascanthus* var. *subcanescens* DC., *C. gerascanthus* sensu Griseb., *C. gerascanthus* forma *martinicensis* Chodat, *C. gerascanthus* forma *micrantha* Chodat, *C. alliodora* var. *boliviana* Chodat & Vischer., *C. andina* Chodat, *C. chamissoniana* var. *complicata* R. & P. ex Chodat., *C. goudoti* Chodat., *C. macrantha* Chodat., *C. cerdana* (R. & P.) R. & S., *Cerdana alliodora* R. & P., *Varronia tuberosa* S. & M., *Lithocardium gerascanthus* var. *alliodorum* Kuntze, *Lithocardium alliodorum* (R. & P.) Kuntze, and *Lithocardium gerascanthus* var. *domingense* (Cham.) Kuntze.

Aguardientillo, ajahatsa (ahahsatsa), amapa, amapa asta (amapa hasta), amapa blanca, amapa bola, anallo caspi, arbol del ajo, asca, auxemma blanca, bohunlanza, bois cypre, bois de Rhodes, bois de roge, bois de rose, bois soumis, bojón, bolaina, botoncillo, brown silver balli, canalete, canalete de humo, capá, capá de olor, capá de sabana, capá prieto, cayly, chaquine, chêne caparo, chevel, chullachaqui blanco, cinchado, claraiba parda, corallilo, cyp, cypre, cypress, d'ou lemon, dze-uí, freijo (frejoes, freijorge), guacimilla, guacimo nogal, hochi, hormiguero, lapochillo, laurel, laurel blanco, laurel de monte, laurel de puna, laurel macho, laurel negro, laurel prieto, louro, louro amarello, mataatiyo, moho, momiguilla, muñeco, nogal, nogal cafetero, pardillo, partago, picana, picana negra, sabanero, salaam, salmwood, smokewood, solera, soleria (solerillo), solerito, Spanish elm, spruce, suchil, tacuraí, tama palo santo, tambor hormiguero, uruazeiro (uraseiro), utaatigo, uurushi numi (murushinim), vara de humo, varía, varía amarilla, varía colorada, varía prieta (Little and Wadsworth 1964)

Cordia alliodora is the most widespread of the 300 species in the genus. It grows naturally from northern Mexico, through Central America and South America, to Paraguay, southern Brazil, and northern Argentina (Greaves and McCarter 1990). *Cordia alliodora* is also found on most of the Caribbean Islands from Cuba to Trinidad but is probably not native to Jamaica (Johnston 1950). The most frequently used name is probably laurel.

In lowland, humid tropical, regions, *C. alliodora* is generally a tall, thin tree with a narrow, open crown, and shows minimal forking forming a single stem to 15 to 20 m. Trees may reach over 40 m in height and over 1 m d.b.h. at overmaturity. However, 50 cm d.b.h. is more common in mature trees (Somarriba and Beer 1987). In seasonally dry, deciduous, and semideciduous forests, the species is smaller and more poorly formed, rarely reaching more than 20 m in height and 30 cm d.b.h. Its range extends from flat coastal lowlands, with deep infertile sands and little organic matter (Entisols or Oxisols), to very dissected, mountainous uplands with deep, fertile, volcanic soils high in organic matter (Andepts). *Cordia alliodora* grows under a wide variety of ecological conditions, varying from very wet (as much as 6000 mm annual precipitation) to seasonally dry (as low as 600 mm annual precipitation and a 7-month dry season). The tree grows from sea level to 1400 m in Central America and to 2000 m at lower latitudes in Colombia. It grows best on well-drained, medium-textured soils where mean annual rainfall exceeds 2,000 mm and the mean annual temperature is about 24 °C. The species does not tolerate poor internal drainage or waterlogging. Although *C. alliodora* will survive under light shade, full overhead light on fertile sites produces vigorous trees capable of rapid early growth. A strong tap root is produced at an early stage but a spreading root system also develops (Schlönvoight 1993). Some suggest this root system allows the tree to withstand exposed conditions (Marshall 1930).

The timber of *C. alliodora* is highly valued and used extensively throughout its natural range. Specific gravity varies from 0.38 to 0.73 (Greaves and McCarter 1990), with densities higher on seasonally dry sites and in provenances from seasonally dry zones (Boshier and Henson 1997). The wood is usually straight-grained and easily seasoned and worked. It is used widely for construction, furniture, flooring, veneer, turnery, and carving. Although it marks easily, the heartwood is moderately to highly resistant to termites and to both brown and white-rot fungi (Greaves and McCarter 1990). In Mexico a decoction of leaves was used as a tonic and stimulant in cases of catarrh and lung infections. In the West Indies pulverized seeds were used in treating cutaneous diseases (Standley 1924). The flowers are considered a major source of nectar by beekeepers in the Caribbean (Crane and others 1984).

The white flowers of *C. alliodora* are hermaphrodite, unspecialized, about 1 cm in length, and occur in large auxiliary or terminal inflorescences with 50 to 3,000 flowers. *Cordia alliodora* may begin flowering at 2 years (Greaves and McCarter 1990), but trees usually reach sexual maturity at approximately 4 to 5 years and do not produce large quantities of seeds until later. One tree produces many flowers daily for 8 to 9 weeks. A large canopy tree may produce as many as 10 million flowers and 1 million seeds in 1 year (Boshier and Lamb 1997). The ovary contains four ovules, but generally only one embryo develops per fruit (Miller 1985). The calyx does not continue to grow after pollination, and the mature fruit is shed complete with calyx and persistent corolla. The latter acts as a parachute aiding dispersal by wind. Several indicators of mature fruit (ripe seed) have been reported: at 2 to 3 weeks before natural seedfall; when flower inflorescences turn brown; when the swollen, protruding seed turns brown; and when the embryo is hard.

Seeds should be collected no less than 2 weeks after the last flowers have opened on a tree. Optimal seed collection time is approximately 7 weeks from the period when flowers have opened and the petals are white. In Costa Rica, seed collected at the beginning of March gave germination of less than 10 percent, rising to over 70 percent by the end of April (Boshier and Lamb 1997). Fallen seeds may be collected from the ground (Marshall 1939), mature seeds may be shaken from the branches onto sheets spread on the ground (Stead 1980), or inflorescences may be cut from trees (Boshier and Lamb 1997). Seeds collected from the ground have low viability. The presence of wind and the location of trees above coffee or cacao often render the shaking of seeds onto sheets impractical. Moreover, shaking branches is no more effective in collecting high-viability seeds than is cutting inflorescences.

Seed yields range from about 0.5 to 2 kg per tree (Jara and Valle 1997, Salazar and Boshier 1989), although in some large-crowned trees they may be as high as 5 kg. Better-formed trees usually have smaller crowns and consequently lower seed yields. Collection costs from well-formed trees in natural stands are high, with yields of 1 to 4 kg of seed per man-day (Cortéz 1990, Jara and Valle 1997).

The initial moisture content of mature *C. alliodora* seeds is around 40 percent (Trino Triviño and others 1990) and must be promptly reduced to below 10 percent. Moisture content can be reduced by drying in the shade or in a drying room. Seeds dried in the sun are cooked, which reduces initial germination rate (Boshier and Lamb 1997). Shade drying reduced the moisture content to 6 to 7 percent in 4 to 6 days, while artificial drying achieved the same reductions in 2.5 days (Samaniego and others 1997a, Trino Triviño and others 1990). During drying, the wings (persistent corolla) can be removed by rubbing seeds between the hands. After drying, seeds can be cleaned by winnowing using the hand or aspirator. The aspirator also removes some empty and immature seeds. *Cordia alliodora* seeds average 40,000 to 100,000 per kg, with high levels of purity (more than 95 percent) possible after processing (Greaves and McCarter 1990, Jara and Valle 1997, Samaniego and others 1997b, Trino Triviño and others 1990).

In Costa Rica, seed storage was the most effective at low temperatures (less than 5 ^{o}C) and in hermetically sealed containers that effectively maintained low moisture content (Boshier and Lamb 1997). In Colombia, hermetically sealed aluminium bags allowed only small fluctuations in the moisture content of stored seeds over 15 months. Polyethylene bags allowed the moisture content of seeds to rise from 7 to 13 percent over the same period; germination of these seeds was relatively poor (Trino Triviño and others 1990). Similarly, seed lots collected for provenance trials and stored for 7 to 8 years, with an initial moisture content below 10 percent, maintained their high initial germination rates (generally over 50 percent and some around 90 percent); one lot with a moisture content around 12 percent showed the initial germination rate (11 percent) declining to 1 percent after 8 years (McCarter 1986). In laboratory tests over a range of temperatures germination was found to be optimum at 28 to 30 ^{o}C, but all pregermination treatments tested resulted in germination inferior to the untreated control (Samaniego and others 1997b).

Seeds can be sowed (approximately 40 to 50 g per m^2; Carpanezzi and others 1982) in germination beds under shade and covered to a depth of about 0.5 cm. First germination occurs within 10 to 20 days, and seedlings are transplanted when the first true leaves appear (Boshier 1984). Planting stock is generally produced as stumps from plants raised in beds or as seedlings in bags. Stumped plants, which must remain in the nursery longer than bagged stock, are less sensitive to adverse conditions during transport and storage and to drought immediately after planting (Greaves and McCarter 1990).

ADDITIONAL INFORMATION

Cordia alliodora has often been cited as *C. alliodora* (R. & P.) Cham., a combination made by De Candolle in 1845. Oken, however, made the combination at an earlier date and should be cited as the authority (Johnston 1950).

Some confusion exists over two common names used in a number of countries: laurel negro and laurel blanco. The author feels the terms are used in two different circumstances. In some cases, they are used to distinguish two different species of standing trees because the heartwood color, the bark color, or both, differ. In other cases, the terms refer to a difference in the heartwood color of the sawn timber of *C. alliodora*. In some countries, such as Costa Rica, the terms are used both ways. This confusion has led some to oppose distinguishing the two types as standing trees (Greaves and McCarter 1990).

Although frequently described as a straight tree (e.g., Greaves and McCarter 1990, Stead 1980), this is rarely the case over most of *C. alliodora's* range, and natural regeneration shows great variation in form characteristics (Boshier and Mesén 1987). The bark is light grey/brown in color and smooth, although in drier regions it tends to be more fissured. Buttressing is generally limited to larger trees and is not pronounced, although it may extend 1 to 1.5 m up the bole on shallow soils. The tree is self-pruned even in open conditions, but the degree of pruning is variable. Some trees have pronounced nodal swellings where branches have been shed. Mature trees are deciduous, even in aseasonal climates, losing their leaves for 1 to 2 months following seed production.

Within the genus, *C. alliodora* is unique in having swollen domatia at the tips of shoot nodes (Miller 1985), which are usually occupied by ants.

Cordia alliodora is a prolific seeder and regenerates easily; it is often found in pure stands after forest clearance. Moderately fire resistant, it also competes in dry forests where crown competition and species diversity are more restricted.

Claims that the first seeds to fall have low viability (Marshall 1930) undoubtedly reflect the fact that initial falls consist mainly of unfertilized flowers. A number of indicators of seed ripeness have been reported. Tschinkel (1967) and Vega (1977) suggest that good seeds can be collected 2 to 3 weeks before natural seeds fall. However, they gave no indication of how to observe this period. Salas and Valencia (1979) describe the time to collect ripe and viable seeds as the period when flower inflorescences turn from white to brown without appearing burnt. Because the color change of the corolla to brown occurs approximately 3 days after pollination, part of an inflorescence may be brown while other flowers on the same inflorescence have not opened. Similarly, inflorescences on the same tree may be simultaneously at different developmental stages. Stead (1980) states that, in the latter stages of development, the seed swells and protrudes out of the enclosing calyx and, in drying, turns from green to brown. To examine the color, seeds must be collected. If seeds are collected, the best way to determine seed ripeness is to remove the embryo and squeeze: it is ripe if hard like a grain of rice, but immature if still soft and translucent.

A variety of seed abnormalities can be found at low frequencies. These include seeds with three cotyledons, fused cotyledons, no radicle, or two to three seeds per fruit when more than one ovule in the flower has been fertilized (Boshier 1992). Seeds are despoiled before dispersal by bruchid beetles (*Amblycerus* spp.), with up to 50 percent of the seeds killed (Opler and Janzen 1983). However, levels of attack vary among trees and years. The larva eats the developing seed embryo and the emerging adult beetle leaves a round hole in the calyx. Although adult beetles emerge during the drying process, a small proportion of live adults and larvae remain inside. Damaged seeds and beetles can be removed in the winnowing process. If the level of attack is high or seeds are for export, a persistent grain storage insecticide can be used to kill late-emerging beetles.

ACKNOWLEDGMENT

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Cordia dodecandra A. DC.

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BORAGINACEAE (BORAGE FAMILY)

No synonyms

Anacahuite, chak'opté, ciricote, cópite, cupape, k'an-k'opte, kopté, siricote, trompillo

Cordia dodecandra is native to America. It is distributed naturally in Mexico, Guatemala, Belize, Honduras, and Cuba. The plant is an important component of dry tropical forests and thickets. It has been introduced in other tropical regions.

Cordia dodecandra is a deciduous tree of up to 30 m in height and 70 cm d.b.h. The trunk is straight and short, with a large, rounded or pyramidal, very dense crown, made up of rising branches. The leaves are simple, alternate, ovate, oblong to fully elliptic or suborbicular, 5.5 to 15 cm long, and 4 to 9 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm. The tree grows wild from sea level up to 900 m.

The species has multiple uses. Its trunk is used as support beams and columns in rural houses. The bark and the wood have medicinal properties; the tea obtained from their infusion is used in traditional medicine to treat coughs, diarrhea, and dysentery. The hard and resistant wood is used for firewood. Due to its yellow color with dark red streaks, the wood is valued in the manufacture of furniture, handicrafts, veneer for plywood, and turned articles. The leaves are used as sandpaper and as soap to clean household utensils. The flowers are honey-bearing, and the fruits are edible; the latter are used to make preserves and jams. They are also used as food for pigs. The tree is frequently used in backyards and is valued as a shade and ornamental tree in streets, parks, and gardens (Aguilar 1966, Barrera 1981, Cabrera and others 1982, Chavelas and González 1985, Escalante 1986, Flores 1983, Rico-Gray and others 1991, Ucán 1983).

The tree begins to yield flowers and fruits between 4 and 5 years of age. Because its geographic distribution is extensive, *C. dodecandra* blooms at different times. In southeastern Mexico, it blooms March through May and fruits May through July or August (Juárez and others 1989). The deep orange flowers are infundibuliform and arranged in panicles. The fruits are drupaceous, conical, 3 to 4 cm long, and orange-yellow in color when ripe and have a fleshy, bittersweet, and fragrant pulp. Inside the hardened pyrene of each fruit are one or two seeds (Cabrera and others 1982, Nash and Moreno 1981, Pennington and Sarukhan 1968). *Cordia dodecandra* pyrenes are conical, lignified, indehiscent, rugose, light brown in color, elliptic or terete in cross section, 2.3 to 2.5 cm long, and 1.5 cm wide. The seeds range from obovoid to lanceolate and are laterally flattened, 1 to 1.5 cm long, 5 to 8 mm wide, and 3 to 4 mm thick.

The fruits are ripe in the month of May, and they remain on the tree until the month of July. The fruits are collected both from the ground or by climbing the tree and using poles with metal hooks to remove them. The pulp is removed from the ripe fruits by hand or with a knife inside a bucket of water. Impurities are removed by flotation and the good pyrenes sink. The pyrenes, free from pulp, are washed in cool water and dried where it is well ventilated. Pyrenes average 410 per kg (Patiño and Villagómez 1976). The seeds remain viable within the pyrene for approximately 13 months when stored under ambient conditions (24 to 30 °C). With longer storage, their viability diminishes quickly (Vega and others 1981).

The germination of the seeds is phanerocotylar. Under humid conditions, the fresh seeds germinate at 90 percent without pretreatment. A heterogeneous sample of seeds germinated approximately 15 days after sowing (Vega and others 1981). In a natural setting, the species propagates by the seeds it produces.

ADDITIONAL INFORMATION

The seed hilum and micropyle are indiscernible. The seedcoat is white, opaque, delicate, crustaceous, and firmly attached to the embryo. The embryo has a straight axis and is symmetrical and white. The two longitudinally pleated or corrugated cotyledons are much shorter than the radicle. The plumule is undifferentiated. The radicle is superior and directed toward the hilum (Johnston 1966, Nowicke 1969, Pennington and Sarukhan 1968, Sprague 1965).

Cordia subcordata Lam.

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BORAGINACEAE (BORAGE FAMILY)

No synonyms

Kou, sea trumpet (Corner 1988, Little and Skolmen 1989)

The genus *Cordia* contains about 250 species. They occur in tropical to warm temperate regions throughout the world, with the greatest diversity of species in the Neotropics (Wagner and others 1990). *Cordia subcordata* is apparently native to Malesia but has been spread throughout the Pacific and along Indian Ocean shores. The species can be found on seashores and adjacent lowlands from east Africa to Polynesia. *Cordia subcordata* closely resembles *C. sebestena* L., a better-known species frequently planted as an ornamental along tropical and subtropical coasts (Little and Skolmen 1989, Wagner and others 1990).

Cordia subcordata is a moderately fast-growing, small evergreen tree with a broad, dense crown. It grows to about 8 to 10 m in height and may attain 60 cm d.b.h. The species grows on soils ranging from coastal sands to clays, tolerates brackish water, and is drought tolerant. It generally occurs near sea level on dry to moderately wet (less than 2000 mm annual rainfall) sites. The tree readily produces shoots from its extensive, shallow root system and may form thickets (Wagner and others 1990).

The wood has a specific gravity of about 0.45 and often has a beautiful grain with wavy dark and light lines and bands (Little and Skolmen 1989, Neal 1965). It is soft, easily worked, and durable. Because the wood does not impart a flavor to foods, it is well-suited for cups, dishes, calabashes, and utensils. It is also used in handicrafts and small items of furniture. *Cordia subcordata* is often planted as an ornamental and shade tree. In Hawaii, where the tree was once more widespread, the flowers were commonly used for leis.

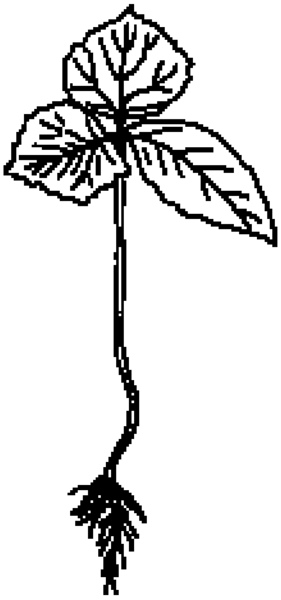
The showy flowers are in open cymes or panicles, with a pale green calyx and orange corolla. *Cordia subcordata* blooms throughout the year, but most heavily in the spring. Flowering may begin within 3 to 5 years of age. The fruit is drupaceous, almost round, green when young, and brown and hard at maturity. The fruits (capsules) are approximately 2.5 cm long, and contain up to four white seeds, each about 10 to 13 mm long.

The fruits can be collected from the ground or picked directly from the trees by hand or with a pruning pole. Specific recommendations for storing *C. subcordata* seed are unavailable. Seeds of other *Cordia* species can retain some viability for up to 1 year when stored in airtight containers (Mandal and others 1985), but sowing fresh seed is recommended. Because the seeds are very difficult to extract without damage, whole capsules are generally sowed.

No pretreatment is required, but germination may be accelerated by clipping off a portion of the hard, dry capsule.

Capsules are sowed at a depth of approximately 1.5 to 2 cm. Germination begins in about 3 to 4 weeks; most seeds will germinate within 6 weeks, but some may take as long as 3 to 4 months (Mandal and others 1985). If more than one seedling germinates from a capsule, thinning may be necessary. When the capsule sufficiently decays, the seedlings should be carefully separated and potted individually.

Seedling growth during the first season is slow, with seedlings typically obtaining a height of about 10 to 15 cm. Seedlings can be outplanted at this height, or retained in the nursery for a second season after which they may reach 1.5 m in height (Hocking 1993, Mandal and others 1985, Singh 1982). Larger seedlings can be top-pruned or trimmed of lower branches before outplanting. Outplanted seedlings perform well in moderate shade. Seedlings may require supplemental watering on drought-prone sites, especially when planted in full sunlight (Mandal and others 1985).



Cornus disciflora DC.

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CORNACEAE (DOGWOOD FAMILY)

Benthamia disciflora (Moc. & Sessé) Nak., *Cornus capitata* Sessé & Moc., *Cornus floccosa* Wanger, *C. disciflora* var., *floccosa* (Wanger Standl.), *Cornus disciflora* f. *floccosa* (Wanger) Rickett

Lloro, llorón

About 40 species of the genus grow in North America, Europe, Asia, and tropical Africa, but only a single species, *Cornus disciflora*, grows in the mountains of tropical America, from Mexico to Panama. Recently, *C. peruvianus* has been reported in Costa Rica (Jiménez and others 1996), and two other species reported in Costa Rica—*C. peruviana* J.F. Macbr. and *Nyssa talamancana* Hammel & N. Zamora—grow in the Talamanca Mountains (Kapelle 1996).

Cornus disciflora is a slow-growing, medium-size tree that reaches 25 m in height and 50 to 60 cm d.b.h. It has a conical trunk; rounded crown; smooth, yellow-gray bark; and foliage of a very peculiar light green color. The small branchlets are conspicuously nodose and very finely appressed-sericeous when young. Leaves are opposite, without stipules, and petiolate; the blade is oblong or ovate-elliptic, acuminate, cuneate, about 7 to 14 cm long and 2 to 6 cm wide, with three to five ascending veins, above opaque and essentially glabrous, and beneath paler and minutely sericeous or tomentose. The species grows in late stages of secondary forest succession, at elevations from 1500 to 2800 m, primarily in moist and wet climates. It grows well in volcanic or alluvial soils, and on slopes of 15 to 40 percent, where the average annual rainfall ranges from 2000 to 2700 mm and the annual temperature average is 14 to 16 °C. It can adapt to a wide range of light conditions, growing in open areas or under more closed canopies.

With a specific gravity of 0.53, the wood of this species is considered heavy. The difference in the colors of *C. disciflora* sapwood and heartwood in dry conditions is striking: sapwood is light pink and heartwood is light brown with black lines. It dries at a moderate rate without defects, is easy to work, and has a smooth surface with a good finish. Though easy to preserve, the wood has very little natural resistance to insects and fungi. The wood is not considered high quality and has been used for low-priced furniture boxes, inside construction, and cement forms (Carpio 1992). It could also be used for railway foundations, firewood, and airplane propellers, and in agroforestry. The bark has been used in home medicine as a tonic and astringent.

Cornus disciflora blooms and produces fruit most of the year (Jiménez and others 1996). However, the highest period of flowering occurs from November through January and fruits mature from September through February, peaking in December (Torres and others 1992). Inflorescences are terminal or subterminal, pedunculate, capituliform, involucrate; flowering heads are about 1 cm in diameter, many-flowered, subtended by two pairs of deciduous, broadly ovate, sericeous bracts about 5 mm long. Flowers are minute, the petals white, the stamens somewhat shorter than the petals and widely exerted. The fruit is a drupe, red to purplish black, broadly oblong-ellipsoid, sparsely sericeous to glabrate, and up to about 10 mm long and 7 mm wide. When the fruits are mature the pericarp becomes purplish black.

The mature fruits are collected from the tree or gathered from the ground and stored on wood tables in the shade. Once they are dry, the seeds are ready for germination (personal observations). Seeds average 2,128 per kg. Germination percentages rarely surpass 40 percent. When seeds are pretreated by wrapping in moss and soaking in cool water for 24 hours or in warm water (70 to 80 °C) for 1 minute, germination occurs sooner, but the germination percentage remains unchanged. However, when seeds are dried for 2 days, soaked in water for 5 days, dried in full sunlight for 2 days, sanded to thin the endocarp, and washed with a chloride solution, germination increased to 80 percent (Torres and others 1992).

The species germinates in the ground in 40 to 45 days. The seedlings are fully developed and ready for transplanting in 85 days. *Cornus* seeds germinate well in beds of pure soil furrows 3 cm apart leaving 1 cm between seeds. The planted furrows should be covered with a 5 mm layer of silty soil. After 85 days the seedlings can be transferred to plastic bags in the shade. The seedlings should be watered frequently, weeded, and protected against insects, such as leafcutter ants, known to be attracted to this species. After a nursery period of at least 5 months and at an approximate height of 20 cm, the seedlings can be outplanted (Torres and others 1992). Some plantations have succeeded well by planting seedlings naturally regenerated. Future planting techniques could include planting bareroot, seedlings, pseudocuttings, or cuttings.

ADDITIONAL INFORMATION

North Americans are shocked when they recognize this southern relative of the northern flowering dogwood, *C. florida* L. (Torres and others 1992, Woodson and Schery 1959). The flowering scales of *C. disciflora*, however, are smaller and are seldom seen because they drop off before they fully open. In Spanish the vernacular name, llorón, means the crying one because local people say that when you put your ear close to the trunk you hear crying.


1cm
1cm

Couratari guianensis Aubl.

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LECYTHIDACEAE (BRAZIL-NUT FAMILY)

Lecythis couratari Spreng. (Systema Vegetabilium 16.4, Cur. Post. 208; 1827); *Couratari panamensis* Standl. (Publications of the Field Columbian Museum, Botanical Series 4(8): 239; 1929); *Couratari pulchra* Sandw. (Bulletin of Miscellaneous Information Kew 1932: 217 1932); *Couratari bragancae* R. Kunth (Das Pflanzenreich IV. 219a (Heft 105): 129; 1939)

Balalabouá, balata blanc, bourrac, braka ingie pipa, cachimbo, coco-cabuyo, congolo-garapelo, copo hediondo, couratari, couroubara, djoemoe, fine-leaf wadara, ingie pipa, ipipjo, irimariye, irimiyar, kabba matjauw djoemoe, kalienja tamere, kariodan, kiesiepolloe joelle malledie, maho cigarre, maho couratari, maho fer, maou, marimari, mori-mori, oelemali, oelemallie, oelemarie, ollemellie, oremerie, oremerivadili, powasa djoemoe, sipoeloejoeroe maladi, tabarí, tauarí, tawary, tawekin oromariri, urimari, wadala, wadara, wadara-kakawalli, waranaka, wataala, watala, wata dje, zwarte ingie pipa (Aublet 1775, Chudnoff 1984, Jiménez 1993, Polak 1992, Record and Hess 1949)

Couratari guianensis is a widespread species; its range of distribution extends from Costa Rica to the coastal forests of eastern Brazil (Mori and others 1990a).

Couratari guianensis is a medium to very large tree that may reach 50 m in height and up to 1 m d.b.h. The bole is straight, cylindrical, and buttressed up to 7 m; it lacks branches in the basal two-thirds. Young branches are short tomentollous, becoming glabrous with age (Mori and others 1990a). The crown is branched and spherical. The bark is light brown, dark brown, or red brown (grayish brown in shade) and lenticellate (lenticels round to elongate), with vertical cracks and slight longitudinal fissures (Polak 1992). The inner bark is 13 to 15 mm thick, brown, laminated, and fibrous due to the high number of phloem fibers. Phyllotaxy is spiral. The tree is deciduous and most leaves abscise before the flowering period. New leaves appear in fluxes and their production is synchronized with the beginning of bloom. Leaves are simple, alternate, petiolate, oblong, obovate-oblong elliptic, entire margin, glabrous adaxially, pubescent abaxially, coriaceous, shiny, and hypostomatic (stomata anisocytic). The leaf apex is round or retuse; the leaf base is round. The species grows well in alluvial and sandy soils and is frequently found in clayey soils and on small, well-drained slopes. The elevation range of the species is 0 to 700 m. It is emergent in the canopy of very humid, nonflooded tropical forests, where temperature range is 24 to 35 °C and annual rainfall is more than 3500 mm.

Fresh sapwood is light brown; heartwood is creamy or light brown, with a pinkish tinge (Chudnoff 1984). The wood is very fibrous with a scent of linseed oil (Polak 1992). Growth rings are conspicuous. The grain is straight or uniformly interlocked; texture is medium to coarse; and luster is high. Silica content is 0.8 percent (Chudnoff 1984). Wood taste is not distinctive. The wood is heavy (green weight 840 to 900 kg per m^3, with 90 to 95 percent of moisture content; specific gravity is 0.49 to 0.57) and strong. Volumetric contraction is normal for its density, and mechanical properties are high. The air-dried wood shows small surface checking and warp. It is easy to work and saw, and it finishes smoothly. Its natural durability is in the medium range and it is easily preserved by either pressure or open tank systems. The wood is excellent for general and heavy construction, carpentry, furniture, veneer and plywood, agricultural tool handles, framing, railroad ties (treated), furniture, and turnery (Chudnoff 1984, Record and Hess 1949). The bark can be used as calking, rolling paper for cigars, boat caulking, native clothing, tinder, and cordage; it is also used in tanning because of its high tannin content (Simpson and Sagoe 1991).

Annual flowering occurs during the rainy season, July through September, when the tree is leafless. Inflorescences are terminal or axillary panicles or racemes, solitary or grouped. The peduncle and the rachis are thick and tomentollous; bracts are lanceolate and deciduous. The flowers are semisessile; pedicels are puberulent and leave a knob (subarticular region) 1 mm long after disarticulating (pedicels split during flower abscission; the abscission zone constitutes the articulation). The flower is hermaphrodite and zygomorphic. The calyx has six sepals; the corolla has six petals alternating with the sepals. The hood is curved inward and outward assuming an S shape (Tsou 1994). The staminal ring consists of 10 to 75 fertile stamens arranged in several whorls surrounding the style (Tsou 1994). The stye is short and straight. The ovary is inferior with three locules. Pollination is carried out by medium-to-large bees. They collect pollen from the hood and the staminal disc (Tsou 1994).

Fruits ripen January to May. Usually, the tree produces one or two fruits per inflorescence. Fruit ripening is quite uniform and crops are annual. The fruit is large and shows strong variation in size and form (20 to 30 cm long by 15 to 20 cm wide). It is a cup-shaped, dry pyxidium, cylindrical and rather triangular in cross section, hard, woody, brown or black, lenticellate; the columella is triangular (Prance and Mori 1978, 1979). There are many seeds in every fruit. Seeds are winged, oblong-elliptic, papery, brown, surrounded by a symmetrical wing, and wind-dispersed. The embryo has two foliaceous cotyledons; the radicle is large.

Fruits are collected from the tree before pyxidium opening. Seeds extracted from the pyxidium should be submerged in running water for 24 hours before sowing. Seed behavior is orthodox. Viability diminishes with increasing dehydration. Seeds do not require special treatment. Germination is 85 to 90 percent for soaked seeds. Germination is epigeal and seedlings are phanerocotylar (if the pair of minute squamiform structures emerging with the plumule are morphologically the cotyledons). The root develops at 30 to 40 days; the seedling taproot is small.

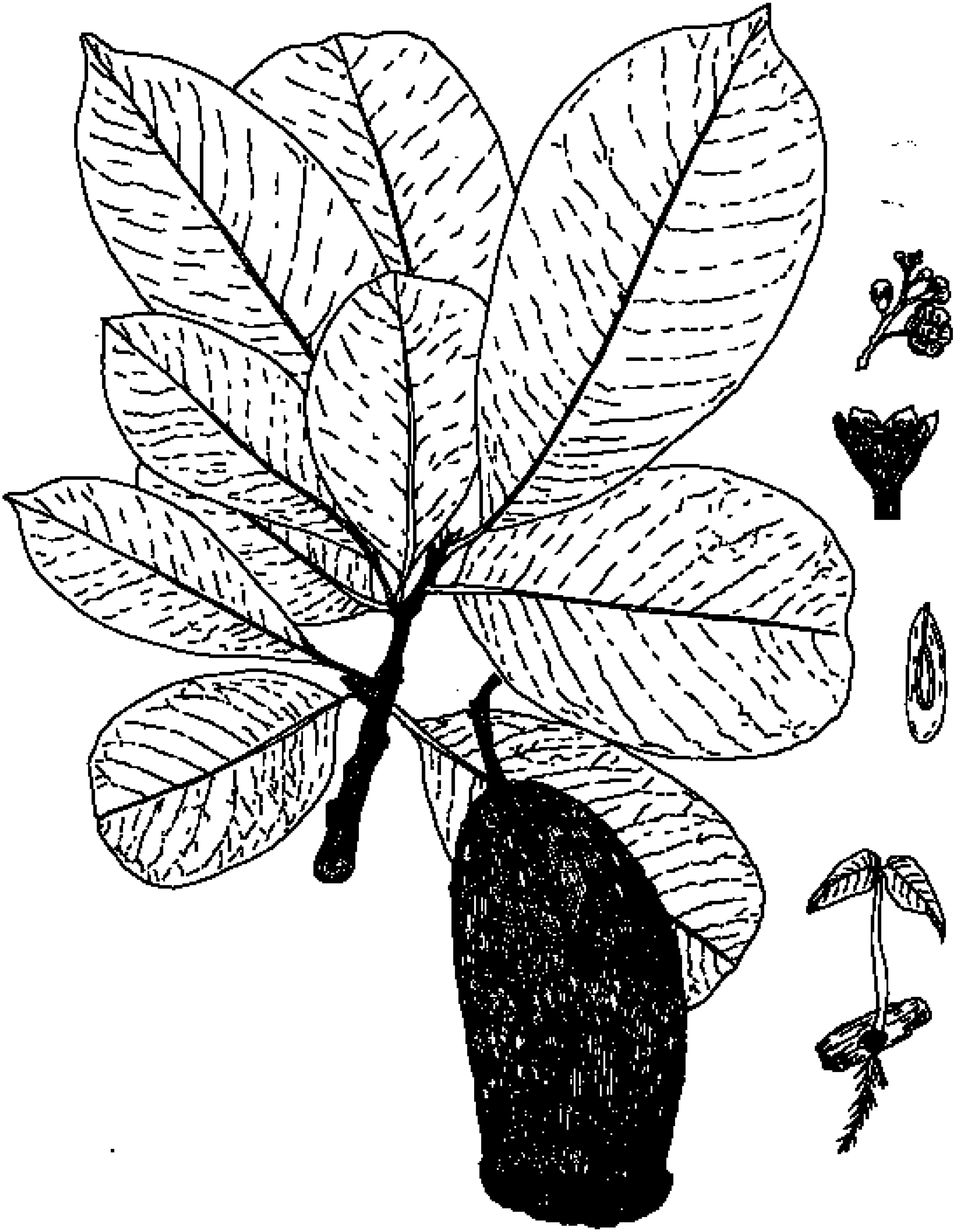
Seeds are sown in beds or plastic bags filled with humid sand or a mixture of soil and sand. Seedlings do well in greenhouses and nurseries, although development is very slow. Seedlings are shade tolerant. The species has not been introduced in reforestation programs, and information on plantation behavior is lacking. The species seems suitable for natural forest management.

ADDITIONAL INFORMATION

The genus name derives from the Caribe term *couratari* (Aublet 1775).

The flower's calyx has six wide ovate lobules; the corolla has six wide elliptic petals, pink or pale purple, fading to white after the anthesis. The androecium has numerous stamens. It is zygomorphic and highly specialized. Filament fusion and degree of specialization produce a complex organ formed by a staminal ring, a ligule (area lacking stamens placed between the staminal ring and the hood) and a hood; this organ is not morphologically equivalent to an androphore or androgynophore. The hood is flat, the proximal being antheriferous. The hood is strongly compressed against the staminal disc, and the flower androecium is considered closed (Mori and others 1990a, Prance and Mori 1979, Tsou 1994). Ovules are anatropous, bitegmic, tenuinucellate, and have a conspicuous funiculus. The embryo sac is of the Polygonum type. Placentation is axilar and ovules develop at the ovary septum base (proximal end). The style is slender and short, with annular expansion toward the distal end. The androecium is closed.

The fruit's pericarp is thick, fibrous, dull, and rough; it is built from ovary, androecium, and perianth tissues. Externally (exocarp), three zones are defined by two rings of scars. The proximal ring, which indicates the calyx position (sepal position) is named calycine ring (calycary, calycinal, or calycine zone). The distal ring is the line of opercular abscission. The zones delineated by the rings are the infracalycine (basal band), the supracalycine (interzonal band), and the deciduous operculum. The infracalycine zone extends from the fruit base to the calycine ring and includes the pedicel scar; the supracalycine zone extends from the calycine ring to the ring of opercular dehiscence. The operculum has a four-ridged inner columella. The ridges are remnants of the ovary septa.



Crescentia cujete L.

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BIGNONIACEAE (BIGONIA FAMILY)

No synonyms

Arbol de las calabazas, ayale, cirián, cuautecomate, güiro, jícara, jícaro, luch, morro, taparo, tecomate, totumo

Native to the tropical and subtropical regions of America, the place of origin of *Crescentia cujete* is unknown because the species has been cultivated in the Yucatan Peninsula since pre-Hispanic times. It may have been cultivated for more than 600 years. Currently, it is observed as a backyard tree in several countries. The species grows on the Caribbean islands and from Mexico through Central America to northern South America. Recently, the tree has been cultivated in the tropical regions of the Old World.

Crescentia cujete is a fast-growing evergreen tree that can reach 10 m in height and 25 cm d.b.h. The short trunk is straight and the open crown consists of twisted, horizontal, or rising branches. The leaves are simple, grouped in bundles, obovate, or spatulate; they have an obtuse apex and an attenuate base. The tree grows in clayey soils with deficient drainage subject to frequent floods. It grows at elevations from sea level to 800 m, in areas with an average annual precipitation between 1500 to 1300 mm and an average annual temperature of 26 °C.

Crescentia cujete is frequently cultivated as an ornamental. The ripe fruits, once dry and clean inside, are used as containers to hold water. When the dry, clean fruits are cut in half, they have a variety of domestic uses, especially as containers to store salt and tortillas. They are valued in the manufacture of handicrafts and musical instruments. The fruit pulp is used as a laxative, emollient, expectorant, and fever reducer. Fresh seeds are ground and mixed with water to make a refreshing drink. The drink has a sweet and pleasant taste. The wood has a specific gravity of 0.6 to 0.8. It is strong, flexible, moderately hard, and heavy. It is used for firewood and construction in rural areas and in the manufacture of handles for agricultural implements (Jarquin and Cervantes 1980, Little and others 1967, Martinez 1959, Niembro 1986, Rico-Gray and others 1991).

Crescentia cujete blooms during the month of June. The flowers are isolated, white or cream colored, and sometimes purple with burdock nervation and a fetid scent. The fruit is a globose, spherical, or ovoid-elliptic capsule; 8 to 20 cm in diameter; and indehiscent; with a hard, and smooth cover and abundant carnose pulp. The fruits grow and ripen slowly, remaining on the tree for 6 or 7 months. Afterwards, they fall to the ground and degrade with time. As fruits ripen, the color changes from green to yellow. When they are over-ripe, their pericarp becomes reddish yellow and their pulp loses moisture. Each fruit contains numerous seeds (Gentry 1982, Little and others 1967, Pennington and Sarukhan 1968). The seeds are obovate, with an emarginate apex, laterally flattened, 7.0 to 7.5 mm long, 5.4 to 7.0 mm wide, and 1.0 to 2.0 mm thick. The seedcoat is dark brown, furrowed with dots, opaque, and coriaceous.

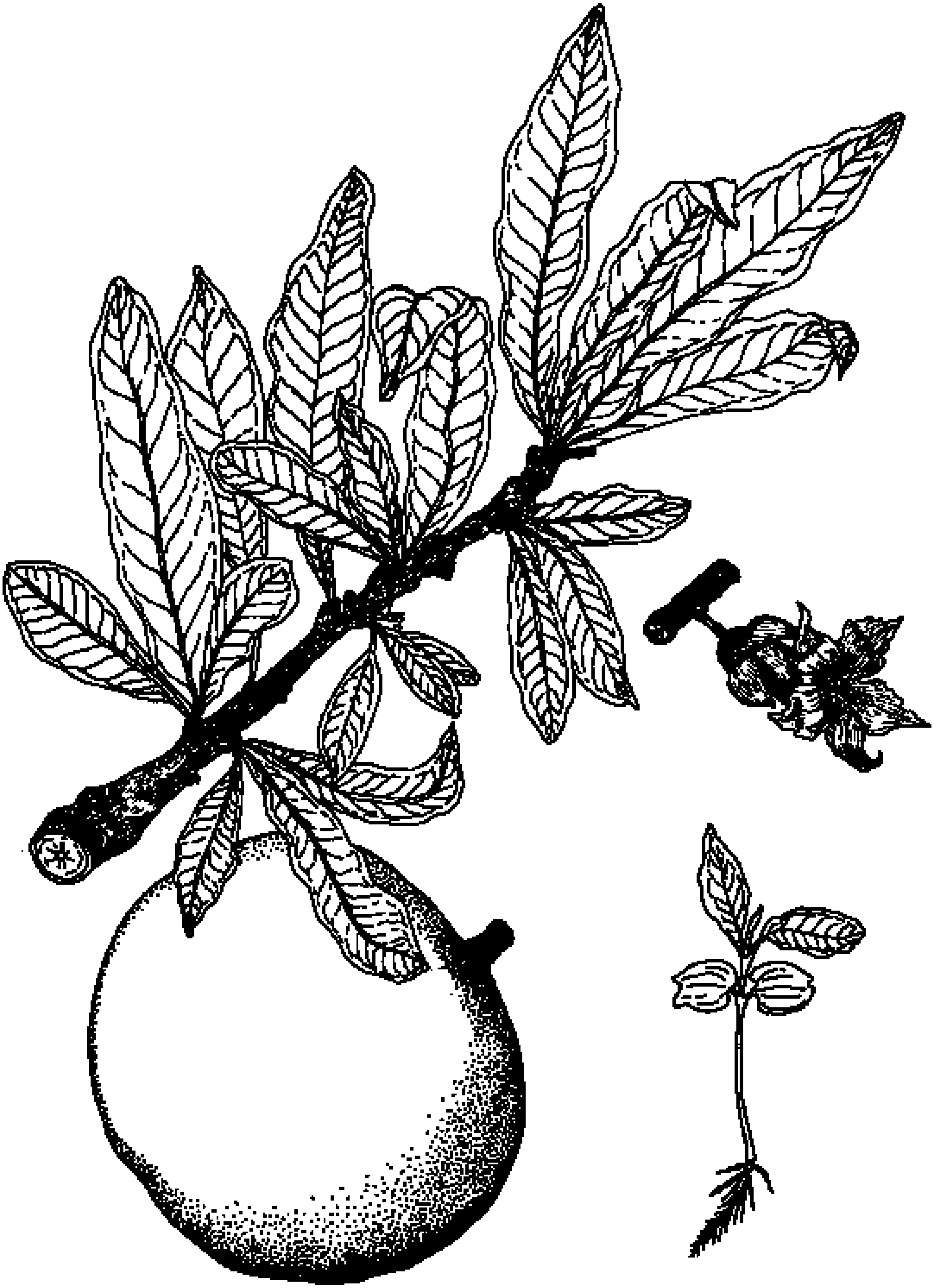
Generally, the fruits are gathered when their yellow color begins to turn reddish yellow. Gathering time is scheduled during the dry season (December through May) when the soils are not flooded and collectors can access the trees. Because the trees are not tall, climbing the trees to gather the fruits is frequently unnecessary. Using a pole with metal hooks while standing on the ground facilitates fruit collection. Because the peel of the fruit is very hard, a hammer is used to break the fruit and extract the seeds. When the fruits are used for handicrafts, the peel is broken delicately using a sharp knife or a hand or electric saw. The fruits themselves are not soaked. The pulp, along with its content of seeds, is soaked for 1 hour to hydrate the seeds and facilitate seed removal. Seeds are removed by hand-squeezing the pulp while washing it with cool water. This process facilitates the loosening of the seeds, which are collected in a strainer. Next, the seeds are washed vigorously under a stream of water to eliminate impurities. In the final step the seeds are dried in the sun for 1 hour or longer, depending on the lighting conditions.

Seeds germinate without any problems 10 to 15 days after sowing. *Crescentia cujete* is easily propagated by seeding and stem cutting. It has a deep radicular system and is very resistant to drought (Hoyos 1979).

ADDITIONAL INFORMATION

The generic name of this plant commemorates Pietro de Crescenzi (1230-1321), a farmer born in Bologna.

The hilum is basal, on one of the lateral surfaces, elliptic, and sometimes surrounded by funicular tissue. The micropyle is indiscernible. The tegmen is light brown, membranous, opaque, and smooth, and firmly adheres to the embryo. There are no endosperm. The white or cream embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are shaped like the seed, slightly emarginate at the apex, whole, expanded, plano-convex in cross section, pulpy, and independent of one another, with an auriculate base. The plumule is undifferentiated. The radicle is globose and partially covered by the cotyledons (Niembro 1982, 1983, 1989).



Dalbergia retusa Hemsl.

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FABACEAE (BEAN FAMILY)

Dalbergia hypoleuca Pittier [Journal of the Washington Academy of Sciences 12(3):62. 1922]; *Dalbergia lineata* Pittier [Journal of the Washington Academy of Sciences 12(3):63. 1922]; *Amerimnon retusum* (Hemsl.)Standl. [Journal of the Washington Academy of Sciences 13(20):442. 1923]; *Amerimnon lineatum* (Pittier) Standl. [Journal of the Washington Academy of Sciences 13(20):442. 1923]

Cocobola, cocobolo, cocobolo prieto, funera, granadillo, nambar, palo negro
(Chudnoff 1984, Holdridge and Poveda 1975)

Dalbergia retusa is distributed in Mexico and the Mesoamerican Pacific region from Guatemala to Panama (Berendsohn and Araniva de González 1989, Chudnoff 1984, Dwyer 1965, Holdridge and Poveda 1975, Janzen and Liesner 1980). *Dalbergia retusa* is a heliophyte, generally a subcanopy species that grows well in open areas. The species grows associated with other tree species, among them *Tabebuia ochracea* (Cham.) Standl., *Astronium graveolens* Jacq., *Tabebuia impetiginosa* (Mart. ex DC.) Standl., *Sideroxylon capiri* (A. DC.) Pittier, and *Swietenia macrophylla* (Jiménez 1993).

Dalbergia retusa is a small to medium-sized tree that reaches 15 to 20 m in height and 40 cm d.b.h. The bole has irregular growth (twisted) and branches at a low height. The crown is wide open with a few slim branches. The bark is blackish with fissures and exfoliates small plates (Holdridge and Poveda 1975, Jiménez 1993). Leaves are alternate, petiolate, and imparipinnate, with 7 to 15 leaflets. Leaflets are alternate, oblong to ovate-oblong, 2.5 to 12 cm long, and 2 to 3.5 cm wide. They are leathery and adaxially shiny. The leaflet base is obtuse; the apex is acuminate, often emarginate; and the margin is revolute; leaf venation is reticulate (Holdridge and Poveda 1975, Jiménez 1993, Record and Hess 1949). The species grows in soils of varying pH, texture, drainage, and fertility. The elevation range of *Dalbergia retusa* is 50 to 300 m. The tree is found on flatlands or moderate slopes in tropical, dry forests with an annual rainfall under 2000 mm and a temperature range of 24 to 30 °C.

The sapwood is whitish and sharply defined and varies in thickness as a result of age. After exposure to light and air, the heartwood usually becomes a deep, rich orange-red with black stripes or some mottling. Wood texture is fine, with straight or interlocked grain. The luster varies from medium to high. The wood has rather high oil content; it is tasteless and slightly pungent and fragrant when worked. The wood is hard, heavy, strong, and sometimes brittle. The basic specific gravity is 0.80 to 0.98; the air-dry density is 750 to 1000 kg per m^3. The wood has excellent drying properties and is free of surface and end checking. Shrinkage is usually low with very low moisture absorption. The wood is easy to work and finishing is smooth. However, wood dust may cause dermatitis or respiratory allergies (Allen and Allen 1981, Chudnoff 1984, Record and Hess 1949). The wood exhibits a high natural polish due to its oil content. Natural durability is high, and the wood is resistant to marine borer attacks. *Dalbergia retusa* is one of the most important woods in the cutlery trade for handles, inlay work, brush backs, musical and scientific instruments, jewelry boxes, chessmen, and other specialized items (Allen and Allen 1981, Chudnoff 1984, Record and Hess 1949).

Flowering occurs after 4 or 5 years, January through May; however, another flush occurs in August and September (Jiménez 1993, Molina and others 1996). Inflorescences are axillary or terminal panicles 4 to 18 cm long, appearing with or before the new leaves. The flowers are zygomorphic, with small caduceus bracts and small bracteoles, which are persistent. The calyx is campanulate, lobed to one-third its length, and slightly bilabiate; the five unequal lobes are acute. The corolla is white and glabrous. The standard is emarginate and clawed; the keel petals are oblong, obtuse, and fused distally. The stamens are fused into a single tube with an open slit distally, conspicuously curved distally, and exceeded by the style.

The ovary is shortly stipitate with one to several ovules; the style is short and distally curved, and the stigma is small.

Ripe fruits are found March to May. The fruit is a long, flat pod, ovate to orbicular, stipitate, generally attenuated at base, 6 to 13 cm long, and 1.5 to 2.5 cm wide. It has a reticulated circular wing with a thin exocarp, a fibrous mesocarp, and a chartaceous endocarp. The fruit is indehiscent with one to five seeds that are oblong, flattened, laterally compressed, 1.4 to 2cm long, and 0.6 to 1.1 cm wide. The seed is 4 to 9 mm long, and 4 to 6 mm wide, dark brown to blackish brown. It is ovoid, flattened, and has a membranous seedcoat (Allen and Allen 1981, De Lima 1990, Holdridge and Poveda 1975, Jiménez 1993, Van Roosmalen 1985). Fruit dispersal is anemochorous and hydrochorous; the latter has been observed in riparian and lacustrine forests (De Lima 1990).

Fruits are collected from the tree or the ground, placed on the floor, and exposed to sunlight for 1 or 2 days for 3 to 4 hours to dry the pericarp and open the samara. Seeds are manually extracted and cleaned. Seeds average from 4,000 to 20,000 per kg.

Seed behavior is orthodox. Seeds can be stored at 6 to 8 percent moisture content in sealed containers at 5 °C. Under these conditions, they remain viable for up to 5 years with 60 percent germination. The seeds are attacked by *Ctenocolum salvini* (Bruchidae, Coleoptera); the larvae develop in young fruits and destroy the embryo. The fungi *Alternaria* and *Aspergillus* also attack seeds.

Seeds can be immersed in running water for 12 to 24 hours before sowing. Seeds that have been stored for some time should be placed in hot water (60 °C) for 1 minute and then transferred to running water at 20 °C for 24 hours (Molina and others 1996). Fresh seeds have 80 to 90 percent germination. Germination is epigeal and seedlings are phanerocotylar. Root protrusion begins at 5 to 8 days.

The seeds are planted at a depth of 1 cm in germination boxes filled with sand. They are later transferred to nursery bags. Seedlings must be transferred to the field at 3 to 5 months, when they reach 25 to 30 cm in height. Early transplanting reduces stress and guarantees rapid plant recovery. Young seedlings (1 to 5 weeks old) are sensitive to dryness and direct sunlight exposure. Pruning of at least 50 percent foliage at the nursery stage is recommended. Seedlings outplant well but show a temporary foliar whitening. The damaged leaves are quickly replaced by new ones (Molina and others 1996). *Dalbergia retusa* is planted at a planting distance of 2 by 2 m (or 3 by 3 m). Due to its high branching rate, the species requires pruning to maintain a desirable shape. Pruning of 2-year-old saplings has provided good results. Seventeen-year-old trees may reach 13 d.b.h. and 8 m in height (Molina and others 1996).

Natural species regeneration is scarce; however, saplings and juveniles up to 4 m can be found in areas periodically exposed to fire. Some of them survive and continue growing after burning.


1cm
1cm
1cm

Decussocarpus rospigliosii (Pilg.) De Laub.

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Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

PODOCARPACEAE (PODOCARPUS FAMILY)

Nageia rospigliosii, Podocarpus rospigliosii Pilger, *Retrophyllum rospigliosii* (Pilg) C.N. Page

Pino, pino colombiano, pino de montaña, pino hayuelo, pino romerón

Decussocarpus rospigliosii grows naturally in the wet forests of the Andes. The life zones where the species predominates are: Pre-Mountainous wet forest (bh-PM), Pre-Mountainous very wet forest (bmh-PM), Low Mountainous wet forest (bh-MB), Low Mountainous very wet forest (bmh-MB), and Mountainous pluvial forest (bp-M).

Decussocarpus rospigliosii is a very slow-growing tree of 30 m in height and 40 cm d.b.h. The trunk has a scaly bark, and branching starts at 3 m. The crown has an oval shape and light green foliage. The leaves are 1 cm, opposite with a whole margin, flattened along the branches, with petioles almost nonexistent. The tree develops better on mildly inclined grounds, fertile river lowlands, plateaus, and small depressions. It grows in wet, clayey, or clayey-sandy, deep, relatively fertile soils with good to slow drainage and acid pH. It is a semi-heliophyte species that does not grow in marshy soils or in edaphic conditions of extreme drought (Corporacion de los Andes 1974). It grows best at elevations between 1500 and 3500 m, where average annual temperatures are between 10 and 18 °C and annual precipitation is between 1500 and 2500 mm. The tree needs constant humidity and cloudiness.

Because the wood of *D. rospigliossi* is easily worked, it is used for furniture, veneer, moldings, wood shaving boards, boxes, and general cabinetry. It is also used for light poles, paper pulp, and pencils.

The cream-colored flowers are 1 cm, and the green ovoid fruits are 3 cm with only one seed. Seeds are gathered only from the ground. During fructification the seeds are found in great quantities under the parent trees. Yellow seeds or seeds with a rotting or completely decomposed testa are more likely to germinate. Seeds are transported in sacks or large boxes. The seeds are carefully cleaned with cool water, and the last remains of the pulpy testa are completely removed. Seeds average 250 to 400 per kg. Seeds are stored in sand under cold conditions.

Seeds may be planted directly from the threshing floor; however, soaking the seeds in room temperature water for 1 to 2 days is recommended. Percentage of purity is 99 percent. Germination percentage in a laboratory ranges between 50 and 60 percent. The germination period is 20 to 30 days.

The seeds can be planted any time of the year, although planting in the rainy season is recommended. Because they are large, the seeds can be planted directly in bags in small holes 2 cm deep and 20 by 20 cm apart. The seeds are attacked by a borer when they are on the ground or in the soil. The seed is covered with well-packed, fine soil, watered abundantly, and provided with shade for 6 months. Watering is repeated as needed, especially during the dry season. Every 4 to 6 weeks, the soil is pricked to maintain it in good physical condition and weeds are eliminated (Lamprecht and Liscano 1957). The lifting of plantules in nurseries must be done in two stages with an interval of 2 to 3 months. The plantules are transplanted into the field when they are 25 to 40 cm high.

The underbrush at the field site must be removed to reduce undesirable competition. However, a complete cleaning can cause excessive growth of the underbrush, which covers the soil like a carpet and can suffocate arboreal vegetation. In half shade, this condition is eliminated.

Planting distance depends on future use of the trees. For conservation of germplasm, a semiregular spacing of 1 by 1 m between plants will provide a rich reserve available for emergencies. To produce a forest, distances of 3 to 5 m may be used. Because the species develops slowly during the first months and the plants are small, herbaceous vegetation must be strictly controlled.

Delonix regia (Bojer ex Hook.) Raf.

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Southern Research Sation,
USDA Forest Service

FABACEAE (BEAN FAMILY)

Poinciana regia Bojer

Acacia, árbol de fuego, árbol del fuego, clavellino, flamboyán, flamboyán colorado, flamboyán rojo, flamboyant, flamboyant-tree, flame-tree, flor de fuego, flor de pavo, framboyán, giant, giant-tree, guacamaya, guacamayo, josefina, July-tree, malinche, poinciana, royal poinciana, tabuchín (Little and Wadsworth 1964, Salas Estrada 1993)

Delonix regia is the most cosmopolitan of the three species in the genus. A native of Madagascar, it now grows in almost every frost-free country and may be the most recognized flowering ornamental tropical tree in the world (Menninger 1962).

Delonix regia is a small to medium-sized tree, typically 7 to 16 m tall and up to 60 cm d.b.h. (Little and Wadsworth 1964). However, the champion Puerto Rican (*D. regia*) tree is 32 m tall and 105 cm d.b.h. (Francis 1994). This tree is easily recognized with prominent buttresses and a briefly deciduous broad, flat crown when grown in full sun. The species grows well in moist soil derived from limestone, where it is common and reproduces well; but it also tolerates well-drained and somewhat droughty conditions (Francis and Liogier 1991).

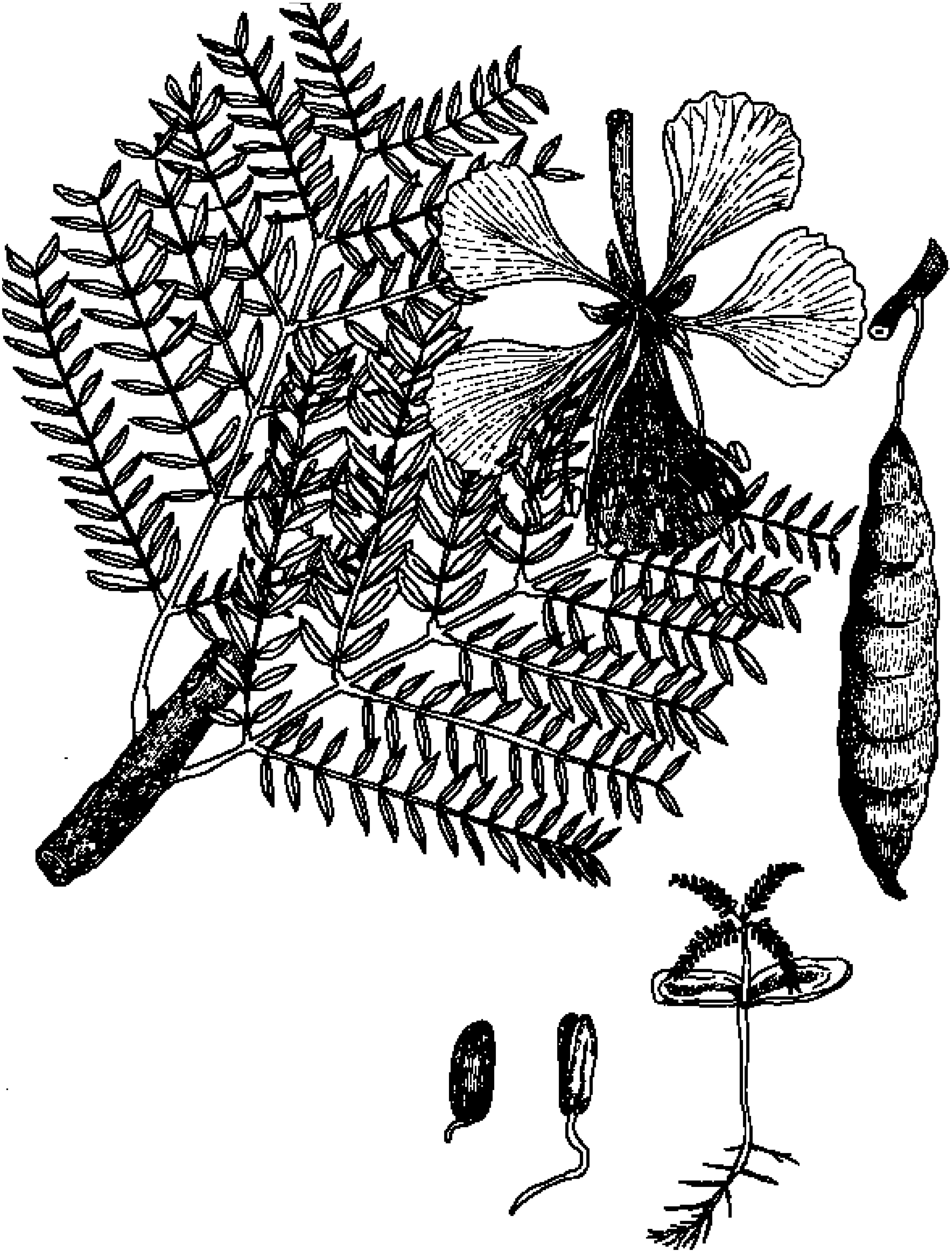
The tree's attractive form and bright, showy flowers as well as the shade it provides make it a popular ornamental throughout the tropics. The predominantly red flowers (with yellow and orange cultivated forms) are commonly used as short-lived cut flowers. The trees remain in flower for several weeks. The trees are often planted along roads to serve as living fence posts or to provide shade. The yellow-brown wood is weak, brittle, and soft, with a specific gravity of about 0.3. It is a poor timber source. *Delonix regia* is widely grown for fuelwood, and the seedpod is edible (Little and Wadsworth 1964, Menninger 1962, Webb and others 1984).

The flowers appear after a dry season when the tree is almost leafless. The five-pointed calyx is hairy and borne on racemes 15 to 25 cm long. Flowers are commonly red but may also be white, yellow, orange, or spotted and range from 8 to 25 cm across. The flowers persist during leaf emergence, resulting in a crown that appears feathery green with dominant, colorful flowers. Seed pods are hard, 35 to 50 cm long, 6 cm wide, and 5 mm thick. They hang tenuously on the trees throughout the year. After 6 months, the mature, dark brown to black pods split lengthwise into two parts (Little and Wadsworth 1964).

Pruning poles are used to collect mature *D. regia* pods. Any unopened pods should be dried for 1 month in full sun, then forced open to remove the seeds which are loosely attached in lateral grooves. *Delonix regia* seeds from Puerto Rico average about 4,500 per kg (Marrero 1949); those from Colombia average only 2,000 to 3,000 per kg (Navarette no date). The dry seeds can be stored in open or closed containers and do not require refrigeration (Francis 1994). Seeds stored for 12 months at 26 °C showed 60 percent germination (Marrero 1949). Webb and others (1984) reported viability after 4 years of storage.

Germination requires scarification by hot water, sulfuric acid, or abrasion. Millat-E-Mustafa (1989) recommends 90 °C for 10 seconds followed by a 24-hour imbibition. A concentrated sulfuric acid soak for 0.5 to 5 hours improved germination for Duarte (1974), while a hot-wire scarification proved superior to other means for Sandiford (1988). All reports of scarified treatments indicated superior results compared to those of controls with no treatment. Seeds germinated within 8 days of collection will have 76 percent germination after 9 weeks.

Seedlings of *D. regia* are ready for outplanting after growing in plastic nursery bags during the wet season, which lasts 3 to 4 months. Saplings to be used as large ornamental potted plants are grown to 2 m, balled, and burlapped. Mature, flowering, and fruiting trees may be grown in 3 to 5 years on good sites (Francis 1994). *Delonix regia* has a shallow but spreading root system which is limiting when selecting planting sites. The trees are susceptible to termites, shoot borers, and heartrot (Webb and others 1984).



Dendropanax arboreus (L.) Decne. & Planch.

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ARALIACEAE (GINSENG FAMILY)

No synonyms

Angélica, banco, bois négresse, galipee, lengua de vaca, mano de danta, mano de león, mano de oso, palo cucharo, palo de burro, palo de pollo, pingüico, quesito, ramón de costa, vaquero

Dendropanax arboreus is native to America. It is distributed naturally from Mexico, across Central America, to northern South America and in the West Indies. It forms part of hot-humid, subhumid, dry tropical forests and part of the secondary vegetation.

Dendropanax arboreus is a fast-growing evergreen tree of up to 30 m in height and 75 cm d.b.h. It has a straight, grooved trunk and an irregular, leafy crown made up of thick, rising branches. The leaves are simple and arranged in spirals. When young, they are trilobate or with a lobe on one side; when adult, they are ovate to fully ovate, oblong elliptic, elliptic or ovate-elliptic, 5 to 26 cm long, and 3 to 13 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatues to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging from between 900 and 1800 mm. The tree grows naturally from sea level to 1700 m.

Because the wood is white or yellowish, strong, and flexible, it is used locally for firewood and in rural construction and carpentry. Specific gravity of the wood is 0.40. In recent years, the species has been in high demand for the manufacturing of veneer, particle boards, tongue depressors, toothpicks, matches, and pulp for paper. It is planted to provide shade in pastures and coffee plantations and to fulfill agroforestry needs. The flowers are honey bearing, and the tea obtained from the infusion of the leaves is used as a remedy in traditional medicine (Aguilar 1966, Cabrera and others 1982, Chudnoff 1979, Escalante 1986, Little and others 1967, Miranda 1976).

Because its geographic distribution is extensive, the *D. arboreus* blooms at different times but especially May through August (Sosa 1979). The tree begins to yield flowers and fruits between 4 and 5 years of age. In southeastern Mexico, the tree blooms precociously and abundantly during the months of July through September and the fruits ripen in the month of December (Juárez and others 1989). The flowers are cream or greenish yellow, fragrant, and arranged in umbel racemes. The abundant fruits are drupaceous, globose, 4 to 8 mm long, slightly depressed, pulpy, and resinous. They change from purple to reddish purple and black when ripe. Each fruit contains 5 to 7 monospermic pyrenes (Cabrera and others 1982, Holdridge and Poveda 1975, Little and others 1967, Pennington and Sarukhan 1968, Sosa 1979). The seeds are inside pyrenes, which constitute the unit of dispersion and sexual propagation of the plant. The pyrenes are plano-convex, laterally flattened, triangular in cross section, crustaceous, brown, indehiscent, smooth, and 5 to 6 mm long. The seeds are subovoid triangular and laterally flattened, similar to orange slices.

The ripe fruits are collected by climbing the trees and using poles with metal hooks to remove them. The pulp is removed from the pulpy fruits by hand inside a bucket of water. Resulting impurities float and are gathered with a strainer. Good pyrenes sink. Subsequently, pyrenes are dried in the sun in ventilated areas for 1 or 2 hours, depending on lighting conditions. Pyrenes average 25,682 per kg (Patiño and Villagómez 1976). The seeds within the pyrenes remain viable for approximately 15 months when stored under ambient conditions (24 to 30 °C). With longer storage their viability quickly diminishes (Vega and others 1981).

The germination of the seeds is phanerocotylar. Under humid conditions, the fresh seeds germinate at 70 percent without pretreatment. A heterogeneous sample of seeds germinated approximately 18 days after sowing (Vega and others 1981). The plant is propagated through its seeds.

ADDITIONAL INFORMATION

The hilum is small and subbasal. The micropyle is indiscernible. The seedcoat is membranous and firmly attached to the pyrene. The endosperm is abundant, pulpy, whole, and translucent. The embryo has a straight axis and is small, symmetrical, white, and near the hilum. There are two ovate or oblong cotyledons. The plumule is undifferentiated. The radicle is superior and directed toward the hilum (Marchal 1967, Smith 1944, Sosa 1979, Standley and Williams 1966).

Diphysa americana (Mill.) M. Sousa

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FABACEAE (BEAN FAMILY)

Colutea americana Mill. (The Gardeners Dictionary, eighth edition, Colutea 5; 1768);
Diphysa robinioides Benth. (Videnskabelige Meddelelser fra Dansk
Naturhistorisk Forening i Kjøbenhavn 1853: 11; 1853)

Achivare, arate, bolsa de gato, carate, cascabelillo, cuachepil, guachipelí, guachipelín, guiloche, huachipilín, huiloche, macano, macano amarillo, naguapate, negrito, palo amarillo, palo santo, retama, retama de cerro, sikró, singrá, stutztzuk, susuk, tsikrá, tsutsuc, urxk, vivaseca, wild ruda, xbabalché, xsusuc (Record and Hess 1949)

Diphysa americana is an American species extending from Mexico to Panama.

Diphysa americana is a slow-growing deciduous tree that reaches 6 to 20 m in height and 30 to 50 cm d.b.h. The crown is spreading, open, and irregular. The bole is rarely straight, basally channeled, and branched; young twigs are grayish green, with numerous elevated, verrucose, longitudinal lenticels. The bark is brown or grayish brown, fissured, and rough; the inner bark is thin, whitish or yellowish, and exudes nonsticky mucilage (Holdridge and Poveda 1975, Salas 1993). Leaves are compound, alternate, imparipinnate, with 11 to 21 membranaceous, peciolate, oblong or oval, and glabrous leaflets; they are entire and eglandular, shiny adaxially and dull, almost grayish green abaxially, and bear small stipules (Allen and Allen 1981, Holdridge and Poveda 1975). The species grows well in well-drained fertile soils as well as in periodically inundated areas with clayey soils. The species is common on flatlands or moderate slopes in tropical dry forests at elevations of 5 to 800 m (Salas 1993). The annual rainfall is under 2500 mm, and the temperature ranges from 24 to 32 °C.

The heartwood has a waxy or oily aspect; it is greenish yellow and turns olive or yellowish brown with drying; the sapwood is yellowish. The dry wood is odorless and tasteless. It is very hard, heavy (basic specific gravity 0.62 to 0.72), tough, and strong, with medium texture, low to medium luster, and irregular grain (Record and Hess 1949). Working properties are moderately good; wood finishing is smooth, and polishing is good. The wood keeps its form and has an excellent natural durability (Record and Hess 1949). Wood properties resemble those of black locust (*Robinia pseudoacacia* L.) and can be used for the same purposes: general carpentry, general construction, floors, furniture, fenceposts, poles, railroad ties, stakes, insulator pins, machine parts, wooden ware, boxes, crates, planing-mill products, treenails, and mine equipment (Allen and Allen 1981, Record and Hess 1949). In Costa Rica, the wood has been used widely to make wood sculptures. In several countries, the timber is used as fuel (Mabberley 1997). The tree is commonly used as an ornamental in parks and along sidewalks. The wood yields a yellow dye (Allen and Allen 1981, Holdridge and Poveda 1975).

Flowering primarily occurs in the dry season, from November through February. In some years, a minor flowering can be observed during the rainy season. Flowers are showy and congested in small, lax, axillary racemes. The calyx is green, campanulate, pentalobed, subtended by two caduceus bracteoles, and turbinate at the base (Allen and Allen 1981). Calyx lobes are unequal: the upper pair is broad and the lower three narrow, the central being longer. The corolla is typically papilionaceous. Petals are deep yellow and unequal; the standard is orbicular, reflexed, and clawed; the wings are oblong and curved, and the keel petals are lunate (Allen and Allen 1981). The androecium has 10 diadelphous stamens. The gynoecium is monocarpellar and stipitate; the ovary is oblong and flattened, with many ovules. The style is curved and glabrous, and the stigma is small (Allen and Allen 1981). Fruits are produced from December through May. Fruit dispersal is anemochorous. Fruits are stalked, flattened, weightless, pale brown, indehiscent pods. The epicarp is papery and expands laterally, forming air chambers (bladders) between successive seeds.

Fruits are collected from the tree in March and April, and seeds must be extracted by hand. Seeds are reniform, light brown or whitish. Seeds average 1,600 to 1,650 per kilogram (Brenes 1994). They are orthodox and can be stored 6 months under ambient temperature in a dry, aerated location. Seeds should be screened and small, malformed, or damaged seeds must be discarded.

Seeds do not require pretreatment. Root protrusion occurs 8 to 10 days after sowing, and the percentage of germination is 80 to 86 percent. Germination is epigeal and seedlings are phanerocotylar.

Seeds can be sown in greenhouse beds or directly in plastic bags filled with soil and sand. In experimental plots or mixed plantations, 6-month-old seedlings are sown at a planting distance of 3 by 3 m. Survival is excellent but growth is slow (Brenes 1994). Branching must be corrected and pruning is recommended in 2- or 3-year-old saplings.

ADDITIONAL INFORMATION

The name *Diphysa* (two bladders) refers to the pair of inflated chambers characterizing the sides of the pod epicarp. The name derives from the Greek di (two) and physa (bladder) (Allen and Allen 1981).

Pericarp expansion occurs in both sides, between the ventral and dorsal sutures. In the mature pod, sutures are found along the center of the flat faces; internally, a central column to which the seed funiculus is attached unites the sutures. The chambers form in the mesocarp aerenchyma. Successive seeds are separated by small septa, which interrupt the lateral air chambers (bladders).


1cm

Diphysa robinioides Benth.

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FABACEAE (BEAN FAMILY)

Diphysa americana (Mill.) *M. Sousa* (Montero Mata 1995)

Guachepilí, guachepilín, guachipilín, palo amarillo (Montero Mata 1995, Witsberger and others 1982)

Diphysa robinioides is distributed from southern Mexico to Panamá and Venezuela (Witsberger and others 1982).

Diphysa robinioides is a deciduous tree 6 to 22 m in height and 30 to 50 cm d.b.h. Usually double-stemmed, the tree has a sparse, irregular crown and bark with deep vertical fissures. *Diphysa robinioides'* alternate, odd, pinnately compound leaves are 3 to 15 cm long. Leaves have from 5 to 27 leaflets. Leaflets are smooth with rounded apex and have a strong smell when rubbed. In Guatemala, the species grows from sea level to 2500 m in diverse soils and climates.

The wood of *Diphysa robinioides* is used for firewood (Guzman 1980) with a specific gravity of 0.965 and high calorific properties (18,810 kj per kg) (Montero Mata 1995). It is an attractive ornamental with brilliant yellow flowers. The heartwood produces a yellow dye. In some Central American countries the trees are used for living fences, posts, or windbreaks. In Nicaragua the species is planted in coffee plantations for shade and timber (Natural Resources Defense Council 1996). The cortex is used for home remedies (González Ayala 1994), especially for treating gastrointestinal diseases (Caceres and others 1990). The foliage is a good source of green manure and sprouts easily after pruning (Montero Mata 1995). Livestock and rabbits feed on the leaves of young and adult trees. Finally, *D. robinioides* is a nitrogen-fixing tree (Allen and Allen 1981, Halliday 1984, Navarrete-Tindall and others 1996) which can be used in agroforestry systems.

Diphysa robinioides flowers in November and fruits from December to May (Witsberger and others 1982). Flowers are yellow, 1.5 cm long, 1 cm wide, and borne in racemes 4 to 7 cm long (Witsberger and others 1982). The indehiscent fruits are inflated oblong pods, forming two bladders on each side of the pod with up to six seeds.

Mature fruits are collected from the ground after they fall or directly from the tree. Seeds are extracted by hand from the fruit and stored under dry and cool conditions (5 °C). Seeds average approximately 50,000 per kg, but 20 to 30 percent of the weight may be broken seeds. Germination is high—91 to 98 percent—without the need for scarification treatments (Montero Mata 1995, Navarrete-Tindall and others 1996).

In nursery production, two seeds are planted in pots or polyethylene black bags in a sunny location, thinned to one seedling, and watered daily. Seedlings grow fast under temperatures between 20 to 30 °C, especially when rhizobial bacteria are present in the soil. Six-month-old seedlings had an average height of 74 cm and 1.4 cm basal stem diameter 4 months after outplanting (Navarrete-Tindall and Van Sambeek, unpublished data). *Diphysa robinioides* is also propagated from large cuttings.

ADDITIONAL INFORMATION

Future research should include progeny and pruning studies to produce fewer-branched individuals for timber production. Studies on root development will help to determine the tree's potential as an ornamental in urban areas.

Dipterocarpus turbinatus Gaertn.

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DIPTEROCARPACEAE (DIPTEROCARP FAMILY)

Dipterocarpus laevis Buch. Ham., *Dipterocarpus jourdainii* Pierre., *Dipterocarpus turbinatus* Dyer

Garjan, gurjan, gurjank uroisal, kaligarjan, kanyin, kanyin wettaung, kanyinni, kherjong, kur oil, kural sal, shweta garjan, tekigurjan, telya garjan, tikya gurjan, tilia gurjan, toligarjan (Brandis 1906, Das 1980, Gamble 1922, Joshi 1980, Regional Office for the Asia and the Pacific 1985, Troup 1921)

Dipterocarpus turbinatus is generally found in the tropical semievergreen, tropical wet evergreen, and tropical moist deciduous forests of Bangladesh, Myanmar, India, and Malaya Peninsula (Champion 1936). Of the 80 species in the genus growing primarily in the Indo-Malayan region (Joshi 1980), four grow in the hill forests of Bangladesh (Das 1980). In Bangladesh the species is scattered in the tropical wet evergreen forests and tropical semievergreen forests of Chittagong, Chittagong Hill Tracts, Cox's Bazar, and Sylhet (Champion 1936, Das 1980) in association with *D. gracilis* Blume, *Chukrassia tabularis* A. Juss, *Hopea odorata* Roxb., *Salmalia insignis* Schott & Endl., etc. In Myanmar, the species has a comparatively wide distribution in tropical semievergreen forests and tropical moist deciduous forests (Champion 1936) in association with *D. alatus, Mangifera* spp., *Syzygium* spp., *Lagerstroemia* spp., *Amoora* spp., *Sterculia alata, Garcinia* spp., *Hopea odorata, Artocarpus chaplasha, Artocarpus lakoocha,* and others, often with an undergrowth of various palms and canes (Troup 1921). In India, the tree is primarily found in the Cochar tropical evergreen forest, Cachar tropical semievergreen forest, Andaman tropical evergreen forest, and Andaman semievergreen forest (Champion and Seth 1968). In Andamans, *D. turbinatus* is found in association with other dipterocarps, including *D. griffithi* Miq., *D. alatusi* Roxb. & G. Don, and *Hopea odorata* with *Artocarpus chaplasha* Roxb., *A. gomeziana* Wall., *Calophyllum spectabile* Willd., *Terminalia bialata* F. Villar, and other trees; and with a dense undergrowth of canes, climbers, and climbing bamboos (Troup 1921). In Tripura, the species occurs sporadically, mixed either with *Shorea robusta* Gaertn. or miscellaneous evergreen and deciduous species, and sometimes occurs in small, pure groups (Joshi 1980).

Dipterocarpus turbinatus is a slow-growing, lofty, evergreen hardwood tree attaining 50 m in height and 159 cm d.b.h. with a clean, cylindrical bole and elevated crown. The species grows in soils that vary from clay to clayey loam on level ground and from sandy loam to coarse sand on hilly ground. Soil pH can range from 4.9 to 5.8. The species grows primarily in the northern and eastern aspects between 15.2 and 457.2 m. In the natural habitat of *D. turbinatus*, the temperature varies from 15.6 to 40.6 °C, and the rainfall varies from 1520 to 5080 mm.

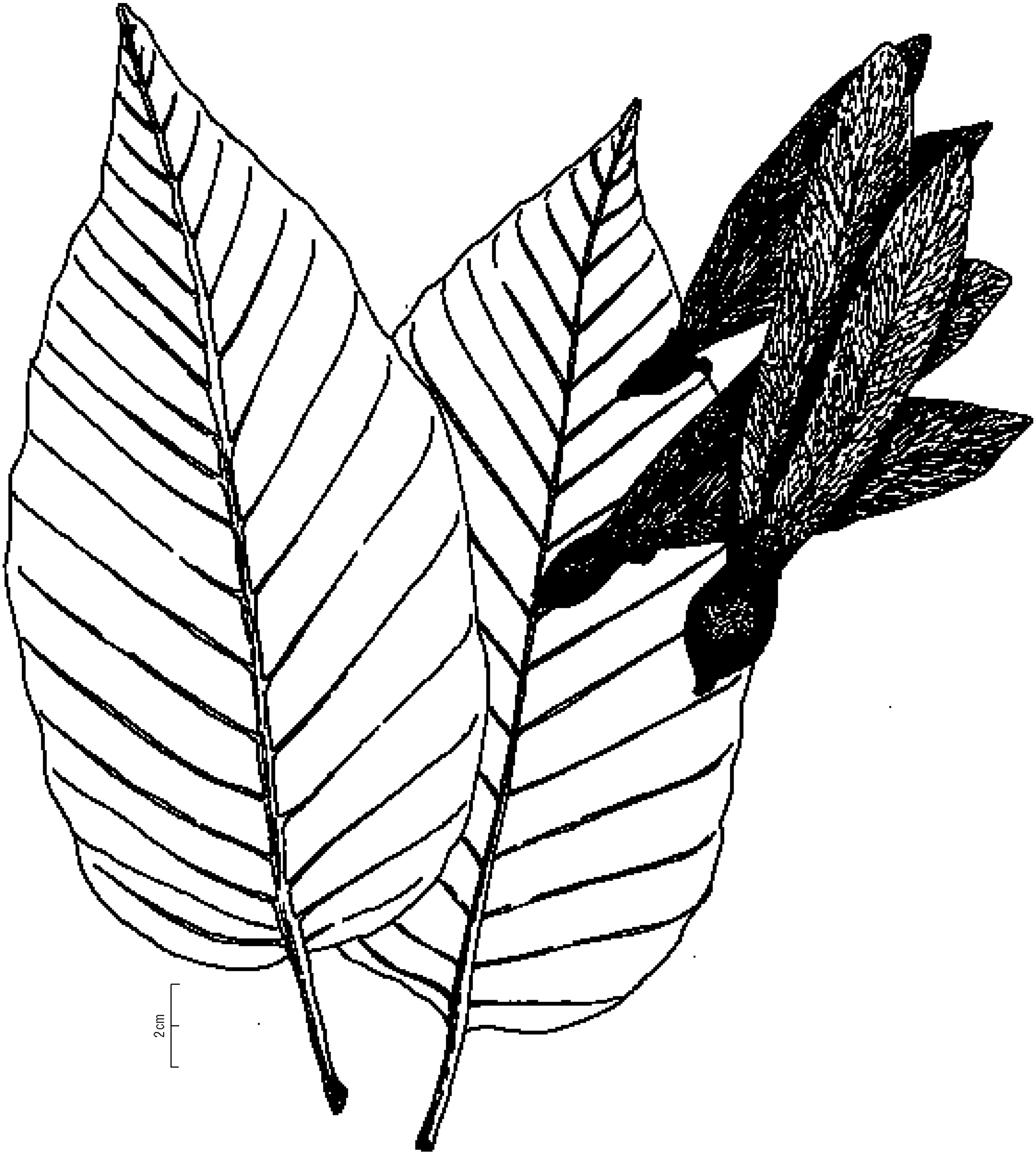
Dipterocarpus turbinatus is basically a timber tree with a specific gravity of 0.655. Sapwood is greyish or brownish white; heartwood is reddish brown with lighter, interrupted, tangential lines (resin canals) at irregular and relatively close intervals, a fairly straight or somewhat interlocked grain, and an even or coarse texture (Regional Office for the Asia and the Pacific 1985). The lumber is moderately easy to air-season but seasons somewhat slowly. To accelerate the seasoning process, the timber is partially air-seasoned and then kiln-dried. The lumber is not durable under exposed conditions and lasts much longer under cover or when treated with preservatives. It is easy to saw and work and polishes well, although it requires a good deal of filling (Chowdhury and Ghosh 1958, Gottwald and Parameswaran 1966, Pearson and Brown 1932). The lumber produces a popular, commercial grade plywood. It is also used as rafters, beams, and planking. In Bangladesh, the lumber is used primarily for railway ties and boat building (Das 1980). In Myanmar, it is popular for dugout canoes (Gamble 1922). After treatment with a preservative the logs make acceptable transmission poles (Joshi 1980). The tree's oleoresin (processed garjan oil) is applied externally to treat ulcers, ringworm, and other cutaneous infections. It is also used to stimulate mucous surfaces and as a diuretic (Kirtikar and Basu 1918, Martindale 1958).

Flowers appear from January through March and occasionally up to April. Flowers are 3 to 3.5 cm long, white or pinkish, and emerge in a few flowered racemes from the axils of fallen leaves. Fruiting occurs in May and June. Fruits swell to 2 to 2.8 cm in diameter and 2.8 to 3.5 cm in length and can be recognized easily because two of the five calyx lobes are enlarged into wings (Gamble 1922, Troup 1921). Fruit ripens and falls from about the middle of May to the middle of June. Seeds have a hygroscopic, spongy, thick, dome-shaped part of the pericarp located just above the embryo (Banik 1980).

The tree's height usually discourages manual collection. Before collection, the ground should be cleaned and all seeds removed. Seeds should be collected daily as they fall to reduce insect attack. In Bangladesh, seeds should be collected between the last week of May and the first week of June and should be sowed within 10 days of collection (Haque and others 1984) because they do not store well. Seeds average about 154 per kg (Chowdhury 1975, Joshi 1980).

The seeds do not require pretreatment. Germination of the seeds is hypogeous. Sowing time and position determine germination success. Straight seedlings and 82.2-percent germination resulted within 3 to 10 days when the seeds were sowed in horizontal, half-buried conditions (Banik 1980). High survival rates in the field are attained when seedlings are grown in containers such as polyethlene bags.

Dipterocarpus turbinatus has been raised in the nursery and outplanted in regeneration areas. Line sowing is recommended if sufficient seeds are available. Shading is unnecessary in the nursery. Seedlings 15 cm high with a ball of earth are outplanted in the regeneration areas during the rainy season. To attain satisfactory survival rates, seedlings must be outplanted immediately after removal from the nursery beds. *Dipterocarpus turbinatus* also propagate by air layering (Rashid and Serajuddoula 1984) and clonal propagation (Smits 1993, Zabala 1994). Because the species is extremely sensitive to fire, adequate fire protection measures must be adopted (Blanford 1915, Homfray 1935). Some larvae, primarily of the order *Lepidoptera,* bore into *D. turbinatus* seeds and fruits (Joshi 1980).


2cm

Dipteryx panamensis (Pittier) Record & Mell

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FABACEAE (BEAN FAMILY)

Coumarouna panamensis Pitt., *Dipteryx oleiforma* Benth., *Oleiocarpon panamensis* (Pittier) Dweyer

Almendro, almendro amarillo, almendro de montaña, almendrón, eboe, tonka bean tree

Dipteryx panamensis is endemic to Costa Rica, Panama, and Colombia and grows primarily in the lowlands of the Atlantic plains.

Dipteryx panamensis is a slow-growing tree that reaches 15 to 50 m in height and 1 to 1.6 m d.b.h. The tree has a trunk with ample basal roots but without buttresses, red-brown and smooth bark with vertical lenticels, ascendant branches, and a semispherical crown. Leaves are alternate, exstipulated, pinnated, with 10 to 20 stipeled leaflets, opposite, and subopposite alternative. The last leaflet or pair of leaflets is in acropetal direction and located 3 to 6 cm from the tip of the rachis. The leaflets are ovate, asymmetrical, slightly sinuated with entire margin, acuminate apex, oblique base; the proximal leaflets tend to be smaller in size. Both surfaces of the leaflets are almost glabrous.

It is an emergent tree, quite abundant in humid and very humid tropical forests, where annual temperatures vary between 24 and 30 °C and annual rainfall from 3500 to 5500 mm. The species grows on very humid plateaus, in alluvial or sandy soils, and sometimes in acid and clayey soils at elevations ranging from 20 to 1300 m.

The wood has a specific gravity of 0.83 to 1.09 and is considered extremely heavy. Transition between sapwood and heartwood is very light and difficult to detect. In green condition the sapwood is whitish and the heartwood yellow; in dry condition, the sapwood is brown-yellow and the heartwood yellow-red. The growth rings are not well defined; the wood has a strong intercrossed grain and median and a waxy texture, and the pores are visible. The rays, the vessels, and the fibers contain an abundance of white, pink, or yellow resinous materials. The wood is dense, hard, very durable, and medium-textured and rates high in mechanical resistance. It dries well with no defects but is difficult to saw and cut due to its weight, density, and crystalline deposit content. It is also difficult to impregnate with preservatives. The wood can be used for industrial floors, bridges, railroad ties, marine construction in waters infested with marine borers, boats, oxcarts, handicrafts, sport implements, springboards, industrial machinery, and agricultural tool handles. In Costa Rica, the wood is used in veneer. The roasted seeds are eaten in some regions of Panama (Standley 1937). As one of the prettier trees in the forest, *D. panamensis* has great potential for use as an ornamental.

The flowering period is dependent on the beginning of the rainy season and varies among regions (Arnáez and Moreira 1995). The flowers are hermaphrodite, zygomorphic, gamosepalous, tubular, and pubescent glandular. The pink flowers are grouped in terminal or lateral panicles, 30 to 50 cm long, with numerous secondary axes. The trees begin to flower and set fruit when they are 11 to 12 years old. Fruits develop in about 4 months, usually during a dry period. The fruits are pods 6 to 8 cm long, 4 to 5 cm wide, and 2 to 3 cm thick. Seeds are cotylecosperm and correspond to the overgrown type. The seed, limited by the size of the pod, ranges from 4.5 to 6 cm long, 3 to 3.5 cm wide, and 1 to 1.6 cm thick.

The fruits are gathered from the ground and approximately 10 percent are well developed well but lack seeds. The fruits collected from the ground usually have exocarpic scars caused by the insects that oviposit in the immature fruit. *Lepiota* aff. *procera mycelia* adhere to the inner surface of the exocarp and the mycelial filaments of the same fungus are present in the fleshy mesocarp. The mature, gold-colored sporocarps of *Lycogala,* and the black sporocarps of *Darcula filum* yeast as well as several insect larvae infect the fruit.

Fresh seeds average between 55 and 60 per kg; dry seeds (38 percent moisture) average 300 per kg (Muller 1995). Seed viability is generally restricted to a period of 9 to 10 days (Flores and Sanchez 1992). Even though the seeds could be recalcitrant, they can endure a certain degree of dryness (Muller

1995). The dry fruits can be stored in moist sawdust for at least 3 months and some seeds will germinate.

Without pretreatment, germination takes 12 to 20 days and is 80 to 90 percent (Rodríquez 1996a). The fruits should be placed on a germination bank or in sand with the peduncle up, taking care that they are half-covered by the medium. Sometimes fruits are planted directly in plastic bags. After 3 to 4 months in the nursery, seedlings can be outplanted. When pseudocuttings are used for reproduction, they must remain in the nursery for at least 6 months. Once seedlings or pseudocuttings are outplanted, they must be weeded periodically.


1cm
1cm
1cm
1cm
1cm

Enterolobium cyclocarpum (Jacq.) Griseb.

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FABACEAE (BEAN FAMILY)

No synonyms

Algarrobo de orejas, árbol de las orejas, caro, costa-mahogany, dormilón, earpod tree, flamboyán extranjero, guancaste, guanacastle, jenízaro, juana, nacaste, nacastle, oreja, oreja de mono orejón, parota, pich, picho

Native to the tropical regions of America, *Enterolobium cyclocarpum* is naturally distributed from central Mexico, across Central America, to the northern part of South America. The species has been introduced and naturalized in the Caribbean islands, Cuba, Puerto Rico, and Haiti (Little and others 1988, Standley and Steyermark 1946a).

Enterolobium cyclocarpum is a deciduous and thornless tree that can reach 30 m in height and 3.5 m d.b.h. The trunk is short and straight with small spurs at the base. The bark has numerous lenticels. The thick, rising branches produce an ample, spreading, and hemispherical crown. The leaves are bipinnate and 15 to 40 cm long, with linear-oblong leaflets 8 to 15 mm long. *Enterolobium cyclocarpum* grows in alkaline, calcareous, sandy, and clayey soils. It grows at elevations from sea level to 900 m. The species prospers where average annual temperatures range between 23 and 28 °C, and average annual precipitaiton ranges between 750 and 2000 mm. The tree requires a dry season 1 to 6 months long.

Enterolobium cyclocarpum is a tree with multiple uses. It is planted in pastures as a shade tree and as a source of forage for cattle. In Central America, the tree is used to shade coffee plantations and to enrich the soil. It is also planted as an ornamental and shade tree on the edges of roads and in parks and gardens. The fruits, boiled unripe seeds, and roasted ripe seeds are edible. Ground seeds provide a flour that contains up to 35 percent protein. The ripe fruits and the bark contain tannin and are used to tan hides. Specific gravity of the wood ranges between 0.34 and 0.6. The wood is easy to work using hand tools. Its uses include furniture and cabinets, veneer, construction, panels, canoes, posts, firewood, and charcoal. Because it is resistant to humidity, the wood is used in ship building. An infusion of the bark is used to reduce fevers. The gum that exudes from the trunk has properties similar to those of gum arabic (Francis 1988, National Academy of Sciences 1979, Niembro 1986).

The flowers are white and arranged in capitula. The tree blooms February through April. The fruits take 3 months to ripen. Ripe fruits can be recognized by the color change in the pericarp from green to dark brown and by the noise the seeds make when the fruits are shaken. The legumes are curved or twisted, laterally flattened, dark brown, shiny, indehiscent, ligneous, and sometimes form a circle 7 to 12 cm in diameter. Each fruit contains 8 to 16 seeds (Holdridge and Poveda 1975, Little and others 1988, Pennington and Sarukhan 1968, Standley and Steyermark 1946a). A tree can yield several kilograms of seeds. The seeds are ovate, laterally flattened, 14.5 to 17.5 mm long, 7.8 to 11.2 mm wide, and 6.2 to 7.2 mm thick. The seedcoat is red-brown, smooth, opaque, cartaceous, very hard, and marked on one of its lateral surfaces by a closed pleurogram or fissural line that follows the contour of the seed. Inside the light brown halo of the pleurogram, the color of the seedcoat changes to a dark brown.

The fruits are usually collected from May through July. Fruits may be collected from the ground or from the trees. A pole with metal hooks is used to remove fruits from trees. Because the fruits are indehiscent they must be broken by hand or macerated. The fruits are ground in wood mortars in the first step to extracting the seeds. The seeds are big and they are easily separated by hand. Small impurities are removed with sieves or by using a vertical column blower. Seeds average 1,100 to 1,170 per kg (Francis 1988, Patiño and Villagómez 1976, Vega and others 1981).

Cleaned of impurities, the seeds are stored in plastic containers at ambient temperature, where they can conserve their viability for a period of 13 months (Vega and others 1981). Stored in hermetically sealed containers in cold chambers at a temperature of 5 °C and a moisture content of 6 to 8 percent, viability is kept for up to 11 years with a germination of 80 percent (Centro Agronómico Tropical de Investigación y Enseñza 1997c).

The seeds have very hard teguments, and they have mechanical latency. The thinning of the teguments can be done mechanically with sandpaper or a knife. However, germination can also be stimulated by submerging the seeds in boiling water for 15 to 30 seconds. Subsequently, they are soaked in water at ambient temperature for 6 to 7 hours. The treated seeds are planted in a seedbed or in polyethylene bags, where they begin to germinate in 4 to 5 days with 80 percent germination. The plantules grow fast and resist desiccation. Francis (1988) notes that the trees are removed from the nursery when they are 6 months old and 50 cm high. However, Centro Agronómico Tropical de Investigación y Enseñza (1997c) recommends outplanting when the plants are 2 to 3 months old and their height ranges from 20 to 25 cm. In general, the plantules do not require special care during cultivation.

ADDITIONAL INFORMATION

Tests done in Costa Rica showed that trees 7.5 to 8 years of age measured 11 to 16 m in height and 8 to 11 cm d.b.h. In southern Mexico, 8-year-old trees had an average height of 8 m and 12 cm d.b.h. In Puerto Rico, 5-year-old trees growing along with other species had a height of 6 m. At 25 years of age, the trees measured 18 m in height and 42 cm d.b.h. (Francis 1988).

The hilum is basal, puntiform, 3 to 5 mm long, and sometimes has a fuliform micropyle. The micropyle is puntiform and set deep. The lens is set deep, on the opposite side of the micropyle and on the path of the vascular bundle. The endosperm is absent. The yellow embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are shaped like the seed, whole, expanded, plano-convex, and independent of one another, with a fissural base. The plumule is well developed in pinnae. The radicle is conical, slightly prominent, and mostly covered by the cotyledons (Hutchinson 1964; Niembro 1982, 1983).


2cm
2cm
1cm
1cm

Erythrina berteroana Urb.

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FABACAEAE (BEAN FAMILY)

Erythrina neglecta (Dwyer and D'Arcy 1980)

Elequeme, gallito, machete, pernila de casa, pito, poró de cerca

The genus *Erythrina* contains more than 60 species (Krukoff and Barneby 1974) distributed through the Tropics and subtropics in a wide variety of habitats (Neill 1988) in both the Old and the New World; its 100 species include *E. berteroana* (Krukoff 1982). *Erythrina berteroana* grows from southern Mexico to Colombia and Venezuela in South America (Dwyer and D'Arcy 1980, Holdridge and Poveda 1975).

Erythrina berteroana is a small, deciduous tree that reaches 12 to 15 m in height and 20 cm d.b.h. (Holdridge and Poveda 1975). The branchlets are smooth, lustrous, and armed with thorns. Leaves are trifoliate with leaflets 5 to 17 cm long, 5 to 20 cm wide, obliquely ovate to ovate rotund or with the terminal leaflets subrhomboidal, as wide or wider than long, shortly acuminate apically, widely cuneate basally, adaxially glabrous, and minutely puberulent beneath, often appearing glaucous. Petiolules are up to 1 cm long, glabrous, and often a different color than the rachis. Petioles are 4 to 15 cm long and glabrous. The tree grows from sea level to about 1800 m, in areas where rainfall ranges from 1500 to 4000 mm per year (Budowski 1997). The tree grows in acid soils (up to pH 4) with high aluminum saturation (more than 50 percent) and in a wide range of temperatures. It is also presumed that in high elevations it is frost resistant (Kass 1994).

Erythrina berteroana wood has a specific gravity of about 0.30 and it is recognized by its abundant axial and radial parenchyma with thin cell walls (Baretta-Kuippers 1982). The timber is light, coarse, and unattractive and lacks durability. In Central America the tree is most frequently used as a living fencepost. It has a more limited use as fodder for cattle and goats (Centro Agronómico Tropical de Investigación y Enseñza 1986b). Crude protein content ranges from 21 to 30 percent with an average of 25 percent, and digestibility ranges from 37 to 57 percent (Kass and others 1993).

Inflorescences are terminal and up to 0.5 m long. The tree flowers December through March. Flowers have a calyx that is narrowly campanulate, 16 mm long and 4 mm wide, stiffly carnose, and minutely puberulent. The banner is elliptic, 80 mm long and 20 mm wide, thick petaloid, and glabrous. The wings are oblong, 10 mm long and 2.5 mm wide; the keels are suborbicular, 8.5 mm long, and 6.5 mm wide. Stamens are diadelphous with an odd stamen free at the base and nine others of two lengths united to the middle of the sheet. The pistil has a slender ovary and a style 30 mm long. The stigma is capitate (Dwyer and D'Arcy 1980). The species is pollinated by hummingbirds (floral nectar has a 25-percent sugar concentration) (Baker and Baker 1982). Fruitification usually runs February through April, later in high elevations. Fruits are capitate and moniliform pods up to 30 cm long and 1.5 cm wide with a 2.5-cm long stipe. Collectors know the pods are mature when the color turns to dark brown. Seeds are red and less than 10 mm long with a black line from the hilum (Krukoff 1982). They have a hard, impermeable seedcoat.

Pods are usually collected directly from the tree between April and July according to elevation. Seeds collected from Santa Maria de Dota (1550 m, 2051 mm annual rainfall) and Laguna Alfaro Ruíz (1800 m, 1921 mm annual rainfall) average between 3,100 and 3,900 per kg (Centro Agronómico Tropical de Investigación y Enseñza 1986b). A single tree in a living fence that is pruned annually may produce 30 to 50 pods or 80 to 120 g of seed per year. Seeds may be stored in cold chambers at 5 °C with a relative humidity of 30 to 40 percent for more than 1 year (Víquez and Camacho 1993).

When *E. berteroana* is propagated by seed, either simple scarification to permit moisture to penetrate the seed or a 12-hour soak in warm water (40 °C) is a necessary pregermination treatment. Germination rates of 85 to 90 percent have been obtained in nursery trials using seeds collected during the previous year and stored in cold chambers at 5 °C with a relative humidity of 30 to 40 percent (Víquez and Camacho 1993).

Germination may be carried out in boxes filled with washed sand, and seedlings may be transplanted to black plastic bags filled with a mix of soil, sand, and compost (2:1:1 in volume). Nursery-grown seedlings can be planted in the field when they reach 20 to 30 cm tall. They can be established either by planting directly in the field or by removing seedlings from nursery beds and planting as bareroot stock, first removing all leaves (Víquez and Camacho 1993).

When vegetatively propagated, large cuttings, 1.5 to 2.5 m long and 6 to 10 cm in diameter, taken from 1- to 2-year-old branches may be planted up to 40 cm deep. This method is used to establish living fences. When the species is grown for forage production, cuttings may be planted closer, perhaps 0.5 by 0.5 m.

The species responds to regular pruning by producing a great volume of large-leafed shoots in 3 to 4 weeks (Russo 1993). Biomass production of 1 km of living fence varied according to pruning frequency: every 4 months produced 2100 kg per km per year of leaves and 1500 of woody biomass; every 6 months produced 1560 kg per km per year of leaves and 2100 of woody biomass and every 8 months produced 1125 kg per km per year of leaves and 2100 of woody biomass (Russo 1990).


2cm

Erythrina edulis Triana ex Micheli

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FABACEAE (BEAN FAMILY)

Erythrina edulis Triana ex Micheli (Jour de Bot. 6:145.1892); *Erythrina edulis* Posada-Arango; *Erythrina esculenta* Spague; *Erythrina lorenoi* F. Macbride; *Erythrina megistophylla* Diels (Secretaria Ejecutiva del Convenio Andrés Bello 1992)

Ante-poroto, balú, baluy, basul, bean tree, bucare, camentsa, Chachafruto, Chachapurutu, frijol de pobre, frijol nopás, frisol, frisol de monte, hijuela, ingano, Juatsembese, nopas, nupo, pajuro, pajurro, pashigua, pashuello, pisonay, poroto, poroton, poruto, sachafruto, sacha-poroto, sachaporuto, sachapuroto, sachapurutu, uswal, zapote de cerro (Acero and Barrera 1996; Barrera 1994a, 1994b; Secretaria Ejecutiva del Convenio Andrés Bello 1992)

Erythrina edulis is one of the 117 species of the genus *Erythrina* reported in the world (Neill 1993). In Colombia, it is one of the 13 species currently reported. *Erythrina edulis* is native to the Andean region and is found in the spur of the Andes mountain range; it is distributed in the sub-Andean forests [according to Cuatrecasas (1958)] or in humid subtropical forests (bh-ST) (Holdridge 1978) from Mexico, across Panama, to Venezuela, Bolivia, Colombia, Ecuador, and Peru.

Erythrina edulis is a leafy bean tree that reaches up to 14 m in height with a crown diameter of up to 7 m when allowed to grow freely. Its main stem is ligneous, and it can reach up to 47 cm d.b.h. (40-year-old trees). The tree grows at free exposure, accepts shade, and has a high demand for water in the first stages of its development. *Erythrina edulis* grows well in association with other trees, in soils with loose sandy texture or in heavy soils with adequate drainage. It does not grow well in acid soils with a pH less than 4.5. Although it is found between 1000 and 3000 m above sea level, the optimal elevation range for its growth is 1600 to 2200 m, with annual rainfall between 1800 and 2200 mm and temperatures between 15 and 24 °C.

Erythrina edulis is considered a multipurpose tree, ideal for agroalimentary programs, for the management of soils and watersheds, and for the stable increase of agroforestry and agropastoral systems. The beauty of the flowers promotes its use as an ornamental tree. Its flowers can also be used in salads and sweets and in infusions taken for anxiety and urinary problems. Its dried flowers can be used in floral arrangements.

Erythrina edulis is used in agroalimentary programs because the flour from the seed has a high protein content. At 23 percent dry basis it has a protein efficiency ratio (PER) of 1.15, which is higher than that of the kidney bean (0.88) or the lentil (0.91). The flour also has an index of essential amino acids (IEA) of 90, which is higher than that of the kidney bean (64) or the vetch (59) (DeSilvestre and Surco 1996). However, because the content of methionine and tryptophan is low, *E. edulis* becomes a complete food only when it is complemented with flours rich in methionine and a tryptophan such as corn, *Zea mays*, and dividivi (sesame seed). The resulting flour is used in cakes, sweets, soups, compotes, fritters, and creams. It also serves as a protein supplement for animals. The leaves, which contain more than 20 percent protein and have an acceptable digestibility of 59 percent that can be improved by combining it with other forages, are used as a protein supplement for ruminants. The complete, cooked fruit is used as pig and bird feed; the cooked seeds as bird feed. The raw seeds are fed to monogastric animals because they contain lectins.

In agroforestry programs, *E. edulis* is planted in rows 5 or 6 m apart to obtain a productivity of up to 170 k of fruits per tree per year in trees over 7 years old (Barrera 1992), in rows alternating with other crops, or as shade for crops. Its leaves decompose easily and serve as green manure. In silvopastoral programs, the species is planted in rows 2.5 or 3 m apart. It also serves as a protein bank when planted in rows at 1.5 by 1.5 m in a homogeneous crop or associated with other species. In Colombia, production of up to 80 tons of edible forage per ha per year has been reported.

The crimson red flowers are grouped in inflorescences defined as phylum racemes. If the soil provides adequate levels of potassium, the tree will flower and fruit at 3 years. An inflorescence has from 180 to 200 complete zygomorphic flowers with short pedicels grouped in triads around the floral axis. Only 15 to 20 percent of the flowers produce fruits, about 8 to 18 legumes per raceme. Legumes are hairless and cylindrical. Those with a diameter of 3 to 3.5 cm and a length of 15 cm will have 2 seeds; with a length of 36 cm, 6 seeds; and up to 55 cm, 9 to 11 seeds.

The greenish-white seed is a huge bean 3 to 7 cm long and 2.0 to 2.5 cm in diameter. It has a concave-convex configuration, made up of two cotyledons united by the flat part. The color of the testa varies with the state of ripeness and the morphotype, from chestnut to a dark-coffee color or from pink to dark red; lighter yellowish and black morphotypes have been observed (Acero and Barrera 1996). The seeds also vary by size. The dimensions are related to the food reserve stored in the cotyledons. A large seed averages a maximum diameter of 2.65 cm, a minimum diameter of 2.02, and a total weight of 26.28 g. A medium seed averages a maximum diameter of 2.03 cm, a minimum diameter of 1.55 cm, a length of 3.98 cm, and a total weight of 11.88 g. A small seed averages a maximum diameter of 1.68 cm, minimum diameter of 1.41 cm, a length of 3 cm, and a total weight of 6.03 g.

Reproduction by sexual seed is successful if seeds are planted promptly after harvest, even with no pregermination treatment. Tests showed 89 percent of emergence in seeds planted 10 days after harvest, 65 percent at 20 days, and 51 percent at 30 days (Mejía and others 1996). Vegetative reproduction of *E. edulis* is also successful by shoot, at 85 percent, and by stem cuttings of 3 to 5 cm in diameter, at 90 percent.

The seeds may be planted in 1 kg bags or can be sown directly if kept clean and protected with a good water supply. The rainy season is the best time for sowing. The seed is placed with the hilum facing down, allowing the back to be protected by a 1 mm layer of soil. The bud emerges in 9 to 15 days. If planted in a bag, the plantule is ready for outplanting in 20 to 40 days.

Lack of water during the first year limits plant growth. With enough water, a plantule 8 months old can reach a height of 2 m. To maintain a protein bank, the seedling should not be pruned until 15 months after the plantule is established.

ADDITIONAL INFORMATION

The cylindrical stem possesses trichomes shaped as thorns and has a shiny green color, starting at the insertion of the roots. At the apex of the main stem of the plantule, the arrangement of the branches from the third knot up changes in 20 to 30 days (Mejía 1993). The leaves are either simple or composite; they are inserted in the knots of the stem or in the lateral branches through petioles. The primary simple leaves appear in the second knot of the main stem; they develop in the seed during embryogenesis. They are opposite, simple, acuminate, and have a shiny green color. The first trifoliolate leaves appear after the knot of the primary leaves. From the third knot onward, trifoliolate leaves are formed to elongate the stem; it can be observed that in the stem there are, at the level of each knot, other organs such as stipules and branches.

The seed is made up of the testa and the embryo, which consists of the plumule, the two primary leaves, the hypocotyl, the two cotyledons, and the radicle. The plumule-radicle complex is located between the cotyledons; it occupies only a very small part of the empty space between the cotyledons.

After the radicle emerges, the epicotyl lengthens, forming an arc; the cotyledons remain covered (hypogeous germination), and finally the bud emerges above the ground with the two real leaves. The leaves develop in the plumule, continuing the growth of the terminal bud.

Nematodes limit the growth and productivity of *E. edulis*. Plantules with nematodes show dwarfism, yellowing, and low production of foliage. In Colombia, the following nematodes have been identified: *Longidorus* sp. (Orjuela and others 1996) and *Helicotylenchus* sp., *Hoplotylus* sp., and *Meloidogyne* sp. (Barrera 1994a, 1994b).

Most of the insects associated with *E. edulis* are found in the foliage and belong to 29 families of 7 orders of insects and 4 acari, establishing diverse types of relationships: Order Lepidopterous, family Tortricidea (borer of the fruit and seed); family Pyralidae (borer of the fruit and seed); possibly *Terestia meticulosalis*; another Pyralidae (borer of the stem of plantules in a tree nursery setting and in the field); an insect of the order Hymenoptera, family Tenthredinidae (skeletonizer of leaves); and one Hemipteran from the family Miridae (sucker of foliage) (Palacios and others 1997).


2cm
2cm

Erythrina fusca Lour.

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FABACEAE (BEAN FAMILY)

Erythrina glauca Willd, *Erythrina caffra*, *Erythrina atrosanguinea*

Agua inmortal, aheyote, amasisa, anahuco, bucare, bucare anauco, búcaro, bucayo, cachimbo, canatagallo, galleto, guiliqueme, maté bravo, maté manso, orornoque, palo prieto, piñon francés, pito, poró, poró blanco, saibo, swamp inmortalle, water inmortalle (Acero 1985, Russo 1993, Sánchez and others 1993)

Erythrina fusca is one of 117 species in the genus. With seeds that float and can be dispersed by oceanic currents, it grows in both the Old and New Worlds. It is amply distributed along the coasts and rivers in the Neotropics, Asia, Oceania, Madagascar, Mascarene, and Africa (Neill 1993, Russo 1993). Seeds are also dispersed to the middle of savannas by large birds and cattle. These animals drink near the trees during periods of rain, dispersing the seeds to other areas during periods of drought. In tropical America, *E. fusca* is indigenous from Guatemala to Peru, Bolivia, Brazil, and Venezuela (Little and others cited by Sánchez and others 1993). It has also been reported in Mexico (Holder and Poveda cited by Russo 1993).

Erythrina fusca is a free-growing tree that can reach 20 m in height. The stems of young *E. fusca* have sharp thorns that become warts or very thick thorns in adult trees. Its leaves are trifoliolate with green folioles on the front and whitish-green folioles on the back, coriaceous or semicoriaceous, ovate with a maximum width of 10 cm and a maximum length of 17 cm. Some authors cite that the tree is deciduous. In Colombia it is considered an evergreen species. In droughts a slight defoliation can be observed, but as soon as flowering begins new leaves appear (Sánchez and others 1993). The species grows in soils either subject to flooding or with shallow phreatic levels. Patches of this species are found in swamps and in areas with periods of rain and drought. *Erythrina fusca* is generally associated with clayey soils, with a neutral pH, and with high saturation of cations, but in some areas it grows very well in ultisol soils with an acid pH and fairly saturated.

Erythrina fusca is used as an ornamental in Costa Rica, Mexico, Venezuela, and Brazil. In Colombia and Costa Rica the tree is used as shade in coffee and cacao plantations and to form living fenceposts. It is also used in agroforestry systems, especially in those areas with extreme climates, high phreatic levels, and difficult soils. In Colombia the generally weak wood is used to make drawers (Acero 1985). The flowers are used as food in Guatemala (Blohm cited by Sánchez and others 1993) and in northeastern Colombia. In Latin America the flowers are used as an ingredient in tortillas, soups, and salads. According to Hasting (cited by Sánchez and others 1993) it is used as a poison in fishing because it possesses at least three alkaloids of phylum curare. In Costa Rica *E. fusca* was used as green manure in parcels of corn and beans at a rate of 16 tons per ha of fresh matter in the first year and the first half of the second year, and crop productivity was good when compared to other treatments (Lebuf 1993). Furthermore, a mulch of *E. fusca* in the soil effected a decrease in runoff and loss of soil compared to other treatments.

Another test in Colombia showed that the productivity of dry biomass of *E. fusca* in monoculture at 2 by 2 spacing and 2,500 trees per ha reached only 2.6 tons per ha, while *Gliricida sepium* (Jacq.) Kunth ex Walp. under the same conditions reached 13.0 tons per ha. Although the content of nitrogen in *E. fusca* (27.4 to 31 g per k) is lower than those of other forages (*E. poeppigiana* (Walp.) O.F. Cook: 37.2 g per k, *Gliricidia sepium*: 39.0 g per k), *E. fusca* does not lose its leaves in the dry season, thus providing forage throughout the year.

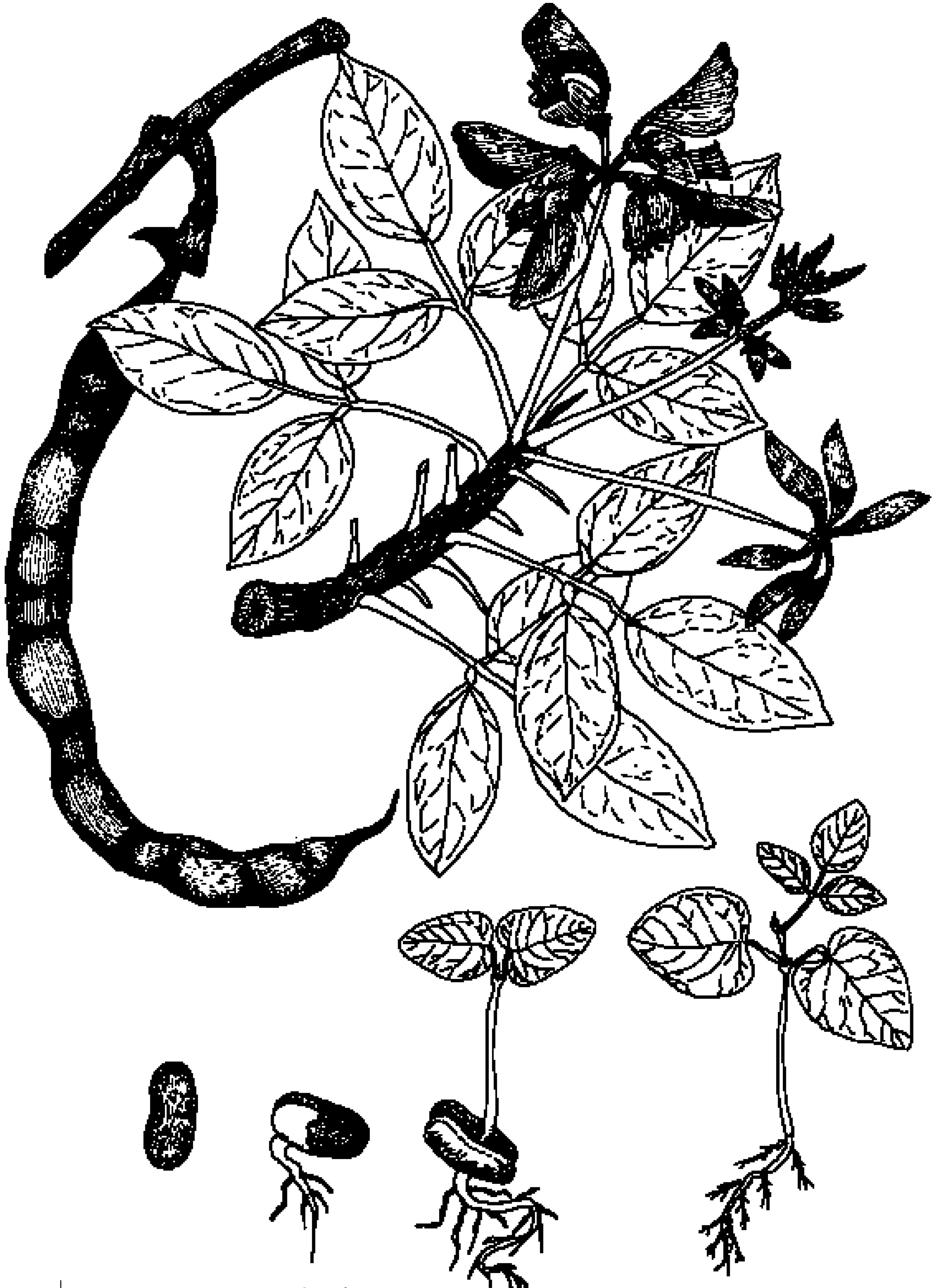
In another test, *E. fusca* showed a 90 percent survival in acid soils (pH 4.3) with a saturation of A1 of 80 percent. When compared to other species inherent to the region (*Albregia saman* and *Delonix regia* (Bojer ex Hook.) Raf.), which have 100 percent survival, *E. fusca* grew better and surpassed them in tolerance against attacks by ants. In spite of these adverse conditions, *E. fusca* retained its leaves (Sánchez and others 1993).

The tree's salmon-colored inflorescence has complete flowers that group in hanging racemes. When the collapsed pods ripen, they twist on their central axes, freeing coffee-colored seeds with black longitudinal stripes. *Erythrina fusca* seeds average about 2,250 per kg.

Most of the *Erythrina* species are easily disseminated through seeds and through cuttings. The soft seedcoat facilitates germination and if the seeds are submerged for 24 hours in water at room temperature, germination is accelerated. Tests in seedbeds showed germination rates of 95 percent for *E. fusca* using seeds stored for 1 year in a cold chamber at 5 °C with a relative humidity of 30 to 40 percent (Viguez and Camacho 1993) or for fresh seeds planted in a medium made up to 50 percent soil and 50 percent sand (Sánchez and others 1993).

Vegetative dissemination is very successful with 2-year-old cuttings 1.5 m long. A 90 percent success rate in the establishment of *E. fusca* has been reported when incisions 20 to 40 cm from the bottom cut are made to stimulate root production (Viguez and Camacho 1993). The cuttings of *E. fusca* may be planted immediately or stored for 2 weeks in a cold room or shaded place. Storage must be vertical.

Even though a complete study of diseases has not been done, a rust whose causing agent is *Dicheirinia binata* has been documented (Figueiredo and others cited by Sánchez and others 1993).



Erythrina poeppigiana (Walp.) O.F. Cook

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FABACEAE (BEAN FAMILY)

Erythrina micropteryx

Amasisa, elequeme, gallito, helequeme, poró extranjero, poró gigante, (Geilfus 1994, Gentry 1993, Holdridge 1970, Holdridge and Poveda 1975, León 1987, Salas 1993)

Erythrina poeppigiana, a tree native to the Tropics of America (from Panama to Bolivia), Africa, and Asia, has been planted in many parts of Central America and the Caribbean (Geilfus 1994, Holdridge 1970, Holdridge and Poveda 1975, León 1987).

Erythrina poeppigiana is a fast-growing tree, reaching 30 to 35 m in height and more than 1 m d.b.h. The gray bark has conical thorns, primarily on the branches and young twigs. The leaves are made up of three wide folioles gathered in long petioles, with two prominent glands among the leaflets; the petiole of the terminal leaf is widened near the lamina. The species grows well in tropical and subtropical zones, in wet and dry forests (Gentry 1993). *Erythrina poeppigiana* is not demanding of soils, growing very well in heavy soils poor in nutrients and adapting to acid soils. It grows in wet and dry areas with a range of precipitation of 800 to 1880 mm, temperatures from 22 to 24° C and elevations from 300 to 1150 m in Nicaragua (Salas 1993).

Erythrina poeppigiana is a species with multiple uses. It is widely used as a shade tree for perennial plantings. It produces a great amount of foliage and when pruned at 4 or 5 m, provides excellent shade for coffee and cacao plantings. Generally, the species is very important in the development of agroforestry systems. The trees grow very quickly, producing a great amount of biomass. Because the roots develop abundant nodulation that allows them to better fix nitrogen, the trees are used in soil conservation and recovery programs (Russo 1984). Used as green manure, they yield abundant foliage (Nygren 1995, Nygren and Ramírez 1995). The species is also used frequently to drain very wet soils (Geilfus 1994). In Costa Rica, up to 20 tons of leaves and stems per ha per year of *Erythrina spp*. have been collected, which is close to 450 kg of nitrogen (approximately 60 sacks of nitrogen, phosphorous, and potassium at 15 percent). The yields of perennial plantings and pastures may be notably improved in association with *Erythrina* species. The species is also used as posts in hedges, wind breaking curtains, props for vegetables, and forage (Geilfus 1994, León 1987). Because the wood is light and lacks durability, its use is limited to general carpentry and the manufacturing of tools, chairs, toys, decorative objects, and kitchen utensils. The bark, seeds, and roots have medicinal properties because they contain some alkaloids. They are also used in insecticides. The roots and parts of the tree are macerated and used to stun fish so they can be caught easily. The trees are planted as ornamentals and the seeds are used in necklaces and ornaments. The flowers are used in apiculture and as a condiment (Gentry 1993, Salas 1993).

Flowers cover the crown during the dry season in February and March, before the tree leafs out. The red or orange flowers are in erect racemes and the upper petal is wide and open. The fruits are pods 10 to 25 cm long, generally twisted, with orange-gray to coffee-colored seeds (Geilfus 1994, Gentry 1993, Holdridge 1970, Holdridge and Poveda 1975, León 1987, Salas 1993).

Erythrina poeppigiana is commonly propagated through the stem cuttings from pruning management in agroforestry systems. The stem cuttings must come from branches no less than 2 years old, in trees 5 to 8 years old. Fortunately, the trees can withstand periodic pruning, sprout quickly, and develop vigorous shoots. Stem cuttings 0.5 to 2 m long are used, and branches that grow vertically or the apex of the main stem are preferred. When propagated through seeds, which may be stored for a long time, the species germinates easily without pretreatment; the seeds may be planted directly in the field (Geilfus 1994, Russo 1984). Seeds number 200 to 7000 per kg.

ADDITIONAL INFORMATION

The genus Erythrina has been located in the subtribe *Erythrininae* of the Phaseolaceae tribe (Fabaceae - Faboideae), along with eight other genera: Strongylodon, Mucuna, Butea, Sphatolobus, Apios, Cochliantus, Rhodopis, and Neorudolphia (Lackey 1981).

Its value as a nitrogen-fixing plant, its rapid growth, its ability to sprout, and its adaptability to relatively acid soils make this a useful alternative in wet tropical areas. Esnaola and Ríos (1994) obtained weight increases of 326 to 820 g per animal per day as they increased the amount of *E. poeppigiana* in the diet of goats raised in stables. They conclude that *E. poeppigiana* leaves are a valuable resource in the nourishment of nursing goats. The studies showed good increases in the weight of milk goats, young goats, and growing kids without the animals showing any signs of toxicity. Rodríguez and others (1984) recommend comparative tests at different locations to establish possible consumption tendencies. *Erythrina poeppigiana* foliage has a raw protein content of more than 100 percent compared to the grasses commonly used in Central America (Benavides 1994, Benavides and Alarcon 1990). Excellent results are obtained when the foliage is combined with high energy foods, such as bananas, because it increases animal weight faster when it is combined with sources of starch rather than simple sugars.

When *E. poeppigiana* is well nodulated with *Bradyrhizobium spp.* it is one of the most efficient nitrogen fixers of all species used in agroforestry (Nygren 1995, Nygren and Ramírez 1995). Its nodules are restored by pruning and apparently, branch pruning influences the economy of nitrogen in the whole system. A large reserve of carbohydrates encourages vigorous sprouting after pruning. If the interval between each pruning is too short to restore this reserve the trees lose vigor.

The dependency of *E. poeppigiana* on mineral nitrogen from the soil during the weeks after pruning indicates that competition for nitrogen is a potential disadvantage of the species. Nygren (1995) found that *E. poeppigiana* and the coffee bean (*Phaseolus vulgaris* L.) compete for nitrogen at the beginning of the cultivation cycle. However, the yield of the bean has been excellent during 10 years of testing. The initial competition may favor the nodulation of the bean, resulting in a good supply of nitrogen in the pod-filling stage, when there is more demand for it. The apparent intolerance of the species to frequent pruning justifies the tradition of pruning only twice per year in coffee plantations.

A smaller biomass of underbrush has been reported growing under the shade of *E. poeppigiana* in contrast to other species, such as the *Gliricidia sepium* (Jacq.) Kunth ex Walp. This smaller biomass can be attributed to a decomposition rate of *E. poeppigiana* leaves that is lower than that of the Gliricidia.

Using *E. poeppigiana* to shade coffee and cacao plants is questionable for three reasons. First, the trees lose their leaves during the dry season; second, the tree's system of superficial roots does not withstand strong winds; and third, the branches are brittle (Geilfus 1994, Salas 1993). If used to shade plantations, pruned trees should be spaced at 6 by 6 m; if they are allowed to grow unpruned, the spacing should be 12 by 12 m.

Eucalyptus brassiana S.T. Blake

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MYRTACEAE (MYRTLE FAMILY)

No synonyms

Eucalipto

Eucalyptus brassiana occurs in the northeastern Cape York Peninsula, Queensland, as far south as Helenvale, Australia, where it grows on seasonally flooded flats and depressions, well-drained rocky slopes and some slightly undulating plains, in woodlands and open forests in poor soils. The species also occurs in southwestern Papua, New Guinea (Flora de Australia 1988).

Eucalyptus brassiana is a fast-growing tree that can reach 30 m in height. In general, its form is poor. The whitish or grayish bark is smooth, and comes loose in narrow strips or fringes. The young branches are hanging and frequently reddish. The young leaves are opposite or alternate, petiolate, widely oval, whole, and glabrous. Adult leaves are lanceolate, sometimes curved, hanging coriaceous, acuminate, 7 to 20 cm long, with a yellowish or reddish middle vein. The tree shows promising growth in loose sandy soils. It grows in moderately deep soils with a medium to low fertility. Calcareous soils delay its growth. It grows at elevations from sea level up to approximately 1000 m, with an average annual temperature of 25 ^{o}C and annual precipitation of 600 to 1400 mm. The species is found in vegetal formations of the Tropical dry forest (bs-T) (Florence 1996).

The wood of *E. brassiana* is used for pulp and in plywood and agglomerate boards. It is also used as crossbeams, long-lasting posts, and pilings and in construction, cabinetmaking, and general carpentry. Finally, it is used as a shade tree and in bee-keeping operations.

The flowers are white, pedicellate, medium, and arranged in axillary umbels that are isolated. Each umbel has many flowers with pedicels or cylindrical peduncles. The hemispheric fruit measures 6 to 10 mm long, with a convex shoot and three valves.

Because knowledge about *E. brassiana* is limited, the following information is about the *Eucalyptus* genus.

The fruits are separated from the branches by hand or scissors and are placed in paper bags. They must be kept well ventilated to prevent attacks by fungi, and they should not be exposed to high temperatures. Fruits can be dried in the open air or in an oven. When dried, the fruits quickly begin their dehiscence.

Eucalyptuses, in general, produce a great quantity of seeds, which vary greatly in size, shape, and color. The ripened seeds can be kept viable for 5 to 30 years if they are stored in sealed containers at a low moisture content (8 to 10 percent) and a temperature of 3 to 5 ^{o}C. Before storing, the seeds must be treated to protect against insects and fungi.

Most *Eucalyptus* seeds germinate well without pregermination treatment, but some species require cold and humid stratification to break latency. This treatment consists of moistening the seeds and placing them in a cold chamber (3 to 5 ^{o}C) for 2 to 10 weeks. The appropriate temperature for germination is 20 ^{o}C. Complete germination occurs in 10 to 21 days, depending on the species.

The substrate for sowing can be sand, vermiculite, or sifted vegetal soil. The substrate must be carefully sterilized before sowing. A simple sterilization method involves using a 3-percent sulfuric acid solution in water, at a rate of 3 L per m^2.

After the seeds are planted, the surface is moderately packed down, covered with a thin layer of sand or fine soil, and watered again. Until the plantules finish emerging (10 to 20 days) the seedbeds must be kept in the shade; they can then be uncovered during the cooler hours. As they strengthen they can be left under direct light and become ready for dibbling. Pesticides must be applied for 30 to 45 days.

Because *Eucalyptus* is very susceptible to competition, especially from grass, the site should be cleaned. Burning after cleaning is a very common practice; removal of woody material facilitates planting, provides good control of the competition, and liberates a great amount of nutrients. However, burning does damage microorganisms in the soil. If the soil is poor or overpastured, plowing, subpaving, or fertilizing is necessary (Prado and Barros 1991).

Eucalyptus camaldulensis Dehnh.

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MYRTACEAE (MYRTLE FAMILY)

Eucalyptus rostrata

Eucalipto

Eucalyptus camaldulensis is native to Australia. Those specimens that originated in Peford and Gibb River, Australia, showed the best growth when planted in some areas of Central America and southwestern America (Lamprecht 1990).

Eucalyptus camaldulensis is a fast-growing tree 25 to 30 m in height and 1 m d.b.h. The crown is generally very sparse. The bark comes loose in the shape of rounded scales, producing a silvery grayish and reddish-brown shaft. The matte green leaves are lanceolate and alternate and measure 15 to 22 cm in length. The species adapts to a wide range of soils, from very poor to periodically flooded. It also grows in soils that are compacted by overpasturing or low annual humidity; however, growth there is not optimal. Changes in soil type within short distances result in very extreme changes in growth. In very shallow or compacted soils, radicular growth is hindered. The trees grow in temperatures ranging from 20 to 28 ^{o}C and elevations ranging from sea level up to 1000 m. In Colombia, the species has been planted where precipitation is between 600 and 2900 mm and it can endure 4- to 8-month-long droughts. It also endures moderately strong winds. It grows in vegetal formations of the Tropical dry to wet forest (bs/bh-T).

Traditionally, this strong wood has been used in heavy construction and for building interiors, wooden rollers, short-fiber pulp, paper, plywood, and agglomerate boards. It is used in cabinetmaking and carpentry and for crossbeams, transmission poles, firewood, and charcoal. It is also planted to shade and protect and to produce excellent-quality honey.

The fruit measures approximately 4 by 6 mm. The seeds are gathered directly from the tree and dried in the sun. Viable seeds average 348,000 per kg. The seeds can be stored up to 9 years if they are placed in hermetic containers at a temperature of 3 to 5 °C and a moisture content of 5.5 to 10 percent.

Normally, the seeds of this species present high germination percentages (greater than 90 percent) without pregermination treatment. Germination in the laboratory occurs in 5 to 16 days (Trujillo 1983).

About 60,000 plantules are obtained from 1 kg of seed in nurseries. The recommended substrate consists of two parts sand and one part soil, which must be disinfected before planting the seeds. Seeds must be sowed deep enough to prevent uncovering when watered, but they must not be too embedded. The plantules are lifted when they are 5 to 7 cm in height.

For all *Eucalyptuses*, the texture of the medium of germination must be fine. A fertile mixture of soils with sand in a proportion of 1:1 must be used. The seeds can also be planted directly into bags using special devices, such as syringes, to place two to four seeds in each bag. The germination period for this method ranges from 4 to 5 days. The plantules grow quickly and reach a height of 40 to 50 cm in 16 to 18 weeks. However, the stems should be pruned to induce more lignification. The plantules require periodic watering in the first stages of development and to prevent damping off, cupric fungicides should be applied.

Weeding and burning of underbrush are recommended before planting. In the first stages of establishment, the presence of underbrush, vertisols, calcareous soils, or sandy soils with low moisture retention limit growth. Recommended planting densities for firewood are 2,500 and 1,600 trees per ha; for other uses, distances of 4 by 4 m between trees are recommended (Martinez 1991). Attacks by defoliating ants, fungi, and cancer delay growth when the trees are planted in very compacted or shallow soils. Locusts and insects can cut trees of up to 3 cm in diameter. Young trees are attacked by many Lepidoptera larvae, termites, and borers, including *Gonipterus sp.* scarab.

Eucalyptus saligna Sm.

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MYRTACEAE (MYRTLE FAMILY)

No synonyms

Eucalyptus

Eucalyptus saligna is a fast-growing, straight-shafted tree that may reach 35 to 55 m in height and 120 to 150 cm d.b.h. The smooth bark has a light tone, frequently with a bluish shine, and it comes loose in long strips down to the base of the shaft. The young leaves measure 3 to 6 cm long and 2 to 3 cm wide and they have short, opposite petioles. The leaves of the older trees are narrow and lanceolate (10 to 20 cm long and 1.5 to 3 wide); they have a fine, uniform nervation, and are alternate. The species requires deep soils with good drainage and clayey, loose clayey, loose sandy or sandy textures; it endures slightly acid pH with a tendency toward neutrality. It grows well in flat to slightly rolling areas. *Eucalyptus saligna* develops best in loose, alluvial muddy-sandy soils, well drained, and of volcanic origin. In Colombia, it grows at elevations between sea level and 2100 m, with temperatures ranging from 2 to 35 °C and an annual average of 22 °C. Annual precipitation must be 800 to 4000 mm, with 4 to 5 months of hydric deficit. It demands light but resists drought periods. The species is moderately resistant to frost. It grows in formations of Tropical wet forest (bh-T), wet and very wet Tropical forest (bh/bmh-T), and Pre-Mountainous wet forest (bh-PM) (Lamprecht 1990, Pereíra 1989).

The wood of *E. saligna* is used in heavy and light construction and for furniture, boxes, and plank molding. It is primarily used for pulp, plywood, and agglomerate boards; in cabinetmaking and carpentry; and as crossbeams, long-lasting posts, and pilings. As round wood, it is used as transmission poles (with a duration of approximately 5 to 10 years), firewood, and charcoal.

Inflorescences develop with approximately 7 to 11 flowers in the axils of the leaves. The fruits are ovoid to cylindrical with an average size of 7 by 5 mm. A valve in the upper part of the fruit opens when the fruit ripens.

Because the trees are tall, manual gathering of seeds is difficult. Viable seeds average 275,150 per kg (Flora de Australia 1988, Lama 1986). Seeds can be stored up to 8 years if they are placed in hermetic containers and kept at 4 °C with a humidity content of 4.3 percent.

Germination in the laboratory occurs in 4 to 16 days. About 60,000 plantules are obtained from 1 kg of seed in nurseries (Trujillo 1983). The recommended substrate is two parts sand and one part soil, which must be disinfected before planting the seeds. Seeds must be sowed deep enough to prevent uncovering when watered, but they must not be too embedded. Plantules are lifted when they are 5 to 7 cm high.

This species can also be propagated by asexual means using spikes from superior trees, rooted in individual containers.

The soil at the planting site should be fertile and the underbrush should be controlled during the first stages of establishment. Very compacted soils or soils with drainage problems must be avoided. Planting densities range from 1,600 to 2,500 trees per ha (Lamprecht 1990, Pereíra 1989). The species is susceptible to attacks by ants and by the *Diaphorte cubensis* fungus (Pinzón 1997).


2cm
1cm

Eucalyptus tereticornis Sm.

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MYRTACEAE (MYRTLE FAMILY)

Eucalyptus umbrellata (Gaertn) Domin.

Blue gum, eucalipto tereticornis, forest red gum, mountain gum,
my sore gum, red iron gum

Eucalyptus tereticornis is located naturally in two areas. In New Guinea, the species grows between 6 and 10° latitude S, at elevations of 0 to 800 m. In Australia, it grows between 15 and 38° latitude S, from Victoria through New South Wales, and in northern Queensland at elevations of 30 to 1000 m. It has been introduced in many tropical and subtropical countries in Africa, Asia, and South America (Aguilar 1966).

Eucalyptus tereticornis is a fast-growing tree that can reach 30 to 45 m in height and 1 to 2 m in diameter. It has a straight shaft with a big crown that is moderately dense. The trunk has a straight base and cylindrical shaft. The smooth, whitish bark comes loose in thin laminas or long strips, producing whitish, gray, or bluish spots in patches and leaving an accumulation of old bark (dark gray, wrinkled) at the base. Leaves are first opposite then alternate, petiolate, narrow lanceolate, frequently curved, sharp-pointed apex, narrow at the base, slightly thick, shiny green on the right and back side, glabrous, with numerous fine veins at an acute angle to the central vein. The species grows in open forests or as scattered trees in alluvial plains and along streams, including brackish waters. It grows better in deep, well-drained, light-textured, neutral, or slightly acid soils. Outside its natural range, the tree has been planted in a great variety of places, including alluvial, muddy, and sandy clay soils (Aguilar 1966, Benitez and Montesinos 1988). It tolerates seasonal floods for short periods and can endure up to 15 freezes per year in the southern part of its natural range. In the South of China and Pakistan the species survives temperatures of -7 °C. The tree is planted amply in areas with summer rainfall and moderate to harsh dry seasons, although it does not tolerate long periods of drought. It thrives where annual precipitation is 800 mm to 1500 mm, but trees have been planted in areas with less rainfall (400 mm in India, 550 mm in Israel, and 580 mm in Zimbabwe) and in areas with considerably more rainfall (2180 mm in Colombia and 3500 mm in Papua New Guinea). It is found at elevations between 0 and 1000 m.

The reddish wood has a uniform texture and intercrossed grain and is difficult to work. With a caloricity of 22,100 kj per kg (5,280 kcal per kg), it makes excellent firewood and charcoal. Because it is hard and heavy (0.75 to 1.0), the wood is used in construction, mining stanchions and posts, drawers, particle boards, fiberboards, railroad ties, and pulp for paper. The wood is immune to termites and dry rot and is, therefore, one of the most durable and valuable woods for construction, especially underground. The trees are also used in the restoration and immobilization of dunes, to control erosion by wind, and as hedges. The species has also been used for the extraction of tannins and oils. The leaves are used for obtaining essential oils, and the flowers, for the production of pollen and honey. In agroforestry, *E. tereticornis* has been used in combination with crops. In Pakistan it has been used in combination with corn, especially during the first 6 to 12 months, and in India, with tapioca (yucca) during the first 2 years. The species is used a lot in forestation and reforestation in India, from the coastal plains to the Himalaya Mountains, and in Western Africa, especially in Zaire.

Each year the tree yields small racemes of white flowers, but only every third or fourth year in spring and summer does it yield abundant florescence. It has simple flowers at the base of the leaves. Each umbel has from 5 to 12 white flowers, scattered over an equal number of pedicels. The floral buds have a semirounded base and a thin, elongated, conical-shaped cover, similar to a horn. It is recognized by the conical, elongated operculum that encloses the fruits before they ripen. The fruits are in numerous seminal capsules, jutting out and curving inward. Each fruit contains numerous small, thin seeds that are approximately 1 mm in diameter and shiny dark brown to black. Seeds average 285,000 to 800,000 per kg with more than 70 to 80 percent viability (Jimenez 1997).

Seeds can be stored for several years at approximately 4 °C temperature and 60-percent relative humidity. The seeds are placed in plastic bags, which are then placed in metallic or glass fiber containers that are well sealed or hermetic.

Seeds do not require pretreatment to germinate; however, natural seeds, in Australia and Papua New Guinea, may need cold and wet stratification to germinate well (Centro Agronómico Tropical de Investigación y Enseñza 1984b). The substrate commonly used for germination is sterilized, fine, river sand. Under controlled conditions, seeds germinate well at alternating temperatures of 20 to 30 °C with 8 hours of light. Excess moisture in the substrate should be avoided to prevent attacks by fungi and bacteria during the germination process. Regeneration by sprouting has been used and can be done three or four times in 10-year shifts (Aguilar 1966).

ADDITIONAL INFORMATION

Yield depends upon humidity. The highest yields have been reported on the borders of canals and under conditions of irrigation. In irrigated plantations in Africa under good conditions, the tree will yield 20 to 25 m^3 per ha per year during the first 15 years; the yield then decreases to 10 to 15 m^3 per ha per year unless the trees are cut down for sprouting.


1cm

Eucalyptus urophylla S.T. Blake

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MYRTACEAE (MYRTLE FAMILY)

No synonyms

Eucalipto

Eucalyptus urophylla is very similar to *E. alba*. It is a fast-growing tree that can reach 15 to 20 m in height and 40 cm d.b.h. The shaft is well shaped. The bark is smooth, with cream or pink spots; the surface is covered by a floury substance. The young leaves are petiolate, ovoid-rounded to elongated, and alternate. In adult trees, the leaves are rather lanceolate. Although the species tolerates chemically poor soils, it must be planted in soils having a loose texture. It does not tolerate very clayey soils with a shallow phreatic layer. It grows better in soils that remain wet during the dry season (Lama 1986). *Eucalyptus urophylla* grows at elevations from sea level to 1200 m, with an average annual temperature of 24 to 28 °C and annual precipitation of 2000 to 3000 mm. It grows in the vegetal formations of the dry Tropical forest (bs-T) and wet Tropical forest (bh-T) (Endo 1992).

The wood is hard and does not split easily. It is used primarily for pulp and boards. It is also used as electrical transmission poles, long-lasting posts, and pilings, in light and heavy construction, cabinet-making and carpentry; and for plywood and agglomerate boards. It is useful in protecting river banks and providing shade. It is also a honey-producing species with good properties. Because the species has no major edaphic requirements, it is appropriate for reforestation, both in flooded soils and in dry soils of low tropical lands.

The fruits are found in rosettes of five to seven. They are separated from the branches by hand or with scissors and are placed in paper bags. They must be kept well ventilated to prevent attacks by fungi and they should not be exposed to high temperatures.

The weight of 1,000 viable seeds ranges from 1.4 to 2.5 g. Viable seeds average 210 to 650 per kg. The ripe seeds can be kept viable for 5 to 20 years if they are stored in sealed containers at a low humidity content (8 to 10 percent) and a temperature of 3 to 5 °C. Before storing, the seeds must be treated for protection against insects and fungi.

Most *Eucalyptus* seeds germinate well without pregermination treatment, but some species require cold and humid stratification to break latency. This treatment consists of moistening the seed and placing it in a cold room (3 to 5 °C) for 2 to 10 weeks. The appropriate temperature for germination is 20 °C. Complete germination occurs in 10 to 21 days, depending on the species. About 108 to 240 plantules are obtained from 1 g of seed in nurseries.

Seeds can be scattered or planted in furrows in seedbeds prepared with a normal substrate (soil and sand 1:1), previously moistened, and provided with shade at the beginning of development. The plantules are dibbled when they reach approximately 3 cm in height. Because the roots must be in clods of earth, dibbling is done to the bags. At the beginning, the planting material must be shaded and kept moist; shade and watering are gradually reduced to prepare the plantule for field planting. The plantules are transplanted when they are approximately 25 cm high at 100 to 150 days.

The underbrush must be removed from the planting site. The soil must be treated by totally breaking it up or digging large holes (50 by 50 by 50 cm). Generally, spacing is 2 by 2 m or 3 by 3 m; occasionally, it is greater. Protection against insects is necessary during the entire growing period. In plantations, growth is hindered by attacks from ants (Lama 1986).

Fraxinus uhdei (Wenz.) Lingelsh.

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OLEACEAE (OLIVE FAMILY)

Franixus americana var. *uhdei* Wenzig, *F. chiapensis* Luncell

Evergreen ash, fresno, shamel ash, tropical ash

Fraxinus uhdei is native to western and southern Mexico, Guatemala, and Honduras. It has been planted as an ornamental in other countries, including Costa Rica, Puerto Rico, and Hawaii.

Fraxinus uhdei is a fast-growing, deciduous tree. It can reach 10 to 20 m in height and 40 to 50 cm d.bh., and very old trees can be larger. The bark is brown, rough, and furrowed, and the crown is pyramidal. The inner bark of *Fraxinus uhdei* is whitish and bitter. The twigs are green, brown when older, and hairless except when young, with paired half-round leaf scars; the foliage is pale green. Leaves are opposite, odd-pinnate, without stipules, 15 to 30 cm long, and composed of 5 to 7 leaflets paired along a slender stalk. Leaflets are serrulate, 5 to 10 cm long, 2 to 5 cm wide, long-pointed at the apex, short-pointed or blunt at the base, finely saw-toothed on the edges, and slightly thickened; the upper surface is green and hairless; the lower surface light green with small hairs along the midvein. The species grows naturally in moist, wet forests and good volcanic soils, at elevations ranging from 500 to 1500 m, with an average annual rainfall of 1800 to 3000 mm and an average temperature of 18 to 23 °C.

The heartwood is brown and is suitable for timber production. It is used for baseball bats, paddles, and tool handles.

The flowers are very small, greenish in axillary panicles, and dioecious; the panicles are located at the sides of the twig, much branched, and 12 to 20 cm. The fruit is a samara with a small, nearly cylindrical, dark brown body, 0.75 cm long at the base, with a light brown wing 2.5 to 3 long and 5 mm wide extending down to about the middle of the body and slightly notched at the apex.

Trujillo (1996a) reported that seeds can be kept for several months in glass containers in hermetic conditions at 4 °C with a moisture content of 7 to 10 percent.

Trees planted artificially are obtained from seedlings of natural regeneration. Some of the planted trees in Puerto Rico were heavily attacked by peach aphis (*Aulacaspis pentagona*) (Little and Wadsworth 1974). The insect *Phassus triangularis* (Lep., Hepiolidae) has been observed boring the piths of this tree (Arguedas and others 1993).


1cm

Gmelina arborea Roxb.

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VERBENACEAE (VERBENA FAMILY)

No synonyms

Gamar, gmelina, gumhar, sor, yemane

Gmelina arborea is native to India, Bangladesh, Sri Lanka, Myanmar, Thailand, southern China, Laos, Cambodia, and Sumatra in Indonesia. The species was introduced into many tropical countries, including the Philippines, Malaysia, Brazil, Gambia, Costa Rica, Burgina Faso, Ivory Coast, Nigeria, and Malawi (National Academy of Sciences 1980, Soerianegara and Lammens 1994).

Gmelina arborea is a fast-growing, deciduous tree that can grow up to 30 m in height and over 80 cm d.b.h. The tree usually grows to about 20 m with a clear bole of 6 to 9 m and a high taper. The species is moderately adaptable and survives well on a wide range of soil types: acid soils, calcareous loams, and lateritic soils. It performs best on fresh, well-drained, fertile soils where rainfall annually varies from 1200 to 4500 mm, temperatures range from 12 to 45 °C, and elevations range from sea level to 1000 m (Lamb 1968, National Academy of Sciences 1980, Smitinand and others 1975, Soerianegara and Lammens 1994).

Gmelina arborea wood is relatively light with a density of 420 to 640 kg per m^3 and a calorific value of about 4800 kcal per kg (National Academy of Science 1980). The straw-colored wood is one of the best utility timbers of the tropics, where it is used in light construction, general carpentry, packaging, furniture, particle board, plywood, and matches. The wood produces average yields of paper with properties superior to those from most hardwood pulps. Its leaves can be used as fodder, and its flowers produce abundant nectar from which high-quality honey is produced (National Academy of Sciences 1980, Smitinand and others 1975, Troup 1921).

Gmelina arborea begins to flower and set fruit at about 6 to 8 years. Clusters of yellowish-brown flowers appear when the trees are generally leafless in January through March, but some trees flower and fruit throughout the year. The panicle is about 30 cm long and appears at terminal and lateral shoots; the bract is about 0.5 cm. The flower is about 2.5 cm in diameter. The fruits ripen during the last few days of April to late May. The fruit is a fleshy, oblong drupe, 2 to 3 cm long. The immature green fruits turn yellow with leathery shining pericarp, sweetish pulp, and a hard, bony, stone when ripe. The stone is 1.5 to 2.0 cm long, pointed at one end, and two- or three-celled with two or three seeds.

The fruits can be collected from the crown canopies or from the forest floor. Because fresh fruits are eagerly devoured by cattle, the seeds can also be collected from their excretion. However, collecting yellowing fruits from the trees is recommended. The fermenting of fallen fruits on the ground may induce a fungi attack that damages the seeds. Collecting ripe fruits from the trees ensures good seed quality from known sources. Tarpaulins or plastic sheets are placed under the trees to collect the mature fruits that fall when the branches are shaken. The fruits are soaked in cold water to facilitate seed extraction by hand or depulper. The Dybvig scarifier successfully extracts the seeds without presoaking. *Gmelina arborea* seeds average 1,250 per kg (Yap and Wong 1983) to 2,750 per kg (Hor and Pukittayacamee 1993). Fresh seeds can be stored in bags in a cool dry place for about 3 months without losing much viability. Fresh seeds show a 90-percent germination rate (Hor and Pukittayacamee 1993).

Seeds are soaked in tap water for 1 day before sowing. Floating seeds should be discarded because they have been aborted, are nonviable, or both. Seeds are sowed in loosened soil and covered thinly (0.5 to 1.0 cm) with soil. Seeds can also be dibbled directly into prepared containers with appropriate media. Germination occurs 7 to 21 days after sowing.

Young seedlings grow quickly and reach appropriate size for outplanting in 2 to 3 months when they are about 40 to 45 cm high. Stump planting is also practiced (Troup 1921). *Gmelina arborea* coppices well after felling. Coppicing shoots are ready for rooted-cutting production when they are about 60 days old. A section of half-leaf single node is commonly used for rooting with or without rooting hormone. However, treatment with rooting hormone may induce earlier and more vigorous rooting than no treatment (Hijoyo 1993). *Gmelina arborea* cuttings root well when the relative humidity is above 80 percent and the temperature is lower than 30 °C.

Goethalsia meiantha (Donn. Sm.) Burret

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TILIACEAE (LINDEN FAMILY)

Luehea meiantha, Goethalsia isthmica

Guácimo blanco

Native to the Philippine islands (Carpio 1992), *Goethalsia meiantha* now grows from Nicaragua to Colombia (Rojas 1983). In Costa Rica the species is common in the Sweet Gulf and the North Huetar region.

Goethalsia meiantha is a medium-size tree with a straight trunk and smooth bark that can reach a height of 15 to 45 m and 35 to 250 cm d.b.h. (Rojas 1983, Standley 1937). The tree grows in clayey soils at elevations from 270 to 900 m in areas where annual precipitation is 4000 mm and average temperature is 26 °C.

The wood is white when green, classified as light (specific gravity is 0.35) and soft and dries quickly without the appearance of major defects. It is easy to work and preserve and it finishes well; however, it has a low resistance to biodegrading organisms. It is used for fenceposts, handles for light tools, boxes, cases, broomsticks, and roof boards and in interior and exterior construction (Carpio 1992). The species ranks second in demand in the match industry, because it is very abundant and grows fast (Rojas 1983).

The flowers appear in August. They show axillary or terminal inflorescence, cyme type; the flowers are hermaphroditic, yellow, and small. The dark green fruits are jointed in threes, indehiscent, and winged. Each fruit is approximately 10 cm long and 6 cm wide, with two locules, and develops one or two pulpy, pyriform seeds. Few seeds are viable, because only one of the three joined fruits has an embryo (Moreira and Arnáez 1992, 1994).

The fruit is collected in February, April, and October. Fruits should be collected directly from the tree when they start to turn dark brown. The fruits are spread on the ground to dry and then planted.


1cm
2cm

Grevillea robusta A. Cunn. ex R. Br.

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PROTEACEAE (PROTEA FAMILY)

No synonyms

Gravilea, grevilea, pino rojo, roble australiano, roble de pelota, roble sedoso, silky oak

Gravilea robusta is naturally distributed in Australia, between latitude 25 and 39° S in Queensland and New South Wales. It can also be found between latitude 13 and 21° S. This species has been planted in tropical and subtropical countries such as Guatemala, Costa Rica (starting at 1000 m), eastern Africa (1200 to 1800 m), Sri Lanka (600 to 2000 m), India (300 to 1800 m), Java (50 to 2000 m), Israel, Cyprus, and South Africa. It grows naturally in coastal rain forests along with *Eucalyptus* sp. or frequently in small, pure patches.

Grevillea robusta is an evergreen tree, reaching heights of 30 to 35 m and diameters of 50 to 60 cm. The shaft is usually straight and very cylindrical, although it has a tendency toward bifurcation. The crown is generally long, narrow, and quite sparse. The limbs are deeply lobed in the upper side, with acute lobes, sometimes reaching the main vein, narrow and whole in the lower side; the back is hairy and whitish; the right side is glabrous. The tree has a strong smell. The bark is dark gray, deeply cracked, and brittle (Centro Agronómico Tropical de Investigación y Enseñza 1984a). The leaves are bipinnately compound and alternate, emanating from 15 to 20 folioles which are narrow and lanceolate, measuring 2.5 cm in length; the right side is smooth, and the back is grayish-silvery (Standley 1931). The tree develops a deep radicle system. It tolerates sandy and acid soils; can develop in shallow and flooded soils, although it does not grow much there and the shaft shape is poor; but clayey, heavy soils are not favorable. It develops well in loose-sandy soils, from fresh to wet, and with a pH between 5 and 7. It prefers soils with a high content of gravel (Benitez and Montesinos 1988, U.S. Department of Agriculture 1974). *Grevillea robusta* can grow at low and high temperatures. The species is considered relatively resistant to frosts. It grows at elevations between 600 and 2000 m. In Australia, it grows where annual rainfall is between 1200 and 1500 mm.

The wood is reddish brown and has beautiful streaks, especially in the knotty parts. It is hard, moderately heavy (specific gravity is 0.56), and flexible, with limited natural durability. It is very difficult to dry; it tends to crack and twist. The wood is used in carpentry, cabinetmaking, veneer, molding, boxes, interior finishes, furniture, sheets, parquet floors, and plywood. Mixed with long-fiber wood, it is used in the cellulose industry. It is especially important as a high-value fuel, especially in semiarid regions. In Australia and in vast areas of other regions where it is cultivated, *G. robusta* is also valued as an ornamental tree for gardens, promenades, street borders, and parks (Standley 1931).

The flowers are orange, arranged in axillary shoots, and up to 2 cm long. A small, lignified follicular fruit grows from the floral peduncles. The fruits are dehiscent, with very irregular ripening. The fructification period occurs May through October, primarily occurring in May and June. The fruit contains one or two thin seeds with a consistency similar to that of paper. Seeds average 50,000 to 150,000 per kg with 60 to 80 percent viability.

Under normal storage conditions, seeds remain viable only 2 to 3 months after being gathered, and germination declines very rapidly. With a physical moisture of 7 to 8 percent, seeds can be stored for up to 2 years at a temperature of approximately 4 ^{O}C and 60 percent relative humidity. The seeds are placed in plastic bags which are then placed in closed containers. Seeds are recalcitrant; they germinate easily in a substrate of sand.


1cm

Guaiacum officinale L.

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ZYGOPHYLLACEAE (CALTROP FAMILY)

No synonyms

Bois de gaoac, bois saint, common lignumvitae, gaïac, gaïac franc, gaïc mâle, guayacán, guayacán colombiano, guayacán de playa, guayacán negro, guayaco, lignumvitae, palo santo, pau santo, pokhout, wayacá (Little and Wadsworth 1964)

The native range of *Guaiacum officinale* includes the South Caicos in the Bahamas, the Greater Antilles, most of the Lesser Antilles, coastal areas of Venezuela and Colombia, and Panama. The species is also native to Aruba, Bonaire, Curacao, and Tobago. Although present in Trinidad and Guyana, it may not be native there. However, because of development, harvest, and fires, *G. officinale* is extinct or near extinction on several Caribbean islands. The tree is planted as an ornamental in Bermuda, Florida, and other tropical areas (Francis 1993).

Guaiacum officinale is a slow-growing, small to medium-sized tree that reaches 3 to 10 m in height. Very old trees nearly 1 m d.b.h. have been reported (Francis 1993). The trunk, which is short and seldom straight, is covered with a smooth, mottled, gray-green bark and topped with a dense crown of dark green leaves. The tree is very hardy in dry and medium-rainfall sites, especially in coastal areas. Rocky limestone areas with 635 to 1570 mm of annual rainfall with a dry season of 2 months or more usually give the best results. If given protection from competing trees, the species will grow more rapidly in deep, rich, medium-textured soils. *Guaiacum officinale* grows from near sea level to 300 or 400 m in elevation (Francis 1993).

Guaiacum officinale sometimes grows in association with a sister species, *G. sanctum* L., but is not known to hybridize with it.

The wood of *G. officinale* is tough, hard, self lubricating, and resistant to sea water. It has a density of 1.20 to 1.36 g per cm^3 air-dried (Longwood 1962) and 1.05 g per cm^3 oven-dried (Chudnoff 1984). The wood was used historically for bushings, bearings, and pulleys for steam and sailing ships; today, it is principally used for carving, cutting boards, mortars, pestles, and charcoal. It has also been used to make a dye. Extracts of this wood have been used for hundreds of years in herbal medicine, although they are dangerous in large doses. For its beautiful flowers, fruits, and foliage, the species is widely planted as an ornamental, especially in the Caribbean area.

Flowering lasts for about 1 month and may occur from early spring to fall in Puerto Rico (Little and Wadsworth 1964) and from March through May in Cuba (Betancourt Barroso 1987). Not all trees in a stand flower at the same time. Trees in one forest planting began flowering and fruiting about 25 years after planting (Francis 1993). The 2-cm-wide blue flowers grow in clusters at the twig terminals. The orange to orange-brown fruits are flattened, two-chambered capsules. At maturity, they split open to expose two seeds that are covered with a red, fleshy aril (Little and Wadsworth 1964). Fruit and seed production is usually abundant. Fruits in one collection in Puerto Rico weighed an average of 0.39 ± 0.11 g each (Francis and Rodríguez 1993).

Fruits that are beginning to split can be picked up from the ground, picked by hand from low trees, or clipped with pruning poles. Usually, the seeds must be removed from the fruits. They can be removed by hand, or the fruits can be dried in the shade, soaked to soften them, and then wet-sieved to remove the pulp (Betancourt Barroso 1987). The seeds are dried and stored at 5 to 8 °C. However, stored seeds begin to lose their viability after 1 month (Betancourt Barroso 1987). An alternative strategy is to germinate the seeds at once and maintain the slow-growing seedlings in the nursery until needed. Air-dried seeds of *G. officinale* collected in Puerto Rico averaged 3,550 seeds per kg (Francis and Rodríguez 1993).

Germination is epigeous and begins within 10 to 12 days after sowing. In Cuba, up to 60 percent of fresh seeds germinate (Betancourt Barroso 1987). A test using Puerto Rican seeds resulted in 9-percent germination of fresh seeds, 5-percent with seeds stored for 1 month at 5 °C, 20-percent with seeds stored for 1 month at 26 °C, and 10-percent with seeds stored for 2 months at 26 °C (Marrero 1949). Another test of Puerto Rican seeds obtained only 7-percent germination in the first month, with an additional 41 percent germinating over the next 9 months (Francis 1993). In a test of several seed pretreatments, cycles of daily soaking and drying for 1 week gave the only improvement in germination over untreated seeds (Cooper 1986).

The seeds are usually germinated in trays or beds and transplanted when 2 to 4 cm in height. Seedlings for forest or ornamental plantings are grown in pots or nursery bags. The potting mix should drain well and contain some lime. Seedlings grow to 20 to 30 cm in 18 to 24 months, when they can be outplanted. Long-term weeding will promote successful forestry plantings. Because grazing and browsing animals carefully avoid the seedlings and saplings, planting in overgrazed areas could be a wise establishment strategy. Fire must be completely excluded.

Guajacum sanctum L.

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ZYGOPHYLLACEAE (CALTROP FAMILY)

Guajacum sanctum (orthographical variation, Missouri Botanical Garden 1999)

Bastard lignum-vitae, guayacán real, palo santo (Chudnoff 1984, Holdridge and Poveda 1975, Record and Hess 1949)

Guajacum sanctum ranges from southern Florida, eastern Mexico through the West Indies, along the west coast of Central America, to northern South America (Burger 1991, Chudnoff 1984, Holdridge and Poveda 1975, Jiménez 1993, Longwood 1962, Record and Hess 1949, Standley and Steyermark 1946). *Guajacum sanctum* is a heliophyte, generally a canopy species that grows well in open areas. In Costa Rica, the species grows in association with other tree species, among them: *Astronium graveolens* Jacq., *Tabebuia ochracea*, *Sideroxylon capiri* (Jiménez 1993). In Nicaragua it is associated with *Phyllostylon brasiliense* Capan. ex Benth. and Hook f., *Haematoxylum brasiletto* H. Karst., and *Caesalpinia coriaria* (Jacq.) Willd. in very hot, dry areas (Salas 1993).

Guajacum sanctum is a slow-growing, small to medium tree that reaches 4 to 25 m in height and up to 60 cm d.b.h. The crown is dense and round, sometimes with distally descendent branches. The external bark is grayish and rugose with longitudinal fissures, and it sometimes exfoliates in plates. The internal bark is light brown and slightly bitter (Holdridge and Poveda 1975, Jiménez 1993, Salas 1993). The leaves are opposite, paripinnate, 3 to 9 cm long with two to six pairs of leaflets; the petiole is 3 to 8 mm long, and the petiole and rachis are up to 5 cm long. The rachis is minutely puberulent or glabrescent and deeply sulcate above. The stipules are 2 to 4 mm long, triangular and acute, appressed, puberulent distally, thick, and persisting. Leaflets are opposite, elliptic, and narrowly oblong to oblong-ovate; the middle leaflets are the longest in each leaf and are bluntly obtuse or rounded to acute at the apex. Leaflets are broad, asymmetric, sessile or subsessile, and unequal on the thick petiolule; leaflets are entire, glabrous, 2 to 3.5 cm long, and 1 to 1.5 cm wide (Burger 1991, Holdridge and Poveda 1975, Jiménez 1993, Salas 1993).

The tree is largely confined to dry, exposed sites, where it is often the predominent species and where the soil is very dry at least part of the year. It grows well in shallow soils, particularly in limestone areas, well-drained low areas, low foothills subject to hot dry winds, and rocky limestone regions (Longwood 1962). *Guajacum sanctum* grows at elevations of 10 to 200 m in Costa Rica and up to 700 m in Nicaragua. It is limited to lowland, decidous, dry tropical forest formations with annual rainfall under 1500 mm and a range of temperatures of 28 to 35 °C.

The heartwood is a dark greenish brown to almost black and is readily distinguished from the narrow, pale yellow or cream-colored sapwood. The heartwood becomes even darker after exposure to air and light. The wood is very fine and uniform in texture with a heavily interlocked grain. It is oily due to a resin content (guaiac content) that constitutes about one-fourth of the dry weight. A slight scent is evident when the wood is warmed or rubbed. Color changes or a fine ripple marking from the interlocked irregular grain occasionally figures it (Longwood 1962).

The wood is extremely hard and heavy. The specific gravity (oven-dry weight/green volume) varies from 1.05 to 1.24. Oven-dry wood has a specific gravity of 1.2 to 1.36. The wood is difficult to dry, and considerable care is required to avoid shakes and end splits. The wood is very difficult to work with hand or machine tools, and a cutting angle of 15° or less is suggested in planing. The wood turns and shapes well and takes a high polish. Because of oily resins, it requires special surface treatments for satisfactory gluing. The heartwood is very resistant to attack by decay fungi, termites, and marine borers. The timber does not require preservation due to its high guaiac resin content and high wood density. The wood is used in bearings, bushing blocks, pulley sheaves, mallet heads, and turnery. Its most noted use is in bearings and bushing blocks for propeller shafts of ships because of its self-lubrication and hardness (Chudnoff 1984, Herrera and Morales 1993, Longwood 1962, Record and Hess 1949). The tree is a source of resins, particularly from the wood and bark, which have guaiacic and benzoic acid. The resins obtained from wood, bark, leaves, and flowers are also used in some pharmaceutical preparations (Herrera and Morales 1993, Salas 1993). However, according to Decree 25700-MINAE, from the Ministry of the Environment of Costa Rica, logging *Guajacum sanctum* is forbidden (Ministerio del Ambiente y Energía 1997).

Flowering occurs during the dry season from February through May and a second flush occurs in November. The tree begins to flower after 6 to 8 years. The inflorescences are fascicles of four to eight flowers at distal nodes with peduncles sparsely and minutely puberulent. The flowers have five petals that are bright blue, broadly obovate, clawed at the base, 8 to 10 mm long, and 6 to 8 mm wide. A disc is usually present, often with extra or intrastaminal glands. The androecium has 10 free stamens, each 6 mm long; the outer stamens are opposite the sepals; anthers are bithecous and dehisce introrsely with longitudinal splits. The pistil is about 10 mm long and solitary, with four to five united carpels, a short stipe, and a slender style; the ovary is obovoid. Fruits have been observed in March, April, June, July, and October (Burger 1991, Holdridge and Poveda 1975, Jiménez 1993). The fruit is a two- to five-lobed or ridged obovoid capsule 14 to 16 mm long and 12 to 18 mm wide. The fruit is fleshy or moist at maturity but dries to a yellowish and lustrous hard surface. The seeds are ellipsoid, about 1 mm long, and brown to black with a red aril (Burger 1991, Holdridge and Poveda 1975, Jiménez 1993, Salas 1993).

Fruits must be collected from the soil very early in the morning to avoid seed predation by rodents. The fruits are placed on the floor and dried for 7 days in the shade; later the fruit pericarp is removed with running water to extract the seeds. The seeds are then dried in the shade and stored in hermetic containers. Seeds average 20,000 per kg.

Fresh seeds have 40 to 60 percent germination in nurseries. Seeds can be stored for 1 month at 5 to 8 °C. They lose viability in less than 1 month if stored at ambient temperature and humidity. Seeds can be immersed in running water (at 20 °C) for 24 hours before sowing. Germination is epigeal, and the seedling is phanerocotylar. Germination begins 6 to 8 days after sowing and ends in 16 to 20 days.

Seeds are planted at a depth of 1 cm in germination boxes filled with sand; when they are 6 cm tall, they are transferred to nursery bags. Seedlings are ready for outplanting 1 year after sowing, when they reach 30 to 40 cm in height. Like *Guajacum officinale*, the primary problem at the nursery is leaf-eating insects: *Kricogonia castalia* (Fabr.), *Iridopsis* sp. and *Gnorimoschema* sp. (Timyam 1996). Regeneration is very good within the forest, with hundreds of seedlings and saplings; however, very few of them manage to survive to maturity (Jiménez 1993).


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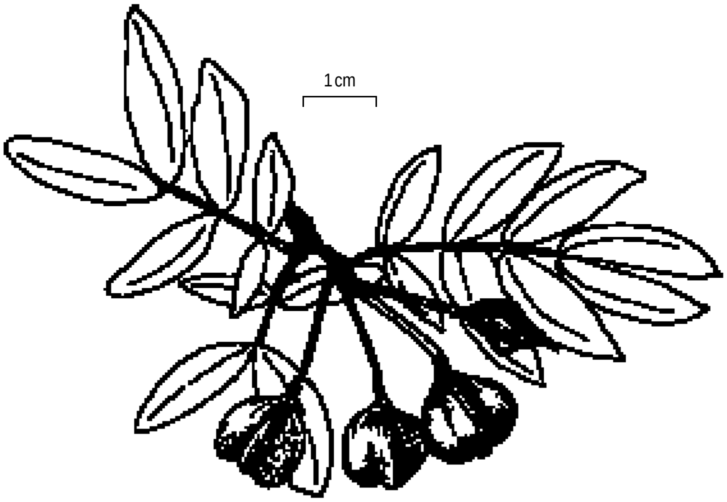
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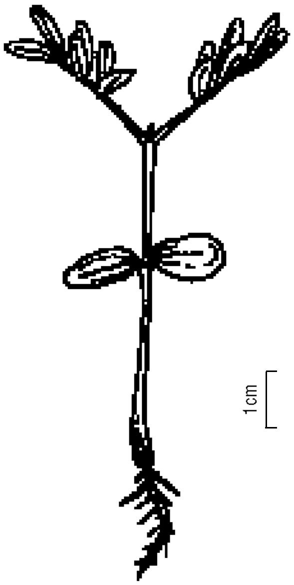
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Guarea glabra Vahl

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MELIACEAE (MAHOGANY FAMILY)

Carapa trijuga Willd. Ex C. DC. (Monographiae Phanerogamarum 1: 564; 1878); *Guarea brachystachya* Sessé & Mociño ex DC. (Prodromus systematis Naturalis Regni Vegetabilis 1: 624; 1824); *Guarea humilis* Bertero ex DC. (Prodromus Systematis Naturalis Regni Vegetabilis 1: 624; 1824); *Guarea swartzii* C. DC. (Prodromus Systematis Naturalis Regni Vegetabilis 1: 624; 1824); *Guarea excelsa* Kunth (Nova Genera et Species Plantarum 7: 227; 1825); *Guarea vahliana* A. Juss. (Mémoires du Muséum d'Histoire Naturelle 19: 240, 282; 1830); *Sapindus glabrescens* Hook. & Arn. (The Botany of Capitan Beechey's Voyage 281; 1838); *Guarea kegelii* Turczaninox (Bulletin de la Societé Impériale des Naturalistes de Moscow 36[1]: 589; 1863); *Guarea fulva* Triana & Planch. (Annales des Sciences Naturelles, Botanique ser. 5 15: 371; 1872); *Guarea fulva* var *mexicana* C. DC. (Monographiae Phanerogamarum 1: 575; 1878); *Guarea bijuga* C. DC. (Monographiae Phanerogamarum 1: 567; 1878); *Guarea filiformis* var. *cinerascens* C. DC. (Monographiae Phanerogamarum 1: 567; 1878); *Guarea filiformis* var. *pallida* C. DC. (Monographiae Phanerogamarum 1: 566; 1878); *Guarea filiformis* Ruiz & Pav. Ex C. DC. (Monographiae Phanerogrmarum 1: 566; 1878); *Guarea purpurea* C. DC. (Monographiae Phanerogamarum 1: 564; 1878); *Guarea schomburgkii* C. DC. (Monographiae Phanerogamarum 1: 565; 1878); *Guarea lherminieri* C. DC. (Bulletin de l'Herbier Boissier ser. 2: 571; 1894); *Guarea luxii* C. DC. (Botanical Gazette 19[1]: 2; 1894); *Guarea palmeri* N. E. Rose ex C. DC. (Botanical Gazette 19: 39; 1894); *Guarea pauciflora* Sessé & Moc. (flora Mexicana 100; 1894); *Guarea tuerckheimii* C. DC. (Botanical Gazette 33[4]: 250; 1902); *Guarea bullata* Radlk. (Bulletin de l'Herbier Boissier ser. 25: 192; 1905); *Guarea donnell-smithiii* C. DC. (Bulletin de l'Herbier Boissier ser. 25: 419; 1905); *Guarea erythrocarpa* C. DC. (Bulletin de l'Herbier Boissier ser. 25: 420; 1905); *Guarea microcarpa* C. DC. (Bulletin de l'Herbier Boissier ser. 25: 420; 1905); *Guarea syringoides* C.H. Wright (Bulletin of Miscellaneous Information Kew 3; 1906); *Guarea rovirosae* C. DC. (Annuaire du Conservatoire et Jardin Botaniques de Genéve 10: 145; 1907); *Guarea virescens* C. DC. (Annuaire du Conservatoire et Jardin Botaniques de Genéve 10: 140; 1907); *Guarea brevianthera* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 1; 1917); *Guarea cook-griggsii* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 2; 1917); *Guarea ternifoliola* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 2; 1917); *Guarea tonduzii* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 4; 1917); *Guarea makrinii* Blake (Contributions from the Gray Herbarium of Harvard University n.s. 53: 57; 1918); *Guarea obtusata* Blake (Proceedings of the Biological Society of Washington 33: 118; 1920); *Guarea chiapensis* Blake (Proceedings of the Biological Society of Washington 34: 116; 1921); *Guarea excelsa* var. *dubia* Blake (Proceedings of the Biological Society of Washington 34: 116; 1921); *Guarea heterophylla* Blake (Proceedings of the Biological Society of Washington 34: 116; 1921); *Guarea polyantha* Blake (Proceedings of the Biological Society of Washington 34: 117; 1921); *Guarea glabrescens* (Hooker & Arn.) Blake (Contributions from the U.S. National Herbarium 23: 559; 1923); *Guarea microcalyx* Harms (Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 429; 1925); *Guarea chiricana* Standl. (Publications of the Field Colombian Museum, Botanical Series 4[8]: 215; 1929); *Guarea matudai* Lundell (Lloydia 2[2]: 93; 1939)

Alligator wood, azote, bejuco colorado, cacahuatillo, cagaste, carapillo, carbon, carbonero, carimbo, cedrillo, cedrillo blanco, cedro macho, chichipate, cola de pavo, coquimbo, cramantree, dorita, duraznillo, guaraguao macho, guaraguillo, hoja blanca, huesillo, mameicillo blanco, pico de oro, pronto alivio, quitacalzon, small redwood, trompillo, wild orange, zapotillo (Pennington and Styles 1975, 1981; Record and Hess 1949; Standley 1938)

Guarea glabra is a neotropical species. Its geographic range extends from Sinaloa and Veracruz in Mexico, along both the Atlantic and Pacific drainages of Central America, to Colombia and Venezuela as far as Amapa in northeastern Brazil (Croat 1978, Pennington and Styles 1981). It is also found along both the Pacific and Amazonian basins of the Andes down to Peru and the southwest area of the Brazilian Amazon, as well as in the Lesser Antilles, Puerto Rico, and Jamaica.

Guarea glabra is a tree that reaches 25 to 30 m in height and more than 1 m d.b.h. The tree is evergreen. The bole is straight with small buttresses; the crown is dense and rounded. The bark is soft and vertically fissured or scaly. It is brown or grayish brown. Internally, the bark is creamy and aromatic. The fresh bark exudes a soft aromatic odor. The mean thickness is 1.3 to 1.6 cm. The young branches are pubescent, becoming glabrous and pale grayish brown or grayish white, with some lenticels (Pennington and Styles 1981). The leaves are compound, pinnate, and may reach 60 cm in length; the terminal bud with intermittent growth is typical of the species of the genus. Some races grow well in bauxite hills. The species is frequently riparian. The range of elevation is from 0 to 2000 m, although the species grows better in lowlands that are periodically inundated. The temperature varies from 18 to 35 °C and the annual precipitation is 1500 to 7000 mm.

Guarea glabra is the most variable species of the genus and has several races along its range of natural distribution.

The wood is brown or reddish brown, aromatic, fine or medium textured, with straight grain, sometimes intercrossed, and moderate luster. The wood's specific gravity is 0.49 to 0.52, varying with the source. The initial moisture content (110 to 119 percent) is too high for its density; the green weight is 980 to 1040 kg per m^3. The volumetric contraction and the tangential/radial contraction ratio are similar to those of *G. grandifolia* DC. The mechanical properties are low or medium. Air drying is moderately fast. The wood dries with few defects (fissures and rollups), is easy to work, and has a smooth finish; brushing is easy and the surfaces obtained are smooth. The heartwood is durable and difficult to preserve. The wood is equivalent to royal mahogany (*Carapa guianensis* Aubl.), apamate (*Tabebuia rosea* (Bertol.) DC.), green ash (*Fraxinus pennsylvanica* Marshall), and red maple (*Acer rubrum* L.) and can be used with success as a substitute for mahogany (*Swietenia macrophylla* King). The timber is mixed and frequently confused with woods of other species in the same genus and with royal mahogany. The wood is used in general construction, carpentry, furniture, window and door frames, cabinets, veneers, molding, floors, and lathed objects (Anonymous 1946, Llach 1971).

Because the flowering pattern is sub-annual, the species has flowers and fruits for several months. It is dioecious and the flowers are unisexual. Inflorescences are axillary or famiflorous pseudospicate panicles. The minor lateral branches are cymes or racemes. The calyx is rotate, pateliform or cyathiform, with four teeth or acute lobes, sometimes rounded. The corolla has four to five petals generally valvate, sometimes imbricate, whitish cream or greenish. The flowers are fragrant and entomophilous. Fruit ripening lasts 3 months and fruit production is correlated to episodic flowering. The main crop occurs January through May. The fruit is a dehiscent capsule, globose, flat at the apex, smooth or rough with a hard, thick pericarp. Dehiscence proceeds basipetally, along the longitudinal grooves, usually producing four to five valves (Van Roosmalen 1985, Wheelwright and others 1984). The endocarp is sugary. There are one to two seeds per locule, shaped like the segment of an orange (Pennington and Styles 1981). Shape and size vary from one fruit to another; seed length usually fluctuates from 1.5 to 3 cm.

Fruits are collected directly from the tree or the ground. Small, malformed, or damaged fruits and seeds must be discarded. Seeds must be kept humid until soaking and further sowing. Seed water content is 38 to 41 percent. Seed behavior is recalcitrant and viability is lost in 6 to 8 days, depending on the loss of moisture content. Germination is hypogeal and the seedling is cryptocotylar. On the forest floor, many fruits and seeds are attacked by insects, guans (large birds), and rodents (Van Roosmalen 1985). Damaged seeds do not germinate. Under greenhouse conditions, germination is good (80 to 82 percent) if healthy, fresh seeds are soaked in running water for 24 hours before sowing. The first evidence of germination is observed 65 to 70 days after sowing.

Seeds are grown in germination chambers or sand beds. The substrate must be kept humid and aerated. The seedlings can be transferred to plastic bags when the plumule is 2 to 3 cm long. The greenhouse and nursery periods must last about

6 months. Seedlings are small, but they are strong and resistant. Growth is slow under full sunlight and shows low capacity to compete with climbers and herbs. Because the species is shade-tolerant, it should be planted under moderate shade or managed with silvicultural techniques and is not appropriate for use in monospecific plantations. *Hypsipyla grandella* and other unidentified predators attack the young shoots and promote seedling mortality.

ADDITIONAL INFORMATION

The petiole and rachis are terete, sometimes adaxially grooved and pubescent. Leaflets are opposite, (1-)2-7(-13) pairs, subcoriaceous, glabrous, and sporadically have glandular dots (Pennington and Styles 1981). The foliar blade is elliptic or oblanceolate, sometimes oblong; the apex is acuminate, acute or rounded, and the base attenuate or acute, sometimes cuneate, obtuse, or rounded. Venation is eucamptodromous, in some cases brochidodromous; midrib flat or depressed, secondary veins ascending, arcuate, usually convergent, tertiary veins prominent (Pennington and Styles 1981).

In the female flower the staminal tube is wide, with undulate or dentate margins, glabrous, with 7 to 10 functional stamens but usually 8. The male flower has small indehiscent antheroids. They lack pollen and the nectary subtending the ovary forms a ring below it; it has a narrow stipe. The pistillate flowers have a reduced nectariferous disc. The gynoecium is tri- to pentalocular but commonly has four locules. Each locule has two superposed ovules, anatropous, bitegmic, and crassinucellate. Some ovules are abortive. The style is short and glabrous (Pennington and Styles 1981).

The seed's embryo is thick and planoconvex with superposed or oblique cotyledons. The radicle is minute, dorsal or lateral, and sometimes included. The sarcotesta and the embryo are rich in lipids.

Germination is gradual and may last 1 or 2 months. The radicle emerges through the micropyle. When the root is 2.0 to 2.5 cm long (65 to 67 days), the cotyledonary petioles begin their extension. They are small, thick, hard, and concave adaxially; the plumule emerges afterwards. Eophylls are opposite. Cotyledonary buds may develop when the main shoot is damaged.

As are all the species of the genus, *G. glabra* is biochemically rich; the limonoid glabretal has been found in leaves and fruits (Taylor 1981).


1cm

Guarea grandifolia DC.

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MELIACEAE (MAHOGANY FAMILY)

Guarea borisii Harms (Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 13: 503; 1937); *Guarea chichon* C. DC. (Annuaire du Conservatoire et Jardin Botaniques de Genéve 10: 147; 1907) *Guarea culebrana* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 5; 1917); *Guarea gigantea* Triana & Planch. (Annales des Sciences Naturelles, Botanique ser. 5[15]: 370; 1872); *Guarea longipetiola* C. DC. (Smithsonian Miscellaneous Collections 68[6]: 5; 1917); *Guarea mancharra* Cuatrec. (Fieldiana, Botany 27[1]: 71; 1950); *Guarea megalantha* Roem. (Familiarum Naturalium Regni Vegetabilis Monographicae 1: 120;' 1846); *Guarea megantha* A. Juss. (Mémoires du Muséum d'Histoire Naturelle 19: 241,292; 1830); *Guarea pittieri* C. DC. (Smithsonian Miscellaneous Collectiosn 68[6]: 6; 1917); *Guarea trompillo* C. DC. (Annuaire du Conservatoire et Jardin Botaniques de Genéve 10: 147; 1907) (W3 Tropicos 1999)

Apae, aycoy, azote, barafa, cabimbo, carapa, carbon, cedrilho, cedrillo, cedrillo blanco, cedrillo cimarrón, cedro macho, chichón de montaña, chohalate, cocora, cramantree, cuaimire, cuamo blanco, cuamo cimarrón, jatauba, javin, kusimsakis, kusipkakis, latapi, latapi de hoja menuda, mancharro, no-choc-che, ocora, piton, pocora, pronto alivio, requia de altura, sabino, tromopillo, trompillo de monte, turubuk, wildake (Croat 1978; Pennington and Styles 1975, 1981; van Roosmalen 1985; Smith 1965; Standley 1938)

The natural distribution of *Guarea grandifolia* extends from Veracruz, Mexico, throughout Central America, to northern South America, reaching the central and western Amazon River Basin (Pennington and Styles 1975, 1981; Standley and Steyermark 1946b). The species is a canopy emergent in the humid and very humid tropical forest.

Guarea grandifolia may reach 50 m in height and over 180 cm in diameter. It has buttresses 3 to 4 m long in the Amazonian forest. The crown is dense, wide, and rounded, with numerous branches. The bark is light brown, dark, brown, or gray (in gallery forests or pastures) and smooth or with vertical light brown fissures. It exfoliates in irregular scales or plates. Internally, it is creamy or yellowish brown. It oxidizes rapidly, becoming brown if exposed to air and light. The fresh bark is characterized by its soft aromatic odor. The mean thickness is 1.2 to 1.5 cm. Leaves are crowded in spirals at the distal end of the branches. They are compound and pinnate and may reach 1.5 m in length. The most important characteristic is the terminal bud with intermittent growth. The leaf has 8 to 34 leaflet pairs, chartaceous or coriaceous, elliptic or elliptic-oblong, sometimes oblanceolate, with entire margin, apex shape variable (acute, acuminate, obtuse or truncate) and truncate, round, cuneate, or attenuate base. *Guarea grandifolia* is a riparian species quite common near streamlets, creeks, and rivers, especially in areas with red clayey or bauxitic soils. It also frequently grows in alluvial banks. The elevation range extends from 0 to 800 m; the temperature range in these forests varies from 22 to 32 °C and the annual rainfall is 3500 to 8000 mm. The species is shade tolerant.

In green condition, the sapwood is yellowish brown; heartwood light brown. After air-drying, the sapwood is light brown and the heartwood brown, pinkish brown, or orange-brown. The wood has fine or medium texture, straight grain sometimes intercrossed, and medium luster; it is odorless and tasteless. The basic specific gravity is 0.50, with variations dependent on wood origin. The average green weight is 1132 kg per m^3. The volumetric contraction is moderate (11.2), and the tangential/radial contraction ratio is favorable (1:5). The mechanical properties are low or medium. Wood air-drying is moderately fast with few defects (cracks and curling). The wood is easily worked and has a soft, smooth finish without brushing defects. It is strong in relation to its weight and has good natural durability. Because the Peteri's coefficient of flexibility is 67 and the Runkel factor 0.84 (group III), the fibers are good for making paper. In America, the timber has the same uses as mahogany (*Swietenia macrophylla*), royal mahogany (*Carapa guianensis* Aubl.), red maple (*Acer rubrum*), or green ash (*Fraxinus pennsylvanica*). The timber is used to make furniture, cabinets, closets, doors, doorframes, windows, moldings, veneers, floors, and lathed objects. The timber is classified as a structural wood of B type, usable in construction designed to support medium or heavy loading (Llach 1971). Bark extracts of *G. grandifolia* are used as an ingredient in the arrow poison made by the Jarawara and Jamamadi tribes living in the Brazilian Amazon area (Prance 1978).

The species is dioecious. Tree blooming starts on the crown side exposed to full sunlight. The flowering pattern is irregular subannual or episodic, and flowering within a population is asynchronous. The number of adult trees flowering in each episode varies, resulting in significant genetic variability. Furthermore, flowering is stepped and the same tree may have flowers and fruits in different developmental stages. Pollination is entomophilous. Floral anthesis occurs at night and the pollination vectors are moths (palaenophily). Inflorescences are axillary or ramiflorous, sometimes cauliflorous, ramified, slender or forming narrow pyramidal thryses. The thryses may be 50 cm long. The flowers are sericeous and short-pedicellate. The calyx has rounded lobes, internally glabrous and appressed puberulous outside. Petals are oblong or lanceolate; they open as a cup during anthesis. The staminal tube is truncate or undulate at margin, glabrous or sparsely pubescent, usually shorter than the corolla. Flowers have a cyathiform, green calyx with three to seven lobes. The corolla has four to seven petals, usually five, white or creamy, valvate or slightly imbircate, reddish with aging. The androecium has a fleshy staminal tube; it has 8 to 12 anthers, generally 10, inserted within a throat.

Fruit production is correlated to episodic flowering. The main crop occurs from February through May. Fruits are thick-pedicellate. They are dehiscent capsules with fleshy pericarp. They are 3.0 to 3.5 cm in diameter and tomentose or glabrous, with dark longitudinal grooves and retuse apexes. Dehiscence proceeds basipetally, along the longitudinal grooves, giving rise to four to eight, usually five, valves. The pericarp is greenish in early stages of development, taking a reddish color near maturity. Mesocarp and endocarp are very fleshy. The pericarp has a high sugar content (approximately 20 percent); sugars are concentrated mainly in the endocarp tissues.

There are one to two seeds per locule, which may reach a length of 2 cm. Seed form and size are variable. They are ellipsoid or truncate at the apex. The seedcoat is bright orange or bright red and is formed by a sarcotesta, a fibrous tegmen, and pachychalazal tissue. Most seed dispersal is endozoochorous and birds are the customary dispersers (Wheelwright and others 1984). Some monkeys and rodents are commensals of fruits and seeds. It is presumed that some fish are possible dispersers of those seeds falling into streams.

Partially open fruits are collected directly off the tree and a careful fruit and seed culling must be done. Small, malformed, or damaged fruits and seeds must be discarded. Fresh seeds can also be collected from the ground.

Seeds must be kept humid before soaking and sowing to maintain their viability. Seeds average 720 per kilogram. The seed water content is approximately 40 percent. Seeds are very recalcitrant and viability is lost in 7 to 8 days, depending on the level of seed dehydration. Germination is hypogeal and the seedling is cryptocotylar. Germination is stepped and may last several months. The radicle protrudes throughout the micropyle, causing the rupture of surrounding tissues. Cotyledonary buds may develop if the main shoot is damaged.

Seeds are sown in germination chambers or sand beds. The seedlings can be transferred to plastic bags when the plumule is 2 to 3 cm long. The greenhouse/nursery period lasts about 6 months. The seedlings are small but strong and resistant.

Because growth is slow under full sunlight and the plant shows low capacity to compete with climbers and herbs, the species is not appropriate for use in monospecific plantations. It must be planted under moderate shade or managed with silvicultural techniques.

ADDITIONAL INFORMATION

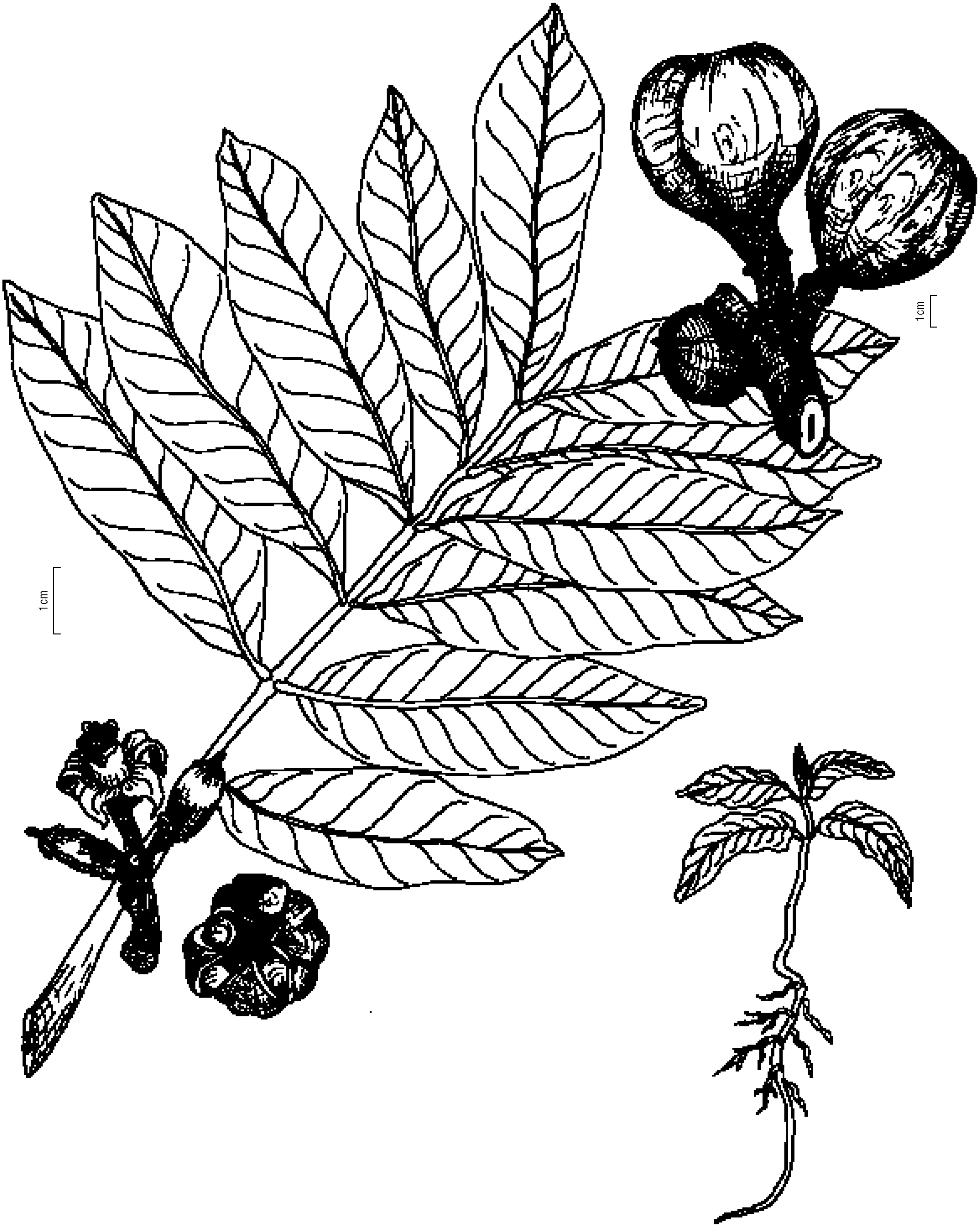
Guarea derives from *guara*, a native name used in Cuba to name the type species of the genus. Allamand rectified the original *Guara* used by Linnaeus (Pennington and Styles 1975, 1981). The species name refers to the large leaf size.

Among the Meliaceae, *Guarea* is one of the genera that has a higher number of species. The meliacins, tetranortriterpenoids, or limonoids (characteristic chemical compounds of the family) are also present in this genus (Taylor 1981). Although many species of the family have biologically active compounds, the *Guarea* limonoids, such as obacunone, show low biological activity against many insects and are unable to inhibit insect growth and activity.

The staminate flower has fertile stamens,; the pistillate flower has indehiscent sterile antheroids. The gynoecium of the pistillate flower is subtended by an annular nectariferous stipe; in the staminate flower, the stipe is longer and narrower. The ovary in the female flower is 5-sulcate, with 4 to 8 locules, sometimes 10. Each locule has two ovules. The style is short and thick, pubescent at the base; the stigma is discoid. Ovules are anatropous, bitegmic, crassinucellate, and superposed. In the male flower, the gynoeciumis narrower; the ovules are well developed but are not functional.

The seed embryo is fleshy, thick, and plano-convex, with large, well-developed cotyledons, superposed or oblique. The radicle is short, dorsal or lateral, sometimes included; the plumule is minute. The seed is endospermic; it is nuclear and oily and is absorbed during seed development. The sarcotesta and the embryo are rich in lipid content.

On the forest floor, insect larvae attack many fruits and seeds; at groundline, guans (large birds) or rodents may damage seeds. *Hypsipyla ferrealis* larvae and other insect larvae develop inside the immature fruits, causing severe damage to developing seeds. Commonly, these damaged seeds do not germinate. Seedlings are shade tolerant and grow well on the forest floor, but the mortality level in young stages is high due to predation. Seedlings growing under full sunlight show slower growth and the leaves have a lighter green color.


1cm
1cm

Haematoxylum campechianum L.

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FABACEAE (BEAN FAMILY)

No synonyms

Bois Campeche, Campeche, Campeche wood, ek, logwood, palo de Campeche,
palo de tinta, palo de tinte, palo negro, tinto

Native to the tropical regions of America, *Haematoxylum campechianum* is naturally distributed on the Yucatan Peninsula in Mexico and in Guatemala and Belize. Within its area of natural distribution, the species forms dense groups called tintales, which grow in soils subject to periodic flooding with deficient drainage (Standley and Steyermark 1946b). The species has been introduced and naturalized across Central America, the Caribbean islands, and northern South America (Stoffers 1973).

Haematoxylum campechianum is an evergreen, thorny tree that can reach 15 m in height and 60 cm d.b.h. It grows at elevations from sea level to 50 m. The trunk has many shoots, branching off near the base. The sparse, spreading, and rounded crown is made up of many rising and twisted branches. The leaves are paripinnate, 3 to 10 cm long, with four to eight cuneate-obovate leaflets 1 to 3 cm long. In the Yucatan Peninsula, the tree grows primarily in flat terrain with clayey soils, deficient drainage, and periodic flooding—commonly known as low wooded. The regions where the tree grows have an average annual temperature of 26 °C with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures occur in April and May; the minimum temperatures in December and January. Average precipitation is approximately 1288 mm, ranging between 900 and 1800 mm.

The wood of this tree is used as a source of the coloring matter called hematoxylin. It is also used as firewood and for posts. The leaves and the young branches are used as forage. The flowers are honey bearing. Frequently, the tree is planted around houses as an ornamental because of its colorful flowers (Niembro 1986, Rico-Gray and others 1991). The wood also has medicinal properties. Because the infusion obtained when it is boiled in water has astringent properties, it is used in traditional medicine as a remedy for diarrhea and dysentery.

The light yellow flowers are arranged in racemes. *Haematoxylum campechianum* blooms September through April, and the fruits (legumes) ripen March through May. The legumes are oblong-lanceolate, 2 to 6 cm long, 6 to 15 mm wide, laterally flattened, rounded or obtuse at the apex, acute at the base, membranous, yellow-gray, and finely reticulate. The fruits are dehiscent, but the pericarps can be broken easily when they are ripe. Each fruit contains one to two seeds (Little and others 1988, Pennington and Sarukhan 1968, Standley and Steyermark 1946b). The seeds are transversally oblong, laterally flattened, 10 to 12 mm long, 3.8 to 3.9 mm wide, and 0.8 to 1 mm thick. The seedcoat is light brown, smooth, opaque, and coriaceous and marked on its lateral surfaces by a green-gray stripe or a longitudinal sinuous depression that is rather deep-set.

The fruits are gathered May through July when the pericarp changes from green to brown and the fruit changes in consistency. Unripe fruits are flexible, and ripe ones are fragile and brittle. Fruits are collected from the trees using poles with metal hooks. Seeds are extracted by breaking the fruits by hand. Small impurities are removed with sieves or using a vertical column blower. Clean seeds average 35,200 to 41,000 per kg (Patiño and Villagómez 1976, Vega and others 1981).

The seeds remain viable naturally for 8 months. They germinate 19 days after sowing at a rate of 48 percent (Vega and others 1981).

ADDITIONAL INFORMATION

The hilum is basal and sometimes covered by remnants of funicular tissue. The micropyle is indiscernible. The lens is prominent, raised, and located on the opposite side of the micropyle. The endosperm is scarce and limited to a very thin layer located on the lateral surfaces of the embryo. The embryo has a straight axis, is almost bilaterally symmetrical, and is yellow to light coffee in color. The cotyledons, shaped like the seed, are whole, expanded, bilobed, flat, foliaceous, and independent of one another. The plumule is partially developed in pinnae. The radicle is prominent, oblong, and completely salient (Hutchinson 1964; Niembro 1982, 1983).


2cm

Heritiera fomes Buch.-Ham.

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STERCULIACEAE (STERCULIA FAMILY)

Heritiera minor Roxb

Jekanazo, pinlekanazo, sunder, sundri (Troup 1921, Gamble 1922)

Heritiera fomes is found in almost all the tropical swamp areas of the world (Zabala 1990b). The tree grows in the Sunderban forests of the Ganges-Brahmaputra Delta in Bangladesh and West Bengal of India, the coasts of Chittagong in Bangladesh, and Arakan (a province of Myanmar), ascending the rivers within tidal limits (Troup 1921). In low-lying areas, undergrowth density varies, being sometimes thick and nearly impenetrable with *Nipa fructicans* Thunb., *Phoenix paludosa* L., *Hibiscus tiliaceus* L., *Pandanus odoratissimus* L.f., *Acanthus ilicifolius* L., *Derris sinuata* Benth. ex Thwaites, and *Acrostichum aureum* L. (Troup 1921).

Heritiera fomes is of moderate size in the Sunderbans, attaining larger dimensions in Myanmar (Troup 1921, Zabala 1990b). At one time, some trees in the Sunderbans were 2 m in girth but, because large trees have been heavily harvested, trees over 1 m in girth are no longer common. Height ranges from 15 to 25 m and d.b.h. from 2.5 to 38 cm depending on site quality (Curtis 1993). A gregarious evergreen tree, *H. fomes* has a buttressed stem and gray, longitudinally cracked bark. The dark green leaves have short petioles and are grouped toward the ends of the branches. The species starts producing pueumatophores at 3 years of age. The species grows in regions with a warm equable climate of 7.22 °C to 37.78 °C and heavy annual rainfall of 1600 mm to 5334 mm (Troup 1921, Zabala 1990b).

Heritiera fomes thrives on clayey soil and in areas situated between the banks of rivers and the low depressions of saucer-shaped islands (Alim 1979). In the Sunderbans, it is the climax species in newly formed inlands with sweet, brackish, and saline water. It is dominant in the slightly saline and moderately saline zone (Zabala 1990b), and thrives in a well-drained soil inundated by tidal water of a low degree of salinity (Khan 1977).

The wood is very hard and close-grained; the sapwood is pale; the heartwood is dark red; and the pores are moderate sized to large, often oval and subdivided into compartments (Gamble 1922). The wood can be used for bridge and house construction, boat-launch building, electric and telephone utility poles, bodies of buses and trucks, anchor logs, scaffolding, pilings, house posts, handles of tools, fuel wood for cooking and burning bricks, flooring, and paneling.

Heritiera fomes flowers in March and April (Rahman 1982). The flowers are unisexual and arranged in panicles (Zabala 1990b). The fruit carpels are 3.81 to 5.08 cm long and 2.54 to 3.81 cm broad; they fall to the ground when they ripen in July and August (Troup 1921). The seeds ripen in June and July (Alim 1979, Das 1979, Hasan and Howlader 1979, Rahman 1982). The tree seeds well and no periodicity has been observed (Hasan and Howlader 1970). The seeds should be collected in July and can be sown directly. Clean seeds average 44 to 53 per kg (Choudhury 1979).

Germination is hypogeous and occurs soon after the carpels fall. Seeds germinate in 7 to 10 days with germination slower during the dry season (Alim 1979). Seeds are removed from pregermination beds when the hypocotyl and numerous roots appear. The pregerminated seeds are sown by dibbling, keeping the epicotyl above the ground (Das 1979). Seedlings can be planted in areas where the soil is considered mature and in areas of intermediate level that are inundated 8 to 9 days in a month during the spring tide. Seedlings will develop vigorously in nurseries that remain submerged for 100 to 200 minutes during each 24-hour period.

Direct sowing of seeds gives the best results (Das 1979, Hasan and Howlader 1979). Initial seedling development is very rapid and seedlings may reach about 0.7 m in 1 month; however, the growth rate then becomes very slow and numerous seedlings die before full establishment (Das and Siddiqi 1985). The taproot may penetrate the ground up to a depth of

18 to 20 cm. One-year-old seedlings planted in areas where the rate of siltation is too high should be spaced at 1.22 by 1.22 m.

ADDITIONAL INFORMATION

Heritiera fomes grows best far away from the high strip along the canals (Troup 1921). It grows very poorly in strongly saline zones, where it will deteriorate rapidly and die off (Zabala 1990b). The species does not prefer regular inundation (Troup 1921) and is classified as medium-to-high submersion tolerant (Hasan and Howlader 1979). *Heritiera fomes* prefers higher ground that is inundated only 4 to 5 days during the spring tide period. The tree should not be grown on sites where water stagnates or on high land that is never inundated (Alim 1979). It is a moderate light demander, enduring more shade in youth than it does later (Alim 1979, Troup 1921). In dense forests of *H. fomes*, undergrowth is practically absent. Natural regeneration appears more successful under moderate cover than where the canopy is too open. Heavy cover, especially matted twining or vines and weeds, as well as shade also hinder natural regeneration (Das and Siddiqi 1985, Zabala 1990b).

The thick, fleshy cotyledons remain within the fibrous wall of the carpel. The stout radical appears first, and the petioles of the cotyledons meanwhile elongate to enable the plumule to emerge. The plumule soon appears, the young shoot elongating and arching until free, when it straightens (Troup 1921).

The roots do not penetrate deeply, but spread laterally not far below the surface, sending up numerous blind suckers or pneumatophores (Zabala 1990b). Coppice reproduction is poor where the trees show the best development and most vigorous growth, as in fresh water forests. Where the growth and development of the tree is poor in the saline soil of salt water forests and on dried ground, coppice growth is vigorous, possibly because the tree expends less energy producing suckers on drier ground (Troup 1921). Das and Siddiqi (1985) report that judicious thinning increases the rate of growth: 12 cm diameter in the best plot in a fresh water area, versus 5.3 cm diameter in the worst plot in a salt water area.

Top dying of *H. fomes* was reported in the Sunderbans working plan (Curtis 1993). Sporadic or patchy occurrence of top dying was noted even earlier (Troup 1921). Top dying of *H. fomes* appears as a decline and dieback of the foliage and twigs in part of the crown. In older trees, one or more of the major branches may die out and dry first. Cracked perennial gall cankers are often associated with dead branches. These top-dying trees are also attacked by borers and wood decay fungi. Cankers are generally more pronounced in mature trees, but are also seen in younger ones (Rahman 1988). Possible causes of top dying are complex and include: (1) reduced fresh water discharge through the Sunderbans as a result of upstream diversion of water by damming and increasing use of ground water for agricultural and industrial purposes; (2) reduced nutrient supply in the Sunderbans (Chowdhury 1984, Imam 1982, Snedaker and others 1977); (3) increased salinity due to reduced fresh water flush (Hannan 1981); (4) a moratorium on felling in the Sunderbans (Rahman 1988); (5) root rot pathogens; and (6) a change in depth and duration of flooding (Rahman 1988). Gibson (1975) recommended that all trees showing early signs of top dying should be felled to clean the area and to ensure maximum utilization of the diseased crop before it is destroyed by insects and rot fungi.

In this species, silvicultural systems produce a girth limit of 1.07 m, and the felling cycle is 20 years. Volume production is about 3 to 5 m^3 per ha per year (Zabala 1990b).

Hernandia sonora L.

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HERNANDIACEAE (HERNANDIA FAMILY)

No synonyms

Aguacatillo, cuajada, guaco, maga, mago, mano de León, tambor, volador

Hernandia sonora is distributed in wet and semideciduous forests of tropical America. It is found from Mexico, across Central America through Costa Rica, in Colombia and Ecuador, and in the West Indies. It grows in the departments of Santa Barbara, Atlantida, Colon, Comayagua, and Cortes (Benitez and Montesinos 1988, Standley 1931).

Hernandia sonora is a tree of up to 28 m in height and 80 cm in diameter. The roots are tabular at the beginning of the shaft, which is straight, cylindrical, and free of branches up to two-thirds of its height. The base is conical or slightly elongated; the crown is umbellated or multiflabellate and evergreen. The tree has clear and open foliage with obliquely rising branches. The bark is yellowish gray or brownish gray and moderately smooth and usually has prominent, rounded, and cracked longitudinal lenticels. It can be recognized by its ovate leaves with long pulvinated petioles, or by its lenticel bark with yellowish chamfer. The leaves are simple, whole, and loosely grouped at the end of the sprigs. Frequently found along river banks and in very wet places in lowland areas, the species grows at elevations from sea level to 500 m. In Honduras it grows in wet forests generally near water springs, up to 500 m.

When the wood dries, it is grayish white; it does not have a characteristic odor or taste. The wood has a straight hilum, thick texture, low shine, and soft grain (Standley 1931). Its specific gravity is 0.28 (very light). The wood has medium dimensional stability. It is easy to saw and work with carpentry machinery, but it does not plane, sand, mold, drill, turn, or chisel well. The wood resists cracking by screws and is easy to work with sharp tools, but saws produce a floccose finish. It is not very durable to biodeterioration, and it is susceptible to stain-causing fungi. The wood dries quickly in the open air, showing slight defects. If the process is neglected, considerable defects may occur. It is easy to preserve through systems of hot-cold bath and vacuum pressure. The wood of *H. sonora* is used for interior finishes, general carpentry, fillers for plywood, boxes and crates, baskets, scaffolds, chips for briquettes, pulp, and paper (Aguilar 1966).

The small, whitish-greenish flowers are axillary cymes. The species blooms and fruits almost all year. The fruits are ellipsoid to ovoid-globular drupes, approximately 2 to 4 cm in diameter, with eight longitudinal aristae, hard, and yellowish or black when ripe. Each fruit contains one seed.

ADDITIONAL INFORMATION

The bevel is 0.5 to 1 cm thick, yellowish or light yellow, with a dark coffee-colored zonal stripe under the rhytidome, turning a darker color with age, fibrous, compact, and soft to moderately hard. The petiole is 5 to 24 cm long, cylindrical, thin, glabrous, and slightly twisted at the apex; both ends are pulvinated (Benitez and Montesinos 1988, Standley 1931). The oval lamina is 10 to 25 cm, acuminate apex, obtuse to rounded; the base is coriaceous. The right side is shiny and dark blue-green, and the back is opaque blue-green; both surfaces are glabrous. The main vein is strongly prominent underneath; a pair of straight basal veins run up to the middle of the lamina; four to five pairs of straight secondary veins are prominent underneath, and camptodrome.

2cm

Hevea brasiliensis Müll. Arg.

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EUPHORBIACEAE (SPURGE FAMILY)

No synonyms

Caucho, hevea, hule, jebe, seringueira

Hevea brasiliensis is a fast-growing tree that reaches 40 m in height and 35 cm d.b.h. The tree has a straight trunk that is column-shaped and thick at the base; the bark is grayish green and branching is regular. The leaves are compound, trifoliate, alternate, dark green above and light green underneath, and have very marked nervation, a long petiole, and a pair of nectarean glands. The shape and composition of the leaves are varietal characteristics. *Hevea brasiliensis* loses its foliage each year, and refoliation has a very attractive copper tone. The radicular system of the tree is made up of the pivot root and two crowns of lateral roots. The species grows well in soils at least 1 m deep with a pH of 4.0 to 6.5. The soil should be well drained and well ventilated. The tree grows on slopes ranging from zero to 70 percent at elevations from sea level to 1200 m. The optimal temperature range for the species is 22 to 30 °C, with an ideal average of 25 °C and a minimum temperature higher than 15 °C. Relative humidity should not exceed 70 to 80 percent (Bustamante and Reyes 1994). Annual precipitation must be between 1500 and 3000 mm; its distribution must be regular with a marked or well-defined annual dry period (preferably 3 to 4 months long), with a hydric deficit of approximately 300 mm that coincides with the defoliation/refoliation cycle. Areas with a high cloudiness index and frequent appearance of the dewpoint are not desirable, and the species requires 1,500 to 1,800 hours of annual sunshine. Winds greater than 8 m per second can damage or topple the tree (Rincon 1996).

Hevea brasiliensis is primarily used for its latex, which is tapped. The wood is used for small boards, matches, packing boxes, compressed wood textiles, round arches, and fuel. In the Colombian Pacific it is used as support beams on the floors of rural houses even though it lacks resistance to attacks by insects and fungi.

The flowers are monoecious, small, light yellow, and grouped in clusters; inflorescence is axillary and lateral in the shape of a panicle. Masculine flowers are 8 to 10 mm long; feminine flowers are larger, 10 to 12 mm long. The fruit is a trilocular capsule containing one seed, rarely with four or six lobules, and 3 to 6 cm in diameter. The seeds are large, quadrangular ovoid, flattened on one or two sides, shiny, grayish or pale in color, with dark coffee-colored spots that are oval, and 2 to 3.5 cm in diameter. They have a spongy tissue that allows them to float, thus contributing to the dissemination of the species. Fruits are collected when they change from green to brown—the time at which the seeds have the most germinative power. Seeds average 180 per kg (Rincon 1996).

Because *H. brasiliensis* has a high content of oil, the seeds quickly lose their germinative power; therefore, planting must occur within 8 days after collection. Fifteen days after collection, the seeds' germination percentage decreases considerably. As a recalcitrant seed, it does not tolerate drying and dies when its humidity content reaches less than 25 percent of its fresh weight. Because a great amount of water is contained in the seed, temperatures less than 5 °C will kill it. If they do not dry out, seeds can survive from a few weeks to a few months. Ventilation should not be limited because the seeds have a high respiration.

Pregermination of the seeds must be done in sawdust beds. Seeds germinate shortly after release from the mother plant and 8 days after being planted. The average germination percentage is 60 percent. The germinator should be 1 m wide by 10 cm high with variable lengths. The germinator is prepared with muddy soil, which is covered with a layer of sawdust. The seeds are placed with their ventral surfaces on the sawdust, 1 cm apart. One thousand seeds will fit into 1 m^2 of germinator. A threshing floor of 1.7 m^2 will produce 1,700 seeds, which provide the 500 plants needed to plant 1 ha. Germination occurs 8 to 10 days after planting, and the plantules are transplanted when they reach an appropriate developmental state. The threshing floors are watered abundantly to maintain humidity and facilitate germination.

Generally, 1 m^2 of germinator produces enough plantules to establish 133.33 m^2 of nursery or 430 m^2 of nursery in bags. The nursery is made up of two parts: the clonal garden and the growing area (nursery proper) (Bustamante and Reyes 1994, Rincon 1996).

In the clonal gardens, small twigs bearing buds for cloning are produced. When the buds, extracted from clones that are highly productive and resistant to diseases, are grafted onto the plantules, with sexual seed (pattern), grafted patterns or stumps are produced. In the field where the selected clones are multiplied, it is established through stumps. (The grafted pattern with the growing bud is released from the soil bare root.)

The planting distance is 1 by 1m. One year after planting, the stems can be used as bud-bearing twigs. Depending on the strength of the plant, one to three twigs per plant can be obtained. The sowing distance has recently been changed to 2 by 2 m, thus decreasing the number of stumps necessary for installation. In the traditional method, two twigs were left at each place; in the new method, four twigs are left. A clonal garden produces material for grafting between 5 and 6 ha of nursery per year for 10 years (Barrero 1984, Bustamante and Reyes 1994, Rincon 1996).

The petioles are cut two days before removing the twigs with leaves; the bud-bearing twigs must be used as soon as possible and must always be protected from the sun. After 1 year, grafted plants in the clonal garden produce 2 m of usable wood and each meter contains approximately 10 viable buds.

ADDITIONAL INFORMATION

The South American leaf blight (*M. ulei*) continues to be an insurmountable obstacle to the establishment of heveaculture in the central basin of the Amazon and constitutes a grave potential threat to production in Southeast Asia and western Africa. Resistant *H. brasiliensis*, *H. pauciflora* (Spruce ex Benth.) Müll. Arg., and *H. benthamiana* Müll. Arg. clones have been used as sources of resistance.

Because *H. brasiliensis* is very susceptible to attacks by the fungus *M. ulei*, escape areas must be described here. The possibility of escaping the fungus occurs when the natural refoliation period of the tree is made to coincide with the low relative humidity of the dry season, until the leaves become resistant at 2 to 3 weeks of age, depending on the clone and the race of the fungus. The concept of escape has been shown to be totally valid. The escape areas are characterized as having a pronounced dry season at least 4 months long, with at least two consecutive months when the relative humidity is less than 65 percent, with a maximum limit of annual hydric deficiency of 300 mm, according to the Thorwaithe Method, and an average annual temperature of 20 ^{o}C. The need for escape does not apply to young plants, which produce new leaves during the rainy months; in this case, chemical control is feasible (Barrero 1984, Bustamante and Reyes 1994, Rincon 1996, Valderrama 1984).


2cm

Hibiscus tiliaceus L.

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Paul Smiths, NY

MALVACEAE (MALLOW FAMILY)

H. tiliaceus f. *albiflorus* (Degener & Greenwell) St. John; *H. tiliaceus* f. *immaculatus* (Degener & Greenwell) St. John; *Paritium tiliaceum* (L.) Juss. ex St. Hill.; *Pariti tiliaceum* (L.) Britton. (Little and Skolmen 1989, Wagner and others 1990)

Emajagua, hau, linden hibiscus, mahoe, majagua de playa, seaside hibiscus (Little and Skolmen 1989, National Academy of Sciences 1983)

The genus *Hibiscus* includes about 200 species distributed primarily in the tropical and subtropical regions of the world. It is a highly variable genus, with relatively few characteristics in common (Wagner and others 1990). *Hibiscus tiliaceus* is one of the most widespread species in the genus, with a pantropical, mainly coastal, distribution. Whether this widespread distribution occurred primarily through natural dispersal or through human intervention is unknown. Seed capsules are well adapted for long-distance dispersal by water. However, the species has been used historically in a wide variety of ways, leading some to suggest that it was also widely distributed by early seafarers.

The fast-growing *Hibiscus tiliaceus* is a small, evergreen polymorphic tree that typically ranges from 4 to 12 m in height and 15 to 20 cm d.b.h. The tree most often has a short, crooked trunk with a broad crown of widely spreading and crooked branches. It may also grow either in a prostrate, spreading form, or more rarely in a taller, straighter form that may reach 20 m in height (Little and Skolmen 1989, Wagner and others 1990). *Hibiscus tiliaceus* is most often found in wet areas along coasts, such as at the mouths of streams or in more saline areas upstream of mangrove forests. It exhibits a high degree of ecophysiological plasticity, however, and can be found in upland mesic forests to about 500 m and along relatively dry coastlines where it is subjected to high levels of salt spray and substrate salinity (Alpha 1994, Little and Skolmen 1989, Whitesell and others 1986). The tree can grow well on mud, marl, sand, and limestone. It attains greater stature on high, well-drained inland sites. On wet sites the lower branches of *H. tiliaceus* often bend down and take root, resulting in essentially impenetrable thickets.

Hibiscus tiliaceus wood is moderately soft and porous, but also moderately heavy (specific gravity about 0.6) and strong. The wood is durable in salt water and has been widely used for canoe outriggers, fishing floats, planks, and pilings. The bark provides a useful fiber that historically had many uses, ranging from cordage to strainers for kava. The flowers, roots, and bark have a number of medicinal properties, and both roots and leaves have reportedly been used as food, especially in times of famine (Little and Skolmen 1989, Neal 1965). The species has also been widely planted in some locations for erosion control, dune stabilization, and as an ornamental (National Academy of Sciences 1983).

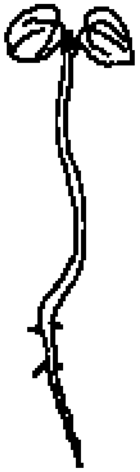
Flowers are borne either in small terminal branching clusters (panicles) or laterally, near the ends of twigs. The showy flowers have yellow petals about 6 to 9 cm long. Flowering occurs throughout the year (Little and Skolmen 1989, Little and Wadsworth 1964). The fruit is an elliptical, long-pointed capsule, typically containing from 5 to 15 brownish-black seeds approximately 0.3 to 0.5 cm long (Nakasone and Rauch 1973, Little and Skolmen 1989). Capsules ripen about 5 to 7 weeks after pollination (Nakasone and Rauch 1973); at maturity they split and break open the calyx and involucre, which remain attached. Seed set often appears to be very low, but no published information on seed set was located.

Capsules should be collected before splitting and air-dried in a paper bag or other container that will minimize seed loss once the capsules open. Capsules can often be readily collected by hand. Seeds of other *Hibiscus* species stored under refrigeration for at least 2 years show a considerable loss of viability (Nakasone and Rauch 1973). Therefore, sowing immediately after removal from the capsules is recommended.

Scarification of the seed coat is recommended to ensure timely germination. Alpha (1994) reported between 50 percent and 70 percent germination within 4 weeks for seeds scarified by sanding lightly with 400 grit sandpaper, compared to 0 percent germination for untreated seeds. Nakasone and Rauch (1973) suggest nicking the seed coat with a knife.

Alpha (1994) reported adequate germination in a range of media, including loamy soil, crushed basalt, and sand. Nakasone and Rauch (1973) recommend transplanting seedlings from germination flats when they reach 5 to 7.5 cm in height. Seedlings can be transplanted into small dibble tubes or pots. Transplanted seedlings should then be kept in partial shade for several weeks before gradually being moved to direct sunlight. Seedlings are ready for outplanting when they reach about 25 to 40 cm.

Hibiscus tiliaceus is also readily, and perhaps more commonly, propagated from cuttings. Both softwood (Dirr 1983) and hardwood (Nakasone and Rauch 1973) cuttings can be used. Treatment of cuttings with indolebutyric acid reportedly improves the rooting of other *Hibiscus* species, but good results have been obtained for untreated cuttings of *Hibiscus tiliaceus* (Cole 1997).



Hura crepitans L.

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EUPHORBIACEAE (SPURGE FAMILY)

No synonyms

Acuapa, acuapar, árbol del diablo, arenillero, arenillo, assacú, betsur, bois du diable, castañeto, catahua, cataua, ceiba amarilla, ceiba blanca, ceiba de leche, ceiba habillo, ceiba lechosa, ceibo, cuatatachi, haba, haba de indio, habilla, habillo, hura wood, igún, jabillo, javarillo, javillo, mil pesos, milinillo, monkey's dinner bell, nune, ochohó, ovillo, pet du diable, possentrie, possum wood, postentrie, rakuda, sablier, salvadera, sandbox tree, seda blanca, trovador, uassacú, uí, wa-cheé-va (Burger and Huft 1995, Record and Hess 1949, Schultes and Raffauf 1990, Standley and Steyermark 1946)

The geographic range of *Hura crepitans* extends from Central America to northern Brazil, Bolivia, and the West Indies (Brako and Zarucchi 1993, Burger and Huft 1995, Foster 1958, Jorsen and León-Yáñez 1999, Longwood 1971, Macbride 1951, Molina 1975, Renner and others 1990). It is found in evergreen and deciduous forests of the Caribbean and Pacific coastal lowlands (Burger and Huft 1995).

The species is a large tree that reaches 45 m in height 3 m d.b.h. In the forest, the tree develops a straight bole; in open places, its growth is faster but the bole is short, thick, branched, and sometimes twisted. The straight bole is cylindrical, without branches in the basal half, buttresses large in basal third. It has a hollow pith. The crown is wide and spreading with horizontal branches and hanging twigs. The bark is smooth, pale gray or light brownish, and densely covered with hard, thick, sharp, conical, broad-based spines. Phylotaxy is spiral. Leaves are simple, with long petioles; blades are ovate, broadly ovate or ovate-orbicular, thick, drying chartaceous, greenish, glabrous, margin serrate or rounded-crenate with 9 to 20 gland-tipped teeth on each side, apex cuspidate-acuminate or cordate-acuminate, base round, cordate or subcordate, with a pair of basal glands, stipules lanceolate or triangular, and deciduous. Venation is pinnate with 7 to 20 secondary veins per semilimb, tertiary veins subparallel (Burger and Huft 1995). The tree reaches its best growth in sandy soils, although it tolerates acid soils with medium to heavy texture and poor drainage. The elevation range is 0 to 800 m.

The wood is moderately light, soft, and sometimes woolly (Longwood 1971). When green the sapwood is light yellowish gray but turns light yellow after drying. The green heartwood is creamy, turning pale yellowish brown upon drying. The innermost heartwood may be darker. The growth rings are demarcated by regular dark stripes. The grain is straight or interlocked; luster is high and texture fine; the wood is odorless and tasteless (Longwood 1971). The wood is light (green weight is 620 to 630 kg per m^3 with an average moisture content of 67 percent; average basic specific gravity is 0.38 (range 0.34 to 0.40) (Bezerra-Marquez and others 1997, Llach 1971, Longwood 1971). Drying is moderately difficult; air-drying prevents the development of sap-stain fungi but produces some warping and slight checking. Sawed boards can be dipped in a fungicide solution before air-drying to prevent these results. Volumetric shrinkage is 7.3 to 7.4 (low and similar to mahogany's 7.7); radial/tangential ratio is 4.5 percent (moderate), and longitudinal shrinkage is 0.48 (into the range of variation expected for this type of wood) (Longwood 1971). The wood is above average in all static-bending properties except stiffness, when compared with species of the same density in green condition. After air-drying the wood increases moderately in all properties except cleavage and tension across the grain; however, improvement is below the level exhibited by other hardwoods from the United States (Longwood 1971). Green wood is moderately difficult to work and must be immediately machined. Chipped and fuzzy grain is common in wood with conspicuous interlocked grain. The wood stains well, nails satisfactorily, and glues easily (Longwood 1971). Natural durability is moderately resistant to fungi (brown rot and white rot) and very susceptible to termite attacks (Llach

1971, Longwood 1971). Impregnation is easy; the wood absorbs up to 20 pounds per cubic foot in hot and cold treatments (Longwood 1971). The wood is used for general carpentry, interior construction, boxes, crates, veneers, plywood, furniture, and joinery. It is suitable as core stock, both utility and face veneer, millwork, and for general use in furniture and joinery where a lightweight, easily worked wood is necessary (Longwood 1971).

The species is rich in lectins and contains a piscicidal compound (Schultes and Raffauf 1990). The sap is inflammatory to sensitive skin, and the seeds are poisonous and used as a purgative (Standley and Steyermark 1946). The milky latex is extremely irritant to the eyes and produces temporary blindness (Hartshorn 1983a, Pittier 1957, Standley and Steyermark 1946). It is used by natives as a remedy for elephantiasis, leprosy, and as a minor fish poison; it may cause blindness and is able to kill anacondas (Longwood 1971, Schultes and Raffauf 1990).

The trees bloom throughout the year, primarily from May through December, although sometimes only through October or November. Inflorescences are unisexual. Staminate inflorescences are narrow, spike-like, conical, terminal, longpedunculate, and 2 to 6 cm long. They have a thick, fleshy rachis and spirals of 60 to 80 congested flowers subtended by red bracts. Male flowers are 3 to 5 cm long, reddish, and apetalous. The androecium has stamens in two or three verticils; with 2 to 15 stamens per whorl. The anthers and pollen are yellow. Pistillate inflorescences have a solitary, dark red flower, 4 to 6 cm long and glabrous. The calyx tube is entire distally. The gynoecium has a maroon stylar column 3 to 5 cm long and fleshy stylar branches, forming a truncate apex with free digitate, radiating stylar branches (Burger and Huft 1995). The ovary is three-locular with axile placentation; there is a single ovule, suspended, solitary, bitegmic, and crassinucellate. Pollination is entomophilous.

Fruit ripening occurs from January to April. The fruit is an explosively dehiscing woody capsule, 3 to 6 cm high, 6 to 12 cm wide, rounded-oblate, depressed in the center around the apex (pumpkin-like), and longitudinally furrowed. Mature fruits split into crescent-shaped segments (cocci), each containing a single seed; the columella is broad and woody (Burger and Huft 1995, Hartshorn 1983a). Seeds are suborbicular with flattened sides, smooth, creamy or pale yellowish, and 3 to 4 cm long; the pericarp is hard.

Fruits must be collected from healthy trees before dehiscence. Seeds collected from the tree or the ground must be soaked for 24 hours. Seed behavior is orthodox.

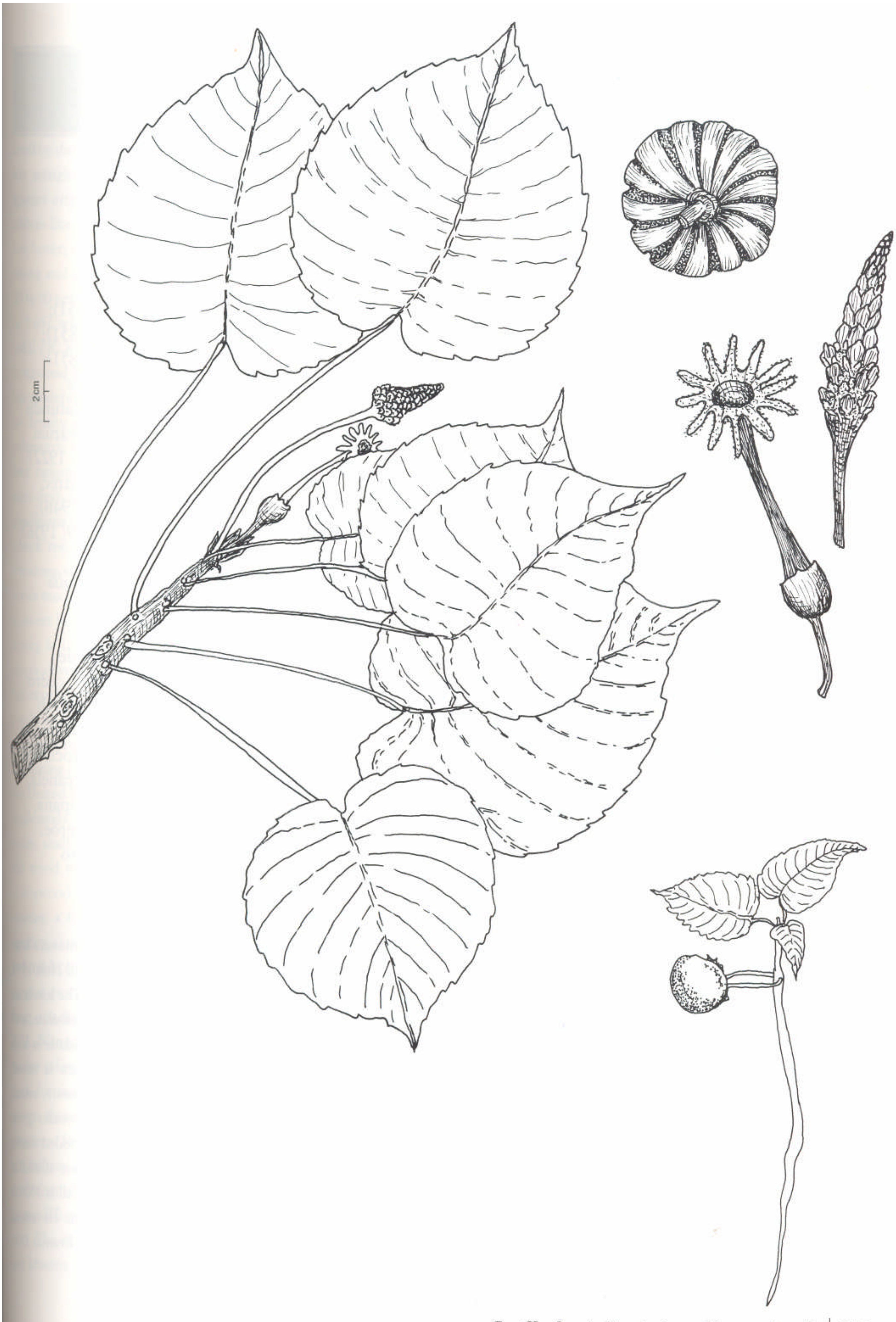
Germination is epigeal and seedlings are cryptocotylar Radicle protrusion occurs in 10 to 12 days. The cotyledons enclosed by the testa elevate from the ground due to hypocotyl elongation.

Seeds do not require special treatments and can be sown in beds or plastic bags filled with humid sand or a mixture of soil and sand. The species is appropriate for use in natural forest regeneration. The seedlings and saplings are shade-tolerant; however, to grow well they require forest clearings to continue their longitudinal growth.

ADDITIONAL INFORMATION

Seed endosperm is nuclear, becoming cellular and thin-walled. The embryo is large, straight, and laterally compressed cotyledons are orbicular, thin, and flat; the radicle is short.

Cotyledonar petiole elongation occurs in the second and third week after root protrusion. The cotyledons enclose the plumule. When they extend longitudinally and bend backwards, they form an inner opening through which the plumule emerges. The cotyledon petioles abscise approximately 1 month later and the seed containing the cotyledonar blades falls down. Seedling growth becomes slower when leaf production begins.


2 cm

Hyeronima alchorneoides Allemão

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EUPHORBIACEAE (SPURGE FAMILY)

Stilaginella laxiflora Tul. (Annales des Sciences Naturelles, Botanique service 3, 15: 244; 1851); *Stilaginella amazonica* Tul. (Annales des Sciences Naturelles, Botanique service 3, 15: 244; 1851); *Stilaginella ferruginea* Tul. (Annales des Sciences Naturelles, Botanique service 3, 15: 244; 1851); *Hyeronima ferruginea* (Tul.) Tul. (Flora Brasiliensis 4 [1]: 334; 1861); *Hyeronima laxiflora* (Tul.) Müll-Arg. (Linnaea 34: 66; 1865); *Hyeronima mollis* Müll-Arg. (Prodromus Systematis Naturalis Regni Vegetabilis 15 [2]: 269; 1866); *Hyeronima caribaea* Urban (Repertorium Specierum Novarum Regni Vegetabilis 16: 139, 1919); *Hyeronima mattogrossensis* Pax & Hoff. (Planzenreich 81: 39; 1922); *Hyeronima heterotrichia* Pax & Hoff. (Planzenreich 81: 39; 1922); *Hyeronima chocoensis* Cuatrec. (Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 7 [25-26]: 52; 1946); *Hyeronima tectissima* L. A. Standl. & L. O. Williams (The Rain Forests of Golfo Dulce 222, t. 29; 1956); *Hyeronima alchorneoides* var. *stipulosa* P. Franco (Botanische Jahrbücher für Systematik, Planzengeschichte und Planzengeographie 111 [3]: 321-323, f. 10; 1990); *Hyeronima ovatifolia* Lundell (Wrightia 4 [4]: 134; 1970)

Aguacatillo, ajo-ajo, ajono, ajowo, amapaia, anoniwana, apamate, aricurqua, bois d’ amande, bois de vin, bois divin, bully tree, cachete toro, cajuela, calun calun, cartan, cartancillo, catatú, cedro macho, chac-te-cook, colorado, coral, curtidor, dalina, dionkoimata, florecillo morado, horseflesh mahogany, itahuba blanca, itahuba colorada, katoelienja, licurana, makoeroerian, malangazote, mapique, mará-gonçalo, margonçalo, mascarey, minua, muiracongalo, nance, nancito, nancitón, okotjo, orocurana, palo chanco, palo curtidor, palo rosa, pantana, piento-bolletrie, pilón, plátano, quina, quindú canela, rosa, sagua, scotch ebo, serdani, soeladan, soeradan, sorodon, suradán, suradanni, surdina, tapana, tapanare, tapierín, tarroema, teloko-enoeroe, tinto morado, tokadie-ballie, torito, troko-enoeroe, trompillo, urucurana, urucurana de leite, urucurana miri, waikwabia, win oudou, zapatero (Flores 1993, Franco 1990, Longwood 1971)

Hyeronima alchorneoides is an important taxon of the neotropical forest, whose center of distribution is located in the Andes (South America). It is found from Belize to the Amazon region and in the West Indies (Brako and Zarucchi 1993, Burger and Huft 1995, Jorgensen and León-Yáñez 1999, Jorgensen and Ulloa 1994, Macbride 1951, Molina 1975, Renner and others 1990). *Hyeronima alchorneoides* is a canopy tree, abundant in humid and very humid tropical forests.

Hyeronima alchorneoides is a tall, evergreen tree, with a straight bole and spreading, extended buttresses on the lower third. It is a tree that may reach up to 50 m in height and 100 to 120 cm d.b.h. The crown is wide and extended. The branches are subterete and angulous. The bark is fissured, hard, brittle, and light brown or reddish brown; it is 0.75 to 0.80 cm thick. Internally, it is pink or red and contains a large amount of tannins. It has a bitter taste (Burger and Huft 1995, Flores 1993, Longwood 1971, Macbride 1951). The leaves are alternate, entire, petiolate (petioles adaxially caniculate, with lepidote indumentum), and stipulate. The leaf blade is wide ovate, wide elliptical, or obovate; the leaf apex is round, obtuse, or acuminate; and the leaf base is attenuate, round, cordate, obtuse, or cuneate. *Hyeronima alchorneoides* grows well in very humid plains that are seasonally flooded during the rainy season. The species grows in soils that are alluvial or clayey and acid. It grows where the annual rainfall is 3500 to 5000 mm and temperatures are 24 to 30 °C. The elevational range of this species is 20 to 900 m (Flores 1993, Franco 1990, Woodson and Schery 1967).

In green wood, the sapwood is reddish brown or pink while the heartwood is dark red, reddish brown, or deep brown, being similar to black walnut (*Juglans nigra*) in appearance (Flores 1993, Longwood 1971). The growth rings are outlined by dark terminal bands formed by thick-walled fibers. It has straight or interlocked grain depending on the site of species origin; wood with interlocked grain has a striped or ribbon-like appearance. Texture is moderately coarse and has low luster; the dry wood is odorless and tasteless. The wood is strong and heavy (green weight 1100 to 1150 kg per m^3; with 85 to 90 percent moisture content; basic specific gravity is 0.60 to 0.65), which is comparable to pignut hickory (*Carya ovata* [Mill.] K. Koch) and white oak (*Quercus alba* L.) (Llach 1971, Longwood 1971, Van der Slooten and others 1971). The wood has moderately high shrinkage compared with woods of similar density and is comparable to white oak in directional and volumetric shrinkage (5.1 to 5.3 percent radially, 9.2 to 94 percent tangentially, 13.3 to 14.5 volumetrically from green to oven-dry). Strength properties are normal in green and air-dry conditions except for deficiencies in work-to-maximum-load (shock resistance), compression and tension across the grain (crushing strength and hardness), and cleavage (splitting). It bends moderately well except in shock resistance, comparable to sweet birch (*Betula lenta* L.) (Longwood 1971). Wood air-drying is fast and easy; however, 38 to 40 percent of wood pieces develop twisting, and 30 percent of them collapse. It has excellent sanding, boring, and mortising properties; very good turning properties; good shaping properties; and poor planing properties. With the exception of planing, wood machining is above the average for 25 domestic hardwoods in the United States (Davis 1949, Longwood 1971). The wood is moderately difficult to work because of its poor planing properties; shallow chipped grain during planing is frequent, and the wood must be scraped well to achieve a smooth finish (Longwood 1971). During brushing, 30 percent of pieces develop a fibrillar appearance and rough grain; 40 percent develop a smooth and flawless surface (Llach 1971). The wood is durable and resistant to termites and white- and brown-rot fungi at ground level but is susceptible to wood-decomposing fungi attacks at underground levels (Llach 1971, Longwood 1971, Wangaard and others 1955). The wood can be used in marine pilings, general heavy construction (interior and exterior), furniture, cabinetwork, decorative veneer, framework, rafters, sheathing in building construction, boat construction, structures for bridges and fences, stakes, barrel construction, and railway ties (Llach 1971, Longwood 1971). The Peteri's coefficient of flexibility is 65, and the Runkel factor is 0.91 [group III: good for making paper (Llach 1971)].

The species is dioecious, and the flowers, unisexual. The tree blooms twice a year, and the primary period of flowering occurs from May to July, with a peak in June. The flowering can vary with rain patterns and range of geographical distribution. Sometimes the species blooms in November, December, or January. The flowers, grouped in axillary panicles of a variable size and number of lateral branches, are inconspicuous and yellowish green. Cross-pollination is obligatory; the floral anthesis takes place in the early morning and many small insects contribute to pollinating the pistillate flowers. Fruits are produced from January to March, sometimes in April. The fruit is drupaceous and turns red or dark purple at maturity. The surface is bright and almost glabrous. The exocarp is thin and membranaceous; the mesocarp is fleshy, soft, and sweet. The endocarp is hard and sclerenchymatous and surrounds the only seed developed in the fruit (Flores 1993). The ripe fruits fall by gravity, alone or in clusters. Birds and monkeys are the main commensals and dispersers. It is possible that seed passage through the bird or monkey digestive system promotes seed germination through endocarp scarification. Seeds are small.

Seeds average 26,400 to 26,500 (seed + endocarp) per kg, with 67 percent moisture content (fresh weight). The percentage of germination is 60 to 70 percent, but varies strongly depending on seed origin. Seeds are viable for 10 to 15 days if moisture and temperature are adequate.

Seed behavior seems recalcitrant and information on seed storage is nonexistent. The species germinates and grows in clearings and well-illuminated places. Seedlings and saplings are not common in the forest understory. Red ants (*Atta cephalotes*), the larvae of *Hylesia alinda*, and other herbivores—deer, mountain goats, and rabbits—attack them. Germination is epigeal and seedlings are phanerocotylar. Under greenhouse conditions, germination occurs at 25 to 30 days; it is gradual. Initially the cotyledons are enclosed in the seedcoat (60 percent of seedlings) but the latter is removed at 45 to 50 days (Arias 1992, Flores 1993).

The species grows well in plantations and has been planted in monospecific plantations with a planting distance of 3 by 3 m. Holes must be 15 cm deep and seedlings must be transplanted in adobe (keeping the surrounding substrate). Plantations must be cleared three to four times during the first year. Seedling mortality in plantations is low, and the species has an efficient autopruning system; however, branches must be trimmed at 9 to 12 months later (Arias 1992, Flores 1993, González 1991). In the Sarapiquí zone (Costa Rica), the annual increase in height is 1.6 m during the first 3 years; diameter increases 2.2 cm annually. About 80 percent of trees have a straight and vigorous bole (Arias 1992, González 1991).

The species is not susceptible to pests and diseases, but several animals predate young seedlings and saplings. Shoot apex damage induces stem bifurcation (Flores 1993).

ADDITIONAL INFORMATION

Hyeronima alchorneoides is the type species of the genus. It was named *Hyeronima* as homage to Jeronimo Serpa, a Brazilian botanist (Flores 1993, Franco 1990).

The leaf's adaxial surface has scarce pubescence (multicellular hairs); the abaxial surface has a densely lepidote indumentum. Venation is pinnate brochidrodromous, with 6 to 12 secondary veins. The midrib is wide, straight, and projects toward the abaxial surface. Secondary veins are parallel and uniformly spaced with a moderate and uniform divergence angle; they branch toward the margin. Tertiary veins are percurrent, branched, and projected abaxially. The leaf is hypostomatic, and the stomata are paracytic. Stipules are variable in shape but always conspicuous, foliaceous, petiolate or sessile, quite permanent, basally wide, fleshy, and commonly inhabited by ants (Flores 1993).

The flower bracts subtending the inflorescence branches tend to be morphologically different from those of the vegetative axes; the proximal are large and foliaceous while the distal are short, triangular, and deltoid. The staminate panicles are corymboid and pedunculate with straight or curved branches. The peduncle is terete and 2 to 4 cm long. Floral bracts are trulate-cocleate. The male flowers have a tetramerous calyx, cupuliform, gamosepalous in the basal third, toothed distally, and densely lepidoted. The disc is annular and massive with a villous margin; stamens are within the disc and the androecium consists of four fertile stamens, sometimes five; anther lobes are pendulous and divergent during the anthesis, and dehiscence is poricidal. The connective is glandular. Pollen grains are tricolporate and perprolate (Flores 1993). The pistillate flower has a short peduncle and a calyx similar to that of the staminate flower, but the annular disc is smaller. The ovary is ovoid, bicarpelar, and covered by peltate scales; each locule contains two ovules; only one develops as a seed. The interlocular septum usually moves toward the cavity with the abortive ovule. The style is vestigial, and the stigma is punctiform and bifid. Ovules are anatropous, bitegmic, and crassinucellate and have an obturator (Flores 1993).

The seed funiculus is vestigial; the testa, thin; and the tegmen, sclerotic. Seed size correlates with fruit size. The seed is endospermic; the endosperm is nuclear but becomes cellular and oily later. The embryo is large in respect to seed size; it is straight, with a small radicle and thin, extended cotyledons. The seeds are rich in lipids (Flores 1993).


1cm
1cm
2cm
2cm
1cm

Hymenaea courbaril L.

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FABACEAE (BEAN FAMILY)

No synonyms

Algarrobo, algarrobo de las Antillas, caguairan, copal, copinol, corobore, courbaril, cuapinol, curbaril, guapinal, guapinol, jatoba, jutaby, jutahy, locus, locust, loksi, nazareno, rode locus, simiri, stinking-toe, West-Indian-locust (Little and Wadsworth 1964)

Of the 17 species in the genus, 16 are found in neotropical America, with *H. courbaril* the most widespread. The one remaining species is African. *Hymenaea courbaril* forms forest associations readily in semideciduous, secondary, moist subtropics (Rzedowski 1981). The species is normally found in open sites from southern Mexico, Central America, and West Indies, to northern South America, and uncommonly in southern Florida. Specifically, it ranges from Cuba and Jamaica to Trinidad and Tobago in the West Indies; and from Mexico through Peru, Bolivia, Brazil, and French Guiana (Little and Wadsworth 1964). It is reported in almost pure stands in Mexico (Weaver 1987).

Hymenaea courbaril is a slow-growing, well-formed tree with a clean trunk. It grows about 1 m per year to about 45 m in height. It develops best on sandy, drained ridges and although found on river banks, it does not grow well in wetlands. The tree grows in a variety of soils from clay to sand but is predominant in oxisols with a pH range from 4.8 to 6.8. Occurring from sea level to about 900 m, it grows best in areas with annual rainfall of 1,900 to 2,150 mm.

Basically a timber tree, *H. courbaril* has a heartwood specific gravity of about 0.70. The wood is strong, hard, tough, and difficult to saw, machine, or carve. The lumber does bend well after steaming. It is commercially useful for flooring, handles, sporting equipment, furniture, and railroad ties (Chudnoff 1984). Indians used the bark for canoes, stripping it in one piece from a large tree (Little and Wadsworth 1964). Although gastronomically unappealing, the seed pulp is a good dietetic sugar source and is high in fiber. In folk medicine, the bark is used as a laxative and the seed pulp as a diarrhea remedy (Liogier 1978). Resistant to white-rot fungi (less to brown-rot) and termites, *H. courbaril* has little resistance to marine borers. The wood does not weather well and requires painting (Francis 1990b, Longwood 1962). It has limited ornamental use as a shade tree in parks and on streets because the heavy seed pods emit an offensive odor as they mature and can cause damage or injury when they fall.

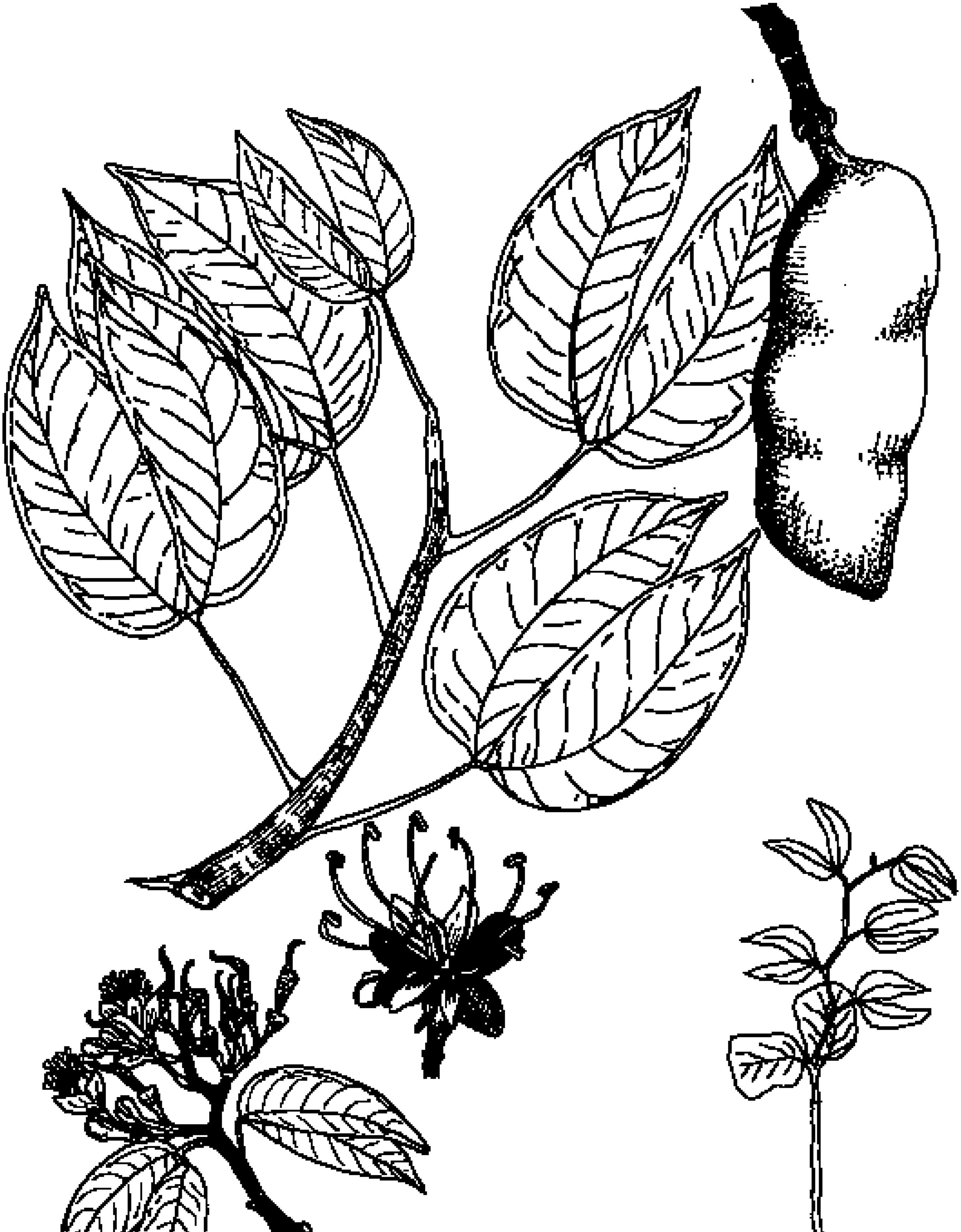
Flowers appear in spring and summer on large trees that grow in full, overhead light. Terminal racemes bear white flowers about 4 cm wide. Mature seed pods 5 to 10 cm long, 2 to 3.5 cm wide, and 2.5 cm thick fall the following spring. The thick, hard seed pods protect three to four large seeds encased in a powdery, cream-colored pulp and do not open naturally (Liogier 1978). Small animals (agouties, peccaries) open the pods to eat both seeds and pulp. The pods also have a protective gum that delays rotting for several months, allowing seeds to imbibe moisture in preparation for germination (Jansen 1983). A single *H. courbaril* tree may produce 100 pods in 1 year but not necessarily every year.

Because tree height usually discourages manual collection, seeds are collected from fresh pods when they fall in the spring (Jansen 1983). Overripening enhances germination during the first 4 months after collection, which may explain why seed pods remain on the tree for 9 months before falling. *Hymenaea courbaril* seeds collected from Puerto Rico average about 253 per kg (Francis 1990), while those from Brazil yield 475 per kg (Pereira 1982). Seeds may be infected by a bruchid beetle [*Pygiopachymerus sp.* (Decelle 1979)], a weevil [*Rhinochenus sp.* (Jansen 1975)], or an ant [*Atta sp.* (Jansen 1983)].

Hymenaea courbaril seeds stored more than 1 year produce acceptable germination percentages. However, storage conditions change with duration. For the first year, seeds should be stored in sealed containers at ambient temperatures (24 to 30 °C). Because humidity becomes excessive within the container, seeds should be refrigerated or kept in unsealed bags after 1 year of storage (Marrero 1943).

Either simple scarification or a 1-hour soak in sulfuric acid is a necessary germination pretreatment (Marshall 1939). After imbibition, seeds may be planted in potting mix for up to 90 percent germination in 14 to 21 days (Marrero 1949, Francis and Rodriguez 1993). Seeds can be germinated at ambient temperature in either potting mixture or sand placed in shallow trays, or on moistened filter or blotter paper in petri dishes.

Containerized stock may be grown in either full sun or 50-percent shade. However, seedlings grown in full sun are ready for outplanting about 2 weeks earlier than those grown in shade (Pereira 1982, Francis 1990). Although *H. courbaril* may be direct-seeded or underplanted, seeding in containers allows greater protection, promoting greater success. A large tap root with a well-developed fibrous net grows deep and may have associated nitrogen-fixing nodules (Allen and Allen 1981).



Inga jinicuil Schltdl. & Cham. ex G. Don

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FABACEAE (BEAN FAMILY)

No synonyms

Chalahuite, chalahuite de monte, coctzán, cuajinicuil, jinicuil, paterno

Native to the tropical regions of Mexico, *Inga jiniciul* is distributed in the states of Puebla, Veracruz, Tabasco, Oaxaca, Guerrero, Michoacán, and Jalisco. The species is part of the mountain mesophyll forests and the gallery forests that grow along rivers.

Inga jinicuil is an evergreen tree that can reach 20 m in height and 50 cm d.b.h. The trunk is straight, and the spreading, round crown consists of rising branches with dense foliage. The leaves are pinnate, made up of six elliptic or lanceolate leaflets, 8 to 11 cm long. The tree is found in areas with deep soils that are rich in organic matter. The climate in which it prospers is humid with an average annual precipitation of 1490 mm, a dry season lasting 1 month, and an average annual temperature of 18 °C. *Inga jinicuil* grows at elevations from 900 to 1500 m.

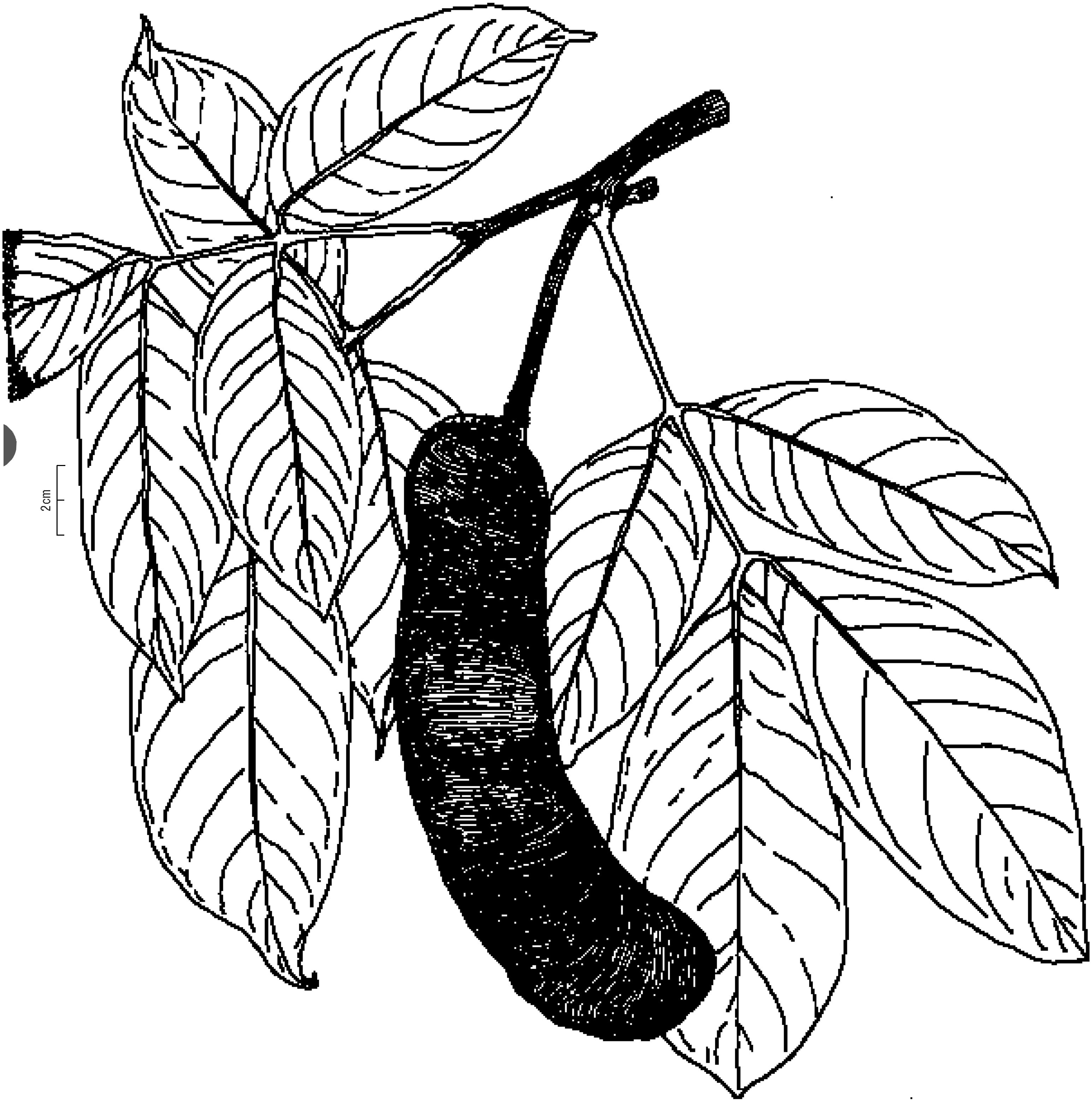
The tree is used primarily for shade in coffee and orange plantations and in hedges to mark boundaries and properties in rural areas. Resistant to freezes, this species fixes atmospheric nitrogen at a rate of 35 to 40 kg per ha per year, a rate that often exceeds that of applied fertilizers (Nair 1993, Roskoski 1981). *Inga jinicuil* is also cultivated as an ornamental tree. The fruits are gathered in large amounts and sold in markets for their pulpy, white, edible seedcoat. The wood is used for firewood and for construction in rural areas. The species has great potential for use in agroforestry systems located in the wet and subhumid regions and tropical highlands with precipitation of 500 to 3000 mm per year and a dry season of 5 to 6 months.

The flowers are fragrant, white or cream, and arranged in colorful capitula. *Inga jinicuil* blooms during the spring and fruits in the fall of the same year. The fruits (legumes) are oblong, arched, 15 to 20 cm long, laterally flattened, thick, green, and dehiscent when ripe. Each fruit contains 12 to 18 seeds (Martinez 1987, Standley 1922). The seeds are oblong, laterally flattened, 24 to 32 mm long, by 12 to 18 mm wide, and 8 to 11 mm thick. The seedcoat is white, cottony, pulpy, sweet, succulent, and easily loosened from the embryo.

The fruits are green and become yellowish green as they ripen. They are not gathered when they are over-ripe because the seeds acquire an unpleasant taste. Poles with metal hooks are used to collect fruits. Children throw stones to knock down fruit or pull down the branches with hemp or jute ropes. The fruits are twisted to separate the valves and extract the seeds. Because the seeds removed from the fruit die quickly from desiccation, they must be planted immediately in a bed of wet moss.

ADDITIONAL INFORMATION

The hilum is basal, and the funiculus adheres to it. The micropyle is indiscernible. The endosperm is absent. The green embryo has a straight axis and is almost bilaterally symmetrical. The cotyledons are ovate or elliptic, whole, expanded, plano-convex in cross section, pulpy, independent, and slightly sinuous in their contact surfaces, with fissured bases. The radicle is conical or pyramidal and totally covered by the cotyledons (Niembro 1992).


2cm

Inga paterno Harms

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FABACEAE (BEAN FAMILY)

No synonyms

Paterno

Inga paterno is native to southern Mexico and Central America (Zarucchi 1986). *Inga paterno* is a fast-growing tree, reaching 10 m to 20 m in height and 44 cm d.b.h. *Inga paterno* has pinnately compound leaves with four to five elongated and entire leaflets (Guzmán 1980). Leaves are copper-red and soft when young, and dark green and rigid when mature. In El Salvador it grows from sea level to 2000 m in moist and well-drained soils. It is found along streams and in riparian zones.

Both the fresh arils and the cooked seeds of *I. paterno* are popular for human consumption in El Salvador. The seeds are used as vegetables in local dishes and are sold fresh or preserved. *Inga paterno* is commonly used for shade in coffee plantations in Central America as are other *Inga* species such as *I. punctata* Willd., *I. oerstidiana* Benth., *I. edulis* Mart., and *I. vera* Willd. (Quintanilla 1997, Witsberger and others 1982). *Inga paterno* branches are used for firewood. Tea made from the fresh bark is given to women to accelerate slow labor during childbirth, and the fresh aril helps to cure constipation (González Ayala 1994). Small animals feed on the seeds, especially the aril. Flowers of *Inga* spp. are a good source of nectar for honeybees and other insects, birds, and bats (Arroyo 1981, Elias 1966). Its branches support wild bromeliads, orchids, and ferns.

Inga paterno flowers are produced during the dry season in El Salvador. The flowers are densely clustered in spikes or heads and have very conspicuous white stamens. Mature fruits are first observed at the end of the dry season in April. Trees first produce fruits at 3 years. Mature fruits are green indehiscent pods, 15 to 30 cm long with 6 to 12 seeds. The soft-green seeds, covered by a sweet and cottony-white aril, are 3 to 5 cm long. The viviparous seeds force the fruits to open at maturity (Allen and Allen 1981). Seeds average 1,200 to 1,400 per kg. Seeds kept inside the pod under cool and moist conditions may be viable for up to 2 months. Without the protection of the pod, seeds are viable for only 1 to 2 weeks (Croat 1978, Lawrence 1993).

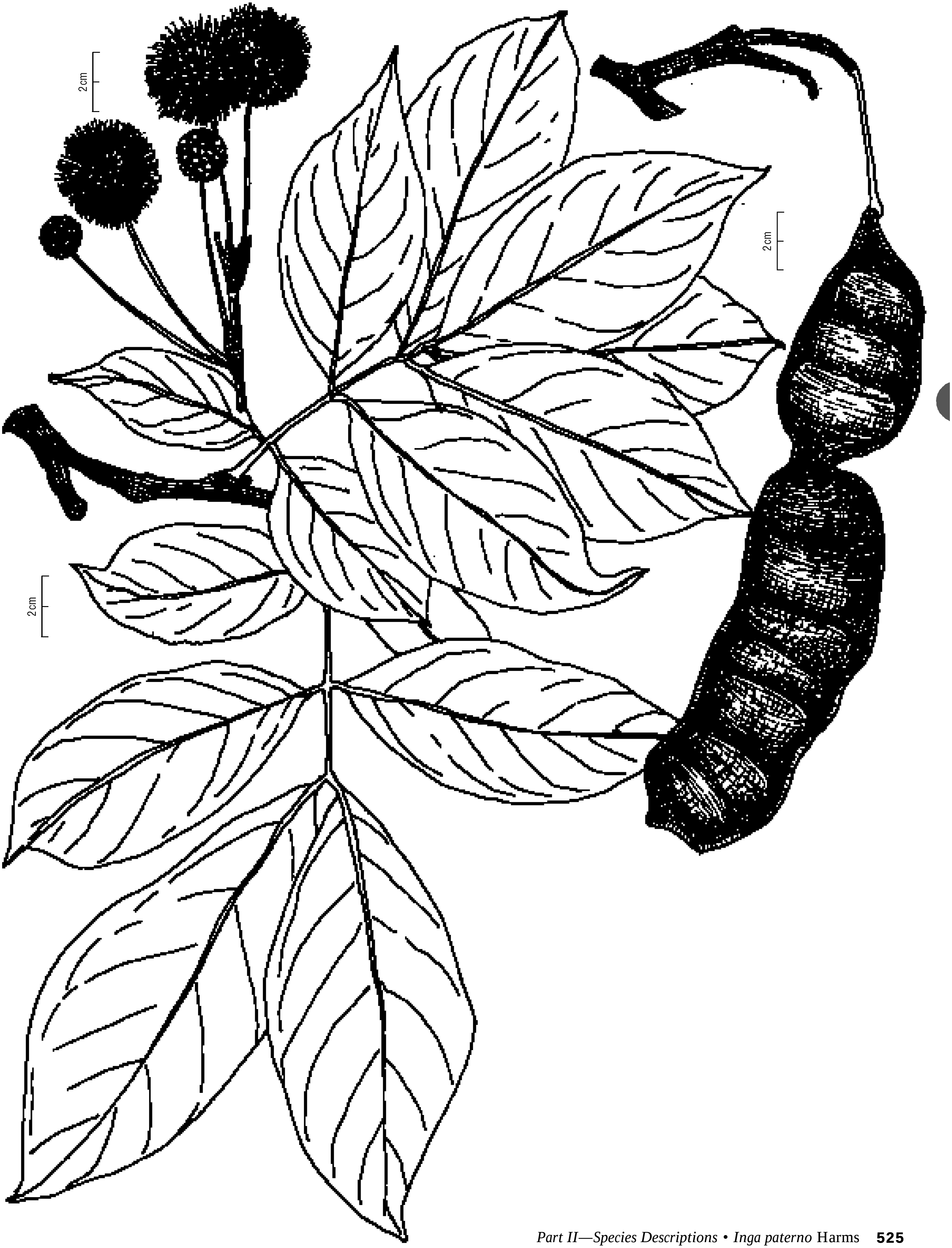
In nursery production, the seeds are planted immediately after extraction from the mature pods. One seed is planted in a polyethylene bag containing soil with high nitrogen content and good drainage. Only the lower part of the seed including the root is inserted in the soil; the upper part with the germinated embryo is left uncovered. One-year-old seedlings, 50 cm or taller, should be outplanted at the beginning of the rainy season in May (Navarette-Tindall, personal observations). Manual weeding around seedlings is required during the first growing season. Chemical herbicides are not recommended.

ADDITIONAL INFORMATION

Inga paterno, like other species of *Inga,* propagate by seed and little is known about other propagation methods. The trees appear to have a lifespan of 20 to 25 years. This short lifespan may be the result of disease or natural aging. Lack of information about genetic diversity for disease resistance has limited the expanded use of *I. paterno* in coffee plantations and agroforestry systems.

Although nodulation has not been documented for *I. paterno* (Halliday 1984, Powell 1997), root nodules were observed in 1-year-old seedlings growing in the plant nursery of the Dirección de Urbanización y Arquitectura in El Salvador. Scanning electron micrographs of the broken nodules of *I. paterno* showed rhizobial bacteria (Navarrete-Tindall and Aragón 1997), similar to those observed in nodules of *Gliricidia sepium* (Navarrete-Tindall 1996). This preliminary information suggests that *I. paterno* is a nitrogen-fixing tree like many other *Inga* species (Allen and Allen 1981, Halliday 1984, Roskoski 1981).

Future studies on nutrient content of the seeds, preservation methods, and availability in markets and plantations could improve seed commercialization.


2cm
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Jacaranda copaia (Aubl.) D. Don

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Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

BIGNONIACEAE (BIGNONIA FAMILY)

Bignonia copaia (Aubl), *Jacaranda copaia* var. *paraensis* Huber

Cedro blanco, chingale, gualanday, pavito, vainillo

Jacaranda copaia is a fast-growing tree 30 m in height and 20 cm d.b.h.; its leaves grow in terminal bundles, erect on top of the crown. The tree grows without much demand for nutrients on flat grounds and hillsides that are moderately to well drained. The species tolerates temporary floods, soils having a sandy-clayey to loose muddy texture and an acid to slightly acid pH. Its growth is delayed in very shallow soils. It adapts to multiple environmental conditions, growing naturally in areas with a marked dry season and in regions, such as the South Pacific, where there is no hydric deficit. In Colombia, it is found from sea level to 1000 m. It grows in areas with an average temperature of 25 ^{o}C and an annual precipitation ranging from 600 to 3000 mm. It grows in formations of the wet and very wet Tropical forest (bh/mh-T) (Venegas 1978). It is a pioneer and colonizing species.

Because the wood of *J. copaia* is easy to finish and work and has a good grain, it is used for decorative boards. It is also used for particleboard, beams, furniture, round arches, pulp, coffins, pencils, matches, crating, musical instruments, toys, and broomsticks (Escobar and Rodriguez 1993). When preserved it can be used for fenceposts. The sap is used as adhesive, varnish, and insect repellent. Because the tree is resistant to fire and termites, it can be used to improve soils.

The pale purple flowers appear at the beginning of summer; the fruit ripens before winter so the seeds can be scattered by the wind.

Seeds can be stored up to 2 months in plastic bags at a moisture content less than 8 percent and a temperature of 4 ^{o}C. A fungicide should be applied to the seeds before storage. Pregermination treatment consists of submerging the seeds in running water for 1 day. Seeds germinate in 5 to 20 days.

About 25,000 plantules are obtained from 1 kg of seeds in nurseries. The recommended substrate consists of two parts sand and one part soil, which must be disinfected before planting the seeds. A substrate of humus with loose texture is used in seedbeds to facilitate germination. Once the seedbed is disinfected with formol or hot water, the seed is planted at a depth no greater than 1 cm and covered with very fine soil.

When the first pair of real leaves are completely developed (1 month after germination), the plantule is transplanted to a coffee bag. The substrate in the bag must be rich in nutrients and have a loose texture. Three months later, plantules approximately 30 cm in height are ready to be outplanted. The ground must be completely cleaned to allow tracing and digging. Soils that are trampled should be plowed or dibbled with holes (Trujillo 1983, Universidad Nacional de Colombia 1988). The recommended planting distance is 3 to 4 m, depending on the type of soil and on the proposed commercial products to be obtained by thinning.

Juglans neotropica Diels

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Santafé de Bogotá, Colombia

JUGLANDACEAE (WALNUT FAMILY)

Jugans andina Triana & Cortés, *Juglans colombiensis* Dode, *Juglans honorei* Dode

Cedro negro, cedro nogal, nogal, nogal bogotano

Juglans neotropica is a slow-growing tree 25 m in height and 40 cm d.b.h. The trunk has a bark with grooves. The crown is oval with light green foliage. The compound leaves are 40 cm long, grouped at the end of branches, and alternate with a serrated border. The species grows in soils of loose texture, muddy, loose-sandy (loose soils), with a neutral to slightly acid pH. It does not tolerate low pH or calcareous soils and needs deep and fertile soils. It has low growth in poor, shallow, and flooded soils. *Juglans neotropica* develops well at an altitude of 1600 to 2500 m, with an average temperature that ranges between 14 and 22 ^{O}C and an annual precipitation of 1000 to 3000 mm that is distributed throughout the year (Acero 1985, Venegas 1978) . The species has a wide ranging ecological distribution; it grows in the Pre-Mountainous wet forest (bh-PM), very wet Pre-Mountainous forest (bmh-PM), Low-Mountainous dry forest (bs-MB), Low-Mountainous wet forest (bh-MB), and Low Mountainous very wet forest (bmh-MB) (Venegas 1978).

The wood of *J. neotropica* is used in decorative veneer, fine cabinetmaking, interior carpentry, turned utensils, and decoration. It is also used in packing boxes and construction and for tri-plex. It is a medicinal species. The seeds are edible, the bark is used for tanning hides, the unripened fruits make yellow dyes, and the ripe fruits make very fine black dyes (Escobar and Rodriguez 1993).

The cream-colored masculine (1 cm) and feminine (2 cm) flowers grow separately on the same tree. The fruit is green, becoming yellowish-green when ripe. It is pulpy, with an almond-type seed, and rich in oil.

The fruits are collected from the ground or from the crown when they have turned yellowish. Gloves must be worn to prevent staining hands. The fruits are soaked in water for 24 to 48 hours but not allowed to ferment; then the loosened pulp is removed manually. Seeds average 50 to 200 per kg. They are stored at 4 to 6 ^{O}C.

The recommended pregermination treatment consists of scarifying the seeds with sandpaper or placing them in moist sand for 4 months at 2 to 6 ^{O}C. Purity percentage is 100 percent. Germination percentage is 40 to 80 percent. Germination is hypogeous. Untreated seeds germinate in 1 to 3 months.

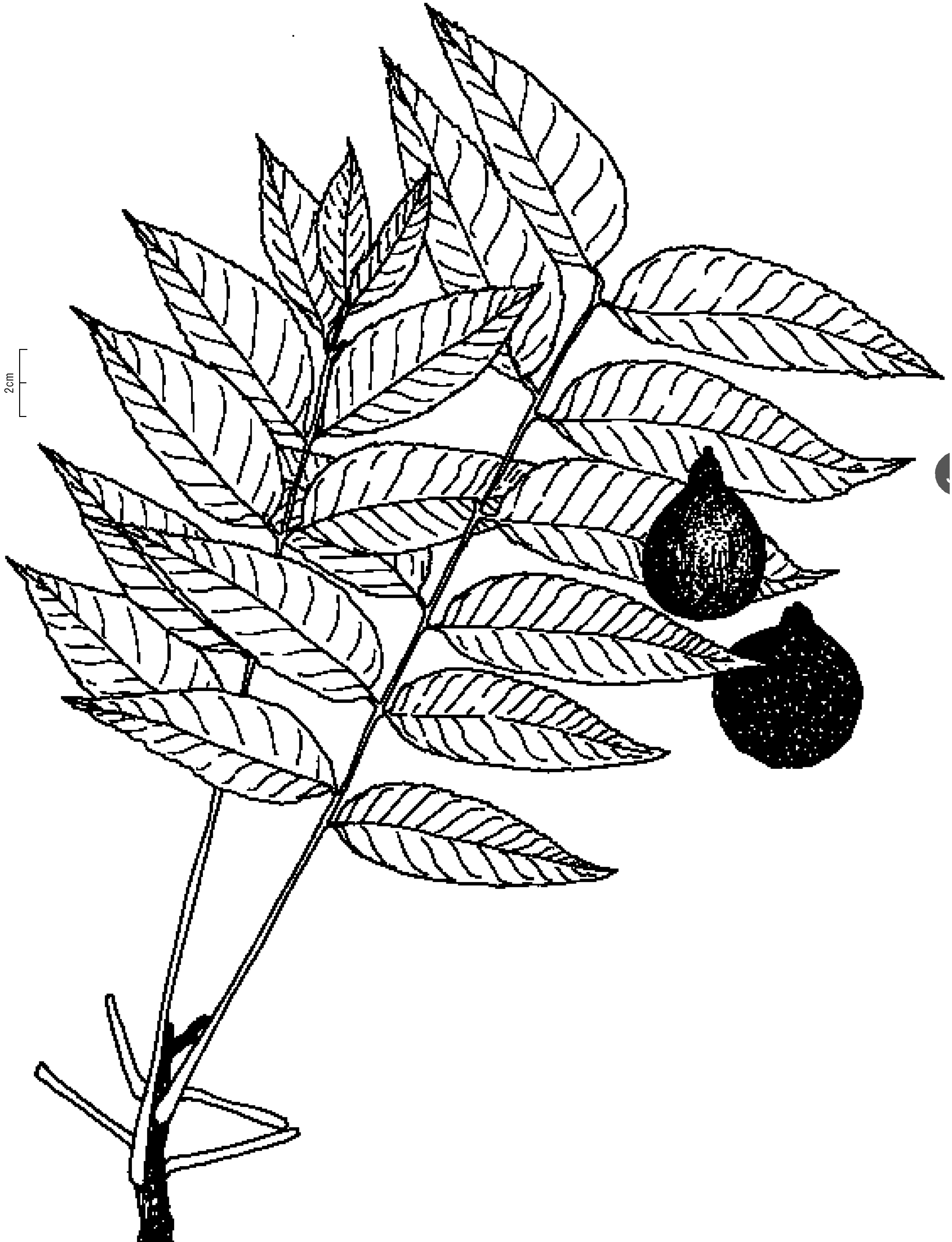
The seeds can be planted directly in bags. If a germinator is used, the planted seeds must be 1 cm apart; the tip must be planted deeply, and covered with 2 to 3 cm of soil and sand. The germination period is 36 days. The species requires medium light for germination (Barreto and others 1990, Montero and Estevez 1983).

In the growing/threshing floors, bags 20 by 30 cm in flat dimension are used; when the plantules are 20 to 40 cm high they are outplanted. The substrate of the growing/threshing floor must have a sandy texture, with fertile soil. Organic and chemical fertilizers may be needed. Seeds can also be planted directly at the site, placing one or two seeds per hole. The tree can also be planted bare root in the form of small, defoliated shoots; the leaves and roots are cut at 25 cm.

The planting site must have optimal edaphoclimatic conditions and available water. Grass and thickets must be removed completely. If the trees are planted far apart the area under the crown must be cleaned. If the trees are planted in a continuous line, a strip about 1 m wide must be cleaned and weeded. To produce a forest, a spacing of 3 by 3 m or 5 by 5 m is recommended (Barreto and others 1990).

ADDITIONAL INFORMATION

This species is very susceptible to fire. It hosts the borer of the cedar species, and its use is restricted in some agroforestry combinations due to allelopathic danger.



2cm

Junglans olanchana Standl. & L.O. Williams

C.R. ALVARADO, C.A. ALVARADO, and O.O. MENDOZA
Jefe Programa Nacional de Viveros Forestales, Administración
Forestal del Estado, Tegucigalpa, Honduras;
Jefe Departamento de Investigación Forestal, Escuela Nacional
de Ciencias Forestales, Siguatepeque, Honduras; and
Gerenta General Semillas Tropicales, Siguatepeque, Honduras

UNGLANDACEAE (WALNUT FAMILY)

No synonyms

Cedro negro, nogal, walnut

Junglans olanchanus is distributed in the wet forests of tropical America, from southern Mexico, across Central America, to the mountain ranges in Colombia, Ecuador, and Peru. It also grows in the mountainous regions of Argentina. In Honduras, it grows in the departments of Atlantida, Colon, Yoro, Olancho, Francisco Morazan, and Comayagua (Centro Agronómico Tropical de Investigación y Enseñza 1997a).

Junglans olanchanus is a semideciduous tree up to 40 m in height and 150 cm or more in diameter. It has a cylindrical, straight shaft that is frequently free of branches for 5 m. Occasionally, the shaft lacks branches for 10 to 15 m. It has an elongated base or one with simple, straight gambas. The crown is dense, umbellated, or multiflabellate. The bark is darkish gray or brownish gray, rough, longitudinally and deeply fissured, and sometimes has cracked anastomoses, which come loose in thick, big, scaly pieces. It has long branches with foliar clusters at the end of the sprigs. The foliage is dark green in color and dense. In Honduras, it grows in wet and very wet forests, preferably in muddy, sandy, and rocky soils, most frequently on the banks of rivers and streams from sea level to 700 m (Aguilar 1966).

In green condition, the duramen is dark coffee-colored, and the alburnum is golden yellow. In dry condition, the duramen is dark coffee-colored, and the alburnum is golden brown or grayish coffee-colored. It has a faint odor and a slightly astringent taste. The wood has a straight hilum, medium texture, low shine, and soft streak. Its specific gravity is 0.49 (moderately heavy), occasionally between 0.42 and 0.50. Total tangential shrinkage is 5.5 percent; total radial shrinkage is 2.8 percent; and tangential/radial shrinkage ratio is 1.96. It is easy to saw and to work with carpentry machinery and hand tools, taking on an excellent finish. It is also easy to turn for veneer and to cut into fine sheets. The duramen is moderately durable, but the alburnum is susceptible to attacks by insects and sea borers. In the open air, the wood dries well but slowly, therefore requiring good ventilation; once it dries, it is dimensionally stable. It is deemed moderately difficult to preserve by pressure methods. The wood of *J. olanchanus* is used for decorative veneer, luxurious furniture, cabinetwork, light construction, cabinetmaking, interior panels, turned articles, musical instruments, decorations, panels, parquet floors, special accessories, and turnery. The nuts from the fruit are edible, and the shell is used to dye leather (Aguilar 1966).

The small yellowish-white flowers are monoecious. The female flowers are in shoots; the males in racemes. The tree blooms March through May. Seeds average 35 to 65 per kg with 50 to 60 percent viabilty.

Seeds can be stored for approximately 4 years without significant loss of viability. The content of physical moisture for their storage ranges from 20 to 40 percent with a relative humidity between 80 and 90 percent (Centro Agronómico Tropical de Investigación y Enseñza 1997a).

Seeds are classified as orthodox. They have a hard testa and require a pregermination treatment to break their natural latency. Three pregermination treatments follow. The seeds can be stratified at 31 to 40 °C. They can be stratified in wet sand and covered with soil and flax luffa. Or, they can be cut and soaked in water. Seeds germinate in a sand substrate in about 4 weeks.

ADDITIONAL INFORMATION

The bevel is 1 to 2 cm thick; brownish red or dark red, fibrous, and hard. The tree has a pleasant odor and exudes a milky latex from the interior layers of the bark.

The petiole and rachis are 40 to 50 cm long. The petiole alone is 7 to 10 cm long, cylindrical, lenticellate, glabrous, and strongly pulvinated at the base. The rachis is cylindrical, slightly thickened at the knots, and glabrous. The petiole is approximately 1 cm long, except the terminal one, which is 2.5 to 3.5 cm long, caniculate, pulvinated, and rosy at the base. It has 4 to 6 pairs of opposite leaflets, and a terminal. The lamina is elliptic-oblong to elliptic-lanceolate, 12 to 22 cm, 6 to 7.5 cm, acuminate apex, cuneate to obtuse base, with whole edges. The right side is shiny and dark green, the back is pale green, and both surfaces are glabrous. The main vein is prominent underneath; there are 10 to 12 pairs of secondary veins that are slightly pulnivated underneath and almost brochidodromous (Aguilar 1966).

Khaya nyasica Stapf ex Baker f.

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University of Wisconsin
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MELIACEAE (MAHOGANY FAMILY)

K. anthotheca (Welw.) (Makuwila 1997)

Acajou, banket, East African mahogany, mkangazi, Mozambique mahogany, muvava, Nyasaland mahogany, red mahogany, Rhodesian mahogany, umbaua

Of the 10 species in the genus, 9 grow in continental Africa and 1 grows in Madagascar and the Comoros. *Khaya nyasica* grows in central, eastern, and southern Africa, including Malawi, Mozambique, South Africa, Tanzania, Zaire, Zambia, and Zimbabwe, where it is found in association with other tree species (Exell and others 1963, Francis 1989a, Storrs 1979). Plantations of this species were tried in Cuba, Florida, Puerto Rico, and Nicaragua (Exell and others 1963, Francis 1989a).

Khaya nyasica is an evergreen to semideciduous tree that occasionally attains 60 m in height and 4.5 m d.b.h. (Greenway 1947). A fast-growing tree, it has reached 36 m in height and 65 cm d.b.h. in 50 years in South Africa (Bussche 1982). Its rounded, heavy crown tops a branchfree, straight bole arising from a basal swelling, occasionally with buttresses. Primarily a riparian tree, *K. nyasica* is found on well-drained alluvial soils and neighboring colluvial slopes (Rendle and others 1911). Suitable soils include clay to sandy loam with a pH from 7 to less than 4 (Francis 1989a). The species grows from near sea level to 1,400 m, with the optimum elevation lying between 700 and 1,000 m. Tolerant of seasonal drought, *K. nyasica* grows best where annual precipitation exceeds 1,000 mm.

The wood of *K. nyasica* is almost pink when fresh, turning to a lustrous reddish-brown when dry (Greenway 1947). Moderately hard and durable, with a specific gravity of about 0.5 to 0.65 g/cm^3 and a straight-to-wavy grain, it air-dries rapidly without much distortion. The wood saws easily, planes hard, and finishes to the rich polish characteristic of American mahoganies (*Swietenia* spp.). It is used for cabinets, furniture, joinery, turnery, paneling, and boats. In its native range, bark preparations are said to cure colds (Greenway 1947), and the seed oil is used to fight head lice. *Khaya nyasica* is grown as an ornamental and as a shade tree in coffee plantations.

The very small, white, and fragrant flowers appear at the end of the dry season and beginning of the wet season (Coates and others 1957, Exell and others 1963, Hack 1950). They are arranged in many-flowered racemes or panicles. The sepals are rounded and overlapping, and the petals are twisted (Greenway 1947). In Puerto Rico, the trees can produce these four- or five-part, unisexual flowers at 24 years (Francis 1989a). The globe-shaped, gray-brown fruits are erect, woody, septifragal capsules up to 8 cm in diameter. When the fruits ripen in spring or early summer (about 9 to 11 months after flowering), they release 20 to 60 seeds. The four- or five-valved capsule opens from the top to release the pale- to reddish-brown, narrowly winged seeds, which measure about 2 to 2.5 by 2.5 to 5 cm.

Seed capsules are clipped from trees when they begin to split. Considering the size and height of mature trees, their fruits must be collected by shooting them down or climbing the tree, or by synchronizing logging with seed maturity. The capsules are sun-dried until they split, and the shells are removed by hand (Francis 1989a, Makuwila 1997). Seeds are air-dried in the shade for an additional five days, when the moisture content should be about 5 to 10 percent (Makuwila 1997). Seeds average about 1,000 to 3,800 per kg.

Because seeds are viable for less than 3 months and are attacked by insects (Mugasha 1978), they must be stored in sealed containers in a refrigerator or sown fresh. Germination is cryptocotylar and takes place in 1 to 4 weeks, with average germination of 30 to 70 percent and sometimes almost 100 percent (Bussche 1982, Makuwila 1997). Large seeds germinate faster and at a higher rate and produce more vigorous seedlings. Seeds can be sown directly into lightly-shaded open beds, into black polyethlene sleeves (10 x 30 cm) with soil containing 50 percent sand (Mugasha 1978), or in a mix of well-but not over-watered compost of semi-decomposed pine bark (or appropriate substitute) and sandy soil (Bussche 1982). Sowing depth is 0.6 to 1.2 cm, and the hilum of the seed must point down to prevent stem curl during germination.

During the first 3 months, shade netting of about 70 percent is required. When seedlings are about 5 cm tall, they are transplanted into large polyethylene bags. After the seedlings are 5 months old, sleeves are pruned monthly with piano wire. In South Africa, seedlings reach 30 to 50 cm and are ready for outplanting at 1 year (Bussche 1982) Seedlings should be planted with minimum root disturbance at 5-by-5 m distance in well-prepared pits surrounded by hoed circles 1 m in diameter, when the second soaking rain of the season occurs (Bussche 1982). To avoid problems with shootborers and sun scorch, this shade-tolerant tree should be planted in small forest clearings or interplanted with fast-growing species. Greenway (1947) transplanted seedlings at 3 to 4 months and 7.5 cm tall. However, he found stump planting or stopping more successful. In this procedure, widely spaced seedlings are usually grown in beds for 18 months to 2 years. When they reach 1.2 to 1.5 m (Mugasha 1978), stumps of about 30-cm shoot and 23-cm taproots are planted at 2.4-by 2.4-m distance (Mugasha 1978).

Lafoensia speciosa (Kunth) DC.

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LYTHRACEAE (LOOSESTRIFE FAMILY)

Lafoensia acuminata

Guayacán amarillo, guayacán de manizales

Lafoensia speciosa is a tree that grows at a medium rate, reaching 15 m in height and 20 cm d.b.h. It has an oval crown and shiny green foliage. The leaves are 10 cm, red when they wither, opposite, with whole margins, short petioles, and a slightly marked nervation. The species grows at elevations between 1300 and 2900 m, with an average temperature of 12 to 24 °C and annual precipitation of 500 to 2000 mm. It demands fertile, well-drained, and wet soils. It grows in the life zones of the Tropical dry forest (bs-T), Pre-Mountainous wet forest (bh-PM), and Low Mountainous wet forest (bh-MB) (Rodriguez 1988).

Lafoensia speciosa is used primarily as an ornamental. It is also planted to protect hydric margins. The wood is used sparingly for posts and furniture and in general construction (Escobar and Rodriguez 1993).

The long-petaled flowers are white and grouped. The fruits are rounded, reddish capsules, 4 cm in diameter, with multiple winged seeds. The seeds have received little study.

After the seeds are soaked in water for 24 hours, they are planted in seedbeds at 2 cm deep and 5 cm apart in lines 10 cm apart. The plantules are transplanted when they reach 20 cm and require shade during early development (Trujillo 1984, Universidad Nacional de Colombia 1988).

When the plants are to be used as ornamentals, the ground must be cleared and the soil must be amended with fertilizer and mulch. When they are to be used as a hedge, the trees are planted 2 to 3 m apart. The site is cleaned and scarified to 15 cm. Poor sites should be fertilized. The tree does not survive frost when young; in dry seasons, the small trees defoliate. It is very demanding in urban zones and suffers attacks from Acarus mites, which suck the sap (Rodriguez 1988).


2cm

Laguncularia racemosa (L.) C.F. Gaertn.

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Paul Smiths College,
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COMBRETACEAE (COMBRETUM FAMILY)

No synonyms

Akira, cinchuite, green turtle-bough, mangel, mangle, mangle amarillo, mangle blanco, mangle bobo, mangle marequita, mangle prieto, manglier blanc, mangue, mangue branco, palétuvier, palo de sal, patabán, white mangrove (Bohorquez 1996, Little and Wadsworth 1964)

Laguncularia is a monotypic genus in a moderately large, tropical, woody family consisting of about 20 genera and 500 species (Tomlinson 1986). The only other mangroves or mangrove associates in the Combretaceae are two Old World species of the genus *Lumnitzera* and the New World species *Conocarpus erectus*. The native range of *L. racemosa* includes the coast of central and southern Florida, Bermuda and most of the West Indies, both coasts of continental tropical America from Mexico south to Brazil and northern Peru, and the coast of West Africa from Senegal to Angola (Chapman 1976, Graham 1964, Little and Wadsworth 1964).

Laguncularia racemosa is a moderately fast-growing, small, evergreen, often multiple-stemmed tree. Usually shorter than 15 m in height and smaller than 30 cm d.b.h., the tree may reach heights of 25 m and 70 cm d.b.h. or more (Jiménez 1985, Nellis 1994). The species is restricted to coastal locations very near sea level. It typically occurs on the landward fringe of mangrove communities but occasionally grows on lower elevation, more frequently flooded sites. It also readily colonizes disturbed sites, where it may form nearly pure stands (Tomlinson 1986). *Laguncularia racemosa* grows on a wide variety of soil types, including silt, clay, sand, peat, and marl (Jimenez 1985). The species grows in areas with average annual rainfall of between 800 and 7000 mm per year and appears to be limited to areas where the coldest average temperatures are above 15.5 °C (Jiménez 1985). The species is often regarded as somewhat weedy in nature and frequently invades sites planted with *R. mangle* or *Avicennia germinans* (L.) L. (Padron 1996).

The wood of *L. racemosa* is moderately heavy (specific gravity is 0.6 to 0.8), hard and strong but not very durable (Little and Wadsworth 1964, Southwell and Bultman 1971). The sapwood is light brown and the heartwood is yellowish brown. The wood is used for a variety of purposes, including small poles, fenceposts, tool handles, fuelwood, and charcoal (Little and Wadsworth 1964). The bark contains a significant amount of tannin suitable for commercial uses (Walsh 1977). *Laguncularia racemosa* has also been referred to as a honey-producing plant (Nellis 1994, p. 111).

The greenish-white, fragrant flowers occur in loose terminal clusters (panicles). Some flowering occurs throughout most of the year, but in Florida and the Caribbean it peaks in May and June. *Laguncularia racemosa* may flower and produce fruit when less than 2 years old and 1.5 m in height (Holdridge 1940a, Little and Wadsworth 1964). *Laguncularia racemosa* has been described as functionally dioecious, with trees having male only or both male and perfect flowers (Tomlinson 1980). Both types of flowers are similar in appearance. The difference between trees with male-only flowers (non-fruiting) and perfect flowers (fruiting), however, is readily apparent in late summer (Tomlinson 1980).

The fruit is slightly fleshy and one-seeded (drupe); it is gray-green or pea green when immature and brownish at maturity (Little and Wadsworth 1964, Rabinowitz 1978a). Fruits are flattened-obovoid-ellipsoid (lens-shaped) and about 2 cm long. The mean weight of fruits collected in Panama was 0.41 g (2,440 per kg) with the pericarp and 0.21 g (4,760 per kg) without the pericarp (Rabinowitz 1978b). Fruits typically mature 2 to 3 months after flowering, with most available from July to October in Florida and the Caribbean (Jimenez 1985, Padron 1996, Tomlinson 1986) and from mid-August to late November in Panama (Rabinowitz 1978a). Rabinowitz (1978a) reported seeing no freshly dropped fruits between December and July. The fruits, which are generally referred to as propagules, float and are widely dispersed by water. The seed sometimes begins germination while still on the tree or while floating in the water, and floating propagules commonly have roots (Little and Wadsworth 1964, Rabinowitz 1978a).

Propagules can be collected directly from the trees, from the soil surface, or while they are floating in open water (Padron 1996, Snedaker and Biber 1996). One useful technique is to spread nets or tarps under the mother trees to capture the propagules as they fall. Propagules should be mature (freshly abscised or about to abscise) and free of insects or physical damage. Little information is available on storage of *L. racemosa* propagules (Snedaker and Biber 1996), but storage for longer than about 10 days is not recommended. Rabinowitz (1978a) found that the capacity of propagules to root declined after about 8 days of simulated dispersal, and the number establishing seedlings dropped dramatically after 10 days.

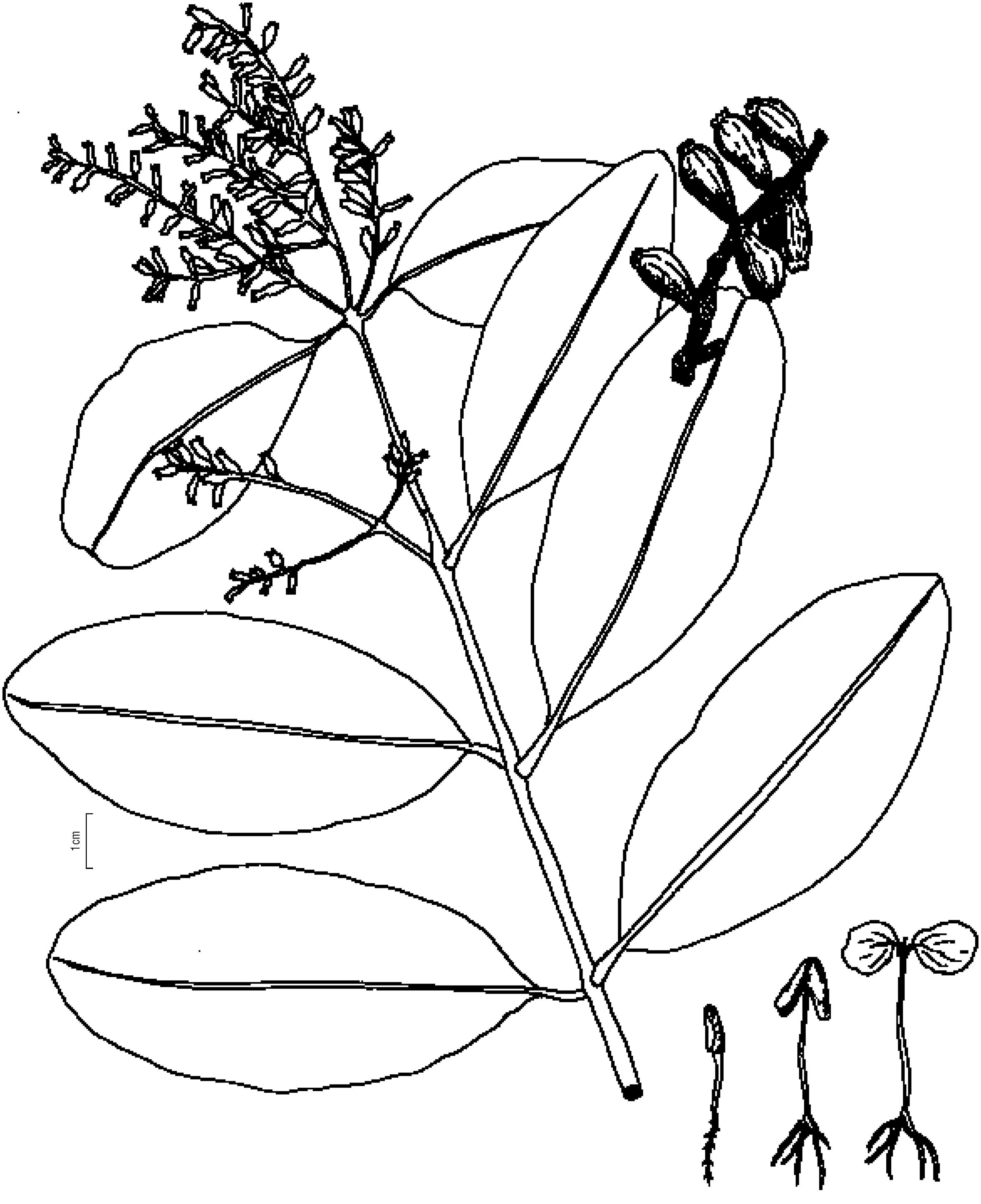
Propagules typically root in 5 to 10 days with no pretreatment. Propagules can also be soaked until the radicle emerges about 1 cm and then sowed by carefully inserting the radicle into the soil (Crewz 1998). If the propagules are soaked before sowing, the water should be changed frequently, ideally every day.

In the nursery, *L. racemosa* propagules are generally sowed in tubes or small pots and grown under ambient conditions. Keeping the pots half-filled with water prepares the seedlings for planting on anaerobic substrates, and periodic watering with brackish or saline water will reduce subsequent planting shock on saline sites. Although easy to grow in nurseries, seedlings are occasionally damaged or killed by scales, aphids, caterpillars, wood and propagule borers, and fungal infections.

Seedlings attain a height of approximately 60 to 90 cm after 1 year in the nursery and can be outplanted. Older, larger seedlings may be sold in 4, 12, 28, or occasionally even 40-liter containers (especially in Florida). To ensure a desirable root-shoot balance when planting, some people trim the terminal bud of larger seedlings once they reach about 1 m (Crewz 1998).

Establishment by direct sowing and by broadcasting propagules has been successful in Cuba (Padron 1996). Success with these techniques may be more limited in Florida, where high losses result when propagules are washed away before anchoring (Lewis and Haines 1981). Success increases on well-protected, low-energy sites and in areas with low levels of seed predation. Large seedlings with well-developed root systems or smaller seedlings in protectors, such as PVC pipes should be planted on exposed sites. In general, however, *L. racemosa* is not as well-suited for exposed sites as are common associates such as *R. mangle* and *A. germinans.*

In all but the most northern parts of its range, *L. racemosa* seedlings or propagules can be planted any time of the year, but cold and dry periods should be avoided (Snedaker and Biber 1996). The best time to plant nursery-grown seedlings produced using fresh water without acclimation to salt may be in seasonally rainy periods, which may reduce the shock caused by sudden exposure to high salinity (Barnett and Crewz 1989). Outplanted seedlings may grow about 60 to 75 cm per year (Barnett and Crewz 1989).


1cm

Lecythis ampla Miers

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LECYTHIDACEAE (BRAZIL-NUT FAMILY)

Lecythis ampullaria Miers (Transactions of the Linnean Society of London 30[2]: 201, t.38, f.1-2; 1874); *Lecythis bogotensis* Miers (Transactions of the Linnean Society of London 30[2]: 203-204, t.41; 1874); *Lecythis costaricensis* Pittier (Contributions from the U.S. National Herbarium 12: 99, t. 6-8, f. 3-4; 1908); *Lecythis curranii* Pittier (Contributions from the U.S. National Herbarium 20[3]: 130; 1918); *Lecythis armiliensis* Pittier (Contributions from the U.S. National Herbarium 26[1]: 9, t.8; 1927); *Lecythis boyacensis* R. Kunth (Das Planzenreich IV. 2190 [Heft 105]: 55-56; 1939)

Coco de mono, coco salero, jícaro, monkey pot, olla de mono, pansuba, sapucaia (Flores 1994d; Mori and others 1978, 1990a; Pittier 1910; Prance and Mori 1978)

Lecythis ampla is an endemic species and its range of distribution extends throughout Central America along the Atlantic watershed, from southern Nicaragua down to Darien, Panama. The geographical range in South America encompasses the Magdalena River Valley and the Choco zone in Colombia, as well as the north coast of Ecuador.

Lecythis ampla is a large tree 45 m in height and 1.0 to 1.6 m d.b.h. The bole is straight and cylindrical and lacks branches in the basal two-thirds. It does not have buttresses but shows short, thick abutments. The crown is branched and spherical. The bark is gray (grayish brown in shady places) and has many sharp vertical fissures. The inner bark is 13 to 15 mm thick, brown, laminated, and fibrous due to the high number of phloem fibers. Phyllotaxy is spiral. The tree is deciduous and most leaves abscise before the flowering period. New leaves appear in fluxes and their production is synchronized with the beginning of bloom. Leaves are simple, alternate, petiolate, narrow elliptic or wide elliptic, glabrous, chartaceous, shiny, and hypostomatic (stomata anisocytic) and have abaxial cuticular papillae. The species grows well in alluvial and sandy soils and is frequently found in clayey soils. It does not grow well in periodically flooded areas or poorly drained soils (Flores 1994d). The elevational range of the species is 0 to 800 m (Flores 1994d, Mori and others 1990a). The species is emergent in the canopy of very humid tropical forests, where temperature range is 24 to 35 °C and annual rainfall is more than 3500 mm.

Sapwood and heartwood are quite different. Sapwood is fibrous, creamy in fresh condition and light brown when dried; heartwood is brown in green condition and reddish brown after drying. Growth rings are inconspicuous. The wood has a straight grain, sometimes interlocked, and a regular texture, and it lacks luster; the radial surfaces are finely banded. It is tasteless and odorless. The wood is heavy (green weight 1200 to 1300 kg per m^3, with 93 to 96 percent moisture content; basic specific gravity is 0.70 to 0.74). Volumetric contraction is normal for its density, and mechanical properties are high. The air-dried wood shows small splittings and twistings. It is moderately difficult to work and saw and does not polish well. The silica content is 0.32 percent. Its natural durability is high and preservation is difficult. The Peteri's coefficient of flexibility is 1.03 and the Runkel factor is 4.6 (group V: not useful for making paper). The wood is excellent for ship construction, agricultural tool handles, frameworks, railroad foundations, furniture and cabinets, turnery, heavy general construction, bridge and marine construction (especially in waters with marine borers), piles, posts, and stakes (Flores 1994d, Herrera and Morales 1993, Llach 1971). The bark can be used as oakum, rolling paper for cigars, boat caulking, native clothing, tinder, and cordage; it is also used in tannery because of its high tannin content (Flores 1994d).

Annual flowering occurs during the rainy season, May through July. Inflorescences are terminal or lateral racemes, solitary or grouped (Flores 1994d). The peduncle and the rachis are thick and lenticellate. The flowers are semisessile; pedicels are puberulent and leave a knob (subarticular region) 1 mm long after disarticulating (pedicels split during flower abscission; the abscission zone constitutes the articulation).

The flower is hermaphrodite and zygomorphic. The flower's calyx has six wide ovate lobules; the corolla has six wide elliptic petals, pink or pale purple, fading to white after the anthesis. The zygomorphic, highly specialized androecium has numerous stamens. Filament fusion as well as the degree of specialization produces a complex organ formed by a staminal ring, a ligule (area lacking stamens placed between the staminal ring and the hood), and a hood; this organ is not morphologically equivalent to an androphore or androgynophore. The staminal ring has 130 to 170 stamens, those of the basal zone being fertile; filaments are 1 to 2 m long and are dilated at the distal end. Anthers are basifixed and 0.5 to 0.6 mm long. The hood is flat, pinkish or light purple, with well-developed appendages, the proximal being antheriferous. The hood is strongly compressed against the staminal disc, and the flower androecium is considered closed (Flores 1994d; Mori and others 1990; Prance and Mori 1977, 1979; Tsou 1994). The hypanthium is puberulous. The ovary is inferior, tetracarpelar, and tetralocular with 4 to 10 ovules developed per locule.

A 10-month fruit development period ends with fruit ripening from March to May. Usually, the tree produces one or two fruits per inflorescence. Fruit ripening is quite uniform and crops are annual. The fruit is large but shows strong variation in size and form (20 to 30 cm long by 15 to 20 cm wide) (Flores 1994d). It is a dry pyxidium or circumscissile capsule, woody and ovoid or oblong. The fruit hangs upside down, so when the operculum abscises and falls on the forest floor, the seeds are exposed. Later, gravity or monkey activity causes the fruit to fall (Flores 1994d ; Prance and Mori 1978, 1979).

The mean number of seeds per fruit is 36. Of these, 25 percent are abortive or of a smaller size. Well-developed seeds are large (5.0 to 5.5 cm long by 2.5 to 3.0 cm in diameter) and ovoid, with a dark brown or black seedcoat, thick and longitudinally ridged; the tegmen is collapsed in the mature seed (Corner 1976, Flores 1994d). The micropyle is formed by the exostome. The seed has a prominent aril, funicular in origin, at the proximal end; it is whitish or creamy, broad, fleshy, and oily (Flores 1994d). Seeds average 150 to 160 per kg, with a moisture content of 46 to 48 percent (Flores 1994d).

Seedcoat removal to promote plumule development is not successful. The application of giberellic acid to intact seed, seems to promote plumule development (Flores 1994d).

Seed behavior is recalcitrant. Viability diminishes with increasing dehydration. Seeds collected from the ground should be separated by size and form and submerged in running water for 24 hours before sowing. Germination is 95 to 96 percent for soaked seeds. The first root, usually adventitious, develops at 45 to 60 days and shows rapid growth; the main root emerges later. Germination is hypogeal and seedlings are phanerocotylar (if the pair of minute squamiform structures emerging with the plumule are morphologically the cotyledons).

Under greenhouse conditions, 11-month-old seedlings reach a height of 25 cm. Seedlings are shade tolerant (Flores 1994d).

The species has not been introduced in reforestation programs, and information on plantation behavior is lacking. Its greenhouse and nursery behavior is very good, although its development is very slow. The species seems suitable for natural forest management (Flores 1994d).

ADDITIONAL INFORMATION

The genus name derives from the Greek *lekythos* and means oil jar. It refers to the urn-like fruits typical of the genus (Flores 1994d). The species is one of four belonging to Sectio Pisonis Mori. The group is collectively known as monkey pots or sapucaias. The group type is *L. pisonis* Cambessèdes (Prance and Mori 1979).

The leaves oxidize and acquire a greenish blue color when damaged. Apex is acuminate, margin crenate, base obtuse or rounded, narrowly decurrent onto the petiole. Venation is pinnate, brochidrodromous with 10 to 15 pairs of secondary veins, forming an acute angle when diverging from the midvein. They arch upwards and fuse distally (Flores 1994d).

Ovules are anatropous, bitegmic, tenuinucellate and have a conspicuous funiculus. The embryo sac is of the Polygonum type. It is surrounded by an endothelium developed from the inner layer of the inner integument. The endothelium plays an active role in nutrient transport from the integuments up to the embryo sac and disappears during seed development. Placentation is axilar and ovules develop at the ovary septum base (proximal end). The style is slender and short, with annular expansion towards the distal end. The androecium is closed. Pollination is carried out by medium to large euglossine bees. They collect pollen from the hood and the staminal disc (Flores 1994d, Tsou 1994).

The fruit's pericarp is thick (2.5 to 3.0 cm), fibrous, reddish brown, dull, and rough; it is built from ovary, androecium, and perianth tissues. Externally (exocarp), three zones are defined by two rings of scars. The proximal ring indicates the calyx position (sepal position) and is named calycine ring (calycary, calycinal, or calycine zone). The distal ring is the line of opercular abscission. The zones delimited by those rings are the infracalycine zone (basal band), the supracalycine (interzonal band), and the deciduous operculum. The infracalycine zone extends from the fruit base up to the calycine ring and includes the pedicel scar; the supracalycine zone extends from the calycine ring up to the ring of opercular dehiscence. The operculum has a four-ridged inner columella. The ridges are remnants of the ovary septa.

Immature seeds have nuclear endosperm which is consumed by the developing embryo; the latter is big, fusiform, massive, undifferentiated, and macropodial and is formed by a fleshy hypocotyl with a thick wall epidermis. Cotyledons, plumule, and radicle are not developed. The hypocotyl stores mainly lipids as a reserve material. The embryo's mean length is 4.0 cm and the mean diameter is 1.5 cm. Plumule development begins when the seedling is 7 months old. A pair of minute (1.0 to 2.0 mm long), opposite, green, squamiform organs appear between the hypocotyl and the plumule; they probably correspond to cotyledons. Protophylls are produced later. Metaphyll production begins at 8 months.

Holes produced by insect attacks are frequently observed and damage extends to heartwood (Flores 1994d).


1cm
2cm
2cm
2cm
2cm

Leucaena leucocephala (Lam.) de Wit

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FABACEAE (BEAN FAMILY)

Acacia biceps DC., *A. caringa* Ham., *A. frondosa* Willd., *A. glauca* DC., *A. leucocephala* DC., *Leucaena blancii* Goyena, *L. glabrata* Rose, *L. glauca* (L.) Benth., *L. greggii* Watson, *L. latisiliqua* (L.) W.T. Gillis, *L. salvadorensis* Standl., *Mimosa glauca* L. (Brewbaker and others 1972, Dassanayake 1980, Hooker 1879, National Research Council 1984, Parrotta 1992b)

Acacia, acacia palida, aroma blanca, aroma boba, aroma mansa, barba de león, bois-lolo, cowbush, grains de lin pays, granadillo bobo, granadino, guaje, hediondilla, jimbay, jumbie-bean, koa haole, leadtree, leucaena, lino, lino criollo, macata, macata blanca, mimosa, monval, panelo, shack-shack, tamarindillo, tantan, tumbarabu, uaxim, West Indies mimosa, white popinac, wild mimosa, wild taman, wild tamarind (Little and Wadsworth 1964, Van den Beldt and Brewbaker 1985)

The genus *Leucaena* consists of about 50 species of trees and shrubs native to tropical and subtropical regions of North and South America, Africa, and the South Pacific; 13 species are endemic to Mexico (Allen and Allen 1981, Brewbaker and others 1972). *Leucaena leucocephala*, originally from the midlands of Guatemala, Honduras, El Salvador, and southern Mexico, was spread by pre-Columbian civilizations throughout the coastal lowlands of Central America from Mexico to Nicaragua. During the Spanish colonial era it was introduced and became naturalized over a much larger area of the tropics. Today, the species is cultivated and naturalized in most countries between latitudes 25°N and 25°S (National Research Council 1984, Van den Beldt and Brewbaker 1985).

Leucaena leucocephala, a fast-growing deciduous species, varies in form from shrubby varieties (common or Hawaiian types) up to 5 m tall to medium-sized trees (giant or Salvadoran types) that reach 8 to 10 m in height and 50 cm d.b.h. (National Research Council 1984, Parrotta 1992b) and have spreading crowns and smooth gray to grayish-brown bark. *Leucaena leucocephala* tolerates a wide range of soil conditions, from skeletal and stony soils to heavy clays, although best growth occurs on well-drained soils with pH from 6.0 to 7.5 (National Research Council 1984, Parrotta 1992b). Although *L. leucocephala* can survive on sites receiving less than 600 mm or more than 2000 mm annual rainfall, it grows best on sites receiving about 1500 mm annual rainfall with a dry season lasting approximately 4 months. It grows well in areas with annual temperatures ranging from 20 to 30 °C with mean monthly minimum and maximum temperatures of 16 and 32 °C, respectively (Allen and Allen 1981, Centro Agronómico Tropical de Investigación Enseñanza 1991b, MacDicken 1988, National Research Council 1984, Van den Beldt and Brewbaker 1985, Webb and others 1984). Primarily a lowland species, it does not grow well above 500 m between 10° and 25° latitudes, nor above 1000 m within 10° of the equator (Van den Beldt and Brewbaker 1985).

A high degree of genetic variability is found in the species and more than 800 varieties have been identified (Brewbaker and others 1972, Hutton and Gray 1959). Growth rates vary greatly among varieties and are strongly influenced by site conditions. Among the larger varieties on good sites, annual stem diameter and height increments generally range from 2.0 to 3.5 cm and 2.6 to 4.0 m, respectively, during the first 5 years. After 5 years, diameter growth rates tend to decline to less than 2.0 cm per year and height growth rates to 2.0 m per year (Parrotta 1992b).

Leucaena leucocephala is cultivated throughout the tropics in block plantations and agroforestry systems primarily for fuelwood and fodder, for soil fertility improvement, and for erosion control in degraded watersheds (National Research Council 1984, Parrotta 1992b). The species has limited value as a timber source, though it is suitable for light construction, boxes, fenceposts, particleboard, and pulp. The softwood is pale yellow and the heartwood light reddish, with a specific gravity of 0.50 to 0.59 (Hu 1986, National Research Council 1984, Parrotta 1992b, Tang 1986).

Flowering phenology varies considerably among varieties and location. The shrubby, common-type varieties flower throughout the year, often starting at 4 to 6 months of age, while the giant varieties flower seasonally, usually once or twice a year starting in the first or second year (Little and Wadsworth 1964, National Research Council 1984, Van den Beldt and Brewbaker 1985). The spherical, whitish flower heads, 2.0 to 2.5 cm in diameter across the spreading, thread-like stamens, are borne on stalks 2 to 3 cm long at the ends or sides of twigs. The abundant fruits, which mature 6 to 9 months after flowering, are flat, thin pods, 10 to 15 cm long and 1.5 to 2.0 cm wide that hold 15 to 20 seeds. The shiny, dark brown seeds are small, flat, teardrop-shaped, 8 mm long, with a thin, durable seedcoat. Seeds are released from the mature, dehiscent pods while still on the tree, although closed or partially open pods may be carried long distances by the wind.

The mature, dark brown seed pods may be collected before dehiscence using pruning poles. They should be sun-dried and then threshed to release seeds; threshing is commonly done by beating the dried pods in cloth bags (Van den Beldt and Brewbaker 1985). Seeds average 17,000 to 21,000 per kg (Centro Agronómico Tropical de Investigación y Enseñanza 1991b, Dijkman 1950, von Carlowitz 1986). Unscarified seeds stored under dry conditions will remain viable for more than 1 year at ambient temperature; at 2 to 6 °C, up to 5 years (Daguma and others 1988, Van den Beldt and Brewbaker 1985).

Although seeds may be sown without pregermination treatment, the following treatments are used to ensure more rapid and uniform germination: (a) immersion in hot water (80 °C) for 3 to 4 minutes followed by soaking in water at room temperature for up to 12 hours; (b) soaking in concentrated sulfuric acid for 15 to 30 minutes; or (c) mechanical scarification by abrading with sandpaper or clipping the seedcoat (Daguma and others 1988, National Research Council 1984). These pregermination treatments may be followed by inoculation with nitrogen-fixing *Rhizobium* bacteria (mixed with finely ground peat) after coating the scarified seeds with a gum arabic or concentrated sugar solution. Presowing inoculation facilitates good field establishment in soils devoid of effective rhizobial strains (National Research Council 1984). Seed germination is commonly 50 to 98 percent for fresh seeds (Daguma and others 1988, von Carlowitz 1986). Scarified seeds germinate 6 to 10 days after sowing (Centro Agronómico Tropical de Investigación y Enseñanza 1991b, Dijkman 1950, von Carlowitz 1986); unscarified seeds germinate 6 to 60 days after sowing (Centro Agronómico Tropical de Investigación y Enseñanza 1991b, Dijkman 1950, von Carlowitz 1986). Germination in *L. leucocephala* is epigeal.

Seeds germinate at or near the soil surface and should not be planted deeper than 1 to 2 cm (National Research Council 1984). Nursery media should be well drained, have good water- and nutrient-holding capacity, and a pH between 5.5 and 7.5 (Van den Beldt and Brewbaker 1985). Light shade is recommended during the first few weeks of seedling development; thereafter full sunlight is recommended (Centro Agronómico Tropical de Investigación y Enseñanza 1991b, Van den Beldt and Brewbaker 1985). Taproot development is rapid in young seedlings. Seedlings generally begin to reach plantable size, 20 cm height, at 10 weeks (Van den Beldt and Brewbaker 1985, Westwood 1987). Seedlings often grow slowly during the first months after planting, and are susceptible to suppression by competing vegetation. Weeding is recommended in plantations until the seedlings overtop competing grasses or herbaceous competitors (Centro Agronómico Tropical de Investigación y Enseñanza 1991b, Van den Beldt and Brewbaker 1985)

Lonchocarpus hondurensis Benth.

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FABACEAE (BEAN FAMILY)

No synonyms

Chaperno, cincho, pellejo de vieja

Lonchocarpus hondurensis grows from Mexico, across Central America, to South America. It also grows in the Caribbean. In Honduras it is found in the departments of Cortes, Atlantida, Colon, Olancho, and Yoro (Jiménez 1995).

Lonchocarpus hondurensis is a semideciduous big tree, reaching 18 to 30 m in height and 30 to 100 cm in diameter. It has an umbellated or multiflabellate crown and dark green, moderately dense foliage. The branches rise obliquely or stretch out, usually bending downward at the end. The trunk is straight, slightly irregular, and cylindrical; the base is elongated or with very small, aliform gambas. The bark is greenish-grayish to light coffee-colored, smooth, horizontal, and dense with lenticels that come loose in thin, small, and irregular pieces. The tree can be recognized by its imparipinnate, alternative leaves and by the blood-red exudation from the interior bark. The species grows in wet, swampy forests, usually along riverbanks or in periodically flooded lowlands.

The alburnum is yellowish, and the duramen is dark brown. The wood does not have a characteristic odor or taste. It has interwoven hilum, medium texture, medium shine, and marked streak. It does not contain silica and is deemed a hardwood. The wood is moderately easy to saw but, due to its high density, is hard to work with machinery and hand tools. Planing is difficult because the grain is interwoven. Tools must be sharp. It is durable to biodeterioration and susceptible to attacks by insects. Drying in the open air is satisfactory, without excessive cracks if the wood is dried slowly. It is difficult to preserve through vacuum-pressure systems. The wood is used for heavy construction, floors, parquet floors, furniture, cabinets, wagons, wheels, tool handles, crossbeams, frameworks, staves, interior walls, transoms, veneer, pilings, boats, turned articles, agricultural tools, and crosspieces for transmission lines and poles and in rural construction (Benitez and Montesinos 1988).

The flowers appear in axillary panicles; flowers are purple-red, small, and very pretty. The tree blooms May through June and fruits June through August. Dehiscent fruits form in small flat pods that are 4 to 6 cm long and 1.5 to 2 cm wide, rounded to cuspidate at the apex, soft to the touch, frequently contracted among the seeds, with thick edges. Each pod contains one to two dark-red seeds. Seeds are orthodox, easy to handle, and formed like a capital C or a half moon. Seeds are corrugated to the touch and average 10,000 to 20,000 per kg with a viability of 80 to 90 percent (Benitez and Montesinos 1988, Standley 1931).

No pregermination treatment is required, and seeds germinate in 8 to 10 days.

ADDITIONAL INFORMATION

The bevel is 1.5 to 2 cm thick, light yellow with brownish-reddish stripes, with a green zonal stripe under the rhytidome, fibrogranular, and moderately hard. It has a faint oily odor. It slowly exudes a blood-red, translucent sap, coming from the interior bark although it is not abundant.

The petiole and rachis are 6 to 10 cm long. The petiole alone is 1.5 to 2.5 cm long, cylindrical, glabrous, and thick, with pulvinated base. The rachis is cylindrical and glabrous. The petiole is approximately 1 cm long, caniculate, thick, and glabrous. There are three to four pairs of opposite leaflets with one terminal that is usually the biggest. The lamina is oblong to oblong-ovate, 6 to 12.5 cm by 3 to 6 cm; the apex is acuminate mucronate; the base is rounded-truncated, with whole edges, and coriaceous; and the right side is opaque green with both surfaces glabrous. The main vein is prominent underneath; 6 to 8 pairs of secondary veins are finely prominent underneath and camptodrome. The reticulum of veins is not very distinctive (Benitez and Montesinos 1988).

2cm
2cm

Lonchocarpus longistylus Pittier

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FABACEAE (BEAN FAMILY)

No synonyms

Balché, bal-ché, palo gusano, saayab, sakiab, xbal-che'

Lonchocarpus longistylus is native to America. The species grows from southeastern Mexico, particularly in the Yucatan Peninsula and Chiapas, south to the region of Peten in Guatemala, forming part of the semideciduous tropical forests. It grows in association with *Brosimum alicastrum* Sw., *Bursera simaruba, Vitex gaumeri* Greenm., *Lysiloma bahamensis* Benth., and *Caesalpinia guameri* Greenm., among others (Martínez 1987, Rzedowski 1978).

Lonchocarpus longistylus is an evergreen or deciduous tree, depending on the availability of water. It can reach up to 18 m in height and 20 to 25 cm d.b.h. The trunk is straight and short, and the large, spreading crown is made up of thin, rising branches with dense foliage. The leaves are composite, imparipinnate, and have 15 oblong or ovate leaflets, 3.5 to 8.5 cm long. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an average annual temperature of 26 °C with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm.

Since pre-Hispanic times, the bark of *L. longistylus* and other species of this genus has been used to prepare an alcoholic beverage with psychotropic properties, known as balché. The bark is soaked in sugary water or water with honey. Once fermented, it is drunk during religious festivities. The bark contains a toxic alkaloid called rotenone, which has insecticidal properties. The tea obtained from the infusion of the leaves is used in traditional medicine to treat coughs and to clean infected wounds. *Lonchocarpus longistylus* is planted as an ornamental in streets, parks, and gardens (Mendieta and del Amo 1981, Miranda 1975, Standley 1930).

Lonchocarpus longistylus blooms during September and October and fruits abundantly the following April through June. The flowers are papilionaceous, purple-violet in color, and arranged in racemes. The fruits are oblong and flattened legumes, indehiscent, and light brown in color when ripe. Each fruit contains one or two seeds (Martínez 1987, Standley 1930). Seeds are reniform, laterally flattened, 12 to 14.5 mm long, 6.8 to 7.0 m wide, and 4.5 to 6.0 mm thick. The seed coat is dark reddish-brown to dark brown, smooth, opaque, and coriaceous.

The ripe brown fruits are collected from the tree using poles with metal hooks or from the ground. The fruits are fragile and the extraction of seeds is done by grinding the fruits by hand. Impurities are removed using sieves or with a vertical column blower. Seeds average 3,943 per kg. Seeds remain viable for approximately 6 months when stored under ambient conditions (24 to 30 °C). With longer storage, their viability quickly diminishes (Vega and others 1981).

Under humid conditions the fresh seeds germinate at 65 percent without pretreatment. A heterogeneous sample of seeds germinated approximately 10 days after sowing (Vega and others 1981).

ADDITIONAL INFORMATION

The hilum is lateral, oblong or elliptic, surrounded by funicular remnants and a darker areola, and has a split. The micropyle is puntiform and very close to the radicular lobe. The lens is opposite to the micropyle, oblong, and dark. The dark yellow embryo has a curved axis and is asymmetrical. The two cotyledons are plano-convex in cross section, pulpy, and oily. The plumule is slightly developed. The radicle is curved and elongated.

Lonchocarpus rugosus Benth.

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FABACEAE (BEAN FAMILY)

No synonyms

Arripin, black cabbage bark, canansin, canasin, catzin, chaperno, chapulaltapa, masicarán, masicarón, matabuy, and matachalpul (Lagos 1977, Witsberger and others 1982)

Lonchocarpus rugosus is native to southern Mexico and Central America. Other *Lonchocarpus* species reported in El Salvador are *L. atropurpureus* Benth., *L. minimiflorus* Donn. Smith, *L. peninsularis* (Donn. Smith) Pittier, *L. phaseolifolius* Benth., and *L. salvadorensis* Pittier (Berendsohn 1989, Witsberger and others 1982).

Lonchocarpus rugosus is a slow-growing, medium-sized tree that may reach 15 m in height. The tree with its broad and dense crown may reach maturity when it is only 2 m tall. *Lonchocarpus rugosus* grows from sea level to 1400 m and is adapted to dry conditions. In El Salvador, it is found only on dry and steep sites, especially in hot, subtropical, humid forests (Witsberger and others 1982).

Lonchocarpus rugosus produces high quality wood used in construction and wooden wagons (Witsberger and others 1982). In Guatemala, a purple dye used to color fabrics is obtained from the bark. This species grows slowly but its round and dense crown could be useful in silvopastoral systems, parks, or other urban areas.

Lonchocarpus rugosus blooms in June and July. The purple-reddish flowers measure 1.1 to 1.3 cm in racemes 7 to 13 cm long, and the fruits are flat legumes or pods 5 to 14 cm long with one to three seeds (Witsberger and others 1982). The indehiscent pods mature from October through December and are very abundant in full-grown trees.

Pods are collected by hand directly from the tree. Seeds from pods collected from the ground are usually infected by weevils. Seeds are extracted by hand and average 6,000 per kg. Seeds kept dry at 5 °C are viable for at least 3 years.

Pregermination treatments may be necessary for fast germination. Only 17 percent of nonscarified 6-month-old seeds germinated 30 days after planting, while more than 30 percent of fresh nonscarified seeds germinated within 10 to 15 days (Navarrete-Tindall and Aragón, unpublished data). Placing seeds in boiling water for 1 to 5 seconds did not improve germination and seeds exposed for 10 to 15 seconds died. Germination was higher in loam soils than in sand, perlite, and fine red basalt. Future research should investigate other scarification treatments including use of lower water temperatures.

In nursery production, one seed is planted in a polyethylene bag containing soil with 10 to 15 percent organic matter. Seedlings vary in growth; 5-month-old seedlings from a single tree reached 8 to 40 cm in height after outplanting at 3 months. The longest leaves were 32 cm and had 9 to 13 leaflets (Navarrete-Tindall and Van Sambeek, unpublished data). Outplanting 6-month- to 1-year-old seedlings should occur during the rainy season. Mechanical weed control is required during the first two years.

ADDITIONAL INFORMATION

Nodulation was observed recently in 3-month-old *L. rugosus* seedlings (Navarrete Tindall and Van Sambeek, unpublished data) suggesting that like other *Lonchocarpus* species the tree is a nitrogen fixer (Allen and Allen 1981). Additional research will determine nitrogen fixation efficiency of the rhizobial bacteria symbiotic to the species.


2cm
2cm

Luehea seemannii Triana & Planch.

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TILIACEAE (BASSWOOD FAMILY)

No synonyms

Caulote, cotonron, guácimo, guácimo colorado, guácimo de montaña, guácimo macho, guácimo molinero, guacimón, guacimón llayo, molinillo, tapasquit, yayo

One of the three species in the genus, *L. seemannii*, grows from Guatemala to Colombia.

Leuhea seemannii is a fast-growing forest tree often reaching more than 30 m in height and 2 m d.b.h. The trunk is often buttressed (up to 2 m in height), and the branches are tomentose. The trunk is irregularly channeled or intercrossed, and the yellow-red bark has a large number of lenticels. Leaves are alternate, stipulate, simple, rather thick-petiolate. The blade is oblong or oblong-elliptic, sometimes slightly oblong-obovate, rounded and asymmetric at the base, acuminate at the apex, margin serrated, 7 to 40 cm long and 3 to 16 cm wide. The upper surface is green and loosely arachnoid to glabrescent; the lower surface is brownish-arachnoid, palminerved, with the nervation more prominent beneath. Young plants in pastures and on cutover land are often little more than shrubs and have much larger juvenile leaves, which may be nearly 30 cm in length (Allen 1956). Large trees very often grow along gallery forests in humid and wet lowlands, but the species also grows in hilly areas up to 600 m. It grows in a wide range of soils and in climates with an annual rainfall from 2000 to 4000 mm and an annual average temperature of 23 to 25 °C.

The wood of *L. seemannii* is whitish, soft, light, and weak and is primarily used as firewood. The macerated young shoots secrete a dense, brown-reddish mucilageous substance in water. This substance is used in small sugarcane mills to agglomerate dirt and debris from boiling juice. The dirt and debris are gathered from the surface of the liquid and used as fertilizer or as pig feed.

Inflorescence of axillary or terminal thyrses, the white or yellowish flowers are 1 to 3 cm and usually appear in January and February (Allen 1956). The fruits usually mature in March and April. Fruit is a ligneus capsule, narrowly elliptic, contracted toward both ends, deeply five-sulcate with five prominent angles, 2 to 2.5 cm long, 1 cm in diameter, shortly brownish-tomentollous, and imperfectly loculicidally five-valvate. The seeds are numerous, small, oblong, about 2.5 to 3 mm long and 1 mm wide, with a wing. The wing is about 8 mm long and 3 mm wide, testa crustaceous, and expands into a large membranaceous wing. The embryo is straight and fleshy.


1 cm
1 cm
1 cm

Magnolia hondurensis A. Molina R.

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MAGNOLIACEAE (MAGNOLIA FAMILY)

No synonyms

Jagua, magnolia

Magnolia hondurensis is an evergreen species from the wet forests of the tropics of Central America; it usually grows in regions with elevations greater than 1000 m (Aguilar 1966).

Magnolia hondurensis is a tree that reaches 20 m in height and 60 cm in diameter. It has a rounded or narrowly umbellated crown, the foliage is very dense, and the branches stretch out obliquely. The shaft is straight, sometimes slightly irregular, and cylindrical with a conical or slightly elongated base. The bark is brownish gray or dark gray, moderately rough with prominent lenticels that come loose in scaly, thin, irregular pieces, displaying brownish lenticels in the new bark. Leaves are simple, whole, alternate, shiny, dark green, and ferruginous or rusty-pubescent underneath.

The wood has white alburnum. The olive-green duramen turns yellowish coffee or greenish coffee in color, with dark purple-coffee or blackish stripes and a fine grain. The wood is used for general construction, interior finishes, furniture, cabinets, doors and windows, veneer and plywood, platforms and structures for ships, turnery, sawn wood, parquet floors, armory, and interiors of heavy vehicles.

The flowers are isolated, axillary, big, and very beautiful with white petals, greenish-yellow stamens, and a fragrant odor. The tree blooms March through April and fruits March through June. The fruits are dehiscent follicles, with large seeds suspended by filiform structures. The yellowish-white seeds are recalcitrant, covered with a soft, membranous tissue, and stuck to the aril. Seeds are cleaned by maceration and continuous washing with water. Seeds average 5,000 to 10,000 per kg with 60 to 70 percent viability.

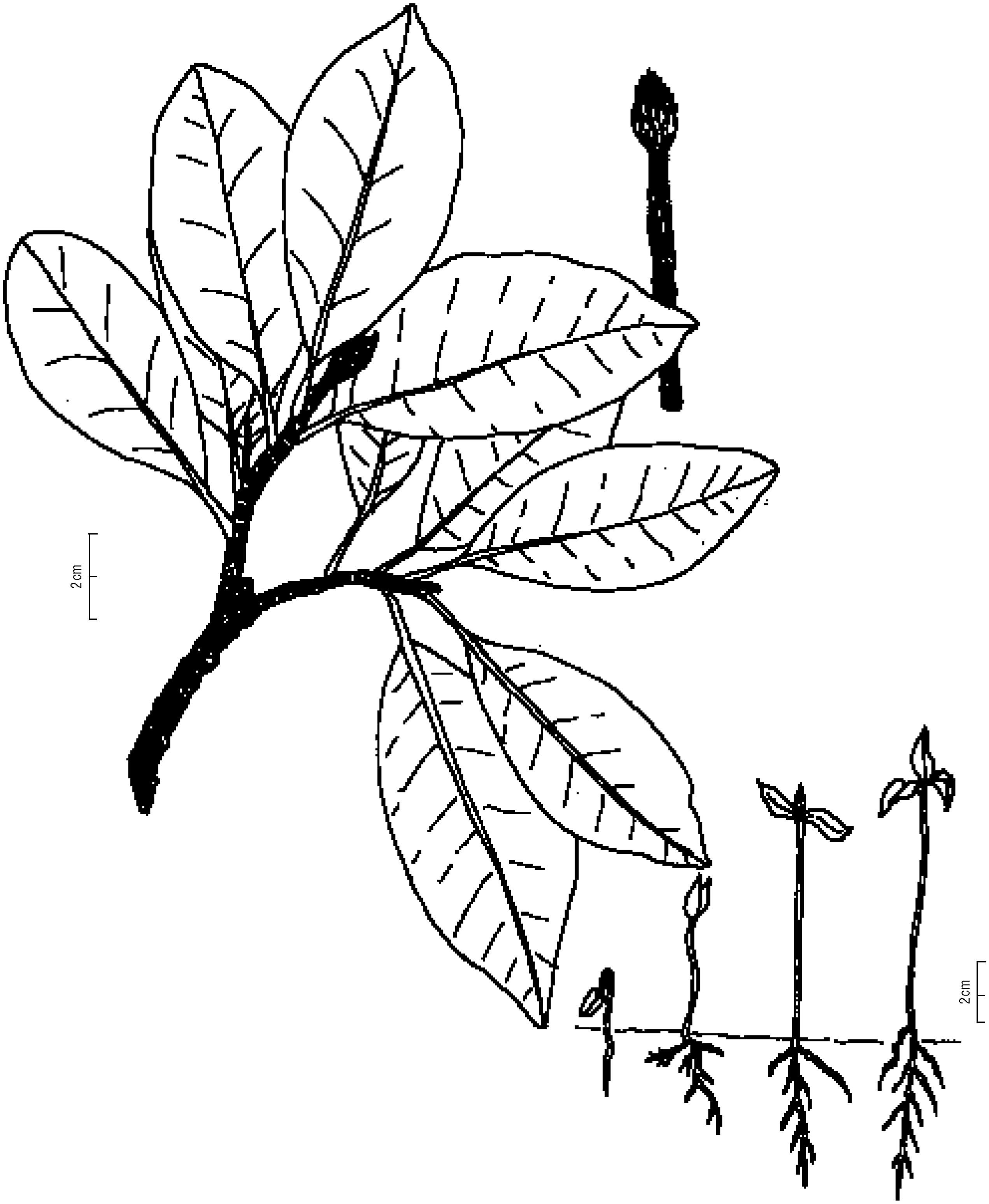
Once clean and dry, seeds can be stored for several years by lowering the levels of physical moisture between 7 and 9 percent and controlling storage conditions (Aguilar 1966).

Pregermination treatments include cutting seeds longitudinally, soaking them in water for 48 hours, or stratifying them in sand.

ADDITIONAL INFORMATION

The bevel is 1.5 to 2 cm thick, opaque yellow to light orange, becoming dark later, granular, moderately hard, and brittle. It has a faint pleasant, bittersweet, odor.

The petiole is 1 to 1.5 cm long, slightly caniculate above, thick, and rusty-pubescent. The stipules are caducous. The lamina is oblong-elliptic or oblong-oval, 10 to 18 cm by 4.4 to 8 cm, short-acuminate to obtuse apex. The base is obtuse, cuneate, and coriaceous and the edges are frequently revolute. The right side is shiny and dark blue-green; the back is ferruginous or rusty-pubescent. The main vein is strongly prominent underneath; 12 to 14 pairs of secondary, parallel, straight veins are slightly prominent underneath and camptodrome. The reticulum of veins is not distinctive.


2cm
2cm

Mammea americana L.

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CLUSIACEAE (MANGOSTEEN FAMILY)

Mammea emarginata Moc. & Sesse ex DC

Abrico do para, abricotier d’Amerique, abricotier des Antilles, mamey, mammee apple, mammy fruit, Saint Domingo apricot (California Rare Fruit Growers 1995, Guzmán 1980)

Mammea americana is native to the West Indies, but is widely cultivated in the tropics in Central America and the Caribbean islands (National Germplasm Repository 1995). It is found in tropical and subtropical life zones in dry and wet forests (Lamberts and Crane 1990).

Mammea americana is a slow-growing tree that reaches from 6 to 20 m in height (Schubert 1985) and 50 cm d.b.h. The crown has a pyramidal shape. This tree has coriaceous, gland dotted, bright, and dark green leaves. Although *M. americana* grows in poor soil (Schubert 1985), it grows best on a rich, well-drained, sandy loam (California Rare Fruit Growers 1995). It requires 109 to 203 mm of rain per year and its optimum temperatures are 19 to 27 °C. It grows at elevations from 70 to 1500 m.

The fleshy fruit pulp of *M. americana* is eaten fresh or used to prepare refreshments, jellies, preserves, or sherbets. The flowers are used in preparing the liqueur Eau de Créole in Santo Domingo. An aqueous solution with the crushed seeds help to kill common fly larva and to control mites and fleas on domestic animals as well as lice in humans (Aguilar Márquez and others 1996, González Ayala 1994, Guzmán 1980). A mash of the cut seeds is used to treat wounds. The wood has a specific weight of 0.878, and it can be used to make furniture (Guzmán 1980). *Mammea americana* is an attractive tree planted for shade or as an ornamental in urban areas (Schubert 1985). *Mammea americana* is a fruit tree with a lot of potential for exportation. Studies on post-harvest storage are necessary to increase the number of commercial plantations.

The flowers are white with four fleshy petals, many stamens, and a single ovary. The fragrant flowers attract honeybees and hummingbirds. The trees may fruit at 6 to 7 years (California Rare Fruit Growers 1995). In Puerto Rico, *M. americana* flowers May through October and fruits are observed most of the year. The fruits are round with orange-yellow pulp. Mature fruits are brown, 7 to 15 cm in diameter, with 2 to 3 seeds that are 2.5 to 4 cm long and 2 to 2.5 cm in diameter.

Seeds are collected by hand from the indehiscent fruit, cleaned of the fleshy pulp, sun-dried for 1 to 2 days, and kept at 5 °C in dry conditions or planted immediately. Seeds average 10 to 20 per kg.

Mammea americana is propagated primarily by seed or by air-layering (California Rare Fruit Growers 1995). One seed is planted in a 15 by 15 cm polyethylene bag containing loamy soil and placed in a sunny location. To avoid fungal growth, half the seed is buried in the soil while the other half is left uncovered. Seeds germinate 1 to 2 months after planting. Seedlings grow quickly and 1-year-old seedlings reach 50 cm in height (California Rare Fruit Growers 1995). One- to 2-year-old seedlings can be outplanted at the beginning of the rainy season in May or June. Manual weeding is recommended during the first year to prevent competition for nutrients and light. Chemical pesticides are not recommended (Navarrete-Tindall 1998).

Manihot dichotoma Ule

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Centro Internacional de Agricultura Tropical, Colombia

EUPHORBIACEAE (SPURGE FAMILY)

No synonyms

No common names

Manihot dichotoma is native to northeastern Brazil in the states of Pernambuco and Bahia, and in northeastern Minas Gerais. As a tree that thrives under dry conditions, *M. dichotoma* grows more frequently in the Sertao (arid and semiarid parts of the Brazilian Caatingo). The species has been introduced in Colombia and also in Miami, FL (Allem 1997).

Manihot dichotoma is a neotropical tree that reaches 3 to 12 m in height and 25 cm d.b.h. Branching pattern is either dichotomous or trichotomous, and its smooth-stemmed branches may become slightly scaly with age (Rogers and Appan 1973).

New variations arising from naturally occurring mutations or genome reorganization are not documented for *Manihot* and can only be assumed to be part of long evolutionary processes as in any other genus (Hershey 1992). *Manihot dichotoma* has been used to form interspecific hybrids with *M. esculenta* as a source of resistance to the African cassava mosaic disease and other viruses (Jennings 1976, Storey and Doughty 1951).

From 1897 to 1916, *M. dichotoma* was an inexpensive source of rubber latex in northeastern Brazil. During this time, the species provided a means of support to 10,000 families in central Bahia, Piaui, Pernambuco, and Ceara, especially from 1903 to 1913. During World War II, interest in the species as a latex producer resurfaced. However, *M. dichotoma* is no longer used as a source of rubber latex (Allem 1997).

Inflorescence is monoecious racemose, short, terminal, and 4 cm long; every part except the interior surface of the tepals is glabrous. Setaceous bractlets and bracts are less than 0.5 cm long, less than 0.2 cm wide, and glabrous with serrated edges. Pistillate flowers (female) are restricted to the base of the inflorescence; tepals are 1.7 cm long, yellowish-green externally, and purplish in the interior part. The ovary has prominent wavy wings. Staminate buds are conical with tepals 1.7 cm long. The color of the tepals is the same as the tepals of the pistillate flowers, with 10 stamens forming two groups of 5 stamens each. The fruits are trilocular capsules of about 1 to 1.5 cm diameter, holding one seed each. The fruit has an epicarp layer and a fleshy mesocarp, which dries out at maturity, and a hard inner endocarp which splits open to release the seeds. After flowering, fruit development and seed set takes from 3 to 5 months (Ospina 1996, Toledo 1963). The obovate seeds are approximately 1.8 cm long, 1.1 cm wide, and 0.8 cm thick. The dark brown seed is smooth; the dorsal is convex with small, light and dark brown spots; the ventral is flat and without spots, with a visible raphe and a small caruncle (0.2 by 0.1 cm), light brown in color, located in the micropylar region (Rogers and Appan 1973). Leaves are glabrous and alternate with caducous stipules of serrated edges less than 1 cm long. Petioles are nonpeltate, approximately 8 cm long, erect, and glabrous with a basal union of the petiole to the lamina of 1 cm. The lamina is slightly coriaceous to membranous with a reticulate waxy pattern on the abaxial surface, camptodrome venation, and glabrous veins. The lamina is palmated with five lobes, three major and two smaller; the median lobes are obovate, frequently pandurate, approximately 8 cm long and 3.5 cm wide with a narrow base about 1 cm wide. The length of the lower lobes is half that of the middle lobes, with acute apex (Rogers and Appan 1973).

Like other *Manihot* species, seeds can be collected on the ground around the tree. To prevent fruit fly damage and seed dispersal, seeds may be collected by placing mesh bags around the peduncle of an inflorescence (Ospina 1996).

Information about germination and longevity in storage is nonexistent; data on other species of the same genus are reported as additional information.

In a 14-month study, it was suggested that the behavior of the sexual seeds of *Manihot* is similar to that of conventional, orthodox seeds. With a moisture content between 4 and 6 percent (wet basis), the seed was stored in sealed packaging under cold conditions (5 °C) without losing viability (Ospina 1996). On the other hand, Hong and others (1996) report that the *M. esculenta* seeds did not lose viability after 14 years in hermetic packaging at –20 °C with 6.1 percent moisture content. In this genus, the seeds differ in degrees of dormancy and many different treatments have been tested to improve germination. For example, treatments with sulfuric acid at 2, 5, and 10 percent resulted in a negative effect for seeds of *M. esculenta* (Institut National pour l'Etude Agronomique du Congo Belge 1952) while evaluation of constant and alternate ranges of temperature reveal that during 21 days, 30 to 38 °C; 8 to 16 hours is the most recommended condition for germination (Ellis and others 1982).

Manihot dichotoma is propagated through seeding and stem cutting.

ADDITIONAL INFORMATION

The stages of germination for *M. esculenta* Crantz, *M. aesculifolia* (Kunth) Pohl, *M. carthaginensis* (Jacq.) Müll. Arg., *M. chlorosticta* Standl. & Goldman, and *M. pseudoglazioii* Pax & K. Hoffm. (Ospina 1996) follow:

Days 3 to 5: The testa break longitudinally and the primary root emerges.

Day 7: The primary root lengthens, some secondary roots appear, and the cotyledons begin to show.

Day 10: More secondary roots appear, and the basal part of the somewhat long hypocotyl broadens.

Days 10 to 12: The roots continue to grow, the short epicotyl (small elongation of the plumule) appears and the cotyledons are partially or totally free of the testa.

Day 15: The cotyledons separate and photosynthesize, and in some cases, the epicotyl may have grown (growth of primary leaves).


2cm

Manihot grahami Hook.

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EUPHORBIACEAE (SPURGE FAMILY)

Janipha loeflingii var *multifida, Manihot tweedieana, Manihot tweedieana* var *lobata, Manihot tweedieana* f. *nana, Manihot lobata, Manihot enneaphylla* (Rogers and Appan 1973)

Guazu mandioca, mandio guazu, mandio quazu, mandioca brava, mandioca do matto, mandioca guazu, manidioca de veado, sacha mandioca

Manihot grahami occurs naturally in southeastern Brazil, northern Argentina, Paraguay, and Uruguay. It was introduced in the Southeastern United States and, although sometimes confused with *M. esculenta*, can be found from eastern Louisiana to Florida (Allem 1997).

Manihot grahami is a shrub with a dense crown, shaped like a parasol. The species can reach 7 m in height, 30 cm at the base, and 25 cm d.b.h. The trunk has a branching pattern, either dichotomous or trichotomous (Rogers and Appan 1973). *Manihot grahami* has nontuberous roots, dark coffee-colored epidermis, and white subepidermis. The reddish-brown, soft bark is approximatley 0.6 cm thick and can be peeled easily off the trunk, releasing a small amount of yellowish-white latex (Rogers and Appan 1973). Young stems are olive green and glabrous and form an obtuse angle. The leaves are alternate with long stipules, filiform, glabrous, and caducous.

New variations arising from naturally occurring mutations or genome reorganization are not documented for *Manihot* and must be assumed to be part of long-term evolutionary processes as in any other genus (Hershey 1992).

Manihot grahami is occasionally used as an ornamental and in botanical gardens.

The inflorescence is in panicle, monoecious, profusely ramified, and frequently 30 cm long; every part is glabrous and possesses setaceous bractlets and bracts. Pistillate flowers (female) are restricted to the lower two-thirds of the inflorescence; pedicels are 2 cm in length; sepals are 1.25 cm in length with a split toward the base in the five lobes; and the subglobose ovary is a glabrous, red-orange disk. The male flowers are a bright yellow-green with brown dots internally and a bright orange, globulous disk toward the base. The fruits (capsules), which are rounded from the base to the apex and measure 1.8 cm in length and 1.9 cm in width, possess septicidal dehiscence. There is no information on fruit and seed development for this species but, like other species within the genus, its fruiting may occur 3 to 5 months after flowering (Ospina 1996, Toledo 1963). The seeds are ovate, approximately 0.1 cm long, 0.8 cm wide, and 0.5 cm thick. These smooth seeds are a light coffee color with dark coffee-colored spots. The dorsal is convex and the ventral is planoconvex. The seeds have a visible raphe and a small, light, coffee-colored caruncle located on the micropylar region (Rogers and Appan 1973).

Like other *Manihot* species, seeds can be collected on the ground around the tree. To prevent fruit fly damage and seed dispersal, seeds may be collected by placing mesh bags around the peduncle of an inflorescence (Ospina 1996).

In a 14-month study, it was suggested that the behavior of the sexual seed of *Manihot* is similar to the conventional type of orthodox seeds. With a moisture content between 4 and 6 percent (wet basis), the seed was stored in sealed packaging under cold conditions (5 °C) without losing viability (Ospina 1996). On the other hand, Hong and others (1996) report that the *M. esculenta* seeds did not lose viability after 14 years in hermetic packaging at –20 °C with 6.1 percent moisture content. In this genus, the seeds differ in degrees of dormancy and many different treatments have been tested to improve germination. For example, treatments with sulfuric acid at 2, 5, and 10 percent resulted in a negative effect on seeds of *M. esculenta* (Institut National pour l'Etude Agronomique du Congo Belge 1952), while evaluation of constant and alternate ranges of temperature revealed that during 21 days, 30 to 38 °C for 8 to 16 hours is the most recommended condition for germination (Ellis and others 1982).

Manihot grahami is propagated by seed. There is no information on how seeds are planted, type of substrate, or special care for the seedlings.

ADDITIONAL INFORMATION

The leaf's petioles are usually very long (aproximately 20 cm), straight, glabrous, and bright yellow-green. The union of the petiole to the leaf lamina is basal; the lamina is greenish and glabrous, with a soft waxy pattern on the abaxial surface; it possesses a camptodrome venation. Prominent veins on the adaxial surface of the lamina are bright yellow and glabrous. The leaf is palmated and has 7 to 11 medium, pandurate, oblong lobes with gradual widening from a narrow base to a prominently widened apical region, which abruptly narrows and ends in a pointed apex. The lobes are 15 to 20 cm long and approximately 0.5 cm wide at the base of the lobes. The lower lobes have a margin similar to the medium lobes but are smaller in size (Rogers and Appan 1973).

As in many other *Manihot* species, *M. grahami* is cyanophorous, and its tissues release varying levels of hydrogen cyanide on crushing. Analysis for *M. esculenta* indicates that although cyanogenesis is genetically determined, it is also influenced by various extrinsic and intrinsic factors such as soil moisture, climate, rates of synthesis, transport, and degradation of cyanogenic materials (Nartey 1978).


1cm

Manilkara zapota (L.) P. Royen

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SAPOTACEAE (SAPODILLA FAMILY)

No synonyms

Chakya, chicle, chico, chicozapote, chictsápotl, mispel, mispu, naseberry, níspero, sak-ya, sapodilla, sapote, sapote blanco, sapote colorado, sapote chico, sapotí, xicontsapotl, ya', zapote, zapotillo

Manilkara zapota is native to America. It is distributed naturally from Mexico, through Central America, to southern Costa Rica, sometimes forming extensive groupings. The plant is an important component of the hot-humid and subhumid tropical forests. The species has been introduced in different tropical and subtropical regions of the New and Old Worlds.

Manilkara zapota is an evergreen tree that can reach 40 m in height and 150 cm d.b.h. The trunk is straight, cylindrical, and grooved in the lower part. The low, irregular, and dense crown is made up of numerous thick and horizontal branches with shiny green foliage. The leaves are simple, gathered at the tips of the branches, elliptic to oblong, 5.5 to 18 cm long, and 2 to 7 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree is found have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm. The tree grows from sea level to 900 m.

Very important in the development of the Mayan culture, *M. zapota* has multiple uses. It is cultivated primarily for its edible fruits, which are considered one of the tastiest fruits of the tropical regions. The coagulated latex that the tree produces is called chicle, a substance the Mayans chewed to quench thirst. For many years, this substance was the raw material for the manufacture of chewing gum, and the tree was intensely exploited in its natural habitat. Because the wood is very hard, heavy (specific gravity is 0.86), and quite durable under adverse environmental conditions, it is used in rural construction and for railroad ties and handles for tools. It has also been used in the manufacture of furniture and as parts of carriages such as wheels for carts. The tree is cultivated extensively in backyards that have hot soils. It is also appreciated as an ornamental in streets, parks, and gardens. The bark contains tannin, and it is used to tan hides. The flowers are honey-bearing (Aguilar 1966, Barrera 1981, Cabrera and others 1982, Chavelas and González 1985, Flores 1993, Hoyos 1979, Little and others 1967, Miranda 1975, Rico-Gray and others 1991, Schubert 1979, von Carlowitz 1991).

The tree begins to yield flowers and fruits between 4 and 5 years of age. Because its geographical distribution is extensive, *M. zapota* blooms at different times but especially June through October, and it fruits from January through April (Pennington and Sarukhan 1968). In southeastern Mexico, the plant blooms May through September and fruits December through April (Juárez and others 1989). The flowers are white, shaped like a goblet or bell, and isolated. The fruits are produced at an annual rate of three to four thousand fruits per tree (Flores 1983). The fruits are rounded, ovoid to globose berries that are brown when ripe, up to 10 cm long, pulpy, sweet, and juicy with milky sap. The pulp is yellowish brown. Each fruit contains one to five seeds (Cabrera and others 1982, Little and others 1967, Pennington and Sarukhan 1968). The seeds are elliptic to obovate, laterally flattened, 16 to 24 mm long, 8 to 16 mm wide, and 4 to 6 mm thick. The seedcoat ranges from light brown to blackish, smooth, shiny, and crustaceous and has a ventral, oblong-linear hilum scar. The hilum scar is narrow, white to yellowish cream in color, 9 to 17 mm long, and 2 mm wide.

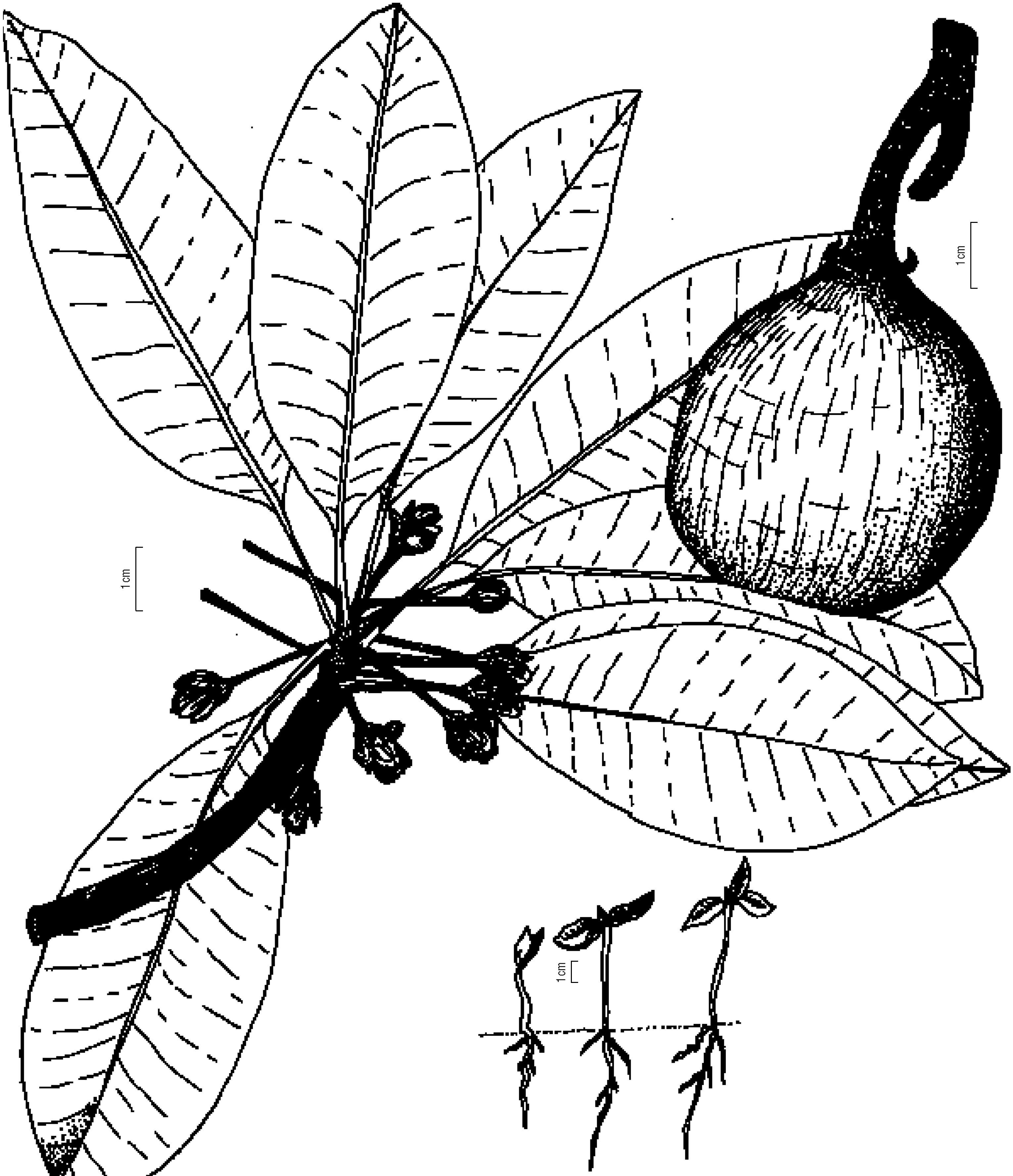
Ripe fruits are collected in March and April either from the ground or by climbing the tree and using poles with metal hooks. The pulp is removed from the fruits by hand inside a bucket of water. Resulting impurities float and are gathered with a strainer. Good seeds sink. Subsequently, the seeds are dried in the sun in ventilated places for 1 or 2 hours depending on light conditions. Seeds average 2,400 to 7,890 per kg (Patiño and Villagómez 1976). Seeds remain viable for approximately 7 months when stored under ambient conditions (24 to 30 °C). With longer storage their viability quickly diminishes (Vega and others 1981).

Under humid conditions the fresh seeds germinate at 11 percent without pretreatment. A heterogeneous sample of seeds germinated 12 days to 5 weeks after sowing (Kennard and Winters 1960, Vega and others 1981).

Manilkara zapota propagates naturally by seeds. However, the species is commercially propagated by aerial shoots, stem cutting, or grafts (von Carlowitz 1991). Models sprouted from seeds are used in grafting (Food and Agriculture Organization 1982).

ADDITIONAL INFORMATION

The hilum is subbasal. The micropyle is indiscernible. The endosperm is abundant, pulpy, whole, and whitish, and surrounds the body of the embryo. The embryo has a straight axis and is asymmetrical, spatulate, and white. There are two expanded, ovate, thin and foliaceous, independent cotyledons, with latex. The plumule is undifferentiated. The radicle is short, obtuse, cylindrical, and well developed (Blackwell 1968, Cronquist 1946, Eyma 1966, Guil 1967, Pennington and Sarukhan 1968, Pilz 1981, Reitz 1968, Standley and Williams 1967, Wood and Channel 1960).


1cm
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Melaleuca quinquenervia (Cav.) S.T. Blake

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MYRTACEAE (MYRTLE FAMILY)

Melaleuca leucodendron (L.) L.

Aceite de cayeput, balsamo de cayeput, belbowie, bottlebrush tree, broad-leaved paperbark, broad-leaved tea-tree, cajeput-tree, capeputi, corcho, five-veined paperbark, melaleuca, numbah, paperbark, paperbark-tree, punk-tree, tea-tree, white bottlebrush

Melaleuca quinquenervia was grouped with nine other species under the name of *M. leucodendron* until 1968. Therefore, precise information about the species before 1968 is limited. The native habitat of *M. quinquenervia* ranges from a latitude of 8 to 34° S. on the east coast of Australia, Papua New Guinea, Irian Jaya, and New Caledonia. In North America, it has become naturalized on a significant scale in southern Florida. Because this species can be an aggressive invader in environments similar to its native habitat, the risk of escape should be assessed before introducing it to a new area (Geary 1998).

Melaleuca quinquenervia is an evergreen tree, commonly 8 to 12 m in height. However, on good plantation sites trees average 18 m in height and 50 cm d.b.h., and the biggest trees reach 24 m in height and 90 cm d.b.h. On dry sites, stands may exist as shrubs. Trunks are moderately straight to crooked. The white bark is thick and spongy and peels in layers. Leaves are entire, narrowly elliptic, 4 to 9 cm long, 2 to 3.5 cm wide, and pungently aromatic, with five faint, nearly parallel veins. The tree is fire tolerant and thrives in continuous to periodically flooded sites (Geary 1998).

In Australia, *M. quinquenervia* grows in level to gently undulating topography along streams and estuaries and in marshes and seasonal swamps, sometimes forming pure stands. The species can grow on a wide variety of soils. In Australia it occurs most frequently on sandstone-derived soils, in Papua New Guinea on highly organic, alluvial clays, and in New Caledonia on well-drained slopes and ridges in the uplands. In Florida, naturalized stands are found on Psammaquents, Aquods, and Saprist soils, which are often shallow and underlain by limestone. Planted trees in Hawaii grow well on calcareous beach sand and on soils derived from basalt ash and lava rock of pH 4.5 to 5.5 (Geary 1998). In its native habitat, *M. quinquenervia* is found mainly from sea level to 100 m, but in New Caledonia extensive stands exist in uplands to an elevation of 1000 m. Mean annual rainfall, which has a summer maximum over most of its habitat, ranges from 900 to 1250 mm. Mean monthly temperatures range from 5 to 32 °C. In the southernmost part of its range, a few light frosts occur per year. As an exotic, the tree grows successfully in plantations where rainfall is 5000 mm and where rainfall with winter maximum occurs (Geary 1998).

Little information is available on racial variation in the species, but the nine related species suggest a great deal of variation that might be exploited through crosses. Variation in the volatile oils is noteworthy (Geary 1998).

The medium-density wood is difficult to season and tends to warp, but it finishes well as a cabinet wood. Without preservative treatment it makes a poor fence post. A major deterrent to use is the high bark-to-wood ratio. Its abundant leaf oil has been used commercially as an essential oil and medicine in its native countries. The bark is useful for its insulating properties and as a mulch. The small crown and distinctive bark have made it a popular ornamental tree. In Florida, the abundant flowering crop has been important to the apiary industry to sustain bee colonies and as a source of honey. Because of its invasive habit in wetlands, the tree is regarded as a pest in Florida and efforts have been made to eradicate it (Geary 1998).

Melaleuca quinquenervia flowers prolifically, and in Florida flowering occurs by age 3. Seedlings less than 1 m tall may bloom. In Florida, some trees are flowering in every month but February, March, and April. Individual trees bloom two to five times a year and pronounced flowering occurs regionally at least twice a year. The insect-pollinated flowers are showy, cream-white spikes in the form of 3 to 8 cm long, 2.5 to 4 cm wide bottlebrushes. The seeds are produced in short, sessile, hard, cylindric capsules, which are aggregated in tightly packed files around the branches. Several seed-bearing sections may alternate with foliage along a branch axis. Seed production is prodigious. On average, 30 seed capsules are produced by one spike of flowers. A branch may hold 8 to 12 of the seed-bearing sections and the capsules may hold seeds for up to 10 years without release. A single capsule may contain 200 to 350 seeds. Seeds are tiny and average 30 million per kg. Capsules release seeds only when subjected to fire, frost, wind breakage, natural pruning, or other damage that disrupts the capsules' vascular systems, causing them to dehisce (Geary 1998).

Published information, if any exists, on seed collection, extraction, cleaning, storage, germination tests, nursery practices, and seedling care is not readily available. However, procedures for another genus of Myrtaceae, *Eucalyptus*, which has similar seed capsules, have been used successfully in Florida for *M. quinquenervia* by the author (Geary and others 1983). Seed collection can be done at any time of year, because individual trees have a wide range of seed ages due to multiple flowering in a year and the retention of seeds for years. Aggregates of seed capsules are clipped from branches and placed in kraft paper bags to dry. This is best accomplished in a hot drying room with low humidity. After the capsules open, the seeds are shaken from them. An efficient method for doing this is to put the capsules in a stovepipe-like cylinder that fits snugly inside a U.S. Standard soil sieve (sieve opening size determined by trial and error). A pan is put on the bottom of the sieve and a lid on the top of the cylinder, and the unit is shaken. The tiny seeds collect in the pan and are free of major debris. No additional cleaning is needed to broadcast sow the seeds, nor is stratification needed because freshly collected seeds germinate.

Seeds stored in sealed containers at 7 °C for several years remain viable. To test germination, a tiny, known weight of seeds is sprinkled on standard blue germination blotters, which are placed in closed plastic boxes lined on the bottom with tissue paper for extra water storage. Germination results are expressed as number of germinations per mg of seed. These results are used to decide the quantity of seeds needed for broadcast sowing.

Seedlings are easy to grow in containers of 47 to 78 cc volume, filled with a potting mix of peat and vermiculite. A very tiny amount of seeds is sown in a container and the seeds are covered with a thin layer of vermiculite. The sown containers are then placed under a plastic or shade cloth shelter for protection from torrential wind or rain. Once seedlings are 3 to 5 cm tall, the shade can be removed and the seedlings thinned back to one per container. Watering depends on local climate. The key to success is to keep the potting mix moist at all times. A 20-20-20 liquid fertilizer is applied frequently to speed growth of the seedlings. After germination, seeds grown in mid-March in southern Florida take about 20 weeks to reach a planting height of about 30 cm. While bareroot seedling production in open beds was not tested, the probability that it can be done successfully is high because natural regeneration of this species on bare, moist soil is easy.

At planting time, seedlings are pulled from the containers at the nursery and packed in vented, waxed-cardboard boxes for transport to the field. A seedling's roots and the potting mix form a firm plug that usually remains intact from seedling pulling through planting.

Metrosideros polymorpha Gaudich.

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MYRTACEAE (MYRTLE FAMILY)

Metrosideros collina (J.R. and G. Forst.) *A. Gray subsp. polymorpha* (Gaud.) Rock.
(Little and Skolmen 1989). See also the extensive list of synonyms in Wagner and others (1990)

Lehua, ‘ohi’a

Metrosideros is a genus of about 50 species. With the exception of one species found in South Africa, all grow in the Pacific from the Philippines, through Papua New Guinea, to New Zealand and on high volcanic islands (Wagner and others 1990). Five species occur in the Hawaiian Islands (Wagner and others 1990). *Metrosideros polymorpha* is native to Hawaii, where it grows on all the main islands except Niihau and Kahoolawe. It is the most abundant and widespread native tree in Hawaii (Adee and Conrad 1990) and grows in association with numerous species in both wet and relatively dry forests.

Metrosideros polymorpha is a slow-growing, evergreen species capable of reaching 24 to 30 m in height and about 1 m d.b.h. It is highly variable in form, however, and on exposed ridges, shallow soils, or poorly drained sites it may grow as a small erect or prostrate shrub (Adee and Conrad 1990, Corn 1979). Its trunk may range in form from straight to twisted and crooked. Because the species can germinate on the trunks of tree ferns and put out numerous roots that reach the ground, it may also have a lower trunk consisting of compact, stilt-like roots. It grows in a wide range of soil types, over a rainfall range from 500 to 11400 mm, and over an elevation range from near sea level to about 2600 m. It is the first tree species to establish on most new lava flows in Hawaii and is also a common component of forests on very old, deep soils. *Metrosideros polymorpha* reaches its best development on relatively level, well-drained sites.

Metrosideros polymorpha is currently treated as a single species, despite its wide morphological and ecological range (Wagner and others 1990). Wagner and others (1990), however, recognize eight varieties with varying geographic distributions, and several other varieties have been described in previous works (Rock 1917, St. John 1979). The extent of hybridization and genetic polymorphism is unknown (Wagner and others 1990).

The heartwood is reddish brown, heavy (specific gravity of about 0.70), of fine and even texture, very hard, and strong. Native Hawaiians used the wood extensively for construction, household implements, and carvings. Principal modern uses include flooring, marine construction, pallets, fenceposts, and fuelwood. The wood’s limitations include excessive shrinkage in drying, density, and the difficulty and expense of harvesting in low-volume stands (Adee and Conrad 1990, Little and Skolmen 1989). Today, *M. polymorpha* is perhaps most highly valued in Hawaii for uses in watershed protection, aesthetics, and habitat for native birds, including several endangered species. *Metrosideros polymorpha* is featured in many Hawaiian songs and legends, and leis are made from the attractive flowers (Neal 1965).

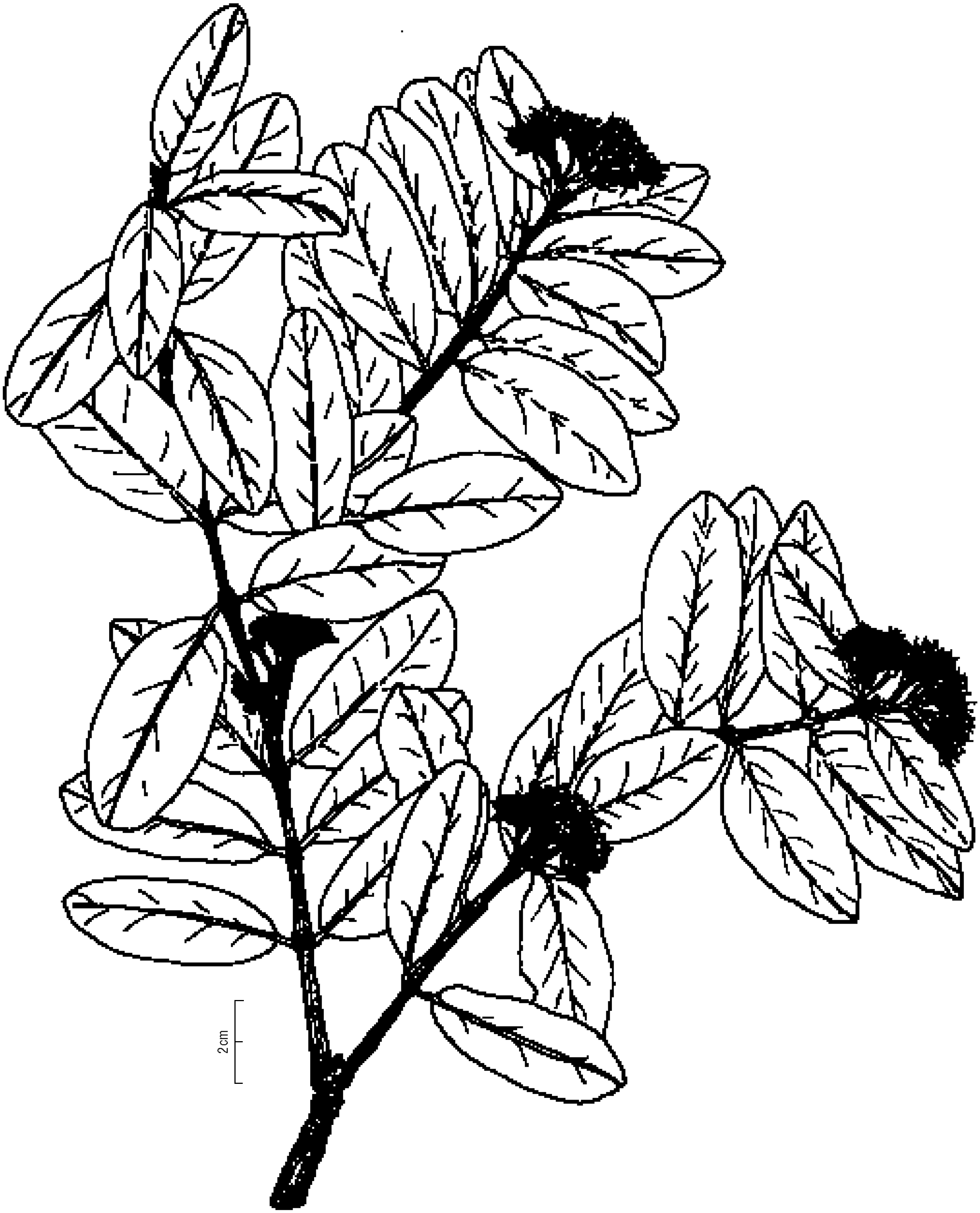
The flowers are borne in a dense, terminal cymose corymb; flowers are most often red, but may be salmon, orange, pink, or yellow. The inflorescence normally has 18 to 24 flowers in different stages of development. Flowering generally peaks in late spring or summer, but some varieties or populations peak in fall or winter, and individual trees or branches may produce flowers at any time during the year (Adee and Conrad 1990). Flowering typically begins first at low elevations, usually in March or early April, and may not peak until July at higher elevations.

Fruits mature approximately 70 to 90 days after flowering (Goo 1997). Fruits are capsules 6 to 10 mm long containing numerous minute seeds (mean fresh weight 57 µg), many of which may be infertile (Dawson 1970, Drake 1993). Seeds should be collected after maturity but before the capsules open; mature capsules have a noticeably swollen appearance and lines are evident where the capsule will dehisce. Although some seed is dispersed throughout the year, on the island of Hawaii (at 700-m elevation) 75 percent of the seeds were dispersed in December and January (Drake 1992a).

Capsules are generally collected directly from trees by hand or with pruning poles. Collected capsules should be air-dried until they begin to open, which typically takes several days to 4 weeks. Capsules should be air-dried in a protected setting, such as in a cardboard box or paper bag, to prevent loss of the minute seeds. Seeds average approximately 1,754,400 per kg. Seeds readily fall out of the capsule after drying. They rapidly lose viability and are best sowed within 1 month after the capsules dehisce. Seeds can be stored in a dry, cool location or under refrigeration, but percent germination may be reduced from the 50- to 60-percent range typical of fresh seeds to less than 10 percent within 1 year (Goo 1997) and nearly 0 percent within 3 years (Corn 1979). No pretreatment of the seeds is necessary.

Seeds are spread onto germination trays filled with commercial potting media, sterile compost, or cinder, and left either uncovered or covered with only a very thin layer of soil. Germination takes approximately 5 to 10 days if the seeds are fresh but may take 4 to 6 weeks for 1-year-old seeds (Corn 1979). Seedlings develop slowly, and it may be several months before seedlings are ready to be transplanted into containers. Seedlings reach an outplanting size of approximately 25 to 30 cm in height in about 1 year. One source reports that seedlings can reach 60 cm tall in 1 year (Bornhorst 1996).

Outplanted seedlings are initially very vulnerable to drought and may require frequent watering (Bornhorst 1996, Corn 1979). *Metrosideros polymorpha* seedlings grow best on well-drained, loose substrates, and often perform poorly on sites with impeded soil drainage, because they are highly susceptible to damping-off fungi (Corn 1979). Because ecotypic variation is great within the species, seed sources should be locations with climatic and soil conditions similar to those of the planting site.


2cm

Michelia champaca L.

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Chittagong University, Bangladesh

MAGNOLIACEAE (MAGNOLIA FAMILY)

Michelia aurantiaca Wall. Champak. Ver.

Champ, champa, champaca, champagam, champaka, champakam, champakamu, champige, chapa, chempaka, Rac-champo, sampige, sempangan, shamba, shembuga, tita-sopa (Balfour 1983, Brandis 1921, Gamble 1922, Troup 1921)

Michelia champaca occurs naturally in the eastern Sub-Himalayan tract (Zabala 1990c). It is a member of a genus with at least a dozen representatives in India and Myanmar (Burma) (Bor 1953). The species is fairly common in Bangladesh, Assam (a province of India), Myanmar, and southern India. It is found from Nepal eastward, including West Bengal (a province of India) and Assam. It is also found on the west coast from Karnataka to Kerala (province of India) (Negi and Gupta 1987). In Bangladesh this species occurs naturally in the tropical wet evergreen forests and tropical semievergreen forests of Chittagong Hill Tracts and Sylhet.

Michelia champaca is a large evergreen tree with a long straight bole (Negi and Gupta 1987) of 18 to 21 m with a close tapering crown composed of ascending branches. It is a medium-growing tree, attaining a height of 33 m or more and under ordinary forest conditions a girth of 2.4 to 3.7 m or more. The bark is light gray, smooth, and about 2 cm thick. Leaves are generally 13 to 25 cm long, 5 to 9 cm wide, lanceolate, sometimes ovate, finely acuminate, glabrous and more or less shining above, glabrescent underneath; the petiole is 1.8 to 3.0 cm long, slightly channeled, and usually pubescent; the old leaves are yellow (Troup 1921). In general it grows in moist, deep, well-drained, good quality soil. It grows in deep valleys and some grow best in foothills (Zabala 1990c). In the Kalimpong Division, it is mixed with other species in gneiss, slates, quartzite, and schist, which weather to a rich, sandy loam soil (Troup 1921). In its natural habitat, *M. champaca* grows in areas where temperatures are 0 to 47.5 °C and annual precipitation is 2250 to 5000 mm or more. It thrives in a damp climate.

Michelia champaca is basically a timber tree. The wood is soft and even-grained. The sapwood is white; the heartwood is light yellowish-brown to olive-brown and somewhat lustrous, without characteristic odor or taste (Anonymous 1976). The heartwood of this species is strong, durable, and capable of taking a high polish (Bor 1953). The wood is light (specific gravity 0.53) and straight grained; even- and medium-textured growth rings are distinct, being delimited by light lines of terminal parenchyma (Troup 1921). The timber is moderately refractory but can be air- or kiln-seasoned without difficulty or degradation, if properly handled. However, the wood discolors slightly and is inclined to become dull. It is also liable to crack with improper care (Troup 1921). The *Michelia* are generally not very durable woods although they have been known to last for fairly long periods when used as posts or under water. The heartwood of *Michelia* sp. is refractory to treatment; side or end penetration is almost nil (Indian Standards Institution 1955). The species is used for packing cases, crates, carriages, furniture, carving, bentwood articles, toys, bobbins, battery separators, pencils, tea chests, and plywood and in ship and boat building (Anonymous 1980b). In India the species is grown as an ornamental and the leaves, flowers, seeds, and fruits are used for essential oils and medicine (Nalawadi and others 1988). The sweetly scented flowers are used in India for hair adornment and for essential oil extraction.

The yellow-flowered variety produces new leaves in March; the white-flowered variety, later in the hot season (Troup 1921). The large, scented, yellow flowers grow singly, each from the base of a leaf. In West Bengal, trees 6 to 12 years old produce flowers and viable seeds, especially in the moister regions of the forest (Troup 1921). The fruit ripens in August or later. Seeds are dark brown and angular, covered with pink fleshy anillus (Zabala 1990c). Seed-year records from the Kurseog and Tista Divisions in West Bengal (India) show a good seed crop almost every year (Troup 1921).

Fruits should be collected in early September. Fruits should be dried in the shade until the seeds are released. If the seeds must be transported, the ripe fruits should be packed in charcoal dust to help keep them fresh (Troup 1921). The pulp is washed from the seeds in water; the floating nonviable seeds are discarded and the clean viable seeds are sown within 2 weeks of collection (Troup 1921, Zabala 1990c).

Seeds are oily and quickly lose viability. Regeneration is poor because the number of seeds that germinate is low (Zabala 1990c). In Dehra Dun, India, fruits were collected in September and spread in the sun to dry. Seeds were released within 3 days and were depulped and dried at room temperature for 1 day. Initial germination of seed lots was 68 percent, and moisture content was 21.2 percent (Bahuguna and others 1987). Germination percentage dropped markedly during storage at 5 °C.

Germination takes from 5 weeks to 4 months. The seedlings are pricked into plastic tubes with a soil and cow dung (3:1) medium when 2 to 4 cm high and left to grow for 1 year in the nursery. Seedlings can be outplanted when they are 30 to 40 cm in height (Zabala 1990c).

In vegetative propagation the Forkert method shows 46.5 percent success, the T-method 44.4 percent, and the Patch method 37 percent, whereas the side veneer method was unsuccessful (Rashid and others 1986). When 8- to 10-month-old seedlings were decapitated 25 to 30 cm from the ground and previously defoliated scions were grafted in early August, 40 percent success was obtained (Nalawadi and others 1988). Extracts of girdled and etiolated shoots contained a higher level of root-promoting substances than shoots that were only girdled or fresh shoots (Gowdam and Jayanthi 1988). *Michelia champaca* can also be propagated by treating fresh or pregirdled and etiolated layers with indole butyric acid. The best rooting (93.3 percent) and survival of rooted layers (92.1 percent) were obtained with pregirdled and etiolated layers treated with indole butyric acid at 5000 ppm (Channaveerappa and Gowda 1984). Roots of 1-year-old *M. champaca* exhibited vesicular-arbuscular mycorrhizas (Thapar and others 1992).

The disease caused by *Rhizoctonia solani* appears in late July (after the monsoon rains set in) and damage may be 70 to 100 percent. Controlling this disease by using appropriate sanitation and cultural methods is recommended. Seedlings can be raised in polypots rather than beds; diseased seedlings can be segregated; infected leaf litter can be removed; and plantations can be weeded during humid months (Mehrotra 1992).

ADDITIONAL INFORMATION

In Lawachara, Bangladesh, *M. champaca* grows well in plantations with *Hopea odarata, Xylia dolabriformis* Benth., and *Artocarpus chaplasha* (Zabala 1990). In West Bengal, India, the species mixed with *Bischofia javanica* Blume and planted under fast-growing deciduous *Chukrasia velutina* Roem. succeeded, and in Assam, India, planting *M. champaca* under *Terminalia myriocarpa* Van Heurok & Müll. Arg. in older plantations also succeeded (Troup 1921).

In the Northern Circle of West Bengal, which includes the Kurseong, Darjeeling, Buxa, Jalpaiguri, Cooch Behar, and Baihunthapur Divisions, *M. champaca* was raised in mixed-taungya plantations (Troup 1921). In *Shorea robusta* (common name Sal) plantations, usually nine lines (1.9 m apart) of sal alternate with *M. champaca, Chikrassia tabularis, Schima,* and other species. *Michelia champaca* and its associates, such as *Exbucklandia populnea, Acer campbellii, Schima, Machilus* spp., and *Cryptomeria* D. Don, were also used in afforestation work in the hills of the Kurseong Division (Troup 1921).

According to Homfray (1936) and De (1940), *M. champaca* does not stand waterlogging; it prefers a well-drained soil. However, in Hugaon Division, Assam (India), in areas too waterlogged for *Shorea robusta*, plantations of *M. champaca* are doing quite well (Troup 1921). According to Homfray (1936) *M. champaca* is sensitive to fire; severe fires may even kill it outright. Even large trees died after exposure to a low ground fire (Bor 1953). *Phomopsis micheliae* causes leaf spot diseases on *Michelia champaca* (Sankaram and others 1987). *Urotylis punctigera*, the *M. champaca* bug, causes appreciable damage in pure plantations. Growing *M. champaca* with other nonsusceptible species prevents intrusion and facilitates direct remedial measures. If necessary, a suitable mixture, such as 1 part nicotine sulfate and 1.8 kg soap in 450 L water, can be sprayed. Dieldrin and DDT water emulsion in very low concentrations can also be used (Troup 1921). Another pest identified as *Rynchothrips champakae* attacks the leaves of *M. champaca*, resulting in the browning and dying of leaves and twigs. The damage, however, is only slight and the plants usually recover (Mathur and Sing 1957).


2cm
2cm

Minquartia guianensis Aubl.

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OLACACEAE (OLAX FAMILY)

Secretania loranthacea Mull-Arg. (Prodromus Systematis Naturalis Regni Vegetabilis 15 [2]: 228; 1866); *Endusa punctata* Radlk. (Sitzungsberichte der Mathematish-Physikalischen Classe [Klasse] der Konigl. Bayer Akademie der Wissenschaften zu München 16: 311; 1886); *Eganthus poeppigii* van Teighem (Journal de Botanique [Morot] 13: 77; 1899); *Minquartia macrophylla* Ducke (Archivos do Instituto Biologico [Sao Paulo] 2: 33; 1935); *Minquartia parvifolia* A. C. Sm. (Brittonia 2: 149; 1936); *Minquartia punctata* (Radlk.) Sleumer (Repertorium Specierum Novarum Regni Vegetabilis 39: 282; 1936)

Acaiquara, acaiquara da varzea, acapd, acari, acaricoara, acariguara, acariquara roxa, acariuba, acary, alata-oedoe, alata-udu, alata-weri, arata o aratta, aratahoehoe, arataweri, arrataweri, baggie-baggie, black manwood, bois agouti, bois incorrupitble, camaroncillo, cricamola, criollo, huacapd, huambula, jewalidanni, kobakedive, konthout, kontoe-hoedoe, maka, makka, mand, mand negro, manwood, mekwa, mincoa, mincouart, minquar, paini yayo, palo criollo, palo de piedra, paramaka, pechiche, pechiche barbasco, plátano, senia'mba quini'cco, tomopio, urana-u-yek, urari, urodibe, wanania, wananin, yuwartu (Aublet 1775, Burger 1983, Sleumer 1984)

Minquartia is a monotypic genus. In Central America, *Minquartia guianensis* grows from southern Nicaragua to Panama; in South America, it is found in the Colombian, Ecuadorian, Brazilian, Peruvian, Venezuelan, and Bolivian Amazon and in the Guianas. The species also inhabits the forests of several Caribbean islands (Brako and Zarucchi 1993, Burger 1983, Hiepko 1993, Jorgensen and León-Yañez 1999, Renner and others 1990, Sleumer 1984, Spichiger and others 1989). *Minquartia guianensis* is an emergent tree, common in the lowland, premontane, and lower montane tropical forests of the Pacific and Atlantic watersheds. It usually grows associated with royal mahogany (C*arapa guianensis* Aubl.), vainillo (*Stryphnodendron microstachyum* Poepp.), oil bean tree (*Pentaclethra macroloba* [Willd.] Kuntze), monkey pot (*Lecythis ampla* Miers), and wild nutmeg (*Virola* Aubl.).

Minquartia guianensis is a large tree that may reach 73 m in height and 180 cm d.b.h. Although the South American trees are small to medium-sized, those from the tropical wet forest in the Corcovado zone (Osa Peninsula, Costa Rica) may reach a height greater than 70 m. The bole is straight and angular and frequently has buttresses and deep, long grooves in the basal third. Trees with a d.b.h. greater than 60 to 80 cm usually have bark and wood perforations and hollow pith colonized by ants and fungi. Young twigs are densely grayish or rusty-puberulent; trichomes are branched. The bark is grayish brown or dark brown. It exfoliates small oblong scales and bears vertical fissures, which may show whitish or yellow latex if cut or damaged. Internally, the bark is whitish or pale yellow, and sugary. It has many laticifers filled with white latex and schizogenous secretory cavities with abundant resin. The latex oxidizes if exposed to air and light. Bark thickness ranges from 1.5 to 2.5 cm (Flores 1994e). Leaves are alternate, simple, stipulate, chartaceous or coriaceous, elliptic, lanceolate or oblong-elliptic, with entire margin, apex cuspidate or abruptly short acuminate with acute or blunt tip, base round-truncate or obtuse; they are short-petiolated; petioles are grooved adaxially. The species may be found in primary, secondary, and gallery forests with alluvial, acid clayey, or sandy soils. It grows well in periodically flooded areas, as well as on slopes. The trees grow where temperatures range from 22 to 35 °C and the annual rainfall varies from 2500 to 6500 mm. The elevation range is 0 to 1000 m.

In green and dry conditions, sapwood is light brownish gray with darker stripes. The heartwood is brown in green condition and turns grayish brown when dried. The transition between sapwood and heartwood is abrupt; they are separated by a clear narrow stripe 1.5 to 2.0 mm in width. *Minquartia* *guianensis* is intensively exploited because of its high wood quality. It has a straight, interlocked, or undulated grain depending on its origin. It has a fine texture and lacks luster. However, under the appropriate angle of incidence, the longitudinal surfaces reflect light. The wood does not have figure and is tasteless and odorless. The wood is very heavy (green weight 1200 to 1300 kg per m^3 with 62 to 68 percent moisture content; basic specific gravity is 0.75). The Peteri's coefficient of flexibility is 88, and the Runkel factor is 2.57 (group V: wood not usable for making paper). Fast drying may cause checking or produce superficial fissures and slight twistings. The wood is difficult to work due to its high density, but it takes a good finish; surfaces with straight grain are smooth after brushing. Differences in radial contraction may be found, depending on wood origin. When in use, the timber shows excellent natural durability and resistance to termites and fungal rotting. Wood preservation is difficult. It is used in heavy general construction, railroad ties, pilings and other marine construction (in waters lacking *Taredo* borers), bridges, posts, sticks, poles for fences and houses, turnery, inlay, and agricultural instruments (Flores 1994e, Llach 1971).

Inflorescence occurs from October to January, and sometimes extends to February; however, its development is delayed during the maturation period of the fruit crop from the previous year. Flowers are grouped in spikes; spikes are solitary in the axile of distal leaves in minor branchlets. Inflorescence is short-pedunculated, with a thick rachis and rusty pubescence. Flowering is irregular or episodic, and flowering within the population is asynchronous (Flores 1994e). The number of trees flowering in each episode is variable. Pollination is carried out by beetles, drones, bees, and sometimes birds. There are many flowers per inflorescence, but few fruits are produced. Flowers are small, perfect, epihypogynous, subsessile, subtended by an ovate bract that is small and deciduous; the flowers are creamy and fragrant. The calyx is pentaerous, gamosepalous, cupuliform, toothed distally, puberulous, and marcescent; it bears numerous basal glands; the corolla is pentamerous, gamosepalous, tubular, campanulate, toothed distally, and covered internally by erect trichomes. The androecium has two verticils, each with five epipetalous stamens; the alternipetalous verticil separates from the corolla above the antipetalous verticil. The ovary is globose, two- to five-locular, dusty ferruginous, and fused to the androecium, perianth, and hypanthium at base; the style is short and the stigma is pentalobed.

Fruit ripening occurs from January to March or April; however, fruits may be found in other months, especially November and December. The fruit is a monospermic drupe, ovoid, reaching 3.0 to 4.5 cm in length and 2.0 to 2.8 cm in width (Flores 1994e, Hiepko 1993). Fruits are dispersed by omnivorous birds, bats, and small rodents; gravity causes some fruits to fall. Bats are attracted by the purplish brown or black color of mature fruits and the rancid odor produced by the fermenting substances of the pericarp (butyric acid) (Flores 1994e). Seeds are ovoid or globose and have a brown seedcoat formed by testa and tegmen.

Fruits must be collected from healthy trees. Seeds average 220 to 240 per kg (seed plus endocarp) with 48 percent water content. Most water is found in the endosperm. Seeds surrounded by the endocarp keep their viability under natural conditions (those prevailing in the humid tropical forest floor: 24 to 30 °C, air humidity 95 percent or more), but viability is gradually lost with increasing dehydration. Fruits average approximately 190 to 200 per kg.

Fresh seeds (seed plus endocarp) must be soaked for 24 hours before sowing. Seed behavior is recalcitrant. Germination is epigeal and the seedling is cryptocotylar. Germination of freshly collected seeds (fruits), soaked 24 hours, is 85 percent. Endocarp removal increases dehydration and speeds embryo death (Flores 1994e).

Seeds do not require special treatment and can be sown in beds or plastic bags filled with humid sand or a mixture of soil and sand. Germination occurs in either the shade or direct sunlight, provided humidity is kept stable. Under greenhouse or nursery conditions, root protrusion begins 4 months after sowing. Four equidistant longitudinal fissures at the distal end of the endocarp are the first signal observed (Flores 1994e). Seedling growth is very slow; 12-month-old seedlings average 40 cm in length (Flores 1994e).

ADDITIONAL INFORMATION

French Guiana was inhabited by the Creoles, descendants of African slaves who were taken to this land by the colonists. They called the *Minquartia guianensis* tree "le minquar de la Guiane." This native name evolved into *Minquartia,* a term used by Aublet (1775) to name the genus in his book Histoire des plantes de la Guiane Françoise (Flores 1994e). The species name refers to the place of origin.

The leaf's adaxial surface is green-olivaceous, sometimes grayish, dull and finely pubescent in young leaves; mature leaves have a bright and glabrous surface. The abaxial surface is dull, verrucose, light grayish green and pubescent; trichomes are dendritic. Leaf blade is amphistomatic; stomata are paracytic. Leaf venation is pinnate eucamptodromous; the midvein is thick, straight, and abaxially prominent. Secondary veins are subparallel with an acute moderate angle (45 to 65°) of divergence with respect to the midvein; tertiary veins are transverse and subparallel, with few branches. Leaf length and width are quite variable (Flores 1994e).

Filaments are glabrous, distally filiform, and adnate to the corolla in the basal third; anthers are globose, minute, and longitudinally dehiscent. Pollen is tricolpate, finely grooved near the pores, angular in polar view and flat ellipsoidal in equatorial view, with a diameter of 23 to 25 mm; exine is smooth (Burger 1983, Hiepko 1993, Sleumer 1984). There is one anatropous, bitegmic, crassinucellate ovule per locule; a single ovule completes its development (Flores 1994e).

The ovary and tissues from the androecium, perianth, and hypanthium form the cup-like basal structure of the fruit wall. The exocarp is thin, membranous, and shiny green with glandular dots in the surface of immature fruits. The mesocarp is fleshy and slightly hard; it has abundant latex and an astringent taste. When fruits mature, the mesocarp softens and acquires a sugary taste. Fruits that fall on the ground undergo a rapid fermentation, acquiring a black coloration, which precedes mesocarp fermentation and rotting. The endocarp is thick, hard, yellowish, woody, and has a well-developed vascular supply; its external surface is irregular.

The seed has a thin testa that splits when root protrusion begins. The tegmen is thin but develops small ruminate invaginations which penetrate the endosperm. It dehydrates and reduces gradually during seed maturation, reaching a papyraceous texture. The endosperm is cellular, massive, hard, whitish, and slightly ruminate; it has a high content of starch and lipids. The embryo is minute (1.6 to 2.0 mm long), rudimentary, pyriform, whitish, with a violaceous basal end, and is surrounded by endosperm (Flores 1994e).

In the 4-month period from sowing to fissure formation and root emergence, the rudimentary embryo develops inside the seed and reaches 1.2 to 1.3 cm in length. It increases to 10 times its initial size and begins hypocotyl and cotyledon development. At 5 months, the embryo initiates root development; the root emerges throughout the endocarp distal opening produced by fissure formation; at least half the root remains inside the seed for several weeks. Cotyledon development increases inside the seed; the cotyledonar blades are fused distally and have an haustorial function. Six-month-old seedlings are 3.0 to 3.2 cm long; they exhibit an intense development of root, hypocotyl, and cotyledons. The cotyledonar blades elongate and widen, developing a complex vascular system inside the seed. The initially whitish blades change with age to pale pink, dark pink, and purplish pink; veins are dark purple (Flores 1994e). In 7-month-old seedlings the hypocotyl increases its development; the seed, surrounded by the endocarp, with the cotyledons enclosed, elevates from the ground. Cotyledonar petiole elongation takes place at 8 months. They enclose the plumule. When they extend longitudinally and bend backwards, they form an inner opening through which the plumule emerges. The cotyledonar petioles abscise approximately 1 month later and the seeds containing the cotyledonar blades and remains of the endosperm fall (Flores 1994e).


1cm
4cm

Moringa oleifera Lam.

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MORINGACEAE (HORSE-RADISH TREE FAMILY)

Moringa pterygosperma Gaertn, *M. moringa* (L.) Millsp., *M. nux-ben* Perr.,
Hyperanthera moringa Willd., *Guilandina moringa* Lam.

Acacia blanc, árbol de las perlas, árbol de los aspáragos, ben ailé, ben tree, benzolive tree, drumstick tree, horseradish tree, marango, moringa pea tree, moringue aptére, mother's best friend, mrongo, never-die, oil of ben tree, palo blanco, paraíso francés, pois quenique, resedá, sohnja, water purifying tree, and many more local common names (Jahn 1986, Little and Wadsworth 1964, Morton 1991, Palada 1996)

One of 14 species in the genus (Verdcourt 1985), *Moringa oleifera* originated in the western Himalayas and eastern Punjab (Brandis 1906) and now grows pantropically, either domesticated or semiwild.

Moringa oleifera is a deciduous-to-evergreen shrub or small tree, rarely reaching 15 m and usually less than 25 cm d.b.h. Initially fast-growing at up to 4.5 m in 9 months, the tree rarely grows older than 20 years (von Maydell 1986). It favors alluvial soils in semiarid regions, thriving at elevations of 800 to 1,200 m, but occurring from lowlands to about 1,500 m. When grown at 1,660 m it fails to develop flowers (Jahn 1991). The species accepts a pH of about 4.5 to 8 and grows well in a wide range of soils except those with saline conditions and stiff clay. It grows best in well-drained sandy loam. *Moringa oleifera* grows well where precipitation is between 760 and 2,150 mm, and when it can access ground water, it will tolerate precipitation levels below 300 mm (Troup 1921).

Moringa oleifera exhibits considerable variability in weight of cotyledons, seed size or yield, and phenology, and especially in the length, appearance, and quality of pods (Duke 1987, Jahn 1989, Morton 1991). Some of this variability is inherent or environmentally controlled, and some may result from long-term vegetative reproduction, as is customary when producing annual plants (Jahn 1989). Pods can be sweet to bitter. One of the best Indian cultivars, Bombay, has curly fruits. Others are characterized by long pods (Chavakacheri Murunga), tender pods (Jaffna), and red-tipped pods (Chem Murunga).

Moringa oleifera is a highly valuable, multipurpose tree, and in parts of the tropics it is cultivated as a vegetatively reproduced annual crop (Jahn 1989). It is used in home gardens or similar agroforestry contexts (Dale and Greenway 1961, Folkard and Sutherland 1996, Keay 1989, Palada 1996), for intercropping and as field borders, windbreaks, live stakes, and live fences. The wood is very soft, burns smoke free, and yields a blue dye. In India, the pulp has been used to make paper. Most of the tree is edible: the tuberous root cores can be substituted for horseradish; the bark (ben gum) can be used as seasoning; and the leaves, young shoots, and fresh or canned fruits can be used as vegetables or pickles and in soups and sauces rich in protein (up to 27 percent), calcium, phosphorus, vitamins A and C, carotene, and the amino acids methionine and cystine (Price 1993). The flowers with their radish-like flavor can be eaten or used to make tea. They also produce a good honey. The seeds can be consumed fresh as peas; or pounded, roasted, or pressed into a sweet, nondesiccating oil (ben oil) of high quality. This oil is used in art, salads, soap, smoke-free lamp fuel, and hairdressing; as a fine lubricant or purgative; and as a fixative for volatile odorous substances in perfumery. The tree's most unique property is the ability of its dry, crushed seeds and seed presscake, which contain polypeptides, to serve as natural coagulants for water treatment (Folkard and Sutherland 1996; Jahn 1989, 1991). With as little as 0.5 to 1.5 seed per liter, turbid, foul water can be rendered clear and potable. The level of purification compares favorably with that obtained using traditional chemical purifiers such as alum. Other applications (Morton 1991) include: using leaves for fodder (poultry, livestock, pigs, and camels) and mulch; using seed presscake as a soil fertilizer/conditioner; using bark for mats, rope fiber, and tanning; and using roots and flowers (Eilert and others 1981) as a natural fungicide against damping-off. Virtually every part of *M. oleifera* is used in some type of native medicine, such as diuretics, skin treatments, and cures for scurvy and various bladder and prostate ailments (Duke 1987, Irvine 1961, von Maydell 1986, Morton 1991). In Cuba the tree is considered an antidote for machineel (*Hippomane mancinella*) poisoning (Bureau of Plant Industry 1915).

The white, cream, pink, purplish, or yellowish flowers are borne in axillary, drooping, 10-to-25 cm long panicles. Each flower is about 2 to 2.5 cm across and exhibits five unequal petals slightly larger than the five reflexed sepals (Keay 1989, von Maydell 1986). Seed-produced plants can start flowering at 8 months. The main flowering period in India is January to April, but many trees are in bloom from September onward (Cowen 1965). In Cuba, Florida, and Nigeria, *M. oleifera* flowers throughout the year (Keay 1989, Menninger 1962, Morton 1991). Flowers usually precede or coincide with fresh leaves in deciduous trees (Brandis 1906). The pendulous fruits (pods or drumsticks) are borne singly or in pairs. They range from 15 to 120 cm, but are usually between 30 and 50 cm long and about 2 cm thick. They are green to purple and bluntly triangular or nearly cylindrical in cross section, exhibit nine ribs, and taper to a point.

Under intensive culture, green pods can be harvested as early as 6 or 7 months after seeding, but in India pods can suffer from attacks of a fruitfly (*Gitonia* spp) (Jahn 1989). Drumsticks mature in about 6 weeks, then open along three valves, revealing 20 to 25 seeds embedded in a dry, white, tissue-like pith, and arranged in a single row. Seeds are round to triangular, brown to black, and usually bear three papery wings. They are less than 2 cm across, including wings.

When dry, the brownish-gray seed pods are collected from the trees and are easily shelled by hand. The sticky film coating the seeds is removed by washing in a strainer. Seeds average about 3,000 to 9,000 per kg (Food and Agriculture Organization 1975, Francis and Rodriguez 1993). A single tree may annually yield 1,500 to 24,000 seeds (Jahn 1989). The germination rate may be as high as 100 percent, but has decreased 10 to 52 percent after 1 month of storage. Some lots show 25 to 60 percent germination after 1 year, but seeds do not survive 2 years of storage (Verma 1973). However, according to Jahn (1986), seeds in sealed jars remain viable for several years and no pretreatment is necessary.

Direct seeding and nursery production are easy (Jahn 1989). Seeds are sowed 1 to 2.5 cm deep under half-shaded conditions, with one to two waterings daily (Verma 1973). A mix of equal parts of black, red, and sandy soil and cow dung is recommended and, if available, a supplement of crushed animal bones (Jahn 1989). Seeds sprout as early as 3 to 4 days, but usually take from 1 to 2 weeks (Francis and Rodriquez 1993, Morton 1991, Price 1993), with best results during hot, moist weather (Jahn 1986).

Seedlings average 25 to 30 cm in two months. At 40 cm or more, which is reached in 3 months, seedlings may be outplanted (Jahn 1989, Price 1993). Outplanting should coincide with the rains. Seedlings should be spaced at 2 by 2 m for annual production, and 4 or 5 m for long-term production. Recommended pit size is about 0.5 by 0.5 by 0.5 m. For intensely managed seedlings such as annuals, 10 kg of farmyard manure and 100 g of urea should be added.

For the most part, selections are propagated vegetatively. The tree coppices well and reproduction from cuttings is easy.


1cm
1cm
2cm
2cm

Myroxylon balsamum (L.) Harms

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FABACEAE (BEAN FAMILY)

Myroxylon balsamum var. *punctatum* (Klotzsch) Harms (Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 43: 97. 1908). *Myroxylon punctatum* Klotzsch (Getreue Darstellung und Beschreibung der in der Arzneykunde Gebräuchlichen Gewächse 14: 12. 1843).
Myroxylon toluiferum Kunth (Nova Genera et Species Plantarum 6: 375. 1824).
Myroxylon toluiferum A. Rich. (Annales des Sciences Naturelles (Paris) 2: 171-172. 1824).
Myrospermum toluiferum (A. Rich.) DC. (Prodromus Systematis Naturalis Regni Vegetabilis 2: 95. 1825)
Toluifera balsamum L. (Species Plantarum 1: 384. 1753)

Bálsamo, bálsamo de San Salvador, bálsamo de tolú, bálsamo del Perú, chirraca, chucte, estoraque, nabá, palo de bálsamo, quina, sándalo, yaga-guienite (Chudnoff 1984, Holdridge and Poveda 1975, Record and Hess 1949)

Myroxylon balsamum occurs from southern Mexico to the Amazonian region of Peru and Brazil (Berendsohn and Araniva de González 1989, Chudnoff 1984, Ducke 1949, Holdridge and Poveda 1975, Macbride 1943, McVaugh 1987, Standley and Steyermark 1946). The tree has been planted for balsam production in West Africa, India, and Sri Lanka. *Myroxylon balsamum* is an emergent tree, typical in the canopy of pristine primary forests.

Myroxylon balsamum is a slow-growing, large tree that reaches up to 45 m in height and 1m d.b.h. The crown is quite round, sometimes open, with dense foliage. The bole is straight with slim, ascending branches and a smooth, grayish brown outer bark bearing abundant lenticels. The inner bark is yellowish and fragrant with a pungent, obnoxious odor (Croat 1978, Holdridge and Poveda 1975). The leaves are alternate, petiolate, imparipinnate, and 8 to 20 cm long including the petiole. The petiole is 1 to 4 cm long and the rachis 5 to 15 cm long. The rachis and petiolules are pubescent and terete. The leaves have five to ten pairs of leaflets that are 3 to 11 cm long, 1.8 to 4 cm wide, lanceolate or elliptic, and alternate on the rachilla. Leaflets have acute to acuminate apex, an obtuse base, and entire margin; they are glabrous, with scattered translucent glandular oil dots or lines (Croat 1978, Holdridge and Poveda 1975). The species is found in evergreen tropical humid forests in low to medium elevations from 100 to 600 m. It grows well on hills or in well-drained areas with moderate slopes with an annual rainfall above 2500 mm and a temperature range of 24 to 30 °C (Croat 1978, Holdridge and Poveda 1975).

The fresh heartwood is reddish brown with an occasional yellowish hue; it turns deep red or purplish upon exposure. It is fairly uniform or striped and sharply demarcated from the white sapwood. The wood is tasteless but has a pronounced, pleasant, spicy, or cedary scent. It is very hard, heavy, tough, and strong. The basic specific gravity (ovendry weight/green volume) is 0.74 to 0.81. Luster is medium to high and golden; texture is medium; and the grain is typically interlocked. The wood is moderately difficult to work but can be finished smoothly with a high natural polish. Radial shrinkage (green to ovendry) is 3.8 percent; tangential shrinkage 6.2 percent; and volumetric shrinkage 10 percent. These values are considered very low for a wood with this density (Record and Hess 1949). The heartwood is reported to be highly resistant to attack by decay fungi (Chudnoff 1984, Record and Hess 1949). Both sapwood and heartwood are difficult to preserve. The wood is used for flooring, furniture, interior trim, and railroad ties (Chudnoff 1984, Record and Hess 1949, Salas 1993). *Myroxylon balsamum* is often used to shade coffee plantations, where it attains a height of 10 m in 10 to 12 years, and 20 m in 25 years. Its vanilla-scented resin, known as bálsamo del Peró, has commercial value. Although formelry credited with great medicinal value, particularly for skin and lung diseases, the balsam is now used chiefly for perfumery, ointments, and proprietary preparations (García 1974, Record and Hess 1949).

Flowering begins after 5 years and occurs February through June. The flowers are whitish, pubescent, medium-sized, entomophilous, and grouped in simple axillary or terminal racemes 20 cm long. The flowers have small caduceus bracts and bracteoles and a campanulate calyx 3.5 to 4.5 mm long, with fine ribs. The flower shows the typical descending aestivation, which is characteristic of the petals of papilionaceous flowers (Polhill and Raven 1978). There are five irregular lobes; the standard is clawed, broad, and orbicular. The wings and keel petals are subequal, free, narrow, and spatulate. The flower has 10 stamens, free or shortly united at the base, which fall with the petals. The anthers are uniform, acuminate, and longer than the filaments. The ovary is stipitate, sparsely villous, with one or two suspended ovules. The style is short, filiform, and incurved and has a well-defined terminal stigma.

The fruit is a flat, indehiscent, samaroid, winged pod that is stipitate, narrowly obovate, 7 to 11 cm long, and 2 cm wide; it narrows toward the base. The pod wings mimic seeds; they are up to 8 cm long and 1 to 2 cm wide and have many veins crowded submedially; the lower wing is narrower than the upper wing. The fruit is monochrome yellowish brown when dried. Fruit dispersal is anemochorous. Dry fruits are found on the ground November to January. The apical seminiferous area is turgid and has one subreniform seed that is 15 to 18 mm long. The seedcoat is membranaceous and compressed by the pericarp. The seed lacks pleurogram and fracture lines (Allen and Allen 1981, Croat 1978, Gunn 1981, Holdridge and Poveda 1975, Polhill and Raven 1978).

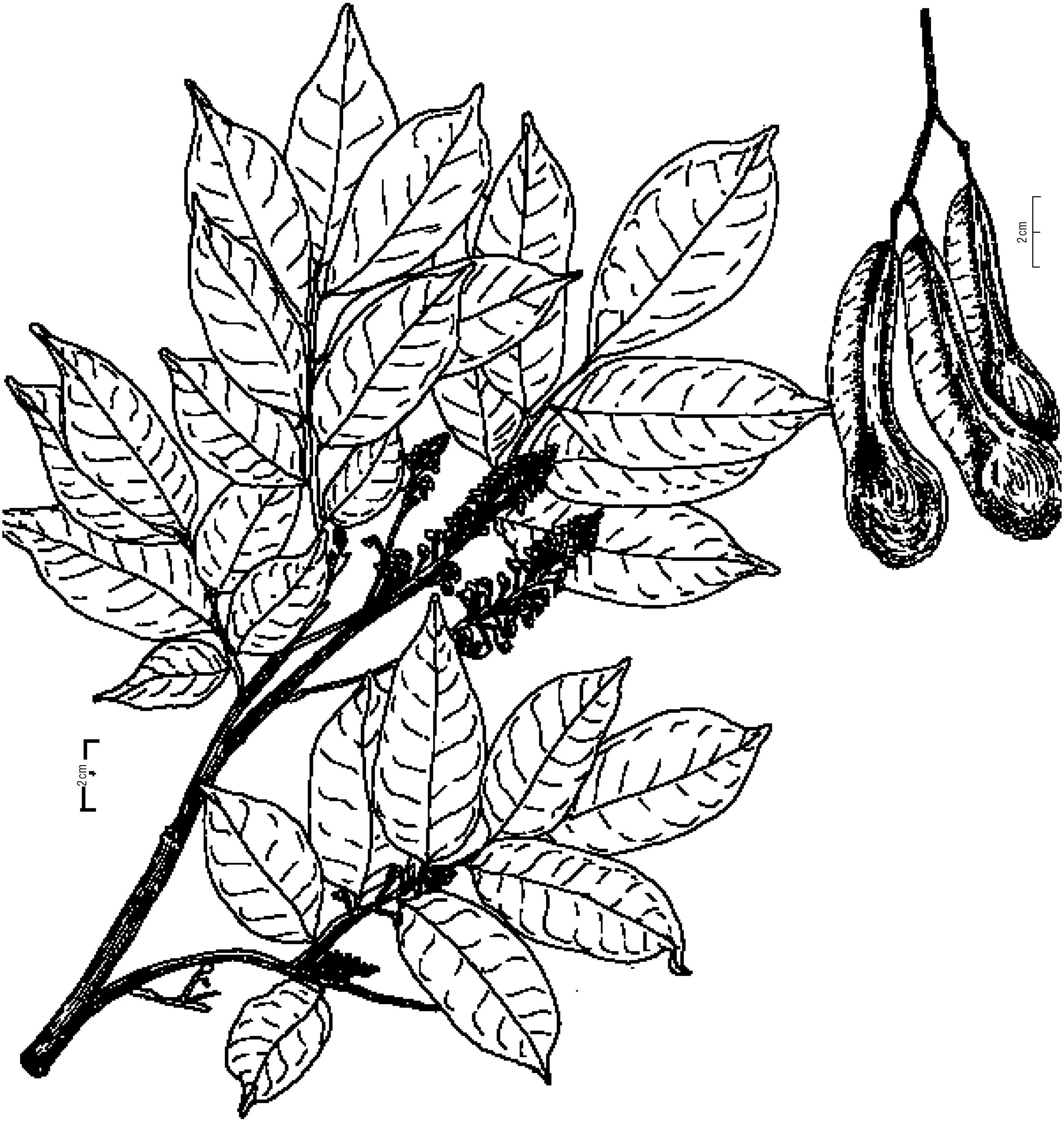
Fruits must be soaked in running water for 24 hours to soften the pericarp and facilitate seed extraction. The species is reproduced by seed. Seed behavior is orthodox. Germination is hypogeal and seedlings are cryptocotylar. Under greenhouse conditions, germination is 60 to 75 percent. Root protrusion begins 8 to 10 days after sowing.

Natural regeneration is abundant mainly under the crown of parent trees, where seeds attain up to 80 percent germination. However, fungi, insect larvae, and other pathogens may cause fruit, seeds, and embryos to rot. The scarce seedlings face low light availability, which hinders their chances for survival; very few reach intermediate ages in the forest.

ADDITIONAL INFORMATION

The Spaniards introduced the balsam produced by *M. balsamum* into Europe in the 16th century. El Salvador is the primary producer of balsam; however, during the colonial era the product was often sent to Peru for shipment to Spain. Balsam harvesting proceeds throughout the year, particularly during the dry season, December to April. The method consists in making numerous V-shaped incisions in the bark and collecting the balsam, which flows through the incisions into vases. Another method involves removing 15 to 25 cm of bark 30 cm above the ground and covering the wound with a piece of cotton cloth to absorb the liquid. When the natural flow ceases, scorching stimulates it. The impregnated rags are boiled in water and pressed. The best trees yield 1.5 to 2.5 kg of balsam per year for almost 30 years, but many trees die as a result of tapping (García 1974, Record and Hess 1949).

The balsam is yellowish brown, transparent, and a little viscous. It often solidifies into small, bright, crystalline pieces, which have a pronounced, pleasant, spicy scent. In addition to resins, the balsam also contains free benzoic acid, benzoic ethers, and a little vanillin. The active components of the balsam are benzilbenzoic and benzilcinnamic ethers (75 percent), cinnamic and benzoic acid (12 to 15 percent), and vanillin (0.08) (García 1974).


2cm
2cm

Ochroma lagopus Sw.

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BOMBACACEAE (KAPOK-TREE FAMILY)

Ochroma bicolor, O. grandifolia, O. pyramidale

Balsa, balso, lana

Ochroma lagopus is a very fast-growing tree that reaches 20 m in height and 20 cm d.b.h. The trunk has a smooth bark, and the tree has an umbellate crown. The opaque green leaves are wide, alternate, and villous, with long, thick petioles and a nervation similar to the palm of a hand. Edaphic requirements are high; optimal growth occurs in soils of alluvial origin with good ventilation and no flooding, or in sandy soils resulting from the meteorization of rocks. The species has a high demand for light, growing as a pioneer species in secondary forests, large clearings, burned acres, or recent alluvial soils. Generally, it requires annual precipitation from 1500 to 3000 mm, temperatures between 22 and 27 °C, and altitudes between sea level and 2000 m. The species can tolerate drought periods of up to 4 months when atmospheric humidity is not lower than 75 percent. This species, a pioneer par excellence, shows abundant natural regeneration (Lamprecht 1990, Venegas 1978).

The wood is difficult to plane and does not hold nails or screws. However, it can be easily glued or saturated. It has a relatively high mechanical resistance, which increases as temperature decreases. For this reason it makes a good insulating and packing material; it was used as insulating material in U.S. spaceships. It is moderately easy to dry in the open air with moderate twisting and cracking. In drying chambers the wood tends to crack, twist, or harden superficially. The wood of *O. lagopus* is also used for boards, toys, sports articles, model airplanes, packing, net floaters, lifeboats, canoes, and signaling buoys. Its fiber is very long and it produces a very valuable, high-yielding pulp. The cellulose is easy to whiten, and the woolly and silky fibers of the seed are used in hats and to fill mattresses. The bark is used in making ropes (Lamprecht 1990, Escobar and Rodriguez 1993).

Ochroma lagopus first fructifies between 3 and 5 years. The white flowers are 10 cm long. The fruits are brown elongated capsules, 18 cm long, with seeds that show hairiness (Camargo 1970).

The seeds cannot be stored and pregermination treatments are required to ensure germination rates greater than 10 percent. The fibers must be removed by hand or by burning. The seeds are then placed in boiling water and the heat source is removed. After soaking in the water for 15 minutes, the seeds must be planted immediately. In nurseries, germination occurs in 10 days.

Because the roots of young plants can be damaged easily, seeds are frequently planted directly in the field (Centro Agronómico Tropical de Investigación Enseñza 1998a, Palacios 1979). The sowing site must be well prepared and free of underbrush. Sowing holes are 3 m apart, and the sowing distance is 3 by 3 m. For direct planting, 15 seeds are placed in each hole. Later, the plants in each hole are thinned. During the plantule's initial phase of development, the site must be kept free of underbrush.

In nurseries the seeds are planted in containers of clayey-sandy soil and lightly covered. When the plantules are 20 to 25 cm high, at about 3 months, they are outplanted (Camargo 1970).

Ochroma pyramidale (Cav. ex Lam.) Urb.

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BOMBACACEAE (KAPOK-TREE FAMILY)

Bombax pyramidale Cav. ex Lam. (Encyclopédie Méthodique, Botanique 2: 552; 1788); *Ochroma lagopus* Sw. (Nova Genera et Species Plantarum seu Prodromus 98; 1788); *Ochroma tomentosa* Humb. & Bonpl. ex Willd. (Enum. Pl. Hort. Reg. Bot. Berol 695; 1809); *Bombax angulata* Sessé & Moc. (Flora Mexicana 169: 1895); *Ochroma concolor* Rowlee (Journal of the Washington Academy of Sciences 9: 161; 1919); *Ochroma grandiflora* Rowlee (Journal of the Washington Academy of Sciences 9: 163; 1919); *Ochroma limonensis* Rowlee (Journal of the Washington Academy of Sciences 9: 163; 1919); *Ochroma velutina* Rowlee (Journal of the Washington Academy of Sciences 9: 164; 1919); *Ochroma bicolor* Rowlee (Journal of the Washington Academy of Sciences 9: 165; 1919); *Ochroma boliviana* Rowlee (Journal of the Washington Academy of Sciences 9: 166; 1919); *Ochroma peruviana* I. M. Johnst. (Contributions from the Gray Herbarium of Harvard University 81: 95; 1928); *Ochroma pyramidale* var. *concolor* (Rowlee) R. Schultes (Botanical Museum Leaflets 9: 177; 1941); *Ochroma tomentosa* var. *ibarrensis* Benoist (Bulletin de la Societé Botanique de France 88: 439; 1941); *Ochroma lagopus* var. *bicolor* (Rowlee) Standl. & Steyerm. (Publications of the Field Museum of Natural History, Botanical Series 23: 62; 1944); *Ochroma lagopus* var. *occigranatensis* Cuatrec. (Phytologia 4: 480; 1954); *Ochroma pyramidale* var. *bicolor* (Rowlee) Brizicky (Tropical Woods 109: 63; 1958)

Algodón, árbol de algodón, balsa, balsa real, balsa wood, balso, bois flot, bombast mahoe, burillo, ceibón botija, ceibón lanero, corkwood, down tree, dum, enea, gatillo, gonote real, guano, jonote real, jopi, jubiguy, lana, lanero, lanilla, mahaudème, maho, mo-hó, mo-ma-há, palo de balsa, pata de liebre, patte de lièvre, pau de balsa, pepe balsa, piú, polak, pomoy, puh, pung, tacarigua, tambor, tami, topa, urú (Pennington and Sarukhán 1968, Record and Hess 1949)

Common in the American lowlands, *Ochroma pyramidale* has a geographic range that extends from southern Mexico to Bolivia and the West Indies (Record and Hess 1949, Whitmore and Hartshorn 1969). The species is an indicator of secondary forests because it occurs in clearings and forest gaps.

Ochroma pyramidale is a fast-growing evergreen tree that may reach 30 m in height and 1.8 m d.b.h. The tree is frequently buttressed. The crown is large, wide, spreading, and sparsely branched; twigs are thick, with leaf and stipule scars, green or greenish brown, lenticellate, with a ferruginous indument, and they exudate a sticky gum (Pennington and Sarukhán 1968). The bark is smooth, with some protuberant linear scars, and grayish, grayish brown, or brown; it has small protuberant lenticels. The inner bark is fibrous, yellowish creme, creamy, or pinkish, turning pinkish brown with age or when exposed to air and light. The average thickness is 8 to 14 mm. Phyllotaxy is spiral. The leaves are simple and stipulate; stipules are broadly ovate and deciduous. It grows well in volcanic or limestone soils that are rich and well drained. The elevation range varies from 0 to 1200 m.

Sapwood is nearly white, creamy, yellowish, or pinkish. The heartwood is pale brown or reddish brown. The wood has a straight grain (sometimes slightly interlocked), high luster, and medium texture. It is odorless and tasteless. The wood is extremely light and has strong variations in weight (basic specific gravity is 0.10 to 0.20). Green wood weighs two or three times more than dry wood. Volumetric contraction is low (6.1 to 10.3) with an unfavorable contraction ratio (2:3). The wood shrinks considerably during seasoning. Wood resistance to endwise compression and static bending is about half that of the best quality spruce (*Picea*) which has a density four or five times greater than *O. pyramidale*. There are woods lighter than

O. pyramidale but they lack its strength (Record and Hess 1949). The wood is stable in use, and changes in atmospheric conditions cause only minor shrinkage or swelling (Longwood 1971). Natural durability is low; the timber is susceptible to termite and fungal attacks. It decays very quickly in contact with the ground and is subject to sapstain if not rapidly dried. The wood is so difficult to air-season that kiln drying is recommended (Longwood 1971). Even this method can produce splitting, warping, casehardening, and a tendency to toast the wood (Longwood 1971). Seasoned wood absorbs water easily if submerged, but this can be prevented with treatments. The heartwood is resistant to preservation but a limited amount of preservative can be injected into it.

Ochroma pyramidale has a good reputation and is the lightest commercial wood in use for different purposes (Longwood 1971). According to Longwood (1971), the wood is used in heat insulation (packing cases for perishable foods, cold storage rooms, aircraft cabins, roof insulation, railway storage cars, refrigerators, water coolers, lining of pith helmets, and packing for armor plate in battleships); buoyancy (rafts, lifebelts, floats for fishing nets and mines, water sports equipment, buoys, and hydroplane floats); sound and vibration insulation (lining for telephone booths, broadcast studios, aircraft, phonograph booths, and subflooring and pads for heavy machinery and other equipment with moving parts); lightness (aircraft streamlining, model airplanes, toys, display models, surgical splints, and theatrical and film sets and accessories); and resilience (protective packing for glass, ceramics, delicate instruments, and furniture). The silky trichomes of the fruit are used to make pillows, mattresses, and cushions; the inner bark provides excellent fibers and the outer bark contains tannins (Record and Hess 1949).

Blooming occurs from December to March. Inflorescences are axillary with a single flower and grouped toward the branch terminal end. The softly scented flowers are hermaphrodite, actinomorphic, pedicellate, pubescent, and three-bracteolate; bracteoles are deciduous. The calyx is infundibuliform, coriaceous, red or purpuraceous, with five imbricate lobules. The corolla has five white petals and is reddish in the margin. It is obovate-spatulate, wide, fleshy, and basally adnate to the staminal column. The androecium has many stamens. The ovary is superior, sessile, and conical and has five locules. There are many ovules per locule; ovules are anatropous, bitegmic, and crassinucellate.

Fruit ripening occurs from March to June. The fruit is a capsule, subligneous, oblong-fusiform, five-angulate, 14 to 28 cm long, 2 to 3 cm in diameter, loculicidally dehiscent, and five-valvate; valves are black, glabrous outside, and densely lanate inside (Pennington and Sarukhán 1968, Whitmore and Hartshorn 1969).

Seeds are dispersed by wind. They are numerous, small, about 5 mm long, pyriform, oily, and imbedded in the pale brown trichomes of the capsule. The embryo is straight and small; cotyledons are thin, with involute margins. Seeds average 100,000 per kg. They must be removed from the mass of hairs inside the fruit. Seed behavior is orthodox.

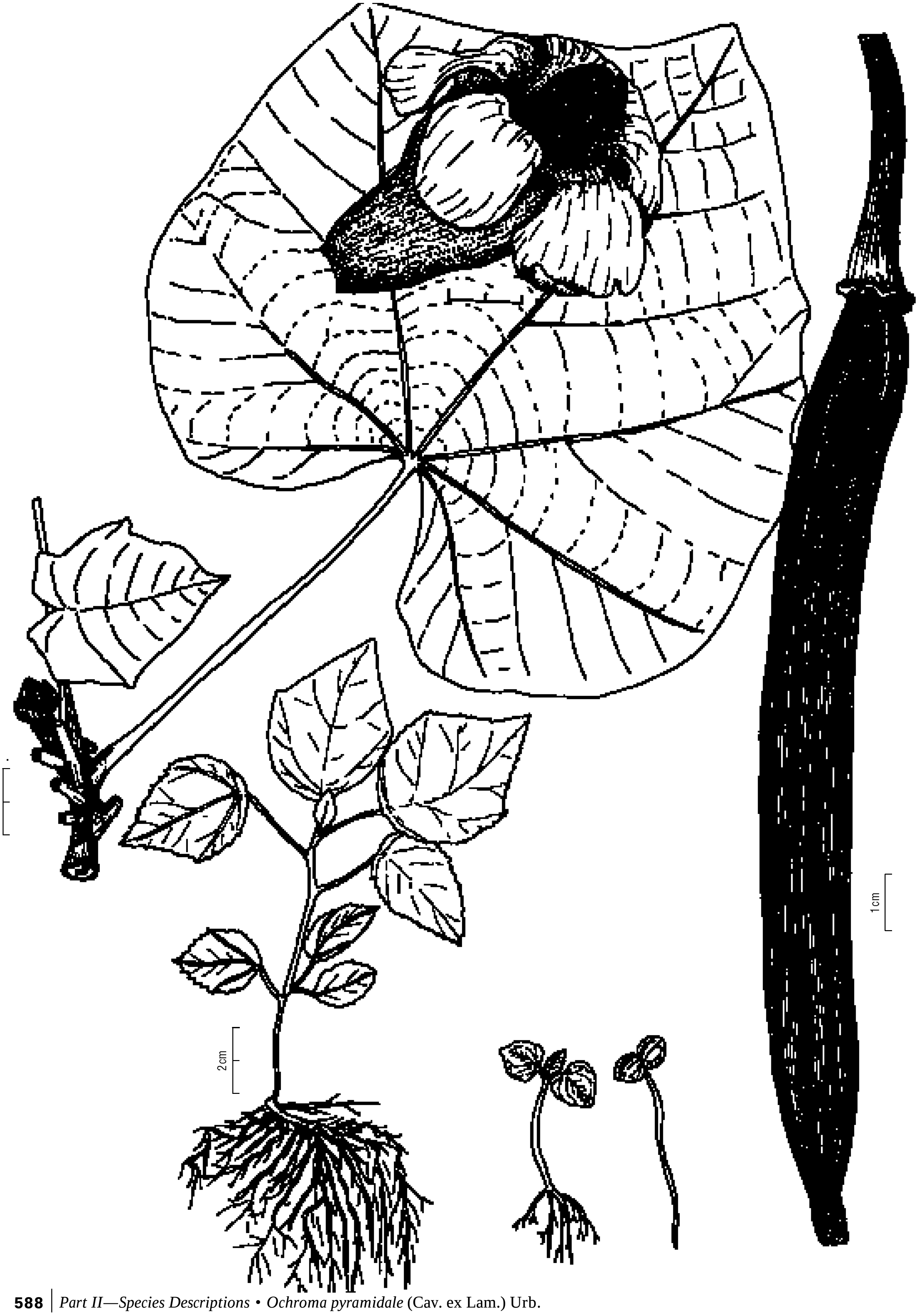
Germination is epigeal and the seedling is phanerocotylar. Seeds must be placed superficially in sand or a porous mixture of substrate and kept under direct sunlight because they are light sensitive. Proper moisture and temperature are necessary. Germination is 70 and 80 percent. Root protrusion occurs in 15 to 22 days. They should be placed in plastic bags when sown because they are very sensitive to transplanting. Until the seedlings are 6 months old, they are easily broken or injured. They are easily damaged in plantations during the first 7 years. Before the sapling reaches this age, the radical system is fibrous; after that, a taproot is developed causing problems in the wood, which changes to a red color and gradually becomes dotty. The bole above the first branch will not produce valuable logs (Record and Hess 1949). The insect *Dysdercus* sp. (F. Pyrrhocoridae) eats the buds, fruits, and seeds.

ADDITIONAL INFORMATION

The most common name applied to this species is balsa. The name means raft and was used by the Spaniards because they observed Indians using the wood to construct rafts (Longwood 1971).

Leaf blades are ovate, wide ovate, ovate-angulate, or three- to five-lobate, and chartaceous. The leaf margin is entire and undulate; the apex or the central lobe obtuse, acute, or acuminate. The leaf base is deeply cordate and sometimes truncate; the upper surface is tomentulose or glabrous; and the abaxial surface, tomentulous with tufted hairs (Pennington and Sarukhán 1968, Whitmore and Hartshorn 1969). Venation is basal actinodromous, with three to five veins diverging radially from the base and some diverging from points at higher levels; veins are prominent beneath. Petioles are long and densely covered by stellate trichomes.

Two corolla lobules are triangular and acute, and three are flabelliform. The stamen filaments form a staminal column, cylindrical, white, enlarged at the base and surrounding the style; it is shortly five-lobate; anthers are sessile, elongated and twisted in a spiral, and extrorse with longitudinal dehiscence. The gynoecium has a filiform style and a stigma slightly exceeding the staminal column; it is spiral and penta-sulcate (Pennington and Sarukhán 1968, Whitmore and Hartshorn 1969).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Ocotea austinii C.K. Allen

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LAURACEAE (LAUREL FAMILY)

Ocotea irazuensis Lundell (Wrightia 5[9]: 339/ 1977)

Bambito rosado, ira colorado, ira rosa

Ocotea austinii is endemic to Costa Rica and Panama. The geographic distribution of the species includes the central volcanic mountain range from Palmira (Alajuela) in the north, throughout the Talamanca mountain range, to the hills in the northeastern Panama (Burger 1990). *Ocotea austinii* is a canopy species, and frequently emergent. The greatest abundance of the species is found in the lower mountain, wet tropical forests characterized by *Quercus* spp. In those forests the species has a density of five to six trees per ha, with trunk diameters above 30 cm.

Ocotea austinii is a tall or medium-sized tree. It may reach 40 m in height and more than 1 m d.b.h. The bole is oval or cylindrical and the base is wide, sometimes with small buttresses. The crown is wide and dense with thick, reddish-brown branches. The bark is deep reddish brown or grayish brown under direct light and irregular in texture. The inner bark is mucilaginous, brittle, pink or reddish colored, and aromatic, with an avocado odor. It exfoliates small plates. The average bark thickness is 1.0 to 1.2 cm. Phyllotaxy is spiral. Leaves are crowded at the branches' distal end. Leaves are subcoriaceous, oblong or elliptic-oblong, abruptly narrowed at the short-acute, acuminate, or obtuse apex. The leaf base is decurrent, with revolute margins. The species grows in well-drained plateaus or flatlands of volcanic origin, with small slopes in an elevation range of 1700 to 3000 m, temperatures between 6 and 20 ° C, and an annual rainfall between 3500 and 8000 mm.

The sapwood is light red in green condition and red in dry condition. The heartwood is deep red in the external layers and pale yellowish red toward the pith. When air-dried, the heartwood takes a reddish-brown color which changes slightly to yellowish red toward the pith. Growth rings are easily seen at first glance and are defined by deeper colored boundary stripes. The wood has a straight grain, sometimes intercrossed, and a uniform, medium texture. The luster is moderate, with silvered glare. The wood does not have figure; it is odorless and tasteless. The reddish-brown wood has good aspect, durability, and moderate heft. The basic specific gravity is 0.48, with slight variations correlated with the zone of origin. In Costa Rica the average weight of green wood is 710 kg per m^3, with 73 percent moisture content; in Panama the average weight is 920 kg per m^3 (57.5 pounds per cubic foot), with 94 percent moisture content. The wood is equivalent to *Ulmus americana* L. (American elm) and *Acer nigrum* Michx. (black maple) woods in its physical and mechanical properties, with the Costa Rican wood being superior to the Panamanian in mechanical properties. The wood is good for making paper. It is easy to work, finishes well, and has a moderate drying time. Its resistance to fungal and insect attack is variable. Wood preservation is difficult. The timber is excellent for making furniture, cabinets, doors, and doorframes. It is also used in turnery, interior and external construction, carpentry, plywood, and boats and ships (Record and Hess 1949, Van der Slooten 1968).

Commonly, numerous trees bloom in February and March or August through November. Frequently, the trees flower and fruit at the same time. Flowers are grouped in axillary inflorescences, in the distal leaf axils of minor branchlets. Inflorescences are determinate, usually pseudoterminal, dibotryoid, 6 to 25 cm long, pedunculate, with peduncles 3 to 12 cm in length, and finely puberulent. Rachis, lateral branches, peduncles, and pedicels are pink or reddish colored. The flowers are actinomorphic and bisexual. They form usually four-flowered umbels at the end of the inflorescence's lateral branches. Flowers are small, densely and minutely puberulent on the outside (calyx and pedicels). The perianth has two, three-tepaloid-cupuliform whorls; tepals are imbricate, fleshy, creamy or yellowish. The hypanthium is obconic and reddish or pink. The androecium has nine functional stamens distributed in three whorls. The gynoecium is monocarpellar, monospermic, glabrous, and creamy or light green. The ovary is void and globose; the style, narrow; and the stigma, discoid. The pollination vectors are beetles (cantharophily).

Most fruits are produced from April to June. Sometimes there is a minor crop in August and September. Fruit dispersal is carried out mainly by birds, mammals (chiropterochory, dyszoochory), and gravity. Over long distances, bats are more efficient dispersers of the fruits and seeds than birds. The fruit is drupaceous. A fleshy receptacle, obconic and reddish, surrounds the fruit base. Fruits average 702 per kg. The seed is large and ovoid. The seedcoat is brown, thin, and formed by testa and tegmen in the early stages; the tegmen is destroyed and reabsorbed during seed development.

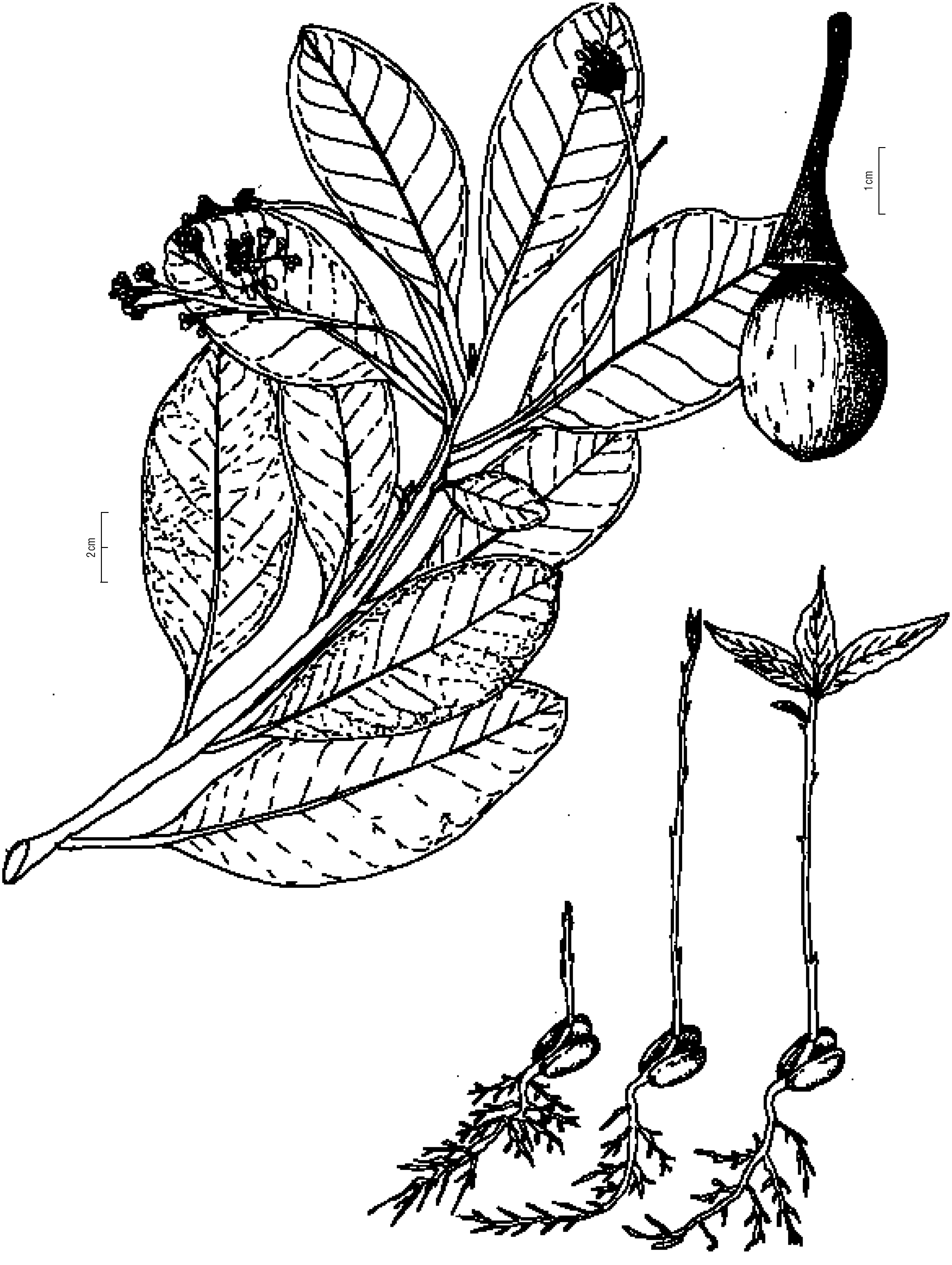
Fruits may be collected from the ground or the trees. The fleshy mesocarp must be removed before sowing the seeds. Seeds average 1,428 to 1,430 per kg. Seed water content is about 49 percent; it is mainly located in the cotyledons. Seed behavior is recalcitrant and viability diminishes with dehydration. Pregermination treatments are not required.

Germination is hypogeal, and seedlings are cryptocotylar. Under natural conditions, germination is good, but seedling mortality is high. Under greenhouse conditions, root protrusion begins 50 days after sowing. Seedlings must be transplanted when they are 4 or 5 months old. Seedling and sapling survival is satisfactory in experimental plantations if they are planted at elevations above 1700 m. The application of foliar fertilizer to 1- to 4-month-old seedlings showed good results.

ADDITIONAL INFORMATION

Ocotea species, including *O. austinii*, store aporphinoid alkaloids of complex biosynthetic origin and derived meolignans, which are structurally varied (Bradbury and others 1983, Castro 1993).

Cross-pollination is obligatory. Flowers are protogynous and the floral mechanism in the family is the synchronized dichogamy (Kubitzki and Kurz 1984). The species of the family have two types of flowering in different individuals. Some have flowers that open the female phase during the morning, closing it at noon. In the afternoon of the same day or the next day, the same flowers open the male phase, closing it at night. In other individuals the flowers open the female phase in the afternoon, closing it at night. The next morning they open the male phase. This mechanism prevents autopollination. If this rhythm is altered by climatic conditions, geitonogamy may occur but the young fruits show early abscission. A postzygotic mechanism of incompatibility has been strongly suggested.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Otoba novogranatensis Moldenke

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MYRISTICACEAE (NUTMEG FAMILY)

Dialyanthera otoba (Humb. & Bonpl.) Warb. (Berichte der Deutschen Botanischen Gesellschaft 13: 89; 1895); *Myristica otoba* Humb. & Bonpl. (Plantae Aequinoctiales 2: 78; 1808-1809); *Otoba otoba* (Humb. & Bonpl.) H. Karst. (Deutsche Flora. Pharmaceutisch-medicinische Botanik 578; 1880-1883)

Aguanillo, bogamani verde, chispiador, coco, fruta dorada, hoja dorada, miguelario, otivo, otoba, otobo, otova, roble, saba, sangre de drago, sebo, white cedar, wine wood, zapatero (García 1974)

The geographic distribution of *Otoba novogranatensis* includes the humid and very humid tropical forests of the coastal lowlands and premontane in Costa Rica, Panama, and Colombia (Gentry 1979, 1993). The species is dominant in the Colombian Amazonian forests with fertile soils. In Costa Rica and Panama, it is abundant in the primary and secondary forests of the Atlantic and Pacific lowlands.

Otoba novogranatensis is a tall tree reaching 40 m in height and more than 1 m d.b.h. (Duke 1962a, 1962b; Gentry 1993, Standley and Steyermark 1949). The bole is straight and cylindrical in the distal two-thirds. It has conspicuous buttresses, especially in swampy areas. The branches extend horizontally on a monopodial axis. The young branches are rugose, strigose, glabrescent, and pubescent. The bark is gray, blackish gray, or reddish gray (in partially shaded places), almost smooth or with vertical fissures, scaly and exfoliates in irregular plates. It is pink internally but becomes red when it comes in contact with sunlight and air. It exudes red, astringent latex. The mean thickness is 3.0 mm. Leaves are simple, entire, petiolated, exstipulated, chartaceous or subcoriaceous, and distributed in a spiral. Leaf blade is wide, elliptic or obovate, apex acuminate or cuspidate, base symmetric, attenuate; it is bright, glabrous, green adaxially, and glaucous. The species grows well in plains or slightly undulate areas, sometimes moderately sloped. It grows well in fertile alluvial soils that are well drained, moderately drained, or inundated for short periods. These inundated areas are close to creeks or rivers. The elevation ranges from sea level to 1100 m, and the temperature range is 22 to 32 °C. The annual rainfall varies from 3500 to 8000 mm.

In green condition, sapwood and heartwood are reddish with small darker stripes. The air-dried wood is intense red or reddish brown. Growth rings are not well defined. The wood grain is straight, sometimes interlocked; the texture is gross, the luster high, and the figure has silvery glare in the radial surface. The wood is tasteless and odorless. It is light or moderately light, with a basic specific gravity of 0.41, varying with tree origin. The average green weight is 740 to 750 kg per m^3, with 81 percent water content; the air-dried wood weighs 490 to 500 kg per m^3. The wood has density, volumetric contraction, and tangential/radial contraction ratio similar to those of wild nutmeg (*Virola koschnyi* Warb.), jaul (*Alnus acuminata* Kunth), and royal mahogany (*Carapa guianensis* Aubl.). The contraction ratio is unfavorable, but better than that of wild nutmeg (Llach 1971, Record and Hess 1949). Air-drying is good; the timber dries with minor fissures and twisting. It is easily worked and the surfaces obtained are smooth. The Runkel factor is 0.48 (group II: very good for making paper) and the Peteri's coefficient of flexibility is 0.61. The wood has low natural durability and is susceptible to insect attacks. Subterranean termites produce severe damage within 1 year. Chromogenous and xylophagous fungi produce rotting in several months. The timber is easily preserved and chemical penetration is uniform. The timber can be used to make boxes and crates. It is also used in carpentry, internal construction, cabinetwork, treated posts, veneers, plywood, lathed objects, and tables (Llach 1971). *Otoba novogranatensis* is used in perfume, candle, and soap manufacture and as medicine and a source of narcotics. Several South American Indian tribes use its resin in their religious ceremonies as part of an hallucinogenic snuff. The resin contains tryptaminic derivatives.

Otoba novogranatensis is dioecious. The pattern of flowering is irregular, subannual or episodic. Flowers have been found in January and February, May through October, and in

December. Both the blooming and the number of physiologically mature trees producing flowers in the different episodes vary in consecutive years. Flowers are small, actinomorphic, pedicellated, and unisexual. They are grouped in panicles or subspicate racemes. The staminate inflorescences are subspicate racemes (one to three per axil) and have variable lengths (average 10 to 12 cm; range 3 to 20 cm). They have many flowers in fascicles or pseudoverticils (subspicate distribution) in the inflorescence axis; there is a terminal pseudoverticil. Each pseudoverticil may have 9 to 15 flowers, commonly 12. Flowers are pedicellated and greenish brown. In male and female flowers the perianth is reduced to a trimerous calyx, inconspicuous, tepaloid, fleshy, yellowish green, and usually pubescent. The male flowers have an androecium with three monadelphous stamens; the filaments are fused, forming a thick column. The pistillate inflorescence has two to five flowers per fascicle, usually four. The female flower is hypogynous, and the calyx is trimerous and tepaloid. The ovary is monocarpellar and the stigma inconspicuous, bilobed, and subsessile; the style is very short and curved. Pollination is entomophilous and the pollination vectors are small coleopterans (cantharophyly, bettles). In both staminate and pistillate flowers, the floral pedicel is short (1 to 6 mm), greenish, glabrous or pubescent. An orbicular bract, precociously deciduous, subtends each fascicle. The ovules are anatropous, almost sessile, bitegmic, and crassinucellate.

The primary fruit crop occurs from December through February, but fruits can be found in other months. The fruiting periods may vary in consecutive years. There are two to four fruits per inflorescence. The fruit is monocarpellar, subglobose or ellipsoid, with a fleshy pericarp, almost glabrous. Fruits open longitudinally in two valves, along the carpellar entral and dorsal sutures. It is difficult to classify the fruit, but it may be considered a fleshy pod. Although fruits and seeds fall by gravity (barochory), most dispersal is ornithochoric and mammaliochoric. The native frugivorous avifauna are attracted by the fruit color display. The contrast between the red-orange aril, the brown-black seed, and the white inner fruit surface is striking. Streams and fish play a minor role in seed dispersal. Birds are the most important dispersers. Seeds are arillate, ellipsoid or ovoid, with acute, sharp distal ends. The aril is intense orange or red and oily with astringent flavor. Commonly, the seeds are 18 to 24 mm long and 16 to 21 mm in diameter, excluding the aril.

Seeds are collected directly from the tree or the ground. A careful seed culling to eliminate small, damaged or malformed seeds improves the percentage of germination. Fresh seeds average 575 to 580 per kg. Seed behavior is recalcitrant and under natural conditions (temperature 26 to 30 °C; environmental humidity no less than 85 percent) seeds may be stored for only a few days. During this period, the germination process continues and embryo growth does not stop. The percentage of germination is 85 percent and the seeds are viable for 10 to 12 days. They dehydrate rapidly and die when the water content drops below 30 percent.

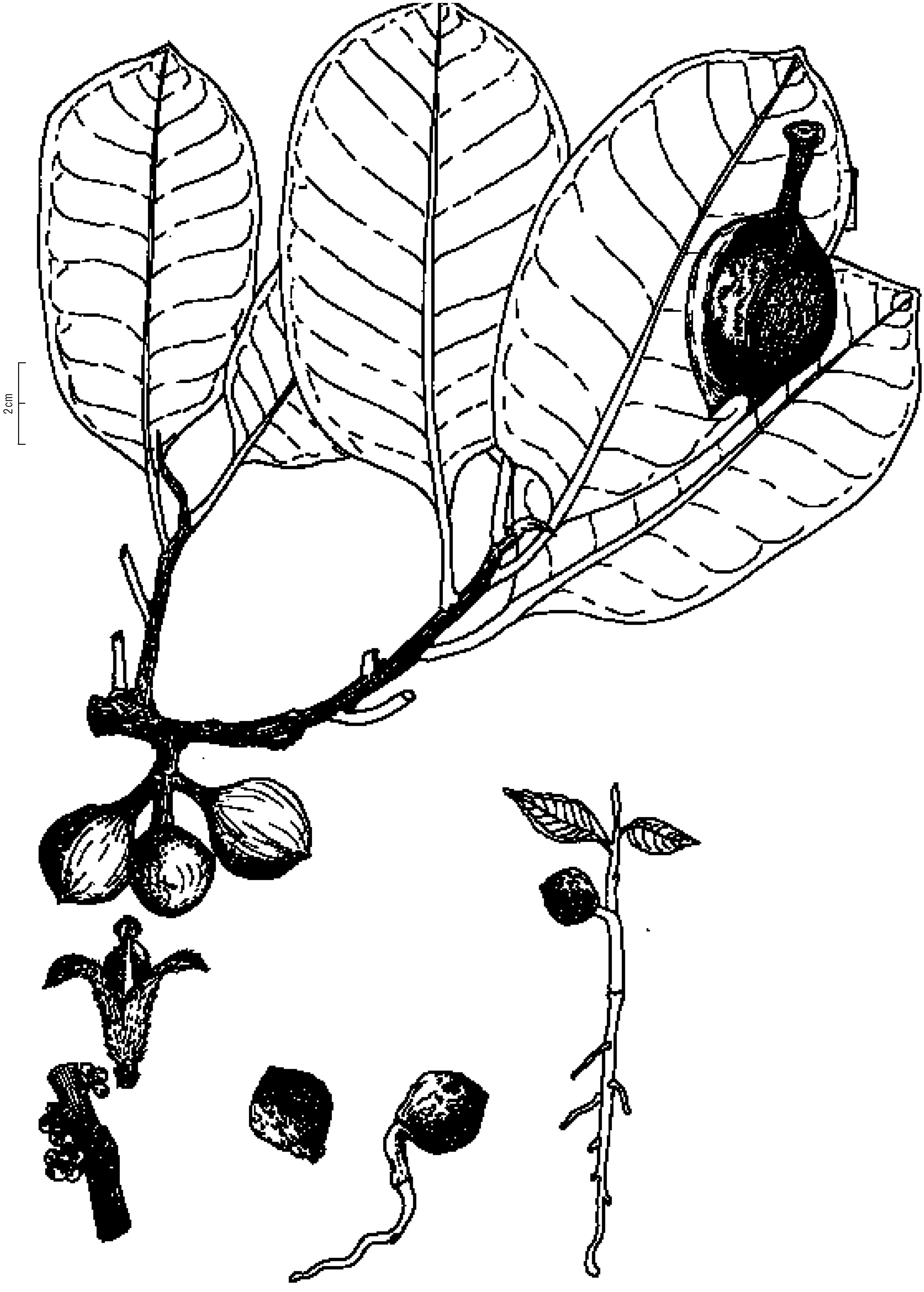
The seeds do not require pregerminative treatments and germinate well in sand beds. Germination is epigeal and the seedling is cryptocotylar. The radicle protrudes throughout the micropylar area 10 to 12 days after sowing. Under natural conditions, seedling mortality is high. In the greenhouse, *O. novogranatensis* seedlings develop faster than those of *Virola koschnyi*. Seedlings must be transferred to plastic bags before eophyll development.

The species probably can be used in monospecific or mixed plantations; it is suitable for natural forest management programs.

ADDITIONAL INFORMATION

Testa and tegmen form the seedcoat. The tegmen is thin in the mature seed and has numerous vascularized invaginations, penetrating the endosperm. The endosperm is whitish, massive, ruminated, soft, and very oily. The seed does not have perisperm. The embryo is microscopic. The haustorial cotyledons remain attached to the seedling for several months; the abscissio layer is formed in the proximal end, when the seedling is 5 to 7 months old.

Weevils (Conotrachelus, Curculionidae) attack many seeds in the ground under the tree crown; weevils also attack the *Virola* seeds. The insect larvae develop in the endosperm and damage the microscopic embryo, precluding germination.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Pachira aquatica Aubl.

J.A. OSPINA
International Center of Tropical Agriculture
Centro Internacional de Agricultura Tropical (CIAT), Colombia

BOMBACACEAE (KAPOK-TREE FAMILY)

No synonyms

Cacao de monte, castaño del chocó, ceiba, ceibón de agua, chila blanca, noli, pumpunjuche, saba, sunzapote, zapote bobo, zapote de agua, zapotolongo, zapotón (Pérez 1956)

Pachira aquatica is native to tropical America (Sánchez and others 1985).

Pachira aquatica is a small to medium-sized deciduous tree that can reach 17 m in height and 90 cm d.b.h. (Encarnación 1983). It has a thick trunk, a cylindrical shaft, and verticillate monopodial ramification in young trees that becomes sympodial in adult trees. The gray external bark is slightly cracked longitudinally with no lenticels, prickles, green areas, or rhytidome. Internal bark is up to 1.5 cm thick and creamy-white and has a heterogeneous texture laminar next to the alburnum followed by an external layer of bundles of fibers that alternate with parenchymatous zones, crossed by numerous orange-colored inclusions. At 25 years, trees are conical and average 11 m in height, 9.2 m in crown diameter. The tree possesses well-developed aletas in specimens described in Mexico (Pennington 1968). It shows digitate, alternate leaves, generally with 4 to 7 folioles of up to 22 by 6 cm, elliptic shape, and jointed petiolules of up to 15 cm in length. The tree grows well in fertile soils (Tokura and others 1996). It grows from sea level to 1300 m with average temperatures of 24 °C or higher and annual precipitation between 1000 and 2000 mm.

Pachira aquatica is used in hedges; it is an excellent ornamental species that flowers, even as a shrub. Tasting similar to European chestnuts (Pérez 1956), the toasted seeds are eaten (Tokura and others 1996). Toasted seeds can also be ground and prepared as a chocolate that tastes good but smells repulsive. The chocolate is nourishing and is used as a tonic. It also contains an edible oil. The young leaves are edible and are soaked in water to produce a liquid used for protection against poisoning and as an antidote for the bites of poisonous animals (Ophidia) (García 1992).

Trees can flower the first time at 3.5 years, and fruits can be harvested when trees are about 4 years. Flowers appear in March and April and September through December (Sanchez and others 1985). The striking, olive green flowers are up to 31 cm long, with five petals, and are exquisitely velvety; the staminal column is subdivided into numerous stamens that resemble a brush. The olive-yellow fruit is elliptic to subglobose and up to 21 by 12 cm, with five valves that have a pulpy consistency and no internal fibers. Robyns (1963) describes the fruit as having seeds wrapped in fibers (kapok). However, Cuatrecasas (1954) and Kroll and Ríos (1992) note that the interior part of the valves (including the seedcoat) has a pulpy consistency. The capsular fruit is similar to the cocoa bean (Tokura and others 1996). The 2.5 by 2 cm seeds have a subglobose shape and a dark brown color (Kroll and Ríos 1992).

The fruits are collected January through March and July through September (Sanchez and others 1985). At 8 years, the tree will yield 127 fruits; at 25 years, 250 fruits (Sanchez and others 1985). The dehiscent fruits release the seeds at maturity, and the seeds are collected directly from the ground. Seeds average 1,900 per kg.

After 25 days and with a purity of 100 percent, germination is 52 percent (Tokura and others 1996). However, precocious germination at 11 days, without pretreatments, has been reported (Sanchez and others 1985).

The seeds are germinated in nurseries and manually transplanted to bags. Plantules reach 30 to 40 cm in about 53 days and are outplanted with 7 by 7-m spacing (Sanchez and others 1985). Plantules should be outplanted in ground that has been plowed and raked. The seedlings require basic care such as adequate watering, fertile ground, and removal of overgrowth. Mature trees do not require special treatment and show good production after 25 years (Sanchez and others 1985).


2cm
1cm

Parkinsonia aculeata L.

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FABACEAE (BEAN FAMILY)

Parkinsonia thornberi M.E. Jones

Acacia, acacia de agûijote, acacia de mesones, arrete-boeuf, boonchi strena, cambrón, cina-cina, cují extranjero, espino del cairo, espino negro, flor de mayo, flor de rayo, goajiro, horsebean, Jerusalem, Jerusalem-thorn, Junco marino, lluvia de oro, madam raíz, madam yass, mataburro, palo de rayo, palo verde, paují, retama, retamola siempre-viva, sauce, sauce espino, sulfatillo, sulfato, wonder tree, yabo, yass

A native of Texas, Arizona, Mexico, and possibly elsewhere, *Parkinsonia aculeata* is widely distributed in tropical America. Once cultivated, the trees spread and naturalized throughout the Southern U.S., southern Argentina, and the Old World tropics. The species also grows throughout the West Indies, where it probably was introduced in Bermuda.

Parkinsona aculeata is a slow-growing tree that usually has a relatively short trunk. This small spiny tree reaches 3 to 6 m in height and 5 to 8 cm d.b.h. The bark is smooth and yellow-green or blue-green, and the branches and twigs are often the same color. The branches begin near the ground with a very open crown of spreading branches. The twigs have paired short spines (stipules) that may remain on the branches and trunk in groups of three or singly. The alternate leaves are twice pinnate (bipinnate), consisting of a very short main axis ending in a spine and one or two pairs of drooping axes. The axes are 10 to 30 cm long, 0.35 cm broad, flat, and slightly thickened. Each dropping strip or streamer bears 20 to 30 pairs of thin, oblong, green, deciduous leaflets and functions as a leaf after the leaflets fall. The foliage is green throughout the year, although the tree appears leafless after the leaflets fall. In Guanacaste, Costa Rica, *P. aculeata* grows in large natural stands in areas that are swampy during the rainy season and very dry during the dry season.

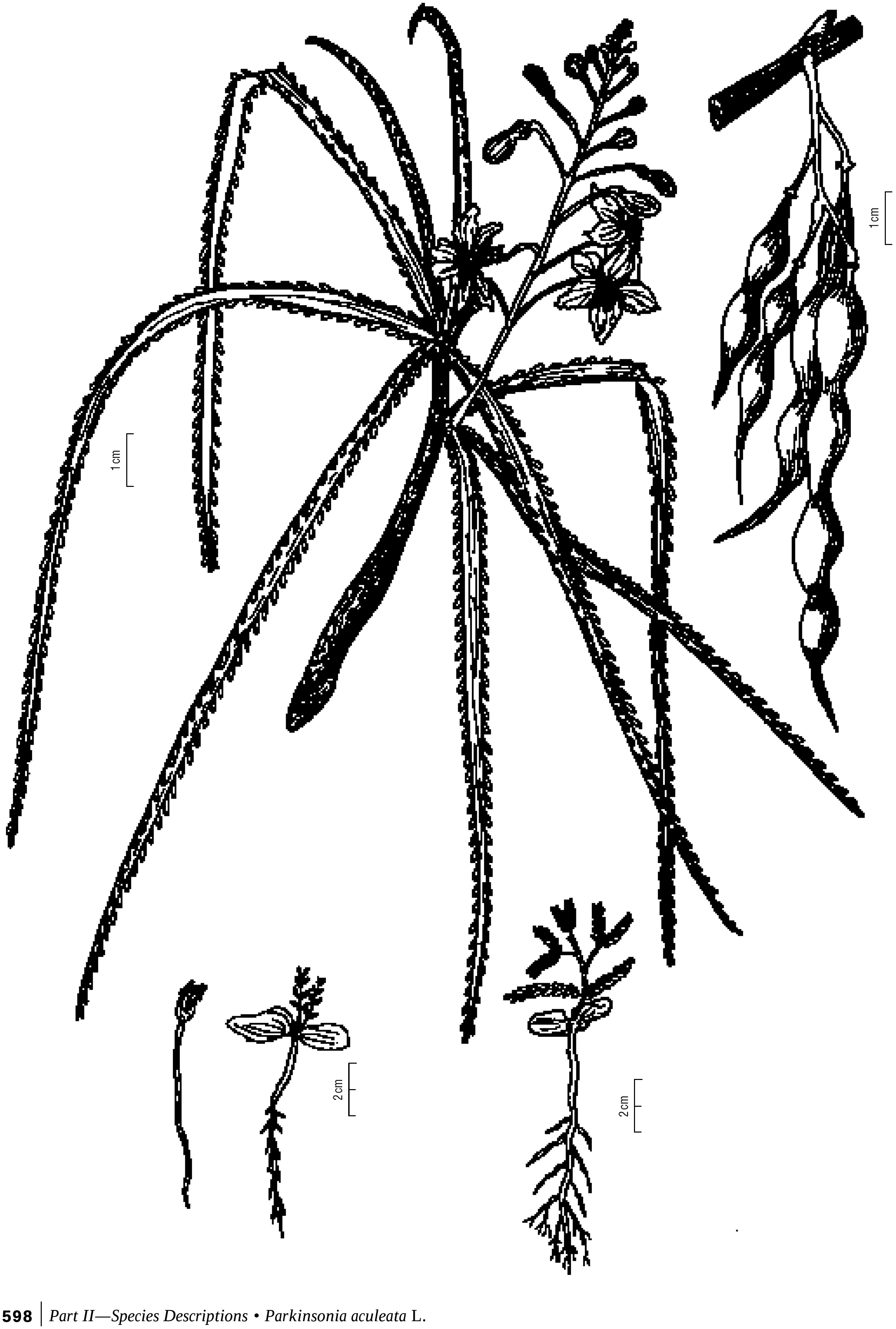
The wood is considered moderately hard, heavy (specific gravity is 0.60), and brittle and is used primarily as firewood. The sapwood of this species is yellowish and thick; the heartwood is light brown or red-brown.

The trees are also grown as spiny living hedges that function as fences, and the foliage and pods are browsed by livestock (Little and Wadsworth 1974). An infusion of the leaves is used in home medicines. Because the tree has peculiar foliage, bending branches, and attractive and abundant yellow flowers, it is also planted as an ornamental in many tropical and subtropical cities.

Parkinsonia aculeata begins to flower and fruit 5 to 6 years after planting. Many slightly beanlike, fragrant yellow flowers are borne on panicles of slender stalks throughout the year. The pods are linear, torulose, striated, dehiscent, 5 to 15 cm long, and constricted between the oblong dark brown seeds, which are 0.90 cm long.

When the pods turn dark brown, they are collected from the trees and placed on blankets in the shade until they dry enough to be opened by hand. *Parkinsona aculeata* seeds retain their viability for at least 9 years when they are stored in hermetic containers at 4 °C and 5.7 percent water content (Trujillo 1996a).

Seed germination is enhanced when the seeds are immersed in boiling water (100 °C) for 5 seconds, then transferred to tap water and soaked for 24 hours (Trujillo 1996b). Seeds are usually germinated in flat boxes filled with sterilized soil. Seedlings are transferred to nursery banks or plastic bags. The seedlings can be outplanted in about 10 to 12 months (personal observations).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1cm
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2cm

Peltogyne purpurea Pittier

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FABACEAE (BEAN FAMILY)

No synonyms

Aromo, morado, nazareno, nene, purple heart

Peltogyne purpurea grows in southern Pacific Costa Rica and in Panama.

Peltogyne purpurea is a very slow-growing, deciduous tree that reaches 35 to 40 m in height and 1 m d.b.h. The trunk is moderately buttressed, and the smooth bark is gray on the surface and pink in the inner layer. Leaves are alternative, stipulate, pinnate, and composed of a single pair of leaflets (occasionally three). The blade is elliptic-lanceolate, long acuminate, leathery, 5 to 8 cm long and 3 to 4 cm wide; the rachis has no terminal growth. The trees are briefly deciduous in late December or early January, the brown leaves being somewhat conspicuous before they fall. The new foliage appears almost immediately and the tree in this condition can be seen for many kilometers (Allen 1956). Found in very humid climates, the tree grows best in the hills or in areas with good soil drainage at elevations from 50 to 500 m. The tree grows in climates with an annual rainfall of 3500 to 5000 mm and average temperatures of 23 to 27 °C.

The wood is heavy (specific gravity is 0.83), difficult to dry, with a moderate twisting and some fissures, and difficult to work and preserve. However, it has a high durability. When dry, the sapwood is gray-yellow-brown, and the heartwood is a brilliant purple when exposed to light (Carpio 1992). The grains are intercrossed; texture is medium to fine; and dark-color strips alternate on radian surfaces. The wood is used for agricultural tools, boats, general carpentry, interior and exterior construction, railway foundations, furniture, cabinetwork, paneling, inlays, flooring, dock fenders, veneer, and ornamental plates (Allen 1956, Carpio 1992). Some of the doors in the National Museum of Costa Rica are made of this fine wood.

Peltogyne purpurea produces small, white, fragrant flowers in subterminal panicles several times from early August through September; each crop of flowers lasts 3 days (Allen 1956). The fruit is a brown, flat, obliquely obovoid-oblong one-seeded pod about 5 cm long that matures in great abundance in early February. Vilchez (1997) studied the phenology of this species in an exploited forest of Peninsula de Osa, Costa Rica, in one of the regions where the tree is relatively abundant. He found that leaf flushing occurs primarily in March and April, after a period of intensive leaf fall (January and February). The tree flowers from May through August, with a peak in June. Mature fruits were observed from November throughout January.

Peltogyne purpurea, one of the most valuable timber trees in southern Costa Rica, is not artificially regenerated. Because timber is harvested only in primary forests, information about nursery practices and seedling care is nonexistent (Nichols and González 1991a, 1991b).


1cm

Pentaclethra macroloba (Willd.) Kuntze

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FABACEAE (BEAN FAMILY)

Acacia macroloba Willd. (Species Plantarum. Editio quarta 4[2]: 1054; 1806); *Mimosa macroloba* (Willd.) Poir. (Encyclopedie Methodique. Botanique...Supplement 2 [1]: 66; 1811); *Acacia aspidioides* G. Meyer (Primitiae Florae Essequeboensis...165; 1818); *Pentaclethra filamentosa* Benth. (Journal of Botany; second series of the Botanical Miscellany 2 [11]: 127-128; 1840); *Pentaclethra brevipila* Benth. (Journal of Botany; second series of the Botanical Miscellany 2 [11]: 128; 1840); *Cailliea macrostachya* Steud. (Flora 26: 759; 1843); *Entada werbaeana* J. Presl. (Epimeliae Botanicae 206; 1849)

Bois mulatre, carbonero, fine-leaf, gavilán, koeroebahara, koeroeballi, koorooballi, koroballi, kroebara, mulato, oil bean tree, palo de aceite, palo mulato, paracachy, paraná-cachy, paroa-caxy, pracaxy, quebracho, sangredo, sangredo falso trysil, wild tamarind (Flores 1994f, Record and Hess 1949, Standley 1937)

Pentaclethra macroloba grows naturally from Nicaragua to the Amazon, including the Guianas and the West Indies (Brako and Zarucchi 1993, Ducke 1949, Schery 1950). It is abundant in coastal lowlands with moderate slope. *Pentaclethra macroloba* is formed by three neotropical disjunctive populations (Hartshorn 1983b). The largest is found in the Amazon lowlands of the Atlantic coast from northeast Venezuela to the Guianas and includes Trinidad and Tobago islands. A second population inhabits western Colombia (Departamento de Chocó) and the humid lowlands of Darien Province, Panama. The last group is located in the Atlantic lowlands of southeast Nicaragua, Costa Rica, and western Panama (Hartshorn 1983b). In the forest, the species grows associated with *Carapa guianensis* (subdominant in the canopy), *Pterocarpus officinalis* Jacq., *Stryphnodendron microstachyum* Poepp., and the palms *Astrocaryum alatum* H.F. Loomis and *Iriartea gigantea* H. Wendland ex Burret (Flores 1994, Hartshorn 1983).

Pentaclethra macroloba is a beautiful, fast-growing, emergent tree, which is dominant in the canopy of the humid tropical forests. It reaches 30 to 35 m in height and 130 cm d.b.h. The bole is cylindrical and grooved at the base; in seasonally flooded places, the tree develops small buttresses. Trees with a bole above 70 cm d.b.h. usually have hollow piths. Branches are rough and strong, and the foliage is feathered. Young shoots are ferruginous (Flores 1994f, Schery 1950). The bark is smooth and grayish brown, with horizontal lenticels. Internally, it is granular and pinkish. Its average thickness is 2 to 3 mm. The phyllotaxis is spiral. The leaves are long, shiny, biparipinnate, stipulate, with a small structure at the distal end. Species density in the forest is close to 50 percent, but decreases with sloping; it is common near rivers, creeks, and seasonally flooded zones. The species grows well in alluvial or residual soils derived from basalts. It is also found in swampy or poorly drained areas with acid soils. In some zones, the tree grows on volcanic rocks covered by a thin layer of volcanic soil. The elevation range of the species varies from 0 to 600 m; the temperature range is 24 to 35 °C, and the average annual rainfall is more than 3500 mm.

Most cambial activity and wood production in the tree occurs in the dry season (December through April) when no flowers are produced (Hazlett 1987). Annual rings are outlined by dark fibrous zones. Heartwood and sapwood are remarkably different. Green sapwood is whitish while heartwood is reddish brown. Air-dried wood has pink sapwood and reddish brown heartwood. The wood has straight or interlocked grain, medium texture, moderate luster, and lacks figure; however, it has an attractive appearance. The wood has high quality; it is heavy (green weight 1090 to 1230 kg per m^3 with 120 to 124 percent moisture content; basic specific gravity is 0.51 to 0.65). Volumetric contraction is moderate, and the tangential contraction:radial contraction ratio is normal. The wood corresponds to the structural type B (Herrera and Morales 1993, Record and Hess 1949). Moisture content is 12 percent. Static flexion is medium; parallel compression of fibers is low; perpendicular compression is medium. Shearing is medium, and Janka hardness (lateral and end strength) is almost medium. It is easy to saw and polishes well. Air-drying is easy and moderately fast (Herrera and Morales 1993). The heaviest wood corresponds to individuals from the extant population in the Atlantic lowlands of Nicaragua, Costa Rica, and Panama. In the Atlantic lowlands of Costa Rica, a subtype has been found: trees are taller, the bole does not bear branches in the basal third, the wood is darker, and wood quality is higher. The natural durability of the wood is moderate and preservation is easy. It resists the attack of subterranean termites from 6 to 7 years, but decays later. It is susceptible to fungal attack at or below ground level 1 year after cutting. Above the ground, rotting occurs 2 years later (Bultman and Southwell 1976).

It is a pretty timber with multiple uses. Several years ago, the Central American countries exported large amounts of this wood to Cuba and other countries where it was used to make telephone poles. The wood is currently used as a substitute for mahogany (*Swietenia macrophylla*); crabwood, empire andiroba or royal mahogany (*Carapa guianensis*); and anaconda or geiger tree (*Cordia alliodora* [Ruiz & Pav.] Oken) to make furniture, cabinets, doors, and window frames. It is also used to make pillars, beams, floors, stairway steps, railroad ties, lathed shapes, and parquet. In rural communities, the wood is used for bridge decking. The bark is a potential source of tannins for fur tanning use. The alkaloid paucine found in bark and seed should be studied to verify the toxicity and medicinal properties ascribed to it by South and Central American Indian groups (Allen and Allen 1981, Flores 1994f). Branches or trunks inadequate for industrial use have been used as firewood (Flores 1994f, Record and Hess 1949).

Pentaclethra macroloba may begin flowering and fruiting at 1 to 2 years. The species blooms primarily from April through May and July and August, although flowers are observed during the entire rainy season. The racemes have numerous flowers (about 200 flowers per raceme), but few fruits develop (Flores 1994f). Flowers are bisexual and monomorphic. They are clustered in dense racemes with a fleshy, spadiciform rachis. Inflorescences are 2 to 4 cm long. Flower maturation is mostly acropetal. The flower is small, sessile, pentamerous, and somewhat coriaceous. The species is cross-pollinated and several small insects are the probable pollinators. One to five flowers per inflorescence set a fruit. The main fruit crop appears in August and September; a minor crop appears in November and December; however, some fruits can be observed in other months.

The fruit is a dehiscent pod, pedicellated, linear, laterally compressed, obtuse at the apex, woody, 20 to 50 cm long, 4 to 6 cm wide, and 1 to 3 cm thick. The exocarp is thin, dull, dark brown, glabrous, and moderately exfoliating; the mesocarp is thick, fibrous, woody, and well vascularized by branches of the dorsal and ventral veins. The endocarp is slightly septate, dull, and light reddish brown. The pedicel is thick, woody, and 1 to 3 cm long. The pod has three to eight seeds. Pod dehiscence is explosive and seed dispersal is autochoric; it begins at the distal end and progresses basipetally along the ventral and dorsal sutures. As the valves move backward, the seeds are expelled 30 to 40 m away (Flores 1994f, Flores and Rivera 1989b).

The seed is ovate or obovate, and laterally compressed; faces are asymmetrical. The seedcoat is brown, dull coriaceous, and unitegmic; the tegmen is absent. The seed is classified as overgrown (Corner 1951) because its growth is limited by pod size. Seeds average 280 to 300 seeds per kg. The seeds contain a high lipid content with industrial potential. The fresh seeds have about 42 to 45 percent moisture content. Seed behavior is recalcitrant. Seeds do not tolerate dessication or drastic temperature fluctuations. They may be stored 4 to 6 days under ambient temperature (24 to 30 °C) and environmental moisture (above 90 percent air moisture).

Germination averages 90 percent, and it can be increased if damaged or faded seeds are discarded. Germination is hypogeal and seedlings are cryptocotylar (partially). Radicle protrusion takes place 8 to 10 days after sowing. Frequently, 10 to 11 insect larvae emerge through small holes on the adaxial surface of the cotyledons, which diminishes seed vigor. If the plumule is damaged, shoot development does not occur (Flores 1994f).

Seeds may be sown in greenhouse beds or plastic bags. Sowing must be superficial, with seeds in a vertical position and the acute end placed within the substrate. They must not be buried. They germinate well under different light regimes and are shade tolerant. Seedlings growing in the forest understory may be successfully transplanted to germination beds, plastic bags, or open areas in the field (Flores 1994f).

The species has been sporadically planted in experimental plots. A planting distance of 3 by 3 m has been used. Sapling growth and survival have not been carefully evaluated. In the forest, the seeds germinate well. The seedlings, saplings, and juveniles of all ages survive under the canopy, but their growth is slow especially during the first 2 years. Insect predation is intense. The species is a pioneer in the regeneration of disturbed areas; under natural regeneration it forms monospecific stands. Three factors may explain its colonizing capacity: nitrogen-fixing by root nodules (Allen and Allen 1981), precocious sexuality, and a series of accessory buds able to replace the damaged main shoot (Flores 1994f). The species appears suitable for natural regeneration and natural forest management.

ADDITIONAL INFORMATION

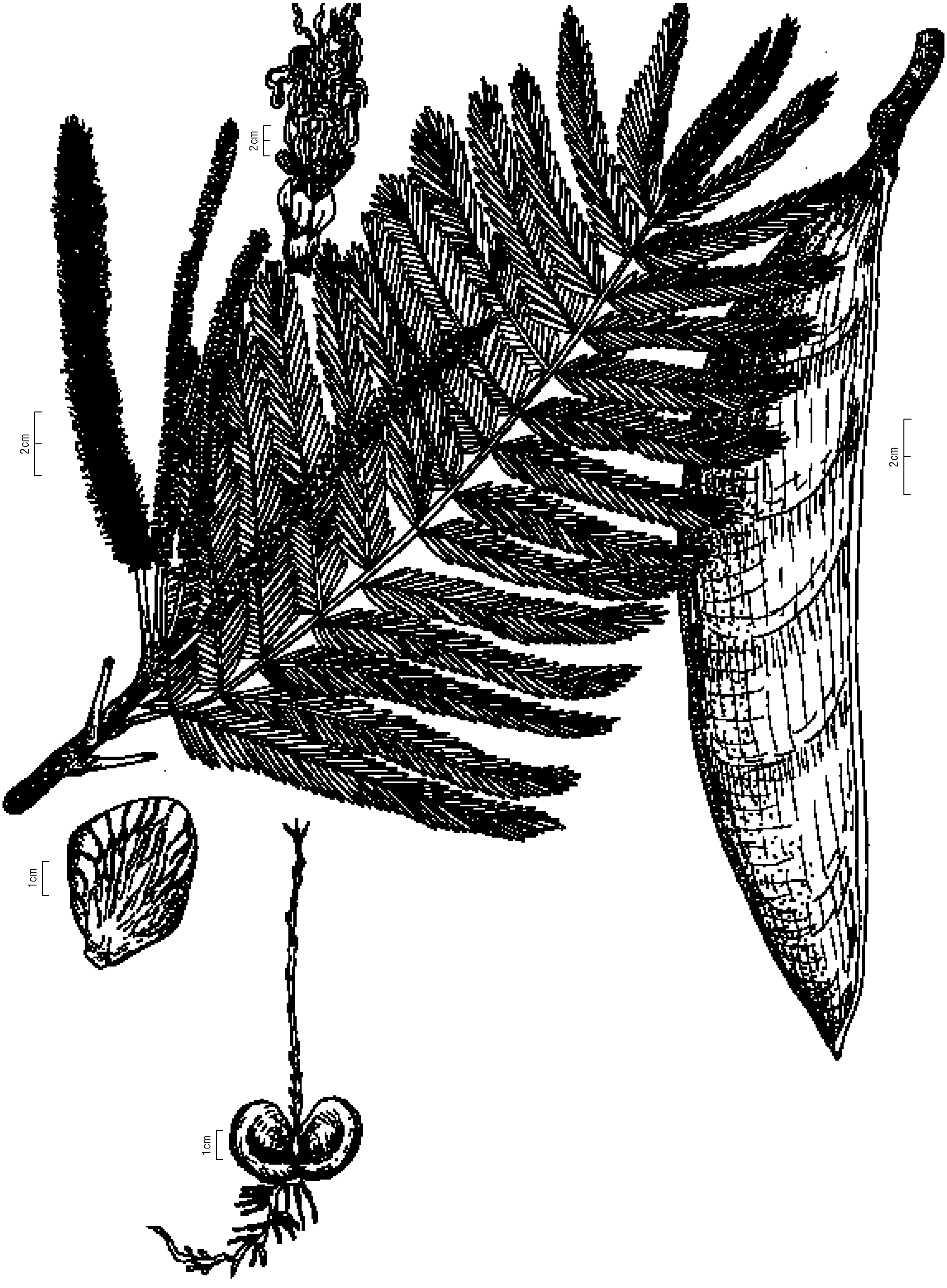
The genus name derives from the Greek roots *pente* (five) and *kleithron* (bolt). It refers to the valvate aestivation of the calyx lobes and to the petal concrescence at the basal third. The species name refers to the large and thick calyx lobes (Allen and Allen 1981, Flores 1994f).

The leaf's petiole is 1 to 7 cm long, pulvinated, semiterete, and adaxially sulcate. The leaf blade has 15 to 20 pairs of opposite pinnae, pulvinulated, and 2 to 10 cm long. The rachis may reach a length of 30 cm; it is pubescent and adaxially channeled. The numerous foliolules per pinna are opposite, semisessile, small, linear-subfalcate, 6 to 9 mm long, and 1 to 2 mm wide. Foliolules are entire with asymmetrical semilimbs and have pubescent margin, acute-acuminate apex, and an asymmetrical base that is oblique, round, truncate, or auriculated. The pinnules are hypostomatic, and the stomata are paracytic (Flores 1994f).

The calyx is cupuliform and purple, and the calyx lobes are pubescent, thick, broad, round distally, with imbricate aestivation, and 1 to 2 mm long. Petals are elliptic, 4 to 5 mm long, coherent at the basal third, pubescent, valvate, and purple but distally greenish. The stamens alternate with the sepals and five white staminodia; stamens are extrorse, white or yellowish, and basally fused to the staminodia. Filaments are filiform and 5 to 7 mm long; the anthers are 1 mm long and whitish, with a prominent distal gland. Anther dehiscence is longitudinal. Pollen grains are liberated in monads; they are triporate (with a diameter of 40 to 45 µm), exine smooth and without reticulum (Guinet 1978). The gynoecium has a conspicuous single style longer than the stamens; the stigma is wide and truncate. The ovary is subsessile, pubescent, free, and monocarpellar, with laminar placentation. It has several bitegmic anatropous ovules. The funiculus is short (2 to 3 mm long), thick, and restrained near the placenta (Flores 1994f).

The seeds lack endosperm and perisperm. The embryo is overgrown. The cotyledons are fleshy, thick, parenchymatic, oily, and slightly concave adaxially; they keep the asymmetry shown externally by the seed. The embryo axis is straight; the reddish plumule is well developed and bears several leaf primordia (Flores 1994f, Flores and Rivera 1989b). The auriculate base of the cotyledons encloses the small radicle.

The hypocotyl is vestigial. Plumule development is fast and may reach a length of 25 to 35 cm in 45 days (Flores 1994f). The seedling produces a spiral of 14 to 17 scales before it gives rise to the first biparipinnate leaf. The axil of each scale has two accessory buds in a descending series. The distal scale as well as the subsequent biparipinnate leaves have a series of three accessory buds. The series of accessory buds enhances the survival of seedlings and saplings (Flores 1994f).


2cm
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2cm
1cm
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Persea americana Mill.

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International Center of Tropical Agriculture
Centro Internacional de Agricultura Tropical (CIAT), Colombia

LAURACEAE (LAUREL FAMILY)

Laurus indica Siebmann, *Persea gratissima* Gaerthner, *P. praecox* Poep. (Pérez 1956)

Aguacate, aguacatillo, alligator, curo, palto, pear (Pérez 1956)

Persea americana originated in the Americas and grows from Chile to Mexico and in the Caribbean Islands. Although concentrated in the Latin American countries, the tree is now cultivated in the Philippines, New Zealand, Australia, South Africa, Kenya, the Ivory Coast, Morocco, Israel, the Canary Islands, and Spain.

Persea americana is a plant of periodic growth where growth rates are affected by local conditions. In areas of constant humidity, *P. americana* grows all year. In drier or cold regions, the tree can go through four annual growth stages and during certain periods can lose a lot of foliage; the main stage usually coincides with flowering. The new growth of shoots or sprigs occurs only on certain parts of the tree. In years with greater growth, the fruit harvest will be reduced; and in several cultivars the yield is markedly biennial. The shoots or sprigs are cylindrical or prismatic and have alternative leaves which have axillary buds. The shape of the leaves varies considerably depending on the position. Wild species can reach 20 m in height. It grows well in soils that are loose, well-drained, slightly acid, and rich in organic matter (Tokura and others 1996). The tree grows at elevations from sea level to 2400 m, with average temperatures of 16 to 24 °C and annual precipitation of 800 to 1700 mm. Wild trees have a spherical crown, while cultivated trees, originating from grafts and subjected to pruning, have a very different appearance.

Persea americana is a very polymorphous species. Certain clonal traits, such as the shape and color of the foliage, contribute to creating a very extensive range of types, and cultivated types can be separated into three groups or races: Mexican, Guatemalan, and West Indian (León 1987). Additional information about these races is presented in the last section of this description.

Persea americana is commercially important as a fruit species. The fruit has very high nutritional qualities; its caloric index is similar to that of the banana. It contains between 5 and 35 percent fat, fundamentally oleic acid, with an index similar to that of the olive. The digestibility coefficient of the fat is similar to that of the fat of cows. The seed has a high content of tannins, and the cortex has vermifuge properties (Gózman 1989).

The flowers emerge in panicles that sprout from the new growth on the apex of the sprigs or from the axil of the leaves. The axis of the panicle is strong and pubescent and carries several deciduous bracts. *Persea americana* yields many thousands of flowers per plant. The panicles open up for long periods of weeks or months. However, the number of flowers that yield fruit is 5 percent or more. The characteristics of the fruit are very changeable, depending on the race and the variety. Pear-shaped fruits predominate, but spherical and ovoid fruits also exist. They are usually asymmetrical, and the side with more fibers or vascular bundles is thicker. The pericarp is made up of a cortex whose thickness and color vary from yellowish green to purple or almost black; the surface varies from smooth and shiny to corrugated and opaque. The mesocarp is a pulpy, soft mass, yellowish-greenish-white in color, with green pigmentation close to the cortex. The ovoid seed occupies a large part of the fruit; it is made up of two pulpy cotyledons and a small embryo; it contains no endosperm. The coat is made up of one to five exterior layers of sclerenchyma and several layers of parenchyma. The outermost layer of parenchyma, next to the sclerenchyma, is stuffed with tannins, which give it the characteristic dark color. The cotyledons consist primarily of parenchyma containing starch and tannins (León 1987).

The time between flowering and harvesting of fruits depends on the race: for the West Indian race it is between 5 and 6 months, for the Guatemalan race between 8 and 10 months, and for the Mexican race between 7 and 10 months

(Gózman 1989). The fruits are collected manually using ladders and scissors or knives. Pulling the fruit off can injure and damage it. Because the fruits are delicate, they should not be put on the ground without protection. The stem should be cut close to the fruit to prevent damage to other fruits when packed. Fruits harvested early should be placed in the dark and refrigerated.

The humidity content in seeds with harvest ripeness is approximately 65 percent. The seeds are recalcitrant and lose their viability 2 to 3 weeks after removal from the fruit. However, the fruits can be stored for periods of more than 8 months in a dry room at 5 °C (Halma and Frolich 1949, Spalding and others 1976). Viability can also be maintained for several months by covering the seeds with a powdered fungicide and storing them in wet sawdust or peat in polyethylene bags at 4 to 5 °C (Verheij and Coronel 1991). The critical humidity content (the point to which one can lower the humidity of the seed without losing its viability) is 57.6 percent for slow drying and 57.4 percent for fast drying (Boyce 1989, Grabe 1989).

The seeds should be pretreated by immersion in water at room temperature for 24 hours (Trujillo 1986). About 70 percent of the seeds germinate underground in an average of 21 days (Tokura and others 1996).

Persea americana may be propagated by seedling or grafting. Grafting is recommended for commercial plantings because the fruits of grafted trees have uniform characteristics in size and shape. The terminal bud graft is the easiest and most successful. To produce healthy and vigorous trees, seeds should be selected from good-sized fruits. These seeds should have a higher coefficient of germination and the subsequent seedlings should grow faster. To prevent dehydration, seeds should be planted immediately after extraction from the fruits. Seeds may be preserved in wooden trays with humid sand between 5 and 7 °C. To prevent disease, seeds should be disinfected in hot water (49 °C for 15 minutes); the ground should be treated with water vapor (90 °C for 4 hours or 60 °C for 6 hours); and all tools should be treated, possibly with sodium hypochlorite (Gózman 1989). *Persea americana* is frequently cultivated on hillsides because minimum temperatures are higher than those on flat ground (Gustafson 1997).

ADDITIONAL INFORMATION

Leaves in the upper part, centered around the apical point of the growth, have bracteal shapes. Farther down the sprig, the internodes are longer and the leaves are more developed. The elongation of a *P. americana* shoot begins after a rest period. The bracts that cover the apex of the growth come loose and the shoot lengthens by first forming leaves in the shape of a bract, separated by short internodes, then forming normal leaves and longer internodes, and finally forming small leaves and shorter internodes. In the axils of the basal leaves, lateral buds can develop. On these, the first internode is excessively long. The shape, color, and pubescence of the leaves vary according to the cultivar. The lamina is ovate-oblong to obovate-oblong, from 5 to 20 cm long by 3 to 12 cm wide; the pubescence changes according to the age of the leaf. The foliage and the new sprigs are densely pubescent; the old leaves are smooth and shiny on the top and pubescent underneath. Leaf color varies by race from dark to green-yellow. The species has a powerful root system that lacks absorbing hairs.

The flowers are hermaphroditic, actinomorphic, greenish-whitish, with short and pubescent pedicels. The perianth is made up of one involucrum, which has interpreted itself as a calyx consisting of six parts that are acute, yellow, pubescent on both surfaces, and arranged in two groups of three. The exterior parts are the largest. It is in fact three sepals and three petals of very similar appearance. There are 12 stamens in four cycles; the first two are external and simple filaments whose anthers open up through four pores located toward the center of the flower. The third cycle consists of three stamens with the pores opened outward; its filaments have, at the base, an orange gland or nectary. The fourth cycle, the innermost one, is made up of staminodia. The pistil is made up of an ovoid, monocarpic, superior, monospermic, unilocular, white, and pubescent ovary, which ends in a short style with a globose stigma.

Low fruit yield occurs because the stigmatia receive a few grains of fecundating pollen when the stamens and the pistils in each flower do not mature uniformly. Cross pollination is essential to reproduction.

Persea americana is a perennial that can produce fruit for 18 to 25 years when it is managed well. The life cycle of the species is divided into four periods. During the period of youth, usually 18 to 24 months, the seedling remains in the nursery. When outplanted, *P. americana* enters the period when growth is accelerated and flowers begin to appear. Between the fourth and fifth year, the plant reaches the full yield period, characterized by high flowering and fruit yield. In the fourth and final period, the fruit yield stabilizes and plantation managers must work to prevent mortality by diseases such as *Phytophthora cinnamoni* Rand (Gózman 1989).

The fruits remain hard on the tree and soften only after collection. Mature fruits soften uniformly while immature fruits shrink, wrinkle, and do not soften properly. Different varieties mature at different rates. Oil content is used to determine fruit maturity for Mexican and Guatemalan varieties; size and weight are used for West Indian varieties. Sometimes the fruit's appearance while on the tree represents the degree of maturity. For the varieties with green skin, a yellow color in the skin and stem and loss of shine indicate maturity. The condition of the seed cover is another useful guide for determining the grade of maturity. If the seed cover is tender and light brown in color, the fruit is mature. To determine when the fruit is soft enough to eat, the button of the stem can be removed and a stick inserted in the opening. If the pulp is soft, the fruit is ready to eat. This test is especially useful for determining the softness of varieties with hard and leathery skin (Gustafson 1997).

The three cultivated races of *P. americana* are West Indian, Guatemalan, and Mexican. The West Indian race is native to Central America and grows at elevations between 0 and 550 m. It is widespread from Florida to Brazil. The race is very sensitive to cold. When the leaves are rubbed, they do not give off an anise smell. The fruits ripen 5 to 6 months after flowering. They are dark green, vary in size according to variety, have an oval shape, weigh from 150 g to 1 kg, and measure between 8 and 30 cm in length. The penduncle is short and conical. The skin is thin but strong, with a thickness of 1.5 to 2 mm, and the surface is shiny and viscous. The pulp varies from soft green to reddish yellow in color and has a fatty content of approximately 5 to 16 percent. Because the seed comes loose from the pulp when the fruit ripens, consumption must occur shortly after harvest.

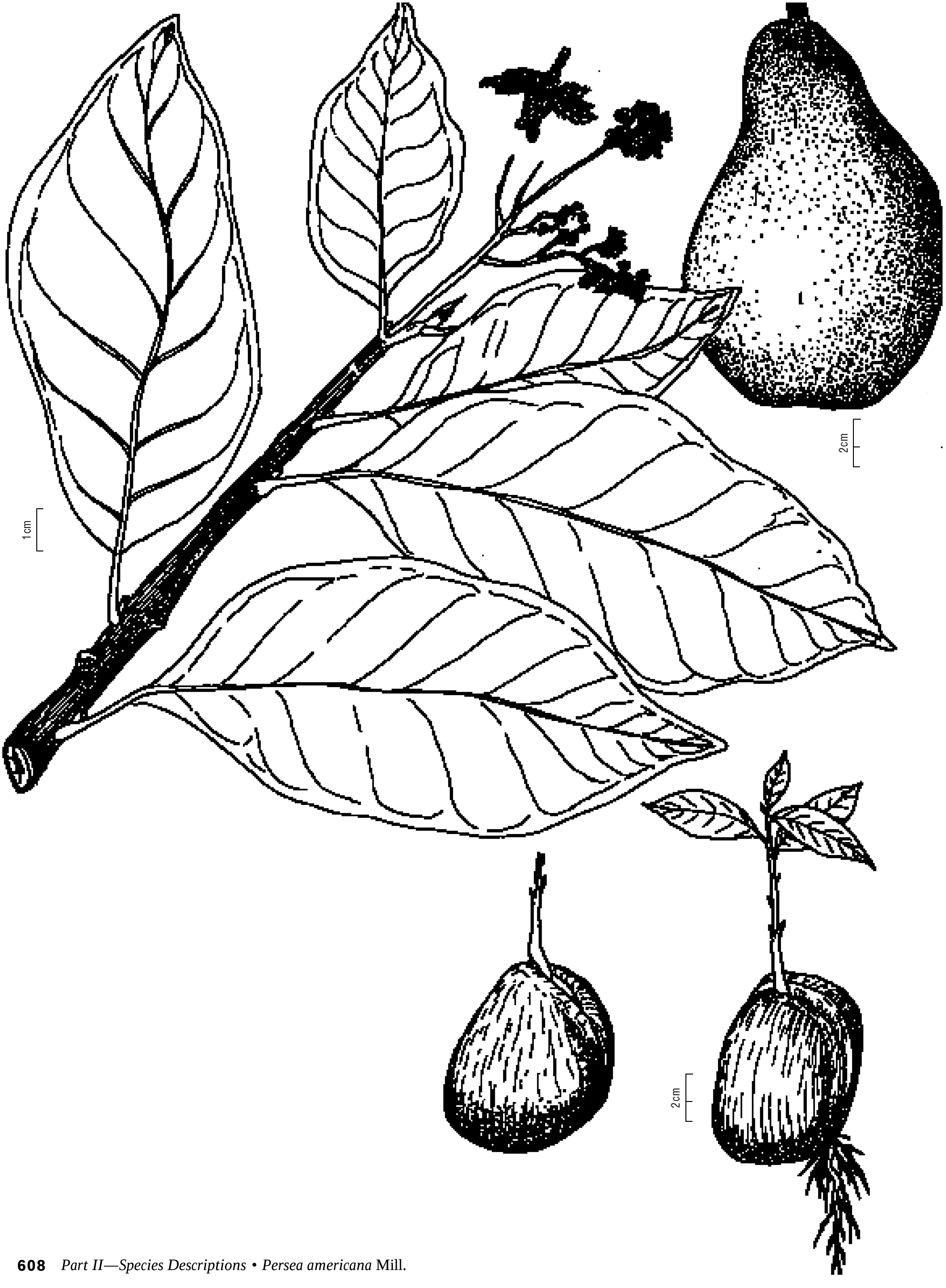
The most important commercial varieties of the West Indian race include the Pollock, the Walden, and the Fuchsia. The Pollock is the most cultivated variety in Venezuela. It was developed in the United States (Florida) with seeds from Cuba. The fruit can be harvested 5 to 6 months after flowering. The variety produces pear-shaped fruits with a smooth, thin peel. The fruit weighs between 858 and 1400 g, has a yellowish pulp with no fibers, and has a fatty content of 2.5 to 5 percent. The seed has a conical shape. The Pollock is adaptable to harsh and temperate climates and to elevations ranging from 400 to 1300 m. The Walden variety yields medium-sized fruits with a smooth, thin, pale green peel, a yellowish pulp with a fatty content of 5 to 10 percent, and weights that range from 250 to 850 g. Plants of the Walden and Fuchsia varieties produce high yields of fruit. The Fuchsia variety has glassy-green fruits with smooth peels and weights ranging between 350 to 550 g.

The Guatemalan race of *P. americana* comes from Central America, Mexico, and Nicaragua at elevations from 500 to 1000 m. It is sensitive to temperate climates because its large, deep green leaves lack essential glands; the leaves also do not give off the anise smell when rubbed. The fruits ripen 8 to 10 months after flowering. They weigh between 100 and 130 g, are generally round, and are attached to the branch by a very long peduncle. Skin thickness varies between 3 and 10 mm; it has a viscous and ligneous consistency and ranges from green to purple to dark colors as it ripens. The pulp has an approximate fatty content of 15 to 20 percent. The seed is very large and round and does not come loose from its cavity, making it possible to preserve the fruit for a relatively long time between harvest and consumption.

Important commercial varieties of the Guatemalan race include the Chouette and the Lola. The Chouette is a hybrid obtained by crossing the West Indian and Guatemalan races; it grows well in the agroecological conditions of Venezuela at altitudes ranging between 500 and 1500 m. The plants yield oval fruits with a harsh peel and wrinkled skin. The fruit can be harvested 8 to 11 months after flowering. The Lola variety adapts well to harsh climates and yields fruit weighing between 250 and 550 g with smooth skin and a fatty content of approximately 18 to 20 percent. Other varieties in this race include the Hass, the Trap, the Hickson, and the Macarthur.

The Mexican race of *P. americana* comes from the cities of Atlixo and Puebla, at altitudes ranging from 1100 to 1950 m. It shows a pronounced resistance to temperate climates. The leaves, smaller than those of the other races, have glands that give off a strong anise smell when the leaves are rubbed. Generally, the flowering occurs during the last months of the year. The fruits ripen 7 to 8 months after flowering and are relatively small, with a weight of 200 to 250 g and a length of 40 to 90 mm. In pubescent flowers, the peduncle is thin, with a uniform diameter throughout its length. The skin is thin, 0.9 to 1.5 mm, with a smooth external surface. The normally light-green skin has dark tonalities depending on variety. The pulp is a little fibrous and has a fatty content ranging from 22 to 25 percent. Given the multiple characteristic traits of this race, many botanists consider it a different variety of *P. americana* (*Drimifolia*).

In Mexico, the Fuerte, the Puebla, and the Gottfriel are important commercial varieties of *P. americana*. The Fuerte is a hybrid of the Mexican and Guatemalan races; it produces medium-sized fruits with a fatty content of 25 to 35 percent. It adapts well to temperate climates at altitudes over 1500 m. The variety Puebla produces medium-sized fruits with an ovoidal shape, a smooth and glossy peel, and a fatty content of 18 to 20 percent. The variety Gottfriel produces pear-shaped, elongated fruits with a purple peel and a thin consistency; it grows well at elevations ranging from 500 to 1500 m.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Pinus caribaea Morelet

V.M. NIETO and J. RODRIGUEZ
Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

PINACEAE (PINE FAMILY)

No synonyms

Pino caribea, pino cubano

Pinus caribaea is a medium-growing tree that reaches 45 m in height and more than 1 m d.b.h. The shafts are generally straight and free of branches. The bark is thick with wide fissures and is reddish brown to ashy brown. This variety has fascicles of three, and in the young trees these fascicles have four to six acicular leaves. The acicular leaves are 15 to 25 cm long and 1.5 mm wide; they are stiff and finely serrated, dark green to yellowish green, and covered with white stripes of stomata. The tree has a pivot root in deep soils, and superficial roots in slightly deep soils. It adapts very well to a wide variety of environments, including degraded, poor, lixiviated, rather low soils with good drainage. The species grows well in acid sandy soils (pH 4.3 to 6.5) and, to a lesser degree, sandy-clayey soils. Generally, moisture in the soil determines development more than the availability of nutrients. The tree grows well in oxisol soils that are not very deep, are saturated with water during the rainy season, and are very dry in the rainless season. In wet climates of the Tropics the species tends to form foxtail. It can tolerate drought for up to 6 months and sporadic floods. However, drought can also cause large losses in young stands (Lamprecht 1990). *Pinus caribaea* grows well where temperatures range from 20 to 27 °C and annual precipitation is between 1000 and 1800 mm. Some trees grow where precipitation is 600 to 3900 mm. In its native region the tree grows from sea level to 850 m; it is occasionally found at 1000 m.

The hard wood of *P. caribaea* is appropriate for floors and all types of construction. Treated with a preservative, the wood is used in mines, pilings, and railroad ties. Primarily used in construction and carpentry, the wood is also dried and turned (Centro Agronómico Tropical de Investigación Enseñza 1994, SEFORVEN 1993). In Villanueva, Casanare, Colombia, wood obtained by precommercial thinning at 8 to 10 years is used in tongue and groove boards and cabinetmaking (portable crates, doors, windows, desks, and bookcases) (Koenig and Venegas 1978, Venegas 1982). It is used for pulp even though its resin content is high. It is traditionally used as firewood and in the manufacture of charcoal. The trees are used as windbreaks and to control erosion and recover soils. Resins are also extracted to produce colophony and turpentine. The seeds of this species have a high commercial value.

The cones are 6 to 14 cm long. The dark grayish seeds are ovoid and winged and sometimes have light brown speckles. Most of the seeds lose their wings. Fire is essential for natural regeneration; however, the young plantules are damaged or killed by fire. Outside its native area, the species rarely regenerates naturally.

Seeds can be stored up to 10 years if placed in hermetic containers at 3 to 4 °C and 6 to 9 percent humidity. A pregermination treatment is unnecessary; however, seeds submerged in water for 12 hours will germinate more uniformly. Germination percentage reaches 80 percent (Trujillo 1984, Wong 1983).

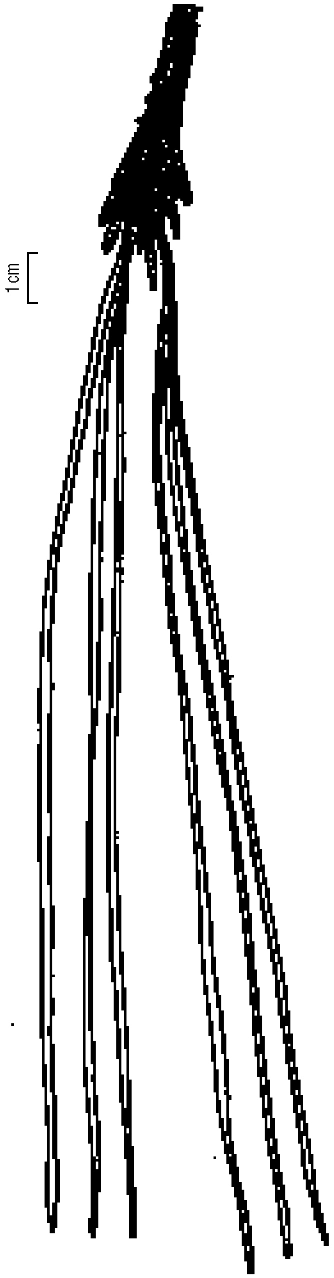
The species can be propagated in nurseries by seeds or bare roots. Seeds are sowed in germinators and transferred to bags; seeds with a high germination percentage can be planted directly in bags. Two hundred seeds are planted per m^2 to ensure that 100 plants per m^2 are produced. Seeds germinate within 17 days. One month after sowing, the soil must be removed from around the plantule. The plantules must also be fertilized with nitrogen, phosphorus, and potassium.

Mycorrhizal fungus must be applied to improve plantule development; an application of 20 g per ha of spores of the *Pisolithus tinctorius* or *Telophoroa terrestri* fungus is also recommended. Furthermore, fertilizers must be applied periodically. Roots should also be routinely pruned, and the plantules should be hardened. Plantules are outplanted when they reach 20 to 30 cm in height.

The planting site should be thoroughly cleared; burning the site produces the best results. In deep soils, holes must be 20 cm deep and 20 cm in diameter. In shallow, compacted soils, holes must be 30 cm in depth and diameter. Up to 80 percent of the roots will remain when outplanting by lifting the plantules with clods of earth on the roots.

Silvicultural treatments during the first 2 years in reforestation of savannas provide fire protection. Removal of underbrush by trampling is also essential. Reforestation of pasture prairies should occur within 6 months after formation of the prairie to inhibit competition from arboreal species and cattle. In intense plantations, Gramineae, such as *Brachiaria*, should be planted.

In the production of trees for pulp, firewood, or small posts, plantules are planted 1,600 per ha, at an initial spacing of 2.5 by 2.5 m. Trees are harvested at 8 to 12 years, with no thinning. In plantations for sawwood, veneer, and large posts, 1,100 trees are planted per ha at 3.0 by 3.0 m. The best trees are pruned during the first years; an initial thinning occurs when the crowns close; and thinning continues until 250 to 400 trees per ha remain. These trees can be harvested at 15 and 25 years (Koenig and Venegas 1978).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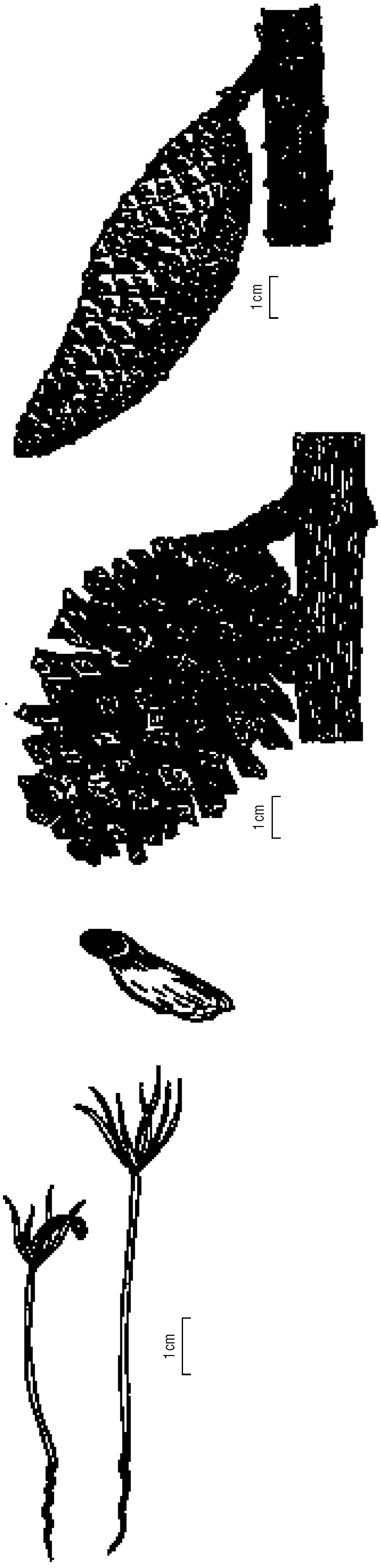
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Pinus chiapensis (Martínez) Andresen

JAVIER LÓPEZ-UPTON and JEFFREY K. DONAHUE
Colegio de Postgraduados, Mexico and
Boise Cascade Corporation, Louisiana

PINACEAE (PINE FAMILY)

P. strobus var. *chiapensis* Martínez (Andresen 1964)

Cuctoj, ocote, palo-pique, pinabete, pinabeto, pino blanco, tonatzin
(Donahue and others 1991, Eguiluz-Piedra 1978, Perry 1991)

Pinus chiapensis has a natural distribution ranging primarily from southwestern Mexico into northern Guatemala; from 15 to 20° N latitude, and 91 to 101° W longitude. In Mexico it is most abundant in the States of Oaxaca and Chiapas; isolated occurrences are also found in Puebla, Guerrero, and Veracruz. In Guatemala, *P. chiapensis* grows in the Departments of El Quiché and Huehuetenango (Donahue and others 1991, Martínez 1948, Perry 1991). *Pinus chiapensis* is considered a rare and endangered species. It now generally consists of small remnant populations of 5 to 20 ha throughout most of its range, with little or no natural regeneration (Donahue 1985). *Pinus chiapensis* forms pure stands or may grow in mixed species stands in association with *P. maximinoi* H. E. Moore, *P. oocarpa* Schiede ex Schtltd., *P. pseudostrobus* Lindl., *P. michoacana* Martínez and *P. pringlei* Shaw at low to mid-elevation sites and with *P. ayacahuite*, *P. patula* var. *longipedunculata, P. pseudostrobus, P. tecunumanii* (Schw.) Eguiluz & J.P. Perry, *P. teocote* Schiede ex Schltdl. & Cham. and *Abies guatemalensis* Rehder at the higher elevations. Associated hardwoods include *Liquidambar styraciflua* L., *Ulmus mexicana* (Liebm.) Planch., *Carpinus caroliniana* Walter, *Fagus mexicana* Martínez, *Cyathaea mexicana* Schltdl. & Cham., and also species of the genera *Quercus, Ostrya, Platanus, Cedrela, Populus, Podocarpus, Clethra,* and *Fraxinus* (Donahue and others 1991, Farjon and Styles 1997, Rzedowski and Vela 1966, Zamora-Serrano and Velasco-Fiscal 1978).

Pinus chiapensis is a fast-growing tree that generally reaches 30 to 40 m in height and 80 to 100 cm d.b.h. (Donahue and others 1991, Martínez 1948, Perry 1991). The species is found at elevations from 150 to 2300 m, most abundantly at 1200 to 1800 m. The tree, typically restricted to the lower slopes and foothills of mountains, is also found frequently in isolated canyons (Donahue and others 1991). *Pinus chiapensis* grows primarily in well-drained sandy loams, sandy clay loams, and clay loams, with pH values of 4.5 to 5.5. These topsoils are generally more than 1 m deep and have good fertility. The species grows in areas where the climate is subtropical to temperate-warmer and usually with high humidity. These areas receive an annual rainfall of 1300 to 2300 mm, occurring primarily from May to October (Dvorak and Donahue 1992, Eguiluz-Piedra 1978). Mean annual temperatures are 20 to 22 °C, maximum temperatures are 40 to 42 °C, and minimum temperatures are 4 to 6 °C (Donahue and others 1991). This species has not been reported to occur naturally in frost zones.

The wood of *P. chiapensis* is soft and light, the sapwood creamy white, and the heartwood slightly darker (Perry 1991), with a specific gravity from 0.34 to 0.38 (Centro Técnico de Evaluación Forestal 1972, Yáñez-Márquez and Caballero-Deloya 1982). It is used for sawn lumber, furniture, doors, window frames, and interior woodwork (Donahue and others 1991, Eguiluz-Piedra 1978).

Pinus chiapensis flowers during March and April (Farjon and Styles 1997, Zamora-Serrano and others 1993). The cones are subcylindrical, tapering toward the apex, mostly straight, often resinous, and 10 to 15 cm long. Their color remains green right up to the time of opening (seed dispersal). They are borne singly or in groups of two and three, on oblique, slender peduncles 25 to 50 mm long, which fall with the cone (Hernández-González 1986, Martínez 1948, Perry 1991). The cone scales are thin, flexible, 31 mm long, and 15 to 34 mm wide (Hernández-González 1986). The cone scale apophysis is prolonged, with the apex often slightly curved inward. The umbo is terminal, without a prickle (Martínez 1948, Perry 1991). Cones of *P. chiapensis* may begin to ripen in July through October, depending on the geographic location. Maturation is indicated when they change from green to brown in color. They may open 1 to 2 weeks after turning brown and are soon deciduous; the seeds are shed immediately. In natural stands in Chiapas, Mexico, 160 kg of cones yield approximately 1 kg of sound seeds (Zamora-Serrano and Velasco-Fiscal 1977). As an exotic planted in trials in Colombia, cones averaged from 0.2 to 3.5 sound seeds (Wright and others 1996). Seeds of *P. chiapensis* are dark brown, occasionally mottled, 4 to 8 mm long, and 3 to 7 mm wide. The seed wings are adnate, strongly attached to the seed, and 20 to 26 mm long (Hernández-González 1986, Martínez 1948, Perry 1991).

Careful planning is required for successful seed collection because the period between cone maturation and seed dispersal is short. Cones are collected in most stands from mid-August to mid-September, using pole-mounted pruners and cutters. Cones are dried by exposing them to the sun for 1 to 2 weeks; however, they must be protected from rainfall during the drying process. Seeds are removed from cones by shaking in a large mechanical tumbler or shaker, or in a small manual shaker for small lots. Seeds are dewinged by rubbing or flailing and cleaned by air screen or floating in water, and should be dried before storage. Special care must be used in processing to avoid damage to the seeds because seed coats are thin. Seeds average 52,000 per kg in Guatemala and 80,000 per kg in Chiapas, Mexico (Perry 1991, Zamora-Serrano and Velasco-Fiscal 1977).

Seeds should be stored in dry conditions at temperatures near 4°C. Donahue and others (1991) note that drying seed to an 8- to 10-percent moisture content enables viability in long-term storage. Seed germination ranges from 17 percent to 85 percent (Carrillo and others 1980, Donahue and others 1991, Zamora-Serrano and others 1993), and viability of seed stored for more than 2 years has shown reduced germination (Lambeth and others 1990, Wright and others 1996).

Germination rates improve with a cold-stratification period of 40 days at 2 °C before sowing (Moreno 1985). If extended pretreatments are not possible, seeds should be soaked overnight in water before sowing. If germination is 85 percent, seeds are sowed in seedbeds at densities of 300 g per m^2; if percentage of germination is less, seeds should be sowed at 400 g per m^2. Alternating temperatures between 22 and 30 °C will provide acceptable germination results (Zamora-Serrano and others 1993). Seeds should be sowed at a depth of 1 cm, in a light and sterile medium that provides good aeration and moisture.

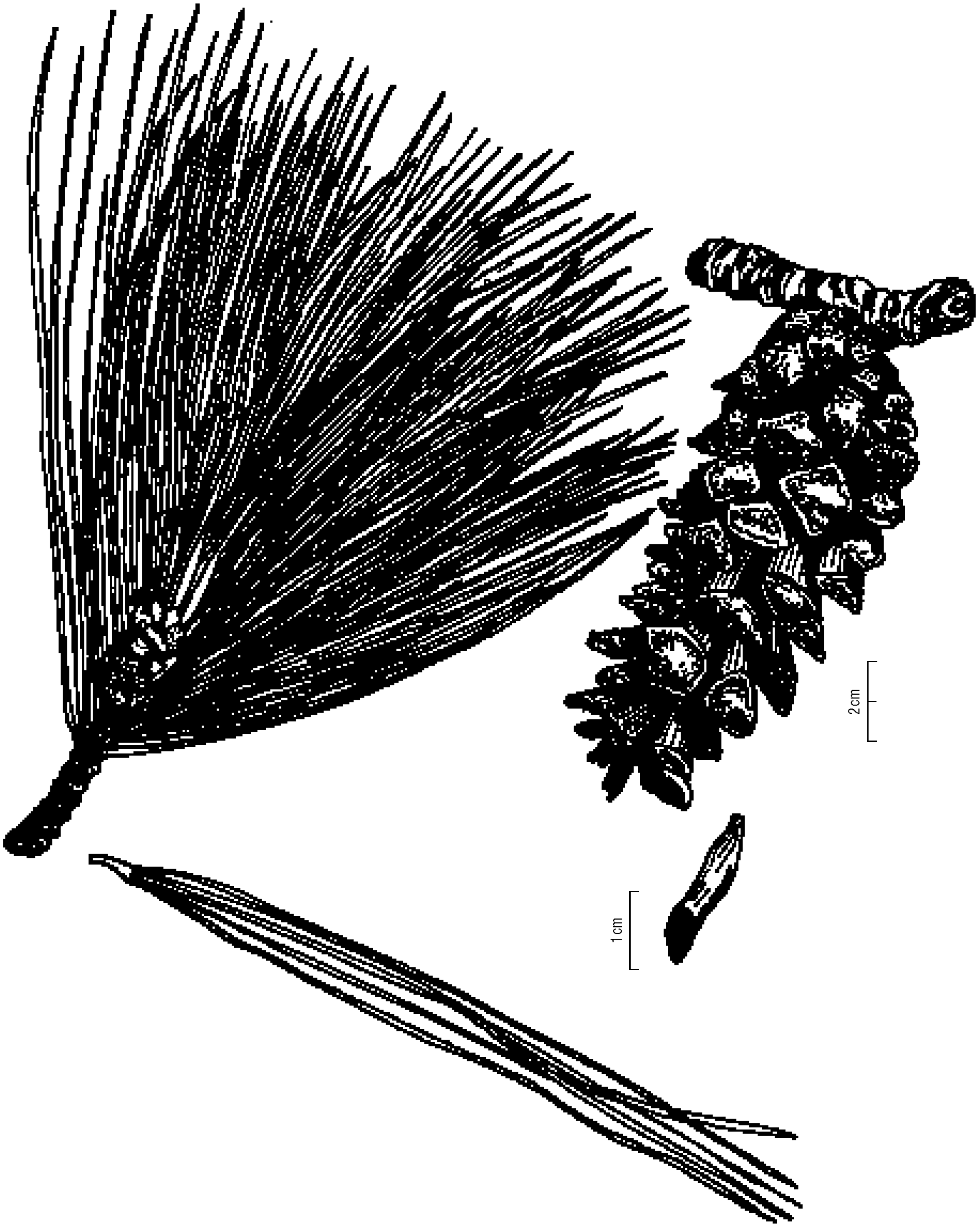
Seedlings of *P. chiapensis* are susceptible to damping off disease. Thus, substrata must be sterile or watering with a fungicide may be needed. As an exotic in Colombia, the species has been found to require 10 to 12 months in the nursery to attain adequate transplant size (Wright and others 1996). In Mexico, nursery stock should be grown between 1000 and 2000 m elevation because the species cannot tolerate frost (Donahue and others 1991).

ADDITIONAL INFORMATION

Pinus chiapensis wood production at 8 years of age in exotic test plots ranged from 12 to 25 m^3 per ha per year (Dvorak and others 1996a). In natural stands, average traqueid length was 2.82 mm, and wood specific gravity from 0.34 to 0.38 (Centro Técnico de Evaluación Forestal 1972, Yáñez-Márquez and Caballero-Deloya 1982). In exotic plantations at 10 years of age, the specific gravity varied from 0.34 to 0.35 (Dvorak and Brouard 1987).

Cones and peduncles from the western extreme of the species distribution in Guerrero have been reported to be longer than in more southerly populations, tending more toward a morphological similarity with *Pinus monticola* Douglas ex D. Don (Rzedowski and Vela 1966). Cone crops can be consistently large, commonly producing up to several kilograms of seed per tree (Donahue and others 1991, Zamora-Serrano and others 1993).

Principal seed insect pests include the moth *Dioryctria erythropasa* and several seed chalcids of the genus *Megastigmus*. Early spring insecticide applications have been shown to control *D. erythropasa. Apolychrosis candidus* Pogue, also a moth, can be an important cone pest (Cibrián-Tovar and others 1995).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Pinus greggii Engelm. ex Parl.

W.S. DVORAK
Central America and Mexico Coniferous Resources Cooperative (CAMCORE)
Department of Forestry, North Carolina State University

PINACEAE (PINE)

No synonyms

Ocote, ocote chino, pino garabatillo, pino garabato, pino prieto
(Flores 1996, López-Upton 1996, Perry 1991)

Pinus greggii is a closed-cone pine that occurs in two distinct geographic regions in Mexico: the States of Coahuila and Nuevo Leon (24° to 25° N latitude) in the northern part of the country (northern population), and in the States of Puebla, San Luis Potosi, Hidalgo, Queretaro, and Veracruz (20° to 21° N) in the central region (southern populations). The reason for the 360-km gap in the species distribution between *P. greggii* trees in the north and south is not readily understood because other pines, like closely related *Pinus patula* Schiede & Schltdl. & Cham., are found in the transition area (Donahue and López-Upton 1996).

Trees from northern and southern populations differ in external needle and cone morphology, flowering patterns, seed size, and monoterpene percentage their native environment (Donahue and López-Upton 1996, Donahue and others 1995, López-Upton and Donahue 1995). Morphologic differences and differences in growth rates between trees from northern and southern populations are even more pronounced when the trees are grown as exotics (Dvorak and others 1996b, Kietzka and others 1996).

Pinus greggii trees from the northern populations occur in small (20 ha), degraded stands on shallow calcareous soils with pH 6.8 to 7.7 (Donahue and López-Upton 1996). These populations exist at elevations from 1900 to 2600 m with annual rainfall between 650 and 750 mm, and the trees are cold and drought tolerant. Trees average only 6 to 15 m in height and 22 to 40 cm d.b.h. at maturity and are often limby and poorly formed. Growth rates of trees in this harsh environment probably average 1 to 2 m^3 per ha per year. *Pinus greggii* trees in northern populations, seldom found with other pines, are more often associated with *Abies spp.*, *Quercus spp.*, and *Pseudotsuga flahaulti* Flous.

The southern populations of *P. greggii* occur in stands of 20 to 5,000 ha on predominantly acidic soils with pH 4.2 to 6.1 (Donahue 1990, Perry 1991). Trees in these populations are found at elevations of 1250 to 2380 m and receive between 1465 to 2380 mm of annual precipitation. *Pinus greggii* from southern populations are as cold tolerant and probably more drought tolerant than *P. patula* but seem less hardy than *P. greggii* from northern populations when planted as an exotic based on early results from progeny tests (Kietzka and others 1996). Trees from southern populations range from 9 to 20 m in height and 25 to 40 cm d.b.h and are of regular to excellent phenotypic quality. Growth rates of 3 to 6 m^3 per ha per year are common. Southern populations are found in close proximity to *P. patula*, *P. teocote* Schiede ex Schlectendal & Chamisso, and a number of *Quercus spp*. (Donahue and others 1995).

Pinus greggii is thought to naturally hybridize with *P. patula* at Jalameco and Carrizal Chico, Hidalgo (Donahue and López-Upton 1996). Artificial hybrids between the two species have been successfully made (Fielding 1960).

In its native environment, the wood of *P. greggii* is whitish to pale yellow in color and of moderate density (0.450 g per cm^3 to 0.550 g per cm^3) based on results from trees assessed between 25 and 30 years of age (Murillo 1988). The wood is used locally for fuel, fence posts, and construction.

Pinus greggii was tested in species trials in approximately 10 countries in the subtropics between the 1960's and 1980's (Dvorak and others 1996b). These introductions apparently included genetic material from the southern populations only. Range-wide provenance and progeny tests of both northern and southern populations of *P. greggii* were carried out in Brazil, Colombia, New Zealand, South Africa, and Zimbabwe in the late 1980's (Dvorak and others 1996b, Kietzka and others 1996). Preliminary results suggest the provenances of northern *P. greggii* should be planted on sites too cold and dry for *P. pat-*

ula; southern sources should be established on sites too dry for *P. patula* (Dvorak and others 1996b, Kietzka and others 1996).

Both northern and southern sources of *P. greggii* are being planted on a limited commercial scale (1000 ha per year) in South Africa, and the tree's popularity as a plantation species is growing (Kietzka 1997). In South Africa, wood from 16-year-old trees of southern sources had properties very similar to *P. patula* in terms of density (0.480 g per cm^3) and percent extractives, and was found to be acceptable for mechanical pulp (Dommisse 1994). Trees of southern sources also had excellent structural quality for saw timber, but poor stem form and high concentrations of knots reduced board quality (Malan 1994).

In its native environment, *P. greggii* begins flower and cone production at approximately 4 to 5 years of age. Trees from the northern populations flower in May or June; those from southern populations in April and May (López-Upton and Donahue 1995). When planted in Brazil and South Africa as an exotic, *P. greggii* trees from northern populations produce a heavy female flower crop 18 months after field planting. The female flowers on trees from northern populations are usually larger and more reddish than those from southern populations. Trees from southern populations may flower as early as 18 months, but more often a light-to-moderate crop of female flowers emerges approximately 24 months after field planting. In southern Brazil, initial heavy flowering at approximately 2 years of age was followed by relatively little flowering for 4 years. Heavy flowering began again at approximately 6 years of age. In South Africa, *P. greggii* flowers twice during the year. The northern sources flower from November to January; information on a second flush is currently unavailable. The main flowering time for the southern populations is September through November and a second flush of predominantly female strobili occurs in February and March (Kietzka 1997). At the Institute of Forest Genetics, Placerville, California, *P. greggii* flowers twice: once in November and again in June (Critchfield 1967).

In Mexico, cones ripen in December and January, approximately 21 months after pollination. Coning is prolific with clusters of 8 to 10 cones common in many portions of the crown (Donahue and López-Upton 1996). Because the species is a serotinous pine, mature cones may stay closed on the tree for several years. In studies conducted in natural stands in Mexico, trees from northern populations were found to have slightly longer cones than those from southern populations (115 mm vs. 105 mm) but had a lower seed potential (92 vs. 116) (López-Upton and Donahue 1995).

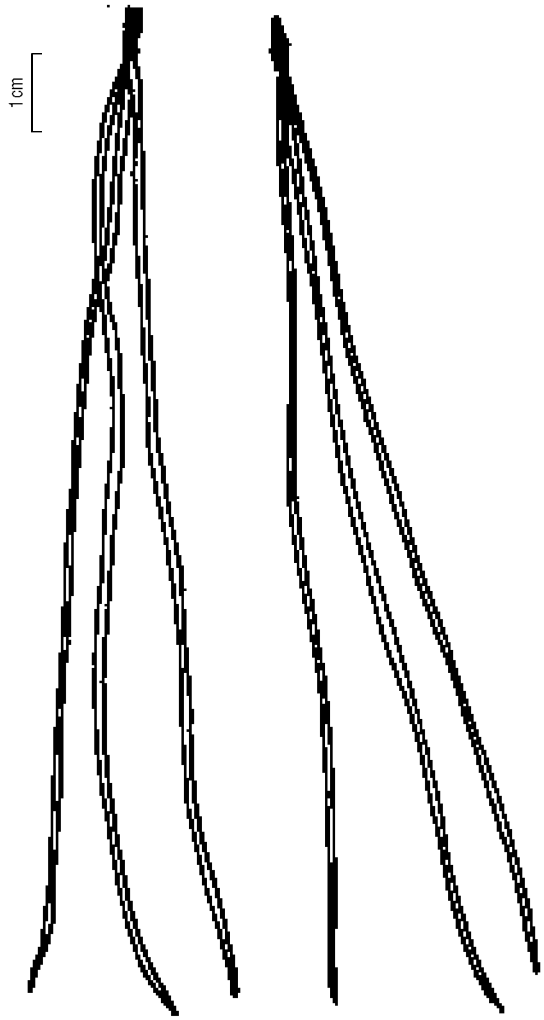
The average number of filled seeds per cone was less for trees in northern populations than in southern populations (46 vs. 74). Trees from northern populations appear to be much more infested with cone and seed insects in natural stands than those of the southern populations, which may explain lower seed yields (López-Upton and Donahue 1995). In South Africa, cones usually ripen in August. Cones from a *P. patula x P. greggii* cross matured 33 months after flowers were pollinated (Kietzka 1997). Future studies will accurately determine reproductive cycles for *P. greggii* across its many new environments.

Cones should be collected when they are light brown, and old cones that are gray should not be harvested. Cones are held tightly on branches and care is needed when removing cones from the trees to avoid damage to future cone crops. In Mexico, cones are removed from branches by tree climbers. Cones that can be reached are pulled off the branches by hand. Cones at the end of long branches are removed using an aluminum or wood pole. The pole has a curved blade at the end that pries or cuts the cones from the branches.

Cones can be air-dried in the sun for several days or placed in a kiln at 45 to 48 °C for 24 to 48 hours. The seeds from trees in northern populations are significantly larger than those from southern populations. Average seed yields for trees in natural stands from northern populations was 55,500 seeds per kg; from southern populations, 67,100 seeds per kg. From a seed orchard in South Africa, 68,000 seeds per kg were obtained from clones of southern sources. No information is available on seed quantities from trees of northern sources when planted as an exotic.

The seeds of *P. greggii* germinate well in moist sand or similar media. Even though cold stratification is not necessary for good germination, studies by Donahue (1990) indicates that a 30-day cold stratification increased the rate of germination for trees from southern populations but had no effect on trees from northern ones. Germination rates of 30 to 70 percent have been found for seeds collected from natural stands in Mexico. In large commercial nurseries in South Africa, *P. greggii* seed is placed in a porous cloth bag in a water bath, pH 5.6, at 28 °C, and compressed air is bubbled through for 24 hours (Kietzka 1997). Excess moisture is toweled off and the seed is sowed.

Seedlings of *P. greggii* from both southern and northern populations intended for outplanting at 10 cm height can be produced in most nurseries in 5 to 6 months. Planting seedlings at this height succeeds in harsh environments in South Africa and lessens the chance for subsequent J-root problems. Seedlings from southern sources will reach shoot heights of 20 to 25 cm in 7 to 8 months, especially in tropical and subtropical environments in Brazil and Colombia. Seedlings from northern sources may take two growing seasons in the nursery to reach these heights because the plants set a resting bud sooner than those from southern provenances.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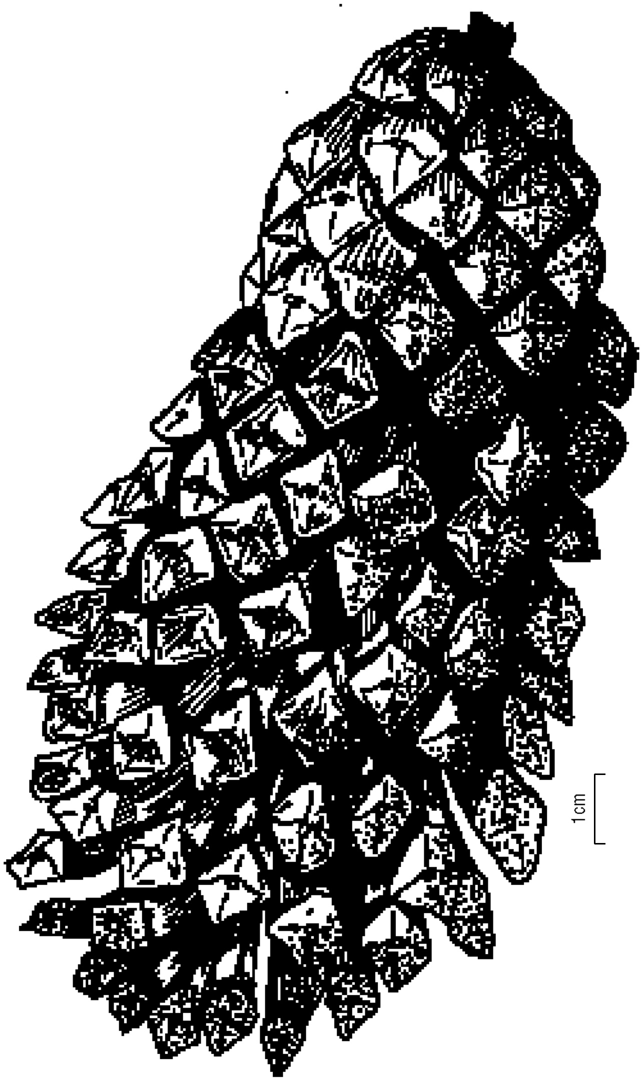
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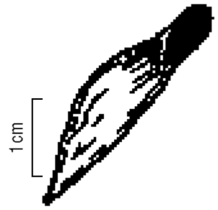
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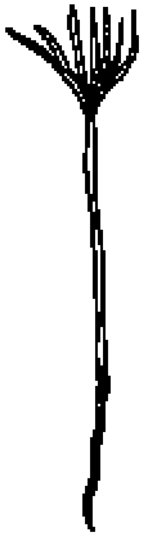

Pinus jaliscana Pérez de la Rosa

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Especialidad Forestal del Colegio de Postgraduados
México

PINACEAE (PINE FAMILY)

P. patula var. *jaliscana* (Pérez de la Rosa) Silba., *P. macvaughii Carbajal*
(Carbajal and McVaugh 1992, Silba 1985)

Jalisco pine, ocote, pino (Perry 1991)

Pinus jaliscana grows only in western Jalisco, Mexico (Carbajal and McVaugh 1992, Pérez de la Rosa 1983). Associate species are *P. oocarpa, P. maximinoi,* and *P. douglasiana* Martínez (Perry 1991).

Pinus jaliscana is a well-formed, fast-growing pine, 20 to 30 m in height (sometimes 35 m) and 50 to 80 cm d.b.h. (Carbajal and McVaugh 1992, Perry 1991). It grows at elevations from 850 to 1650 m in semitropical to tropical climates with annual rainfall amounts of 1000 to 1500 mm and mean annual temperatures of 22 to 26 °C (Pérez de la Rosa 1983). The best trees grow on deep, well-drained soils of granite origin (Perry 1991).

The wood is hard, strong, and resinous. It is used for general construction and fuelwood (Perry 1991).

Pinus jaliscana cones are oblique (sometimes markedly oblique), almost symmetrical, pendent, and tapered toward the base. Cones are 3 to 9 cm in length, 2.3 to 2.8 cm in diameter when closed (4 to 6 cm when open), and 35 to 60 g in weight. They are borne singly, in pairs, or sometimes in groups of three on slender, strong peduncles 10 to 15 mm long that are twisted downward. Cones are serotinous and persistent. Maturation is indicated when they change from green to brown in color. Cones mature in the second year and ripe cones begin to appear in November, but cones may remain closed for some years (Carbajal and McVaugh 1992, Pérez de la Rosa 1983, Perry 1991). Seeds are dark brown, 4 to 6 mm long, and about 4 mm wide. The seed wings are pale brown, articulate, 10 to 17 mm long, and 5 to 8 mm wide (Pérez de la Rosa 1983, Perry 1991).

Cones are collected from the tree using pole-mounted pruners and cutters. Cones are dried by exposing them to the sun for 1 to 2 weeks; however, they must be protected from rainfall during the drying process. When cones remain closed on the tree for 1 year or more, their color changes to gray. When this occurs, one of the following methods may be needed to accelerate the opening of cones and collection of seed: placing cones in boiling water for 10 to 30 seconds, or placing them in a cone-drying kiln for 1 day at temperatures of 50 °C or less. Seeds are removed from cones by shaking in a large mechanical tumbler or shaker, or in a small manual shaker for small lots. Seeds are dewinged by rubbing or flailing, cleaned by air screen or floating in water, and should be dried before storage. Care must be used in processing with mechanical dewingers to avoid damaging the seeds. Seeds average 120,000 per kg (Perry 1991).

Seeds must be stored in dry, cool (4 °C), and airtight conditions. Seed pretreatment involves soaking them in water overnight before sowing. Seeds should be sowed at a depth of 0.9 cm in a light, sterile, and acid medium that provides good aeration and moisture. A temperature of 20 to 30 °C will provide acceptable germination. Like many other pine species, seedlings are susceptible to damping off, thus substrata must be sterile or watering with a fungicide may be needed.

Pinus leiophylla Schiede ex Schltdl. & Cham.

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PINACEAE (PINE FAMILY)

P. leiophylla Schiede and Dieppe; *P. gracilis* Roezl (Farjon 1984)

Ocote, ocote prieto, pino chino, smooth-leaved pine (Perry 1991, Martínez 1948)

Pinus leiophylla is native to Mexico, extending from Chihuahua in northwestern Mexico southward along the Sierra Madre Occidental into Oaxaca and along the Volcanic Axis in central Mexico (Martínez 1948, Perry 1991). *Pinus leiophylla* rarely forms pure stands; associate species are *P. engelmannii* Carrière, *P. arizonica* Engelm., *P. teocote, P. lumholtzii* B.L. Rob. & Fernald, *Juniperus* sp., and *Quercus* sp. in north Mexico, and *P. montezumae* Lamb., *P. ayacahuite, P. pseudostrobus, P. michoacana, P. patula* Schiede & Deppe ex Schltdl. & Cham., *P. oaxacana* Mirov, *Abies religiosa, A. guatemalensis, Quercus* sp., *Arbutus* sp., and several hardwood species in central Mexico (Eguiluz-Piedra 1978, Perry 1991).

Pinus leiophylla grows at a moderate rate to 20 to 30 m in height, occasionally reaching 35 m, and 35 to 80 cm d.b.h. (Perry 1991). It will grow on marginal sites or areas covered by volcanic rock, but the best trees grow on deep, well-drained soils of volcanic origin (Martínez 1948). The tree grows at elevations from 1600 to 3000 m but is most often found between 2200 and 2750 m. The species grows in temperate to temperate-warmer climates, where temperatures drop to freezing during the coldest winter months (Perry 1991). It is found where temperatures range from -15 to 38 °C and annual rainfall from May to October is 700 to 1500 mm (Eguiluz-Piedra 1978).

The wood is relatively dense, heavy, and hard, and very resinous with a pale brown heartwood. Wood specific gravity is 0.44 to 0.51 (Echenique-Manrique and Díaz-Gómez 1969, Murillo 1988, Zobel 1965). It is used for general construction, railway ties, and fuelwood (Eguiluz-Piedra 1978, Perry 1991).

Pinus leiophylla begins reproducing at 5 to 6 years and flowers from February through April (Jasso-Mata and Jiménez-Casas 1994, Jasso-Mata and others 1995, Patiño-Valera 1973). Cones are ovoid to ovoid-conical, symmetrical, and reflexed. When fresh they are a lustrous or yellowish brown, 4 to 8 cm, and 3.5 cm thick when closed. The cones are borne singly or, most often, in groups of two, three, and four on stout peduncles 5 to 15 mm long (Carbajal and McVaugh 1992, Martínez 1948, Perry 1991). Cones mature in the third year and are persistent for 2 to 3 years (Martínez 1948). Cone scales are 5 to 8 mm wide, thin, stiff, strong, and not flexible; the apophysis is flat but somewhat thickened along the apical margin; and the umbo is dorsal, and generally flat to depressed (Perry 1991). Seeds disperse from December through February when the purplish brown cones are ripe. The number of sound seeds per cone is 11 to 18, with a mean of 13. The percentage of sound seeds (per cone) is 15 to 20 percent, while that of empty seeds is 17 to 43 percent (Aldrete and López-Upton 1993). In one natural—but not pure—stand in eastern México, Delgado (1994) found 9 sound seeds out of 53 potential seeds per cone, seed efficiency of 17 percent, and 95-percent germination. Seeds are grayish to black, 3 to 4.5 mm long, and about 3 mm wide; the seed wing is yellowish, articulate, 10 to 17 mm long, and 5 to 8 mm wide (Carbajal and McVaugh 1992, Martínez 1948, Perry 1991).

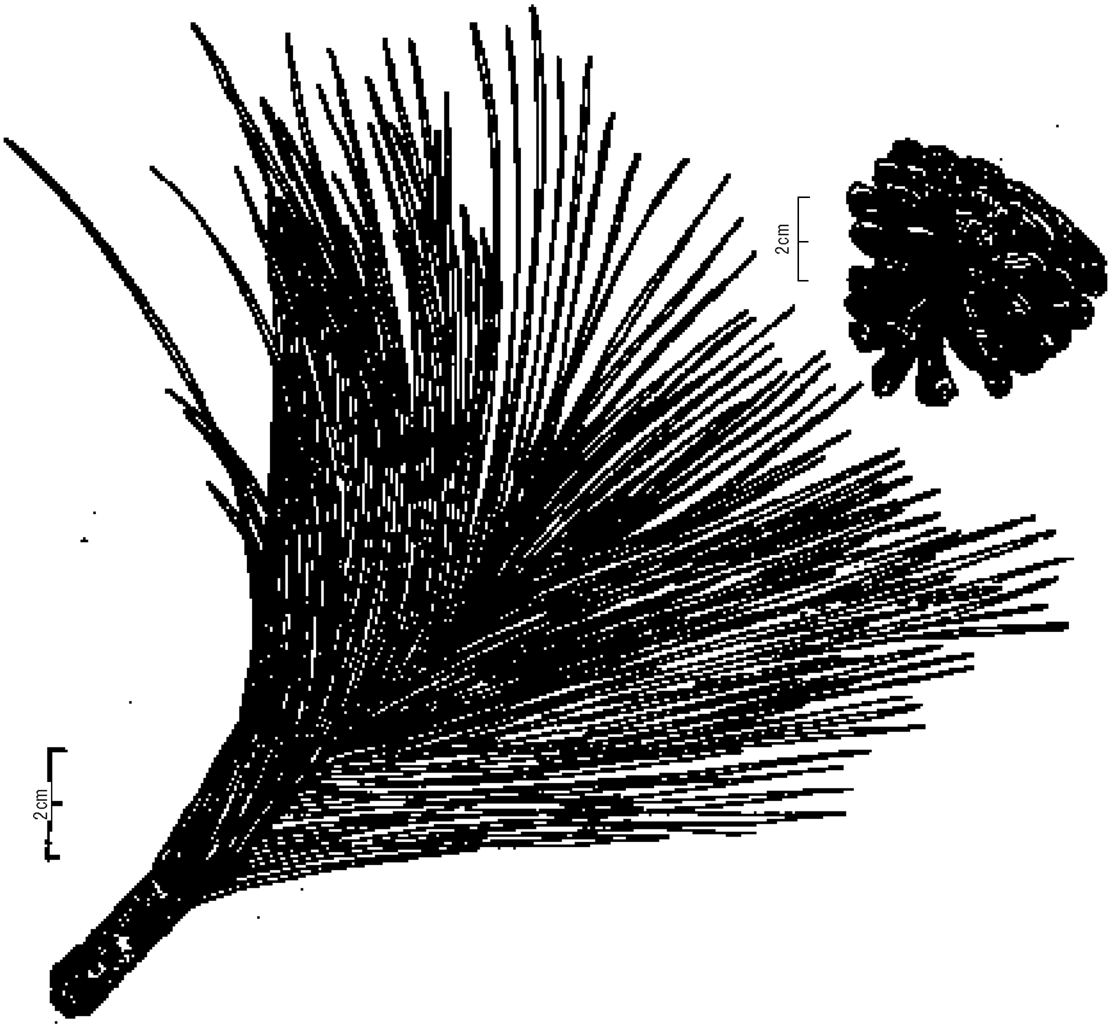
To achieve 95-percent germination, cones should be collected from mid-December through mid-February (Aldrete and López-Upton 1993). Cones are collected from the tree using pole-mounted pruners and cutters. Cones are dried by exposing them to the sun for 1 to 2 weeks; however, they must be protected from rainfall during the drying process. Seeds are removed from cones by shaking in a large mechanical tumbler or shaker, or in a small manual shaker for small lots. Seeds are dewinged by rubbing or flailing, cleaned by air screen or floating in water, and should be dried before storage. Care must be used in processing with mechanical dewingers to avoid damaging the seeds. Seeds average 85,000 per kg (Perry 1991). Seeds must be stored in dry, cool (4 °C), and airtight conditions.

Seed pretreatment involves soaking overnight in water before sowing. Seeds must be sowed at a depth of 1 cm, in a light, sterile medium that provides good aeration and moisture. The best sowing time is May to July with 65 to 72 percent emergence (Catalán-Sánchez 1987). Germination of 62 percent (Patiño-Valera 1973) increases to 95 percent when the seeds are cleaned. Seeds are sowed in seedbeds at densities from 12,000 to 15,000 per m^2 or 300 g per m^2 (Zamora-Serrano and others 1993). A temperature of 20 to 30 °C will provide acceptable results for germination. Seedlings are susceptible to damping off. Thus, substrata must be sterile or watering with a fungicide may be needed. The ectomycorrhizal fungi *Pisolithus tinctorius* (Pers.) Coker et Couch improves seedling field performance (Marx 1975).

ADDITIONAL INFORMATION

This species produces epicormic shoots on the trunk and is able to sprout from the root collar (Perry 1991).

Pinus leiophylla consistently produces a moderate cone crop every year, but the interval between large cone crops is 3 to 5 years (Zamora-Serrano and others 1993). Cones are susceptible to the fungus *Caeoma conigenum* Heds. et Hunt (Martínez 1948, Perry 1991). Important insect pests are *Conophthorus conicolens* Wood, which can destroy 16 to 60 percent of conelets, cones, and seeds, and *Leptoglossus occidentalis* Heidemann. Other cone pests include *Conotrachelus neomexicanus* Fall, *Dioryctria erythropasa* (Dyar), *D. pinicolella* Amsel, *Apolychrosis synchysis* Pogue, *A. ambogonium* Pogue, and *Megastigmus* sp. (Cibrián-Tovar and others 1995, Delgado 1994).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Pinus maximinoi H.E. Moore

JAVIER LÓPEZ-UPTON and JEFFREY K. DONAHUE
Colegio de Postgraduados, México
Boise Cascade Corporation, Louisiana

PINACEAE (PINE FAMILY)

P. tenuifolia Benth. *P. pseudostrobus* var. *tenuifolia* Shaw., *P. douglasiana* var. *maximinoi* (H.E. Moore) Silba. (Carbajal and McVaugh 1992, Farjon and Styles 1997, Martínez 1948, Stead and Styles 1984)

Cantaj, ocote, pino candelillo, pino canis, pino llorón, tzin (Carbajal and McVaugh 1992, Dvorak and Donahue 1988, Eguiluz-Piedra 1978, Perry 1991)

Pinus maximinoi is widely distributed in the Pacific Coast states of México and Central America; from Sinaloa, México to northern Nicaragua (Dvorak and Donahue 1992, Martínez 1948, Perry 1991). The species grows in pure stands or in association with *P. oocarpa, P. douglasiana, P. pseudostrobus, P. tecunumanii, P. michoacana, P. leiophylla* Schiede & Deppe, *P. montezumae, P. patula* var. *longipedunculata, P. ayacahuite, Abies hickelii, Quercus* spp., *Liquidambar styraciflua, Juniperus* spp., and *Arbutus* spp. (Dvorak and Donahue 1988, Eguiluz-Piedra 1978, Farjon and Styles 1997, Perry 1991).

Pinus maximinoi is a fast-growing pine, reaching 20 to 40 m in height and 40 to 100 cm d.b.h. The trunk is usually straight and clear of branches (Carbajal and McVaugh 1992, Perry 1991). This pine grows at elevations of 600 to 2400 m. However, in relation to growth and phenotypic quality, the best stands are found at 800 to 1500 m, on seaward-facing slopes, with deep and fertile well-drained soils. Topsoil pH values typically range from 4.2 to 6.5, while subsoils may reach pH 8.0. Textures are normally sandy clay loams to clays for surface soil horizons and clays for subsoil horizons (Dvorak and Donahue 1988). The species grows in climates varying from temperate-warmer to subtropical humid (Carbajal and McVaugh 1992); annual rainfall on these sites ranges from approximately 1000 to 2100 mm (Dvorak and Donahue 1988). Mean annual temperatures vary from 17 to 22 °C. Maximum temperatures reach 40 °C, and minimum temperatures drop to -1 °C (Eguiluz-Piedra 1978). *Pinus maximinoi* does not appear to tolerate freezing temperatures (Dvorak and Donahue 1988).

The wood of *P. maximinoi* is soft and light; the sapwood is pale yellowish white, and the heartwood is slightly darker (Perry 1991). Specific gravity density in trials in Colombia varied from 0.32 to 0.51 and in South Africa from 0.49 to 0.50 (Wright and Baylis 1993, Wright and Osorio 1993, Wright and Wessels 1992). Its potential uses include paper, firewood, resin extracts, and hewn timbers for roof supports and doorways (Eguiluz-Piedra 1978, Perry 1991, Wright and Wessels 1992).

When planted as an exotic in Colombia, the species begins reproducing at 4 years (Osorio 1998, personal communication); in Mexico the species does not appear as precocious. The tree flowers in January and February in Mexico and in February and March in Central America (Farjon and Styles 1997; Zamora-Serrano and others 1993). Cones are long-ovoid, asymmetrical and oblique, 5 to 8 cm long and 4.5 to 7 cm wide after opening. The light brown, lustrous cones develop in groups of three or four, on oblique peduncles 10 to 15 mm long, which fall with the cone (Carbajal and McVaugh 1992, Martínez 1948, Perry 1991). The cone scales are weak, 18 to 22 mm long, and 8 to 15 mm wide. The cone scale apophysis is usually flat, 2 to 4 mm high, and indistinctly or transversely keeled; the umbo is small and depressed, with a deciduous prickle (Carbajal and McVaugh 1992, Perry 1991). Cones ripen from late December through March. Maturation is noted as the cone color changes from light green to dark green. They are ready for collection when the cone scale is soft enough to allow penetration by a fingernail and the seedwing has a brownish color. Cones open upon maturation and are soon deciduous. In the native environment, cones of *P. maximinoi* may contain up to 40 filled seeds. As an exotic planted in trials in Colombia, cones averaged four filled seeds (Arce and Isaza 1996). Seeds of *P. maximinoi* are dark brown, 5 to 7 mm long, and about 4 mm wide. The seed wings are pale yellowish-brown, articulate, and 16 to 20 mm long (Martínez 1948, Perry 1991).

Cones are collected during the first two weeks of April (Dvorak and Donahue 1988). Cones are removed from the tree using pole-mounted pruners and cutters. Cones are dried by exposing them to the sun for 1 to 2 weeks (Zamora-Serrano and others 1993). Seeds are removed from the cones by shaking in a large mechanical tumbler or shaker, or in a small manual shaker for small lots. Seeds are dewinged by rubbing or flailing and cleaned by air screen or floating in water. Care must be used with mechanical dewingers to avoid damage to the seeds. Sound seeds should be dried down to 8 to 10 percent moisture content before storage. They should be stored in dry, airtight, and cool (4 °C) conditions. Seed size follows a strong clinal variation pattern: larger in size in Honduras (55,000 seeds per kg from Tatumbla) and smaller in Mexico (100,000 seeds per kg in Oaxaca) (Dvorak and Donahue 1988). Zamora-Serrano and others (1993) report 84,200 seeds per kg in Chiapas, Mexico.

Seeds should be soaked overnight in water before sowing. Germination rates increase favorably when seeds are subjected to a cold-stratification period of 40 days at 2 °C before sowing (Moreno 1985). Seeds should be sowed at 1 cm deep in a light, sterile medium that provides good aeration and moisture. If the germination rate is more than 75 percent, 300 g per m^2 will provide adequate density in seedbeds (Zamora-Serrano and others 1993). The recommended temperature for optimum germination is 25 °C, but a temperature between 20 and 25 °C will provide acceptable results (Belcher 1985). Germination varies by provenance, ranging from 65 percent to 80 percent (Belcher 1985, Patiño-Valera 1973, Zamora-Serrano and others 1993). Seedlings are susceptible to damping off. Thus, substrata must be sterile or watering with a fungicide may be needed.

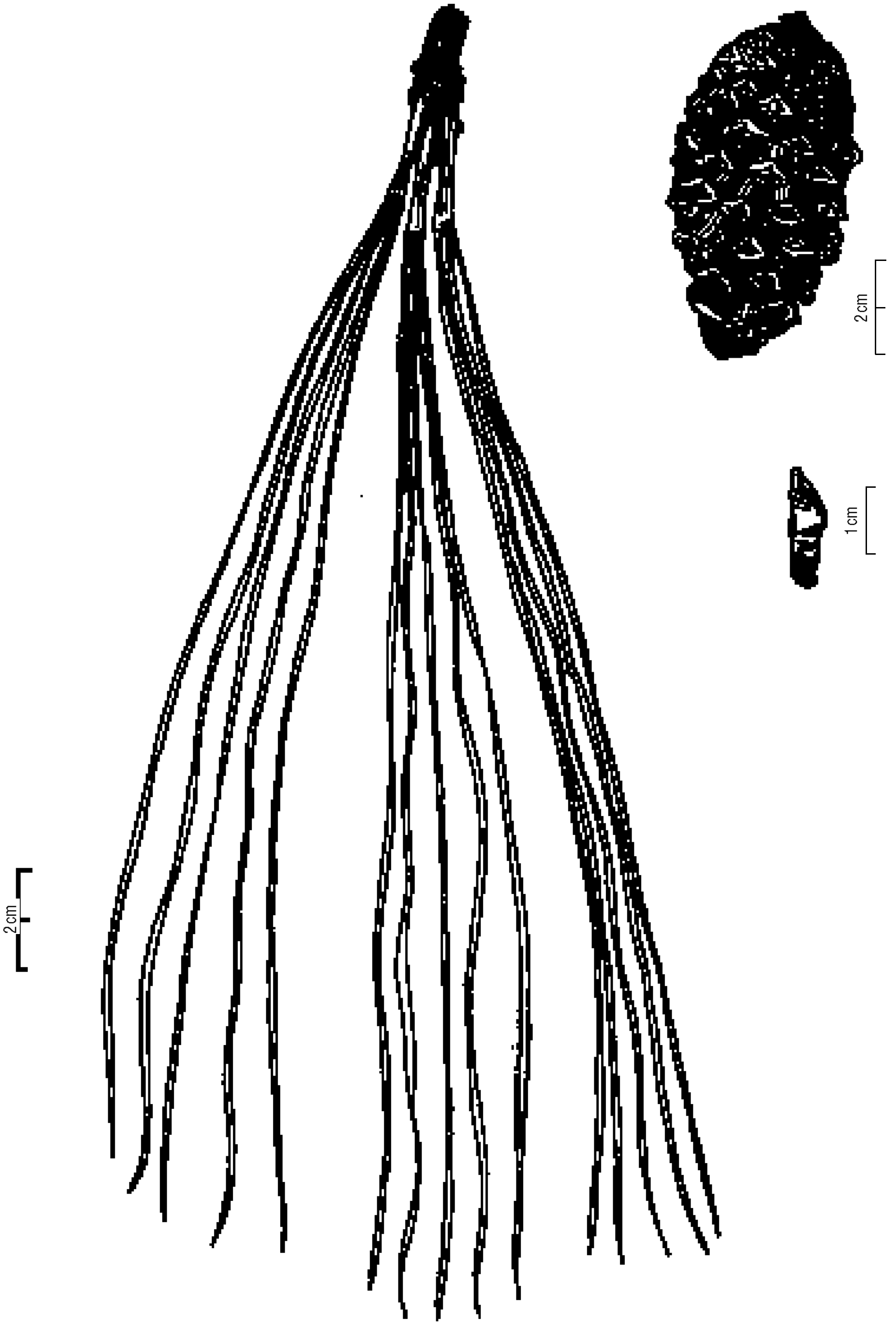
ADDITIONAL INFORMATION

Cone and leaf traits are used to distinguish *P. maximinoi* from *P. pseudostrobus*. The leaf hypoderm intrusions across the chlorenchyma to the endoderm are good distinguishing characteristics of the two species (Mittak and Perry 1979, Stead 1983).

Planted as an exotic in Colombia, wood production in test plots at 5 years ranged from 17 to 30 m^3 per ha per year (Dvorak and Donahue 1988, Wright and others 1992).

The size of cone crops is usually small every year compared to other hard pines (Dvorak and Donahue 1988). The interval between large cone crops is from 3 to 5 years (Zamora-Serrano and others 1993).

Leptoglossus occidentalis Heidemann, a seedbug, is the most important insect pest of conelets, cones, and seeds. *Tetyra bipunctata* Herrich-Schaeffer, a coneworm, is the primary cause of empty seeds. *Cecidomyia bisetosa* Gagné, a moth, causes cone death. Larvae of the moths *Cydia montezuma* Miller, *Dioryctria erythropasa* Dyar, *Cecidomia bisetosa*, and several seed chalcids in the genus *Megastigmus* are capable of producing serious seed losses in orchards (Cibrián-Tovar and others 1986, 1995). Applications of insecticides in early spring control *D. erythropasa*. Systemic insecticide applications have been successful in reducing *C. bisetosa* damage (Cibrián-Tovar and others 1986, 1995). Cones are also susceptible to the fungus *Cronartium conigenum* (Pat.) Heds. and Hunt and *C. comandrae* Peck. (Mead and others 1978).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Pinus montezumae Lamb.

ARNULFO ALDRETE
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PINACEAE (PINE FAMILY)

Pinus occidentalis, P. devoniana, P. russeliana, P. macrophylla, P. filifolia, P. sinclairii, P. grenvilleae, P. gordoniana, P. wincesteriana, P. rudis, P. ehrenbergii, P. lindleyana, P. donnell-smithii (Eguiluz 1978; Shaw 1909, 1914). At present, the complete taxonomic group referred as *Pinus montezumae* includes the typic species *Pinus montezumae* Lamb., as well as two more variants described as *Pinus montezumae* var. *Lindleyi*, and *Pinus montezumae* form *macrocarpa* (Eguiluz 1978, Loock 1950, Martínez 1948, Mirov 1967, Perry 1991)

Chalmaite blanco, juncia, montezuma pine, ocote, ocote escobetón, pino, pino blanco, pino de moctezuma, pino real, rough-branched Mexican pine (Eguiluz 1977, 1978; Perry 1991)

Pinus montezumae thrives on the slopes and in the valleys of the Great Cross Range in Mexico which extends from Colima State on the Pacific Coast through Veracruz State on the Gulf of Mexico. The species extends north toward the Sierra Madre Occidental, reaching Durango State and the Sierra Madre Oriental up to Coahuila State (Martínez 1948, Perry 1991) and south to Guatemala and El Salvador (Mirov 1967).

Pinus montezumae is a large pine that reaches 20 to 25 m in height and 30 to 80 cm d.b.h. It grows under a variety of conditions at mean temperatures from 10 to 24 °C and elevations from 1150 to 3150 m. However, the best growing conditions for this species are volcanic soils at 2500 m.

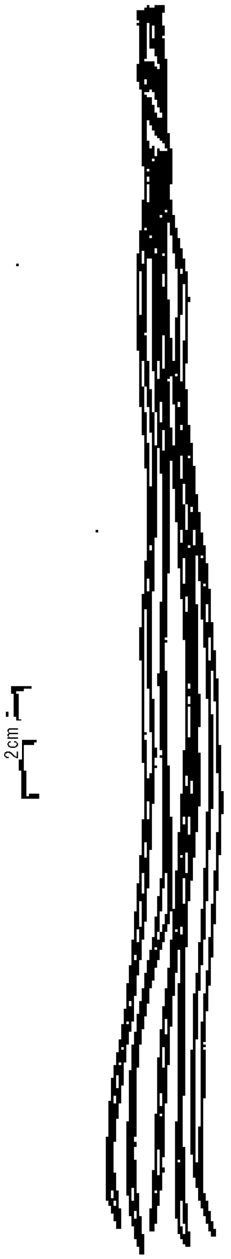
Pinus montezumae can be found growing in pure stands or associated with other pine species such as *P. pseudostrobus, P. rudis, P. hartweggii, P. leiophylla, P. douglasiana, P. michoacana, P. lawsonii* Roezl. ex Gordon, and *P. ayacahuite*, and several hardwood species (Eguiluz 1978, Rzedowski 1983). The species crosses naturally with some of its associated species forming many hybrids (Hernández 1967, Jasso 1982, Perry 1991).

Pinus montezumae is one of the most important timber species in Mexico. Its wood is hard, heavy, and resinous with a density of 0.74 kg per m^3 (Eguiluz 1978); the color varies from yellowish white in the sapwood to light brown in the heartwood (Perry 1991). It is used for rough timber, hewn timber, plywood, firewood, pulp and in construction (Eguiluz 1978, Rzedowski 1983).

Flowering occurs February through April; pollen dispersion, in March and April occasionally extending until May. Male flowers form bud-terminal groups varying from one to five flowers per bud. Female flowers are produced in lateral or subterminal buds. The buds are solitary or form groups of two or three (Jasso 1982). Cones develop and mature during the fall of the same year, in November and December and occasionally in winter (Niembro 1979, Patiño 1973, Pérez 1988). The cones of *Pinus montezumae* vary from long ovoid to conical-ovoid or conoid. They are slightly asymmetric and curved, 8.5 to 15 cm long, and 7 to 10 cm wide after opening. They are lustrous, arranged in pairs or groups of three, and extended or slightly hanging on short peduncles 10 to 15 mm long. The numerous cone scales are thick, hard, stiff, 25 to 35 mm long, and 13 to 17 mm wide; the umbo dorsal is slightly raised. The cones have a mean fresh weight of 135 g and mean dry weight of 88 g, with an average of 144 seeds per cone; only 52 percent of these are fully filled seeds (Musálem 1984). Seeds are slightly triangular, small, dark brown, 6 to 7 mm long, and about 3 to 4 mm wide with an articulated, pale brown seed wing about 20 mm long and 7 mm wide (Martínez 1948, Perry 1991). Acosta and Musálem (1986) found that dispersion occurs from early February to late June. The maximum dispersion of fully filled seeds occurs during mid-March, when more than 50 percent of the fully filled seeds dispersed can be obtained. Most of the high-quality seeds are dispersed within 25 m of the seed tree, dispersing at about 104,000 seeds per ha; seed quality decreases with the distance of dispersion in open growth conditions (Acosta 1986).

Generally, *Pinus montezumae* produces good cone crops every 5 or 6 years; occasionally two good crops are produced in successive years. The best time to collect mature cones is from early December through mid-January (Ramírez 1985). Collected cones are dried in the sun for a few days; the seeds can then be easily extracted by hand. Clean seeds average 46,000 per kg (Patiño 1973). Seeds should be stored in large metal cans at temperatures near 4 °C.

The most common pregermination treatment involves soaking the seeds during the 24 hours before sowing. Seeds can be sown at a depth of 0.5 to 2.0 cm (Carrillo 1986, Galván and Martínez 1985). The average time for germination is 20.9 days with a germination rate of 65 percent (Caballero 1966). Seedlings are susceptible to damping-off; consequently, a fungicide should be applied (Galván and Martínez 1985).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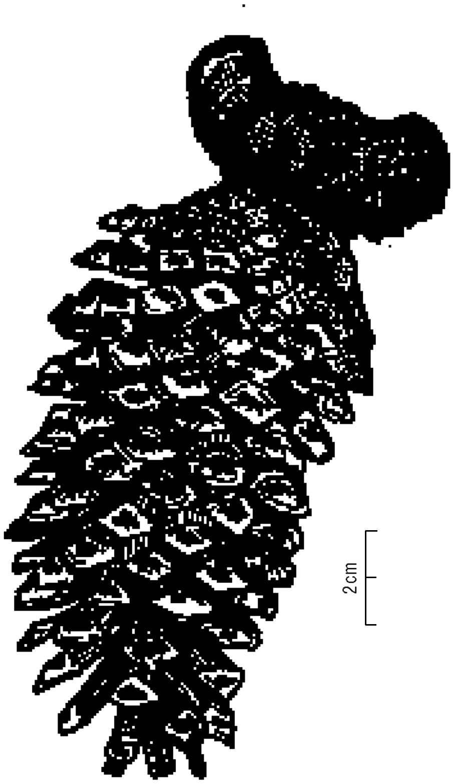
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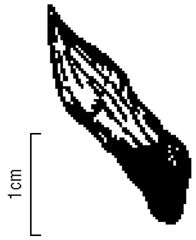
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Pinus oocarpa Schiede ex Schltdl.

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PINACEAE (PINE FAMILY)

No synonyms

Chaj, chictaj, ichtaj, ocote, ocote chino, pino, pino amarillo, pino avellano, pino colorado, pino ocote, pino prieto, tocj (Gutiérrez 1996, Martínez 1979, Perry 1991, Peters 1977, Zamora 1981)

Pinus oocarpa is a closed-cone pine native to Mexico and Central America (Perry 1991). It has a geographic range of 3000 km from Sinaloa, Mexico (28°20'N latitude) to central Nicaragua (12°40'N latitude) and is the most common pine in the southern half of Mexico and Central America. It constitutes approximately 45 percent of the pine forests of Chiapas (Zamora 1981), 50 percent of Guatemala, 66 percent of Honduras (Wolffsohn 1984), 90 percent of Nicaragua (Greaves 1979), and 60 percent of El Salvador. It is also found in several locations in the interior highlands of Belize.

Pinus oocarpa is phenotypically an extremely variable species in its native environment because it has evolved under diverse climatic and edaphic patterns over its 3000-km geographic distribution. It occurs from 350 to 2500 m elevation in Mexico and Central America but reaches its best development between 1200 to 1800 m. Along the northwest coast of Mexico it occurs in areas with as little as 600 to 800 mm of annual rainfall (Pérez de la Rosa 1998). In southern and eastern Mexico and most of Central America it generally occurs in areas of 1000 to 1500 mm of annual precipitation with dry seasons of up to 5 months. In some locations where *P. oocarpa* is found, like Ocotal Chico, Veracruz, Mexico, annual rainfall amounts exceed 2250 mm. *Pinus oocarpa* is most often found on shallow, sandy clay soils of moderate soil acidity (pH 4.0 to 6.5) that are well drained. The species distribution appears to be very dependent on the existence of frequently occurring fires.

Trees of *P. oocarpa* can be recognized in their native habitats by their irregular crowns, thick, gray, platy bark, ovoid-shaped cones with a large, thick peduncle, and needles in fascicles of five. On deep, well-drained soils and with good rainfall regimes, *P. oocarpa* is a medium-to-large tree about 20 to 35 m in height and 45 to 80 cm d.b.h. The species reaches its best development in eastern Guatemala, Honduras, and northern Nicaragua where soils are deep and annual rainfalls are above 1200 mm. The growth rates of *P. oocarpa* in natural stands in these regions are approximately 3 to 4 m^3 per ha per year. In northern Mexico, where the climate is drier than in most parts of Central America, trees reach only 10 to 15 m height and are generally poorly formed. Trees are also often less than 10 to 12 m height where they grow on shallow, eroded soil on ridge tops, or at elevations below 800 to 900 m (Zamora 1981). The growth rate of *P. oocarpa* in these dry regions is approximately 1 m^3 per ha per year.

Pinus oocarpa crosses naturally with both *P. caribaea* var. *hondurensis* (Sénécl) Barr. & Golf. and *P. tecunumanii* Eguiluz & J. P. Perry, and a number of hybrid swarms exist in Central America (Furman and others 1996, Squillace and Perry 1992). Artificial crosses among all three pine species have been successfully made for years in Queensland, Australia (Nikles 1989).

The wood of *P. oocarpa* is whitish yellow. Wood density is moderate and provenance averages range from 0.450 to 0.550 g per cm^3 for trees 30 to 60 years of age throughout Mexico and Central America. Local industries and farmers have used the wood for plywood, construction lumber, packing boxes, soft drink boxes, broomstick handles, Popsicle sticks, railroad ties, and posts (Zamora 1981). However, its greatest use in the region is for fuel wood and kindling (ocote) as well as for resin production.

Since the early 1970's, *P. oocarpa* has been extensively studied for provenance variation in adaptability and productivity (Dvorak and Donahue 1992, Greaves 1979). Results of the field studies suggest that provenances from Honduras and the Sierra de las Minas region of eastern Guatemala are generally the best volume performers (Birks and Barnes 1990). Outstanding sources of what was once called *P. oocarpa* from Nicaragua, like Camelias, San Rafael del Norte, and Yucul, have now been classified as *Pinus tecunumanii* (McCarter and Birks 1985). Similarly, what was once called *P. oocarpa* var. *ochoterenae* on the Mountain Pine Ridge, Belize (McCarter and Birks 1985), and in Chiapas, Mexico, is now called *Pinus tecunumanii* (Dvorak and Raymond 1991) even though not all taxonomists agree with the reclassifications (Squillace and Perry 1992).

An estimated several hundred thousand hectares of *P. oocarpa* are planted in the tropics, primarily Brazil, as an exotic. The productivity of the species as an exotic ranges from 10 to 18 m^3 per ha per year across many sites, with wood density of 0.420 to 0.500 g per cm^3 at 10 to 15 years of age. Continued interest in *P. oocarpa* as a plantation species declined in the early to mid-1980's because provenances of *P. tecunumanii* and *P. caribaea* var. *hondurensis* were found that were superior (Crockford 1990, Dvorak and others 1993, Dvorak and Shaw 1992). The disadvantages of *P. oocarpa* as a plantation species include its slow initial growth on some sites, poor wind firmness, susceptibility to nutrient deficiencies and needle diseases, and a relatively light crown that permits a continuous weedy understory to develop, increasing the fire danger. Recent problems of stem breakage in *P. tecunumanii* have once again stimulated interest in planting more *P. oocarpa*. Growers like its good wood quality, its ability to sprout from cut stumps, and the ease with which it vegetatively propagates, as well as its usefulness in developing hybrids with other tropical and subtropical pines.

Flowering of *P. oocarpa* begins in November in most of Central America and Mexico, and reaches its peak in late December and early January. Flowering always begins earliest in the driest areas or at the lowest elevations (Zamora 1981). Changes in climatic patterns, such as those brought about by El Niño, can cause flowering to occur as early as September in Central America (Houkal 1983). In northern Mexico, cones of *P. oocarpa* occur singly or occasionally in clusters of two or three (Pérez de la Rosa 1998). In southern (Chiapas) Mexico and Central America, cones are usually borne in clusters of three or four and the main crop matures from January through March, even though some cones can be found ripening on the tree most of the year. Generally there are several flushes of cones from December through April, but the ones that mature during February and March contain the most filled seeds. Because seeds usually fall to the ground in March, April, and May just prior to the onset of the rainy season (Wolffsohn 1984), old cones from past-year crops should not be collected.

In Central America and Mexico, mature cones are collected by tree climbers with poles. The poles have an S-shaped hook or sharp blade at one end, which is used to force the cones from the branch. At harvest, cones have a fresh weight moisture content of 20 to 25 percent (Robbins 1985). Cones can be placed directly in the sun to air-dry, the most common method used in Mexico and Central America. The amount of sunlight and the air temperature affect when cones open, usually in 3 to 5 days. During the air-drying process, the cones should be raked or moved around so all sides are exposed to the sun. Cone scales not exposed to the sun may remain closed. Cones stored in burlap bags or sugar sacks for several weeks may case harden and remain closed even when subjected to high temperatures.

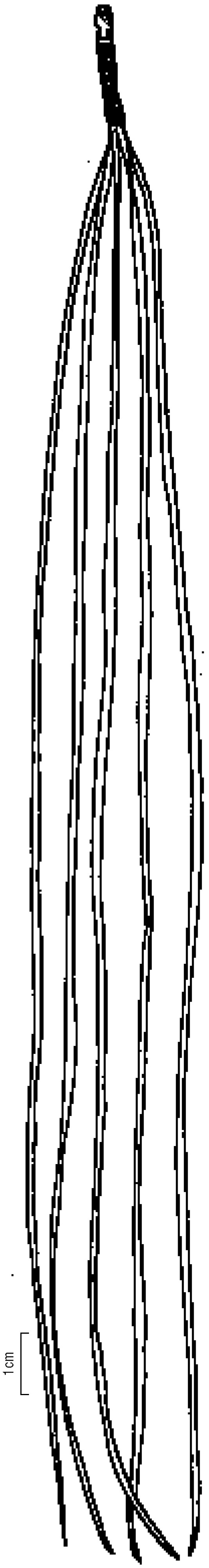
Cones of *P. oocarpa* will open quickly when placed in a kiln or tobacco drying barn at 40 to 44 °C for 24 hours. *Pinus oocarpa* can withstand kiln temperatures of 50 °C for 12 to 18 hours without loss of viability (Robbins 1985). Higher temperatures are not recommended. Because the seeds have thin coats that can be easily split or cracked, great care is needed if dewinging the seed by hand.

The seed potential of *Pinus oocarpa* is approximately 140 seeds per cone (Houkal 1983). Seed set is relatively low in natural stands. Several studies in Guatemala and Honduras revealed approximately 15 to 35 filled seeds per cone or a seed efficiency rate of about 12 to 30 percent (Houkal 1983, Hudson and others 1981, Ordoñez 1981, Robbins 1983, Wilkinson 1983). The number of seeds per kg for *P. oocarpa* was between 43,600 and 49,000 in Chiapas, Mexico (Zamora 1981), 51,000 in Honduras (Wolffsohn 1984) and 56,000 to 77,450 in Guatemala. In Guatemala, seed size was found to decrease with increasing elevation.

When *P. oocarpa* is planted as an exotic near the equator, seed yields are poor but improve with increasing latitude. In Colombia (2°N latitude), Arce and Isaza (1996) found only seven filled seeds per cone in stands 12 to 21 years of age established between 1360 and 1800 m elevation. *Pinus oocarpa* averaged approximately 25 filled seeds per cone in Venezuela (10° to 11°N latitude) in stands 10 to 12 years of age when established above 800 m elevation. The seed production of *P. oocarpa* is usually better than that of *P. caribaea* var. *hondurensis* at tropical low latitudes.

Seeds of *P. oocarpa* can be stored for a number of years at 4 °C if moisture content has been reduced to 6 to 9 percent after collection and the seeds are packaged properly. Commercial forestry nurseries soak seeds for 24 hours before sowing to improve both the rate and the percentage of germination. Cold stratification of seeds is unnecessary before germination for most provenances. However, some level of cold stratification may prove beneficial for the most northern sources of the species in Mexico.

Seeds will begin to germinate in 7 to 10 days using standard laboratory techniques (germinating seeds on moist filter paper in petri dishes) or nursery techniques (germinating seeds in moist sand). *Pinus oocarpa* seedlings usually reach a field planting height of 20 to 25 cm in 5 to 7 months. Plants tend to become bushy shortly after field establishment and remain that way for several years before a dominant terminal leader develops. Weeds should be well controlled during this period. Seedlings will resprout after heavy browsing by deer, and saplings will resprout from the base after either freezes or fires of low intensity. *Pinus oocarpa* should not be considered a cold-tolerant species.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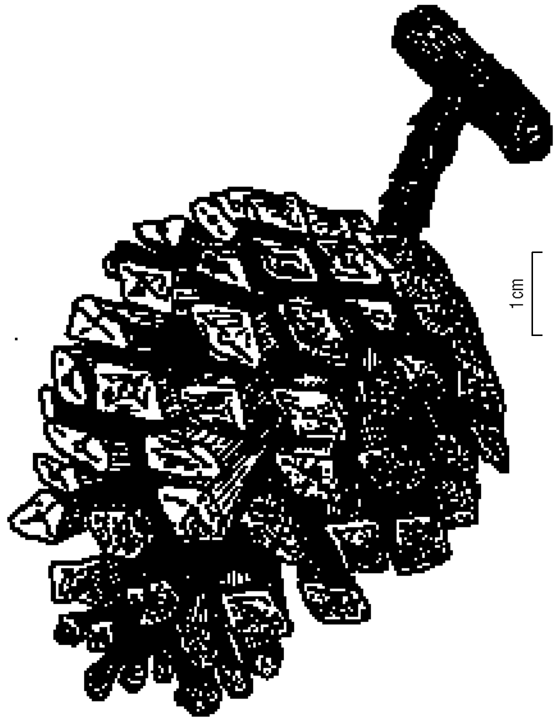
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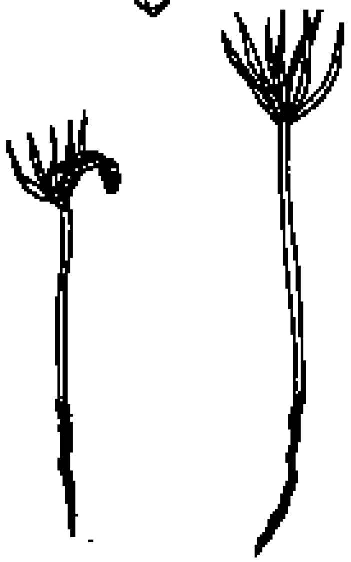

Pinus patula Schiede & Schltdl. & Cham.

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PINACEAE (PINE FAMILY)

No synonyms

Ocote colorado, ocote macho, pino chino, pino colorado, pino llorón, pino triste, pino xalocote (Patiño and Kageyama 1991, Paz Perez and de la Olvera 1981, Perry 1991)

Pinus patula var. *patula* occurs primarily in the Sierra Madre Oriental in the eastern part of Mexico between 18° and 24°N latitude. A closely related variety, *P. patula* var. *longipeduculata* Loock ex Martínez, is found primarily in the Sierra Madre del Sur in southern and western Mexico between 16°N and 17°N latitude. Because the seeds of both varieties can be handled in a similar fashion, they are referred to here as simply *P. patula*. When important differences occur between the two varieties, the varietal names will be used.

Pinus patula grows in both pure and mixed stands in association with *Abies* sp., *Carya* sp., *Juniperus* sp., *Liquidambar styraciflua* L., *Quercus* spp., *P. ayacahuite* Ehrenb., *P. douglasiana* Mart., *P. leiophylla* Schiede ex Schlectendal & Chamisso, *P. montezumae* Lamb., *P. pseudostrobus* Lindl., *P. rudis* Endl., *P. teocote* Schiede ex Schlectendal & Chamisso, and *Taxus* sp.

Pinus patula, a closed-cone pine with straight stem form, reddish flaky bark, and pale-green, pendent foliage, can reach a height of 35 m and 80 cm d.b.h. It grows on fertile, well-drained soils on mountain ridges and slopes in cloud forest environments at elevations between 1490 and 3100 m (Dvorak and Donahue 1992) but is most common between 2100 and 2800 m (Perry 1991). It generally occupies sites that receive between 1000 and 2000 mm of annual precipitation with distinct dry seasons of up to 4 months. Growth rates of trees of *P. patula* in natural stands may be as high as 8 m^3 per ha per year on the best sites. *Pinus patula* var. *patula* and sources of var. *longipeduculata* from northern Oaxaca are cold tolerant and can withstand hard freezes. However, sources of *P. patula* var. *longipedunculata* Loock in Martínez from southern and western Oaxaca are more susceptible to cold weather and suffered freeze damage when planted in field trials in South Africa. (Dvorak and others 1995).

The wood sampled from mature trees of *P. patula* in natural stands in Mexico is yellowish white in color and of moderate density: 0.440 to 0.600 kg per cm^3 (Quiñones 1974, Zobel 1965). It is used locally for posts, boards, boat frames, fruit boxes, mining timbers, telegraph poles, veneer, plywood, pulp, containers for exported products, furniture, and fuelwood (Patiño and Kageyama 1991, Romero 1991).

Pinus patula, tested in trials and pilot plantings as an exotic species in more than 20 countries (Wormald 1975), is now a major plantation species in southern Africa and the mountains of northern South America where more than 1.0 million ha are estimated to have been planted (Birks and Barnes 1991). Almost 300,000 ha are under operational management in South Africa (South African Department of Environmental Affairs 1993). Intensive provenance and progeny tests of *P. patula* have been initiated by the Central America and Mexico Coniferous Resources Cooperative (CAMCORE), North Carolina State University, including 23 sources and 593 open-pollinated families (Dvorak and others 1995). Results from studies in Brazil, Colombia, and South Africa indicate that provenances from the central part of the species range in Hidalgo, Puebla, and Veracruz are generally more productive than sources from far northern or southern Mexico when grown as an exotic (Dvorak 1997). *Pinus patula* was found to be more resistant to drought than the southern pine *P. taeda* L. and as tolerant as *P. elliottii* Engelm. in southern Africa (Morris and Molony 1993) but was more susceptible to damage or death from waterlogged soils. *Pinus patula* is very susceptible to the needle disease *Sphaeropsis sapinea* (formerly *Diplodia pinea*) in southern Brazil and South Africa.

Pinus patula appears to hybridize naturally with *P. greggii* Engelm. ex Parl. in Hidalgo, Mexico (Donahue and others 1995, Dvorak and others 1996b). Successful artificial crosses of *P.*

patula have been made with *P. greggii, P. oocarpa* Schiede ex Schlectendal, *P. tecunumanii* Eguiluz and J. P. Perry, and *P. radiata* D. Don (Critchfield 1967, Fielding 1960, Stanger 1994).

The species is grown primarily in plantations for pulp, paper, and sawtimber but is also used by some for charcoal (Wright 1994). The wood from plantation-grown *P. patula* is whitish to yellow whitish with a slightly pinkish heartwood (Dommisse 1994). The wood density of trees between 13 and 16 years of age in Brazil, Colombia, and South Africa was 0.389 g per cm^3, 0.400 g per cm^3, and 0.395 g per cm^3, respectively (Wright 1994). In South Africa, *P. patula* wood had the lowest percent extractives of 11 Southern United States and Mexican pine species studied (Dommisse 1994).

In its native range *P. patula* flowers from January to April (Patiño and Kageyama 1991, Romero 1991). Cones are collected from December to March, approximately 22 to 24 months after pollination. Climbers use a pole with an S-shaped hook or a sharp blade at the end to remove the cones. The maximum seed potential of *P. patula* is approximately 125 seeds per cone and for the variety *longepedunculata*, which has smaller cones, 95 seeds per cone. In its native range, the species is considered to be a shy cone and seed producer. Patiño and Kageyama (1991) indicate that cone and seed production in native stands begins when trees are approximately 15 years old. Only 22 filled seeds per cone were obtained from samples of open-pollinated *P. patula* trees in natural stands in Mexico (Barrett 1972).

As an exotic species in South Africa and Zimbabwe, *P. patula* flowers during September and October (Barnes and Mullin 1974, Van der Sijde and Denison 1967) with a second, less pronounced peak from January through May. In Colombia, male and female strobili are produced every month of the year with the greatest occurrence in July and August (Isaza 1996). Seed yields have often been higher in environments where *P. patula* has been planted as an exotic than in natural stands. Thirty-six to 66 filled seeds per cone were obtained in two separate studies in South Africa in plantations 7 to 11 years of age (Hagedorn and Raubenheimer 1996, Kanzler 1992), 45 to 50 filled seeds per cone were obtained in seed orchards 10 to 13 years of age in Zimbabwe (Barnes and Mullin 1974, Geary and Pattinson 1969), and 55 filled seeds per cone were found in 45-year-old plantations in Queensland, Australia (Dieters 1996).

The number of filled seeds per cone appears to be influenced by latitude and elevation of the planting site. In Colombia (2°N latitude), the best seed production was obtained between 1750 and 2500 m elevation; it then decreased at greater elevations (Arce and Isaza 1996, Lambeth and Vallejo 1988). In South Africa (25° to 30°S latitude) the number of filled seeds per cone increased from 1300 to 1500 m but decreased thereafter as elevation increased. In addition, cone yields increased with decreasing latitude (Stanger 1994) and a mean annual temperature between 13 and 16 °C was considered best for good seed production by Barnes and Mullin (1974).

Results from artificial crosses of *P. patula* in South Africa and Zimbabwe showed poorer yields per cone than for open-pollinated experiments. Strobili abortion rate was thought to be high because of the sensitivity of strobili to high temperatures in pollination bags (Van der Sijde and Denison 1967).

Cones should be collected when they are light brown. Cone crops may remain on trees for several years and old cones that are gray should not be collected because the seeds can be of poor quality.

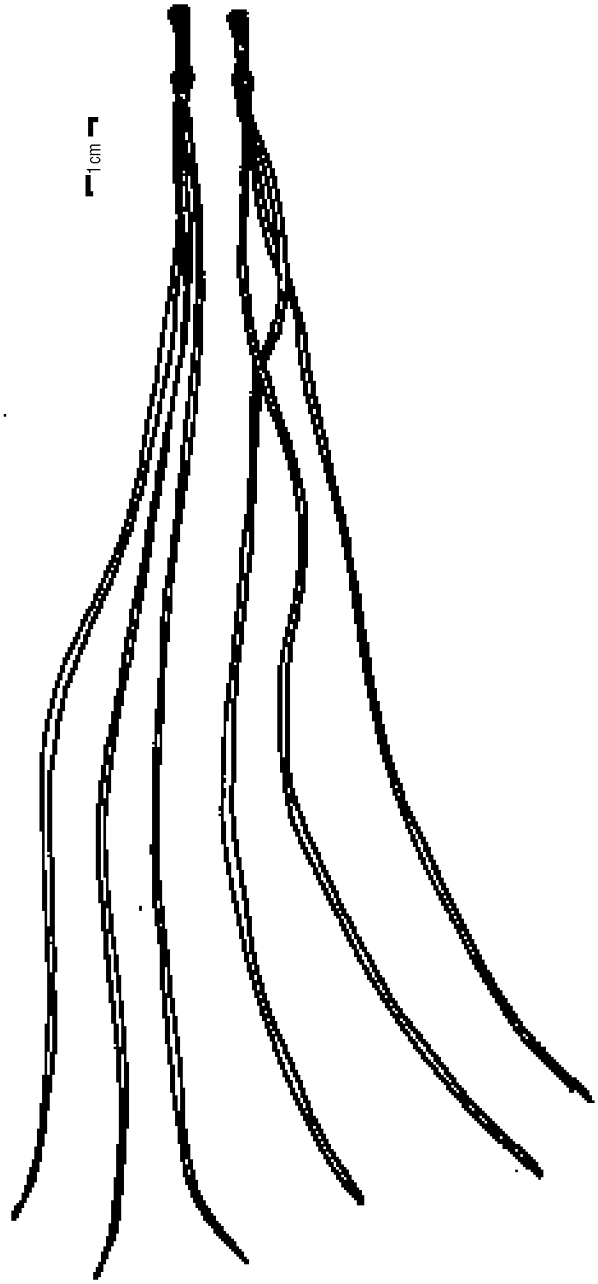
Seeds can be extracted by air- or kiln-drying the cones. In air-drying, cones are placed on tarps or in boxes or trays in an area with good air circulation. In many places in Mexico, cones are placed on a cement patio and dried directly in the sun. The amount of sunlight and the air temperature affect when the cones will open, usually in 2 to 7 days. In Zimbabwe and many other locations in southern Africa, cones are placed in a wood frame structure covered with clear polythene sheets. The plastic cover increases the air temperature in the shed and the cones usually open in 1 to 3 days (Marunda 1996). In South Africa, one practice involves placing cones in boiling water for 30 to 60 seconds and then kiln-drying them at 45 to 48 °C for 24 to 48 hours (Van der Merwe 1996). Accidentally boiling the unsheathed seeds will kill them instantly (Ghosh and others 1974b).

An average of 117,000 seeds per kg were obtained in natural stands in Mexico by Barrett (1972), with a range from 97,000 to 157,000 seeds per kg depending on the provenance. The CAMCORE Cooperative found an average of 118,000 seeds per kg in natural stands, with a range by provenance from 97,200 to 129,700 seeds per kg. The number of seeds per kg from plantations and seed orchards in South Africa and Zimbabwe ranged from 92,000 to 114,000 (Barnes and Mullin 1974, Van der Merwe 1996). Seeds kept at moisture contents between 6 and 9 percent remain viable for years if properly stored at 4 °C.

Seeds will begin to germinate without any cold stratification 7 to 10 days after placement in germination chambers, boxes, or nursery beds. Daniels and van der Sijde (1975) increased germination of *P. patula* seed 5 percent by cold stratification at 4 °C for 7 weeks, followed by storage at room temperature for 2 weeks. This practice is seldom followed in commercial operations. Soaking seeds in water at room temperature for 18 hours before sowing improves germination (Ghosh and others 1974a). The South African Pulp and Paper Industry Ltd. organization in South Africa soaks *P. patula* seeds in 1 percent hydrogen peroxide at 25 °C for 24 to 48 hours to promote consistently high germination (Bayley 1997). Large commercial forestry organizations in South Africa also place seeds in cloth bags in a swirling water bath (pH 5.6) at approximately 28 °C and force compressed air to bubble through for 24 hours before sowing the seeds. This practice both improves and promotes more uniform germination (Kietzka 1997). Percent germination of fresh or well-stored seed is generally above 85 percent in South Africa and Zimbabwe.

Pinus patula seeds germinate well in many different nursery media including decomposed *P. patula* bark (South African Pulp and Paper Industry Forests Research Report 1994) but not in sawdust and cow manure (Ghosh and others 1974b). Because the species seems somewhat sensitive to J-rooting, larger container sizes are recommended. A commercial forestry nursery in Colombia uses plastic tubes with 106 ml capacity for growing *P. patula* seedlings operationally and a slightly larger black plastic bag, 8 x 13 cm with 204 ml capacity, for plants intended to be sold to local farmers (Arce 1996). In South Africa, one nursery uses a 49-tubelet solid tray with dimensions of 340 mm x 340 mm for growing *P. patula* (Bayley 1997). The tubes have a diameter of 40 mm and a depth of 80 mm and contain five root-training ridges equidistantly spaced on the inner side of the cavities. Recently, nurseries in both southern Africa and northern South America have started to plant *P. patula* seedlings into the field when they reach 10 to 15 cm shoot height to lessen the probability of root development problems. Seedlings grow to plantable height in 4 to 7 months.

Pinus patula seedlings appear more sensitive to imbalances of nutrients in nursery soils and of watering regimes than Southern United States' pines (Sang Arap and Munga 1973, Van der Merwe 1996). Furthermore, seedlings are susceptible to different species of *Fusarium*. Pitch canker (*Fusarium subglutinans* f. sp *pini*) caused great mortality in a commercial *P. patula* nursery in South Africa in the early 1990's (South African Pulp and Paper Industry Forests Research Report 1993, Viljoen and Wingfield 1994). The species propagates easily from seedling cuttings and both pilot and operational rooted-cutting programs are in place in Colombia and South Africa.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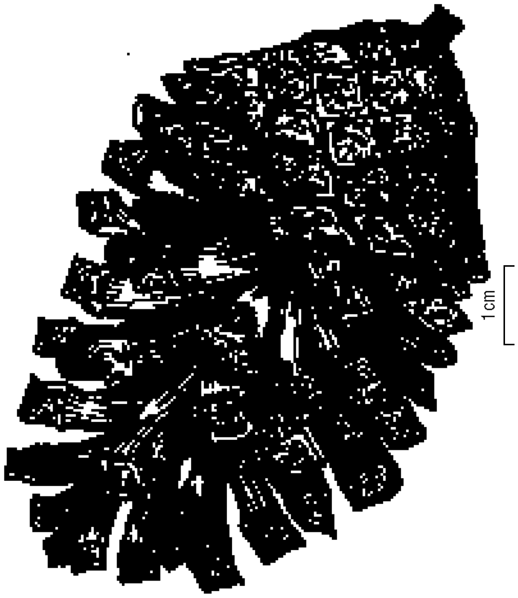
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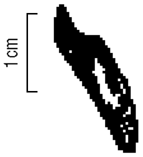
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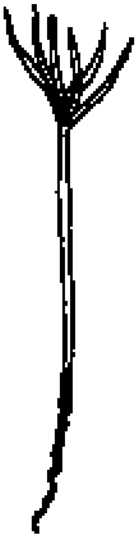

Pinus pseudostrobus Lindl.

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Especialidad Forestal del Colegio de Postgraduados
México

PINACEAE (PINE FAMILY)

P. orizabae Gordon (Martínez 1948, Stead and Styles 1984)

False Weymouth pine, macochyaj, macohtai, pino blanco, pino lacio, pino liso, pino real
(Carbajal and McVaugh 1992, Eguiluz-Piedra 1978, Farjon 1984, Perry 1991)

Pinus pseudostrobus is primarily a Mexican pine although its range reaches the high mountains in Guatemala. It is chiefly distributed along the Volcanic Axis Mountains in Central Mexico (Martínez 1948, Perry 1991). *Pinus pseudostrobus* forms pure stands or grows in association with *P. montezumae, P. douglasiana, P. michoacana, P. maximinoi, P. leiophylla, P. ayacahuite, P. patula, P. cembroides* Zucc., *P. rudis, P. pringlei, Abies religiosa* (Kunth) Schltr. & Cham., *Quercus* sp., *Arbutus* sp., *Juniperus* sp., *Buddleia* sp., and *Dasylirion* sp. (Eguiluz-Piedra 1978, Perry 1991).

Pinus pseudostrobus is one of Mexico's finest pines with its usually straight, branchless trunk. It is a fast-growing tree that reaches 30 to 40 m or more in height and 40 to 80 cm d.b.h. (Perry 1991, Stead and Styles 1984). The species grows at elevations from 1600 to 3250 m, but the best stands are found at 2500 m on deep volcanic soils. This tree can also be found in swallow and calcareous soils. *Pinus pseudostrobus* grows in temperate to temperate-warmer climates, where temperatures may drop to freezing during the coldest winter months. The species is found where temperatures range from -9 to 40 °C and annual rainfall from May to October is 600 to 2000 mm (Eguiluz-Piedra 1978, Martínez 1948, Perry 1991).

No geographic races have been reported, but the species can naturally hybridize with *P. montezumae.* (Perry 1991)

The wood is light, soft, strong, and yellow, with a specific gravity 0.32 to 0.51 and high pulp yields. It is widely used for general construction, hewn timber, decorative items, pulp, and firewood (Eguiluz-Piedra 1978, Perry 1991, Wright and Malan 1991, Wright and Wessels 1992, Zobel 1965).

The species begins reproducing at 6 to 7 years and flowers in February and March (Patiño-Valera 1973). Cones are ovoid or long-ovoid, slightly curved, almost symmetrical, not reflexed, 8 to 12 cm long and 5 to 8 cm wide. Cones are borne singly, or sometimes in groups of two and three, on short peduncles 10 mm long or more. Cones open when mature and soon fall, leaving the peduncles with some basal scales. Cone scales are thin, hard, 30 to 35 mm long, and 15 to 18 mm wide. The apophysis is raised-to-flat, 2 to 8 mm in height, and lightly transversely keeled; the umbo is dorsal, small, occasionally depressed, not prominent, and armed with a small, weak, deciduous prickle (Carbajal and McVaugh 1992, Martínez 1948, Perry 1991, Stead and Styles 1984). Maturation is indicated when the cones change from green to brown in color. The number of sound seeds per cone is 25 to 82 (mean 48). The percentage of sound seeds (per cone) is 20 to 43 percent; empty seeds, 3 to 23 percent (Aldrete and López-Upton 1993). Delgado (1994) found, in eastern México, 12 sound seeds per cone out of 73 potential seeds, seed efficiency of 16 percent, and 95 percent germination in one natural but affected location. Seeds are dark brown, 6 mm long, about 4 mm wide; the seed wings are pale brown, articulate, 20 to 23 mm long, and 6 to 12 mm wide (Carbajal and McVaugh 1992, Martínez 1948).

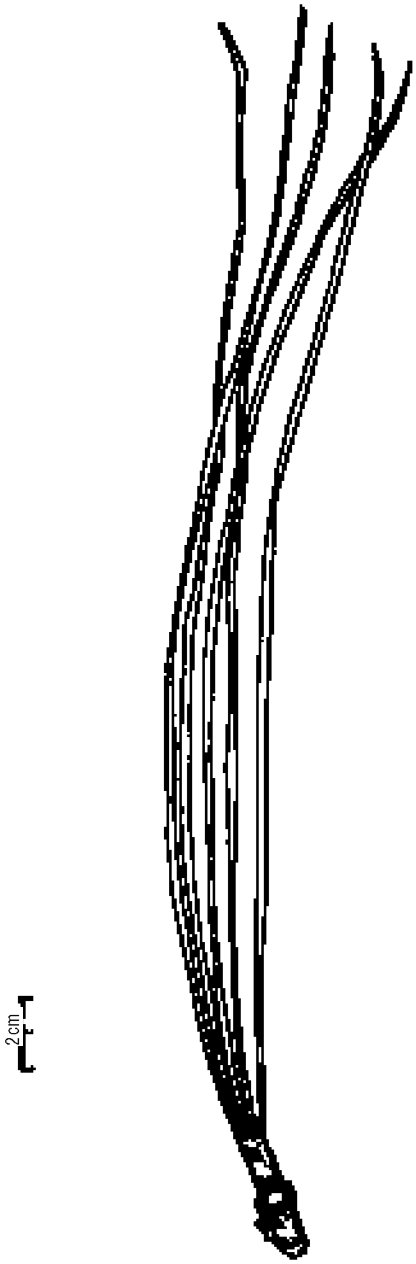
Cones mature in the second year, and ripe cones begin to appear from December to February, but the best time for collection is from January to mid-February (Aldrete and López-Upton 1993). Cones are collected from the tree using pole-mounted pruners and cutters. Cones are dried by exposing them to the sun for 4 to 6 weeks (Patiño-Valera 1973); however, they must be protected from rainfall during the drying process. Seeds are removed from cones by shaking in a large mechanical tumbler or shaker, or in a small manual shaker for small lots. Seeds are dewinged by rubbing or flailing, cleaned by air screen or floating in water, and should be dried before storage. Care must be used in processing with mechanical dewingers to avoid damaging the seeds. In central Mexico, seeds average 53,705 per kg. In Chiapas, México, seeds average 44,500 per kg (Patiño-Valera 1973, Zamora-Serrano and others 1993). Seeds must be stored in dry, cool (4 °C), and airtight conditions.

Seeds are pretreated by soaking overnight in water before sowing. Seeds should be sown at a depth of 1 cm, in seedbeds at densities from 12,000 to 15,000 per m^2 or 400 g (Zamora-Serrano and others 1993). The sowing medium must be sterile and light, providing aeration and moisture. The uncleaned-seed percent germination is 65 (Patiño-Valera 1973); the sound-seed percent germination is from 70 to 95 depending on provenance (Aldrete and López-Upton 1993). The best temperature for germination is 25 °C, which results in 50 percent germination in 8 days and 90 percent germination in 12 days. However, alternating temperatures between 20° and 30 °C will provide acceptable results (Belcher 1985). Seedlings are susceptible to damping off. Thus, substrata must be sterile or watering with a fungicide may be needed. The ectomycorrhizal fungi *Pisolithus tinctorius* (Pers.) Coker et Couch improves seedling field performance in both fertile and adverse sites (Valdés 1986).

ADDITIONAL INFORMATION

Pinus pseudostrobus wood production is 12 to 30 m^3 per ha per yr (Pancel 1993). There are 5,827 closed cones per m^3 (Patiño-Valera 1973). The interval between large cone crops is from 3 to 5 years (Zamora-Serrano and others 1993).

Leptoglossus occidentalis Heidemann and *Conophthorus ponderosae* Hopkins are the most important insect pests of conelets, cones, and seeds. *Tetyra bipunctata* (Herrich-Schaeffer) produces empty seeds. *Cecidomyia bisetosa* Gagné causes cone death. Larvae of *Cydia montezuma* Miller and *Megastigmus albifrons* Wik feed on seeds (Cibrián-Tovar and others 1995). Seeds and saplings are severely affected by the fungus *Shaeropsis sapinea* (Fr.) Dyko & Sutton (Rees and Webber 1988).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Pinus tecunumanii Eguiluz & J. P. Perry

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PINACEAE (PINE FAMILY)

Pinus patula ssp. *tecunumanii* (Eguiluz & Perry) Styles, *Pinus oocarpa* var. *ochoterenae* (Mart.)

Pino colorado, pino de las Sierras, pino ocote, pino rojo (Gutiérrez 1996)

Pinus tecunumanii is a closed-cone pine that occurs from Chiapas, Mexico (17°02’N) to central Nicaragua (12°42’N) in a series of disjunct populations (Dvorak and Donahue 1992). The species’ geographic range can be divided into two large subpopulations based on subtle morphologic and adaptability differences: high-elevation populations that occur from approximately 1500 to 2900 m elevation, and low-elevation populations that are found at 450 m to 1500 m (Dvorak and others 1989).

Mature trees from high-elevation populations can reach 55 m in height and more than 100 cm d.b.h. on the deep, fertile soils of the montane cloud forests of Guatemala and Honduras (Eguiluz and Perry 1983). The tree is easily recognized by its small crown and its thick, gray, furrowed bark near the base with thin, gray, flaky bark higher on the stem. It has a very straight stem form, small cones borne in ones and twos on long, thin peduncles, and needles in fascicles of mainly four (Eguiluz and Perry 1983). *Pinus tecunumanii* trees from high-elevation populations are often found in areas with greater than 1500 mm of annual rainfall and grow in association with *Liquidambar styraciflua* L., *P. ayacahuite* Ehren., *P. maximinoi* H. E. Moore, *P. oocarpa* Schiede ex Schlechtendal, and *Quercus* spp. The growth rate of trees of *P. tecunumanii* in high-elevation areas ranges from 5 to 8 m^3 per ha per year.

Trees from the low-elevation populations seldom grow larger than 30 m in height and 60 cm d.b.h., have less flaky bark and poorer stem form than their high-elevation counterparts, and often produce cones in clusters of threes or fours. On dry sites in Honduras and Nicaragua, *P. tecunumanii* is practically indistinguishable from *P. oocarpa* and, some taxonomists refer to the low-elevation sources as *P. oocarpa* var. *ochoterenae* (Squillace and Perry 1992). Trees from low-elevation sources grow in areas with 1000 to 1800 mm annual precipitation in association with *P. oocarpa*, *P. caribaea* var. *hondurensis* (Sénécl) Barr. and Golf., and *P. maximinoi*. The growth rate of trees from the low-elevation sources in Central America is approximately 3 to 8 m^3 per ha per year.

Molecular marker studies show a clear separation between high- and low-elevation populations of *P. tecunumanii* and suggest that the species may share a close evolutionary history with both *P. oocarpa* and *P. caribaea* var. *hondurensis* (Furman and others 1996). The Central America and Mexico Coniferous Resources Cooperative (CAMCORE), North Carolina State University, is keeping the two groups of *P. tecunumanii* separate for breeding purposes (Central America and Mexico Coniferous Resources Cooperative 1996). It is widely assumed, based on field observations, that *P. tecunumanii* crosses naturally with *P. patula* var. *longipedunculata* Loock ex Martínez, *P. oocarpa*, and *P. caribaea* var. *hondurensis* in its native habitat where the species occur sympatrically. Artificial hybrid crosses between *P. tecunumanii* and *P. caribaea, P. elliottii, P. oocarpa,* and *P. patula* have been made successfully by several institutions in the tropics and subtropics (Mather 1996, Nikles and Robinson 1989, Stanger 1994).

Pinus tecunumanii has a yellowish wood much like some of the southern pines from the United States. In natural stands, trees that averaged at least 30 years old had wood density that ranged from 0.510 g per cm^3 to 0.560 g per cm^3 (Eguiluz and Zobel 1986). In Mexico and Central America the wood is used for saw timber, framing, pallets, broom sticks, fuel wood, and kindling for fires.

Since 1980, *P. tecunumanii* has been the most widely tested Mexican and Central American pine in the tropics and subtropics, with more than 50 provenances and the progeny from 2,000 mother trees in field trials (Dvorak 1993). Results from the international series of trials established by CAMCORE indicated a 32-percent difference in volume performance between the best and worst high-elevation source of *P.*

tecunumanii (Central America and Mexico Coniferous Resources Cooperative 1997). The best high-elevation source was from San Jeronimo, Guatemala, and the best low-elevation sources were from Villa Santa, Honduras and Yucul, Nicaragua (Hodge and Dvorak 1998).

The low-elevation sources of *P. tecunumanii* are superior in productivity to high-elevation sources in Colombia, but these differences do not appear in South Africa. *Pinus tecunumanii* is only planted on a small scale as an exotic in places like Colombia and South Africa because of the high levels of stem breakage (Dvorak and Raymond 1991, Parfitt 1996). The wood of *P. tecunumanii* from both high- and low-elevation sources, when planted as an exotic, has proven to be acceptable for sawn timber, kraft, and thermomechanical pulp (Malan and Hoon 1991, Wright and others 1995).

With the possible exception of the Rancho Nuevo, Chiapas provenance, *P. tecunumanii,* shows little resistance to frost when planted as an exotic (Dvorak and Donahue 1992). The low-elevation *P. tecunumanii* sources appear to be more drought tolerant than *P. elliottii* on the sandy soils of Zululand, South Africa (Mather 1996), but are much more susceptible to *Phytophthora* root rot on the wetter sites than either *P. elliottii* or *P. caribaea*. *Pinus tecunumanii* appears to be much more resistant to *Sphaeropsis sapinea* in southern Brazil than does either *P. greggii* or *P. patula.*

In Central America and southern Mexico, *P. tecunumanii* produces male and female strobili from December through March and cones can be collected from January through March, 22 to 24 months later. Cones are usually borne in as many as three flushes, but those collected in mid-season (February) seem to have the highest percentage of filled seed. Cones should be collected when they are brown. If collected too green, the seeds have a pinkish tinge and germinate poorly. Cones are collected by tree climbers with poles. The poles have an S-shaped blade at the end, and cones are cut or broken from the branches. *Pinus tecunumanii* cones can be placed directly in the sun or an oven to open. Success in opening has even been achieved by placing cones inside a vehicle and turning on the heater. To oven-dry cones, maintaining a temperature of 40 °C for 24 hours is recommended.

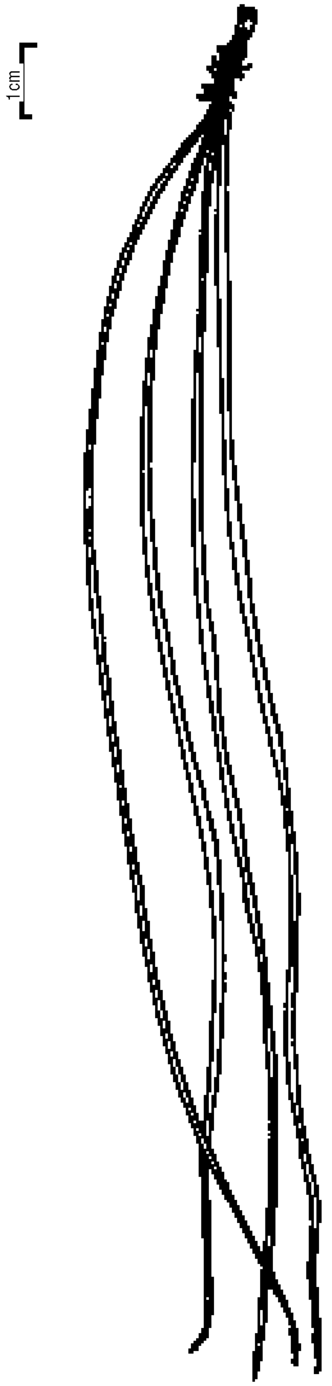
The high-elevation sources of *P. tecunumanii* are very shy cone producers in Mexico and Central America. A large tree (40 m tall) may have fewer than 50 mature cones that average only six filled seeds each (Dvorak and Lambeth 1993). Trees from low-elevation sources are generally more prolific cone producers and average approximately 30 filled seeds per cone. The maximum seed potential for cones from high- and low-elevation collection sites is 90 and 95, respectively (Dvorak and Lambeth 1993). Seeds from trees of high-elevation populations tend to be smaller than those from low-elevation sources. The average number of seeds per kg for high-elevation populations is 88,250; for low-elevation, 76,215.

Flowering time and duration of *P. tecunumanii* grown as an exotic has not been well-studied. However, in South Africa, a 2- to 3-week difference in flowering periods appears between clones of high- and low-elevation material when grown in the same seed orchard. In Colombia, flowers appear throughout the year, with a peak in August. Cone and seed production of *P. tecunumanii* is poor near the equator and northern latitudes but improves in southern latitudes. Regions for cone and seed production are best between 17° and 28°S in coastal Australia, Brazil, South Africa, and the highlands of Zimbabwe (Dvorak and Lambeth 1993). Seed orchards of *P. tecunumanii* established in Brazil, Costa Rica, Colombia, South Africa, and Zimbabwe are just beginning to produce seeds. In Colombia, studies are being implemented to determine how applications of gibberellins affect flowering. Scions of *P. tecunumanii* have been successfully grafted onto root stock of *P. elliottii* in South Africa (Mather 1996) and of *P. patula* and *P. oocarpa* in several regions. Grafting *P. tecunumanii* scions onto *P. taeda* L. rootstock failed in Brazil.

Seed storage and handling procedures for *P. tecunumanii* are similar to those used for many of the other hard tropical pines. Seeds stored in a plastic, air-tight container at 4 °C and with a moisture content of 6 to 9 percent should remain viable for years. However, *P. tecunumanii* has a thin seed coat that can be cracked, chipped, or split easily by rough handling, and care must be used during seed processing.

Seeds of *P. tecunumanii* can be easily germinated when laid on moist filter paper in petri dishes and placed in a germinator for 7 days. The seeds also readily germinate when placed in open boxes that contain moist sand. Normal germination for seeds from natural stands is approximately 75 percent. Commercial forestry programs sometimes soak seeds in water at room temperature for 24 hours before sowing. Germination begins 7 to 10 days after sowing.

Pinus tecunumanii will grow successfully in a number of different soil media including decomposed *P. patula* bark. Soil that is high in organic matter and holds water for long periods tends to slow or stunt the growth of *P. tecunumanii* (Dvorak 1985). The development and architecture of the root system is strongly influenced by container shape and size. The species is very susceptible to J-rooting, and trees have been observed falling over from root strangulation after 2 to 3 years in the field in Brazil, Colombia, Venezuela, and southern Africa when planted as an exotic. *Pinus tecunumanii* does not appear to produce a deep taproot (Dvorak 1990). To improve root development and seedling quality, nurseries are beginning to use large containers with ridged interiors and to outplant seedlings at a small size, usually between 12 to 15 cm shoot height. Cuttings from seedling stools root easily in most tropical environments (Easley and Lambeth 1989, Osorio 1992), and large improvements in productivity and uniformity will be achievable through replication of the best clones.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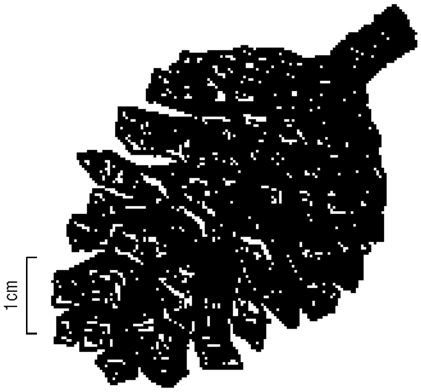
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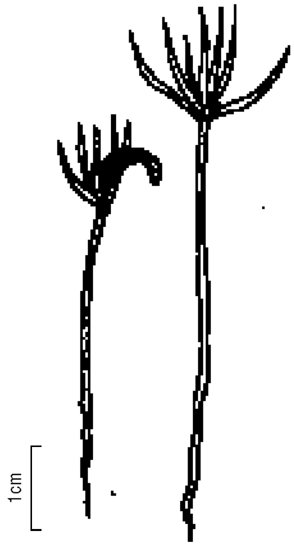
1cm

Platymiscium pinnatum (Jacq.) Dugand

L.A. FOURNIER
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FABACEAE (BEAN FAMILY)

No synonyms

Cachimbo, coyote, cristobal, granadillo, hormigo, ñambar, quira, quirei, sangrillo, swamp kaway

Platymiscium pinnatum grows from Central America to northern South America (Colombia, Venezuela, and Ecuador).

Platymiscium pinnatum is a slow-growing tree up to 35 m in height and 1 m d.b.h. It has a rounded crown and rough, green-gray bark. Leaves are opposite and odd-pinnate with stipules and with three to five short-petiolate leaflets. The broadly ovate-acute or acuminate glabrous leaflets are 5 to 20 cm long and 3 to 5 cm wide. The trees are usually deciduous during the dry season, December through April. The species grows primarily on the hills and the mountain slopes with good drainage in the dry, moist, and wet climates of the lowlands. The tree grows in different types of soils and is adapted to a wide range of rainfall (1500 to 3000 mm per year), an annual average temperature of 23 to 26 °C, and elevations from sea level to 600 m.

The hard, strong wood of *P. pinnatum* is considered moderate to heavy with a specific gravity of 0.50 to 0.86. The transition from sapwood to heartwood is gradual; when dry the sapwood is dark yellow and the heartwood is red-brown. The grains are oblique and slightly intercrossed, the texture is fine, and the luster is moderate. It is easy to dry and preserve, has good workability, and shows no defects during the drying process. The wood is naturally durable and resists decay. It is used for high-quality flooring, paneling, furniture, crafts, and veneer and in cabinetwork and heavy construction. Because the wood is durable even in contact with the ground, it has been used for railroad ties in Colombia (Allen 1956).

The small, pale-orange flowers are produced from December through April, and sometimes in May. The flowers appear in clusters of slender racemes from the subterminal or axillary defoliate nodes, rendering the trees very conspicuous and attractive from a distance (Allen 1956). The fruits are indehiscent pods about 7 cm long that mature within 30 days (Allen 1956). The pods are flat, rather leathery, and elliptic or nearly oblong. They each contain one seed.

Production of this fine timber tree is primarily from natural forests, and information on nursery practices and seedling care is nonexistent. Nevertheless, the seedlings of *P. pinnatum* that are growing naturally in the forest can be outplanted (personal observation).

Fusarium roseum, a fungus, has been reported as a parasite of the foliage of this species (Arguedas and others 1993).


1cm
1cm
1cm

Podocarpus montanus (Humb. & Bonpl. ex Willd.) Lodd.

V.M. NIETO AND J. RODRIGUEZ
Corporacion Nacional de Invesitgacion of Forestal
Santafé de Bogotá, Colombia

PODOCARPACEAE (PODOCARPUS FAMILY)

Nageia montana, Podocarpus taxifolia, Prumnopitys montana, Stachycarpus montana, Taxus montana

Pino de montaña, pino de pacho, pino hayuelo, pino romerón

Podocarpus montanus is a very slow-growing tree that reaches 15 m in height and 30 cm d.b.h. The crown is semi-round and not very dense; the bark is purple to blackish, scaly, and covered with shoots. The evergreen leaves are alternate, narrow, coriaceous, bluish in the lower part, inserted in spiral but stretched out in two series on a plane, 12 to 22 mm long by 2.5 to 3 mm wide, with a groove over the prominent central vein. The tree adapts to poor soils with good drainage, acid pH, and loose clayey texture. It grows at elevations from 1900 to 3000 m with an average annual temperature of 8 to 16 °C and annual precipitation of 600 to 3000 mm. It tolerates short frosts. It adapts to the life zones of the Low Mountainous dry forest (bs-MB), Low Mountainous wet forest (bh-MB), Low Mountainous very wet forest (bmh-MB), Mountainous wet forest (bh-M), and Montainous very wet forest (bmh-M).

The wood of *P. montanus* is used for veneer, furniture, lath, posts, wood shaving boards, and in cabinet-making. It is also used as pulp for paper and in pencils (Corporacion de Los Andes 1974, Lamprecht and Liscano 1957, Marin 1998).

The strobiles are dioecious. The masculine flowers are elongated, cylindrical, and numerous; 1 to 5 cm long; and sessile or on a short peduncle. The feminine flowers are very small and isolated at the tips of the branches. The cones (fruits) are globose, 1 to 2 cm long, 0.8 to 1 cm wide, smooth, soft, and shiny dark green when not ripe. They turn orange-yellow when ripe. Clean seeds are 8 mm long and 5 mm wide (Marin 1998).

The cones are collected from the tree or the ground. Old cones or seeds are not collected because the seeds are frequently attacked by a borer on the ground. Seeds are stored at 3 to 4 °C. Seed purity percentage is 99 percent. Germination is epigeal. Germination percentage is 45 to 60 percent, and seeds germinate in 3 months.

Podocarpus montanus is propagated through its seeds. Because the seeds are relatively large, they can be planted in bags. The planting hole should be 2 cm deep and separated from other holes by 20 cm. The seeds are covered with fine, well packed soil, watered abundantly, and shaded during the first 6 months.

Plantules are lifted in two stages, with an interval of 2 to 3 months. Periodically (4 to 6 weeks), the ground is pricked to maintain a good physical condition, and weeds are eliminated. When the plantules are 25 to 40 cm high, they are outplanted. The planting site should be relatively clean; however, excessive cleaning can promote the growth of an underbrush that suffocates arboreal vegetation.

Planting distances vary. For conservation of germplasm, a semiregular spacing of 1 by 1 m between plants is used. To produce a forest, distances of 3 to 5 m can be used.

Polylepis besseri Hieron.

W.A. PATTERSON IV
Returned Peace Corps Volunteer, Bolivia

ROSACEAE (ROSA FAMILY)

P. crista-galli Bitter, *P. triacontandra* Bitter, *P. incana* H.B.K. ssp. *brachypoda* Bitter, ssp. *incarum* Bitter, ssp. *subtusalbida* Bitter, *P. racemosa* Ruíz & Pavón var. *lanata* Kuntze, and var. *tomentosa* Kuntze

Coloradito, keñua, keru, keshua, kewiña, q'ueñua, queñua, quenuina, queuñua, quewiña, quinhuar, quiñual, quiñuar, yagual

Distribution of the genus is restricted to the Andean corridor of South America from Venezuela, south to northern Argentina and Chile. *Polylepis besseri* forests most commonly occur in small (1 to several ha) isolated patches surrounded by high-elevation grasslands and agriculture. Characteristically forming open-structure, monotypic forests at high elevations in the Andes of South America, *P. besseri* is also found in association with *Buddleja* sp., *Escallonia* sp., and *Gynoxis* sp. (Fjeldsa and Krabbe 1990).

A slow-growing tree tolerant of wind, freezing temperatures, solar radiation, and moderate drought, *P. besseri* thrives in some of the harshest tropical environments. Depending on environmental factors, the species can vary from shrub to small tree and range in height from 3 to 10 m with an average of 7 m. Commonly occurring as a low, multibranched cup with a crown diameter of 4 m, *P. besseri* also grows in a more erect, cupped form with a single trunk reaching a maximum d.b.h. of 45 cm. Rusty colored, papery, flaking bark combines with the tree's contorted growth form to give a unique appearance. The tree prefers rocky, well-drained soils, usually on steep slopes of sandy loams, and tolerates moderate acidity and nutrient-poor soils. As a major primary source of organic matter, *P. besseri* is important in forming and protecting soils in climatic zones with characteristically sparse vegetation (Borter 1994). *Polylepis besseri* typically grows at elevations between 3000 to 4000 m in areas with rainfall ranging from 300 to 1200 mm (Borter 1994). These trees grow at higher elevations than any other tree in the world (Killeen and others 1993), surviving as high as 5200 m on the slopes of Nevado Sajama in Potosi, Bolivia. As an evergreen tree that does not resprout and has low fire tolerance, *P. besseri* is highly susceptible to the pressures of agricultural expansion and fuelwood consumption.

Frequent hybridizing within the *Polylepis* genus causes much confusion in species identification, the most common *P. besseri* crosses being with *P. tomentella* Wedd., *P. (aff.) australis* Bitter, and various subspecies (Killeen and others 1993).

Though often twisted and poorly formed, *P. besseri* wood has an attractive reddish color and is very strong and durable. The specific gravity of *P. besseri* wood is not found in the literature, but experience shows that it is a relatively dense wood and resistant to rot. In a study of all tree species in the highlands of Bolivia, *P. besseri* proved to be the most frequently and widely used based on a series of questions asked of subsistence farmers (Ledezma 1994). Traditional uses include: charcoal, home construction, tools, plows, firewood, cooking utensils, soil conservation and improvement, wind and frost protection, paddle wheels for water-powered mills, fenceposts, urban forestry, medicine for colds, musical instruments, and dyes for clothing (Arze and Weeda 1996, Borter 1994, Fossati 1996, Ledezma 1994).

Polylepis besseri can flower any time of the year with a peak flowering season March through May (Fossati 1996). Flowers are generally red and without petals, arranged in axillary racemes of 1 to 70 flowers. Each flower produces a single fruit 7 to 10 mm long. The fruit consists of 3 turbine-shaped wings running along the axis of the seedcoat and a single, ovular seed that is pointed at one end and 3 to 5 mm long (Killeen and others 1993). The fruits dry on the tree in 5 to 6 months, providing the greatest amount of ripe seed from August through November (Fossati 1996).

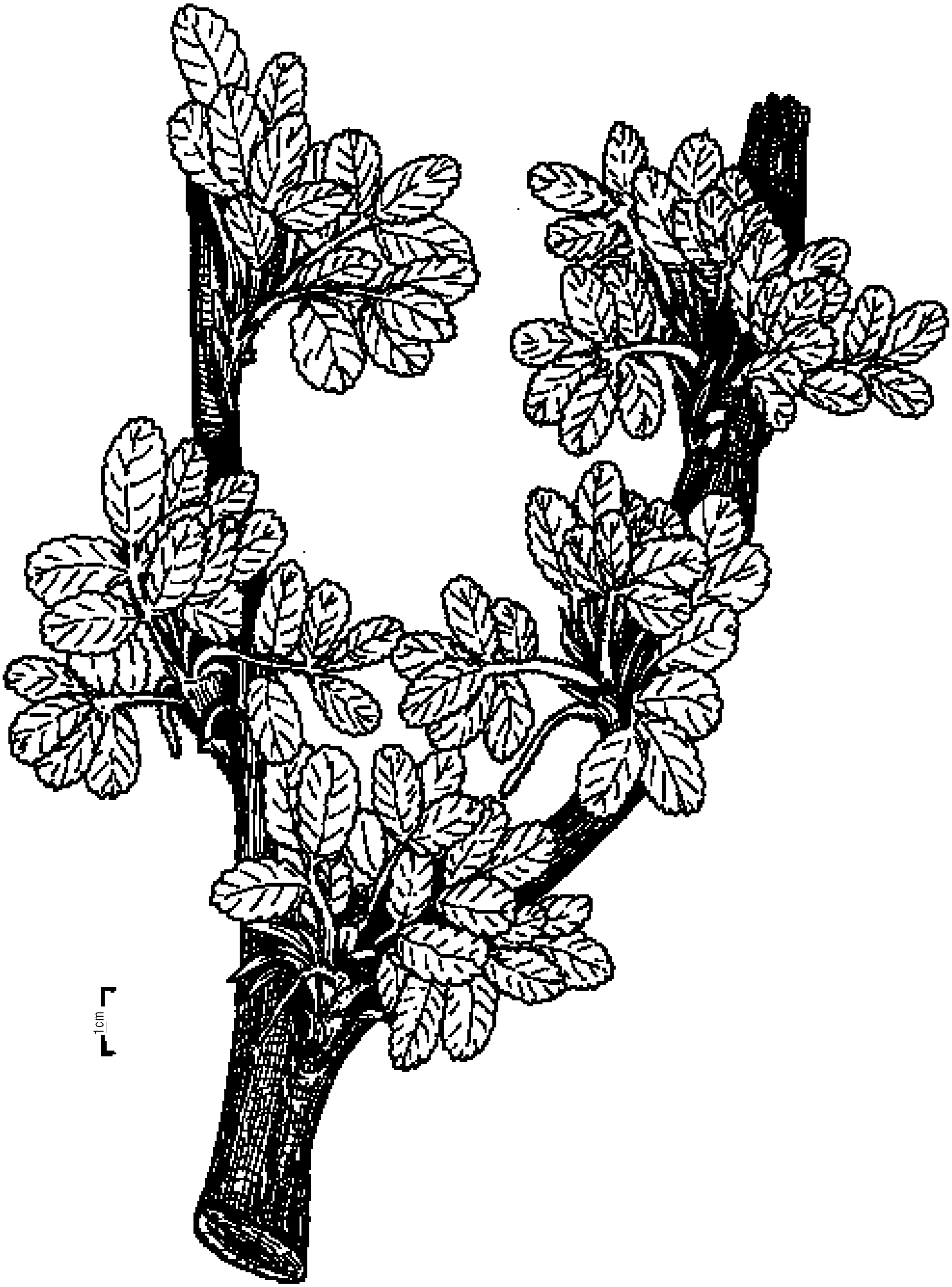
Ripe seeds from *P. besseri* must be collected after they are dry but before they fall to the ground, because of their very small size. Seeds are commonly collected from select branches cut as firewood; no special tools are needed since this species does not exceed 10 m in height and is easily scaled. Seeds average 80,000 to 120,000 per kg (Borter 1994). Seeds have a very low germination rate (2 to 15 percent) with no satisfactory pregermination treatments known. Because the germination rate diminishes rapidly in storage, limited seedbed production can be achieved only through planting in substrates of high sand and organic matter content immediately after collection.

The preferred method of seedling production is possible when parent trees are available locally. The soils beneath the trees are cleared of all vegetation and loosened before the seeds drop. Naturally germinated seedlings can then be extracted and transported in small plastic bags sprinkled with water to a nearby nursery, where they can be transplanted to containers for future development (Fossati 1996). Seedlings in containers should be shaded at first, then grown in full sunlight after they have adapted to transplantation. Normally, seedlings develop in the nursery for 12 to 18 months. An alternative method involves cutting 1- to 2-year-old branches into 15- to 25-cm lengths at the start of the rainy season, soaking them for 24 hours in water or root-inducing hormone, and either planting the cuttings in a sandy soil mixture in nursery containers or directly planting them in the field (Mamani and Apaza 1995).

Although established *P. besseri* trees are extremely resistant to harsh climates, seedlings require protection from drought, wind, and grazing animals. Because growth is very slow, these trees need many years to establish, an obvious disadvantage to reforestation efforts. Given their adaptation to reproduction within the shelter of monotypic stands, the best *P. besseri* management strategy may be to prevent complete deforestation and manage for sustained natural reproduction within existing forests.

ADDITIONAL INFORMATION

The cause of the small size and isolated nature of *P. besseri* forests is the subject of some debate. One theory holds that *P. besseri* competes best in high-elevation microsites of rocky, well-drained, frost-free soils with microclimates of nightly mists and cold air drainage—in effect creating low-elevation microenvironments at high elevations (Simpson 1977). Alternatively, paleobotanical and historical evidence suggests that *P. besseri* forests were once much more extensive, and that burning, grazing, and other anthropic pressures have greatly reduced their area during the last 3,000 years, particularly over the last several hundred years (Fjeldsa and Kessler 1996, Fjeldsa and Krabbe 1990). Because of its unique position as the highest growing tree in the Andes, the genus *P. besseri* is extremely important both ecologically and as a human resource (Ledezma 1994, Ridgley and Tudor 1989). *Polylepis besseri* provides a rare source of high-elevation forest habitat, which several species of avifauna rely on exclusively (Fjeldsa and Krabbe 1990, Ridgley and Tudor 1989).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Pouteria campechiana (Kunth) Baehni

ANÍBAL NIEMBRO ROCAS
Instituto de Ecología, A.C.
Xalapa, Veracruz, México

SAPOTACEAE (SAPODILLA FAMILY)

No synonyms

Canishte, k'anixté, mamey de Campeche, zapote amarillo, zapuyul

Pouteria campechiana is native to America. It is distributed naturally in Mexico and Central America, where it forms part of the wet and subhumid tropical forests.

Pouteria campechiana is an evergreen tree that reaches 30 m in height and 30 cm at d.b.h. The trunk is straight with an irregular and dense crown, made up of thin and horizontal branches. The leaves are simple, alternate, gathered at the tips of the branches, oblanceolate to oblanceolate-oblong, 6 to 25 cm long, and 2.5 to 8 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree grows have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm. The species grows at elevations near sea level.

Because the tree is appreciated for its edible fruits, it is planted in yards and orchards. The wood is hard and resistant, and it is used for firewood and in rural construction (Barrera 1981, Cabrera and others 1982, Chavelas and González 1985, Escalante 1986, Flores 1993).

The tree begins to yield flowers and fruits between 4 and 5 years of age. In southeastern Mexico, *P. campechiana* blooms May through June, and fruits between July and November (Juarez and others 1989). The flowers are light green, sweet-smelling, and arranged in small axillary fascicles. The fruits are pyriform or subglobose berries, up to 7 cm long, 2.5 to 5 cm in diameter, yellow when ripe, and pulpy, with a thin peel and a yellowish, sweet-tasting pulp. Each fruit contains 3 to 5 seeds (Cabrera and others 1982, Miranda 1975, Pennington and Sarukhan 1968). The seeds are ovoid to globose, terete in cross section, and 2 to 4 cm in diameter. The seedcoat is light brown in color, smooth, shiny, and osseous. It has a long and large lateral hilum scar that is white or yellowish-cream in color and occupies part of the body of the seed.

From August through October, the fruits are collected either directly from the ground or by climbing the trees and using poles with metal hooks. The pulp is removed from the pulpy fruits by hand inside a bucket of water. Resulting impurities float and are gathered with a strainer. Good seeds sink. Subsequently, the seeds are dried in the sun in ventilated places for 1 or 2 hours, depending on the lighting conditions. Seeds average 490 per kg. Seeds remain viable for approximately 9 months when stored under ambient conditions (24 to 30 °C). With longer storage seed viability quickly diminishes (Vega and others 1981).

The germination of the seeds is cryptocotylar. To improve germination, the seedcoat should be broken before sowing. The fresh seeds germinate at 18 percent. A heterogeneous sample of seeds germinated 68 days after sowing (Vega and others 1981).

ADDITIONAL INFORMATION

The seed hilum is subbasal. The micropyle is indiscernible. The embryo has a straight axis; is relatively symmetrical and cream-colored with pink hues; and fills the seed cavity. The two massive cotyledons are pulpy, shaped like the seed, plano-convex in cross section, and strongly attached to one another, with smooth surfaces, sinuous contact surfaces, and latex. The plumule is undifferentiated. The radicle is small and conical or puntiform (Cronquist 1946, Eyma 1966, Guil 1967, Pennington and Sarukhan 1968, Pilz 1981, Reitz 1968, Wood and Channel 1960).


2cm

Pouteria sapota (Jacq.) H.E. Moore & Stearn

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Xalapa, Veracruz, México

SAPOTACEAE (SAPODILLA FAMILY)

No synonyms

Mamey, mamey colorado, zapote mamey

Pouteria sapota is native to America. The precise area of its natural distribution is unknown because the species has been introduced and cultivated throughout tropical America since pre-Hispanic times. It grows from Mexico through Central America, to northern South America and in the West Indies.

Pouteria sapota is a deciduous tree that can reach 40 m in height and 80 cm d.b.h. The trunk is straight and sometimes has spurs. The pyramidal crown is made up of horizontal, separated branches. The leaves are simple, alternate, gathered on the tips of the branches, obovate or oblanceolate, sometimes slightly curved, 10 to 50 cm long, and 7.5 to 16 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The plant prefers sandy-loamy, deep, and fertile soils. The regions where the tree grows have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May, the minimum temperatures to the months of December and January. Average annual precipitation is approximately 1299 mm, ranging between 900 and 1800 mm.

Pouteria sapota produces one of the most delicious fruits in the tropics. It is eaten raw and is used in jams, drinks, and ice creams. The oil contained in the seeds is used to treat dandruff and to stimulate hair growth. The strong, hard, and compact wood is used in rural construction and for firewood, stakes, boards, beams, and furniture. The tree is frequently cultivated in backyards (Aguilar 1966, Barrera 1981, Chavelas and González 1985, Flores 1993, Hoyos 1979, Miranda 1976, Rico-Gray and others 1991).

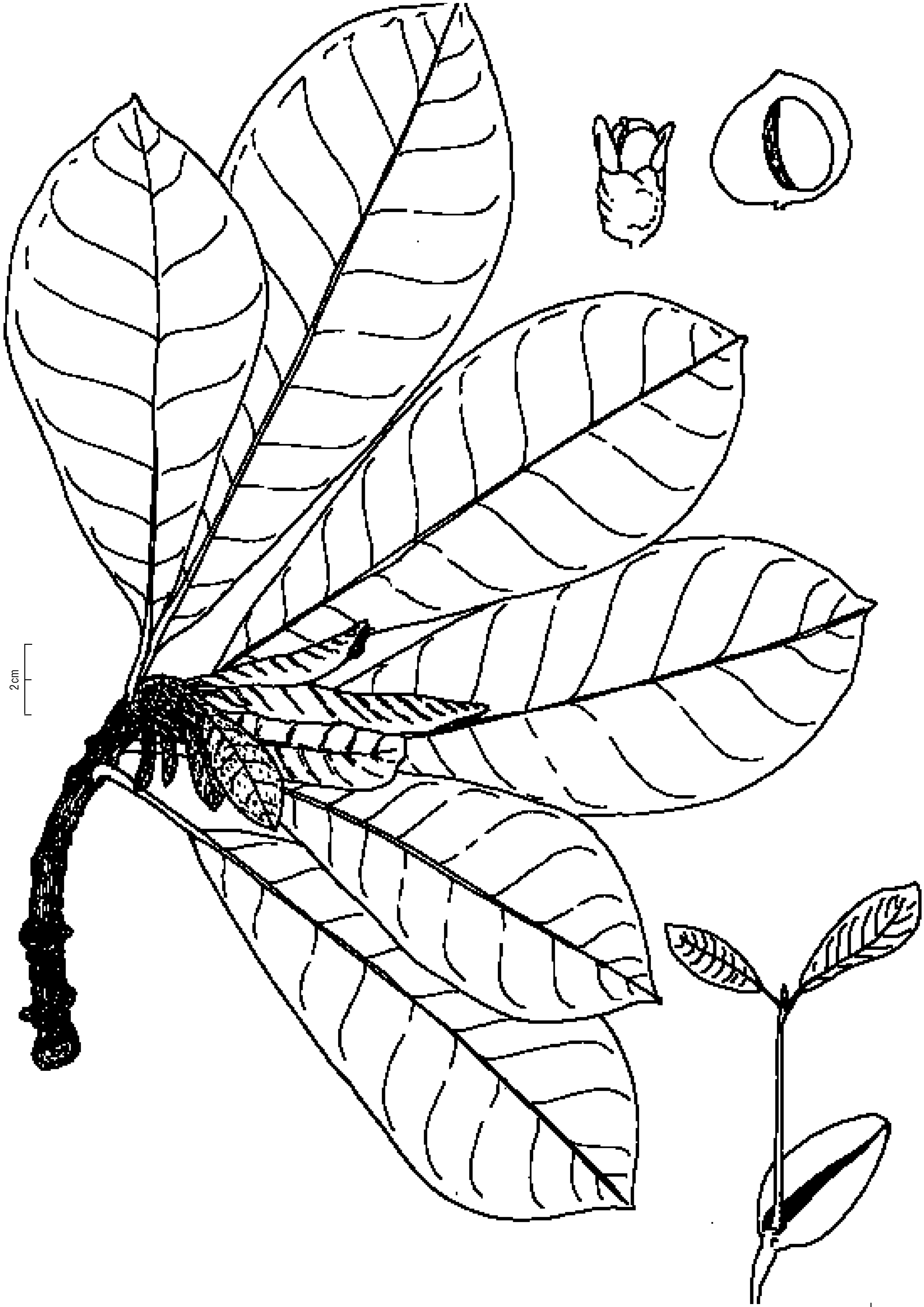
The tree blooms August through October and fruits December through March (Pennington and Sarukhan 1968). The fruits are often seen in the markets during April and May (Martínez 1959). The flowers are white to greenish-cream, almost sessile, and gathered at the axils of the fallen leaves. The trees begin to yield fruits at 8 to 10 years (Kennard and Winters 1960, Miranda 1976). The fruits are globose or ovoid berries, up to 20 cm long, 7.0 to 12 cm in diameter, reddish brown when ripe, and pulpy, with a thick and rough peel and a red-orange or pink pulp; the pulp has a sweet and pleasant taste. Each fruit normally contains one seed (Pennington and Sarukhan 1968). Seeds are ellipsoid to ellipsoid-ovate, acute on the tips, terete in cross section or slightly flattened laterally, 8 to 10 cm long, and 3 to 6 cm wide. The seedcoat ranges in color from brown to black; is smooth, shiny, and osseous; and has a lateral, long, and large hilum scar that is white to yellowish cream in color and occupies part of the body of the seed.

The way to gather fruits depends on the size of the tree. If the tree is short, the fruits are gathered from the ground, using wooden poles with metal hooks. If the tree is tall, gatherers must climb to its crown. The pulp is removed from the pulpy fruits by hand inside a bucket of water. Resulting impurities float and are gathered with a strainer. Good seeds sink. Subsequently, the seeds are dried in the sun in ventilated places for 1 or 2 hours, depending on the lighting conditions.

This tropical species is easily propagated from its seeds, which sometimes germinate inside the fruit. Removing the testa before sowing shortens germination time. Germination is cryptocotylar, and the growth of the plantule is slow. The seeds are planted in seedbeds or directly in containers, placing the thinner part of the seed downward.

ADDITIONAL INFORMATION

The hilum is subbasal. The micropyle is indiscernible. The embryo has a straight axis, is relatively symmetrical and cream-colored with pink hues, and fills the seed cavity. The two cotyledons are massive, pulpy, shaped like the seed, plano-convex in cross section, and strongly attached to one another, with rugose surfaces, sinuous contact surfaces, and latex. The plumule is undifferentiated. The radicle is small and conical or puntiform (Eyma 1966, Guil 1967, Pennington and Sarukhan 1968, Reitz 1968, Wood and Channel 1960).


2cm

Prioria copaifera Griseb.

C. SANDÍ and E.M. FLORES
Escuela de Agricultura del Trópico Húmedo and
Academia Nacional de Ciencias de Costa Rica, Costa Rica, respectively

FABACEAE (BEAN FAMILY)

No synonyms

Amansa mujer, camíbar, canime, cativo, cativo blanco, cativo negro, cautivo, floresa,
Spanish walnut, tabasara, taito, trementino (Record and Hess 1949)

The genus is monotypic and its geographic range extends from Nicaragua to Colombia (Jiménez 1993). It is also found in Jamaica. The cativales, stands of *Prioria copaifera* trees, form a belt 1 to 3 km wide in the land behind the mangrove fringe, along the Caribbean coast of western Panama and Costa Rica. Stands of the species are also found in the lower valleys of some of the larger rivers (Record and Hess 1949). The tree grows associated with *Pterocarpus officinalis, Carapa guianensis, Pentaclethra macroloba*, and the palm *Raphia taedigera* (Mart.) Mart.; when it grows on slopes, it also associates with *Dussia cuscatlanica* and *Carapa guianensis* (Jiménez 1993). In Costa Rica it is protected as a threatened species (Jiménez 1993).

Prioria copaifera is a tall canopy tree, unarmed, reaching 40 m in height and 100 to 150 cm d.b.h. The bole is straight, cylindrical, and without buttresses (Holdridge and Poveda 1975). The bark is gray, smooth, and thick (2.0 to 3.0 cm). The inner bark is reddish. Leaves are paripinnate, long petiolate, with two pairs of pellucid-dotted leathery leaflets, pellucid-dotted, leathery, elliptic-acuminate, asymmetrical base, with translucid dots, stipulate, and dark green; stipules are scaly and fugacious. The tree grows on rich loamy soils along coastal plains, on slopes, on river banks seasonally flooded, or in swamps. The common elevation range is from 0 to 40 m, although it can be found at elevations up to 150 m (Jiménez 1993).

Transition from sapwood to heartwood is inconspicuous. The green wood is light brownish gray; air-dried wood is light yellowish gray. A false heart in the pith is frequent; it is usually dark reddish brown. Growth rings are outlined by fine, light stripes (Richter 1973). The grain is straight or interlocked depending on wood origin; texture is medium or coarse; luster is low; and the wood lacks figure and is odorless and tasteless after drying. The wood is moderately heavy: green weight is 855 kg per m^3, with a moisture content of 91 percent; basic specific gravity is 0.45 (range 0.38 to 0.46) (Llach 1971). Air-drying is fast with only slight defects. Working properties are average. The polish is not very good when the grain is interlocked. The mechanical properties of *P. copaifera* are similar to those of yellow poplar (*Liriodendron tulipifera* L.), but the former is superior in hardness and compression through the grain. Natural durability is low; it is quite susceptible to termite and fungal attacks and marine borers; it is not suitable for exterior construction. Wood preservation is easy. The wood can be used in carpentry, cabinetwork, and interior construction and to make boxes, cases, and boards. The Peteri's coefficient of flexibility is 37 and the Runkel factor 0.28 (group II: very good for making paper) (Richter 1973). The timber has high quality. The dark brown, resinous gum obtained by cutting the bole has a stinging taste and is used by natives as a fly-trap. The natives claim it can also be used to trap bats, birds, and other small animals. The resin is also used to heal cuts and bites and as a general antiseptic (Pittier 1957, Record and Hess 1949). The seeds are edible and eaten locally.

Flowering occurs from December to May and September through November, with variations along the geographic range. The inflorescences are long panicled spikes, bracteate, and terminal in twigs; they have spike-like branches bearing many flowers. Flowers are small, creamy or whitish, fragrant, and sessile, with two-lobed, cup-shaped bracteoles. The flower is apetalous. The calyx is tubular, short, five-lobed, orbicular, petaloid, and imbricate. The androecium has 10 stamens that are free and unequal. The gynoecium is sessile or short-stalked, monocarpellar, and biovulate. Fruits are produced in February and March and September through November. The fruit is a brown pod, obliquely obovate-orbicular, 6 (10) -12 cm long by 6 (7)—8 cm wide, woody, and indehiscent, containing a single seed. The pod is laterally compressed; one side is convex and the other concave. Seeds are flat, large, overgrown, exospermic, with undifferentiated testa, and surrounded by the pod; pod dimensions limit the seed and embryo growth. Fresh seeds (seed plus pericarp) average 30 to 35 per kg.

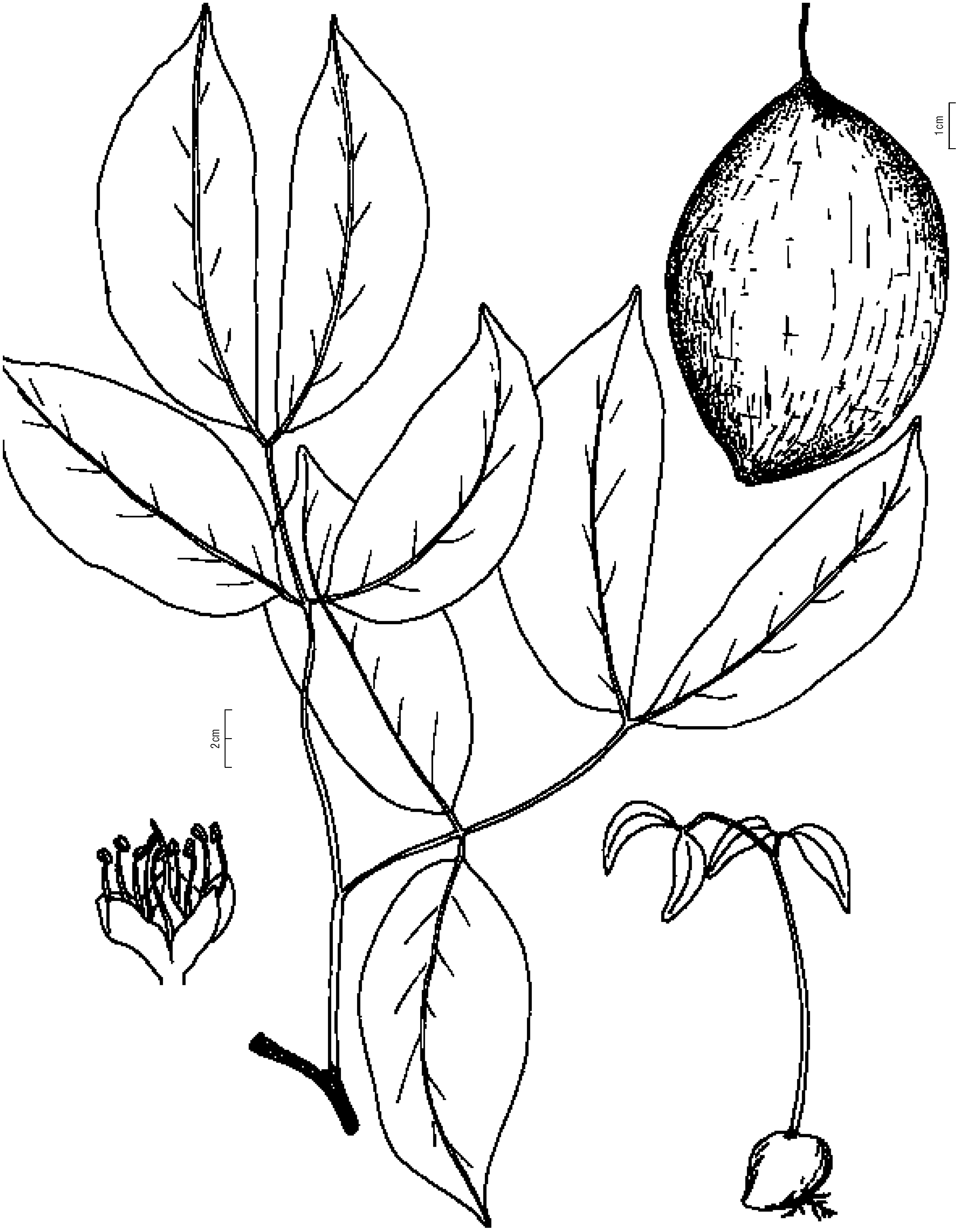
Seed behavior is recalcitrant. Germination is hypogeal and seedlings are cryptocotylar. Root protrusion occurs 30 to 40 days after sowing. The percentage of germination is greater than 85 percent.

Although the species has been propagated in small stands, it seems more suitable to natural forest management or to increasing forest richness.

ADDITIONAL INFORMATION

The genus was named for the British botanist R. Ch. A. Prior. *P. copaifera* Griseb. is the type of the genus.

Anthers are thick and apiculate with a thick connective. In the gynoecium, the style is short and awl-shaped; the stigma is inconspicuous. The embryo is large; cotyledons are thick and fleshy; the embryo axis is straight and conspicuous.


1cm
2cm

Prosopis juliflora (Sw.) DC.

CRISTINA GARIBALDI
Department of Botany, University of Panamá, Panamá

FABACEAE (BEAN FAMILY)

P. chilensis (Mol.) Stuntz; *Ceratonia chilensis* Mol.; *Mimosa juliflora* Swartz

Acacia de catarina, algarroba, amansa caballo, cambrón, carbón, catzimec, chachaca, guatapana, manca-caballo, mesquite, nacascol, plumo de oro, trupillo, yaque (Centro Agronómico Tropical de Investigación Enseñza 1984a, 1984b; Geilfus 1994; Holdridge 1970; Woodson and Schery 1950b)

Prosopis juliflora is native to the West Indies, Central America, and northern South America (Venezuela and Colombia), but it has been planted in arid zones in many parts of the World. It is the only species of the genus in Central America, where it is confined to the dryer regions of the Pacific slope (Woodson and Schery 1950). In Panama, the species grows in the remnants of forests on the Pacific slope corresponding to the life zones of the tropical dry forest and dry premontane forest. In India, it is an invader species that competes with native species (Sharma and Dakshini 1996).

Prosopis juliflora is a fast-growing, deciduous tree or shrub that is thorny and has a wide crown and deep roots. Zigzag branching, stretched out over the crown, is characteristic of the species (Drake 1993a). The tree can reach between 3 and 12 m in height and up to 45 d.b.h., depending on where it grows. It frequently grows as a shrub, with the trunk twisted and the crown broadened in the shape of a parasol. Its leaves are pinnately compound and very dark green. Characteristic thorns, produced by modified stipules, occur only in pairs in the foliar nodes. The species grows in very hot, dry climates, with temperatures up to 48 °C and annual precipitation from 150 to 750 mm. It is found from sea level to 1500 m. The roots penetrate to great depths in the soil searching for the required water. If root growth is not obstructed, the tree can grow in a variety of soils, including saline and alkaline areas and in sandy and rocky soils (Drake 1993a, Geilfus 1994). The tissue of *P. juliflora* is photosynthetically active throughout the year, presenting a superficial and widespread radicle system through which the tree fully exploits the available hydric resource. The species shows water potentials more negative than *P. tamarugo* Phil., a species native to the Atacama desert. Its low nutritional requirements and its resistance to hydric deficit give *P. juliflora* a great plasticity of response, which allows its wide distribution in arid and semiarid zones of tropical America (Alarcón and Díaz 1993).

Prosopis is considered a rather old genus, with divergence into several lineages. When these lineages were isolated, partial speciation occurred. There exists a good number of intermediate forms and hybridization with related species, which makes distinction among species in the field more difficult (Burkart and Simpson 1977, Drake 1993a).

The wood is hard, heavy (specific gravity is 0.70 or more), durable, and resistant to rotting. It finishes well and has been widely used for door and window frames and other woodwork and carpentry articles (Centro Agronómico Tropical de Investigación Enseñza 1984, 1984b). The wood is also used in rural construction and for posts and tool handles. The species has great value in agroecosystems in very dry locations where it is used for firewood and charcoal. The high caloric capacity of the alburnum produces a high quality charcoal and small-dimension wood yields between 5 and 15 tons per ha per year (Drake 1993a). The flowers are an important source of nectar for the production of high quality honey. The bark is a good source of tannin, and rubber can be obtained from the trunk (Woodson and Schery 1950). The legumes and the seeds are used as cattle feed, and the species produces 20 to 40 tons per ha per year, beginning at 2 to 3 years of age. The pods have also been ground and used as flour. Because *P. juliflora* resists drought and fixes nitrogen, it is valuable in agrosilvopastoril, mining projects, dune stabilization, and the recovery of degraded soils.

The flowers are grouped in sprigs; they are regular and the corolla is pentamerous. The pods are long, pulpy, and yellowish when ripe (Burkart and Simpson 1977).

The seeds are extracted from ripening pods that have been collected from the trees and allowed to dry. It is not necessary to separate the seeds from the mesocarp. The pods are broken up into pieces by beating with a stick or trampling by cattle, and the pod pieces are sown in place of seed. Adequately stored seeds can survive for 20 to 30 years without losing viability. Seeds should be scarified with a solution of sulfuric acid at 20 percent for 1 hour. Seeds can also be soaked in concentrated sulfuric acid for 20 minutes or covered with boiling water and soaked for 24 hours. *Prosopis juliflora* reproduces well through direct sowing of the pretreated seeds or through root shoots. Germination after pretreatment is usually 75 to 95 percent. Seeds are planted by direct sowing whenever sufficient rainfall is available. Rooted cuttings in polybags also do well. For hedges, seeds are sown about 10 cm apart in two lines about 50 cm part; or polybag plants are planted 30 cm apart in two rows 50 cm apart (Drake 1993a).

In forest plantations developed to produce firewood or to control erosion, plantules should be spaced at 3 by 3 m; good yields have also been obtained with a spacing of 1 by 1 m. The trees should be protected from fire until a thick bark has formed, which occurs in the third year (Centro Agronómico Tropical de Investigación Enseñza 1984a, 1984b; Drake 1993a).

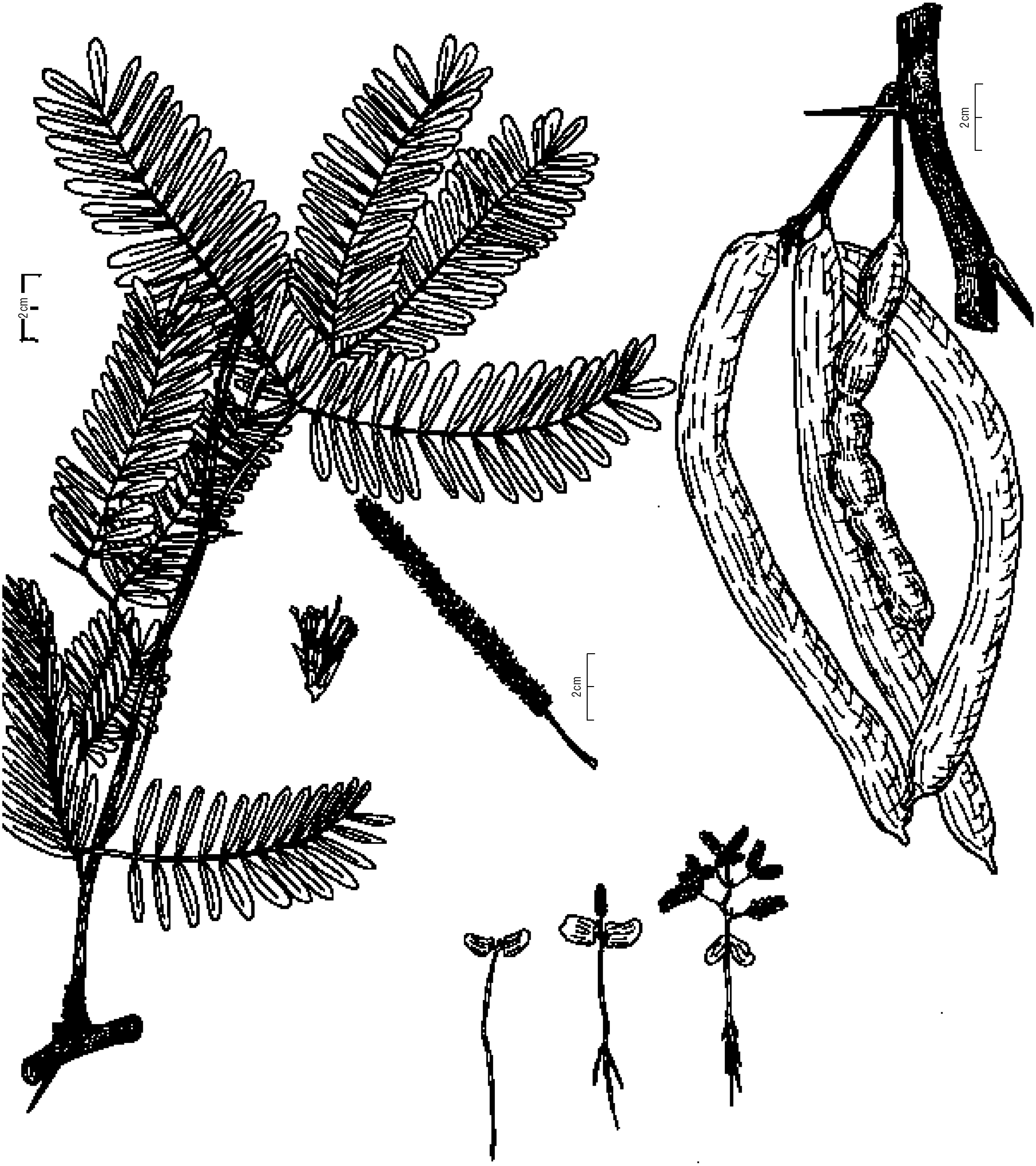
The plantules have a good capability to compete with the underbrush, but *Coleoptera* harm part of the seed crops. Generally, the species is considered a very aggressive invader that competes for the soil humidity. Because *P. juliflora* is difficult to eradicate and because it may eliminate native species, it should be sown only in arid problematic areas, where soils must be recovered or protected from erosion (Centro Agronómico Tropical de Investigación Enseñza 1984a, 1984b; Drake 1993a).

ADDITIONAL INFORMATION

The taxonomy of this genus is obscure; some species native to North America, initially classified with this name, are currently known as *P. velutina* Wooton and *P. glandulosa* (Centro Agronómico Tropical de Investigación Enseñza 1984a, 1984b). Because the diverse species of the genus in South America exhibit all the traits found in North America and in the Old World and because of the chemical composition of the species, some suggest the genus originated in South America (Burkart and Simpson 1977). In the dry areas of Central America, two varieties of the species have been reported (Burkart and Simpson, 1977). *Prosopis juliflora* (Sw.) DC. has two pairs of axial thorns on the folious nodes. The variety *inermis* (H.B.K.) Burkart has no thorns or small thorns distributed along the branches, with pubescent folioles; it apparently belongs to varieties derived from forms with thorns.

The species grows rapidly; yields of 75 to 100 tons per ha in 15-year rotations have been obtained; in 10 years, yields of between 50 and 60 tons per ha are expected. The trees sprout easily (Geilfus 1994).

In natural regeneration of *P. juliflora* the seeds are dispersed by cattle or by wild animals that eat the pods. Germination is stimulated as the seeds pass through the digestive tracts of these animals. Substances within these digestive tracts apparently stimulate dormancy, promoting germination.


2cm
2cm
2cm

Prumnopitys standleyi (Buchholz & Gray) de Laub.

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PODOCARPACEAE (CIPRECILLO FAMILY)

Podocarpus standlley, Podocarpus montanus

Ciprecillo, cobola, lorito (Rojas and others 1992a)

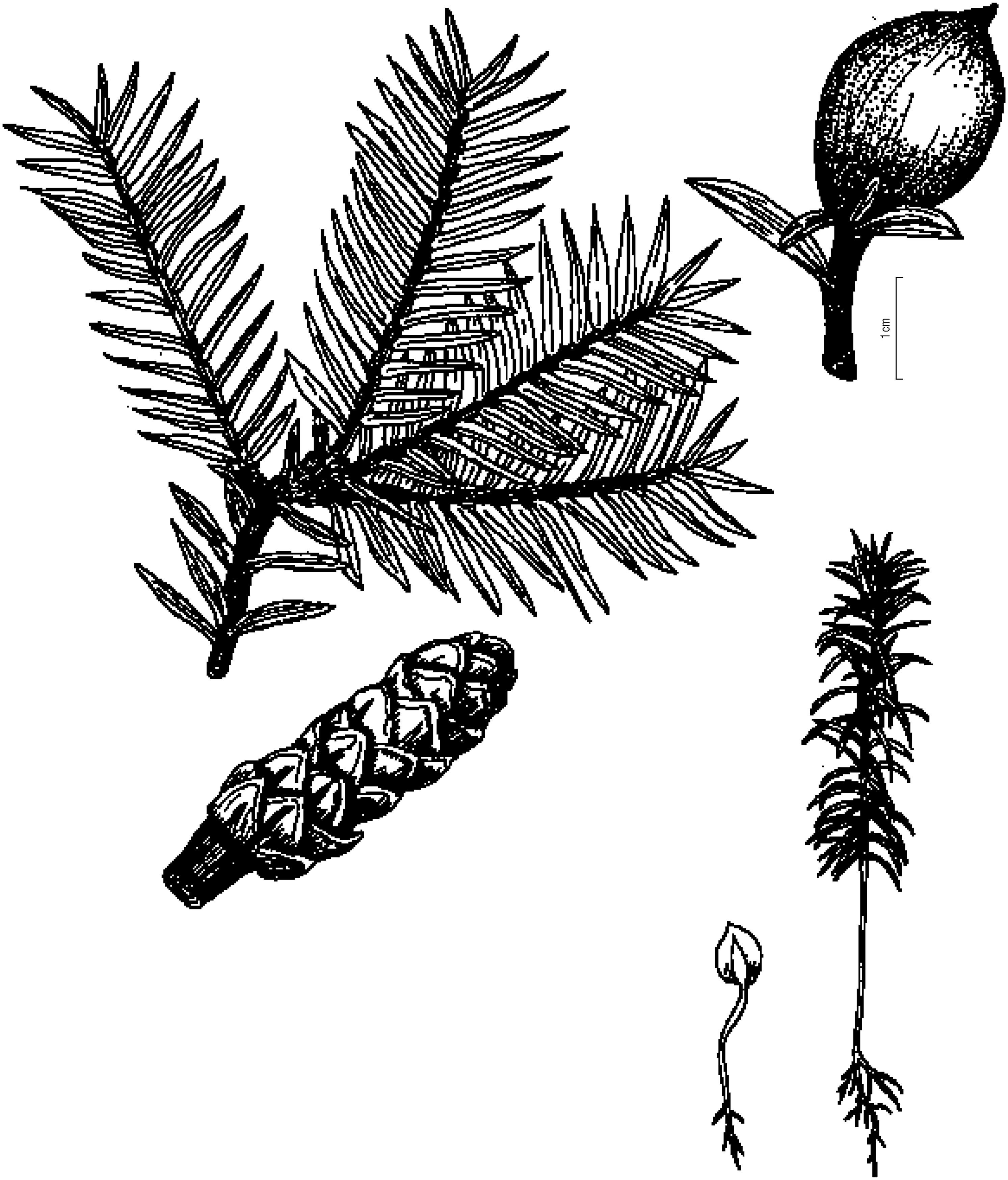
Prumnopitys standleyi grows naturally from Costa Rica to Bolivia; however, this species is taxonomically confused with species of the genus *Podocarpus* (from South America). It is a climax forest species that grows in wet zones at moderate to high elevations (Carpio 1992).

Prumnopitys standleyi is a tall, slow-growing tree that reaches 20 m in height and 75 to 150 cm d.b.h. The trees vary in shape and trunk form. The species grows at 2000 to 3200 m on very wet, low-mountainous grounds, on pluvious montane, and especially on very wet montane. It grows where annual precipitation is 2000 to 4000 mm and temperatures range from 3 to 25 °C (Budowski 1954). It is resistant to strong winds (Rojas and others 1992a).

With a specific gravity of 0.555, the wood of *P. standleyi* is considered heavy. It dries fast without defects. Easy to dry and preserve, the wood's texture is uniform and fine (Carpio 1992, Standley 1938). The wood is used in construction and in pulp for paper and for boxes, floors, indoor decorations, veneer, farming tools, fenceposts, firewood, coal, and furniture (Budowski 1954, Carpio 1992, Rojas and others 1992a).

As a rare species (0.1 to 1 per ha) (Slooten 1969), *P. standleyi* regenerates poorly. In males, some strobili are produced in the branch terminals; in females, they are produced in the axial leaves. The male structure measures about 0.97 cm long by 0.23 cm wide. These structures have numerous polliniferous sacks located in the strobila scales, producing 50 or more in only one branch. In the female strobili, two bracts are held by a peduncle that merges and folds the egg cell on the top of a receptacle. The seed is simple; it is covered by a scale and by an ovulary scale. Seeds are 0.9 cm long and 0.7 cm wide (Arnáez and Moreira 1992, Rojas and others 1992a).

Preliminary observations reveal that seeds ripen in 5 months. Seeds are ready for harvest in April. Seeds are soaked in water at 22 °C for 24 hours. Germination is epigeal. The seedlings show numerous nodules in their roots.


1cm

Prunus annularis Koehne

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ROSACEAE (ROSE FAMILY)

No synonyms

Ciruelo, duraznillo, mariquita

One of the more than 100 species in the genus *Prunus* that grow throughout North, Central, and South America, *Prunus annularis* grows only in Costa Rica and in Chiriqui, Panamá (Standley 1950). In Costa Rica, it commonly grows at the base of the Poas and Barba volcanoes and the Talamanca range (Arnáez and others 1992).

Prunus annularis is an evergreen, medium-sized, slow-growing tree with a straight or irregular trunk. Cylindrical in form, the tree can reach 5 to 12 m in height and 20 to 50 cm d.b.h. Commonly found in clear spots in the forests, it requires deep, well-drained soils. *Prunus annularis* grows at elevations from 900 to 3200 m in rainy areas of the humid mountainous forests, and in very wet areas that receive 1000 to 3500 mm annual precipitation with temperatures of 4 to 27 °C.

Prunus annularis is a timber tree. Its grain is interwoven. The sapwood and heartwood of *P. annularis* differ slightly. The wood has a medium-to-thick texture and medium luster and is pink when dried. Easy to work, the wood is used for coal, floors, and girders and in construction. The trees are planted as windbreaks, live fences, and ornamentals (Arnáez and others 1992).

Prunus annularis flowers in November and December. The white flowers appear in racemes. Its fruits are drupes with a light-colored exocarp and a meaty mesocarp. The drupes, 1.5 cm long and 1.30 to 1.70 cm wide, turn red when they ripen February through April. Each drupe contains one seed, 1.06 cm long and 0.78 cm wide. The seed cover is wrinkled with small longitudinal grooves. Birds may scatter the seeds or the seeds may fall. Natural regeneration was observed under the father tree; however, 2 months after germination many seeds die from fungus attack, such as talluelo disease. Seeds scattered by birds in separate areas and isolated spots survive (Arnáez and others 1992). *Prunus annularis* also resprouts in branches and cut trees.

Ripe fruits are collected by climbing the tree or by using an extension pruner. Collected fruits are separated from the branches and are transported in blanket sacks. The seeds are soaked in water for 24 hours to facilitate pulp removal. Seeds are dried in the sun. Seeds average 6,523 per kg. Seeds can be stored for a few months but less than 1 year (Arnáez and others 1992).

To ensure homogeneous germination, seeds should be soaked in water at 22 °C for 24 hours. Soaked seeds germinate in 22 days with 50 percent success. They germinate at room temperature (22 °C) in a previously sterilized substrate mixture of soil and sand (Arnáez and Moreira 1992, Arnáez and others 1992).

The seedlings are placed in the shade; in 21 days seedlings are transplanted to plastic bags and should remain in the shade. The species can also be reproduced using a bare-root or a transplant. Controlling weeds and watering will produce healthy and vigorous seedlings in 3 or 4 months. Plagues and diseases are not a risk to plantations although an ant of the genus *Atta* eats the leaves.


2cm
1cm

Pseudobombax ellipticum (Kunth) Dugand

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Facultad de Agronomía, Universidad de El Salvador

BOMBACACEAE (BOMBAX FAMILY)

Bombax ellipticum H.B.K., *Carolinea insignis* (Guzmán 1980, Witsberger and others 1982)

Acoque, amapola, árbol de doncellas, árbol de señoritas, calinchuche, clavelina, jilinsuche, matías, pilinsuchil, pumpo, shaving bush, shilo, shilo blanco, shilo colorado (Carr 1998a, 1998b; Guzmán 1980; Witsberger and others 1982)

Pseudobombax ellipticum is native to southern Mexico, El Salvador, Guatemala, and Honduras and has been introduced in the Caribbean and Hawaiian islands and southern Florida (Carr 1998a, 1998b).

Pseudobombax elipticum is a tree that can reach 18 m in height and 1.3 m d.b.h. Its branches are close to the base of the stem. It is a deciduous tree with succulent stems, and leaves that are palmately compound with five leaflets. The species grows well in dry and rocky habitats or poor soils and is shade intolerant. *Pseudobombax ellipticum* grows at elevations from sea level to 1800 m (Witsberger and others 1982).

The wood of *P. ellipticum* is used for firewood and in the handicraft of carving dishes. The seeds contain carbohydrates and can be consumed if toasted. In El Salvador, the tea of the flowers is used for gastrointestinal ailments and the tea of the fresh bark is used to treat diabetes (González 1994, Guzmán 1980). The tree is grown as an ornamental in Florida and Hawaii (Kuck and Tongg 1960), and the attractive flowers are used to decorate homes and churches in Central America. The fine fibers of the fruits of several species of the Bombacaceae family, including *P. ellipticum,* are used to fill pillows and mattresses. The fibers have also been used to insulate refrigerators (Salter 1956). The tree may be used as living fence in rural areas.

In El Salvador, *P. ellipticum* loses its leaves December through May and flowers in December or January; its fruits mature in January and February (Witsberger and others 1982). In Hawaii, it blooms in March (Kuck and Tongg 1960). The pink or white flowers are solitary and have numerous stamens; the elongated fruits are dehiscent capsules containing numerous seeds. The seeds are wind dispersed.

The fruits are collected manually from the tree before opening and dried to extract the seeds. The small seeds are manually separated from the fibers and stored under cool and dry conditions (Aragón 1998).

Pseudobombax ellipticum is propagated by seeds and cuttings. Seeds require sunny locations for germination. The cuttings, 40 to 100 cm in length and 2 to 5 cm in diameter, are easily rooted when planted in bags of sand and watered daily or when planted directly in the field (Salter 1956).

ADDITIONAL INFORMATION

Three other important species in the Bombacaceae family are *Ceiba petandra* (L.) Gaerth, *Ochroma lagopus,* and *Bombacopsis quinatum* (Jacq.) Dugand. *Ceiba petandra* is a multiple-use tree and is the source of the fine, cotton-like fiber kapok. It is the national tree of Guatemala (Rojas 1993, Watson and Dallwitz 1992a, 1992b). *Ochroma lagopus*, or balsa, is a well-known tree that produces one of the world's hardest light woods. *Bombacopsis quinatum* (synonym *Bombax quinatum*) is a tree that produces good quality wood and has been extensively studied in Central America. This last species is easily propagated in plantations (Centro Agronómico Tropical de Investigación Enseñza 1991a) and has many botanical characteristics similar to those of *P. ellipticum*. Designing field studies of *P. ellipticum* similar to those of *B. quinatum* are necessary to evaluate the growth rate and propagation methods.


1cm
1cm
1cm

Pseudosamanea guachapele (Kunth) Harms

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Academia Nacional de Ciencias de Costa Rica, Costa Rica

FABACEAE (BEAN FAMILY)

Acacia guachapele Kunth (Nova Genera et Species Plantarum 6: 281-282; 1823); *Acacia guachapele* (Kunth) Dugand (Nova Genera et Species Plantarum 6: 281-282; 1823); *Lysiloma guachapele* (Kunth) Benth. (Transactions of the Linnean Society of London 30(3): 533; 1875); *Pithecellobium longepedatum* Pittier (Contributions from the U.S. National Herbarium 20[12]: 464-465; 1922); *Samanea samaningua* Pittier (Arboles y arbustos nuevos de Venezuela 4-5: 54; 1925); *Albizia longepedata* (Pittier) Britton and Rose ex Record (Tropical Woods 11: 14; 1927); *Pithecollobium samaningua* (Pittier) J.F. Macbr. (Candollea 6: 4; 1934); *Pithecolobium guachapele* (Kunth) J.F. Macbr. (Field Museum of Natural History, Botanical Series 13[3/1]: 54; 1943); *Albizia guachapele* (Kunth) Dugand (Phytologia 13: 389; 1966)

Cadeno, cenízaro macho, gavilán, genízaro macho, guachapele, guamarillo, guayaquil, samaningua, tabaca (Record and Hess 1949, Salas-Estrada 1993, Zamora 1991)

The geographical range of *Pseudosamanea guachapele* extends from southern Mexico, throughout Central America, to Ecuador in South America (Holdridge and Poveda 1975, Zamora 1991).

Pseudosamanea guachapele is a medium-to-tall tree reaching 20 to 30 m in height and 50 to 100 cm d.b.h. The crown is extended and flat; the young twigs are ferrugineous tomentose and the bark is light gray, with wide plates between fissures (Bentham 1875, Holdridge and Poveda 1975, Zamora 1991). The leaves are bipinnate, paripinnate, with 2-(4-5)-6 pairs of opposite or subopposite pinnae, each with 3 to 9 pairs of foliolules (pinnules). *Pseudosamanea guachapele* is a canopy (emergent) tree and rare (abundance of 0.1 to 0.01 per ha or between 1 per 10 ha and 1 per 100 ha). The species grows primarily on plateaus or flatlands with slopes of 5 percent or less and alluvial or sandy soils with good or moderate drainage (Hartshorn and Poveda 1983, Nichols and González 1992a, 1992b). Although usually found at low elevations, *Pseudosamanea guachapele* can grow at elevations of 1200 m. This tree is typical of the tropical dry forests of the Pacific lowlands in Central America and grows where temperatures range from 22 to 32 ^{o}C (mean annual biotemperature above 24 ^{o}C) and rainfall fluctuates from 1000 to 2500 mm.

The dry heartwood is reddish gray and the sapwood brownish gray. The wood has straight or interlocked grain with dark stripes, low luster, and medium texture. The figure has glare in the radial surface and dark vertical lines. The wood is heavy (green weight 1200 to 1300 kg per m^3, with 60 to 62 percent of moisture; specific gravity is 0.65 to 0.70). Odor and taste are noncharacteristic (Creemers and Lemckert 1981). Volumetric contraction is low (9.9 to 10.2), and the mechanical properties are medium. The air-dried wood splits on the sides and ends. The wood is moderately easy to work; it saws and polishes well. The natural durability is medium, but the wood impregnates well. The treated wood can be used in heavy construction, posts, fences, floors, furniture, railroad foundations, boxes, and handles. It is good for papermaking (Runkel Factor = 0.51; Peteri's Coefficient = 52 to 53). The wood is also used as firewood. *Pseudosamanea guachapele* is a nitrogen-fixing tree with possibilities for greater use (Nichols and Rodríguez 1990). The species has been used primarily in monospecific plantations, although some experiments introduced it in mixed plantations, grasslands, and tacotales (lands in early natural regeneration) to improve soils (Nichols and González 1992a, 1992b).

The tree commonly flowers from December through March along its geographical range. The flowers are crowded in pedunculate, umbellate inflorescences; peduncles are ferruginous (Bentham 1875, Holdridge and Poveda 1975). Flowers are white or creamy, and pentamerous. The calyx is gamosepalous, valvate, narrow-campanulate, toothed apically, pubescent, and 6 to 7 mm long (Bentham 1875, Holdridge and

Poveda 1975, Zamora 1991). The receptacle is subglobose; the corolla is gamopetalous, valvate, infundibular, pubescent, and 9 to 10 mm long (Bentham 1875, Zamora 1991).

Pseudosamanea guachapele usually produces pods February through May. The pod is thin, flat, chartaceous, widely oblong-linear, 15 to 20 cm long, and 2.5 to 3.5 cm wide. Dehiscence takes place along the ventral suture while the dorsal suture, thicker than the ventral, remains indivisible; the valves reflex tardily (Bentham 1875). Pericarp is golden brown or yellowish, silky pubescent, and slightly wrinkled transversely. The mesocarp is inconspicuous, and the endocarp is shiny, whitish, and nonseptate. Pods usually average 12 to 13 seeds; the seeds are transverse, not overlapping, in one series; the funiculus is long, filiform, whitish, coiling or plicate (Gunn 1984). Seeds are ovate, laterally compressed, 0.8 to 0.9 cm long, 0.45 to 0.55 cm wide, 1.0 to 1.2 cm thick, and without funicular aril. The testa is thick, slightly glossy, creamy, monochrome (if fresh and healthy), and hard, with pleurogram, linea fissura open at the micropylar end, and fracture lines.

The pods must be collected before dehiscence, placed in open sacks, and exposed to full sunlight. Once the pods are open, the seeds are removed by hand (Nichols and González 1992a, 1992b). Seeds average 22,000 to 24,220 per kg (Centro Agronómico Tropical de Investigación Enseñza 1985, Nichols and Rodríguez 1990, Ramírez and Morillo 1987), depending on the site of collection and moisture content of the seeds. The seeds are hard and orthodox, and viability under storage at ambient temperature (24 to 32 ^{O}C) slowly declines. The seeds are frequently attacked by weevils (Nichols and González 1992a, 1992b).

Seeds can be stored for 2 years and maintain acceptable germination success. Lighter colored seeds germinate better; those with a dark areole in the lateral faces do not germinate well because the embryo is dehydrated. Fresh seeds have 70 percent germination with no pretreatment (Centro Agronómico Tropical de Investigación Enseñza 1985). Tresemer (1989) reported 60 percent germination of seeds sown directly in plastic bags with germination beginning in 4 to 8 days. Seeds soaked in hot water (80 ^{O}C) for 1 minute followed by a bath in lukewarm water (30 to 40 ^{O}C) for 24 hours have 82 percent germination if damaged seeds are discarded. After imbibition the seeds must be sown in greenhouse beds filled with sand at ambient temperature. The radicle protrudes in 3 to 5 days and germination is quite uniform. In another method, the seedcoat end opposite to the micropyle is cut and the seeds are placed in running water for several hours. Germination after this pretreatment has been greater than 90 percent (Nichols and González 1992a, 1992b). Germination is epigeal and the seedling is cryptocotylar. The first eophyll is pinnate. Seedlings must be transplanted to plastic bags before the first eophyll completes its expansion.

Some seeds have been sown directly in the soil, and the seedlings outplanted as pseudosticks. If the seedlings develop in bags, they must be outplanted in 2 to 3 months (Nichols and González 1992a, 1992b). In the field, the seedling roots are attacked by joboto (insect larvae of *Phyllophaga* spp.), and the foliage is eaten by ants (*Atta* spp. and *Acromymex* spp.). Another insect (unidentified) eats the bark, forming rings around the shoot; bark and phloem damage frequently result in sapling death (Nichols and González 1992a, 1992b). Seedling survival in plantations is about 90 percent; survival diminishes drastically if the seedlings are unhealthy or the plantation does not perform appropriate maintenance procedures. The plantation must be cleared three to four times during the first year, and saplings require axis selection and pruning of undesired shoots (Nichols and González 1992a, 1992b). Planting distance is usually 3 by 3 m. Longitudinal growth in the first year is approximately 1 m. On the Osa Peninsula, 9-year-old juveniles reached 12 to 14 m in height and 10 to 12 cm d.b.h. (Tresemer 1989). In the dry tropical forest areas of Costa Rica, seedlings produced from Costa Rican seeds grow faster than those from Honduran seeds; 3-year-old saplings reached an average height of 3.53 m and an average d.b.h. of 6 cm (Paterson and others 1996a).

ADDITIONAL INFORMATION

Leaf foliolules are pubescent, ovate, and obovate, with the upper semilimb 2:1 trullate. The apex is round or emarginate, the base is irregular, and the blade silky pubescent abaxially. The petiole is ferruginous tomentose and pulvinate, with an extrafloral nectary in the middle. The pulvinus is adaxial, basal, and oblong. The rachis bears extrafloral nectaries toward the distal end. The petiolules bear basal and adaxial pulvinuli. The stipules are large, membranous, and sometimes long persistent, although finally falling away (Bentham 1875, Zamora 1991).

The androecium has 15 to 20 stamens; the stamens are long, monadelphous, and basally adnate to the corolla, forming a tube; each anther has a few polyads of pollen in each locule (Bentham 1875, Guinet 1981, Nilsen 1981). The gynoecium is monocarpellar, and placentation is laminar. The gynoecium has several anatropous, bitegmic, crassinucellate ovules.

The flowers are presumably pollinated by moths, although sometimes they are visited by birds. The pollen has internal pores, nonequatorial apertures of the simple porate type, exine areolate and tectum perforate (Guinet 1981).

The seed hilum is concealed by funicular remnants.

Endosperm and perisperm are absent. The embryo is large, laterally compressed, and investing; the embryo axis is slightly reflexed and the plumule is well developed with several foliar primordia. The cotyledons are large, thick, and ovate, with a simple, irregular split over the radicle, concealing all but the tip of the radicle. Many seeds are damaged by insect larvae while in the pod.


1cm
1cm

Pterocarpus indicus Willd.

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FABACEAE (BEAN FAMILY)

Pterocarpus wallichii Wight & Arn., *P. pallidus* Blanco, *P. papuanus* F.V.M., *P. blancoi* Merr., *P. pubescens* Merr., *P. carolinensis* Kaneh. *P. casteelsii* De Wild. var. *ealensis* Hauman, *P. echinatus* Pers., *P. obtusatus* Miq., *P. vidalianus* rolfe, *P. klemmei* Merr.

Angsana, India padauk, linggoa, narra, Papua New Guinea rosewood, pradoo, terocarpo, sena (National Academy of Sciences 1979)

Pterocarpus indicus occupies a native range stretching from southern Burma through peninsular Thailand, Vietnam, Malasia, Sumatra, West Java, Borneo, the Philippines, Sunda Islands, the Moluccas, New Guinea, the Andaman Islands of India, the Solomons, and the Carolinas (Rojo 1977). The tree is widely scattered or uncommon in its native forest habitat.

Pterocarpus indicus is a large tree that tends to have a short, clear bole, a spreading crown, especially when open-grown, and a large buttress. Of a moderate growth rate, mature trees of the species may exceed 30 m in height and 1 m d.b.h. *Pterocarpus indicus* grows in areas receiving about 1200 mm to 3000 mm mean annual precipitation, only minor seasonal temperature variation (around 27 °C mean monthly temperature), and from near sea level to 1300 m elevation (Asiddao and Nestor 1958). Soils from sandy loams to clays with pH from neutral to very strongly acid are suitable.

The species is divided into two forms: *P. indicus* forma *indicus* Willd. and *P. indicus* forma *echinatus* (Pers.) Rojo. They are distinguished by spines on the seed-bearing part of the fruit of the latter. The spiny-seeded form grows on Luzon island in the Philippines and possibly the Celebes, Ambon, Andora, Wetar, and Kisar islands (Rojo 1977). *Pterocarpus indicus* is very closely related to *P. macrocarpus* Kurz. Because the leaves and flowers are almost identical, the fruits are used to differentiate between the two species. Where the ranges of the two species merge, they are indistinguishable. The species is also linked with the endemic *P. santalinus* Linn. of the Andaman Islands (Rojo 1977).

Pterocarpus indicus is highly valued as an ornamental and shade tree throughout the moist tropics. This unusually pleasing tree tolerates the partially compacted fill in which urban trees are frequently planted, and grows relatively rapidly in most urban habitats. However, because its roots become large and grow near the surface, it should be planted several meters away from sidewalks and other structures. It has been planted as a shade tree for at least 200 years in Malaysia (Nitrogen Fixing Tree Association 1992). The colorful (from yellow to deep red) wood ranks among the most valuable woods in the world. It shapes well, takes a high polish, and resists termites and rot. It is used to produce furniture, cabinetwork, paneling, carvings, and flooring.

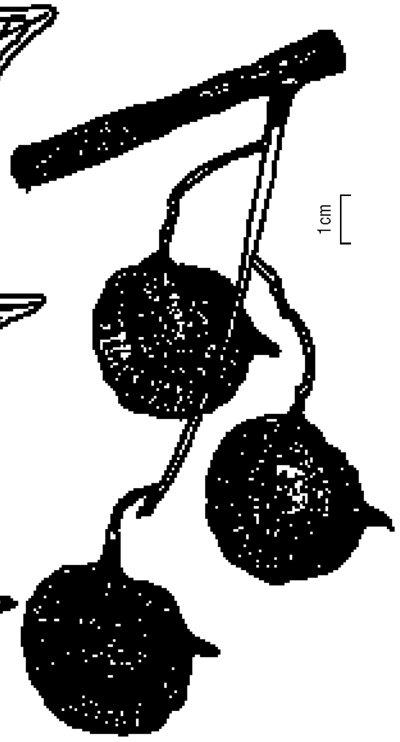
Open-grown trees usually begin flowering and fruiting between 5 and 10 years of age. The sweet-scented yellow flowers are produced copiously in panicles and racemes. Individual flowers measure about 17 mm across. The buds on individual trees come to full size and responding to some unknown trigger, all flower on the same day (Nitrogen Fixing Tree Association 1992). The season of flowering varies considerably throughout the native range and is reported to occur from July through September in the Philippines (Asiddao and Nestor 1958). The flowers are pollinated by honey bees and other insects. *Pterocarpus indicus* fruits are lenticular-shaped pods with a flat wing that circles its edge. The pods have a diameter of 4 to 7 cm (Rojo 1977). They mature about 6 months after flowering and fall off the trees gradually over several months. A group of medium-sized trees in the Philippines produced an average of 181 L of pods annually (Asiddao and Nestor 1958).

At maturity, the pods dry and turn from greenish yellow to light tan and can be clipped from low-growing trees with pruning poles. Because the fruits and their seeds do not deteriorate for several months after falling, they may be collected efficiently from the ground after most of the crop has fallen. The pods are air-dried and stored in plastic bags with or without refrigeration. Air-dried samples of *P. indicus* forma *indica* and *P. indicus* forma *echinata* pods collected from one tree each in Puerto Rico yielded 2,816 and 1,697 pods per kg, respectively. The seeds from the latter sample were extracted and found to hold an average of 2 seeds per fruit but ranged from 1 to 4 seeds per fruit. The seeds weighed an average of 0.0763 grams or 13,000 seeds per kg. Air-dried seeds in their pods will still germinate after 1 year of storage at room temperature.

No pregermination treatment is necessary. A germination rate of 24 percent was reported in the Philippines (Asiddao and Nestor 1958). A sample of *P. indicus* forma *echinata* in Puerto Rico gave 57-percent germination which started in 5 days and took 3 months to complete. Shelled seeds of the closely related *P. macrocarpus* germinate quickly, uniformly, and with percentages of 70 to 90 percent (Francis 1989c). Because shelling the fragile seeds from the tough pods is difficult by hand and currently impossible mechanically, pods are sowed with seeds inside.

Pods are lightly covered with potting mixture in germination beds or trays and kept moist until germination. Planting seeds with the pods requires thinning the plants soon after emergence. When true leaves develop, the seedlings are transplanted into nursery bags or pots filled with a potting mixture. Seedlings about 0.5 m in height are suitable for most forestry plantings. Stump plants are also used effectively to establish plantations (Maun 1980). New plantations must be kept weed-free for 1 to 2 years and protected from vines for an additional year or more until the crowns begin to shade the understory. Seedlings intended for ornamentals are often grown in 12- to 15-L plastic pots until they reach 2 to 3 m in height before transplanting. Cuttings of the species can be rooted. In the Philippines, branch cuttings of *P. indicus* about 8 cm in diameter are rooted after hormone treatment to produce instant trees (Dalmacio and others 1978).


1cm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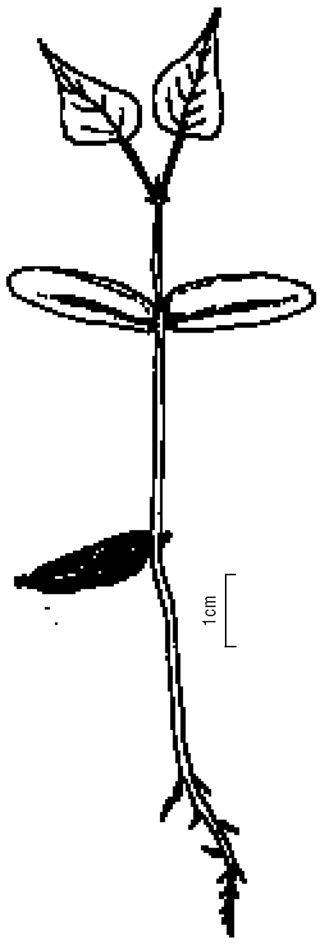
1cm

Pterocarpus macrocarpus Kurz

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USDA Forest Service

FABACEAE (BEAN FAMILY)

Lingoum macrocarpum (Kurz) O. Ktze., *Lingoum cambodianum* Pierre, *Lingoum glaucinum* Pierre, *Lingoum gracile* Pierre, *Lingoum oblongum* Pierre, *Lingoum parvifolium* Pierre, *Lingoum pedatum* Pierre, *Pterocarpus cambodianus* Pierre var. *calcicolus* Craib

Burma padauk, pradu, terocarpus

Pterocarpus macrocarpus grows naturally throughout the greater part of Burma, northern Thailand, Kampuchea, and into Vietnam (Carrapiett 1960, Hundley 1956, Suvarnasuddi 1950). It is an associate with *Tectona grandis* L.f. in moist to dry deciduous forests.

Pterocarpus macrocarpus is a large tree with a medium growth rate. It develops long and relatively straight boles in closed forest, but as an open-grown tree, tends to have short boles and spreading crowns. In their native range, these trees seldom exceed 30 m in height and 70 cm d.b.h. (Hundley 1956). However, as ornamentals, *P. macrocarpus* trees may reach impressive sizes. A tree approximately 64 years old in Puerto Rico measured 39 m in height and 1.7 m d.b.h. (Francis 1989c). Suitable soils include sandy loams through clays with pH ranging from neutral to very strongly acid. Rainfall throughout the native range varies from about 1000 to 2000 mm per year (Kermode and others 1975). The tree grows from near sea level to 670 m elevation. Mean monthly temperatures are fairly uniform at about 24 °C. (Francis 1989c). Because it grows somewhat more slowly than its fiercely competitive associates, *P. macrocarpus* usually must survive years of suppression as a sapling or pole until disturbance creates a canopy gap through which it can grow. As a result, the species makes up only a small percentage of the canopy trees in its native habitat (Hundley 1956).

Pterocarpus macrocarpus is closely related to *P. indicus* Willd., and it is difficult to distinguish between the two species by leaf and flower morphology alone (Rojo 1977). The fruits of *P. macrocarpus* are usually larger, darker, and have more pronounced central veins than *P. indicus*, but where the native ranges merge and at the extremes of natural seed variation, differentiating between the species is difficult. No hybrids have been reported.

Pterocarpus macrocarpus produces a timber with heartwood that varies from golden brown to brick red. It is comparable in workability to inferior quality teak. Used for furniture, cabinetry, flooring, ship timbers, cart wheels, tool handles, house framing, and posts (Chudnoff 1984, Hundley 1956, Rendle 1970), the wood is very resistant to termites and rot (Carrapiett 1960). A visually pleasing tree, *P. macrocarpus* is planted throughout the moist tropics as an ornamental and shade tree (Rojo 1972). However, older trees have large roots that run along the surface of wet or clayey soil and have a high propensity to damage sidewalks and curbs (Francis and others 1996).

Flowering and fruiting usually begins in open-grown trees between 5 and 10 years of age. The sweet-scented yellow flowers are produced copiously in panicles and racemes. Individual flowers measure about 1.6 cm across. They are pollinated by honey bees and other insects. The fruit of *P. macrocarpus* is a lenticular-shaped pod with a flat wing that circles its edge. These pods have a diameter of 4.5 to 7.5 cm. Large trees may produce one to several quintals of pods annually.

At maturity, the pods dry and turn from greenish yellow to light brown and can be clipped from low-growing trees with pruning poles. Fruits mature about 6 months after flowering and fall off the trees gradually over several months. Because the fruits and their seeds do not deteriorate for several months after falling, they may be collected efficiently from the ground when most of the crop has fallen. The pods are air-dried and stored in plastic bags with or without refrigeration. A sample of air-dried pods of *P. macrocarpus* collected in Puerto Rico yielded 1,067 pods per kg (Francis 1989c) and an average of 2.6 seeds per pod (Francis 1989c). Air-dried seeds in their pods will still germinate after 1 year of storage at room temperature. The pods are tough and the seeds are fragile, making extraction impossible mechanically and difficult by hand. Shelled seeds average 11,500 per kg (Francis and Rodríguez 1993).

The seeds are usually planted in the pods without any pretreatment. Germination is epigeous. In a comparison study, shelled seeds germinated in 5 days, with 70-percent germination within 2 weeks. Unshelled seeds began germination in 11 days with 64 seedlings per 100 pods germinating within 2 months. In a test in Burma, shelled seeds gave 80- to 90-percent germination. Moreover, seeds from pods that had lain on the ground for 1 year germinated better than new pods collected from the tree (Hundley 1956). The best temperature regime seems to be about 30 °C day and 25 °C night (Liengsiri and Hellum 1988).

Lightly covered with a high-organic potting mix in germination trays or beds, the seeds begin to grow through the pods about 1 to 2 weeks after planting. The remaining seeds continue to germinate for several weeks. Using seeds in the pods sometimes requires thinning the plants soon after emergence. When true leaves develop, seedlings are transplanted into 1- to 2-L nursery bags filled with potting mixture. After growing under light shade for a few months, the seedlings reach about 0.5 m in height and are ready to outplant (Francis 1989). In Burma, seedlings in plantations grew from 0.6 to 1.2 m the first year and added another 1.2 to 2.1 m in the second (Hundley 1956). In Puerto Rico, 30 planted trees in a small forest plantation that was situated on clay soil over porous limestone averaged 1.3 m in height 14 months after outplanting (Francis 1989c). Seedlings intended for ornamental use are often grown in 12- to 20-L plastic pots until they reach 2 to 3 m in height before outplanting.


2cm
2cm
1cm

Quercus copeyensis C.H. Mull.

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FAGACEAE (BEECH FAMILY)

Quercus costaricensis f. *kuntzei* Tret, *Q. copeyensis* Muller emend E. Little,
Q. aata auctores in herbs as to Costa Rica

Roble, roble barcino, roble blanco, roble colorado

Quercus copeyensis ranges from central Costa Rica (Talamanca range) to Chiriquí, Panama.

Quercus copeyensis is a slow-growing tree between 8 and 35 m in height and 1 m d.b.h. The crown is rounded with dark green foliage, the bole is usually straight, and the gray bark forms flat scales. Leaves are alternate, simple deciduous, and often clustered at the end of the branches. The lamina are quite variable: 4 to 15 cm long, 2 to 6.5 cm broad, elliptic to oblong, obovate or occasionally oblanceolate, bluntly acute to rounded at the apex, tapering to obtuse, cuneate or slightly rounded base, and drying stiffly chartaceous to subcoriaceous. In its range *Q. copeyensis* is the dominant tree of the wet, evergreen, lower montane and montane rainforest between 1810 and 3000 m. *Quercus copeyensis* grows in silty-clay, deep soils of low fertility and a very low pH (3.5 to 4.6) (Camacho and Orozco 1998). The annual rainfall in the distribution range of this species is 2500 to 3200 mm, and the average annual temperature varies from 12 to 18 °C.

Quercus copeyensis wood varies from heavy to very heavy with a specific gravity of 0.59 to 0.63. As it dries, the sapwood changes from white-yellow to pale brown; the heartwood from pink to brown-red. It is difficult to work and although it dries with moderate speed, serious defects develop during the process. Difficult to treat with preservatives, the wood has a natural resistance to decay. The wood is used for docks, pilings, bridges, railway foundations, poles, mine posts, flooring, charcoal, and wine barrels. For many years (1940 to 1970) *Q. copeyensis* was the most important raw material for charcoal in Costa Rica, but substantial reductions of its natural stands rendered the species less important (Kapelle 1996).

Quercus copeyensis flowers in February and September, and fruits mature in April, June, July, and October (Jiménez and others 1996). Male spikes are catkins 3 to 12 cm long, and the flowers become distinct on the glabrous or sparsely puberulent rachis. Female spikes are 2 to 6 cm long and 2 mm thick. Each spike has 4 to 10 flowers. Fruiting spikes are 2 to 8 cm long and 20 mm broad at the apex. The cup tapers gradually to the base, is thin at the edge, and reportedly encloses one-third to one-half of the mature acorn.

ADDITIONAL INFORMATION

Quercus copeyensis is included in the white oak group. The gray bark with flat scales marks this species as a white oak and distinguishes it from *Q. costaricensis* Liebm., a black oak with similar foliage.

In central Costa Rica, *Q. copeyensis* attains an immense size and is the tallest tree along the Panamerican Highway where it traverses the Talamanca range.

Eutachypter psidii (Lep., Lasiocampidae) reportedly attacks the foliage of this species (Arguedas and others 1993).


2cm

Quercus costaricensis Liebm.

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Technological Institute of Costa Rica, Cartago, Costa Rica

FAGACEAE (OAK FAMILY)

Quercus frazuensis, Quercus endres

No common names

Quercus costaricensis grows in Panama and Costa Rica.

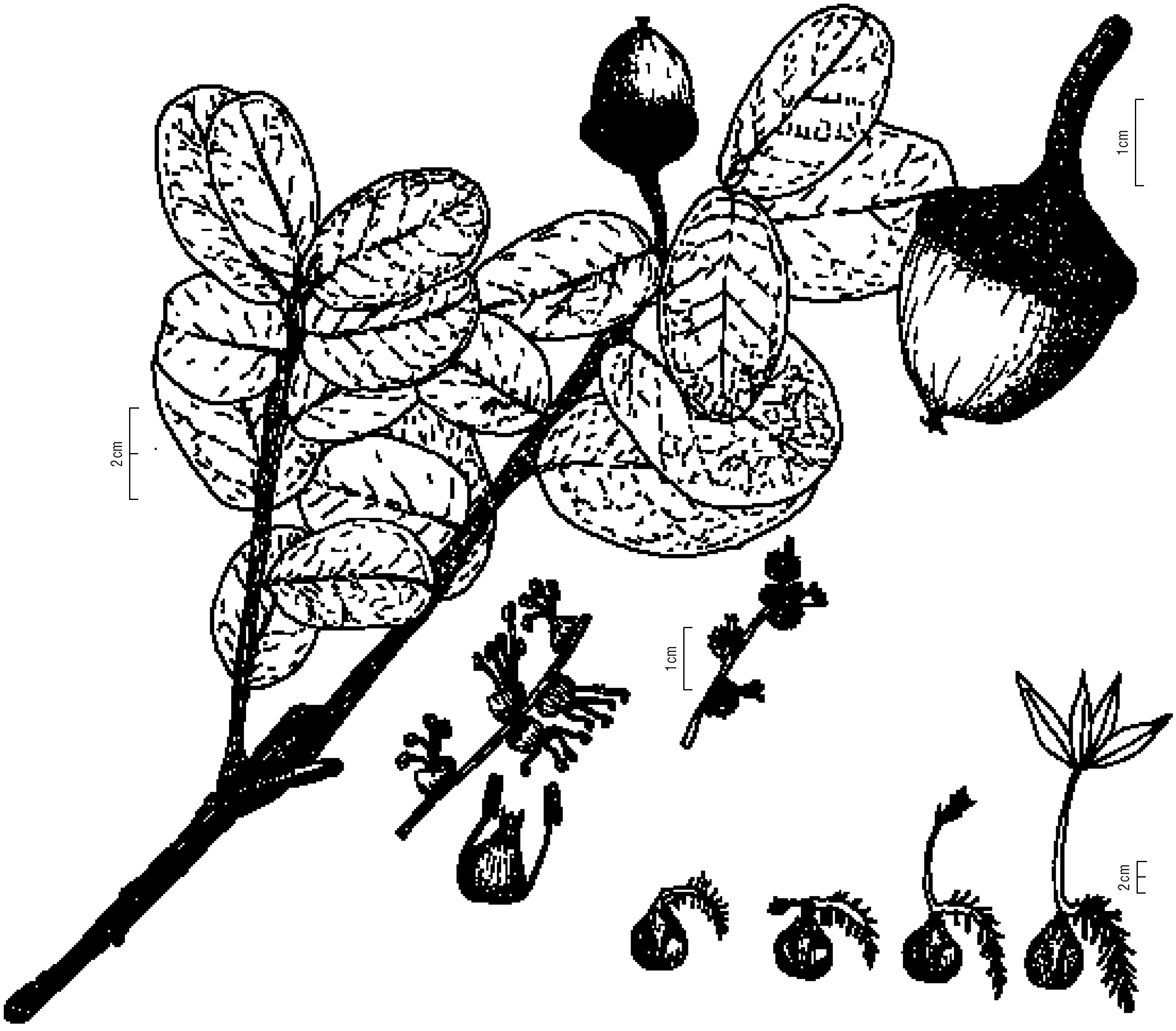
Quercus costaricensis is a large tree that can reach 44 m in height and 60 to 90 cm d.b.h. The tree has a conical, cylindrical, or straight trunk. It has coriaceous leaves with prints on the adaxial surface. The pubescences in the abaxial surface have abundant alternate stipules (Burger 1977). This species grows in wet, rainy mountainous forests at elevations between 2200 and 3300 m, where temperatures range from 0 to 20 °C and annual precipitation is 1000 to 4000 mm.

Quercus costaricensis wood ranges from heavy to very heavy (specific gravity 0.59 to 0.63). The wood dries moderately fast and shows some regular cracks and a strong collapse. It is difficult to work and preserve; however, it has a strong natural resistance, especially to fungus attack (Carpio 1992). It has regular quality for making paper and is used for farm tools, keels, bridges, wharf pilings, mine beams, and underwater posts. It is excellent for charcoal (Carpio 1992, Torres and others 1992, Van der Slooten 1968).

The tree produces green flowers in bunches from August through November. The female inflorescenses are located in the branch terminals. The sepals and petals form a resistant perianth with numerous bracts. The male inflorescences average 4 to 9 cm in length and are located at the base of branches where there are stipules. They are amentaceous (Arnáez and Moreira 1992). The brown fruit is 1.5 to 2.3 cm long and 1.3 to 4.4 cm wide. This acorn is oval to globular with a wide and discoidal proximal part showing a rough surface. The brown pericarp is coriaceous with a large amount of druse (crystal). Mature fruits are green or brown and the cupule separates easily. The fruits contain one to three seeds, but usually only one seed germinates (Arnáez and Moreira 1992). The oval seeds are approximately 2.11 cm long and 2.7 cm wide and are classified as megasperm (more than 10 mm in size). The top is brown. Its embryo is straight and cylindrical. The size of fruit and seeds varies within the same tree.

Fruits, which ripen from November through January, are usually collected from the ground or from the tree by shaking the branches. Fruits are transported in nylon sacks. If fruit must be preserved, it must be wrapped in moss to prevent dehydration (Torres and others 1992). In Costa Rica, seeds average 41 per kg. The seeds cannot be stored because storage damages the embryo and at 15 °C metabolic activity accelerates (Quirós 1990).

Pretreatments are unnecessary. Germination is hipogeal and begins 7 days after the fruit is planted (Quirós 1990). The rate of germination is 90 percent. The fruits are planted in a substrate of sandy-frank texture that is high in organic matter. Because seedlings show vigorous radical systems, the bed of substrate soils should be deep. Seedlings should be watered twice daily, and transferred to plastic bags 12 days after sowing. Plagues or diseases have not been detected in the plants; however, continuous weed control is recommended (Torres and others 1992).


2cm
1cm
1cm
2cm

Quercus humboldtii Bonpl.

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Corporacion Nacional de Investigacion of Forestal
Santafé de Bogotá, Colombia

FAGACEAE (BEECH FAMILY)

No synonyms

Encino, roble, roble amarillo, roble blanco, roble colorado, roble negro

Quercus humboldtii has a wide geographical distribution from South Texas in the United States to Esmeraldas in Ecuador. Because *Q. humboldtii* forms a relatively stable association with respect to composition and structure, pure stands of the species are common. In natural forests, the species is dominant. Its natural regeneration is quite vast in areas where moisture is high in the raw humus (primarily decomposing oak leaves), especially in forest clearings and peripheries where sunlight is abundant.

Quercus humboldtii is a slow-growing tree that reaches 30 m in height and 35 to 40 cm d.b.h. The trunk is thick with a rugose and blackish bark. The crown is rounded and the foliage is light green. The leaves are 14 cm long, grouped in bundles, and alternate, with a wavy margin and short petioles. *Quercus humboldtii* can grow in soils that are moderately fertile and deep and in those that are degraded and almost barren. However, it prospers in clayey and heavy soils with high acidity (pH 5.8 to 7.0) and a thick layer of humus. These soils are not very deep and drain well (Barreto and Herrera 1990). The tree grows well in areas with temperatures of 16 to 24 °C and average annual precipitation between 1500 and 2500 mm, with a relative humidity of 40 to 70 percent. It is found in elevations ranging from 1000 to 3600 m. In South America, it is restricted to high and humid parts of the Andean orographic system of three mountain ranges, at elevations ranging from 1900 to 2900 and 3200 m.

Because the wood of *Q. humboldtii* resists weathering, it is used for posts, railroad ties, handles for tools, and wooden rollers. It is also used as charcoal and firewood. Being hard and heavy, the wood is also used to make handles for agricultural tools. Considered a high-quality wood, it is used in fine furniture, cabinetmaking, and decorative veneer. In Colombia, it is used for railroad ties, levers for mines, heavy construction, shafts and handles for tools, and barrels. The bark is used in industrial tanning. Because the trees adapt to degraded soils, they are used to preserve natural resources.

The flowers are cream in color; fruits are oval, and brown, with the base shaped as a goblet and one dark-green seed. Fructification can occur when the trees are 2 m in height. However, the process commonly starts at 4 to 5 m in height. Once begun, fructification occurs annually. The seed is the size of an acorn, ovoid and globose, 2 to 3 cm in diameter by 5 to 7 cm in length; its pericarp has a coriaceous consistency. The dark-green seeds turn brown or dark coffee color when they are ripe (Barreto and Herrera 1990).

Seeds are collected during February, March, and August. Because seeds gathered from the ground have low viability, seeds should be collected from the tree or by shaking the branches. These large seeds do not disperse well. Seeds average 150 per kg.

Seeds should be stored in a cold, dry environment (relative humity less than 12 percent). However, storing these recalcitrant seeds directly in water at a low temperature or stratifying them in wet sand, moss, or sawdust to prevent attacks by fungi or insects has shown good results. Moisture content at the moment of storage is about 21 percent, and seeds remain viable less than 4 months (Barreto and Herrera 1990).

Although the seeds do not require pregermination treatment, washing the seeds before planting is recommended. The seeds can be placed in 10 °C water for 4 days before planting. Germination percentage is 80 percent when the seeds are fresh; seeds germinate in 30 to 50 days. Germination is hypogeal, and two cotyledons unfold in 60 to 65 days.

Seeds may be sowed in the threshing floor, but sowing in 20 by 30 cm bags or in seedbeds of soil and loose sand is recommended. Soil from a natural oak grove is best. Seeds are sowed 5 cm apart to a depth equal to the seed's smallest diameter. Seeds should be covered lightly and watered abundantly. Although the species thrives in sunlight, some shade should be provided to prevent the burning of stems and bark. When the plantules reach a height of 10 to 15 cm in seedbeds, they must be transplanted to bags and watered and shaded for 30 days. The plants must be outplanted when they reach 60 to 80 cm in height.

Quercus humboldtii can also be propagated by stem cuttings, shoots, or bareroots. Shoots from the roots are cut 30 to 35 cm from the ground. Trees greater than 50 cm d.b.h. have lost their sprouting capacity.

Because the species is resistant to pests and grows rapidly, no special care is required.

ADDITIONAL INFORMATION

In Colombia, *Q. humboldtii* has been subjected to intense felling. However, some trees still grow in the central region of the country, in the high zones of the central and eastern mountain ranges, and more abundantly in some regions of the southern region.


1cm
2cm

Quercus oleoides Schltdl. & Cham.

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FAGACEAE (BEECH FAMILY)

No synonyms

Encino, encino prieto, roble, roble blanco, tesmol, tresmoles, yagpsuy

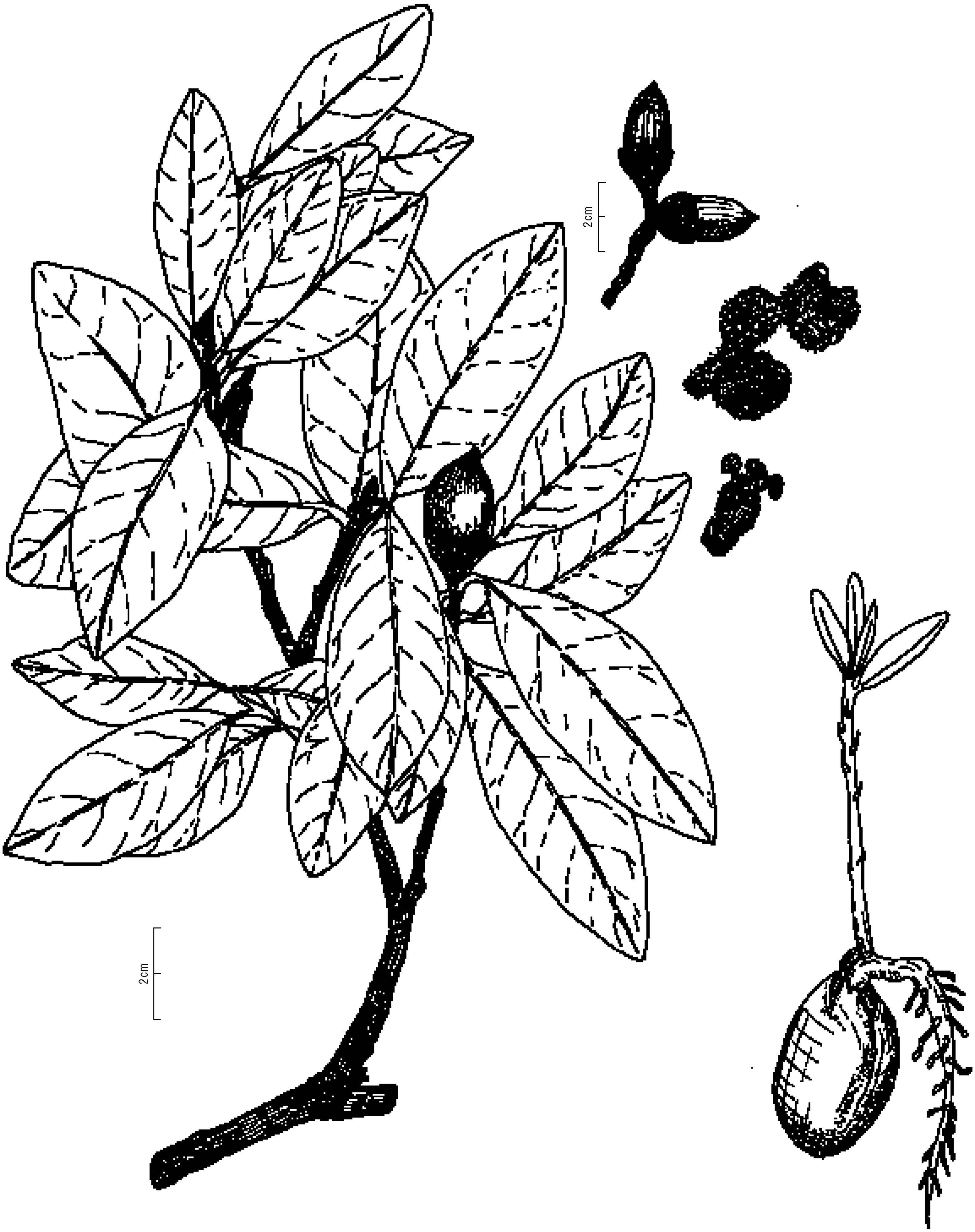
Quercus oleoides grows in dry forests and pastureland from Guanacaste, Costa Rica to Tamaulipas, Mexico in a series of distinct populations (Burger 1977, Montoya 1966). In Honduras, Belize, and Nicaragua the tree grows in association with *Pinus caribaea* Morelet in woodlands or open forests, and is sometimes more abundant when fire occurs frequently.

Quercus oleoides is a slow-growing tree, reaching 8 to 15 m in height and up to 60 cm d.b.h. This often many-branched tree has a dense crown, cylindrical trunk, and dark gray, smooth bark with some furrows. The twigs are 1 to 2 mm thick and fluted; they develop densely short-stellate-tomentose, and turn glabrate or persistently puberulent gray; the lenticels are rarely evident, the stipules caducous. Leaves are evergreen, thick, hard, 4 to 11 cm long, 2 to 5 cm wide, oblong or elliptic to slightly obovate and are pale gray with minute, canescent, stellate hairs. Their shape is obtuse to rounded and emarginate, abruptly obtuse to acute or cuneate at the base. Biological and edaphic factors appear more important to the range of distribution of the species than climatic differences (Montoya 1966). In Costa Rica, this species is very abundant in young volcanic soils developed on gray tuffs. In Mexico, it has been reported growing in sandy soils with good drainage, as well as in clay soils with poor drainage (Pennington and Sarukhan 1968). *Quercus oleoides* Schltdl. & Cham. grows from sea level up to 500 m and in climates with a range of annual rainfall of 1500 to 2500 m and an average temperature of 23 to 25 °C.

The species exhibits great variability in vegetative and reproductive characteristics (Montoya 1966). *Quercus oleoides* from Guatemala is considered related to *Q. virginiana* Mill., and *Q. sagraeana* Nutt. from Pinar del Río, Cuba, is probably a hybrid of *Q. oleoides* from Mexico and *Q. germinata* from the Southeastern United States (Muller 1955).

The wood of *Q. oleoides* is extremely heavy with a specific gravity of 0.86. Dry sapwood is white; heartwood is brown. The wood has intercrossed grains, medium texture, and little luster. The pores are conspicuous, usually solitary, and distributed in continuous strips on the transverse surface. The wood dries slowly and suffers strong contractions during the process. It is difficult to work and preserve, but has high natural durability. It is used for railway foundations, bridges, fenceposts, wine barrels, mine posts, agricultural tools, and charcoal.

Quercus oleoides flowers from December through May. Male catkins are 3 to 4 cm long, the puberulent rachis are rather closely flowered; and the anthers are about 1 mm long on very short filaments. Female catkins are 3 to 30 mm long with one to six flowers 7 mm long. Fruits mature 1 year after flowering and are single or with several others on a peduncle 5 to 50 mm thick; the cup is 7 to 12 mm long and 12 to 17 mm broad. The mature fruits have been collected from July throughout January.


2cm
2cm

Quercus oocarpa Liebm.

L.A. FOURNIER
Escuela de Biología, Universidad de Costa Rica

FAGACEAE (BEECH FAMILY)

Quercus warscewiczii Liebm., Q. yunkeri Trel.

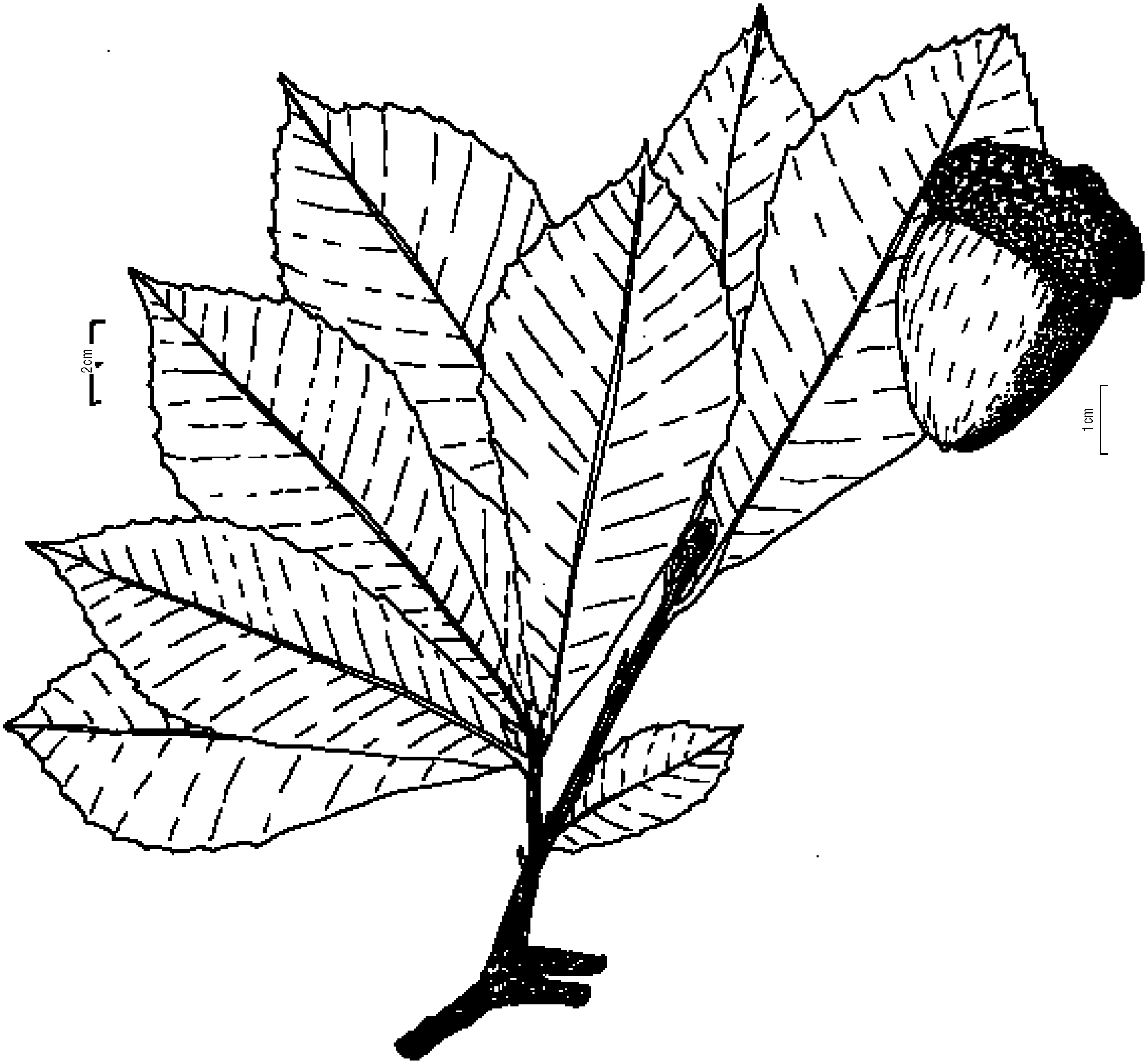
Encino, roble, roble blanco

Quercus oocarpa is easily differentiated from other oak species in the region by its very pale-colored lower leaf surface. Closely related, *Q. insignis* M. Martens & Galeotti and *Q. oocarpa* share much of the same habitat in Costa Rica and much of the same range, which may indicate the two are the same (Burger 1977). *Quercus tomentocaulis* Muller, from Honduras, and *Q. oocarpa* are probably the same species (Burger 1977).

Quercus oocarpa is a slow-growing tree that reaches 6 to 30 m in height and up to 60 cm d.b.h. The tree has a tall trunk, rounded crown, and brown bark that sheds in strips. The twigs are coarse, fluted, develop from densely fulvous-tomentose, and become glabrate and gray or light brown with a few scarcely evident lenticels. The buds are round and glabrate, stipules caducous. Leaves are alternative, apparently evergreen, thin and papery or rather firm, 10 to 30 cm long, 3 to 14 cm wide, oblanceolate to obovate or narrowly elliptic, attenuately acute at the apex, narrowly rounded or cunneate at the base, undulate or sharply low-dentate, except the entire base. The very pale-colored lower leaf surface is a characteristic that easily separates this oak species from others in the region. *Quercus oocarpa* grows in a wide range of soils, all of them rich in organic matter. It grows in moist and wet lower montane and montane forests from 700 to 2300 m but is more abundant from 1400 to 1900 m. The species occurs in climates with an annual rainfall from 2200 to 3000 mm and a temperature of 14 to 18 °C.

The wood of *Q. oocarpa* is heavy (specific gravity is 0.67). The dry sapwood is white and the heartwood is brown. The wood has a straight grain, rough texture, and poor luster. The figure shows very attractive mottling on the radial surface, and the pores are solitary or arranged in bands. The wood dries at a moderate rate, suffering some defects during the process. It is not easy to work or preserve but has good natural durability. The wood is used primarily for flooring, agricultural tools, charcoal, fenceposts, railway foundations, wine barrels, and mine posts.

The species flowers primarily in March (Jiménez and others 1996) and mature acorns have been observed in May, July, September, and November, suggesting blooming may occur in other months. In a recent study in the central mountains of Costa Rica (1700 m), *Q. oocarpa* bloomed from March throughout August with peak flowering in April and July (Madrigal 1997). Fruits observed from May through January were more abundant than those from August through November, peaking in September and October. Male catkins are 3 to 7 cm long and flowers remain crowded distally on the densely tomentose rachis. Female flowers are on short, 5 to 30 mm spikes about 5 mm long. Fruits are usually solitary; the cup is 2 to 3 cm long, 3 to 4 cm broad, but probably becoming larger, gradually tapering, and bowl-shaped; the acorn is 4 to 5 cm long and 2 to 5 cm thick at maturity (Burger 1977).


2cm
1cm

Quercus seemannii Liebm.

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FAGACEAE (BEECH FAMILY)

Quercus eugenifolia Liebm., *Q. granulata* Liebm., *Q. citrifolia* Liebm., *Q. bumelioides* Liebm. Fide Trelease, *Q. borucanas* Trel., *Q. eugenifolia* f. *petiolata* Trel., *Q. boquetensis* Stand., *Q. panamandinaeae* Muller pro parte as to stems and leaves only, *Q. sapotaefolia* as to Costa Rica, *Q. chiriquiensis* Trel. ex C.H. Muller

Encino, encino blanco, roble

Quercus seemannii grows in Central America.

Quercus seemannii is a slow-growing tree that reaches 6 to 25 m in height and 40 to 60 cm (in some cases, 1 m) d.b.h. The trunk is cylindrical or slightly furrowed; the crown, round and dense; the smooth bark, gray or brown; and the foliage, dark green. Twigs are 1 to 2.5 mm thick, fluted from sparsely pubescent, and soon glabrate and dark red-brown buds with prominent light lenticels. The buds are 2 to 4 mm long, ovoid or elongated, acute, glabrous, and light brown; the lingulate stipes are soon caducous. Leaves are subevergreen, thin but rather hard, and alternate. Sometimes persisting for a short time after new flushes of growth, leaves are 4 to 8 cm long (sometimes 16 cm) to 4 cm broad. The blade is narrowly oblong to elliptic, lanceolate or narrowly obovate, usually tapering gradually to the acute and aristate apex. Occasionally, it is blunt and rounded on the same stem or on different trees, tapering to the acute base or, rarely, obtuse and contracted abruptly at the petiole. The margin is entire, usually becoming revolute. The lamina evolves from chartaceous to subcoriaceous. The tree grows in premontane, lower montane, and montane wet and rain forests between 1400 and 2400 m, but it is occasionally found as low as 1100 m and as high as 3100 m. This area of distribution includes a wide variety of soil types and climatic conditions (2000 to 3500 mm of annual rainfall and 8 to 22 °C average temperature).

Quercus seemannii is considered a complex species due to its considerable variability (Burger 1977). This species probably integrates with *Q. gulielmi-trealease* C.H. Müll and hybridizes with *Q. rapurahuensis* Trel. and *Q. tonduzii* Seemen. *Quercus seemannii* and its close relatives in Costa Rica are related to entire-leafed black oaks (subgenus *Erythrobalanus*) of northern Central America. These species combine to make up the most difficult complex in Central America's oaks.

The wood of *Q. seemannii* is heavy with a specific gravity of 0.67. Sapwood is white-yellow to white; the heartwood is dark-brown to brown with well-defined growth rings (Van der Slooten and others 1969). The heartwood has a straight grain, rough texture, and a good figure in the radial surface, although its luster is poor (Carpio 1992). It dries at a moderate rate, with serious defects. It is hard to work and preserve but has good natural durability. The wood is used for flooring, agricultural tools, charcoal, poles, mine posts, wine barrels, and railway foundations.

Flowering of *Q. seemannii* reaches its highest peak during the month of March when leaf fall is high and rainfall is very low. However, two additional flowering peaks occur (Céspedes 1986), one at the beginning of the rainy season (May) and one during the transition period between the rainy and the dry seasons. Staminate catkins 3 to 10 cm long are loosely flowered; the flowers are attached to minute and sparsely puberulent rachis, and the apiculate anthers are slightly exerted. Pistillate catkins are about 1 cm long, anther flowers are solitary or in groups of two to four. A good crop of acorns appears in January and February, the largest crop occurs in May and June, and a small crop occurs in August and September. Fruits mature within 1 year. They are subsessile or on very short peduncles, and solitary or in groups of two to four. The light brown acorns are 10 to 18 mm long, 8 to 14 mm thick, broadly ovoid to hemispheric, and about one-fourth to one-third included in the cup.

Quercus seemannii has good capacity for natural regeneration and is commonly found growing in almost pure natural stands. It is a common practice in Costa Rica to collect seedlings from the natural forests and outplant them in small plantations without any nursery care (personal observation). The seedlings of natural regeneration are also kept in small nurseries for 6 months before being outplanted.

ADDITIONAL INFORMATION

One individual tree planted on the campus of the University of Costa Rica in San Pedro de Montes de Oca (Premontane, 1200 m) has grown at a rate comparable to trees growing in the natural range of the species (16 m in height and 60 cm d.b.h. in 32 years).

Céspedes (1986) carried out a detailed phenological study of this tree species in a lower montane moist forest of the central mountains of Costa Rica (1700 m, 2148 mm average rainfall, and 16 °C average annual temperature). He observed that leaf flushing is very low during the dry season (December through April), but a large amount of new foliage is produced at the beginning of the wet season in May. A lesser peak of vegetative growth was observed during the wettest months of September and October. Leaf fall occurs throughout the year but peaks during the dry season.

Dirphiopsis flora (Lep., Saturniidae) attacks the foliage of this species in Costa Rica (Arguedas and others 1993).


1cm
2cm

Rhizophora mangle L.

JAMES A. ALLEN
Paul Smiths College,
Paul Smiths, NY

RHIZOPHORACEAE (MANGROVE FAMILY)

Rhizophora mangle var. *samoensis* Hochr., *R. samoensis* (Hochr.) Salvoza

Mangle, mangle caballero, mangle colorado, mangle de chifle, mangle gateador, mangle injerto, mangle rojo, mangle salado, mangle zapatero, manglier, manglier rouge, mangro, mangue sapateiro, mangue vermelho, palétuvier rouge, red mangrove (Bohorquez 1996, Little and Wadsworth 1964)

The genus *Rhizophora* comprises six to eight species and three or four hybrids (Duke 1992, Tomlinson 1986). All members of this pantropical genus are considered true mangroves and are limited in distribution to the intertidal zone. The native range of *R. mangle* includes the coast of central and southern Florida, Bermuda and most of the West Indies, both coasts of continental tropical America from Mexico south to Brazil and northern Peru, and the coast of West Africa from Senegal to Angola (Chapman 1976, Little and Wadsworth 1964). *Rhizophora mangle* has also been introduced in several other locations, including Hawaii (Allen 1998) and Tahiti. *Rhizophora mangle* may also be native to western Pacific Islands from New Caledonia to American Samoa, but the taxonomic status of these populations is not completely clear and they have been treated both as a variety of *R. mangle* and as a separate species, *Rhizophora samoensis* (Tomlinson 1986).

Rhizophora mangle is a small to medium-sized tree of 10 to 20 m in height and 10 to 30 cm d.b.h. However, it may exceed 40 m in height and 70 cm d.b.h. on productive sites where hurricanes are infrequent. It is capable of moderately fast growth (1 to 1.5 m per year) on productive sites (Jimenez 1985). Its most characteristic feature is the mass of branched, arching, stilt (also called prop or aerial) roots, which may spread so profusely that they make *R. mangle* forests practically impenetrable. *Rhizophora mangle* is restricted to coastal environments, particularly low-energy, protected, intertidal sites with soft, muddy substrates. It also grows on other types of substrates, such as peat, marl, and sand, and occasionally on rocky and moderate-energy shorelines (Chapman 1976, Odum and others 1982). While salt-tolerant, its growth is impaired above about 35 parts per thousand (ppt) salinity, and mortality may occur above 60 ppt. The species grows in areas with average annual rainfall of about 800 to 10,000 mm per year and appears to be limited to areas with average temperatures of about 21 to 30 °C (Jimenez 1985). *Rhizophora mangle* often dominates the seaward side of mangrove forests, where it may form monospecific stands. Farther inland it more frequently mixes with other mangrove species (Odum and others 1982).

There is some controversy over the taxonomic status of *R. harrisonii*, which some consider a hybrid between *R. mangle* and *R. racemosa* (Jimenez 1985, Tomlinson 1986).

The wood of *R. mangle* is hard and very heavy, with a specific gravity of 0.9 to 1.2. The sapwood is light brown, and the heartwood is reddish brown or dark brown. The wood is used for pilings, posts, poles, cabinets, fuel, and charcoal and in shipbuilding. The wood is durable in the soil but susceptible to dry-wood termites (Little and Wadsworth 1964) and marine borers (Southwell and Bultman 1971). The bark has been used commercially as a source of tannin and various dyes and also to produce medicines (Little and Wadsworth 1964, Morton 1965).

Flowers are borne in axillary clusters, which have been characterized as simple cymes (*e.g.*, Wagner and others 1990) or as a modified dichasium (Gill and Tomlinson 1969). There are two to four flowers per cluster; typically clusters are three-flowered, with a terminal and a lateral pair of flowers, although the terminal flower is commonly absent (Gill and Tomlinson 1969). Flowers have a small, bell-shaped, pale yellow base (hypanthium); four widely spreading, leathery, and persistent pale yellow sepals approximately 10 to 15 mm long; and four narrow, downwardly curved petals that are initially whitish or pale yellow but turn brown. Flowers may be found throughout the year, but in southern Florida flowers are most abundant July through September (Gill and Tomlinson 1971).

Rhizophora mangle may begin flowering by 6 years of age, and possibly as young as 3 to 5 years; flowering has been reported in saplings as small as 0.5 to 1 m in height (Gill and Tomlinson 1969). Pollen appears to be dispersed primarily by wind (Tomlinson 1986, Tomlinson and others 1979).

Rhizophora mangle is viviparous, meaning that the species produces seeds that germinate on the parent plant. The dispersal unit, a viviparous seedling, is called a propagule. Following fertilization, from 4 to 7 months are required for emergence of the hypocotyl (Gill and Tomlinson 1971). Another 4 to 6 months typically elapse between appearance of the hypocotyl and abscission, by which time the propagule is between 8 and 30 cm in length. Fresh propagules range in weight from about 3 to 35 grams (29 to 333 per kg). Published mean weights of propagules include 7.8 g (scrub mangroves, Florida; Lin and Sternberg 1995), 13.1 g (tall mangroves, Florida; Lin and Sternberg 1995), 14.0 g (Panama; Rabinowitz 1978), and 23.3 g (Florida; Smith and Snedaker 1995).

Propagules can be collected directly from trees, from the ground, or from water surfaces. Propagules collected from trees should be fully developed and nearing abscission; these propagules usually detach from the pericarp with a gentle pull. Collected propagules should be bright green (except the lower portion, which is normally brown), have no roots or damaged plumules, and be free of other visible damage and/or discoloration (Bohorquez 1996, Snedaker and Biber 1996). Propagules with evidence of attack by the borer *Coccotrypes* (syn. *Poecilips*) *rhizophorae* (small emergence holes) should be discarded. Although propagules are available throughout the year, there is usually a pronounced peak of propagule availability. In Florida and the Caribbean, more propagules are available August through October (Padron 1996, Snedaker and Biber 1996).

Propagules may be stored for at least 3 to 4 weeks in moist containers (Snedaker and Biber 1996). Propagules stored indoors in open containers—with a small amount of water in the container and the propagules covered with moist paper towels—remained viable for 2 months (Crewz 1998). Experiments with storage of other *Rhizophora* species suggest that it may be possible to store *R. mangle* propagules for periods longer than 2 months. Kogo and others (1985), for example, reported better than 80-percent survival of *Rhizophora stylosa* propagules stored for 71 days in an air-conditioned room in closed plastic bags, in tap water and in 2- and 4-percent sea water. *Rhizophora mangle* propagules kept floating or submerged in water for up to 1 year have reportedly been grown successfully (Davis 1940).

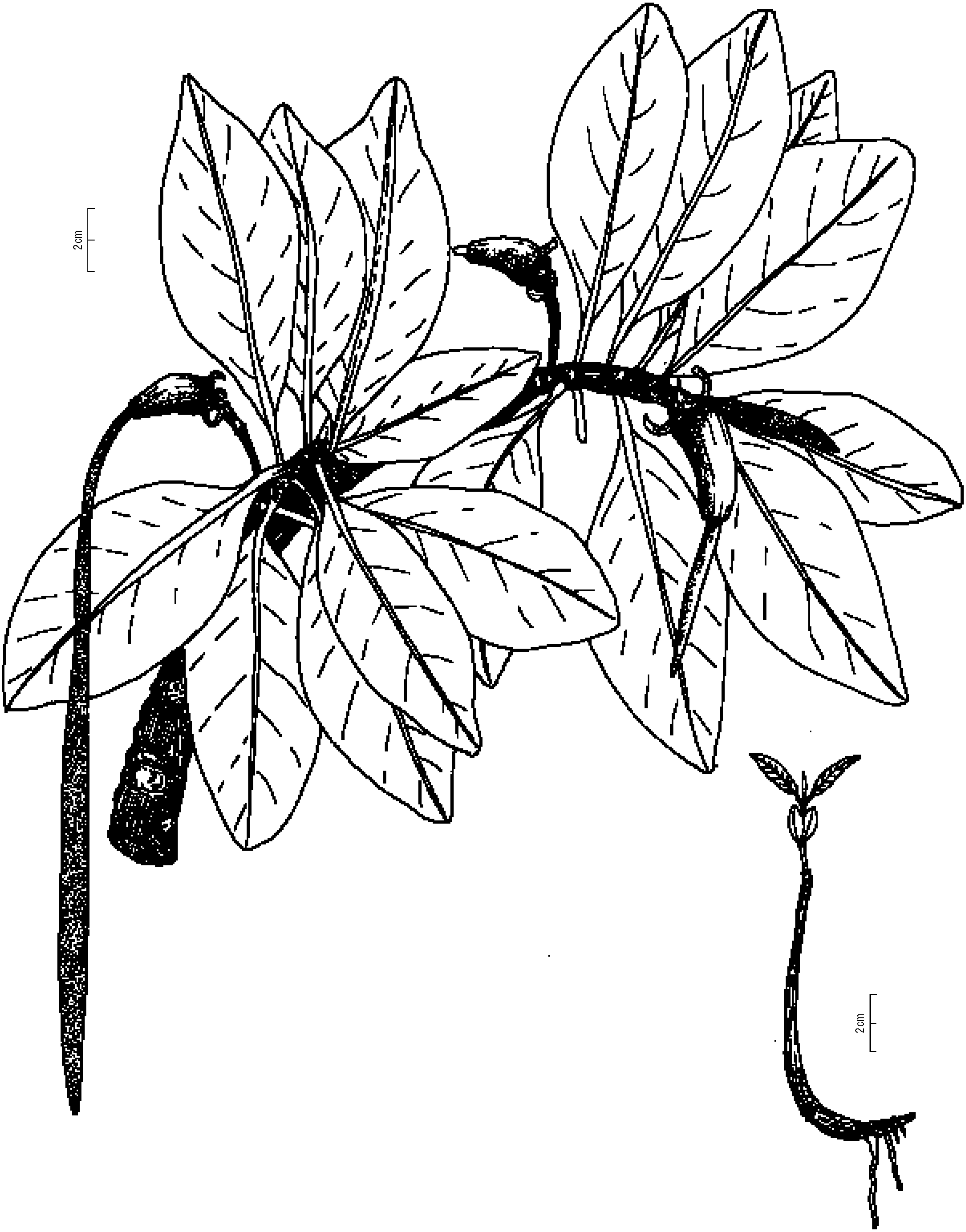
Germination without pretreatment may exceed 90 percent. Although pretreatment is unnecessary, the propagules can be soaked in water for 2 weeks or until root buds develop at the tip of the radicle (Crewz 1998).

In the nursery, *R. mangle* propagules are generally sown in tubes or small pots and grown under ambient conditions (Reark 1983). Keeping the pots half-filled with water prepares the seedlings for planting on anaerobic substrates and occasional watering with brackish or saline water (e.g., 15 ppt) will help to reduce subsequent planting shock on saline sites. Use of saline water may also help reduce the number of pathogens affecting seedlings in the nursery. Although easy to grow in nurseries, seedlings are occasionally damaged or killed by scales, aphids, caterpillars, wood/propagule borers, and fungal infections.

Seedlings of approximately 30 to 60 cm in height are produced after 1 year in the nursery and can be outplanted. Older, larger seedlings may be sold in 4, 12, 28, or even 40-liter containers.

Direct planting of propagules in the field is a low-cost method that has shown reasonably good success (Lewis 1990). Propagules are sown to a depth of about one-fourth to one-third of their length, although growth may be better when propagules are sown to a depth of only about 2.5 to 4 cm. Survival is best on well-protected, low-energy sites and in areas with low levels of propagule predation. On exposed sites or sites that frequently flood > 20 cm, direct sowing is more likely to fail. Planting large seedlings with well-developed root systems (Goforth and Thomas 1980, Snedaker and Biber 1996) or smaller seedlings within protectors, such as PVC pipes, may increase survival rates.

In all but the most northern parts of its range, *R. mangle* seedlings or propagules can be planted any time of the year, but cold and dry periods should be avoided (Snedaker and Biber 1996). The best time to plant nursery-grown seedlings produced without acclimation to salt water may be in seasonally rainy periods, which may reduce the shock caused by sudden exposure to high salinity (Barnett and Crewz 1989).


2 cm
2 cm

Roupala montana Aubl.

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Escuela de Biología, Universidad de Costa Rica

PROTEACEAE (PROTEA FAMILY)

Roupala pyrifolia Salisb. & Knight, *Rhopala media* R. Br., Rh. Dentata R. Br., *Rhopala complicata* Kunth, *Rhopala ovalis* Pohl, Pl. Bras., *Rhopala macropoda* Klotzsch & Karst, *Rhopala gardneri* Meissn., *Rhopala martii* Meissn, *Rhopala martii* var. *Simplicifolia* Meissn, *Rhopala frondosa* Rich ex. Meissn, *Rhopala tomentosa* a. *integrifolia* Meissn, *Rhopala boissieriana* Meissn, *Rhopala veraguensis* Klotzsch es Meissn, *Roupala borealist* Hemsl., *Roupala dariensis* Pitt., *Roupala panamensis* Pitt., *Roupala discolor* Rusby, *Roupala dissimilis* Pitt., *Roupala repanda* Lundell, *Roupala montana* var *dentata* (R. Br.) Sleumer

Danta hediondo, danto, danto carne, ratón, ratoncillo, zorrillo, zorrillo hediondo

One of about 50 species in an American genus, *Roupala montana* is distributed from the Isthmus of Tehuantepec, Mexico to Brazil.

Roupala montana is a slow-growing, medium-size tree that reaches 8 to 25 m in height and 40 to 70 cm d.b.h. The tree has a cylindrical trunk, some low branching, and a rounded crown that is dense with dark green foliage. The gray-brown bark is smooth with narrow furrows in old mature trees. The young stems are terete, ferrugineous-strigillose, and glabrescent. Leaves are very heteromorphic; alternate juvenile leaves are pinnately compound, and generally larger than the adult form. The number of leaflets is extremely variable even on a single branchlet; the margin is generally coarsely serrate or sometimes undulate; and the veins are conspicuous. Adult leaves are ovate, 5 to 12 cm long, 2 to 9 cm broad, acute or acuminate at the apex, cuneate to more or less obtuse at the base, often decurrent upon the petiole, subcoriaceous, ferrugineous-strigillose and glabrescent above and below. The fresh wood and crushed leaves or branchlets have a strong odor like that of ground fish or tuna fish, as described by those doing the testing. Although *R. montana* occurs in a wide range of soil types, it grows best in soils with good drainage. This species grows in moist and wet forests from the lowlands up to 144 m (Nevling 1960). The climatic conditions in which the species grows have an annual rainfall of 1500 to 3000 mm and an average temperature of 18 to 25 °C.

The small, creamy-white flowers are produced from late January through April in terminal or axillary racemes of many flowers. The rachis are 6 to 18 cm long and tomentose, and the flowers are borne singly or in pairs. The fruit is a flat follicle, obliquely bivalvate, often minutely spurred at the base, 2.5 to 4 cm long, about 1.5 cm broad, and glabrous. Follicle dehiscence occurs from the end of March through April, liberating the winged seeds that germinate at the beginning of the wet season at the end of May. Winged seeds are oval, 1.5 cm long, and 0.8 cm broad.


2cm
2cm

Roystonea borinquena O.F. Cook

K.F. CONNOR and J.K. FRANCIS
Southern Research Station
and International Institute of Tropical Forestry
USDA Forest Service

ARECACEAE (PALM FAMILY)

No synonyms

Mountain-cabbage, palma de costa, palma de yaguas, palma real,
Puerto Rico royal palm, royalpalm

Roystonea borinquena is native to Puerto Rico, the Puerto Rican island of Vieques, St. Croix in the U.S. Virgin Islands, and possibly Tortola in the British Virgin Islands (Francis 1992, Little and Wadsworth 1964). A widely planted ornamental, *R. borinquena* may have naturalized in the British Virgin Islands and in St. Thomas and St. John, U.S. Virgin Islands (Francis 1992).

Roystonea borinquena is a rapidly growing tree with an average height of 12 to 18 m in Puerto Rico, but it can reach 26.4 m (Francis 1992). Young trees can average 1-m height growth annually. Diameters range from 25 to 70 cm; maximum age is 80 to 110 years. The tree has a smooth, gray trunk with a swollen base and gracefully drooping fronds. The upper trunk is encased in a green column of leaf sheaths 1 to 3 m long. The pinnate leaves have short petioles and a sheath and blade 2.4 to 3.7 m long. The youngest leaflet projects as a spire above the others (Little and Wadsworth 1964), and pinnae grow from the rachis in two planes (Bailey and Bailey 1978). In Puerto Rico, natural regeneration is most aggressive on the slopes and valleys of moist limestone hills (Francis 1992). The species regenerates naturally in areas annually receiving 1250 to 2500 mm of precipitation; its native range has a mean annual temperature of 25 °C and is frost free.

Roystonea borinquena is a common sight in the island cities. The species' ability to withstand a polluted atmosphere and to grow well on either moist, well-drained soils or partially compacted fill dirt enhances its value as a landscape plant (Francis 1992). Ultisols, Alfisols, Inceptisols, and Oxisols are important soil order habitats. Roots will not damage sidewalks or curbs even when the trees are planted in constricted spaces. Palm lumber was once widely used in rural construction, and the leaves were used as a roof thatch. Dry leaf sheaths (yaguas) can be spread out flat to make sides of buildings (Little and Wadsworth 1964). The wood, when used as lumber, is susceptible to attack by the dry-wood termite *Cryptotermes brevis* (Francis 1992, Little and Wadsworth 1964, Wolcott 1946).

Flowering can begin as early as the seventh year, and trees can bloom throughout the year. The length of the inflorescence reaches up to 1 m (Little and Wadsworth 1964). The whitish male and female flowers form on the same panicle, with male flowers of each tree opening and falling before the female flowers to prevent self-fertilization. The twice-branched, drooping panicles of *R. borinquena* develop from large, narrow buds located at the base of the leaves. The panicles develop inside a dark brown sheath 0.9 to 1.5 m long (Francis 1992, Little and Wadsworth 1964). According to Bailey and Bailey (1978) and Braun (1983), there are scales on the axes bearing the flowers (rachillae). Generally, each female flower forms between two male flowers on the panicle (Francis 1992, Little and Wadsworth 1964). The male flowers have three small, broad sepals, three blunt-pointed petals, and six to nine stamens with purple anthers; the females have three small, broad sepals, and a tubular corolla (Little and Wadsworth 1964). The stalkless male flowers measure 13 mm across, while the smaller female flowers measure 3.2 mm across. The greenish-yellow fruit are 13 mm long and about 10 mm in diameter (Little and Wadsworth 1964). Fruits ripen to a brownish-purple color and contain one light brown elliptic seed that is 8 mm long, hard, and oily. The flowers are an important nectar source for honey bees, and the fruits a fat-rich food for birds (Francis 1992, Little and Wadsworth 1964). Seeds are commonly dispersed by birds, rodents, water, and domestic animals.

Fruits are easily collected from the ground beneath open-grown trees. Seeds average 2,980 per kg (Francis and

Rodríguez 1993). Seeds can be stored for 1 to 2 months in sealed containers at room temperature and for longer periods of time under refrigeration at 3 to 4 °C. On a suitable site, natural regeneration may be so abundant that the one- or two-leafed plants may be mistaken for grass. Seeds sowed in trays of sand with no pretreatment and kept at ambient temperatures (24 to 30 °C) averaged 80 percent germination after 14 days. Germination is hypogeous (Francis 1992) and may take up to 2 months after sowing. The radicle emerges first, the shoot about 3 weeks later. Under natural conditions, the first seeds may not germinate for 50 to 60 days, with others delayed for an additional 100 days (Braun 1983).

Seedlings grown in nurseries should be kept in full sunlight (Francis 1992). Seedlings can be transplanted at any size but need protection from weeds and grass until they have formed a stem and have overgrown the competition. *Roystonea borinquena* seedlings kept in full sunlight averaged 30 cm in height after 6 months and 90 cm after 15 months; they can be grown to heights of 1.5 m or more in 4-L containers (Francis 1992). Large trees can be dug up with a backhoe and transplanted. Survival is high as long as trees are braced and frequently watered. High mortality results if young trees with only a few basal leaves or short trunks are moved without a protective earth ball and left without shade and water (Francis 1992). The tree apparently has no serious insect pests.

ADDITIONAL INFORMATION

Braun (1983)and Little and Wadsworth (1964) note *R. borinquena* heights reaching only 18 m and diameters of 30 to 61 cm for the species, while Bailey and Bailey (1978) report heights reaching at least 15 m. Because of its ability to withstand high, hurricane-force winds, the species sometimes dominates the forest canopy despite its short stature (Francis 1992).

Although trees flower and fruit throughout the year, suppressed and intermediate trees may never bear fruit. Francis (1992) reports that, in a survey of 100 open-grown *R. borinquena* trees, 35 percent bore no fruit while the remainder bore an average of 3.2 panicles, which produced from 6,000 to 12,000 fruits each. Fruits contained, on the average, 6.48 mg per 100 mg starch and 44.38 mg per 100 mg lipid.

Seeds of *R. borinquena* yield 19.65 mg per 100 mg of oil; the oil is made up of 31.8 percent lauric, 27.2 percent oleic, 9.6 percent myristic, 8.4 percent linoleic, 7.8 percent caprylic, 7.8 percent palmitic, 4.8 percent capric, and 2.6 percent stearic fatty acids.


1cm
2cm

Roystonea regia (Kunth) O.F. Cook

K.F. CONNOR
Southern Research Station,
USDA Forest Service

ARECACEAE (PALM FAMILY)

Oreodoxa regia (HBK); *Roystonea elata* (Bartr.) F. Harper [Florida royal palm]1;
Roystonea jenmanii (C.H. Wright) Burret; *Roystonea ventricosa* (C.H. Wright) Burret

Cuban royal palm, konnings palm, palma de yagua cubana, palma de yaguas,
palma real, palma real cubana, royalpalm

Species of the genus *Roystonea* grow in the subtropical moist and subtropical wet life zones (Holdridge 1967). *Roystonea regia* is a native of Cuba, now naturalized in Hawaii (Neal 1965) and in Collier, Dade, and Monroe counties in Florida (Little 1979, West and Arnold 1952), where it grows on moist, rich hammocks.

Roystonea regia can reach 15 to 34.5 m in height and 61 cm in diameter (Bailey and Bailey 1976, Neal 1965, West and Arnold 1952). The stout, smooth trunk is not always straight, and many short air roots are attached at the base. The upper trunk is encased in a green column of leaf sheaths 1 to 3 m long. The pinnate leaves have short petioles and a sheath and blade 2.4 to 3.7 m long. Pinnae grow in several planes along the rachis of each *R. regia* leaf, while in *R. borinquena* O.F. Cook, pinnae grow from the rachis in two planes (Bailey and Bailey 1978). Growth is rapid if the tree is placed in fertile soil with adequate water and full sun (Braun 1983).

Roystonea regia is primarily valued as an ornamental. The seeds contain oil that is sold commercially (Moscoso 1945) or used for livestock feed (Little and others 1974). The leaves are used for thatching, and the wood can be used for construction.

Flowers develop from buds formed on the trunk below the leaves. In Florida, trees flower in the spring and fruits mature in the fall (West and Arnold 1952). The fragrant flowers are borne on a many-branched panicle. Both the male and the female flowers form on the same panicle, with male flowers of each tree opening and falling before the female flowers to prevent self-fertilization. Generally, each female flower forms between two male flowers on the panicle (Francis 1992). The male flowers have three minute, broad sepals, three blunt-pointed petals measuring 6.4 mm long, six to nine stamens with purple anthers, and a rudimentary pistil (Little and others 1974). The smaller female flowers have three small, broad sepals and a tubular corolla. They also bear six sterile stamens and a pistil with three styles. Bailey and Bailey (1976) observed trees with dull red to purple flowers, while West and Arnold (1952) and Little and others (1974) describe trees bearing white flowers. The violet-purple fruits are smooth, ovate, and measure 13 mm in length. Each fruit bears a single light brown, thin seed embedded in brown fibrous flesh (Neal 1965, West and Arnold 1952).

In Puerto Rico, birds or bats often feed on the oily pericarp; if seeds are shed with pericarp intact, detritis-eating animals clean the seed when rotting is well advanced, leaving only a papery shell that is easily removed (Francis 1998). Thus, large quantities of cleaned seeds can be collected from the ground under seed-bearing trees.

The best method for long-term seed storage involves the following steps: select clean, half-ripe to ripe seeds; air dry seeds at 80 to 90 percent relative humidity; treat with a fungicide; and seal tightly in polyethylene containers held at room temperature (23 °C). The seeds of *Roystonea* may be intermediate in their storage behavior, neither orthodox nor recalcitrant (Ellis and others 1991a). Drying the seeds to a low moisture content or storing them below 0 °C may result in damage.

Under natural conditions, the first seeds may not germinate for 50 to 60 days, with others delayed for an additional 100 days (Braun 1983). Presoaking *R. regia* seeds in 1,000 ppm GA_3 solution for 48 hours slightly increases the rate of germination but also results in abnormally elongated seedlings (Broschat and Donselman 1988). Clean seeds germinated at 30 to 35 °C provide the best results.

ADDITIONAL INFORMATION

Although *R. regia* is noted for its stature and symmetry, there is some variation in reported height growth. Neal (1965) lists heights reaching only 15 to 21 m in Hawaii, while West and Arnold (1952) report heights of 24 to 34.5 m and up to 61 cm in diameter in Florida. Bailey and Bailey (1978) note maximum heights of 23 m.

Little and Wadsworth (1964) contend that a characteristic distinguishing *R. regia* from *R. borinquena* is that the former lacks the swollen trunk of the latter; however, West and Arnold (1952) and Neal (1965) report the swollen base, and Neal (1965) and Braun (1983) the swollen middle trunk in *R. regia*. According to Bailey and Bailey (1978) and Braun (1983), one feature that distinguishes *R. regia* from *R. borinquena* is the absence of scales on the axes bearing the flowers (rachillae) of *R. regia*. The length of the inflorescence also seems to differ, with that of *R. borinquena* reaching up to 1 m (Little and Wadsworth 1964), but that of *R. regia* reaching only 0.6 to 0.8 m (Braun 1983, West and Arnold 1952).


1cm
1cm

Samanea saman (Jacq.) Merr.

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FABACEAE (BEAN FAMILY)

Acacia propinqua A. Rich. (Histoire Physique, Politique et Naturelle de l'Ile de Cuba, Botanique.-Plantes Vasculaires 1: 466; 1845); *Albizia saman* (Jacq.) F. Muell. (Selected Plants, ed. 2: 12; 1876; annot. as Albizzia); *Calliandra saman* (Jacq.) Griseb. (Flora of the British West Indian Islands 225; 1860); *Enterolobium saman* (Jacq.) Prain ex King (Journal of the Asiatic Society of Bengal, Part 2, Natural History 66: 252; 1897); *Fueilléea saman* (Jacq.) Kuntze (Revisio Generum Plantarum 1: 189; 1891); *Inga cinerea* Humb. & Bonpl. ex Willd. (Species Plantarum, editio quarta 4[2]: 1024; 1806); *Inga salutaris* Kunth (Nova Genera et Species Plantarum 6: 304; 1823); *Inga saman* (Jacq.) Willd. (Species Plantarum, editio quarta 4[2]: 1024; 1806); *Mimosa saman* Jacq. (Fragmenta Botanica 15, t.9; 1800); *Pithecellobium saman* (Jacq.) Benth. (London Journal of Botany 3: 216; 1844); *Zygia saman* (Jacq. Lyons (Plant Names, Scientific and Popular [ed. 2]: 503; 1907)

Algarrobo, algarrobo del país, almacigo blanco, árbol de lluvia (arbre a pluie), bordao de velho, carabali, carito, carreto, carreto real, cenícero, cenísero, cenísero claro, cenísero oscuro, cenízaro, compano, cow tamarind, daugení, dormilón, French tamarind, genízaro, gipio, gouannegoul, guango, huacamayo-chico, lara, monkey pod, rain-tree, regenboom (Dutch), saaman, sama, samán, samán blanco, samán negro, samana, tabaca, tabaca de monte, urero, urero macho, urero negro, zorra (National Academy of Sciences 1979, Record and Hess 1949)

Samanea saman is a widely cultivated tree, indigenous to the dry American tropics, which extend from Mexico, through Central America, down to Venezuela and Colombia in South America (Allen and Allen 1981, Woodson and Schery 1950). Its widespread distribution could be the result of seed dispersal by cattle, horses, and man (Janzen and Martin 1982). The tree is an occasional or frequent element of the canopy in primary dry tropical forests and transitional to humid forests.

Samanea saman is a large tree reaching 50 m in height and 250 cm d.b.h., with a branch spread of about 60 m in very old trees. Commonly, the trees are 25 to 35 m in height and 40 to 120 cm d.b.h. (Holdridge and Poveda 1975, National Academy of Sciences 1979, Salas-Estrada 1993). The crown is wide spreading and umbrella-shaped with feathery foliage. The tree is deciduous in deciduous forests and evergreen in rain forests; flowering and refoliation are synchronized (Janzen 1983e). The young twigs are green or gray, aureo-pubescent, becoming glabrate with spare lenticels. They can be hollowed and inhabited by ants (Salas-Estrada 1993, Woodson and Schery 1950, Zamora 1991). The bole is irregular and twisted; the basal third is branch free. The bark is blackish gray with vertical fissures and horizontal cracks forming blocks in young trees and narrow scaly plates in old trees; the inner bark is whitish, light pink, or light brown and fibrous, with a fresh potato scent and bitter taste (Holdridge and Poveda 1975, Salas-Estrada 1993). Leaves are compound, alternate, bipinnate, paripinnate, 12 to 36 cm long, and 13 to 34 cm wide, with two to six pairs of pinnae. Each pinna bears two to eight pairs of opposite pinnules. Pinnules are sessile, oblong, elliptic or rhombic, and 1.5 to 6.0 cm long by 1.0 by 3.0 cm wide; they have entire margin, obtuse apex, and acute and unequal base (Brenes 1994, Salas-Estrada 1993).

The tree grows on plateaus and flatlands (slopes of 5 percent or less) with moderate drainage, where temperatures range from 20 to 38 °C and annual rainfall fluctuates from 600 to 2500 mm with a mean of 1400 mm (Hartshorn and Poveda 1983, National Academy of Sciences 1979). It is also found in open country, cultivated areas, and pastures and is used as a shade and garden tree (Janzen 1983e). It can survive 2 to 6 months of dryness. The species is indifferent to soil texture and pH, but good or adequate drainage is important (Brenes 1994). The elevation range is 0 to 1100 m.

The sapwood is light yellowish gray in green condition and the heartwood is reddish brown. In dry condition the sapwood is orange-gray and the heartwood is grayish brown (Laboratorio de Productos Forestales 1981). The wood has a slightly interlocked grain with wide stripes, medium texture, regular luster, and figure characterized by overlapping arcs; it is odorless and tasteless. Frequently, the wood has blue stain spots due to fungal attack (Laboratorio de Productos Forestales 1981). The species has a strong, hard, moderately heavy wood with a basic specific gravity of 0.45 to 0.53. The green wood varies from 0.72 to 0.88 g per cm^3 (Laboratorio de Productos Forestales 1981). The volumetric contraction is low (1.8), and the mechanical properties vary from very low to medium; the wood is of the structural type C. It is moderately easy to work, saw, and polish although it presents rolling grain (Herrera and Morales 1993). The wood is comparable to that of black walnut (*Juglans nigra*; National Academy of Sciences 1979) and *Enterolobium cyclocarpum* (Jacq.) Griseb. (Cozzo 1951). Air-drying is moderately slow; it takes 24 to 29 weeks depending on ambient temperature and moisture (Laboratorio Productos Forestales 1981); the wood shows some twisting and fissures at the ends and moderate splitting on the sides. The sapwood is very susceptible to insect and fungi attack while the heartwood is moderately resistant (Herrera and Morales 1993). Wood impregnation is easy; the sapwood is completely and uniformly penetrated. The Runkel factor is 0.78 and the Peteri's coefficient 16 to 18; the wood is good for making paper (Laboratorio de Productos Forestales 1981). The wood is harvested commercially in Costa Rica and other countries of the Mesoamerican region for bowls, trays, carvings, furniture, veneers, posts (treated wood), paneling and turnery; Hawaii is well-known for its monkey pod bowls (National Academy of Sciences 1979). In Central America the wood is used for two-wheeled carts (Allen and Allen 1918).

Samanea saman is a nitrogen-fixing tree (National Academy of Sciences 1979, Nitrogen Fixing Tree Association 1987b). The pods have edible pulp; when ripe the pulp is soft and sugary with a licorice-like flavor attractive to children. The foliage and young twigs have a high protein content (24 to 30 percent) and the fruits have 13 to 18 percent (Herrera and Morales 1993). The pods can also be dried and ground into a meal excellent as animal fodder (National Academy of Sciences 1979). In silvo-pasture systems, the tree provides shade and nutritious pods for livestock and fosters the growth of nearby grasses (National Academy of Sciences 1979). The bark, seeds, and flowers produce a saponin-like alkaloid, pithecolobine (samanin D), $C_{22}H_{46}N_4O_2$ (Allen and Allen 1981, Van Italie 1932, Varshney and Khanna 1978, Varshney and Vyas 1976, Weisner and others 1953). The boiled bark is applied externally to cure constipation (Grijalva 1992). Although the tree is not currently used in reforestation programs, established plantations are successful.

The tree flowers January through May, with variations along its geographic range. The flowering peak occurs in April and May. In Central America, the species may bloom in May or June. The flowers are small, pinkish or whitish, hermaphrodite, and crowded in axillary, subterminal or terminal umbellate inflorescences, 4.5 to 5.5 cm long (Holdridge and Poveda 1975, Salas-Estrada 1993, Zamora 1991). The calyx is pentamerous and gamosepalous; the corolla is gamopetalous, valvate, and infundibular (Bentham 1875, Holdridge and Poveda 1975, Zamora 1991). The androecium has many stamens; gynoecium is monocarpellar, and placentation is laminar. Pollination is entomophilous and bees are the primary pollinators, although some butterflies are common visitors and perhaps pollinate some flowers (Brenes 1994).

The fruit is a pod. It initiates development immediately after pollination, but after reaching a length of 3 to 4 cm begins an 8-month period of dormancy. It resumes growth at the end of the rainy season, reaching maturity in the forthcoming dry season. Fruit ripening occurs February through May and the main crop occurs in April and May. The pod is indehiscent, woody, flat, 10 to 25 cm long, straight or curved, 2.5 to 3.5 cm wide, and almost 1 cm thick. A pair of thick, woody valves with prominent ventral and dorsal sutures forms the fruit's pericarp. The epicarp is reddish brown or brown, glossy, and slightly carved on the lateral surfaces; the mesocarp is poorly developed and indistinguishable; the endocarp is dull, septate, and forms a sticky pulp that is whitish, creamy, or light brown. Seeds are separated by the endocarp septa.

The seeds are oblong, laterally compressed, 1.0 cm long, 0.7 cm wide, and 0.5 cm thick. The yield of viable seeds per fruit is about 20 percent; 15 percent are abortive seeds and the remainder are damaged by different insect larvae and weevils.

The pods must be collected February through April and placed in open sacks. Seeds are extracted by hand. They must be removed from the pod immediately and washed in running water; after washing, they are exposed to full sunlight for several hours. Seeds average 4,000 to 5,000 per kg (Brenes 1994). The sweet, sticky endocarp promotes an intense insect attack which must be avoided (Brenes 1994). Seed behavior is orthodox and moisture content in fresh seeds varies from 12 to 18 percent. Seeds can be stored at 4 °C with 6 to 8 percent moisture content. Seeds stored at 5 °C keep their viability longer than 1 year (Quiroz and Chavarría 1990).

Fresh seed germination is about 36 to 50 percent without pregerminative treatment. Seeds soaked in hot water (80 °C) for 1 minute followed by a bath in lukewarm after (30 to 40 ° C) for 24 hours produce 90 to 100 percent germination if damaged seeds have been discarded. After imbibition the seeds are sown in greenhouse beds filled with sand, in plastic bags or directly in the soil. Germination is epigeal and the seedling is phanerocotylar. Radicle protrusion occurs in 4 to 5 days and is quite uniform in pretreated seeds. In the nursery, seedlings are predated by defoliating lepidopterans (*Ascalapha odorata* and *Mocis latipes*) (Brenes 1994).

In monospecific plantations with close spacing, the species grows well and branching diminishes, providing longer and straighter boles (National Academy of Sciences 1979). Initial growth is slow, but survival is good. Two months after planting, the seedlings begin to grow and look vigorous. Pseudocuttings or bare-root seedlings are commonly planted with success. In Estación Experimental Horizontes (Guanacaste, Costa Rica), the best results have been reached using seedlings planted in plastic bags and transplanted in adobe (Brenes 1994). Pruning has been employed in 2-year-old saplings to improve tree form by diminishing undesirable branching. Growth in height and diameter is fast in the first years. In the mixed experimental plantations of Estación Experimental Horizontes (*Enterolobium cyclocarpum, Simarouba glauca* DC., *Hymenaea courbaril* L., *Samanea saman),* the 2-year-old trees reached an average height of 2.93 m; in monospecific plantations located in Nicoya, Guanacaste, the juveniles planted at a distance of 3 by 3 m reached a height of 4.78 m and 6.6 cm d.b.h. (Brenes 1994).

ADDITIONAL INFORMATION

The Spanish term *saman* derives from the French Caribbean vernacular *zamang* which means rain tree (Allen and Allen 1981). This name is used because it “rains from the branches the juice of the cicadas” and the grass is green beneath the canopy (Hargreaves and Hargreaves 1965, National Academy of Sciences 1979).

Leaf petiole is ferruginous, and pulvinate basally. The pulvinus is adaxial and oblong. The rachis is wide and also pulvinate. Petiolules have basal adaxial pulvinuli. Leaf blades are shiny, almost glabrous, green or dark green adaxially, ferruginous, and silky pubescent abaxially. The leaves are nyctinastic, closing at night.

Flowers are short pedunculate; peducles are tomentose and sulcate. The calyx is valvate, campanulate, toothed, pubescent, and greenish; the receptacle is subglobose. Stamens are long, pinkish distally, and basally adnate to the corolla, forming a tube. There are several ovules; the ovules are anatopous, bitegmis, and crassinucellated. In the umbel, the central flower differs morphologically from the others; its perinth is different and the gynoecium does not complete its development.

Seeds are perpendicular to the pod and have a thick, glossy, brown, halonate, dichrome (if fresh and healthy), and hard testa. The lateral faces have a yellowish brown pleurogram, a linear fissura, and fracture lines. The linear fissura opens at the micropylar end. Endosperm and perisperm are lacking. The embryo is large, straight, laterally compressed; the plumule is well developed; cotyledons are large, thick, fleshy, ovate, concealing all but the tip of the radicle.

The bruchid *Merobruchis columbinus* oviposits the immature fruits and the developing larvae damage and kill 50 to 70 percent of developing seeds. If the fruit is opened and the seeds are exposed, *Stator limbatus* oviposits them (Janzen 1977, 1983e).

Santalum freycinetianum Gaudich.

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SANTALACEAE (SANDALWOOD FAMILY)

S. freycinetianum var. *auwahiaense* Stemmermann; *S. freycinetianum* var. *lanaiense* Rock; *S. freycinetianum* var. *longifolium* (Meurisse) Degener; *S. freycinetianum* var. *pyrularium* (A. Gray) Stemmermann; *S. involutum* St. John.; *S. lanaiense* (Rock) Rock; *S. longifolium* Meurisse; *S. majus* St. John; *S. pyrularium* A. Gray; *S. pyrularium* var. *sphaerolithos* Skottsb. (Wagner and others 1990)

Freycinet sandalwood, ‘iliahi

Santalum L. is a genus of about 25 species growing from India and Nepal to Australia and Polynesia, four of which are native to Hawaii (Wagner and others 1990). The native range of *S. freycinetianum* includes the Hawaiian islands of Oahu, Kauai, Lanai, Maui, and Molokai.

Santalum freycinetianum is capable of reaching approximately 25 m in height and 90 cm d.b.h. (Little and Skolmen 1989) but is typically much smaller. This relatively slow-growing evergreen is characterized by slender, often drooping branches and narrowly elliptical gray-green leaves. It grows on a range of volcanic soils but does not become established on poorly drained sites. Most often found on slopes and ridges, the species can be locally common in dry, mesic, and wet forests with mean annual rainfall between 500 and 3800 mm. It is most often found growing between 250 and 950 m but has been found at elevations as low as 15 m (Applegate and others 1990, Wagner and others 1990). Like other members of the genus *Santalum*, it is hemiparasitic on the roots of other plants.

Like many other Hawaiian plant species, *S. freycinetianum* is highly variable, and its taxonomic status might still be considered unresolved. Currently, three morphologically overlapping varieties are recognized: *S. f.* var. *freycinetianum*, *S. f.* var. *lanaiense*, and *S. f.* var. *pyrularium*. The varieties vary in their geographic range and the site types on which they grow (Applegate and others 1990, Wagner and others 1990). Further information on the taxonomic status of Hawaiian sandalwoods is provided by Wagner and others (1990) and Stemmerman (1980a, 1980b; 1990).

Santalum freycinetianum is highly valued for the oil contained in its heartwood, which gives the wood an attractive fragrance. The wood, which is hard, heavy, yellow-brown in color, and fine textured, is used for ornamental carvings and fine furniture (Little and Skolmen 1989). Like the other sandalwoods, the oil is extracted for use in perfumes, incense, and medicines (Applegate and others 1990, Little and Skolmen 1989).

The weakly fragrant red flowers, each about 6 to 15 cm long, are borne in terminal or lateral clusters (cymes). Flowering generally peaks in the late summer and fall, but flowering also occurs in late winter and early spring. The single-seeded fruits (drupes) are 8 to 17 mm long and reddish-purple to black at maturity. Other sandalwoods (e.g., *S. album* L.) begin producing viable seeds at about 5 years (Applegate and others 1990), but information specific to *S. freycinetianum* is unavailable.

The general recommendations for propagating sandalwoods (Applegate and others 1990, Utomo and others 1990) are believed applicable to *S. freycinetianum*. Seeds should be collected directly from trees by hand or with pruning poles but can be collected from the ground. The seeds should be depulped by washing in water and treated with a disinfectant or fungicide. Seeds should be sowed immediately or dried in the sun or an oven before storage. Seeds can be stored in a dry, cool location or dried to approximately 8 percent moisture content and refrigerated at about 5 °C. Sandalwoods can be successfully stored under refrigeration for several years.

Like other sandalwoods, *S. freycinetianum* is difficult to propagate. Although considerable progress has been made over the last 10 to 15 years, unresolved questions remain about seed dormancy, seedling nutrition, and using host plants. Because untreated seeds may take from several months to well over 1 year to germinate (Hirano 1990), seed pretreatment is recommended. Presoaking in water for 3 to 5 days helps; however, complete removal of the seedcoat (Nagaveni and Srimathi 1980), soaking for 8 to 12 hours in 0.05 to 0.1 percent gibberellic acid (Applegate and others 1990, Nagaveni and Srimathi 1981), manual scarification followed by soaking in water (Applegate and others 1990), or acid scarification (Nagaveni and Srimathi 1980) are reportedly more effective. Full light has been shown to enhance germination of *S. album* (Utomo and others 1990), but no information on the light requirements of *S. freycinetianum* is available.

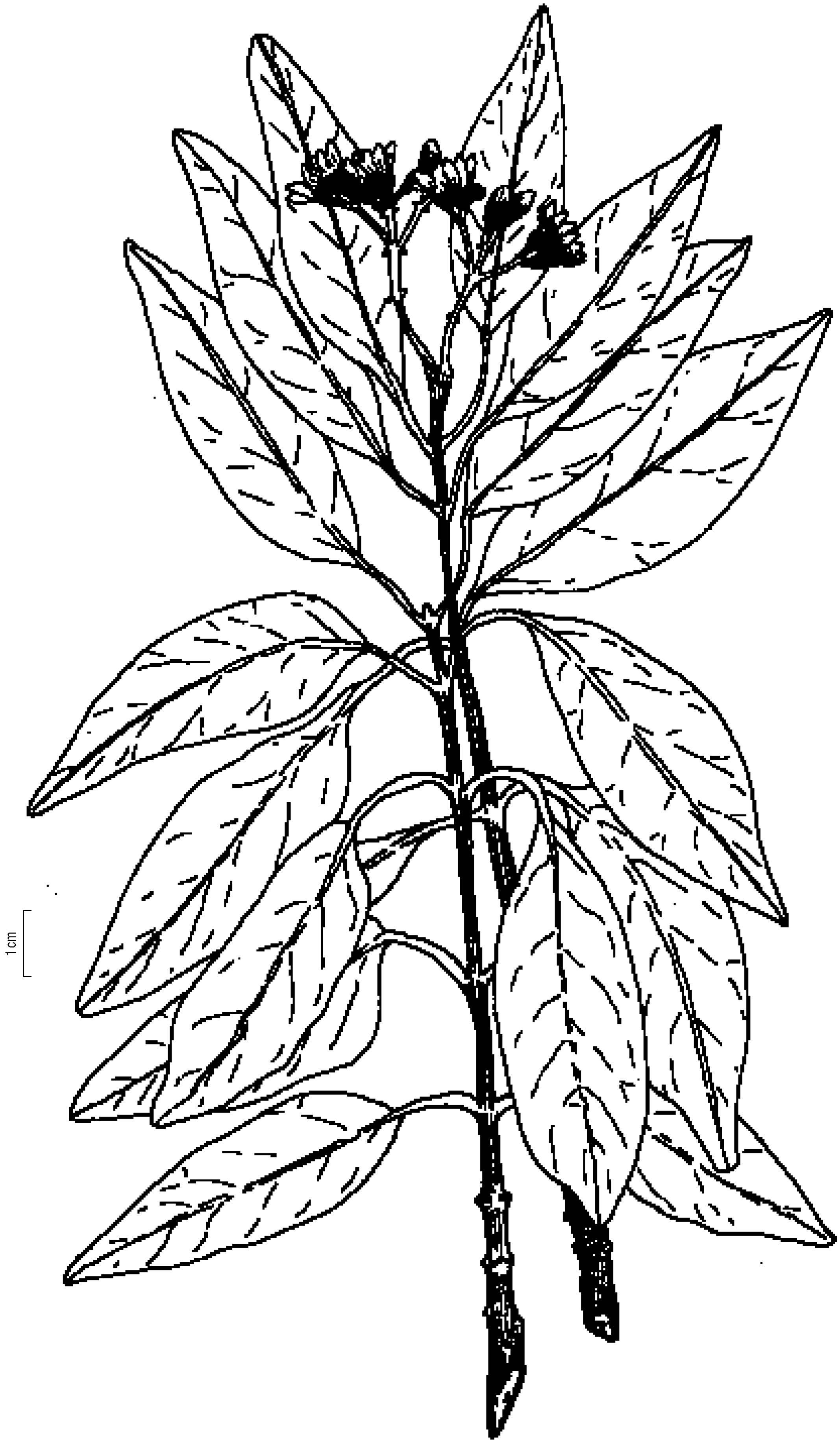
Seed should be sowed in a sterile media such as vermiculite, well-drained potting mix, or sterilized sand-soil mixture. Optimal temperature for germination of some sandalwoods appears to be about 25 °C, and one effective technique involves bottom-heating germination beds to maintain the temperature at this optimal level (Applegate and others 1990). *Santalum freycinetianum* seedlings are susceptible to both fungi and nematodes, and applications of appropriate pesticides may be necessary. Careful attention must be paid to seedling nutrition in this hemiparasitic species. Hirano (1990) reported that seedlings of three sandalwood species (two native to Hawaii, but not including *S. freycinetianum*) developed severely chlorotic leaves that did not respond to a foliar (20-20-20) fertilizer. They did, however, improve significantly with the application of chelated iron. Seedlings should be kept in partial shade (30 to 50 percent) and protected from stressors such as temperature extremes, frost, and wind.

When seedlings reach the four-leaf stage, they can be transplanted into containers, such as a 13-x 30-cm pot, filled with a well-drained potting mixture. A primary host plant may also be transplanted into the pot. Potential host plants include native Hawaiian species such as *Acacia koa* A. Gray, *A. koaia*, *or Dodonaea viscosa* Jacq., or nonnative species such as *Leucaena luecocephala* (Applegate and others 1990, Scheffel 1990). Seedlings have also been grown successfully with no primary host plants for at least 18 months (Hirano 1990), and primary host plants are not currently used in Hawaii Division of Forestry and Wildlife nurseries (Lum 1997). Seedlings reach adequate size for outplanting about 8 to 9 months after transplanting.

In the field, seedlings should be planted near potential host plants. In some situations, such as *S. austrocalendonicum* plantations in New Caledonia, secondary host species are established on plantation sites 1 year before the sandalwoods are outplanted (Applegate and others 1990). In commercial sandalwood plantations, seedlings are outplanted at 4 to 5 m spacings. Plantation practices have not been documented for *S. freycinetianum* or other Hawaiian sandalwoods. Seedlings are generally planted within existing vegetation near potentially suitable hosts; the best host may be *Acacia koa*. Success is generally good (Scheffel 1990), especially in locations where seedlings can be watered occasionally and weed competition is controlled. Periodic trimming of the secondary host may benefit seedlings.

ADDITIONAL INFORMATION

In Hawaii, sandalwood populations were decimated in the early 1800’s during a period of intensive harvesting that had far-reaching environmental and socioeconomic consequences (Merlin and Ravenswaay 1990). Although the sandalwoods have partially recovered, relatively few large trees are found and the distribution is more restricted than it was in the early 19th century.


1cm

Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin

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ARALIACEAE (GINSENG FAMILY)

Didymopanax morototoni

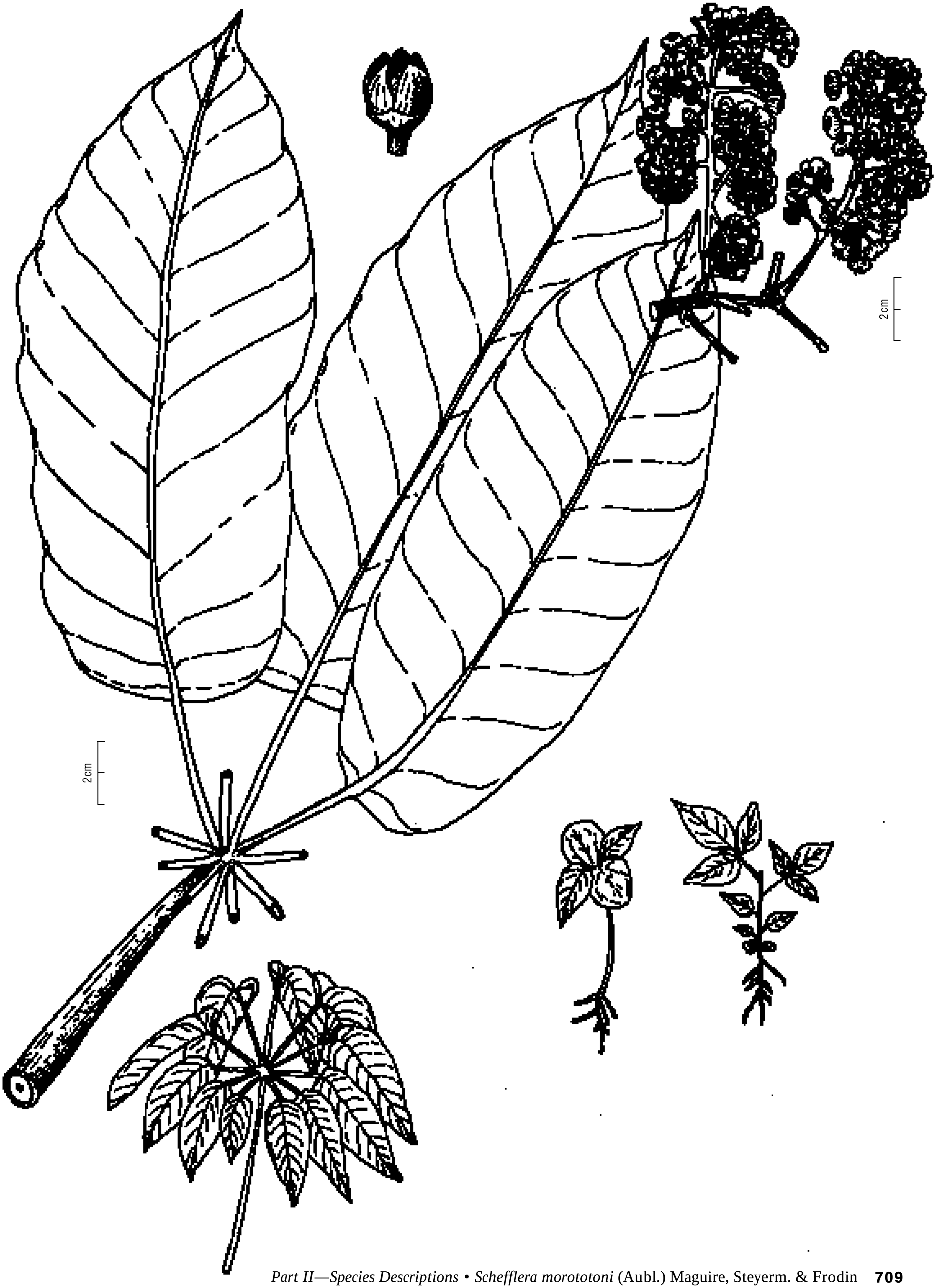
Ambay guasu, ambay guazu, aralie grandes feuilles, arriero, bois canot, bois trembler, cacheta, chancaro blanco, costilla de danto, gavalan, gorgoran, mandioqueira, mangabe, matchwood, mountain trumpet, morototo, palo de sable, pava, pavilla, probado, roble blanco, sable, sablito, trembler, trompette male, yagrumo macho, zapaton

Schefflera morototoni is naturally dispersed in Mexico, Panamá, Brazil, Bolivia, Paraguay, and northeastern Argentina. It thrives in the tropical-subtropical broadleaf forests of tropical America.

Schefflera morototoni is a tree that can reach 25 m in height and 40 to 80 cm d.b.h. The smooth, cream-colored bark has big lenticels. The trunk has many rings which are formed by leaf scars. The crown has an umbrella shape; the foliage appears as clusters of leaves in the upper part of the branches. Leaves are alternate and palmate with 9 to 13 oblong leaflets, each with a long petiole. The leaves measure 25 to 40 cm long by 15 to 35 cm wide; the leaflets measure 8 to 25 cm long by 4 to 12 cm wide. The upper face of the leaves is dark green; the inside face is gray-white and downy. A sun-loving species, *S. morototoni* requires deep, semihumid, and mesohygrophilic soils. It grows where annual precipitation is 1500 mm or more. In the subtropics, the species will tolerate a few low-intensity frosts; elsewhere, it grows where the mean annual temperature is 18 °C. The species has average longevity.

The wood is light brown, sometimes grayish with gold glints; has a medium density of 450 kg per m^3; and is very useful for veneer and plywood. The wood does not perform well outdoors because it does not resist fungal attacks.

The inflorescence is a raceme 5 to 12 cm long with umbels 1 to 5 cm long; the greenish-white flowers are 3- to 6-mm-long hermaphrodites. The fruit, a rounded drupe 5 to 10 mm in diameter and grayish in color, contains 2 to 3 seeds.


2cm
2cm

Schinus molle L.

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ANACARDIACEAE (CASHEW FAMILY)

Schinus huingan Mol., *Schinus molle* L. var. *Huingan* (Mol.), *Schinus molle* var. *areira* (L.) DC

Aguaraiba en guarani, aguaribay, arbol de la vida, arbol del Peru, balsamo, cullash, cuyash, false pimiento, gualeguay, huaribay, huigan, huignan, huinan, lentisco del Peru, molle, molli, muelle, mulle, mulli, orighan, pepper-tree, pimentero, pimiento, pimiento de Bolivia, pirwi, tancar (Fossati 1996, Navi 1989, Schulte and others 1992)

In the genus, 27 species are distributed from Mexico to Argentina (Lindley 1993). *Schinus molle* embraces most of this range, extending from Central America, through Colombia, Ecuador, Peru, and Bolivia, and into Chile, Argentina, Paraguay, and Uruguay (Schulte and others 1992).

Schinus molle is an attractive tree with a strong, usually erect trunk supporting a full, dense, leafy canopy. It grows rapidly at about 1 m per year to a height of 20 m with a corresponding trunk diameter that ranges from 30 to 80 cm (Borja and Lasso 1990, Schulte and others 1992). Found growing in a wide spectrum of soils from sands to clays, alkaline to saline, this tree develops well on steep dry slopes, ravines, valleys, and areas composed of rocky and shallow soils (Soux 1987). This tolerance range is in part due to an extensive radial and vertical root system, which can penetrate to 30 m in depth (Navi 1989). Growing at elevations from 1000 to 3400 m, *S. molle* grows well where temperatures range from 15 to 28 °C and rainfall is between 300 and 700 mm per year (Borja and Lasso 1990, Fossati 1996).

Schinus molle is a tree of many uses. The wood is resinous, heavy, hard, fine textured, and resistant to termites. It has an average density of 0.669 g per cm^3 (Schulte and others 1992). The wood is used for posts and interior floors; farm implements, such as ploughs, yokes, and tool handles; rustic furniture; and home construction (Borja and Lasso 1990, Borter 1994). Because the wood burns slowly and emits uniform heat, it is considered a good fuel source. The tree's pendulant, informal branches and clusters of red-rose fruits add to its value as an ornamental. When fermented, the fruits make a refreshing alcoholic drink known as chicha de molle. The dried fruits are boiled to produce honey de molle which, when fermented, yields a vinegar-like substance (Schulte and others 1992). The fresh leaves, bark, and roots of the tree are used to alleviate or cure rheumatism, bronchial infections, high blood pressure, ulcers, tumors, anxiety, and inflammations of the skin (Centro Equatoriana de Servicios Agricolas 1993, Schulte and others 1992). Indigenous inhabitants of rural Bolivia decorate newlyweds with the branches of S. molle to confer perpetuity; also, in certain religious ceremonies, small branches are placed in the caps of the participants to establish a ritual relationship with their ancestors and the souls of the dead (Food and Agriculture Organization/Holanda/Cochabamba Departmental Forestal 1992).

Schinus molle begins to flower at 3 years in the Cochabamba Valley (elevation 2500 m) of Bolivia (Urquidi 1998). Flowering begins in August and continues until February (Fossati 1996). The inflorescence is a terminal panicle 8 to 20 cm in length that bears yellowish- to greenish-white, unisexual or hermaphroditic flowers (Unidad Evaluacion de Bosques y Unidad Planificacion y Monitoreo 1996, Urquidi 1988). The fruits, borne by racemes, are small, globose drupes, red-purple in color and about 4 to 6 mm in diameter (Fossati 1996, Schulte and others 1992). Fruits appear in October; each contains one round seed that is 3 to 5 mm in diameter and maroon to black in color and tastes similar to pepper (Fossati 1996, Navi 1989). Fruits drop to the ground upon maturity. A wide variety of birds eat the fruits and disperse the seeds (Soux 1987).

The mature, reddish-rose-colored fruits are collected by hand from the pendulant branches in April and May from trees at least 8 m in height (Fossati 1996, Schulte and others 1992). After collection, fruits are dried in the sun for 5 to 7 days and then rubbed by hand to release the thin husk. *Schinus molle* seeds average about 36,000 per kg (Fossati 1996). Stored in sealed glass jars or similar containers and kept in a dry, dark, cool environment, the seeds retain viability for about 2 years (Navi 1989).

Seeds are coated with a sweet and sticky substance that can attract insects. This substance must be removed before planting. Typically, the seeds are soaked in water at room temperature for 48 to 72 hours (Schulte and others 1992). Treated seeds germinate in 20 to 25 days with a germination rate of 50 to 80 percent (Schulte and others 1992).

Seeds of *S. molle* should be planted in beds of a loose substrate and topped with straw until germination (Schulte and others 1992). After germination, a shading system should be used to regulate the intensity of light reaching the seedlings (Schulte and others 1992). Seedlings may be moved to containers in 4 to 6 weeks (Navi 1989). When plants reach 30 cm, they are ready for outplanting (Soux 1987). Young plants should be protected from grazing animals. In areas with good soil and sufficient rainfall, direct seeding is feasible (Schulte and others 1992).


2cm
2cm

Senna siamea (Lam.) H.S. Irwin & Barneby

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FABACEAE (BEAN FAMILY)

No synonyms

Bombay black-wood, casia amarilla, casia de Siam, casia siamea, johar, juar, kassod, kassod-tree, minjri, mjohoro, msunobari, mti, muong, sheku, siamese cassia, taray ulaya, vakai, wa, yellow casia

Senna siamea is native to Southeast Asia from India, Sri Lanka, and Thailand to Indonesia, Burma, and Malaysia and forms part of the warm and wet tropical forests. The species has been introduced in Africa and America.

Senna siamea is an evergreen tree that is fast-growing and short-lived. Under optimal conditions, it can reach 30 m in height and 30 cm d.b.h. The tree has a straight trunk and a rounded or irregular and spreading, multibranched crown with dense foliage. The leaves are pinnate, 23 to 33 cm long, and made up of 5 to 14 pairs of lanceolate, oblong or ovate-elliptic leaflets, 3 to 7 cm long and 12 to 20 mm wide. The species requires soils that are deep, well-drained, and rich in organic matter for good development. Average annual precipitation is 1137 mm with a minimum precipitation of 500 mm and a maximum of 2800 mm. Average annual temperature is 24.2 °C, with a minimum of 19.9 °C and a maximum of 27.7 °C and a dry season that lasts 4 to 6 months and rain in the summer. The tree grows naturally from sea level to 600 m. It endures seasonal flooding, salinity, and continuous exposure to wind and shade. However, it is not very resistant to cold and drought (Nair 1984, von Carlowitz 1991).

Senna siamea has multiple uses. In its native habitat it is used to establish windbreaks and to provide shade to coffee plantations. It has also been planted to recover degraded soils. *Senna siamea* is customarily planted in lanes with corn and cotton because the foliage is rich in organic matter and serves as green manure. Because it grows fast, the species is planted in wet tropical regions to produce firewood (National Academy of Sciences 1980). Good-quality plantations yield approximately 175 m^3 per ha of high calorific power (Food and Agriculture Organization 1957). The wood is also used for poles, turned articles, furniture, and pulp for paper and in rural construction. The bark contains tannin and is used to tan hides. The flowers, rich in nectar, are honey bearing. The foliage, fruits, and seeds are fatal to pigs, but cattle and sheep are not affected by their toxicity (Hoyos 1979, Nair 1993, Parrotta and Francis 1990).

In its native habitat, *S. siamea* blooms precociously and abundantly from June to January. Outside its area of natural distribution, the tree blooms and fruits at different times of the year, depending upon the environment. The flowers have yellow petals and are arranged in racemes or panicles. *Senna siamea* begins to fruit at 5 years. The fruits are hanging, linear, plano-compressed legumes, 5 to 30 cm long, 12 to 20 mm wide, bicarinate, coriaceous or subwoody, and dark brown and dehiscent when ripe. Each fruit contains approximately 25 seeds (Holdridge and Poveda 1975, Irwin and Barneby 1982, Little 1983). The seeds range in shape from circular to obovate and in some cases are vaguely elliptic and laterally flattened. Seed size ranges from 6.5 to 8 or 9 mm long, 5.5 to 6.0 mm wide, and 0.8 to 1.0 mm thick. The seedcoat is dark brown, smooth, shiny, and cartaceous, and 3.3 to 4.5 mm long by 0.9 to 1.2 mm wide, with a closed, oblong-elliptic pleurogram on each of its lateral surfaces.

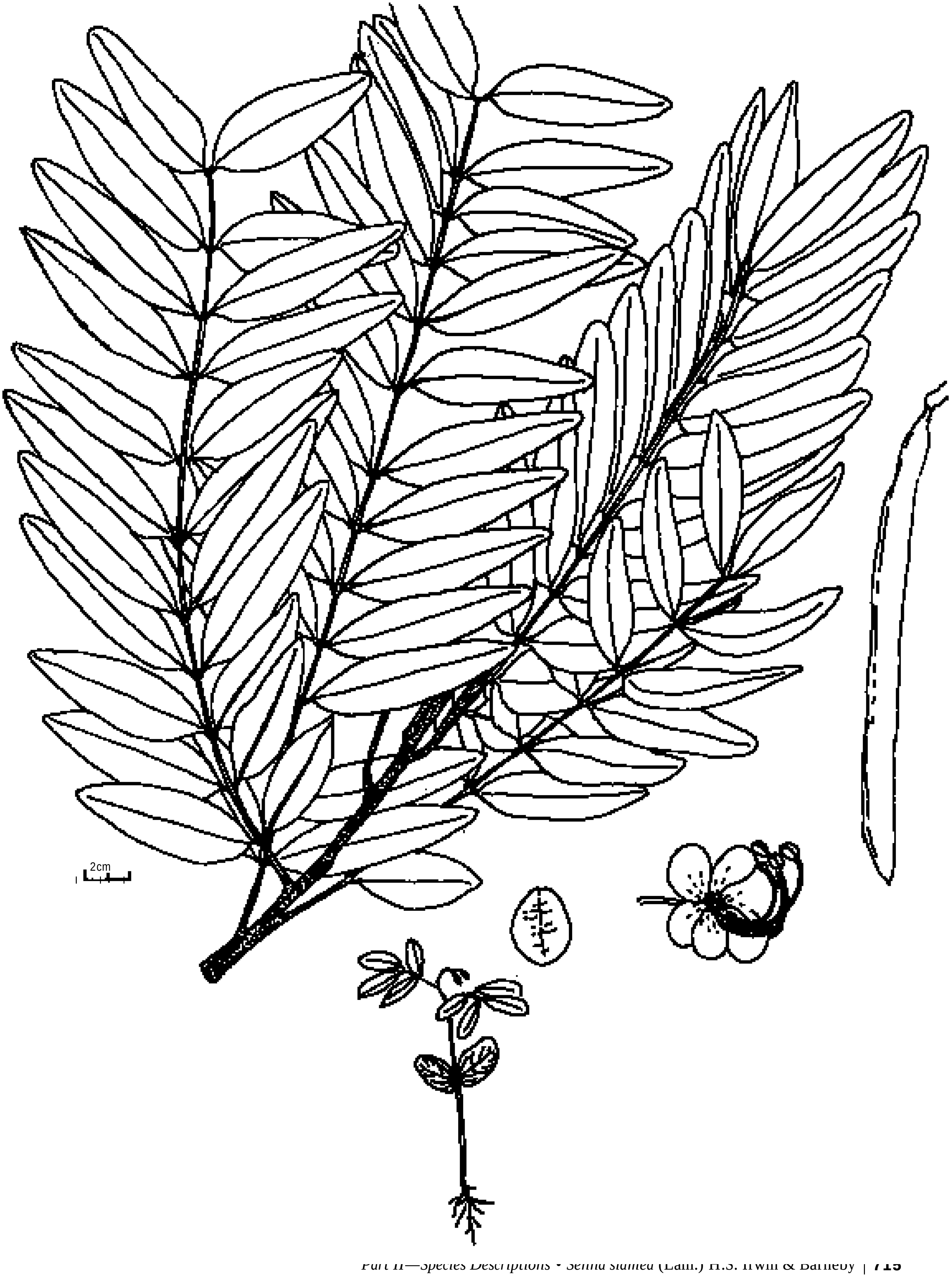
Fruits are collected before they ripen and release their seeds. Collectors climb the trees and use poles with metal hooks to remove fruit. Fruits are placed in boxes in the sun to dry and open. Fruits are fragile, and the extraction of seeds is done by grinding the fruits by hand. Impurities are removed using sieves or a vertical column blower. Seeds average 30,000 to 45,000 per kg. They remain viable for several years when stored under ambient conditions (24 to 30 °C) (Parrotta and Francis 1990). According to some studies developed in the International Centre for Research in Agroforestry (International Center for Research in Agroforestry 1992), seeds maintain their viability for 1 year when viability begins to decrease.

The germination of seeds is phanerocotylar. Fresh seeds germinate at 50 to 90 percent without pretreatment. Old seeds must undergo various pregerminative treatments such as: (1) immersion in concentrated sulfuric acid for 5 to 15 minutes; (2) soaking in water at ambient temperature for 48 hours; or (3) immersion in boiling water for 1 minute and then soaking in water at ambient temperature for 6 hours (von Carlowitz 1991). Seeds germinate 4 days to 6 weeks after sowing.

In nurseries, seeds are planted in seedbeds and when the plantules reach a height of 7 to 10 cm, they are transplanted to black polyethylene containers. In about 3 months, when seedlings reach a height of 25 cm and a diameter of 2.6 mm at the base of the stem, they are outplanted (Parrotta and Francis 1990). *Senna siamea* also regenerates by stump shoots after the trees have been cut down (Irwin and Barneby 1982).

ADDITIONAL INFORMATION

The hilum is subbasal. The micropyle is indiscernible. The endosperm is whole, cornaceous, whitish, and translucent, and located on the lateral surfaces of the embryo. The embryo has a straight axis and is spatulate, almost bilaterally symmetrical, and greenish yellow in color. The two cotyledons are shaped like the seed, whole, equal, expanded, flat, pulpy, and independent of one another, with an auriculate base. The plumule is rudimentary. The radicle is conical and not covered by the cotyledons (Irwin and Barneby 1982).


2cm

Spathodea campanulata P. Beauv.

K.F. CONNOR and J.K. FRANCIS
Southern Research Station
and International Institute of Tropical Forestry
USDA Forest Service

BIGNONIACEAE (BIGNONIA FAMILY)

Spathodea nilotica Seem.

African tulip tree, firebell, fountain tree, rarningobche, spathodea, tulipàn Africano, tuliptree

Spathodea campanulata grows naturally in the secondary forests of the high forest zone and in the deciduous, transition, and savanna forests of equatorial Africa. Its native range extends along the Pacific Coast of Africa from Ghana to Angola and inland across the humid center of the continent to southern Sudan and Uganda (Irvine 1961). The species has been successfully planted outside its natural range (Little and Wadsworth 1964, Mahecha and Echeverri 1983). At a minimum, it has naturalized in Colombia (Mahecha and Echeverri 1983), Costa Rica (Holdridge 1942), Puerto Rico (Liogier and Martorell 1982), Cuba (White 1951), Jamaica (Streets 1962), Sri Lanka (Worthington 1959), Guam (McConnell and Muniappan 1991), and Hawaii (Little and Skolmen 1989).

Spathodea campanulata is a medium-sized tree that commonly reaches a height of 21 m (Neal 1948) and 1.75 m d.b.h. (Francis 1990a); however, in some parts of West Africa it may reach a height of 30 m (Unwin [no date]). It can grow very rapidly, increasing annually by as much as 5 cm in diameter (Little and Skolmen 1989). In Puerto Rico, the largest member of this species measures 35 m tall and 1.75 m d.b.h. (Francis 1990a). In Hawaii, large trees of *S. campanulata* form narrow buttresses at the base. The species may reach heights of 15 to 24 m and diameters of 0.3 to 0.5 m (Little and Skolmen 1989). *Spathodea campanulata* leaves are large, 31 to 61 cm long, and composed of 5 to 19 leaflets (Little and Skolmen 1989) (fig. 1). Leaflets range in length from 7.5 to 15 cm and in width from 4 to 7.5 cm. Lower surfaces are covered with rust-colored hairs. In Puerto Rico, the species develops best in fertile, deep, well-drained loams but will also colonize heavily eroded sites (Francis 1990a). It is frost sensitive and in its native range grows in areas with warm uniform temperatures where the mean temperature of the coldest month is about 27 °C and the mean of the warmest month is about 30 °C (Francis 1990a). In Puerto Rico, it grows from near sea level to 1200 m (Francis 1990a).

No hybrids or geographic races have been reported, although it is possible that *S. nilotica* Seem., the Uganda flame tree, may prove to be a variety of *S. campanulata* (Francis 1990a).

Throughout the humid tropics, *S. campanulata's* large, brilliant, flame-orange flowers have made it one of the most popular flowering ornamentals. The wood of this fast-growing species is light, soft, and little used. Heart and butt rots are common in trees older than 20 to 25 years that have suffered mechanical or fire damage. Planting near roads or buildings is not advised, because the trees become hollow with age and have shallow root systems.

The 10-cm-long, irregularly bell-shaped flowers appear on each terminal raceme on trees as young as 3 to 4 years of age (Francis 1990a). Yellow-flowering trees have also been reported (Francis 1990a, Little and Skolmen 1989, Menninger and others 1976). Flowering time varies, depending on location. In India, flowering occurs from early January until early March, with peak flowering in mid-February (Nalawadi and others 1980). In southern Africa, flowers appear in fall and winter, while in the Caribbean, trees bloom from late winter to early summer (Francis 1990a). In Hawaii, flowering and fruiting may occur throughout the year (Little and Skolmen 1989). The oddly flattened flowers have a light brown, curved, pointed calix and four pale yellow stamens with brown anthers. One to four boat-shaped green to brown pods, 15 to 25 cm long, usually develop from each flower cluster (Eggeling 1947, Little and Wadsworth 1964). Pods are 4 cm wide and 22 mm thick (Little and Skolmen 1989), and seeds mature 5 months after flowering (Francis 1990a). The seeds are light brown, lightweight, and surrounded by a membranous wing.

The mature brown pods should be collected while closed and air-dried until they split open (Francis 1990a). The majority of species in this genus are orthodox and the seeds should store well. Seeds average from 125,000 (Holdridge 1942) to 290,000 (Francis and Rodríguez 1993) per kg.

Germination is epigeous and may begin in as little as 2 days. Germinating seeds are fragile and should not be covered by more than a dusting of peat or fine sand. Francis and Rodríguez (1993) report germination of 38 percent for *S. campanulata* seeds sowed on the surface of wet potting soil in a covered tray and kept at ambient (24 to 30 °C) temperatures.

When seedlings were placed under 50-percent shade, they developed the first true leaves 2 months after germination (Francis 1990a). When transplanted into nursery beds at 25-percent shade, the seedlings attained a plantable size of 35 cm tall in 5 months. Francis (1990a) concluded that a regimen with more sunlight would probably have reduced the time required to reach plantable size. The species may also be propagated by cuttings and root cuttings. It is a prolific root sprouter (Little and Skolmen 1989).


1cm
2cm
2cm

Stryphnodendron excelsum Harms

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FABACEAE (BEAN FAMILY)

Stryphnodendron microstachyum Poepp & Endl., *S. inaequale* Benth., *S. purpureum* Ducke

Vainilla

Stryphnodendron excelsum grows on both coasts from Nicaragua to Panama.

Stryphnodendron excelsum is a canopy tree that may reach 35 m in height and 1 m d.b.h. The tree has a reddish outer bark and a light yellow inner bark. Large trees are buttressed at the base, and the crown is rounded and irregular. Leaves are alternate, bipinnate, 15 to 35 cm long, with 8 to 15 pairs of opposite or subopposite pinnae 10 to 13 cm long. The pinnulae are alternate and subopposite, dorsiventral, 8 to 12 mm long, oblong or oblong-lanceolated, asymmetrical base, entire margin, and obtuse or emarginated apex (Flores 1992b). The rate of growth is fast, and the tree grows well in acid soils. The species grows at elevations up to 700 m, in areas with annual precipitation from 3500 to 5500 mm and a mean annual temperature between 24 and 30 °C (Flores 1992b, Holdridge and Poveda 1975).

The wood is soft and light, with specific gravity of 0.34 to 0.44. The wood is whitish to light brownish yellow or pink, odorless, and tasteless, with no differences between the heartwood and the sapwood in dry conditions. The grain is straight to slightly interlocked and fine textured, with irregular growth rings (2 rings per cm), diffuse porosity, and multiple pores in radial and tangential lines. The timber is easy to work, with high strength in relation to density, and is used for frame construction, pallets for banana export, and furniture, boxes, molds, and posts (Acuña and Flores 1987, Carpio 1992, Solís 1992).

Inflorescences are racimes, 10 to 15 cm long, grouped in axilar fascicles in the branch distal end. The flowers are small, 3 to 4 mm long, sessile, actinomorphic and hermaphrodite, with yellowish green calyx. The trees flower March through July and fruitification normally begins in November. Fruits are straight pods, 10 to 20 cm long, 1 to 1.5 cm wide, marginally dehiscent, with endocarp septate. Fruits mature from November to May. Collectors know the pods are mature when the color turns to brown.

Pods may be collected off the ground; however, collecting directly from the tree prevents animal or insect damage to pods. Pods are collected between December and February (Asociación Costarricense para el Estudio de las Especies Forestales Nativas 1994, Flores 1992b). A single tree may produce from 8,000 to 15,000 pods (90 to 160 pods per kg), with 9 to 16 seeds per pod, or 17 to 26 kg of seeds annually. Seeds average 9,000 per kg when moisture content is near 18 percent. Mean seed moisture content for a sample of 19 trees was recently reported at 15.25 percent (Müeller 1997). Seeds with reduced moisture content (6.5 percent) kept at -15 °C can be stored for 2 years. Germination rates were over 90 percent when seeds were stored at temperatures from -15 °C to 4 °C with moisture content between 6.5 and 10 percent (Müeller 1997).

Seed viability may range between 30 and 60 percent without pregermination treatment, to more than 95 percent when pretreated by cutting the seed testa. The germination is epigeous and occurs in steps. Up to 60 percent of the seeds may germinate during the first 10 to 30 days. Fewer numbers germinate weeks or months later. High variability in germination between trees and even within the same tree has been reported (Asociación Costarricense para el Estudio de las Especies Forestales Nativas 1994, Arias 1992, Flores 1992b, Müeller 1997, Rodríquez 1995, Serrano 1994).

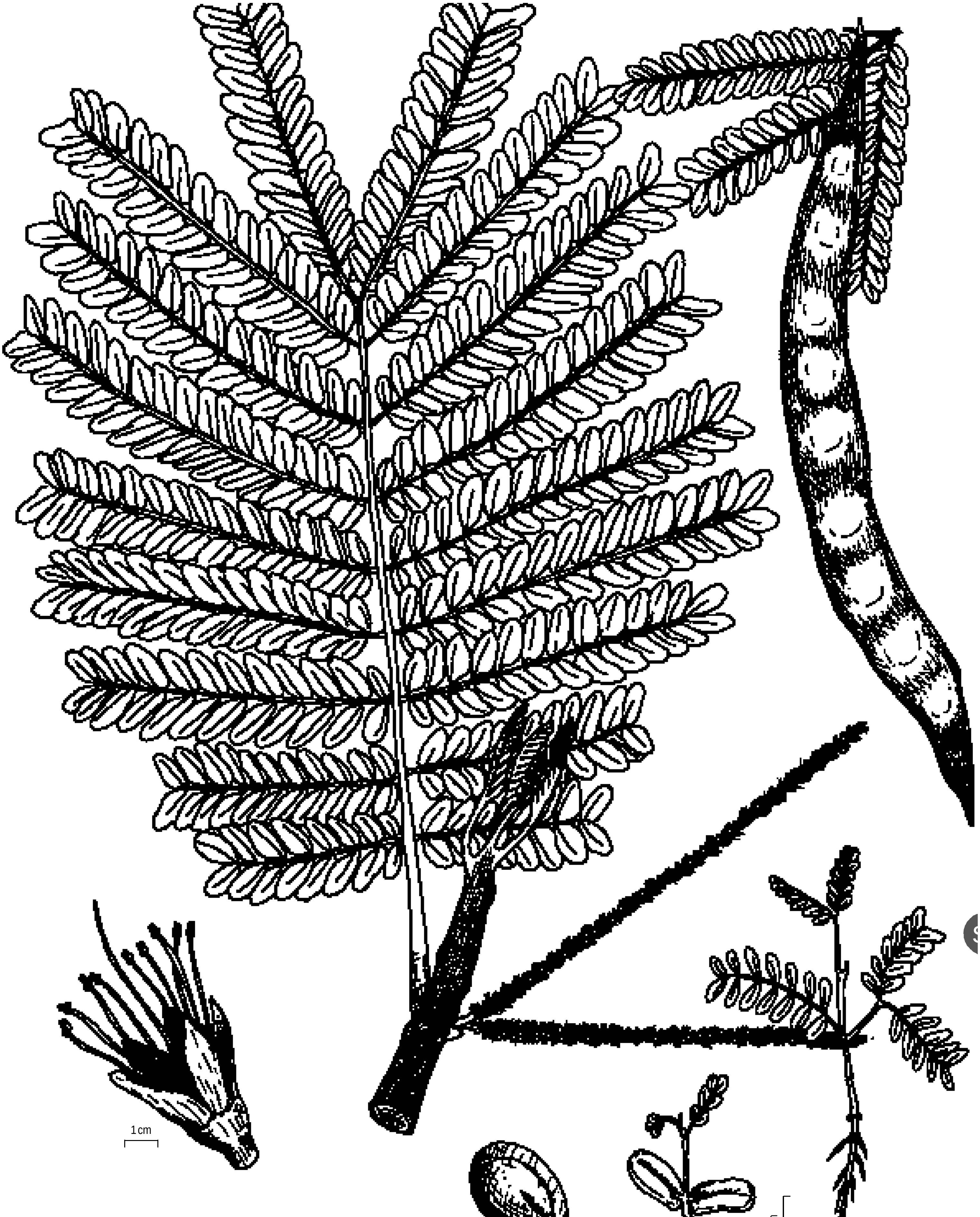
Seeds are sown in germination boxes filled with washed sand. Small seedlings (5 cm height) are transplanted to nursery potting bags with a potting medium composed of soil, sand, and compost in equal parts. Seedlings require half shade. When they reach 15 to 20 cm in height, seedlings may be planted. Trees in plantations may be infected by a vascular fungi, *Nectria* spp (Arguedas 1997).

ADDITIONAL INFORMATION

Species screening trials and demonstration plots of several tropical timber species including *S. excelsum* have been established in Costa Rica (Butterfield 1993). EARTH College (10° 12= North, 83° 37= West; 26 °C mean annual temperature; 3400 mm annual precipitation; 50 m above sea level), in the Province of Limón, Costa Rica, has established several plots. Data on average d.b.h. and height of vainillo trees from the demonstration plots seven years after planting are presented below (data taken from Russo 1997, 1999).

Age	Average d.b.h. cm	Average height m
1	3.2	1.6
2	8.3	4.7
3	12.2	7.5
4	16.7	10.0
5	21.9	12.6
6	24.4	16.4
7	26.7	19.8

Roots of *S. excelsum* interact with the azotrophic bacteria of the Rhizobiaceae, forming small nodules. According to Baker and Montagnini (1994), who estimated the proportion of nitrogen derived from the atmosphere (pNda) using a ^{15}N dilution methodology, more than half of the N contained in the leaves (51.9 percent in 22-month-old plants) comes from N fixation. In addition, vesicular-arbuscular mycorrhizae (VAM) are present in its roots. Janos (1980) characterized the species as an obligate mycothroph. In the EARTH plots, 48 percent of the roots evaluated showed evidence of VAM (Russo 1995).


1cm
1cm

Swietenia macrophylla King

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MELIACEAE (MAHOGANY FAMILY)

No synonyms

Acajou Amerique, acajou du Honduras, aguano, British Honduras mahogany, caoba, caoba centroamericana, caoba hondureña, Central American mahogany, chacalte, chiculte, cóbano, gateado, Honduras mahogany, mahogany, mara, mogno, oruro, rosadillo, venadillo, zopilote

Native to the tropical regions of America, *Swietenia macrophylla* is naturally distributed from southern Mexico, through Central America, to northern South America. The species forms part of the semideciduous tropical forests found along a coastal strip of the Atlantic slope, without reaching the Pacific slope, where *S. humilis* Zucc. is distributed.

Swietenia macrophylla reaches 45 to 60 m in height and 80 cm d.b.h. In exceptional cases, specimens can be found with a d.b.h. of up to 3 m. The trunk is straight and cylindrical, slightly grooved, with well-developed spurs. The open, rounded crown has thick, rising branches, and thick, dense foliage. The leaves are usually paripinnate, sometimes imparipinnate, 12 to 45 cm long, and made up of 3 to 6 pairs of lanceolate or ovate leaflets. The leaflets are asymmetric, 5 to 12 cm long, and 2 to 5 cm wide, with a whole margin and an acute or acuminate apex. The tree prefers rich, deep, and well-drained soils, with moisture available most of the year. Whether the tree is deciduous or evergreen depends on water availability. The species grows at elevations from sea level to 1400 m, in areas with an average annual precipitation of 1600 to 4000 mm, an average annual temperature of 23 to 28 °C, and a dry season that lasts 0 to 4 months.

Swietenia macrophylla produces one of the finest woods in the world. The wood is easy to work using hand tools. Specific gravity of the wood ranges from 0.40 to 0.85. It acquires a good polish and does not crack or bend, making it valuable in the manufacture of quality furniture. An infusion made with the bark is used to treat diarrhea and fevers (Niembro 1986).

The yellow-green flowers of both sexes are in the same inflorescence and arranged in panicles. The season of flowering and fruiting differs with geographic location. In the States of Campeche, Quintana Roo, and Yucatan in Mexico, the tree blooms April through June, and the fruits ripen January through March of the following year. The fruits ripen during the dry season, when the trees begin to lose part of their foliage and the warm air dries the fruits and promotes dehiscence. The fruits are capsular, oblong, or ovoid; 11.6 to 38.7 cm long; 6.7 to 12.0 cm in diameter; dehiscent; and light gray to brown with four to five valves (Holdridge and Poveda 1975, Pennington and Sarukhan 1968). Each fruit contains 22 to 71 developed seeds (Niembro 1995b). The mahogany seeds are samaroid, bulky at their base, 7 to 12 cm long, and 2 to 2.5 cm wide including the wing. The bulky part is comose, laterally flattened, and vaguely rhombic on cross section. The seedcoat is differentiated in testa and tegmen.

Fruits are collected before the valves open. In southeast Mexico, particularly in the States of Campeche, Quintana Roo, and Yucatan, the mahogany fruits are gathered January through March. When the fruits are ripe, the pericarp changes to a light coffee color just before the valves open and release the seeds. Collectors carefully climb the trees and, working above the fruits, use poles with metal hooks to cut them from the trees. The fruits are transported in jute sacks to the processing plant. The fruits are placed in wood boxes with metal mesh bottoms and set in well-ventilated sheds to facilitate air circulation and prevent the growth of microorganisms. The valves begin to open on the second or third day, releasing the seeds. Seed wings are removed by hand to facilitate handling and reduce volume. The wing is broken 1 cm above its base, and the seeds without wings are placed in a container. Impurities, such as pieces of fruit, branches, leaves, and aborted seeds, are removed by using sieves or a vertical column blower. Seeds average 1,235 to 3,246 per kg (Patiño and Villagómez 1976, Vega and others 1981). This wide range in number of seeds per kg indicates that the seeds differ in size and fresh weight.

According to King and Roberts (1979), mahogany seeds are recalcitrant because loss of moisture irreversibly damages their viability. Gómez (1996) reports that the humidity content of the seeds, the container type, and the storage temperature significantly affect viability in less than 1 year. Drying fruits in the sun should be avoided because it reduces humidity content, hence viability. However, recent studies (Centro Agronómico Tropical de Investigación y Enseñza 1997d) show that the seeds are orthodox and that they maintain their germinative capacity up to 7 or 8 months when stored at ambient conditions. Stored in a refrigerator in hermetically sealed plastic bags, seeds remain viable for over 4 years. If they are stored at 4 °C with a moisture content of 4 percent, they conserve their germinative capacity for 8 years.

Niembro (1997a) compared germination of mahogany seeds after they had been stored in three different ways for 120 days. The results showed that seeds stored in hermetically closed bags in a refrigerator at a temperature of 8 °C germinated at 75 percent, whereas seeds stored under ambient conditions without any protection germinated at 62 percent. The fresh weight of mahogany seeds significantly affects germination and growth of the plantules. Niembro (1997b) also found that heavier seeds germinate more quickly, producing bigger and more vigorous plantules. Position at planting is also important to germination. In numerous places, it is customary to plant seeds with the base facing downward and the wing facing upward. This practice is not recommended because the frequency of pig tails, or roots shaped like a J, increases (Niembro 1997c). Actually, planting the seed with the wing pointing downward and the base pointing upward helps germination and decreases the incidence of pig tails (Liegel and Venator 1987, Niembro 1997d).

Seed germination is hypogeal or cryptocotylar (Duke 1969). The seeds do not show a latency period (Lamb 1966) and do not require pretreatment (Liegel and Venator 1987). Under favorable conditions (fertile soil, periodic watering, without attacks by pests and diseases at the nursery site), the newly gathered, fresh seeds germinate 10 to 28 days after sowing (Liegel and Venator 1987, Marrero 1949), with germination at 70 to 90 percent. In the Forest Tree Seeds Laboratory in the China Experimental Field of the National Institute of Forest, Agricultural, and Cattle Research, located in Campeche, Mexico, seeds are placed in germinators with continuous light and a constant temperature of 28 °C. Under these conditions mahogany seeds begin to germinate 15 and 18 days after sowing. Germination is considered complete 6 weeks after sowing.

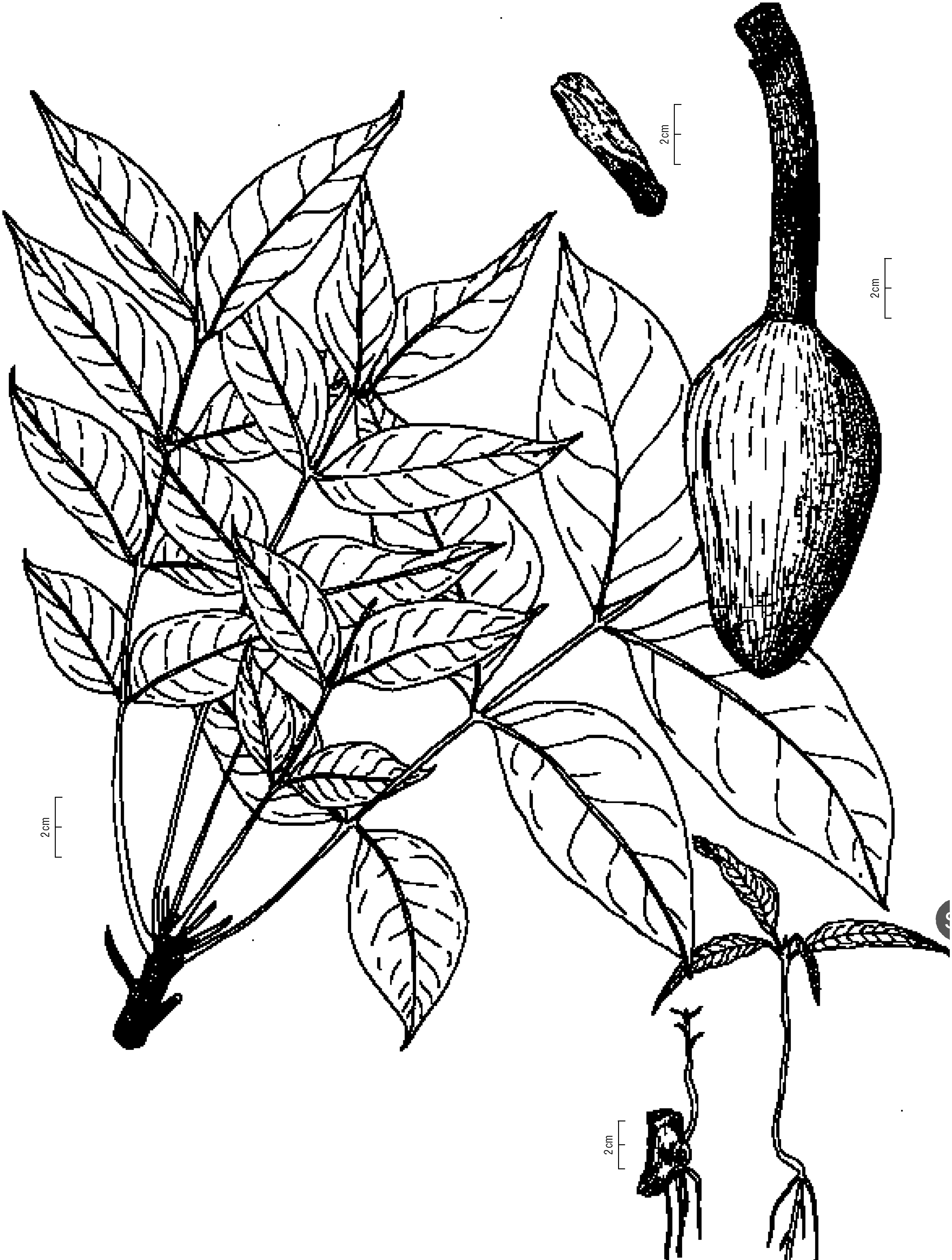
The containers used for the propagation of mahogany are black polyethylene bags which measure 20 by 10 cm. The medium used is a mixture of soil, sand, and compost whose proportions vary among nurseries. *Swietenia macrophylla* is usually propagated by direct planting in containers. Seeds should be planted in March to ensure seedlings will be ready for outplanting at the beginning of the rainy season in July. Mixtures of soil and sand, compost, wood sawdust, rice husks, bark of trees, and agricultural haulm should be used as substrates (Patiño and others 1993a).

ADDITIONAL INFORMATION

The seed testa is light brown to red-brown, smooth, opaque, cartaceous, and internally full of numerous air pockets. The testa expands toward the apex in a thin, brittle, lateral wing, which results from an overgrown raphe-exostome. The tegmen is cream or white, granular, opaque, and firmly joined to the embryo. The hilum is at the end of the wing, set deep, and puntiform, and sometimes has remnants of funicular tissue. The vascular bundle is prominent, descending along the wing, and connected to the embryo in a prominent chalaza that is seen as a black, longitudinal protuberance located at the extreme opposite to the radicle. The micropyle is indiscernible. The endosperm is whole, white, thin, and pulpy, and firmly surrounds the embryo. The embryo is transversal, almost bilaterally symmetrical, and white, with a straight axis. The cotyledons are obovate, compressed, expanded, whole, flat, foliaceous, and merged to each other along their adaxial surface. The plumule is undifferentiated. The radicle is small, globose, and slightly prominent (Alvarenga and Flores 1988, Corner 1976, Niembro 1982, Pennington and Styles 1981, Pennington and van Rijn 1984, Standley and Steyermark 1946b, Stoffers 1984, Wilson 1924).

Germination begins with the distension and outward arching of the point of insertion of the cotyledons with the axis of the embryo because a type of petioles is formed among these structures. Subsequently, the epicotyl and the radicle lengthen. The plumule, made up of two leaves, begins to grow and differentiate when the epicotyl is 1 to 3 cm long. In this stage of growth, very fast changes occur in the morphology and physiology of the stem. The first two leaves increase in size and change from red to green—indicating the appearance of photosynthetic pigments. Simultaneously, the radicle develops secondary roots, thus finishing the germination phase. The plantules continue to grow and develop new leaves that provide nutrients for the tree.

Some seeds have two functional embryos (polyembryony), one usually smaller than the other, which germinate almost simultaneously and produce two plantules of unequal sizes. If the plantules are separated at the right time, they can grow and develop. The occurrence of polyembryony is low. In the China Experimental Field, only 3 out of 500 seedlings (0.6 percent) showed polyembryony.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Swietenia macrophylla x mahogani

JOHN K. FRANCIS
International Institute of Tropical Forestry,
USDA Forest Service

MELIACEAE (MAHOGANY FAMILY)

Swietenia x aubrevilleana Stehlé & Cusin

Caoba hibrido, hybrid mahogany

Because the ranges of the parent species did not merge, hybrids did not occur before the mahoganies were widely planted; consequently, *Swietenia macrophylla* x *mahogani* has no native range. However, when *S. macrophylla* King and *S. mahogani* (L.) Jacq. grow or are planted near each other, the probability that hybridization will occur is high. The hybrid is quite common in Puerto Rico and has been reported to have occurred naturally in Cuba (Marquetti and others 1975) and Martinique (Stehlé 1946). Controlled pollination was used to produce hybrids in Taiwan (Lee 1968). Plantations of hybrids have been established in St. Croix, U.S. Virgin Islands (Weaver and Francis 1988), and Puerto Rico, and seeds have been shipped widely throughout the Caribbean and around the world.

First recognized in Puerto Rico in 1935 (Whitmore and Hinojosa 1977), the hybrid *S. macrophylla* x *mahogani* is a fast-growing tree with a straight trunk and a moderately dense crown. Although the known stands and individuals of *S. macrophylla* x *mahogani* are relatively young, heights of 30 m and diameters of nearly 1 m have been reached. Much larger diameters appear possible as the trees age. The inherent variability of the population gives *S. macrophylla* x *mahogani* a very wide ecological amplitude. Mean annual precipitation totals ranging from 700 to 3000 mm and a considerable range of soil textures, pH, and soil nutrient regimes are tolerated. Sites to avoid have soils that have been eroded down to subsoil, compacted soils, or waterlogged soils. The hybrid outgrew and outsurvived both *S. macrophylla* and *S. mahogani* on moist and dry forest sites in St. Croix in the first two growing seasons (Nobles and Briscoe 1966). Growth of the hybrid did not differ significantly from *S. macrophylla* during the first three growing seasons in wet forests of Puerto Rico (Bauer 1987).

Swietenia macrophylla x *mahogani* is not yet abundant enough to be considered a commercial species. Small numbers of trees are cut in Puerto Rico, and the wood is mixed and sold with other mahoganies to use in making furniture, cabinetry, doors, musical instruments, trim, turnary items, and carvings. In a recent study of the specific gravity of plantation-grown trees, *S. mahogani* averaged 0.58 and the hybrid averaged 0.55; *S. macrophylla* averaged 0.47, differing significantly from the former two (Francis in press). The hybrid is used in conservation, shade, and ornamental plantings. Its rapid growth and near-surface roots preclude it from use near sidewalks, curbs, and other structures (Francis and others 1996).

Planted trees begin flowering and fruiting between 10 and 25 years of age. Flowering generally occurs during the dry season or summer in Puerto Rico and fruits ripen during the winter. The small, greenish-yellow flowers grow in panicles arising from the leaf axils near the tips of branches. Because of the relatively even climate in Puerto Rico and the inherently diverse hybrids, trees with fruit can be found at almost any time of the year. The fruits are capsules that split into five parts to release the seeds. Theoretically, the capsules can vary in size from that of one parent to that of the other, or 6.5 to 17.5 cm in length. Lengths of 12 to 16 cm are more typical.

Seed collections are made when a few of the capsules on a tree have opened. At ripening, the color of the capsule changes from greenish gray to gray-brown, red-brown, or brown. The color change is sometimes too difficult to see to judge ripening. However, during collection, capsules with a discernible green shade should be avoided. Using pruning poles, step ladders, or high-lift buckets, capsules are clipped from the trees. They are then sun-dried until partially open. The capsules are then broken open and the seeds removed and further dried over screens in a shaded, well-ventilated area. Bauer (1987) noted 1,538 seeds per kg for dewinged seed and Francis and Rodríguez (1993) measured 2,580 seeds per kg for whole, air-dried seeds.

The seeds are stored in sealed containers. Bauer (1987) found no difference in germination between seed stored for 6 months at 24 °C and seed refrigerated for 6 months at 5 °C.

Pregermination treatments are unnecessary. The seeds of *S. macrophylla* x *mahogani* may be germinated on fine sand, sandy soil, or potting mix in germination trays, germination beds, or directly in nursery bags or pots. Any germination media should be sterilized to prevent damping-off problems. Seeds may be scattered and lightly covered (1 cm deep) or inserted individually part way into the soil. Germination begins in about 17 days (Francis and Rodríguez 1993) and is completed about 50 days after sowing (Bauer 1987). Germination rates of 83 percent (fresh seed) and 73 percent (seed stored 6 months) have been reported (Bauer 1987, Francis and Rodríguez 1993).

New seedlings in germination trays or beds can be transplanted to pots, nursery bags, or nursery beds after they develop two or three leaves. Outplanting of seedlings about 50 cm in height is recommended for large, solid-block plantings. Nursery seedlings reach that height in 6 to 10 months. Seedlings from 50 to 100 cm in height are recommended for line planting. Seedlings to be used as ornamentals should be 1 to 1.5 m or more in height before outplanting. Bare-root seedlings and stump plants are suitable for moist and wet forest sites if soils are moist at the time of planting and will remain moist for several months. Seedlings must not dry out or heat up before planting. For dry sites, bagged or potted seedlings are recommended. Seedlings must be protected from weeds and grass for about 2 years after planting and cleaned annually of vines until the crowns shade the understory.

ADDITIONAL INFORMATION

Observers in St. Croix noted that seedling leaf size of putative hybrids fell midway between those of the apparent parents (Briscoe and Lamb 1962). Research in Cuba has shown that leaf size of seedlings is manifest according to the 1:2:1 ratio of classic Mendelian genetics (Marquetti and others 1975). In plantations of older putative hybrid trees, the variation in leaf size ranging from that of *S. macrophylla* to that of *S. mahogani* is readily apparent. The capsule size also varies in like manner, but is not necessarily coupled with leaf size. Trees with small leaves may have large capsules, and trees with large leaves may have small capsules. Variation, though less obvious, may be seen in form, limb structure and number, and bark pattern.


1cm
1cm
2cm

Swietenia mahogani C. DC.

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MELIACEAE (MAHOGANY FAMILY)

No synonyms

Acajou, acajou de Saint Domigo, caoba, caoba de Santo Domingo, caobilla, madeira, mahogany, mahogany du pays, mahogany petites feuilles, mahok, mahoni, small-leaf mahogany, Spanish mahogany, West Indian mahogany, West Indies mahogany (Little and Wadsworth 1964)

The native range of *Swietenia mahogani* includes the southern tip of Florida, the Florida Keys, the Bahamas, Cuba, Jamaica, and the island of Hispaniola. The species is planted as an ornamental outside its native range in Florida, several Caribbean islands, Hawaii, India, Sri Lanka, and Fiji. It has naturalized or escaped in a number of sites in Puerto Rico and the U.S. Virgin Islands (Francis 1991).

Swietenia mahogani is a medium to large tree with a straight to crooked bole and a limby crown. Although most trees commonly seen are medium-sized, this long-lived species can grow to very large sizes. A planted tree more than 200 years old in St. Croix, U.S. Virgin Islands, has reached 2 m d.b.h. and 25 m in height (Weaver and Francis 1988). Diameter growth may vary from 0.3 to 1.4 cm per year, depending on climate, soils, competition, and age (Francis 1991). The species grows on a wide variety of sites. Areas that receive mean annual rainfalls of 760 to 1780 mm are best. *Swietenia mahogani* colonize areas that receive salt spray; soils that have developed from marl, porous limestone, coastal sands, or serpentine rocks; and soils with pH between about 5.0 and 8.5. However, *S. mahogani* plantations on soils with pH of 5.0 or below and rainfall above about 2250 mm per year died out completely in Puerto Rico (Francis 1991). Ornamentals in parts of Florida tolerate infrequent light frosts.

Geographic races have not been reported, but hybrids occur whenever it is planted near *S. macrophylla* and *S. humilis* trees (Whitmore and Hinojosa 1977).

Before 400 years of exploitation of the natural stands, *S. mahogani* wood was the best known and most prized tropical wood in the world for cabinet making. Small quantities of logs are still harvested from plantations, roadside plantings, and depleted natural stands (Francis 1991). The heartwood has a deep, rich, red or brown color (Longwood 1962) and an oven-dried specific gravity that is typically about 0.6 (Heck 1937, Kyoch and Norton 1938). The wood dries without warping and checking and can be worked easily with hand and power tools. It is used to make and repair fine furniture, for balustrades, trim, carving, and crafts. Small trees and limbs are used for making fenceposts, charcoal, and firewood. The tree is grown as a shade tree and ornamental in the West Indies and elsewhere in the tropics (Francis 1991).

Flowering and fruiting of plantation trees starts at 12 to 13 years of age (Lamb 1966). Only dominant and codominant trees flower. Flowering occurs in spring and early summer (Little and Wadsworth 1964). The flowers are unisexual and the trees are monoecious, with male and female flowers present in each inflorescence (Lee 1967, Styles 1972). The flowers are apparently pollinated by bees and moths (Styles and Khosla 1976). The fruit is a brown, egg- to pear-shaped capsule about 6 to 10 cm long (Schubert and Zambrana 1978). Large trees may produce over 100 capsules, but seed production is irregular from year to year. The fruits ripen during the winter (Little and Wadsworth 1964). When fully ripe, the woody shell splits into five sections from the base upward and falls off to release the seeds. The winged seeds (samaras) are 5 to 6 cm long and tan to reddish brown in color (Bisse 1981). A capsule may contain up to 60 seeds. Fifty capsules sampled in Puerto Rico averaged 39 ± 1.3 seeds and ranged from 19 to 56 seeds (Francis 1991).

Seeds are collected when a few of the capsules on a tree have opened. At ripening, the color of the capsule changes from greenish gray to gray-brown, red-brown, or brown; during collection, capsules with a discernible green shade should be avoided. Pruning poles, ladders, or high-lift buckets are used to collect capsules from the trees. The capsules are sun-dried until partially open; they are then broken open and the seeds are removed and further dried over screens in a shaded, well-ventilated area. Air-dried seeds average about 7,000 per kg (Marrero 1949). The seeds are placed in sealed containers and may be stored at room temperature for about 2 months. If longer storage is needed, the seed should be refrigerated. Evidence from *S. macrophylla* indicates that storage for longer than 1 year should not be attempted (Marrero 1943). *Swietenia mahogani* appears to have similar seed characteristics.

No pregermination treatments are necessary. Germination is hypogeal. The seeds will germinate in almost any moist media. An average of 70-percent germination was noted in tests in Puerto Rico, and an average of 18 days passed before the first seeds germinated (Marrero 1949).

A sound approach to nursery germination is to scatter fresh seeds on moist, sterile potting mix in trays or beds and cover with about 1 cm of potting mix. New seedlings are transplanted from the germination trays or beds to pots, nursery bags, or nursery beds after they develop two or three leaves. Nursery seedlings reach about 20 cm in 6 months and about 60 m in 1 year. Outplanting of seedlings from 30 to 50 cm in height is recommended for large, solid-block plantings. Seedlings from 50 to 100 cm in height are recommended for line planting. Seedlings to be used as ornamentals should be 1 to 1.5 m or more in height before outplanting. Bare-root seedlings and stump plants are suitable for sites if soils are moist at the time of planting and will remain so for several months. Seedlings must not dry out or heat up before planting. For dry sites, bagged or potted seedlings are recommended. Seedlings must be protected from weeds and grass for 2 to 3 years after planting and from vines and invading tree species for as long as necessary.


2cm
2cm
2cm

Symphonia globulifera L. f.

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CLUSIACEAE (MANGOSTEEN FAMILY)

Maronobea coccinea Aubl., *Maronobea esculenta* Arrudo

Barillo, bogum, botoncillo, cerillo, cero, leche amarillo, marillo, pimientillo, sambogum, varillo

Symphonia globulifera is widespread in tropical America, Africa, and Madagascar, showing little variation throughout its range. In tropical America, the tree is distributed from southern Mexico to northern South America. In Panama, *S. globulifera* more frequently grows along the Atlantic coast (D'Arcy 1980), but in Costa Rica it also grows in the wet Pacific lowlands (Hurtado 1996).

Symphonia globulifera is a slow-growing, medium-to-tall tree that can reach 20 to 30 m in height (average height is 15 m) and 0.30 to 1 d.b.h. In Finca La Selva, Costa Rica, the species is small at less than 10 in height, but in Tortuguero National Park and Braulio Carrillo National Park, it is a tall tree. The trunk is long, straight, and cylindrical; it often has short, stout, stilt-like roots at its lower part. The bark is furrowed and the crown is dense and narrow. An abundant yellow sap is present in all parts of the tree. Leaves are opposite, without stipules, lanceolate or oblong, acuminate, glabrous, and leathery, with very short petioles and cuneate bases. The blade is 5 to 11 cm long and 1.5 to 3 cm wide; the costa is impressed above and elevated beneath; and the numerous lateral nerves are straight and parallel. The larger trees grow in mixed evergreen, wet forests (3500 to 5000 mm annual rainfall, 23 to 26 °C average temperature) from sea level to 900 m (Allen 1956). Smaller specimens forming nearly pure, often very extensive, stands occur in areas of freshwater swamps.

The wood of *S. globulifera* is heavy (specific gravity is 0.56) and dries at a moderate rate without major defects. The dry sapwood is gray-yellow, and dry heartwood is brown-yellow (Carpio 1992). The grains are generally straight, although some are intercrossed; the texture is medium-rough and the luster is regular. The figure has very conspicuous lines and arches in the radial surface and mottling in the tangential plane; the pores are usually solitary and not very conspicuous. The wood has good workability and possesses a high natural durability. However, treating with preservatives is difficult. It is used for furniture, bridges, fenceposts, turning, barrels for solids, railway ties, boats and ships, boxes, crates, veneer, and wood pulp (Carpio 1992). The latex is used for making candles and torches, caulking boats, and treating ulcers (Allen 1956). It also yields an ammonia-soluble khaki dye used in British Guyana to give leather a rich, brown color.

Symphonia globulifera flowers from early July to the end of February, and individual trees remain in bloom for almost 2 months (Allen 1956). The waxy, blood red, nearly globose flowers are borne in dense heads at the end of short lateral branches. The flowers are very showy from a distance, abundant, and secrete nectar only during the bisexual period (Hurtado 1996, Pascarella 1992). In Peninsual de Osa, Costa Rica, the most abundant crop of fruit appears during April and May (dry season) (Hurtado 1996). Fruits are subglobose, 2 to 4 cm long, surmounted by the persistent style and branches, leathery, and brown or yellow. Fruits contain one to three ellipsoid or subglobose seeds.

Seeds in natural conditions germinate in less than 30 days (Hurtado 1996). Seedlings are shade tolerant during early stages of growth, but require more light to grow and develop in later stages.

Tabebuia donnell-smithii Rose

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BIGNONIACEAE (BIGNONIA FAMILY)

Cybistax donnell smithii (Rose) Seibert, *Cybistax millsii* Miranda, *Roseodendron dennell-smithii* (Rose) Miranda, *Roseodendron millsii* (Miranda) Miranda, *Tabebuia millsii* (Miranda)

Cacho de venado, comida de culebra, copal, cortez, cortez blanco, duranza, flor de zope, gold tree, palo blanco, primavera, white mahogany (Andrino and others 1991, Gentry 1992, Standley 1926, Witsberger and others 1982)

Tabebuia donnell-smithii is naturally distributed from Mexico to El Salvador, Honduras, Colombia, and Venezuela (Gentry 1992). It has been planted as an ornamental in the Hawaiian islands (Carr 1998, Kuck and Tongg 1960). There are approximately 100 species in the genus *Tabebuia* (Gentry 1992). *Tabebuia chrysea* S.F. Blake or roble amarillo is endemic to the dry forests of northern California and northwestern Venezuela. *Tabebuia rosea* (Bertol.) DC., one of the national trees of El Salvador, is appreciated for its high-quality wood and beautiful flower display (Rojas 1993).

Tabebuia donnell-smithii is a tree with a straight trunk that reaches up to 35 in height (Standley 1926). This tree can be harvested for wood at 35 years (Andrino and others 1991). It is a deciduous tree with leaves from May through January. The leaves are palmately compound with five to seven leaflets. Leaves lack the stellate hairs present in other species of *Tabebuia*. According to Gentry (1992), this tree grows from sea level to 900 m. Andrino and others (1991) report that it grows from 800 to 2000 m and in areas with annual precipitation from 1500 to 4000 mm.

Known in the trade as white mahogany (Standley 1926), the fine wood of *T. donnell-smithii* has a medium texture. According to Gentry (1983), the wood is one of the hardest and heaviest of the Neotropics. It is used worldwide for veneer, furniture, household utensils, flooring, and cabinetwork (Andrino and others 1991, Carr 1998). It is planted as an ornamental because the beautiful, striking yellow flowers bloom when the tree is free of leaves (Navarrete-Tindall 1997). Flowers last less than 1 week.

Tabebuia donnell-smithii flowers briefly in December and April and fruits in May and June (Witsberger and others 1982). The yellow, tubular flowers are produced in panicles; the fruits are cylindrical, elongated, and dehiscent capsules that contain many winged seeds that are dispersed by wind.

Fruits are collected before they open and dried before the seeds are extracted. Seeds are separated manually from the fruits.

Tabebuia donnell-smithii is propagated by seeds and cuttings. One or two seeds are planted in polyethylene bags containing soil with good drainage and watered regularly. Seeds germinate in 12 to 18 days and germination rate is 46 to 47 percent in El Salvador (Jara 1996). Seedlings can be outplanted in May or at the beginning of the rainy season, when they are 2.5 to 5 cm tall and have two or more true leaves. Cuttings 25 to 199 cm tall can be planted in polyethylene bags and watered regularly (Andrino and others 1991) or can be rooted directly in the field without the addition of growth regulators.

Tabebuia guayacan (Seem.) Hemsl.

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BIGNONIACEAE (BIGNONIA FAMILY)

Tecoma guayacan Seem

Cortez, corteza, guayacán

Distributed from southern Mexico to Colombia, T*abebuia guayacan* is very abundant in Costa Rica and Panama.

Tabebuia guayacan is a fast-growing, medium-to-large tree that reaches 25 to 50 m in height and 40 to 60 cm d.b.h.; it sometimes grows to 2 m d.b.h. The trunk is straight and cylindrical with prominent stilt roots, and the apex crown is rounded. The bark, light tan or buff to gray-brown in color, is split by long, shallow, vertical furrows with the plates between furrows broken into scales. The twigs are subtetragonal and glabrous; the nodes have no interpetiolar glands or pseudostipules. Leaves are opposite and palmate with five to seven leaflets (usually five) and without stipules. The leaflets are lanceolate to ovate, acuminate and basally rounded to obtuse. The terminal leaflets are 9 to 30 cm long and 3.7 to 15.5 cm wide; the intermediate leaflet is 8 to 30 cm long and 2.8 to 15 cm wide; the lateral leaflets are 6 to 21.5 cm long and 2.1 to 10.7 cm wide. Leaflets are often partially divided if not completely divided into seven leaflets. The basal pair is smaller, entire (or serrulate in seedlings), membranaceous, minutely lepidote (at least beneath) and stellate-pubescent with multicellular trichomes in the axils of lateral nerves beneath. The species grows in the tropical moist forest, sometimes reaching the premontane wet forest. Even though the tree requires humid and warm climates for good growth, it prefers the soils with good drainage often found in hilly areas.

The wood of *T. guayacan* is considered extremely heavy with a specific gravity of 0.85. The sapwood is light orange when dry; heartwood is dark brown with some olive-green traces. The grains are very intercrossed in narrow bands, and the wood has a medium texture and poor luster. The figure consists of fine stripes in the radial surface, and the pores are primarily solitary and inconspicuous (Carpio 1992). The wood dries quickly with severe to moderate defects in the ends. It is difficult to work and preserve but has good natural durability. It is used for railway ties, heavy flooring, boats, furniture feet, agricultural tools, sport items, and dock pilings.

Tabebuia guayacan blooms primarily from late March to May; occasional individual blooms appear during the wet season (May through November). Inflorescence is a terminal panicle, the flowers in twos or threes on the branches, with caducous bracts. The flowers have a very faint odor, the calyx is campanulate, and the corolla is yellow with reddish penciling on the throat. The fruit is a linear-cylindrical capsule, 29 to 61 cm long, 1.0 to 2.9 cm wide, essentially glabrous, inconspicuously lepidote or thick-stellate pubescent. Seeds are 0.9 to 1.1 cm long and 3.5 to 4.0 cm wide; the wings are hyaline-membranaceous and sharply demarcated from the seed body. Seeds are released late in the dry season at the beginning of the wet season.

Information on propagating *T. guayacan* is nonexistent; however, some data about reproduction of related species is presented in the next section.

ADDITIONAL INFORMATION

The species can be recognized vegetatively by the stellate trichomes beneath the axils of the lateral nerves of an otherwise glabrous leaflet and by its tendency to have seven leaflets (Gentry 1973). It is closely related to *T. serratifolia* from South America, which has simple trichomes in the axils of the lateral nerves and longer trichomes inside the corolla tube. In Costa Rica the species is sometimes confused with *T. ochracea* subsp. *Necochrysantha,* which also has yellow flowers.

When *T. rosea* and *T. ochracea* subsp. *neochrysantha* seeds are immersed for 24 hours in water at room temperature, germination percentage improves (Trujillo 1996a). The seeds of *T. ochracea* subsp. *neochrysantha* when hermetically kept in plastic bags in a cool chamber at 5 °C maintain their viability for 3 to 6 months. When placed in glass containers kept at 18 °C, their viability can be maintained for 1 year. *Tabebuia rosea* seeds can remain viable for 2 years.


2cm
2cm

Tabebuia rosea (Bertol.) DC.

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BIGNONIACEAE (BIGONIA FAMILY)

Couralia rosea (Bertol.) Donn. Sm. (Botanical Gazette 20: 9; 1895); *Sparattosperma rosea* (Bertol.) Miers (Proceedings of the Royal Horticultural Society of London 3: 99; 1863); *Tabebuia mexicana* (C. Mart. ex DC.) Hemsl. (Biologia Centrali-Americani, Botany. 2: 495; 1882); *Tabebuia pentaphylla* (L.) Hemsl. (Biologia Centrali-Americani, Botany 2: 495; 1882); *Tabebuia punctatissima* (Kraenzl.) Standl. (Tropical Woods 36: 18; 1933); Tecoma evenia Donn. Sm. (Botanical Gazette 20[1] 8; 1895); *Tecoma mexicana* C. Mart. ex DC. (Prodromus Systematis Naturalis Regni Vegetabilis 9: 218; 1845); *Tecoma punctatissima* Kraenzl. (Repertorium Specierum Novarum Regni Vegetabilis 17: 221; 1921); *Tecoma rosea* Bertol. (Novi Commentarii Academiae Scientiarum Instituti Bononiensis 4: 425; 1840)

Amapa, amapa rosa, amapola, apamate, cachahua, cul, hokab, ícotl, kokab, li-ma-ña, macuelis de bajo, macuelizo, macuil, macuilís, macuilixuatl, maculigua, maculís, maculishuate, maculiz, maculiz prieto, mano de león, maqueliz, maquile, maquilicua, maquilís, matilisquate, mayflower, orumo, palo blanco, palo de rosa, palo yugo, primavera, roble, roble blanco, roble colorado, roble de sabana, roble de San Luis, roble de yugo, roble del río, roble macuelizo, roble morado, roble prieto, roble sabanero, rosa morada, satanicua, tural, yaxté (Gentry 1992, Pennington and Saruhkán 1968, Pittier 1957, Record and Hess 1949, Standley 1938)

Tabebuia rosea is native to continental America and common from wet lowlands to dry uplands, from southern Mexico to Venezuela and coastal Ecuador (Gentry 1992). The species can be found in essentially pure stands, as isolated trees, or in a mixed forest (Longwood 1971).

Tabebuia rosea is a tall, fast-growing tree reaching 25 to 30 m high and 1 m d.b.h. The crown is wide, stratified, and irregular, with a few thick, horizontal branches; the bole is straight, sometimes channeled at base. Branching is sympodial; twigs are subtetragonal (Gentry 1992). The bark is gray, blackish or grayish brown, rough and narrowly fissured vertically, with corky ridges (Gentry 1992); the inner bark is creamy or pinkish, fibrous, bitter, with a mint odor, and 20 to 30 cm thick (Pennington and Saruhkán 1968, Salas 1993). Leaves are decussate, compound, digitate, long petiolate, and deciduous. Each leaf has five leaflets unequal in size; the central leaflet is the larger. Petioles and petiolules are pulvinate. They are elliptic-oblong, obovate, or oblong-ovate, with acute or acuminate apex, entire margin, and obtuse base. Leaflet surface is lepidote adaxially and abaxially, although sometimes it can be glabrous (Salas-Estrada 1993, Whitmore and Hartshorn 1969). Leaves are dropped March through June. *Tabebuia rosea* is found in deep and superficial soils, but grows better in well-drained soils with a light texture. The soil pH is variable. Although the species grows in a great variety of habitats, it is frequent in periodically inundated forests or soils with moderate or low drainage. The elevation range is from sea level to 1200 m, the temperature 20 to 30 °C, and the annual rainfall above 500 mm.

The sapwood is creamy, yellowish or brownish; the heartwood is light brown with a grayish or golden hue (Longwood 1971). The wood is strong and quite heavy; the basic specific gravity is 0.48 to 0.60. Fine brown lines of parenchyma give the wood a distinctive figure on the radial surface and a feather-like pattern in the tangential surface (Longwood 1971). It has medium to coarse texture, straight or interlocked grain, and medium luster and is tasteless and odorless in dry condition. Air seasoning is fast and causes small surface checking and slight warping (Longwood 1971). The wood is easy to work except in planing and has a moderate rate of shrinkage (intermediate: between mahogany and black walnut) (Longwood 1971). The wood can be sawed, shaped, bored, and turned with excellent results; planing requires some care to avoid torn and chipped grain (Longwood 1971). Natural durability is medium. The wood is moderately resistant to white-rot fungi, resistant to brown-rot fungi, and susceptible to termite and marine borers (Herrera and Morales 1993, Longwood 1971). Wood preservation is easy. The wood is used in general construction, for furniture, interior trim, paneling, cabinetwork, flooring, boat decking, millwork, handles of sporting goods, agricultural implements, paddles, shingles, face veneers, carts, boxes, and crates (Herrera and Morales 1993, Longwood 1971). It is classified as a structural wood type B (Herrera and Morales 1993). The species has been used as an ornamental and shade tree, but it can be used with success in commercial plantations (Pennington and Saruhkán 1968).

Flowering occurs in January and February, and pollination is entomophilous. Flowers are hermaphrodite, zygomorphic, and solitary or grouped in small, lax, terminal inflorescences, with a pair of bracts subtending each dichotomy (Gentry 1992). Flowers are large and showy. The calyx is greenish or greenish brown, tubular, and bilabial. The corolla is basally funnelform-campanulate, pentalobed, membranaceous, with the limb spreading; it is whitish at base and pink, magenta, or almost white distally, with a yellow throat opening (Gentry 1992). The androecium has four stamens, didynamous, with tecae divaricate, alternating with the corolla lobes and inserted in the corolla tube. A staminode is also present. Anther dehiscence is longitudinal. The gynoecium is surrounded by a thick nectary. The ovary is linear and bilocular with many ovules biseriate in each locule; the style is long and the stigma, bifid.

Fruits mature February through April. The fruit is a long, slender, linear-cylindrical, brown, bivalve, loculicide capsule that is linear or linear-oblong, 18 to 35 cm long, 15 mm in diameter, and attenuate at both ends; the calyx is persistent (Flores 1999, Gentry 1992, Salas 1993). Seeds are whitish, thin, with broad, hyaline-membranaceous wings; seed dispersal is anemochorous.

Fruits are collected from the tree before opening. The seeds are removed from the pods and can be stored at ambient temperature and humidity for several months. Seeds average 40,000 to 45,000 per kg; water content in fresh seeds is 12 to 13 percent. Seed behavior is orthodox and the percentage of germination varies from 75 to almost 100 percent.

Seeds do not require special treatment. Germination occurs either in shade or direct sunlight, provided humidity is kept stable. Germination is epigeal and seedlings are phanerocotylar. Seed imbibition lasts 24 hours; root emergence occurs 3 to 4 days after sowing.

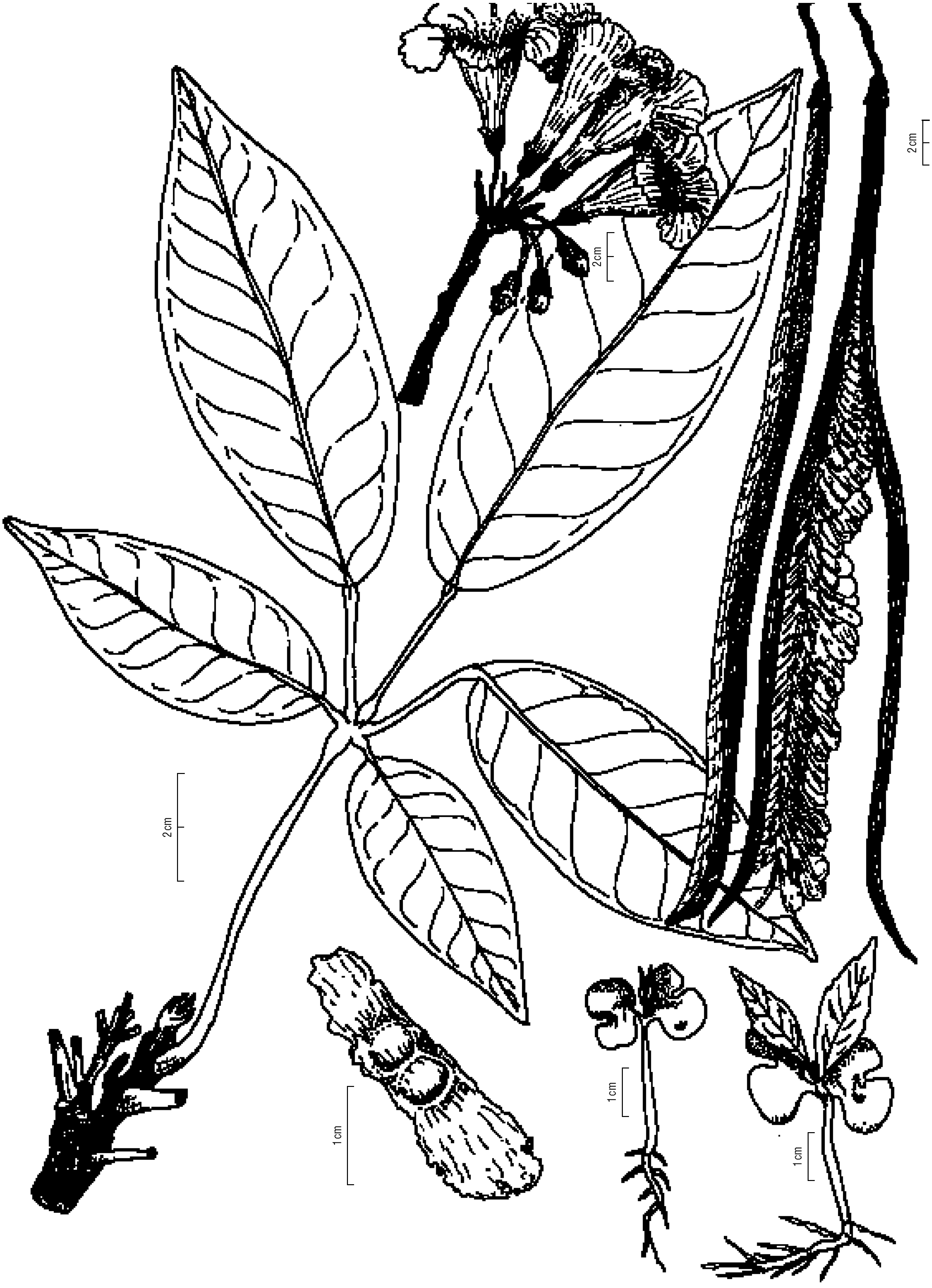
Seeds can be sown under partial shade in beds or plastic bags filled with humid sand or a mixture of soil and sand. Seedling development is fast and the small seedlings can be transplanted to plastic bags 8 days after sprouting. Outplanting can be done when seedlings are 3 to 5 months old. The planting distance used in monospecific plantations is 3 by 3 m (González and others 1990) and survival is above 80 percent. *Tabebuia rosea* can also be planted as a pseudostick (Nichols and González 1991b). The trees do not require pruning, and no predators or parasites damaging seedlings have been reported. The tendency to stem bifurcation exhibited by juveniles in plantations must be controlled with appropriate silvicultural practices (Nichols and González 1991b).

Seedling survival is 98 percent in plantations in Sarapiquí, Heredia, Costa Rica. Average annual increase in d.b.h. is 1.7 cm and average increase in height is 1.5 m (González and others 1990). Ten-year-old juveniles reached 9.4 cm d.b.h. and 8.7 m in height in a monospecific plantation located in Pejibaye, Pérez Zeledón, Costa Rica.

ADDITIONAL INFORMATION

Tabebuia rosea was previously identified as *T. pentaphylla* (L.) Hemsl. in several Central American countries. *Tabebuia pentaphylla* grows in the Antilles (Holdridge and Poveda 1975).

Because the wood is similar to oak, it has been called roble, which means oak (Holdridge and Poveda 1975). The wood has some resemblance to white ash (*Fraxinus americana*) (Longwood 1971).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Talisia oliviformis (Kunth) Radlk.

ANÍBAL NIEMBRO ROCAS
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SAPINDACEAE (SOAPBERRY FAMILY)

No synonyms

Cotoperiz, guaya, huaya, keneb uayum, uayab, wayam

Talisia oliviformis is native to America. It is distributed naturally from Mexico, across Central America, to northern South America, and in the West Indies. The plant is an important component of wet and subhumid tropical forests.

Talisia oliviformis is a deciduous, dioecious tree up to 20 m in height and 50 cm d.b.h. The tree grows slowly and has a long life (Hoyos 1979). The trunk is straight, slightly grooved, and has small spurs at the base. The crown is pyramidal, very dense, and made up of rising branches. The leaves are generally paripinnate, 5 to 15 cm long, and made up of 1 to 2 pairs of elliptic, oblanceolate or obovate leaflets, 3 to 8.5 cm long and 1.5 to 4.5 cm wide. In the Yucatan Peninsula, the tree grows in calcareous soils with outcropping rocks, forming part of the tropical forest. The regions where the tree grows have an average annual temperature of 26 °C, with a maximum temperature of 36.7 °C and a minimum temperature of 14.9 °C. The maximum temperatures correspond to the months of April and May; the minimum temperatures, to the months of December and January. Average annual precipitation is approximately 1288 mm, ranging between 900 and 1800 mm. The tree grows from sea level to 150 m.

Talisia oliviformis is a tree with multiple uses. Its bittersweet, edible fruits are sold in markets. The leaves serve as forage for domestic animals, and the wood is used for firewood and in rural construction. The flowers are honey bearing. *Talisia oliviformis* is planted in backyards and orchards. It is also cultivated as an ornamental and a shade tree in streets, parks, and gardens (Aguilar 1966, Barrera 1981, Cabrera and others 1982, Chavelas and González 1985, Escalante 1986, Flores 1993, Hoyos 1979, Rico-Gray and others 1991).

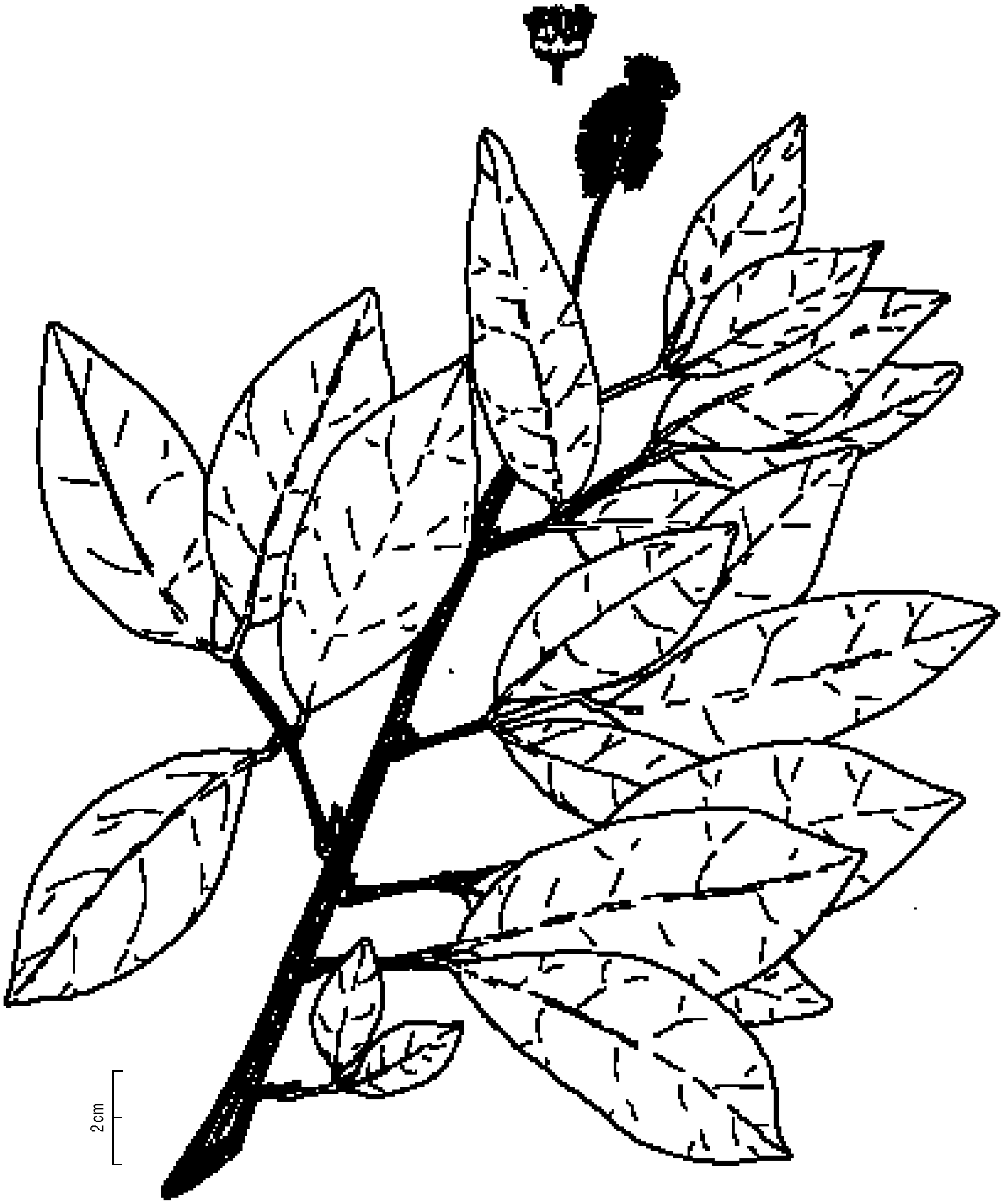
Because its geographical distribution is extensive, *T. oliviformis* blooms at different times of the year. Trees begin to yield flowers and fruits between 5 and 6 years of age. In southeastern Mexico, the plant blooms from February to May and fruits from April through June (Cabrera and others 1982, Juárez and others 1989, Pennington and Sarukhan 1968). The flowers are sweet smelling, yellow-cream or yellowish green in color, and arranged in panicles. The fruits are globose berries, 1.5 to 2.5 cm long, and yellowish green when ripe, with a fleshy, thin, and sweet pulp. Each fruit contains one seed (Cabrera and others 1982, Pennington and Sarukhan 1968). The seeds range in shape from ovoid to globose or ellipsoid and are 1 to 1.5 cm long and in diameter. They are surrounded by a pulpy, whole, succulent aril that is yellow in color. The seed coat is light brown, smooth, opaque, and crustaceous.

The fruits are collected in April and May by climbing the trees and using poles with metal hooks. The pulp is removed from the pulpy fruits by hand inside a bucket of water. Resulting impurities float and are gathered with a strainer. Good seeds sink. Subsequently, the seeds are dried in the sun in ventilated locations for 1 or 2 hours, depending on the lighting conditions. Seeds average 355 per kg and remain viable for approximately 9 months when stored under ambient conditions (24 to 30 °C). Longer storage quickly diminishes seed viability (Vega and others 1981).

The germination of the seeds is cryptocotylar. Under humid conditions, fresh seeds germinate at 80 percent without pretreatment. A heterogeneous sample of seeds germinated approximately 12 days after sowing (Vega and others 1981).

ADDITIONAL INFORMATION

The hilum is basal and vaguely elliptic or circular. The micropyle is indiscernible. The embryo has a curved axis and is asymmetrical, white or cream in color, with expanded cotyledons. There are two massive, unequal, pulpy cotyledons. The plumule is undifferentiated. The radicle is ligulate (Pennington and Sarukhan 1968, Standley and Steyermark 1949, Vittien 1937).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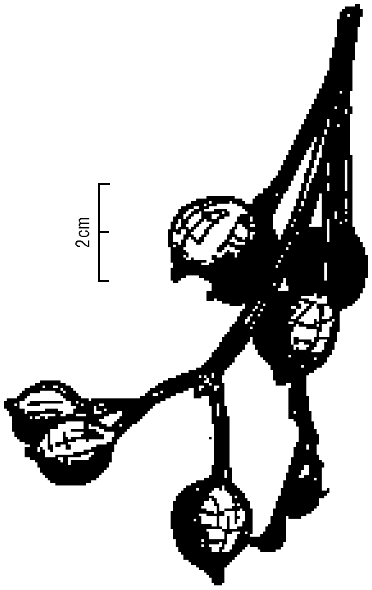
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Tamarindus indica L.

H.G. SCHABEL
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University of Wisconsin
Stevens Point, WI

FABACEAE (BEAN FAMILY)

T. occidentalis Gaertn., *T. officinalis* Hook

Indian date, Madeira mahogany, tamarin, tamarind, tamarindier, tamarindo, tamarinier

The only species in the genus (Léonard 1957), *Tamarindus indica* originated in the Old World Tropics but now grows pantropically (Parrotta 1990). It is frequently associated with baobab (von Maydell 1986, Morton 1987).

Tamarindus indica is a slow-growing, occasionally deciduous to mostly evergreen, short-trunked tree with a dome-shaped crown up to 9 m wide. It attains 30 m in height and up to 1.5 m d.b.h. (Anonymous 1982a, 1982b; von Maydell 1986; Morton 1987). This wind-resistant and long-lived tree thrives in semiarid—including alkaline, slightly saline, and poor—soils. It grows from sea level to about 1,500 m, with a preference for riparian, well-drained sites in woodlands, alluvial flats, scarp slopes, and deciduous thickets and around termite mounds.

Tamarindus indica is genetically broad, as reflected primarily in the variability of its fruits; these range from small to large and sweet to acidic. Interesting genetic types are reported in Southeast Asia and a red-fruited variety, known as *T. indica rhodocarpa*, grows in India (Anonymous 1979, Morton 1987, Parrotta 1990).

Tamarindus indica is a multipurpose tree (Anonymous 1979, von Maydell 1986, Parrotta 1990). Because it has a wide, dense crown and attractive shape, tamarind is an excellent shade and ornamental tree (Schubert 1979), even as a potted indoor plant. Due to heavy shading and supposedly allelopathic properties, *T. indica* suppresses understory vegetation and is used as a firebreak species in Indian forest plantations (Troup 1921). The sapwood is bright yellow and the dark brown to purple, heavy heartwood (specific gravity of 0.8 to 1.22 g/cm^3) is hard to work but easy to polish and bend. It is generally borer and termite-proof and suitable for furniture, pestles, mortars, carts, boats, wheels, hubs, utensils, turnery, tools, toys, and panels (Troup 1921). It also makes excellent fuelwood and charcoal for both fuel and gunpowder. The ashes and bark are used for tanning; the bark also provides extractives for making ink or fixing dyes. The flowers yield good honey and a yellow dye, while leaves make a red dye. Flowers, foliage, and immature pods can be added to soups, curries, stews, and salads and are browsed by livestock (Anonymous 1982a, 1982b). Seeds can be peeled, roasted, or boiled but are considered famine food (Storrs 1979). They also contain a pectin used for jelling fruits; stabilizing ice cream, mayonnaise, and cheese; and sizing textiles, paper, and jute products. Seed oil is suitable for food, varnish, and lamp fuel, while the seed husk yields a fish poison. The tree's best known use, however, relates to the pulp of the pod, which is eaten fresh or as an ingredient in fruit drinks, jams, chewing gum, confections, chutney, curries, preserves, ice cream, syrups, and condiments such as barbecue and Worchestershire sauces. The fruit is particularly rich in vitamins B and C and calcium (Lefèvre 1971). Overripe fruit pulp is used to clean silver, copper, and brass. Medicinally, *T. indica* is used as a cure for fevers, intestinal ailments, and biliary disorders (von Maydell 1986, Storrs 1979).

Flowers usually appear with new leaves in spring and summer. In Sri Lanka and India, two flowering periods—one in the spring and the other in the fall—have been reported (Troup 1921). The flowers are carried in small, terminal, glabrous, 5-cm-long racemes. They are pale yellow with pink, red, or brown stripes, 3 to 5 cm long, and about 2.5 cm wide (Noad and Birnie 1994). Fruits ripen about 10 months later in trees as young as 4 years (Lefèvre 1971). Mature seed pods range from 6 to 20 cm long, 1.9 to 2.5 cm wide, and 1 to 3 cm thick, are straight to curved, scaly, gray to rusty brown, and oval in cross section. They are irregularly constricted between the 1 to 10 seeds contained within (von Maydell 1986). Seeds are hard, shiny brown to blackish, with a large patch of a different color shade on each face. They are obovate-orbicular, compressed, about 1.6 cm long, and embedded in a sticky, fibrous, yellow to red-brown pulp.

Fruits are collected only when they are fresh and ripe as indicated by a buff, brittle epicarp (Cowen 1965). Pods are shaken from the tree or if reachable fruit pedicels are clipped (Morton 1987). Average annual fruit yields from an adult tree are 150 to 200 kg (Anonymous 1979). Immediately after fruit harvest, seeds can be separated easily from the shell and fibrous pulp under water. Seeds average 600 to 3,000 per kg (Anonymous 1992, Food and Agriculture Organization 1975, von Maydell 1986, Teel 1984). Seeds store well in dry sand, remaining viable for at least 2 years if kept in closed vessels for protection from insects, including *Calandra (Sitophilus) linearis, Caryedon cerratus, Corcyra cephalonia, Pachymerus (Coryoborus) gonogra, Paralipsa gularis,* and *Rhyzopertha dominica* (Lefèvrre 1971, Morton 1987, Parrotta 1990, Teel 1984).

Seeds often germinate at 90 percent success (Teel 1984). Germination can be accelerated by nicking seed coats, by soaking seeds for 24 hours in water (Food and Agriculture Organization 1975), or by boiling seeds for 7 minutes and cooling them slowly (von Maydell 1986).

Seeds, covered with about 1.5 cm of loose, sandy loam or loam/sand mix, are germinated in porous soil in bags or raised seedbeds, but direct sowing is also acceptable (Szolnoki 1985). Within 5 to 15 days (Marrero 1949, Troup 1921), they germinate epigeously into Sloanea subtype seedlings (Burger 1972, de Vogel 1980). As soon as cotyledons show, seedlings require light shading until they reach about 35 cm. The dirty yellow taproots grow more than 30 cm within 2 months, and seedling growth is often equally rapid for the first 2.5 to 3 m (Szolnoki 1985). As a result, nursery time can be limited to 3 to 6 months (Anonymous 1992, Teel 1984). To allow lifting with a sufficiently large rootball, seedlings should be spaced at a minimum of 30 cm (von Maydell 1986). With the beginning of rains, when seedlings are more than 80 cm in height, they can be transplanted at 10 to 20 m spacings (Morton 1987).

Tamarindus indica can also be successfully reproduced by rootsuckers, air- and stem-layering, grafting, and cuttings (Anonymous 1979, von Maydell 1986, Morton 1987, Troup 1921). Trees with exceptionally good fruit should be propagated vegetatively (von Maydell 1986).

1cm
1cm
1cm

Tectona grandis L.f.

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International Institute of Tropical Forestry,
USDA Forest Service

VERBENACEAE (VERBENA FAMILY)

No synonyms

Teak, teca, teck

Tectona grandis occupies two areas of native range: the western portion includes most of peninsular India and the eastern portion includes parts of Burma, Laos, and Thailand (Weaver 1993). It has been cultivated since ancient times in Asia and today the species is planted in much of the moist tropics. *Tectona grandis* has naturalized in at least the Philippines, Java (Little and Wadsworth 1964), and Puerto Rico (Francis and Liogier 1991).

Tectona grandis is a large deciduous tree that reaches maximum heights of 30 to 40 m and diameters of 2 m (Chanda Bacha 1977). Although varying considerably by habitat, the trees individually and by stands demonstrate a moderate growth rate. The tree has large, yellow-green leaves, a medium-dense foliage, a medium-to-narrow crown, and a straight trunk covered by tan-to-gray scaly bark. It grows in a wide variety of soils if they are well drained, are not compacted or have a shallow hardpan, and are not seriously depleted of nutrients. *Tectona grandis* tolerates a wide range of climates, but grows best in a warm, moist, tropical climate (1250 to 3000 mm of mean annual precipitation) with a marked dry season of 3 to 6 months (Webb and others 1984). Trees of the species are not harmed by infrequent light frosts (Weaver 1993).

Although *T. grandis* is not divided into subspecies or varieties, a number of different habitat-correlated populations can be distinguished by both morphological characteristics and adaptability (Wellendorf and Lauridsen 1986).

The heartwood of *T. grandis* is golden brown with a distinct grain and has a specific gravity of 0.55. It dries with little degradation and is easily worked with hand or power tools (Longwood 1961). The untreated wood weathers well, resists rot, and is not attacked by dry-wood termites. These superlative properties make it one of the best known and most valuable woods in the world. The wood is used for furniture, flooring, joinery, trim, doors, paneling, carving, musical instruments, turnery, vats, boat masts and decks, railway sleepers, mine props, fuel, and fence posts (Weaver 1993). Trees of the species are also used as ornamental and shade trees.

In Thailand, flowering begins between ages 8 and 10 (Hedegart and others 1975). The small, white, perfect flowers are borne on short pedicels, in large, erect, terminal panicles, about 2 months after the dry season has ended and the leaves have emerged. Flowering generally takes place for 2 months or more between June and September. The fruits ripen 2-1/2 to 3 months later (Chable 1969, Mahapol 1954, Troup 1921). The fruit consists of a subglobose, four-lobed, hard, bony stone about 1.2 cm in diameter, surrounded by a thick, felty, light brown covering, the whole enclosed in an inflated papery involucre. The stone (often called a nut) contains 1 to 3, rarely 4, seeds, and has a central cavity. Researchers in one study found that the number of seeds per stone averaged 1.7 (Schubert 1974). In a survey of the fruits in 23 provenances in India, 51 percent had no seeds, 35 percent had one seed, 12 percent had two seeds, 2 percent had three seeds, and 0.4 percent had four seeds (Gupta and Kumar 1976). In India, good seed crops are produced by plantations less than 20 years old (Troup 1921).

The bladder-like involucres turn from green to brown when the seeds are ripe and gradually fall to the ground during the next dry season. The fruits can be swept or picked up as they fall, clipped from the trees with pruning poles, or shaken from the branches. Fruits can be spread in the sun or in ventilated sheds to dry. The involucre can be removed by mechanical dehusking or by working a cloth bag half-filled with dried fruits against the ground with a foot and then winnowing to separate the fruits from the chaff. *Tectona grandis* fruits in Honduras average 705 per kg with involucres intact and 880 per kg with the involucres removed (Chable 1969). In other parts of the world, the number of clean fruits per kg varies from a low of 880 to a high of 3,070 (Champion and

Brasnett 1958, Parry 1956). The seeds make up about 3 percent of the weight of the cleaned fruits (Dabral 1976). The fruits retain their viability for about 2 years in sacks in dry warehouses (Kushalappa 1977). High seed moisture content or high atmospheric humidity will shorten the storage life considerably. Long periods of storage have not been necessary in most areas because *T. grandis* produces good seed crops almost every year (Mahapol 1954, Troup 1921).

Cut tests of fruit from 56 collections across the range of *T. grandis* revealed a potential mean viability of 71 percent with a range of 40 to 96 percent (Danish/Food and Agriculture Organization Forest Tree Seed Centre 1973). Germination of fruits in nursery beds in various parts of the world has varied from 0 to 96 percent in periods varying from 10 days to 3 months. Seeds extracted from fruits and treated with fungicide gave a germination of 54 percent in 12 days (Dabral 1976). But because seed extraction is difficult, and untreated *T. grandis* seeds have protracted, often low and unpredictable germination, some fruit pregermination treatment is usually applied to the fruit. A number of pretreatments have been effective:

• Soaking the fruits in water for several days or alternately wetting and drying have proven effective (Schubert 1974, Troup 1921). In one test, clean fruits pretreated by five cycles of alternately soaking in water for 24 hours and drying in the sun for 48 hours, were sowed. Germination began 18 days after sowing, increased for 15 days, and gradually decreased. The germination rate 68 days after sowing was 61 percent. Weathering of the epicarp and mesocarp helped germination (Schubert 1974).

• Innoculating seeds with *Scytalidium* sp., a cellulolytic fungus isolated from teak litter, and keeping them moist for 21 days resulted in 96-percent germination compared to 20-percent for uninoculated controls (Dadwal and Jamaluddin 1988).

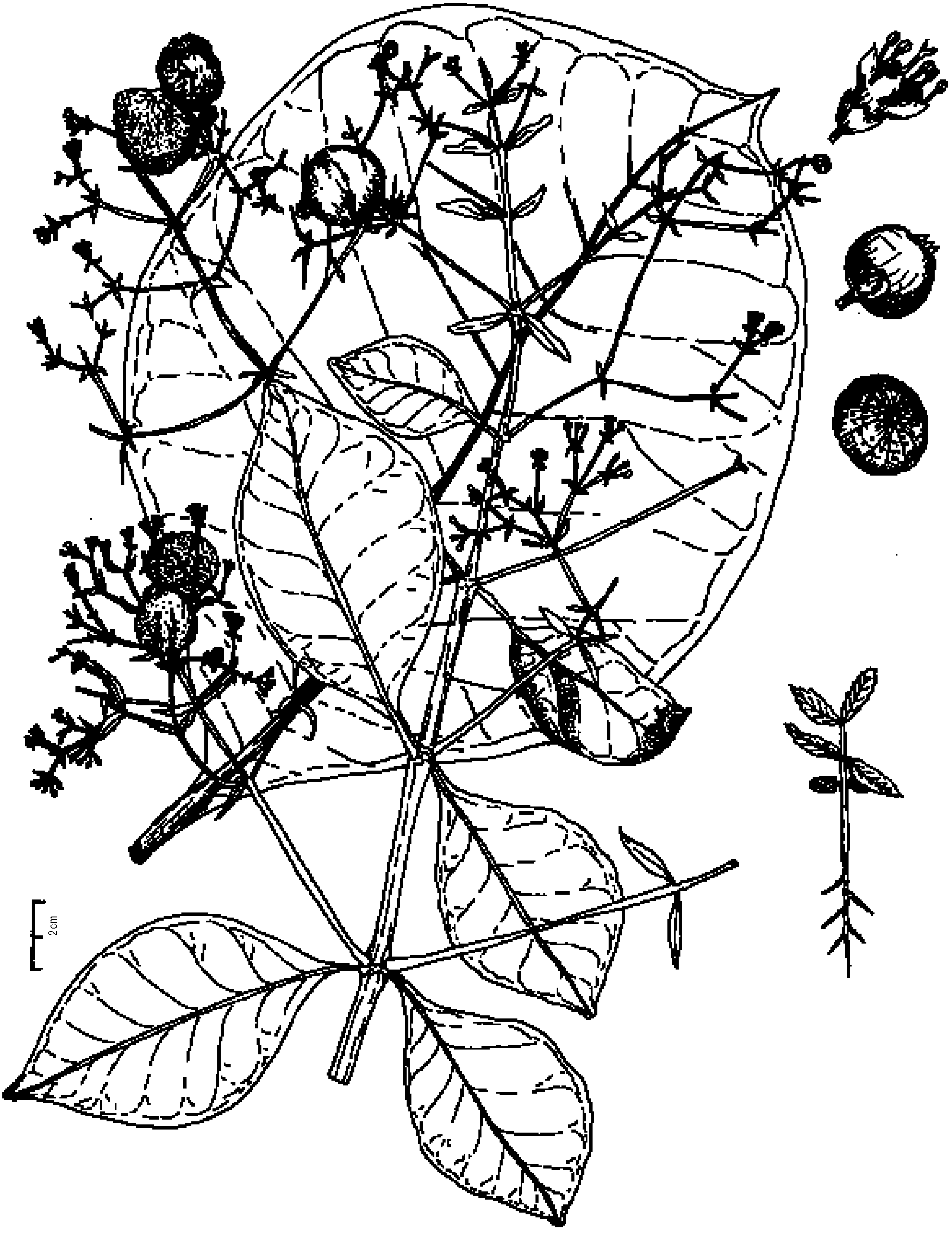
• Treating with indoleacetic acid and gibberellic acid, alone and in combination at various concentrations, increased germination 5 to 12 percent over controls (21-percent germination) (Uanikrishnan and Rajeeve 1990).

• Soaking fruits from 11 Indian provenances in a nutrient solution resulted in a higher seedling yield (34 percent) than control (18 percent), water soaking (30 percent), or scarification (28 percent). Gupta and Pattanath (1975) felt that nutrient deficiencies in some of the sources resulted in lower germination or early seedling failure.

• Storing seeds for several months improves germination. Some seed lots that were stored for several months germinated better than fresh seeds (Champion and Brasnett 1958, Mahapol 1954, Troup 1921), probably because they needed a period of afterripening (Schubert 1974).

Size of fruit and region of origin also affect germination rates. Because large fruits tend to have a greater number of seeds than smaller fruits, they yield a significantly higher number of seedlings per fruit. Banik (1977) recommends that fruits smaller than 14 mm in diameter be culled. Seeds from dry regions are frequently more difficult to germinate (Troup 1921). Germination is epigeal (Troup 1921).

Tectona grandis fruits are usually broadcast in nursery beds and covered with 1.2 to 2.5 cm of sand, soil, or sawdust (Schubert 1974, White and Cameron [n.d.]). A temperature of 30 °C during germination appears to be optimal for the seeds (Dabral 1976). A seedling yield of about 25 percent can be expected from good seed (White and Cameron [n.d.]). The beds should be kept moist. Once the seedlings have become established, watering should gradually be reduced. Stump plants (seedlings with the tops removed) or potted plants grown in plastic nursery bags are usually used in field plantings. Direct seeding is also practiced but requires prepared seed spots. Early growth is slow and mortality is often high (Weaver 1993). The stump plants are grown in the nursery until they reach 1.2 to 2.5 cm in diameter at the root collar; the top is cut back to about 2.5 cm, and the tap root cut back to 18 or 20 cm in length (Schubert 1974, White and Cameron [n.d.]). Ideally, plants of suitable size can be grown in 6 to 9 months. In Thailand (Kushalappa 1977) and India (Gupta and Pattanath 1975), some nurseries undercut the beds and remove seedlings large enough for stump plants after 1 year, allowing the remaining seedlings to grow an additional year after which the whole bed is harvested. Sowing of the nursery beds should be timed to ensure the proper size for planting at the start of the rainy season. Another approach involves harvesting in the dry season, storing the dormant stumps in beds of dry sand for 3 months, and planting at the start of the wet season (Kushalappa 1977). After outplanting, seedlings must be weeded for 1 to 2 years until they are well above weeds, grasses, and vines.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Terminalia amazonia (J.F. Gmel.) Exell

E.M. FLORES
Academia Nacional de Ciencias de Costa Rica, Costa Rica

COMBRETACEAE (INDIAN ALMOND FAMILY)

Chuncoa amazonia J.F. Gmel. (Systema Naturae, ed 13 2: 702; 1791); *Chuncoa amazonica* J.F. Gmel. (systema Naturae, ed 13 2: 702; 1791); *Gimbernatea obovata* Ruiz & Pav. (Flora Peruvianae et Chilensis Prodromus 138; 1794); *Chuncoa obovata* (Ruiz & Pav.) Pers. (1168 1: 486; 1805); *Terminalia obovata* (Ruiz & Pav.) Steud. (Nomenclator Botanicus.Editio secunda 2: 668; 1841); *Terminalia excelsa* Liebm. ex Hemsl. (Biologia Centrali-Americani, …Botany…1: 402; 1880); *Myrobalanus obovatus* (Ruiz & Pav.) Kuntze (Revisio Generum Planatarum 237; 1891); *Terminalia odontoptera* van Heurck & Mòll. Arg. (Observationes Botanicae 217; 1871); *Terminalia hayesii* Pittier (Contributions from the U.S. National Herbarium 18 [6]: 239; 1917)

Aceituno, adamaram, alasuhabu, almendro, amarillo, amarillo carabazuelo, amarillo caraqueío, amarillo carruajero, amarillo del río, amarillo pijua, amarillo real, amarillo sólido, amarillón, anangostii, araca, araca d'agua, arispin, arpino, boesi-amandra, broadleaf, bullywood, canolté, canshán, canxán, canxón, carboncillo, chicharro, chicharrón, chicharrón amarillo, chicharrón de monte, chicharrón prieto, cochun, coffee mortar, cuiarana, fukadi, gindja-oedoe, guaba, guayabí amarillo, guayabí-ré, guayabí-saiyu, guayabillo, guayabo, guayabo de montaña, guayabo león, guayo, hill fukadi, jucarillo, karalawai jakoenepele, langousi, lanza, lanza amarilla, lapachillo, mapurite blanco, mashipe, membrillo, merendiba branca, nagosse, nagossi, naharu, nangocy, naranjo, nargusta, níspero macho, olivier mangue, palo amarillo, palo prieto, pardillo negro, pau mulato brancho, poirier, pookadi, puete, querebere, rifari, roble amarillo, roble coral, sarandí amarillo, shapana, sombrerete, suchi amarillo, swamp fukadi, tanibouca, tepesóchil, volador, white olivier, yumbin, yumbingue (Flores 1994h, Longwood 1971, Record and Hess 1949)

Terminalia amazonia is an emergent tree in the canopy of the humid tropical forests, common on slopes and flat lowlands. The geographic range of the species extends from Mexico in the Atlantic watershed to the Guianas in South America (Brako and Zarucchi 1993, Flores 1994h, Hall and Seymour 1978, Jorgensen and León-Yáñez 1999). It also grows in the Antilles (Trinidad-Tobago).

The species is a tall, evergreen, fast-growing tree reaching more than 50 m in height in the Amazonian and Central American forests and up to 70 m in the evergreen forests of Mexico (Flores 1994h, Macbride 1941, Pennington and Sarukhán 1968, Standley and Williams 1962). The bole is quite straight, asymmetrical, and frequently grooved in the basal third. It has conspicuous buttresses, which are longer and wider when the species grows in seasonally flooded or swampy areas. The axis is monopodial; the branches arising at the end of each growth flux are sympodial and plagiotropic (Hallé and others 1978). When they become old, the distal end turns downward; this is a distinctive characteristic of the species (Flores 1994h). The bark is thin (1 cm), dull, and grayish brown or grayish yellow and has shallow vertical fissures. It exfoliates medium-sized flecking plates. Phyllotaxy is spiral; internode reduction leads to spur shoot formation at the branch end. Leaves are petiolate, simple, exstipulated, coriaceous or chartaceous, obovate, depressed obovate or oblanceolate, with entire margin, abruptly acuminate, round or obtuse apex, and attenuate base. They are slightly pubescent, especially abaxially. The leaf is hypostomatic; stomata are anomocytic. The foliar ptyxis is conduplicate; young leaves are reddish brown. Leaf size and shape vary within a given tree or spur shoot. Trees inhabiting nearly dry zones lose their foliage; the production of new leaves is synchronized with blooming (Flores 1994h). The species is frequently riparian and grows well in red or dark soils that are lateritic, deep, and derived from alluvial or igneous materials. It grows in clay, sandy, or poor soils, but it reaches its best growth in clay soils (Flores 1994h, Longwood 1971, Pennington and Sarukhán 1968, Record and Hess 1949, Woodson and Schery 1958). The temperature range in these areas is 22 to 35 °C and the annual rainfall 600 to 1500 mm. The elevation varies from 40 to 1200 m.

The sapwood is pale grayish yellow in green condition, and the heartwood is darker; in dry condition, the sapwood is orange or yellowish and the heartwood is reddish yellow, brownish yellow, light yellowish brown, or yellowish olive, with darker reddish stripes. The wood oxidizes rapidly when exposed to air and light (Flores 1994h). It has straight or interlocked grain, medium-to-high luster, medium texture; it is odorless and tasteless (Flores 1994h, Llach 1971, Longwood 1971, Picado and others 1983). The wood is heavy or very heavy (green weight 1020 to 1100 kg per m^3, with 50 to 80 percent moisture content; basic specific gravity is 0.51 to 0.70). The timber has high quality and good physical and mechanical properties. Volumetric contraction (12.5) is moderate for the wood density; the radial contraction is low (4.8), and the tangential is normal (7.9) (Flores 1994h, Llach 1971, Longwood 1971, Picado and others 1983). Drying is moderately difficult, but it varies with wood origin. The wood may show splitting, checking, and slight warping. Working properties are medium; finishing of radial planes is difficult. Natural durability varies with origin. Resistance to fungal and termite attack is moderate. The wood is difficult to impregnate and preserve. Of the trees with diameters of more than 60 cm, 90 percent have hollow piths. The timber is used in heavy general construction, interior and exterior construction, cabinetwork, floors, bridge foundations, beams, fences, veneers, parquet, barrels, railroad ties, and ships. It is also suitable for making paper (Peteri's coefficient of flexibility is 76; Runkel factor is 0.82) (Llach 1971, Longwood 1971, Picado and others 1983).

Blooming occurs from January through April, with variations in the beginning and ending of the flowering period along the geographic range of the species. The inflorescences arise from the axil of spur shoot leaves. They are racemes bearing numerous flowers whose rachis may reach a length of 15 to 16 cm. The rachis and peduncle have ferruginous pubescence. Flowers are protogynous and the species is allogamous. Flowers are hermaphroditic, actinomorphic, and epigynous. They are shortly pedicellated. The calyx is pentamerous, gamosepalous, tubular, pentasulcate, pubescent, and yellowish green or whitish; it is fused to the androecium and gynoecium in the basal two-thirds. The distal-free third is cupuliform; calyx lobes are deltoid and pubescent on both surfaces. The androecium has 10 stamens distributed in 2 whorls; the external whorl alternates with the sepals while the inner verticil is opposite to the sepals. There is an annular, nectariferous, pentalobate disc surrounding the style; its secretion is slightly sugary. The gynoecium is unilocular, with two anatropous, bitegmic, crassinucellate ovules; placentation is suspended. Pollination seems to be entomophilous with medium-size bees acting as pollinating agents (Bawa and others 1982); however, there is a strong possibility of a partial anemophilous pollination (Flores 1994h).

Fruit ripening occurs from February through May, although regional variations occur. Most flowers develop a fruit, but many fruits lack seeds. The fruit is a short, pedicellate, five-winged samara. The two larger wings extend transfersely while the three smaller wings are sometimes vestigial; there are two on one side of the samara while the remaining one is on the opposite surface. The samara is pubescent, especially in the center. The exocarp is thin and papyraceous, the mesocarp is parenchymatic, and the endocarp fibrous and woody (Flores 1994h). Fruits are wind-dispersed and because of their aerodynamic design are considered rolling autogyros (Augspurger 1986). Fruit weight is 4.0 to 4.6 mg. Fruits average approximately 200,000 per kg.

The seed is enclosed by the fibrous endocarp. It is cylindrical-oblanceolate or cylindrical-elliptic and has a long funiculus. The seedcoat is dull and yellow. The percentage of fruits containing seeds ranges from 0 to 40 percent, depending on the entry, and approximately 8 percent are not viable. Fruits collected in stands with several trees have a higher number of viable seeds than fruits coming from isolated parent trees. Fruits collected from the tree have a higher moisture content and sometimes are immature; those lacking seeds are lighter (Flores 1994h).

Seed-producing trees must be selected from stands, and tree diameters must be more than 70 cm. Samaras must be mature and dry; seeds from immature samaras do not germinate well. Determining the period of seed viability is very difficult due to the high and variable percentage of sterile fruits in different fruit entries and because the seed is enclosed by the samara.

Germination is epigeal and the seedling is phanerocotylar. Under greenhouse and nursery conditions, germination is gradual. The radicle emerges at 60 to 70 days.

Samaras must be sown in boxes filed with sand, germination beds, or bancales. They require moderate shade and constant moisture. Seedling survival in the nursery is about 95 percent, with approximately 10 percent having a slower growth rate (Flores 1994h). The seedlings must be transplanted to plastic bags before the first eophyll extends. The bags must be kept under moderate shade for 2 to 3 weeks. Soil fertilization or application of foliar nutrients increases seedling growth and vigor. The seedlings can be transferred to the field 8 to 12 months after germination. Root and leaf pruning before outplanting is convenient. When seedlings are placed in beds, two root prunings are recommended: one when the seedling is 20 cm long, another 1 month before transplanting. Seedlings and saplings must be transferred to the field in adobe.

Terminalia amazonia has been planted at distances of 3 by 3 m, sometimes 2 by 2 m. In experimental plots located in the northern zone of Costa Rica, sapling longitudinal growth averaged 1.2 m per year and annual diameter growth was 1.4 cm; the annual increment in basal area was 0.5 m^2 per ha. In southern Costa Rica, 14-year-old trees reached an average diameter of 12.7 cm and a height of 12.4 m (Flores 1994h). Seedlings and saplings in nurseries and plantations are predated by ants (*Atta cephalotes, Acromyrmex*); they cause shoot damage and may promote shoot branching (Flores 1994h, Nichols and González 1992).

ADDITIONAL INFORMATION

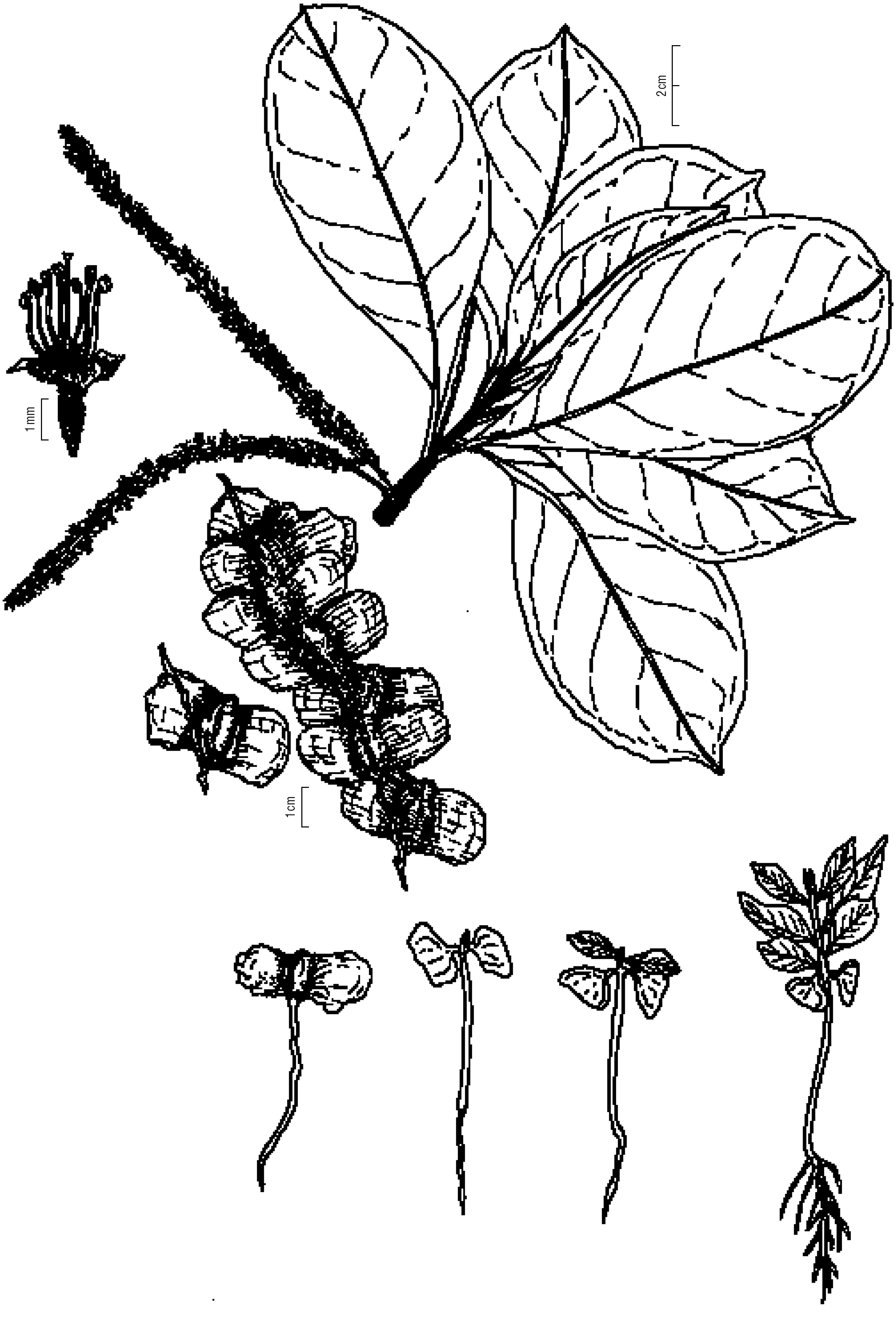
Linnaeus named this genus *Terminalia* because of the peculiar system of branching and the production of leaves at the distal end of each spur shoot. The name of the species refers to the origin of the specimen type (Flores 1994h). *Terminalia amazonia* is the most widely distributed neotropical species of the genus.

There are two to six marginal extrafloral nectaries at the leaf base proximal end and numerous abaxial domatia, surrounded by ferruginous trichomes. The areoles have translucent dots; they correspond to mesophyll idioblasts. Venation is eucamptodromous. The midrib is thick with a straight course, and projects abaxially; the secondary veins have an acute angle of divergence with respect to the midvein. Tertiary veins are transverse and form an angle of 80 to 90° with respect to the midvein; the pattern is distinctive for this species.

Stamen filaments are 2.0 to 2.5 mm long; they are filiform, glabrous, and yellowish. The anthers are subglobose, small (0.3 to 0.4 mm long), extrorse, dorsifixed, and yellow; anther dehiscence is longitudinal. Pollen is abundant and liberated in monads; pollen grains are hexacolpate, and the exine is slightly ornamented. The style is thin and glabrous; the stigma is truncate, glandular, hollow and greenish yellow (Flores 1994h, Pennington and Sarukhán 1968, Woodson and Schery 1958).

Testa and tegmen form the seed. The mature seed is exospermic and lacks perisperm. The endosperm is nuclear and is absorbed during embryo development. The embryo is small, oblong, and whitish. It is straight and has contorted foliar cotyledons. Although the ovary has two ovules, only a single ovule develops, is fertilized, and forms a seed.

After 6 to 8 days, the hypocotyl begins its development; the cotyledons appear 10 to 12 days later. The pericarp and the seedcoat fall down 6 to 7 days later. Cotyledons are reniform, pedicellated, green, and foliaceous. After they are outside, they continue growing for several days. They remain attached to the seedling for more than 3 months; abscission takes place at the petiole base (Flores 1994h). The eophylls have conduplicate ptyxis; they are geenish brown or reddish brown. The first flux of growth ends 4 to 5 months later and the first group of plagiotropic lateral branches is produced.


2cm
1mm
1cm

Terminalia catappa L.

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COMBRETACEAE (COMBRETUM FAMILY)

Catappa domestica Rumph. (Herbarium Amboinense 1:174-176, t. 68; 1741); *Terminalia badamia* sensu Tul. (Annales des Sciences Naturalles, Botanique, ser. 4, 6: 92; 1856); *Terminalia rubrigemnis* Tul. (Annales des Sciences Naturalles, Botanique, ser. 4, 6: 102; 1856)

Almendro, almendro de playa, badam, Barbados almond, Indian almond, ketapang, talisai, wild almond (Chudnoff 1984, Perrier de la Bathie 1954, Tulasne 1856)

Terminalia catappa is a tropical species that is widely distributed in the Indo-Malayan region, extending to the Philippines; it has been widely planted throughout the Tropics, often becoming naturalized (Chudnoff 1984). It is found primarily along the coastal lands forming part of the littoral woodland community.

The species is a fast-growing, medium-sized, deciduous tree that reaches 12 to 25 m in height and 60 to 70 cm d.b.h. (Perrier de la Bathie 1954). The bole is quite straight, asymmetrical, and frequently grooved in the basal third. The axis is monopodial; the branches arising at the end of each growth flux are sympodial and plagiotropic, forming a pagoda crown (Hallé and others 1978). The bark is thin (0.9 cm), dull, and grayish brown with vertical fissures. Internally, it is yellowish. It has a fibrous texture and a slightly bitter taste. Phyllotaxy is spiral; internode reduction leads to spur shoot formation at the branch end. Leaves are petiolate, simple, exstipulated, coriaceous, obovate or oblanceolate, with entire margin, acuminate apex, and attenuate base. There are numerous abaxial domatia. In some parts of the geographic range, the tree loses its leaves twice a year; they turn yellow and then red as they senesce (Tomlinson 1986). The tree grows in sandy, clay, or poor soils, although it reaches its best growth in sandy soils. The species grows well at elevations of 0 to 1200 m.

The sapwood is pale yellowish in green condition, and the heartwood is darker; in dry conditions the sapwood is yellowish brown, and the heartwood is brownish yellow or reddish. The wood oxidizes rapidly when exposed to air and light. It has straight or interlocked grain, medium to high luster, medium texture; it is odorless and tasteless. The wood is heavy (green weight 1000 to 1020 kg per m^3 with 50 to 61 percent moisture content; basic specific gravity is 0.48 to 0.62). The timber is of good quality and has good physical and mechanical properties (Longwood 1971). Drying is rapid with a moderate amount of warping and little or no checking (Chudnoff 1984). Shrinkage, green to oven-dry, is: radial 4.5 percent, tangential 5.7 percent, volumetric 10.3 percent (Chudnoff 1984). The timber saws and machines easily but torn and fuzzy grain is common in planing, shaping, and turning; it sands to a fairly good surface (Chudnoff 1984). Natural durability varies with origin, but it is classified as perishable. Resistance to fungal attack is moderate, but it is very susceptible to dry-wood termite attack (Chudnoff 1984). Sapwood absorption of preservative oils is obtained using an open-tank treatment (Chudnoff 1984). The timber can be used in general light construction, furniture, cabinetwork, flooring, beams, decorative veneers, parquet, barrels, and railroad ties. *Terminalia catappa* is used primarily as an ornamental, shade, and salt-tolerant street tree, but the leaves provide food for the Tasar silkworm, and the seeds are edible like almonds with similar oils (Hutchinson 1969, Lawrence 1969, Mabberley 1997, Schery 1963). Fruits, roots, and bark are used as a source of myrobalan, a tannin used in blends for calf, goat, and sheepskin tanning (Mabberley 1997, Schery 1963).

Blooming occurs from November through March, with variations at the beginning and conclusion of the flowering period along the geographic range of the species. The tree is andromonoecious and the inflorescences arise from the axil of spur shoot leaves (Tomlinson 1986). Flowers are male or perfect, borne in axillary spikes; male flowers are distal while perfect flowers are proximal. Male flowers lack any conspicuous pistillode; perfect flowers include a well-developed ovary (Tomlinson 1986). Flowers are epigynous and shortly pedicellate. The calyx (in both types) is pentamerous, lobed, gamosepalous, tubular, creamy, whitish, or yellowish. In perfect flowers, it is fused to the androecium and gynoecium in the basal third. The distal free third is cupuliform; calyx lobes are deltoid and pubescent in both surfaces. The androecium has 10 stamens distributed in two whorls; the external whorl alternates with the sepals while the inner verticil is opposite from the sepals. The gynoecium is unilocular, with two anatropous, bitegmic, crassinucellate ovules; placentation is suspended. Fruits ripen from January through April, although regional variations occur. The fruit is short pedicellate and almond shaped, 5 to 7 cm long, with a shallow lateral ridge. The exocarp is shiny and coriaceous; the mesocarp, fleshy and fibrous; and the endocarp, woody. The sea, bats, rodents, monkeys, and some large birds disperse the fruits.

The seed is enclosed by the fibrous endocarp. It is cylindrical-oblanceolate or cylindrical-elliptic and has a long funiculus. The seedcoat is dull and whitish and is formed by the testa and tegmen. The embryo contained in the walnut-like fruit has a good flavor resembling the hazelnut (*Corylus* spp.) (Schery 1963). The period of seed viability is unknown.

Germination is hypogeal and the seedling is cryptocotylar. Under greenhouse and nursery conditions, germination is gradual. The radicle emerges at 65 to 75 days. Seedling survival in the nursery is about 90 percent.

Fruits must be sown in boxes filled with sand, germination beds, or bancales. They require moderate shade and constant moisture. The seedlings must be transplanted to plastic bags before the first eophyll extends. Soil fertilization or application of foliar nutrients increases seedling growth and vigor. The seedlings can be transplanted 8 to 12 months after germination. Seedlings and saplings must be transferred to the field in adobe.

ADDITIONAL INFORMATION

Leaf venation is eucamptodromous. The midrib is thick with a straight course, and projects abaxially; the secondary veins have an acute angle of divergence with respect to the midvein. The leaf is hypostomatic; stomata are anomocytic. The foliar ptyxis is conduplicate; leaf size and shape vary within a given tree or spur shoot. The abaxial surface bears domatia.

Stamen filaments are 2.0 to 2.5 mm long; they are filiform, glabrous, and whitish. The anthers are subglobose, small (0.3 to 0.4 mm long), extrorse, dorsifixed, and yellow; anther dehiscence is longitudinal. Pollen is abundant and liberated in monads. An annular nectariferous disc surrounds the style; its secretion is slightly sugary. The style is thin and glabrous; the stigma is truncate, glandular, hollow, and yellowish.

The mature seed is exospermic and lacks perisperm. The endosperm is nuclear and is absorbed during embryo development. The embryo is conspicuous, oblong, and whitish. It is straight and has contorted, foliar cotyledons. Although the ovary has two ovules, only a single ovule develops, is fertilized, and forms a seed.

After 8 to 9 days, the hypocotyl begins its development, the endocarp valves open, and the cotyledons emerge. Cotyledons are reniform, pedicellate, green, and foliaceous; as soon as they are outside they begin to grow and continue growing for several days. They remain attached to the seedling for more than 3 months; abscission takes place at the petiole base. The first flux of growth ends at 6 months and the first fan of plagiotropic lateral branches is produced.


2cm
2cm

Terminalia oblonga (Ruiz & Pav.) Steud.

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COMBRETACEAE (INDIAN ALMOND FAMILY)

Gimbernatia oblonga Ruiz & Pav. (Flora Peruvianae, et Chilensis Prodromus 274; 1798); *Chuncoa oblonga* (Ruiz & Pav.) Pers. (Syn. Pl. 1: 486; 1805); *Terminalia tarapotensis* van Heurck & Müll.-Arg.(Observationes Botanicae 213; 1871); *Terminalia chiriquensis* Pittier (Contributions from the U.S. National Herbarium 18 [6]: 238; 1917)

Guayaba de montaña, guayabo de monte, guayabo negro, guayabón, huesillo, surá, yacushapana amarilla (Flores 1994i, Hall and Seymour 1978, Record and Hess 1949)

Terminalia oblonga is one of the emergent trees in the canopy of the humid tropical forests. The geographic range of the species extends from Honduras to the Amazon in South America (Brako and Zarucchi 1993, Flores 1994i, Hall and Seymour 1978, Jorgensen and León-Yáñez 1999, Longwood 1971, Macbride 1941, Standley and Williams 1962, Woodson and Schery 1958).

Terminalia oblonga is a large tree, reaching 25 to 45 m in height and 150 cm d.b.h., with a symmetrical bole in the distal two-thirds of its length (Flores 1994i, Standley and Williams 1962). The basal third is asymmetrical, with conspicuous buttresses more than 2 m in height. The axis is monopodial; the branches arising at the end of each growth flux are sympodial and plagiotropic (Hallé and others 1978). The branches are twisted and bend upward more than in *T. amazonia* (J.F. Gmel.) Exell (Flores 1994i). The bark exfoliates large and thin plates. The fallen plates are reddish brown or brown; the new bark is yellowish, almost white, and has a smooth texture. The average thickness is 5 mm (Flores 1994i). Phyllotaxy is spiral; internode reduction leads to spur shoot formation at the branch end. Leaves are petiolated, simple, exstipulated, membranaceous, sometimes chartaceous, oblong, obovate, oblanceolate or wide elliptic, with entire margin, acuminate apex, and attenuate leaf base. They are slightly pubescent, especially abaxially. The leaf is hypostomatic; stomata are anomocytic. The foliar ptyxis is conduplicate; young leaves are reddish brown. Leaf size and shape vary within a given tree or spur shoot. The species grows in well-drained alluvial soils of lowlands and coastal plains and frequently, is a constitutive member of the riparian flora; the temperature range is 24 to 35 °C, and the annual rainfall varies from 1500 to 3500 mm. The elevation range is 20 to 500 m (Flores 1994i). Trees inhabiting nearly dry zones lose their foliage; the production of new leaves is synchronized with blooming (Flores 1994i).

The sapwood is creamy in green condition, and the heartwood is grayish brown; in dry condition, the sapwood is yellowish gray, and the heartwood remains grayishbrown. The wood oxidizes rapidly when exposed to air and light (Flores 1994i). Annual rings are not distinctive. It has straight or slightly undulate grain, medium luster, medium texture, and striped figure; the fresh wood smells unpleasant but is tasteless (Flores 1994i, Llach 1971, Longwood 1971, Picado and others 1983). The wood is heavy or very heavy (green weight 1120 to 1180 kg per m^3, with 50 to 71 percent moisture content). The timber has high quality and good physical and mechanical properties. Volumetric contraction (12.5) is moderate for the wood density; the radial contraction is low (4.8); and the tangential, normal (7.9) (Flores 1994i, Llach 1971, Longwood 1971, Picado and others 1983). Drying is moderately difficult but varies with wood origin. The wood may show splitting, checking, and slight warping. Working properties are medium; finishing of radial planes is difficult. Natural durability varies with origin. Resistance to fungal attack is moderate; however, the wood is susceptible to termites. It is difficult to impregnate and preserve. Many trees with diameters above 60 cm have hollow piths. The timber is used in heavy general construction, interior and exterior construction, cabinetwork, floors, bridge foundations, beams, fences, veneers, parquet, barrels, railroad ties, and ships. It is also suitable for making paper (Peteri's coefficient of flexibility is 76; Runkel factor is 0.82) (Llach 1971, Longwood 1971, Picado and others 1983).

Blooming occurs December through February, with variations at the beginning and end of the flowering period along the geographic range of the species; a minor blooming occurs in August and September. The inflorescences are axillary. They are racemes 5 to 20 cm long, bearing numerous flowers grouped in pseudowhorls. A small bract subtends each flower. Flowers are bisexual, actinomorphic, epigynous, and sweetly scented. The receptacle is cup-shaped. The corolla is absent. The calyx is pentamerous, gamosepalous, tubular, and yellowish; it is fused to the androecium and gynoecium in the basal two-thirds. The distal-free third is cupuliform; calyx lobes are deltoid and pubescent in both surfaces. The androecium has 10 stamens exerted, distributed in two whorls; the external whorl alternates with the sepals while the inner verticil is opposite the sepals. There is an annular nectariferous disc surrounding the style; its secretion is slightly sugary. The gynoecium is unilocular with two anatropous, bitegmic, crassinucellate ovules; placentation is suspended. Pollination seems to be entomophilous with medium-size bees acting as pollinator agents (Bawa and others 1982); however, there is a strong possibility of partial anemophilous pollination (Flores 1994i).

Fruit ripening occurs from January to March and in September and October, although there are regional variations. Most flowers develop a fruit, but many fruits lack seeds. The fruit is a three-winged, pale yellow samara. The two larger wings, with a round or obtuse distal end, extend transversely, while the third is vestigial and carinate. The samara is pubescent, especially in the center. The exocarp is thin and papyraceous; the mesocarp is parenchymatic; and the endocarp, fibrous and woody (Flores 1994i). Fruits are wind-dispersed and because of their aerodynamic design are considered rolling autogyros (Augspurger 1986). Fruit weight is 52 to 56 mg. Fruits average approximately 18,000 per kg. The seed is enclosed in a triangular cavity surrounded by the fibrous endocarp. It is oblanceolate and has a long funiculus. The seedcoat is dull and dark yellow. The percentage of fruits containing seeds ranges from 50 to 60 percent, depending on the entry, and approximately 6 percent of them are not viable.

Fruits collected in stands with several trees have a higher number of viable seeds than those coming from isolated parent trees (Flores 1994i). Fruits collected from the tree have a higher moisture content and sometimes are immature; those lacking seed are lighter (Flores 1994i). Seed-producing trees must be selected from stands and the tree diameters must be more than 70 cm. Samaras must be mature and dry; seeds from immature samaras do not germinate well. Determining the period of seed viability is very difficult due to the high and variable percentage of sterile fruits in different fruit entries and because the seed is enclosed by the samara.

Germination is epigeal and the seedling is phanerocotylar. Under greenhouse and nursery conditions, germination is gradual. The radicle emerges at 50 to 60 days.

Samaras must be sown in boxes filled with sand, germination beds, or bancales. They require moderate shade and constant moisture. Seedling survival in the nursery is about 95 percent, and approximately 12 to 15 percent have a slower growth (Flores 1994i). The seedlings must be transplanted to plastic bags before the first eophyll extends. Plastic bags must be kept under moderate shade for 2 to 3 weeks. Soil fertilization or application of foliar nutrients increases seedling growth and vigor. The seedlings can be transferred to the field 8 to 12 months after germination. Root and leaf pruning before outplanting is recommended. When seedlings are placed in bancales, two root prunings are required: one when the seedling is 20 cm long and another 1 month before transplanting. Seedlings and saplings must be transferred to the field in adobe.

Terminalia oblonga has been planted at a planting distance of 3 by 3 m, sometimes 2 by 2 m. The species does well in monospecific plantations (Flores 1994i). Seedlings and saplings in nurseries and plantations are predated by ants *(Atta cephalotes, Acromyrmex*), which cause shoot damage and may promote shoot branching (Flores 1994i, Nichols and González 1992).

ADDITIONAL INFORMATION

The genus name, given by Linnaeus, refers to the branching pattern and the production of spur shoots. The species name is based on the leaf shape. In Central America, the species has been identified frequently as *T. lucida* Hoffm. ex Mart; nevertheless, the South American species differs from it in fruit morphology.

The leaves have numerous abaxial domatia, surrounded by trichome clusters. The areoles have translucent dots; they correspond to mesophyll idioblasts. Venation is eucamptodromous. The midrib is thick, with a straight course and projects abaxially; the secondary veins have an acute angle of divergence with respect to the midvein. Tertiary veins are transverse and form an angle of 80 to 90° with respect to the midvein; the pattern is distinctive for this species.

Stamen filaments are 2.0 to 2.5 mm long; they are filiform, glabrous, and yellowish. The anthers are subglobose, small (2.2 to 2.5 mm long), extrorse, dorsifixed, and yellow; anther dehiscence is longitudinal. Pollen is abundant and liberated in monads. In the gynoecium, the style is narrow and filiform with gold trichomes; the stigma is truncate, glandular, hollow, and reddish yellow (Flores 1994i).

Testa and tegmen form the seedcoat. The mature seed is exospermic and lacks perisperm. The endosperm is nuclear and is absorbed during embryo development. The embryo is small, oblong, and whitish. It is straight and has contorted foliar cotyledons. Although the ovary has two ovules, only a single ovule develops, is fertilized, and forms a seed.

After 5 to 8 days, the hypocotyl begins its development; cotyledon emergence occurs 9 to 12 days later. The pericarp and the seedcoat fall down 5 to 6 days later. Cotyledons are reniform, green, and foliaceous; after they are outside, they continue growing for several days. They remain attached to the seedling for more than 3 months; abscission takes place at the petiole base (Flores 1994i). The eophylls have conduplicate ptyxis; they are greenish brown or reddish brown. The first flux of growth ends 5 months later, and the first group of plagiotropic lateral branches is produced.


1cm
2cm
2cm

Thespesia grandiflora DC.

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MALVACEAE (MALLOW FAMILY)

Montezuma speciocissima Sessé and Moc., *M. grandiflora* DC., and
Maga grandiflora (DC.) Urban (Francis 1989d)

Maga, maga colorada, purple haiti-haiti, tulipán de Japón (Little and Wadsworth 1964)

Thespesia grandiflora is endemic to Puerto Rico. The original extent of the species on the Island before the advent of humans is unknown, but it was probably common only in the moist limestone region (Francis 1989d). Because of deforestation and disturbance, the species has become common throughout the moist and wet areas of Puerto Rico.

Thespesia grandiflora is an attractive, small to medium-sized tree with dark green foliage and large, dark pink or red flowers. In natural forests, boles of this tree are generally straight, round, and free of limbs for 3 m or more. However, few exceed 20 m in height and 50 cm d.b.h. Open-grown and ornamental trees tend to be short with rounded crowns. The species grows on soils ranging from mildly alkaline to strongly acid, with textures ranging from sandy loams to clays. Natural trees grow best on colluvial lower slopes of limestone hills and the alluvial bottoms between the hills. *Thespesia grandiflora* grows in areas of Puerto Rico with mean annual precipitations ranging from 1250 to 2500 mm and mean annual temperature from 20 to 27 °C.

Thespesia grandiflora is planted as an ornamental in Florida, Hawaii, Honduras, and on several of the Caribbean Islands (Francis 1989d, Little and Wadsworth 1964). The large, trumpet-shaped flowers, dark green, heart-shaped leaves, and moderate size make *T. grandiflora* a very desirable ornamental tree. The species also produces a valuable wood, somewhat similar in appearance and working quality to old growth mahogany (Little and Wadsworth 1964). The wood, which is durable and highly resistant to dry-wood termites (Wolcott 1940), is used for furniture, crafts, and musical instruments.

Open-grown *T. grandiflora* are reported to begin flowering between 5 and 10 years of age (Francis 1989d). Flowering and fruiting proceeds throughout the year except when limited by periods of low rainfall and drought stress. The flowers are 7.5 to 9.0 cm long and 9.0 to 13 cm broad with five overlapping petals. The flowers are borne singly on long petioles from leaf bases. The fruits develop and ripen within a few weeks. The fruit is smooth and green, subglobose, and 3 to 5 cm in diameter. From 1 to 12 brown seeds are embedded within a white, fleshy matrix. *Thespesia grandiflora* depends on fruit bats and birds for dispersal.

The fruits can be clipped from trees with pruning poles. Seeds can also be extracted from uneaten fruits that fall to the ground or picked up from the ground after being dropped by bats or birds, but they are usually scattered. Fruits are ripe when pliable to the touch, but ripening is not indicated by a color change and it is difficult to tell which fruits to pick at a distance. In addition, fruits ripen individually so that only a few fruits are ripe at any one time, and in Puerto Rico most are taken by foraging bats soon after ripening. However, fruits sufficiently developed will ripen a few days after picking. Good seeds have a cinnamon-brown color with a waxy luster and are free of fungal spots. Lighter or darker colors denote immaturity or overmaturity and loss of viability (Marrero 1949). Fresh seed weights of 2,500 per kg and air-dried weights of 3,900 seeds per kg have been reported (Francis 1989d).

Nursery workers normally clean the seeds by hand, a fairly rapid process. Cleaning with macerators may damage the fragile seeds. The seeds of *T. grandiflora* are highly recalcitrant. The folded cotyledons are active and turn green within the seed as germination begins. The seeds begin germinating 5 to 7 days after the fruit ripens (Francis 1989d). Because seeds picked up from the ground may already have the radicle exposed, moist paper towels or other moistened material should be placed in the collection container during transport and the seeds should be sowed as soon as possible. Viability of *T. grandiflora* seeds can be extended to almost 4 months by drying to

62.5-percent moisture and storing at 2 to 4 °C (Marrero 1942).

No pregermination treatments are necessary. Seeds may be sowed in germination trays, beds, or directly in the containers and lightly covered in ordinary potting mix. Marrero (1942) reports 70 to 80 percent of fresh seeds germinate, but that he obtained just 20-percent germination of seeds stored at room temperature for 2 weeks. Francis and Rodríguez (1993) reported 80-percent germination beginning 6 days after sowing. Germination is epigeal.

If seeds are germinated in germination trays or beds, they are transplanted to nursery bags or pots after the first true leaves emerge. *Thespesia grandiflora* seedlings develop rapidly in partial shade, reaching 20 cm in height in 3 months and 40 cm in height in 6 months (Francis 1989d). The seedlings should be moved into full sun a few weeks before outplanting. Seedling stock from 15 to 50 cm can be used to establish plantations. Plantations must be weeded for 1 to 2 years after outplanting and vines must be removed for an additional 1 or 2 years. Trees destined to become ornamentals are often grown in pots until they attain 1 to 2.5 m in height, when they should be planted in deep, well-aerated, and fertile soil. Planting in semicompacted construction fill will result in failure.


2cm

Thespesia populnea (L.) Sol. ex Corrêa

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MALVACEAE (MALLOW FAMILY)

Hibiscus populneus Linn.

Álamo, álamo blanco, algodón de monte, beach maho, bosch-katoen, catalpa, clamor, clemón, cork-tree, cremón, emajagüilla, frescura, grós hahaut, haiti-haiti, jaqueca, John-Bull-tree, macoi, mahault de Londres, maho, mahot bord-de-mer, majagua de Florida, majagüilla, otaheita, palo de jaqueca, palu santu, portiatree, santa maría, seaside mahoe, Spanish cork, tuliptree (Little and Wadsworth 1964)

Fifteen species of *Thespesia* are scattered throughout the tropics (Whitmore 1972). Although the original native range of *Thespesia populnea* is not known precisely, it probably included the coastal tropics of the Old World from the East Coast of Africa through Polynesia (Parrotta 1994). Today, the species has naturalized throughout most of the world's tropical coastal areas.

Thespesia populnea is a small tree with a short crooked bole, furrowed gray bark, and a dense crown of yellow-green, heart-shaped leaves. On dry sandy or rocky coastal sites, it frequently forms shrubby thickets. A 0.6-m annual height growth of young stands on a moist site was reported by Whitesell and Walters (1976). Individual trees on fertile sites may reach 18 m in height and 50 cm d.b.h., but normally trees are much smaller. Although it may grow singly in mixed stands, *T. populnea* is more frequently found in pure patches or making up a high percentage of stems in small stands. Suitable natural habitat includes coastal sands through clays and rocky headlands in areas that receive from 500 to 1600 mm of mean annual precipitation. Dry seasons may last up to 8 months (Parrotta 1994). The species also colonizes salty soils just above mangrove forests. Light frosts are tolerated.

Thespesia populnea is a diploid species with 26 chromosomes (Krishnappa and Geetha 1977). Until recently, *T. populneoides* (Roxb.) Kosteletsky was considered to be a population of *T. populnea* (Fosberg and Sachet 1972); it is distinguished by its dehiscent fruits, long pedicels, a broad sinus at the leaf base, and coppery or bronzed leaves.

Thespesia populnea is an important ornamental tree in coastal areas throughout the tropics and it is planted in upland areas as well. A very hearty species that tolerates calcarious, salty, gravelly, and semicompacted soils and the pollution of metropolitan areas, this small tree is often planted in confined spaces and in groups in seminatural landscape designs. It is also used to reforest disturbed coastal areas and stabilize coastal dunes. The heartwood, which is dark reddish brown to chocolate brown (Record and Hess 1943), has a specific gravity of 0.55 to 0.89 (Chowdhury and Ghosh 1958, Skolmen 1974) and is easily dried, shaped, and finished. The wood sometimes is used to make fine furniture. Because the trees available for harvest are small and wood prices are high, the wood is usually reserved for carving and manufacturing small decorative items. Small stems are cut for fenceposts, and the tree is sometimes cultivated as a living fencepost. *Thespesia populnea* has many applications in herbal medicine. The fibrous bark is used for cordage and basketry in many underdeveloped areas (Parrotta 1994).

Trees as young as 1 or 2 years old may begin flowering. Flowering proceeds from spring through fall or throughout the year in the absence of dry or cool seasons. The pale yellow, 5-cm trumpet-shaped flowers are born laterally on twigs (Little and Wadsworth 1964). The fruits are flattened, five-celled capsules 2.5 to 5 cm in diameter. Within the capsules are several hairy brown seeds about 1 cm long and 0.6 cm broad. The seeds are dispersed by wind and water (Parrotta 1994). A collection of ovendried fruits from Puerto Rico averaged 3.3 g per fruit (Parrotta 1994). A sample of 50 fruits collected in Puerto Rico contained from 1 to 11 seeds per fruit with a mean of 5.7 ± 0.4 seeds per fruit (Parrotta 1994). The fruits turn black when ripe (Parrotta 1994).

Because the fruits remain on the tree for some time after ripening and often remain intact on the ground for weeks to months before disintegrating, seed may be collected almost any time during the year. The fruits are picked from the ground or by hand from low trees. Fruits can be clipped from taller trees with pruning poles. If the fruits are not thoroughly dry, they should be placed in the sun for 1 or more days. Small samples may be easily shelled by hand. Larger samples can be threshed by placing the dry fruits in burlap bags, working them underfoot, and then separating by screening and blowing. Reported fresh (essentially air-dried) seed weights range from 3,500 to 6,700 seeds per kg (Francis and Rodríguez 1993, Parrotta 1994, Rashid 1975, von Carlowitz 1986). Data are lacking on seed storage; however, short-term storage in sealed containers has not been detrimental. Refrigeration in sealed containers is recommended for longer-term storage.

No pregermination treatment is needed (Parrotta 1994). The germination rate of fresh seed has been reported as 65 to 79 percent; it begins about 8 days after sowing (Francis and Rodríguez 1993, Parrotta 1994, Ricardi and others 1977). Germination is epigeal.

Seeds may be sowed and lightly covered in fine sand, well-drained soil, or potting mix. Seeds are normally germinated in germination trays or beds and transplanted into nursery bags or pots after the first true leaves develop. Seedlings develop a long, wiry taproot with numerous fine laterals. They may be outplanted after reaching 15 cm, about 3 months after sowing (Parrotta 1994). Seedlings intended for use as ornamentals are outplanted when 0.5 to 1.5 m in height. Bare-root seedlings are also planted. On fertile sites, continuous protection from weeds is necessary for 2 years or more; on very sandy or poor sites, little weeding may be necessary.


2cm
2cm

Trichanthera gigantea (Bonpl.) Nees

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ACANTHACEAE (ACANTHUS FAMILY)

Ruella gigantea

Aro, cajeto, nacedero, quiebra barriga

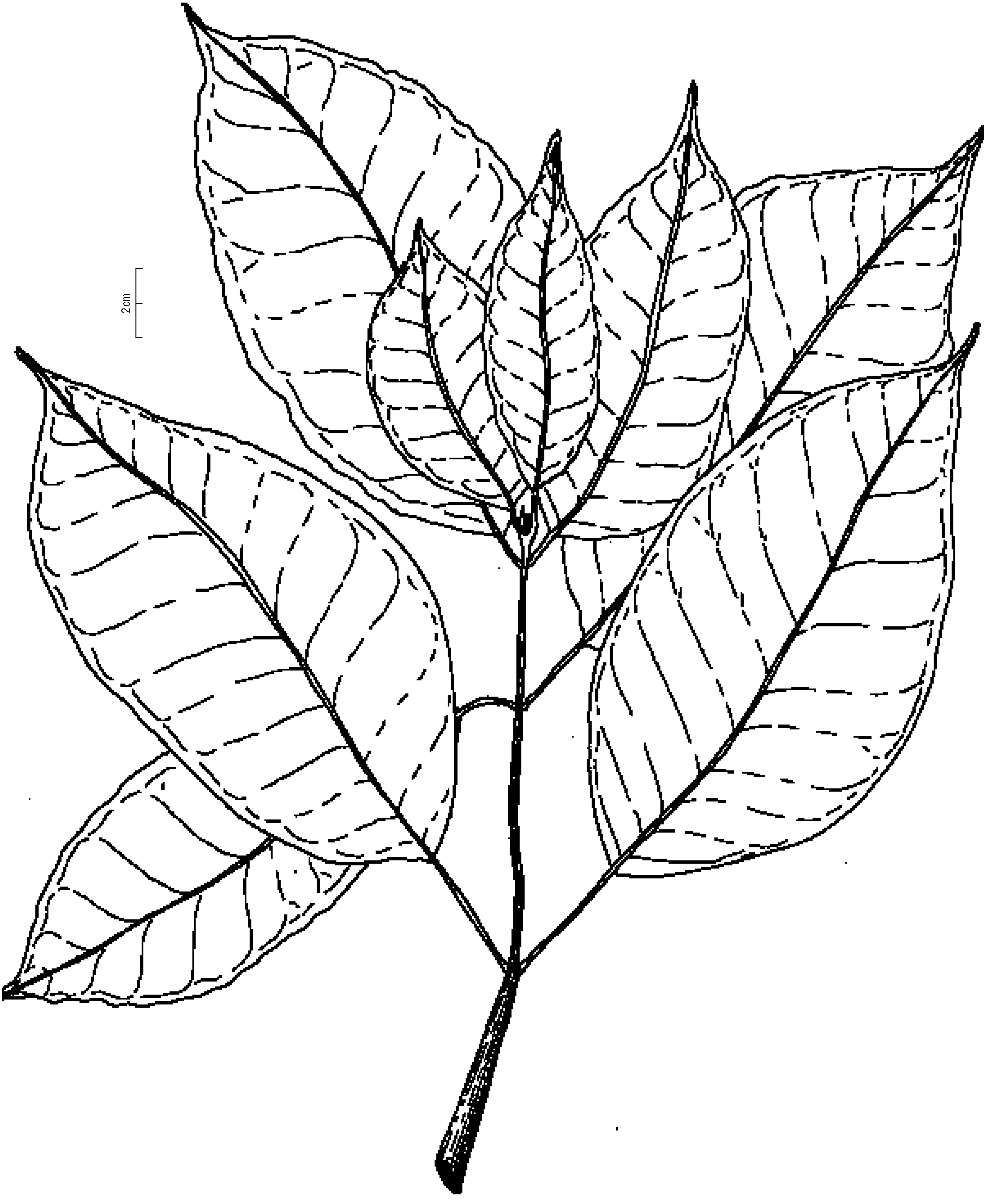
Trichanthera gigantea is a very-fast-growing tree that reaches 8 m in height and 30 cm d.b.h. The trunk has a yellowish-gray bark; branching starts at 2 m. The crown has a pyramidal shape, and the foliage is dark green. The leaves are 14 cm, opposite, and villous, with serrated margins. The tree grows in low-fertility soils with a pH greater than 4.5; loose, loose clayey, or loose sandy textures; and good to slow drainage. It grows at elevations from 600 to 1700 m, with temperatures ranging from 19 to 24 °C and an average annual precipitation of 1400 to 2800 mm. *Trichanthera gigantea* grows in vegetal formations of the Tropical dry forest (bs-T), Tropical wet forest (bh-T), Pre-Mountainous wet forest (bh-PM), and Pre-Mountainous very wet forest (Gomez 1992, Rodriguez 1988).

The yellowish-white wood is not durable in contact with the ground and has a specific weight of 0.7. Parts of the tree are used as medicine and forage for cattle, horses, and pigs. In agroforestry, the trees are used as hedges, protectors of water springs, and shade for coffee. The wood is not used because the tree is too small (Escobar and Rodriguez 1993).

The red flowers are 3 cm, similar to bells, and grouped; fruits are round brown capsules with several seeds. Seeds average 4,000,000 per kg. Purity is 75 to 80 percent, germination is 1 to 2 percent, and seeds germinate in 25 to 35 days (Rodriguez 1988).

Trichanthera gigantea is propagated through seeds or stem cuttings. Seeds are planted in large bags with a capacity of more than 5 kg. The plantules remain in the nursery for 6 months. They are outplanted when they are large enough to compete with the underbrush. The most common method of propagation is stem cutting. Stem cuttings from trees are at least 40 to 50 cm in length and 3 to 5 cm in diameter. Taking the stem cuttings from the lowest part of the branch will reduce dehydration. Stems cut obliquely will more readily grow roots. The point of the stem cutting exposed to the sun should be covered with paraffin or other material that will prevent dehydration. The stem cutting must be planted 15 cm deep immediately after cutting. Stem cuttings, tools, and soil should be disinfected.

The planting site must be totally cleaned, and poor soils should be fertilized with an organic fertilizer. The stem cuttings must be planted during the rainy season. If the species is used as a hedge, large stem cuttings more than 1 m long and more than 2 cm in diameter can be planted 1.5 to 3 m apart. If the plantation is a protein bank, distances of 0.5 by 0.5 m or 1 by 1 m can be used; for shade, a sowing distance of 5 to 10 m is advisable (Corporacion de Defensa de la Meseta de Bucaramanga 1989).


2cm

Triplaris melaenodendron (Bertol.) Standl. & Steyerm.

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POLYGONACEAE (BUCKWHEAT FAMILY)

Triplaris americana L., *Triplaris auriculata, Triplaris macombii, Triplaris macombii* var. *rufescens,*
Velasquezia melaenodendron

Canilla de mula, flor de arco, flor de garrobo, formigueira, gallito, guayabito, guayabo, holy tree,
hormigo, hormiguero, long John, Marv’s tree, mierenhout, mulato, palo mulato,
pálo santo, santa Rosa, tabaco, tabaco de monte, tabacon, tangarana, vara santa, volador
(Chudnoff 1984, Standley and others 1975, Witsberger and others 1982)

Most of the 25 species in this genus grow in South America. *Triplaris melaenodendron* ranges from southern Mexico, through Guatemala, El Salvador, Nicaragua, and Costa Rica, to Panama (Chudnoff 1984, Standley and others 1946). It grows abundantly on the Pacific Coast, sometimes lining the roads, and in the Department of Santa Rosa, Guatemala.

Triplaris melaenodendron is a small to medium-sized tree of about 6 to 12 m in height (sometimes reaching 16 m) with a rounded crown. The branches, which are primarily hollow and septate, are inhabited by savage ants (Gentry 1993). *Triplaris melaenodendron* has large alternate leaves, decidous ocrea, and short petioles. The limb is elliptic to oval-elliptic, about 17 to 35 cm long and 8 to 16 cm wide, pubescent to short-pilose on the underside and glabrous on the upperside. Because the pale gray bark is coarsely mottled, one common name is mulato. The tree grows in thickets or forests at low elevations. It grows well between sea level and 250 m.

The yellowish wood is moderately light and soft but firm, with a straight grain and medium texture. The sapwood is not distinct from the heartwood, which is pale gray brown to pinkish brown and without distinctive odor or taste. The moisture content is about 12 percent. The wood is easy to work and takes a good polish, but it is not resistant to attack by decay fungi and is vulnerable to dry-wood termites. Tests in Venezuela show this wood is difficult to treat with preservatives. The wood is used for furniture components, boxes, crates, fiberboard, particleboard, and interior construction (Aguilar 1966, Chudnoff 1984, Morales 1986, Witsberger and others 1982).

The dioecious flowers appear December through January. Male flowers form lateral and terminal spikes, 2 to 14 cm long, with numerous small greenish flowers, consisting of a pilose calyx 4 mm long with six lobes and nine stamens. Female flowers form lateral and terminal racemes in large panicles. The red or rose-colored flowers consist of a calyx tube about 1.5 cm long; three outer lobulated segments, up to 3 cm long; three free, small, and narrow inner segments; and a triangled superior ovary that contains only one ovule. Flowers lack petals (Heywood 1993). Fruits appear from February through July (Witsberger and others 1982). The fruit is a triangled nut surrounded by a peristent calyx about 4 cm long (Maas and others 1988). The color of the fruit is reddish brown; the calyx tube is enlarged, and the three lobes act as wings for dispersion by wind.

Triplaris melaenodenron fruits [nuts, achenes (Laurence 1951), or samaras (Gentry 1993)] are very light, and 50 seeds (nuts) weigh about 3.2 g. Because one raceme holds about 50 fruits, one tree may bear several hundred.

Because statistics on germination are limited, researchers at the Instituto de Investigaciones, Universidad del Valle de Guatemala initiated a preliminary study. This study investigates possible methods of inducing germination and subsequent germination rates. A summary of the methods and initial results follows. In three experiments that used no germination pretreatments, temperatures were maintained at 20 to 21 °C. In the first experiment, seeds (nuts) were planted 1 cm deep in rotted, organic material. One seed germinated in 10 days, and cotyledons appeared 3 days later. In the second experiment, 10 seeds were placed on humid filter paper in a petri dish. Nine seeds geminated within 17 days, which represents a 90 percent germination rate. In the third experiment, 10 seeds were planted in compact soil; 5 seeds germinated and cotyledons appeared within 18 days.


2 cm

Ulmus mexicana (Liebm.) Planch.

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ULMACEAE (ELM FAMILY)

Chaetopetelea mexican L. (Carpio 1992, Pennington and Sarukhan 1968)

Cenizo, chuchum, cuerillo, ilite, itza, mezcal, nuculpat, olmo, palo de baqueta, patalillo, pepelote chaperno, sacpacche, sacpucte, tiacaciahuitt, tirra o ira blanco, tzapasnaca, zempoalehuati (Niembro 1986, Pennington and Sarukhan 1968)

Ulmus mexicana grows in wet forests and on very wet mountains and premountains from Mexico, through Central America, to Panama (Niembro 1986, Pennington and Sarukhan 1968).

Ulmus mexicana is a medium-sized tree with a straight, cylindrical trunk and buttress. The tree usually grows to 20 to 40 m in height; however, in Mexico, it can reach 84 m in height and 1.5 to 2.5 m d.b.h. (Niembro 1986). The species grows in volvanic, calcareous, and metamorphic soils. It may grow on slopes between 15 and 60° in well-drained and rocky soils. *Ulmus mexicana* grows at elevations of 800 to 2200 m in zones where annual precipitation is 1900 to 3800 mm and median temperatures are 16 to 20 °C (Burger 1970, Standley 1938).

Considered a timber tree, the wood is hard and heavy (specific gravity 0.55). The sapwood and heartwood are clearly defined and growth rings are visible after drying. The wood is difficult to dry and twists and collapses during the process. It is easy to work and preserve and has excellent natural durability. The wood's silica content of 0.35 can damage tools (Carpio 1992, Ritcher 1971). The wood is used for farming tools, floors, railroad ties, wharfs, cupboards, interior decorations, furniture, tool handles, wood, and coal (Carpio 1992, Moreira and others 1992). Cattle eat the branches and foliage (Niembro 1986). *Ulmus mexicano* is planted as a shade and ornamental tree.

The tree flowers November through January. Each raceme contains nine inflorescences, and every inflorescence has 40 flowers. Every umbel is formed by four flowers with a reddish-gray calyx. Its perianth is dark green and 10.2 cm long. The fruits (samara) are 0.89 cm long and 0.23 cm wide and have numerous trichomes. The seeds are beige. Seed production is abundant and seed predators have not been observed. Seeds are dispersed by the wind; however, strong winds have resulted in the loss of whole harvests (Arnáez and Moreira 1992, Moreira and others 1992). Natural regeneration is poor (Hartshorn and Poveda 1983).

Green or yellowish-brown fruits are collected February through April. Collectors climb the tree and use an extension pruner to remove the fruit. In an alternative method, a rope is thrown over a branch and the branch is shaken, releasing the fruits which are collected on a blanket placed under the tree. The seeds can be separated manually or dried in the sun, and then shaken into a sack to separate them from the fruits. Seeds average 727 per kg. They should be planted immediately. When seeds are stored at 5 °C, viability can be lost quickly (Moreira and others 1992).

This species does not require pregermination treatment; however, soaking seeds in water at 22 °C for 24 hours improves germination, which is 90 percent 12 days after planting. The planting mix should be a substrate of 50 percent loose soil and 50 percent previously sterilized sand (Moreira and others 1992).

Four weeks after sowing, seedlings should be transplanted into plastic bags and placed in the shade. Seedlings are hardened at 3 months and growth then accelerates. Weed control and protection from the wind and sun improve plant development. Incidences of plagues and diseases have not been detected (Moreira and others 1992).


2 cm

Virola koschnyi Warb.

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MYRISTICACEAE (NUTMEG FAMILY)

Virola merendonis Pittier (Contributions from the US National Herbarium 20: 453; 1922)

Banak, bogabani, bogamaní, cebo, cedrillo, cedro bastardo, drago, fruta dorada, miguelarillo, mollejo, sangre, sangre drago, tabeque, wild nutmeg (Flores 1992c, Longwood 1971)

Central America, including Belize, is the natural range of *Virola koschnyi* (Duke 1962a, 1962b; Standley and Steyermark 1946). The tree is common along the Atlantic and Pacific lowlands and is an element of the upper canopy in the lowland moist and wet tropical forests. It is also frequent in primary and secondary forests.

Virola koschnyi is a tree that reaches 30 to 45 m in height and 1.0 to 1.5 m d.b.h. The bole is straight and cylindrical in the distal two-thirds; the basal third has heavy buttresses of 1.0 to 3.0 m. The branch system extends horizontally and forms an extended flat crown over the strong monopodial axis (Flores 1992c). The bark is reddish or brownish red, with a moderate or rough texture and small vertical fissures. The inner part is smooth and spongy and contains sour, watery, yellow-red latex. The exudate acquires a brownish red color. The average bark thickness is 1.0 to 1.3 cm (Flores 1992c). The leaves are simple, petiolated, alternate, exstipulated, coriaceous, obovate or lanceolate shaped, with a symmetrical or attenuate base, cuspidate or acuminate apex, entire margin, and pinnate brochidodromous venation. It reaches the best growth in zones with alluvial or sandy soils, where it forms monospecific stands; however, it can be found growing in clay soils, poor in litter, acidic (pH = 5.0 to 5.7), with high levels of iron and aluminum and a low content of primary elements such as phosphorous and potassium (Chávez and others 1991, Flores 1992c). The tree grows where temperatures range from 24 to 35 °C and the annual rainfall is 3500 to 6000 mm. The elevation range of the species if 10 to 1200 m, with the highest density found below 500 m. It inhabits the lower part of hills and the edges of rivers and ravines.

The transition from sapwood to heartwood is gradual. The sapwood is clear yellowish gray in green condition, and the heartwood is grayish orange; in dry condition, the heartwood is light and golden brown, grayish orange or grayish red. It resembles some of the light-colored mahoganies (Longwood 1971). Growth rings are seen easily as narrow, regular, dark bands. The wood has moderate texture, homogeneous and uniform, straight grain, low luster, and attractive figure due to the combination of the silver jasper with the dark-colored rays. The green wood is slightly aromatic and tasteless (Flores 1992c). It is moderately light (green weight 725 to 780 kg per m^3; with 77 to 102 percent moisture content; basic specific gravity is 0.44) (Herrera and Morales 1993, Llach 1971, Longwood 1971). The wood has good dimensional stability; air-drying is fast; it is easy to saw and has excellent brushing properties. It does not present defects when worked by hand or by machine. The wood has low resistance to fungal and termite attacks, as well as attacks from other insects; however, it is easy to impregnate and preservative penetration is fast, complete, and uniform. After cutting, it cannot remain on the ground for long periods because it is attacked severely by fungi (*Polyporus, Hexagonia, Pignoporus, Xylaria, Candelaria, Daldinia, Trametes*) (Flores 1992c). The wood is used primarily in plywood; however, it can be used also in boards, panels, cabinetwork, furniture, poles, boxes, matches, and ship ornaments (Flores 1992c, Llach 1971, Longwood 1971). According to Peteri's coefficient of elasticity and the Runkel factor, the wood corresponds to group II and is suitable for the production of pulp for paper (Van der Slooten 1971). The South American Indians were aware of the hallucinating properties of the resins obtained from the bark, the fruit, and the leaves of different species of *Virola*. Diverse Indian tribes have used these resins and extracts in their rituals and ceremonies for several centuries (Flores 1992c, Schultes and Hoffman 1983, Schultes and Raffauf 1990).

The trees bloom from September to November, although they frequently bear flowers in December. The trees bloom intensively every 2 years. Anthesis occurs in the early morning and pollination is entomophilous. Flowers are unisexual, actinomorphic, small, pedicellated, and clustered in short axillary panicles. Fruit development lasts 6 months. Fruit ripening occurs primarily in February and March, although there is a smaller crop in June. Fruits are fleshy, bivalve, subglobose or elliptic, dehiscent, 22 to 30 mm wide, and 30 to 35 mm long. There are variations in fruit size among different trees growing in the same area as well as on the same tree. Most seed dispersal is carried out by birds and mammals; gravity causes some fruits to fall. Some tropical fish disperse the fruits that fall into rivers (Flores 1992c, Howe and Vande Kerckhove 1980). Seeds are ovate, 15 to 25 mm long by 14 to 20 mm wide, surrounded by a laciniate aril, exostomic, funicular in origin, and reddish orange.

Seed weight varies from 1.6 to 3.4 g, and seeds average 400 to 600 per kg, depending on size and moisture content (Flores 1992c). Seed behavior is recalcitrant. Germination is 80 to 85 percent, and seed viability lasts 1 to 12 days. In fresh seeds, the moisture content is 26 to 28 percent. Seed viability declines when moisture content is reduced by more than 20 percent. Germination is epigeal and seedlings are cryptocotylar (Flores and Rivera 1989a). Radicle protrusion occurs in 11 to 14 days (Flores 1992c).

Under natural conditions, 95 percent of seedlings die in the first 12 weeks due to insect and mammal predation. Seedlings are shade tolerant but demonstrate a vigorous growth in forest clearings. Seedling growth is slow the first 4 years and then increases. Six-month-old seedlings have an average height of 50 cm; 6-year-old saplings have an average height of 10 to 11 m and a diameter of 13 to 14 cm (Chávez and others 1991, Flores 1992c).

Fresh seeds without an aril must be sown in sand beds or plastic bags filled with substrate. Production in bags takes about 5 months. The species can be used in monospecific plantations or mixed with other species. The planting distance commonly used is 3 by 3 m. The site must be cleaned every 4 months during the first year after seedlings are transplanted. Soil fertilization with nitrogen-phosphorous-potassium (10-30-10; 50 g per tree) improves growth and sapling vigor (Flores 1992c).

ADDITIONAL INFORMATION

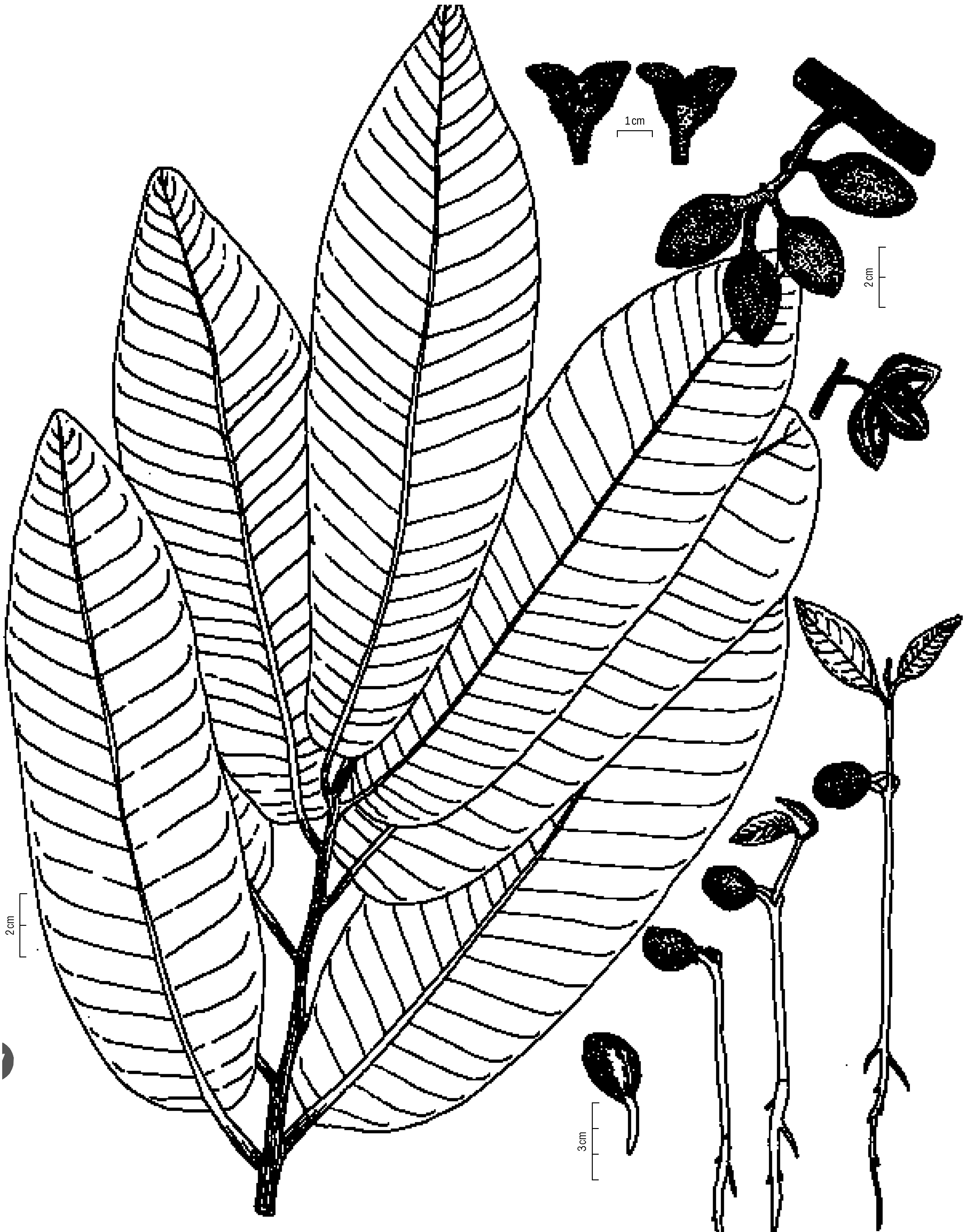
The genus name derives from the Latin *viriola* (bracelet), in reference to the aril surrounding the seed.

The midvein is thick, straight, secondary veins are parallel among them and uniformly spaced, each 1.0 to 1.1 cm; the angle of divergence with respect to the midvein is moderate and uniform. Tertiary veins are simple and transverse. Petioles are adaxially grooved. Young leaves and twigs are pubescenct and ferruginous; hairs are of the candelabrum type. The leaves are hypostomatic; stomata are of the paracytic (rubiaceous) type.

The panicles have membranaceous, deciduous bracts, 4 to 5 mm long. Floral perianth is reduced; calyx is trimerous, campanualte, tepaloid, gamosepalous, yellowish, and 2 to 3 mm long; sepals are crenate, with ciliate margin, and adaxially strigose. Staminate inflorescences have several flowers; each flower has three monadelphous, syngenesious stamens 2.0 to 2.5 mm long; anthers are elliptic and basifixed, with longitudinal dehiscence. Pistillate inflorescences have three to seven flowers; female flowers are hypogynous and monocarpic; the unilocular gynoecium encloses a single ovule; the ovule is anatropous, bitegmic, crassinucellated, and nearly sessile. Placentation is pseudobasal (Flores 1992c).

Fruit exocarp is coriaceous and brown-ferruginous, with stellate trichomes; mesocarp-endocarp is whitish, fleshy, with essential oils strongly aromatic and irritating. These oils are formed by benzofuranoid neolignans (Lemus and Castro 1989). The epidermal tissue surrounding the locule is shiny and irregular due to the impression left by the seed aril.

Seedcoat is formed by a hard testa and a ruminate tegmen. The exotesta is creamy or light brown, soft, and vascularized; the mesotesta is black, hard, lignified, and highly vascularized. The endotesta is sclerenchymatous and lignified. The tegmen is fleshy, massive, highly vascularized, and ruminated penetrating the endosperm. It dehydrates and thins with fruit ripening, acquiring a papiraceous texture (Flores 1992c). The endosperm is white, ruminated, massive, and oily. It is nuclear in the immature seed and cellular in the mature seed. The seed lacks perisperm. The embryo is straight, basal, capitate, and minute (1.0 to 3.0 mm long), with vestigial and divergent cotyledons. They develop and become haustorial during germination (Flores 1992c).


1cm
2cm
2cm
3cm

Vochysia ferruginea Mart.

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Deutsche Gesellschaft für Technische Zusammenarbeit -
Cooperación en los Sectores Forestal y Maderero, Costa Rica, respectively

VOCHYSIACEAE (VOCHYSIA FAMILY)

Cucullaria ferruginea (Mart.) Spreng. 1987 and *Vochysia tomentosa* Seem. 1852 (Flores 1993a)

Areno colorado, barbachele, botarrama, cedro rama, chancho colorado, dormilón, flor de mayo, laguno, malagueto, mayo, mayo colorado, mecri, orcano, palo de mayo rosado, palo malín, palo santo, pegle, quaruba, quillu-sisa, saladillo, sorogá, tecla, yumeri, zopilote

In Central America *Vochysia ferruginea* grows in Nicaragua, Costa Rica, and Panama. In South America its distribution ranges from Colombia and Venezuela to Ecuador, Peru, Brazil, and the Guayanas (Whitmore and Hartshorn 1969). Other species frequently growing in association with *V. ferruginea* are *Laetia procera* (Poepp.) Eichler., *Goethalsia meiantha* (Donn. Sm.) Burret, *Pentaclethra macroloba* (Willd.) Kuntze, and *Simarouba amara* Aubl. (Manta 1988).

Vochysia ferruginea is a fast-growing, medium-to-tall tree that reaches 20 to 34 m in height and 40 to 80 cm d.b.h. The tree has a clear trunk up to one-half its total height and a dense, wide crown formed by ascendant branches. Growth rates in plantations in Costa Rica range from 2.7 cm to 4.8 cm d.b.h. per year and from 1.8 m to 3.2 m in height per year during the first 3 years (Rodríguez 1997). It grows well on poor, acidic but well-drained soils. It grows naturally in upper slope soils and on well-drained ridges but adapts to other conditions. In its natural habitat, *V. ferruginea* grows in humid lowland forests with annual rainfalls ranging from 2500 to 5000 mm and temperatures between 24 and 30 °C. Growing at elevations between sea level and 1500 m, the tree is common in the medium strata of the primary rainforest and is frequently found in secondary forests (Finegan and Sabogal 1988). It also grows on abandoned pastures and invades forest clearings. Natural regeneration of the species is abundant, often resulting in nearly pure stands. *Vochysia ferruginea* belongs to the group of fast-growing species that establish themselves under the forest canopy but require gaps in the canopy for their development (Manta 1988).

The wood is relatively light, with a density of 0.33 to 0.42 g per cm^3 and a medium specific gravity of 0.37. It has an attractive light brown color with beige to rose-colored veining and is easy to work with. The wood dries easily and relatively fast and is moderately resistant to insects and fungi (Instituto Nicaraguense de Recursos Naturales y del Ambiente 1992). It is used for boxes, furniture, boards, panels, veneer, window frames, and toys and in cabinet making (Carpio 1992).

In the northern region of Costa Rica, *V. ferruginea* flowers in May and June (Arnáez and Moreira 1995) and in the southern region between March and May. Occasionally, flowering is observed in September and October (Asociación Costarricense para el Estudio de las Especies Forestales Nativas 1994). The inflorescences are narrow, densely pubescent, axillar or terminal panicles and are composed of numerous showy, dark yellow, zygomorphic flowers. The obovate or oblong fruits are capsules 2 to 4 cm long that consist of three compartments, one for each seed. However, the fruits usually contain only two seeds; the third compartment is either empty or the seed is only partially developed. The one-winged seeds are laterally compressed, 2 to 3 cm long, and brown. They are surrounded by a membranous testa and contain no endosperm. Seed sizes vary greatly among individual trees (Müller 1997).

In the northern region of Costa Rica, fruits are collected in the months of September and October. Fruiting varies widely among individual trees and among years. The ripe capsules open while still on the tree. Therefore, they must be collected as soon as the seams between the three compartments turn visibly brown. The fruit panicles are cut from the ends of the branches with telescopic pruning shears.

After collection, the fruits are dried on screens in well-ventilated, open areas with no direct sunlight. After 1 to 3 days, the capsules open and the seeds can be extracted manually or by shaking the screens (Rodríguez 1996). Because all fruits on a tree do not open simultaneously, about 50 percent of the collected fruits do not open and must be discarded (Müller 1997). In northern Costa Rica, the number of fruits per kg averages 831 and an average of 748 seeds can be extracted from each kg of fruits. The seeds contain an average of 3.7 percent impurities, rudimentary seeds, and wings. The extra wings (1.7 percent on the average) stick to the slightly fuzzy wings of the intact seeds and cannot be separated by seed blowers or screens (Müller 1997). In northern Costa Rica, seeds average 32,130 per kg. The average 1,000-seed weight is 32 g, and the moisture content of fresh seeds is 25 percent.

Seeds should be stored without drying at 15 °C for no longer than 3 months. Under natural conditions, seeds lose their viability in less than 1 month (Rodríguez 1996). They can be dried to 4 percent moisture content without losing viability but remain sensitive to temperatures below 10 °C. After 1 month of storage at 7 percent moisture content, the germination percentage was still high (70 to 80 percent); however, it dropped drastically after 3 months of storage (Müller, 1997). Storage beyond 3 months does not seem to be possible because seeds lose almost all viability.

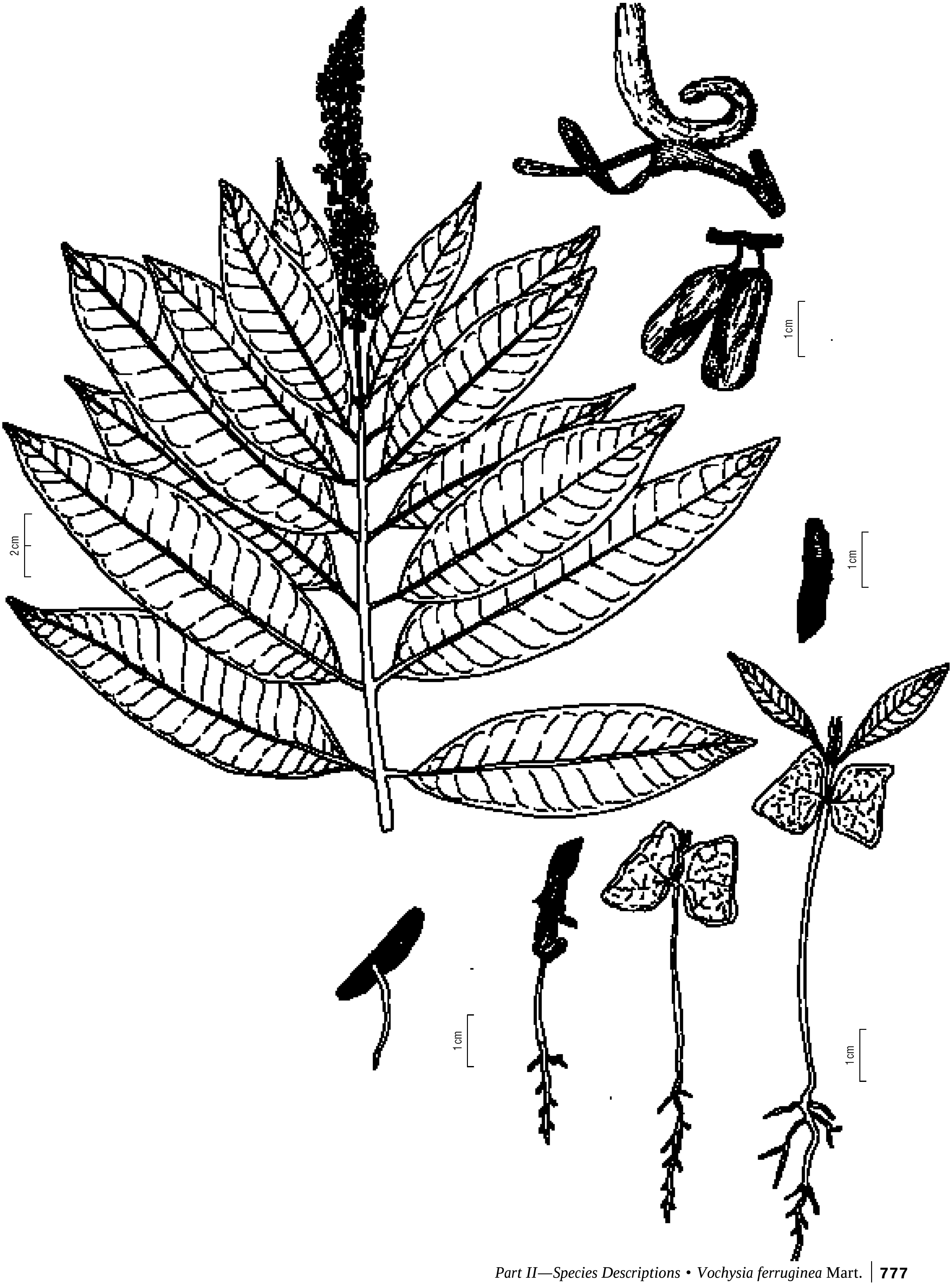
Seeds do not require pretreatment to improve germination (Rodríguez 1996). Under laboratory conditions and sowed flat on top of sterilized sand, they begin to germinate after 4 or 5 days. The germination rate is highest on the seventh day, and after approximately 16 to 18 days, germination is complete. The average germination percentage under these conditions is 97 percent, and often reaches 100 percent (based on germination tests with 4 x 50 seeds, in germination chambers with 12 hours light at 29 °C and 12 hours darkness at 24 °C) (Müller 1997).

In the nursery, seeds of *V. ferruginea* are usually sowed in germination beds, using a mix of sand and soil, which facilitates subsequent transplanting. To control plant density, seeds should be sowed individually in a horizontal position. They are then slightly covered with the substrate. The seedlings are transplanted when the first two real leaves develop. Most nurseries produce seedlings in plastic bags, which are ready for outplanting after 4 to 5 months (Rodríguez 1997). Experiments with stump planting (in Costa Rica: pseudoestacas) have not been successful (Ulate 1996).

ADDITIONAL INFORMATION

Depredation of the unripe fruits by parrots is a serious problem in Costa Rica. It often results in significant losses because parrots can destroy the seed crop of a tree within a few hours.

According to chemical analysis carried out by the Universidad Nacional and the Universidad de Costa Rica, the seeds contain 34.4 percent lipids, 9.9 percent proteins, and 2.4 percent starch. Similar results were obtained elsewhere (Flores 1993a).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Vochysia guatemalensis Donn. Sm.

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VOCHYSIACEAE (VOCHYSIA FAMILY)

Vochysia hondurensis Sprague, *V. guatemalensis* Standl., *V. hondurensis* Standl.

Barba chele, chanco blanco, corosillo, emeri, emery, flor de mayo, ira de agua, maca blanca, magnolia, mayo blanco, mecri, palo bayo, palo de agua, palo de chancho, palo de tecolote, robanchab, ruanchap, sangrillo, san juan, san juan blanco, san juan peludo, san juanillo, san pedrano, sayuc, sebo

Vochysia guatemalensis ranges naturally from Veracruz, Mexico, to Panama. The trees are frequently found in monospecific stands or in patches with *V. ferruginea* Mart. and *V. allenii* Standl. & L.O. Williams. The species has been associated with secondary vegetation (Flores 1993b), but in Costa Rica it grows in primary forests.

Vochysia guatemalensis is a fast-growing tree that can reach 40 m in height and 0.70 to 1 m d.b.h. It has a straight, smooth, cylindrical trunk without branches in the basal two-thirds and without buttresses. The gray bark is slightly scaly, and the crown is very dense with a round or depressed shape. During the dry season the tree is partially defoliated and smaller branches are pruned naturally. Leaves are simple, petiolated, stipulated, coriaceous, and four-whorled (sometimes three-whorled or opposite or decussate on branches producing inflorescences); the petiole is slender and canaliculate. The blade is obovate, symmetrical, with entire margin, obtuse to rounded apex, decurrent base and pinnate venation, with a strong dimensional variation that fluctuates between 9 to 15 cm long and 4 to 5 cm wide. *Vochysia guatemalensis* grows well in clay, acidic (pH 5.0 to 6.0) soils with a high concentration of iron and aluminum. The species grows from the lowlands to 1100 m in the humid and very humid forests of the coastal plains. Temperature varies from 24 to 30 °C; and annual rainfall, from 3000 to 5000 mm.

The wood of *V. guatemalensis* is light (specific gravity 0.35) but strong and has adequate dimensional stability and a moderate drying rate. It dries well and without defects. The wood is easy to machine and cut but develops a slight scrolling of the finish when brushed. The silica content is very high and affects the saws and cutting tools. The wood is very resistant to fungal decay or insect attack but rots easily if exposed to severe weather. If it lies on the ground, the wood decays rapidly. However, this wood is easy to impregnate with preservatives, reaching acceptable or complete penetration. The wood is used for boxes, cabinetwork, and pulp for papermaking. In Belize, the wood is exported to the United States where it is used to make veneer. *Vochysia guatemalensis* is also used to build canoes in the region of Izabal Lake, Guatemala (Flores 1993b).

Vochysia guatemalensis flowers March through June, with additional flowering in October and November and sometimes in February. The trees begin to flower and fruit at the age of 12 to 13 years. The yellow flowers are clustered in terminal or axillary panicles 10 to 20 cm in length with composite ramifications; they are hermaphrodite, zygomorphic, and fragrant. The yellow-brown fruit is a loculicidal, thick, obovate or oblong capsule, 4.8 to 5.8 cm in length, deeply trisulcate, angulose, and verrucose. The capsule is trilocular and contains two seeds per locule. Fruits ripen August through October, but a small crop of fruits ripen in March. The seeds are laterally compressed, winged, and anemochorous.

The fruits should be collected before dehiscence directly from the tree from seed-producing trees with a d.b.h. of 50 cm or more. They can be stored in the shade until they open, and the seeds can be removed manually. Seed abortion is uncommon and approximately 10 percent of the seeds are nonviable. In Costa Rica, fresh seeds (45 to 55 percent moisture) average 3,500 to 4,500 per kg, and dry seeds (8 to 10 percent moisture) average 7,000 to 8,000 per kg (Corea 1994). Viability lasts from 2 to 3 months if seeds are stored at 24 to 26 °C with good aeration. If the moisture content is reduced to 25 percent, seeds can maintain high viability (75 percent) for 4 to 6 months (Flores 1993b). When seeds are stored for 1 month at a low temperature (3 °C) and a high moisture content (32 percent) viability drops rapidly (to 9 percent).

Seeds do not require pregermination treatments and a germination of 85 to 90 percent is obtained under greenhouse conditions. Germination is epigeal and the seedling is phanerocotylar. Under natural conditions, germination is rapid and begins in 8 to 9 days. Nevertheless, most seedlings die in the following month, primarily from ant predation (*Atta* spp.) but also from cricket and grasshopper attacks.

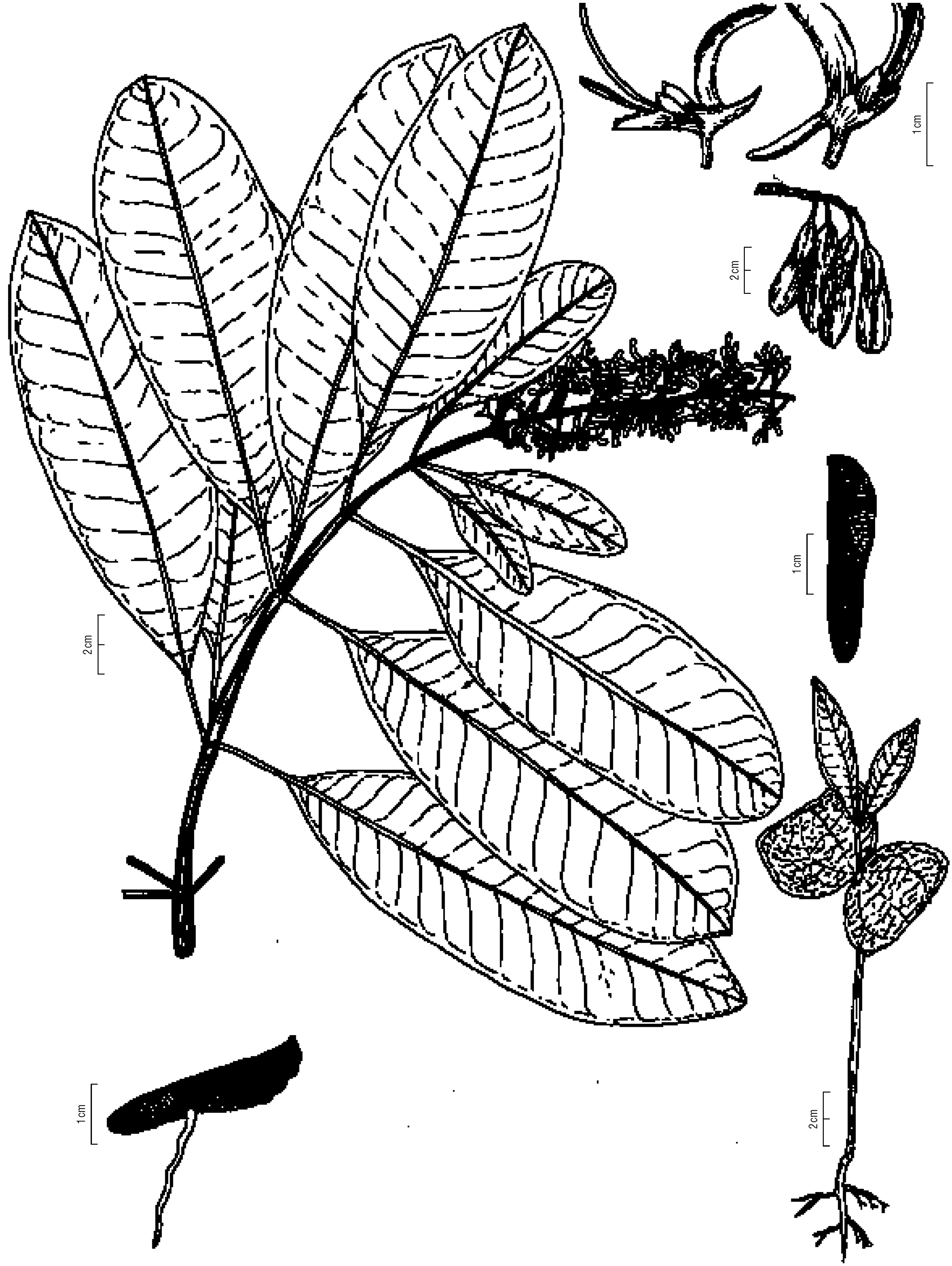
The seeds are planted in boxes full of damp sand. After germination, seedlings should be fertilized (soil or foliar fertilization) because they have high nutritional requirements. Seedlings must be transferred to bags before eophylls develop to reduce leaf withering. At 6 to 7 months the seedlings should be outplanted. Delay should be avoided because the roots grow quickly.

ADDITIONAL INFORMATION

The species is autocompatible and seems to be autogamous, but some nectarivorous insects extract nectar from the spur and pollinate some of the flowers. Many young fruits are eaten by birds and mammals, substantially reducing seed production.

Propagation by pseudografting twigs and naked root seedlings has not been successful (Flores 1993b). However, research continues and Corea (1994) believes using juvenile succulent cuttings for rooting will prove successful.

Chaverri and others (1997) found in a 5-year-old plantation of *V. guatemalensis* in Tabarcia, Costa Rica (premontane moist forest) that almost all of the trees had some insect damage, but in 80 percent the severity was less than 20 percent. The majority of the caterpillars were captured on young leaves, and the larvae were classified as belonging to eight species. Associated with them, six species of parasitoids or hyperparasitoids were detected.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Zanthoxylum kellermanii P. Wilson

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RUTACEAE (RUE FAMILY)

Zanthoxylum mayanum Standl., *Z. panamense* P. Wilson

Acabu, alcabu, arcabu, lagartillo, lagarto, prickly holly, rabo de lagarto, tachuelillo

Zanthoxylum kellermanii grows from southern Mexico to Colombia and Venezuela.

Zanthoxylum kellermanii is a fast-growing tree that reaches 15 to 30 m in height and up to 80 cm d.b.h. The trunk is straight and cylindrical. The brown-gray bark has few suberized lenticels and is armed with vertically flattened prickles. The crown is rounded with ascending branches. The branchlets are strigilate to glabrate, and sometimes armed with small, sharp prickles. Leaves are alternate, without stipules, odd- or rarely even-pinnate, and 17.5 cm long. Petiole and rachis are occasionally armed with yellowish prickles, caniculate above, and minutely puberulent to strigose or glabrous. Leaflets are 6 to 17 cm long, opposite or subopposite, obovate or elliptic to oblong, abruptly acuminate or rounded apically, cuneate and inequilateral basally, the margin entire to obscurely crenulate, more or less revolute, subcoriaceous, lustrous above and paler beneath, and minutely puberulent or strigose to glabrous. Leaflets occasionally have one or more sharp yellowish prickles beneath on the midrib; they may be subsessile or have a petiolule up to 7 mm long. The blade is pellucid and punctate throughout, with punctations of two sizes. The species grows in a wide range of soil types but is better adapted to those with good drainage. In Mexico, the tree grows in deep lateritic soils with good drainage (Pennington and Sarukhan 1968). The species is found in the wet lowlands at elevations of 50 to 500 m, annual rainfall of 3000 to 5000 mm, and average temperature of 23 to 26 °C.

Zanthoxylum kellermanii may be closely related to *Z. mayanum* (Pennington and Sarukhan 1968). Moreover, this species may not be specifically distinct from *Z. panamense* (Porter and Elias 1979), a species of the monsoon forest and evergreen seasonal forests found primarily on the Caribbean side of the Continental Divide. In this description, *Z. mayanum* and *Z. panamense* are synonyms for *Z. kellermanii*; nevertheless, further field and herbarium studies will provide a more precise answer to this taxonomic question.

The rather hard and moderately heavy (specific gravity 0.39) yellow wood is used for fine cabinetwork because it has a very attractive jasper (Pennington and Sarukhan 1968). The wood has also been used in the construction of houses in rural Mexico.

Zanthoxylum kellermanii flowers in April and June and August through October (Porter and Elias 1979). Staminate panicles are axillary, crowded subterminally, many-branched, and 25 cm long with green-white flowers. Carpellate panicles are terminal, branched, 18 to 14 cm long, with puberulent or strigose branches and green female flowers with a three-lobed, globose ovary. Brown to dark red, subglobose fruits have one to four follicles and are punctate glandular, strigilate, and 3 to 6 mm in diameter. Seeds are subglobose, black, lustrous, and minutely pitted. The tree fruits in April, May, July through September, November, and December (Porter and Elias 1979). The fruits can be collected December through January, and good crops have been observed every 2 years (Segundo Encuentro Regional Sobre Especies Forestales Nativas de la Zona Norte y Atlantica de Costa Rica 1994).

Fruits are collected by hand from the ground or the tree. Fruits are laid on blankets in the shade to promote fruit dehiscence. Once the seeds have accumulated on the blankets, the empty fruits are gathered by hand and the seeds are ready for planting in nursery banks. Fruits from *Z. kellermanii* collected from the ground during the months of March and April produce an average yield of 21,600 seeds per kg with a moisture content of 53 percent.

Germination is epigeous and generally occurs 35 to 90 days after planting with a germination rate of 47 percent (Nichols and Gonzalez 1991a, 1991b). When seeds are washed in a soap solution, which apparently eliminates an oily film that covers the seed, germination is 90 to 100 percent (Rodríquez 1996b). However, germination percentage also appears to vary by the provenance and the year of collection, even in the same individual tree. After pretreatment, seeds planted in good-textured soil (silty sand) germinate in 45 to 90 days. River sand can also be used as the germination substrate.

After 90 days the seedlings are transferred to plastic bags filled with a sandy-clay soil and placed in the shade for 15 to 30 days. Seedlings can be outplanted after 6 months in the nursery.

Three species of insects, *Achyloides bursirus* (Lep., Hesperiidae), *Atta cephalotes* (Hym., Formicidae), and *Papilio anchisidiades* (Lep., Papilionidae) attack the foliage of *Z. kellermanii* (Arguedas and others 1993).


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SUPPLEMENTAL SPECIES DRAWINGS

Each species was planned to have both a comprehensive description and botanical illustrations. However, some species were not described as planned while their details were drawn by the artist. These species are included in this section for reference by botanical drawings only.


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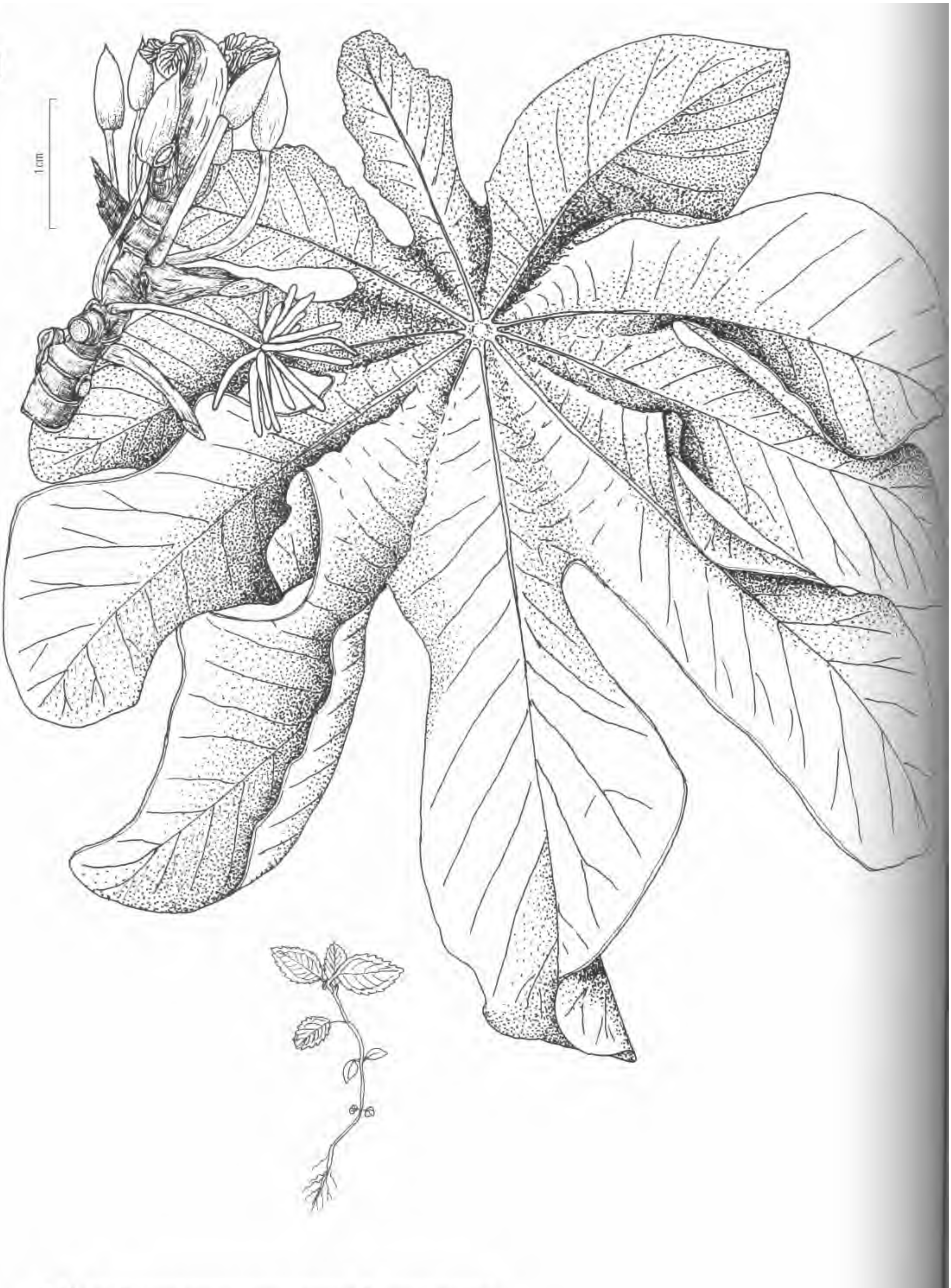
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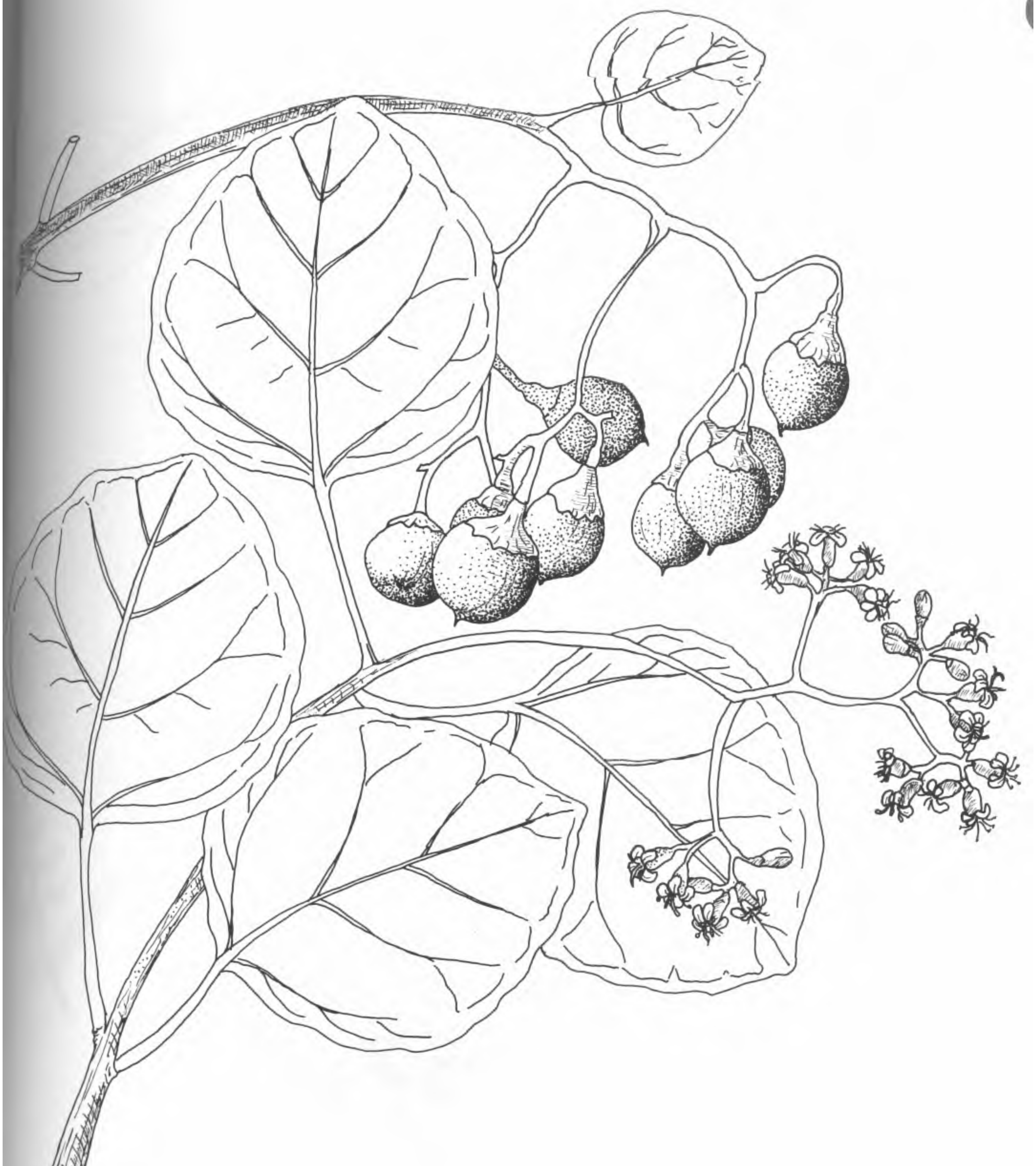

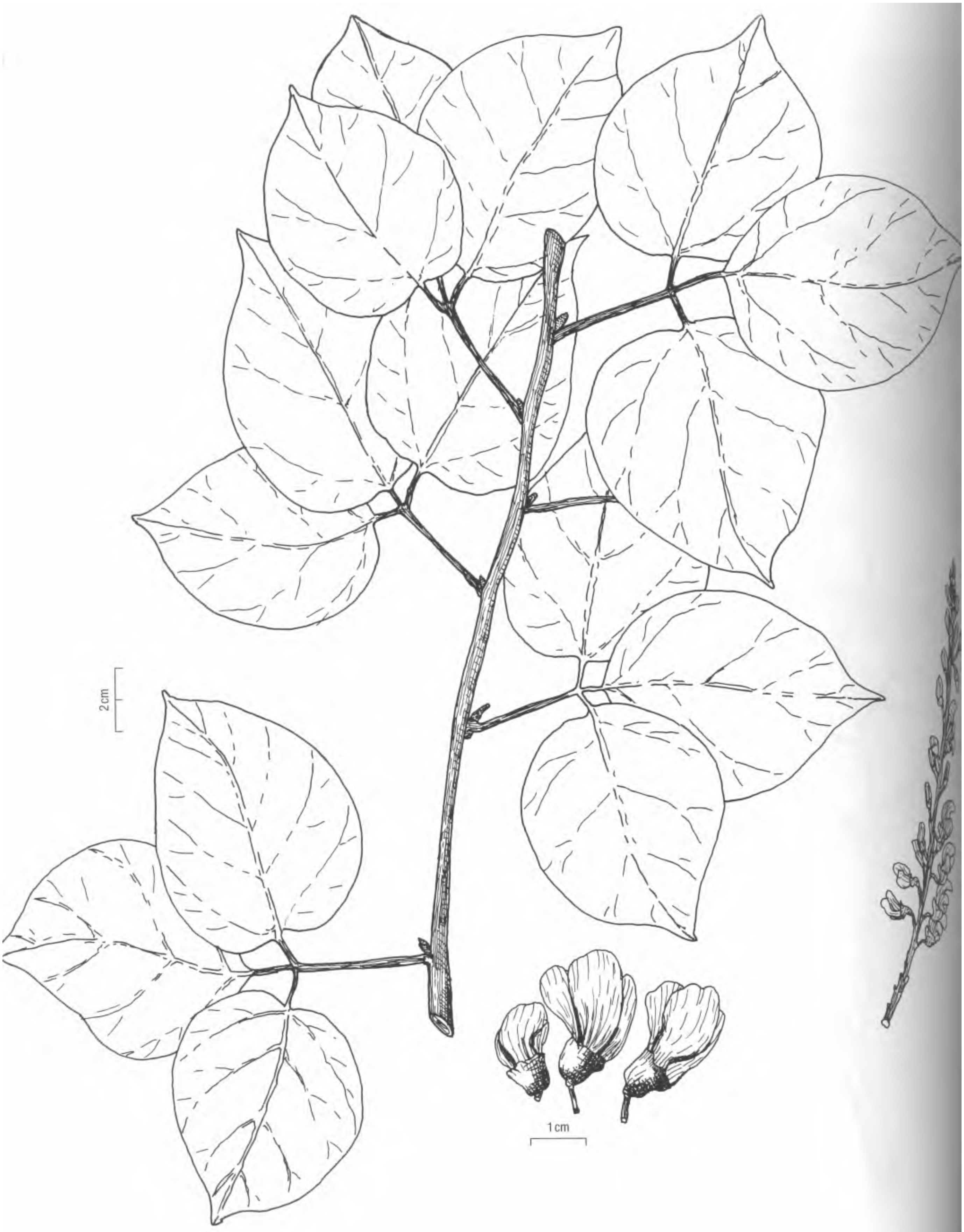
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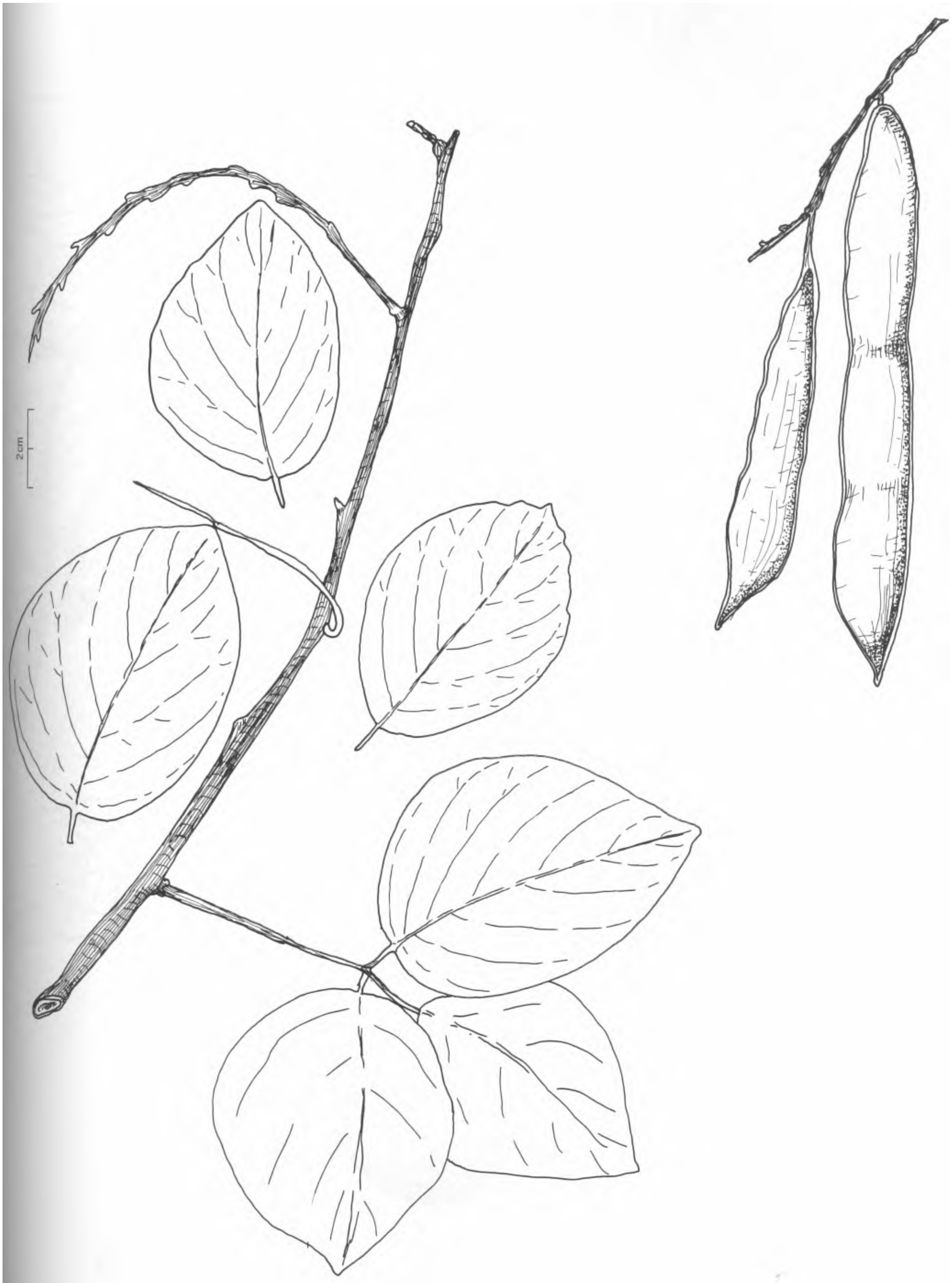
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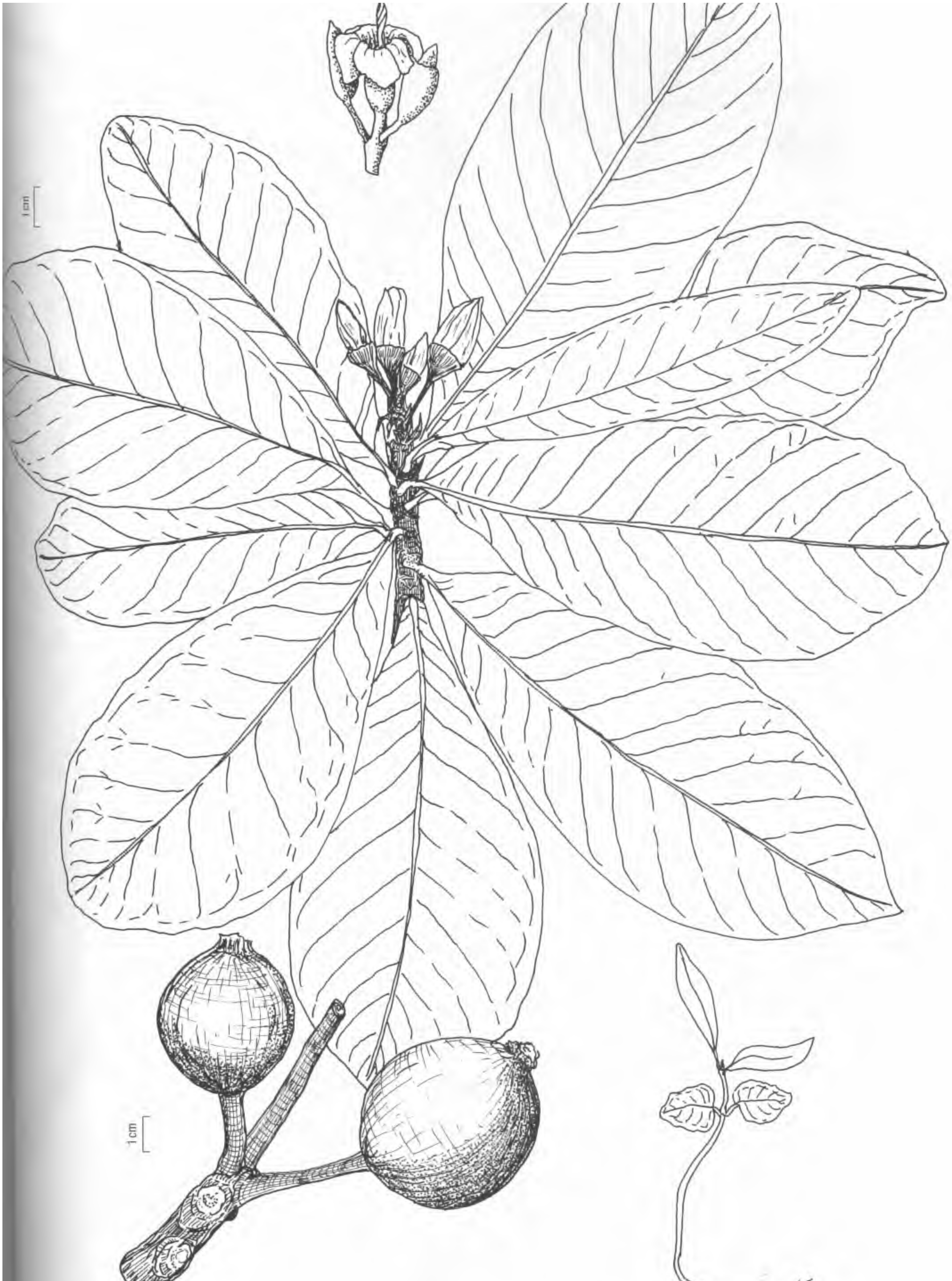
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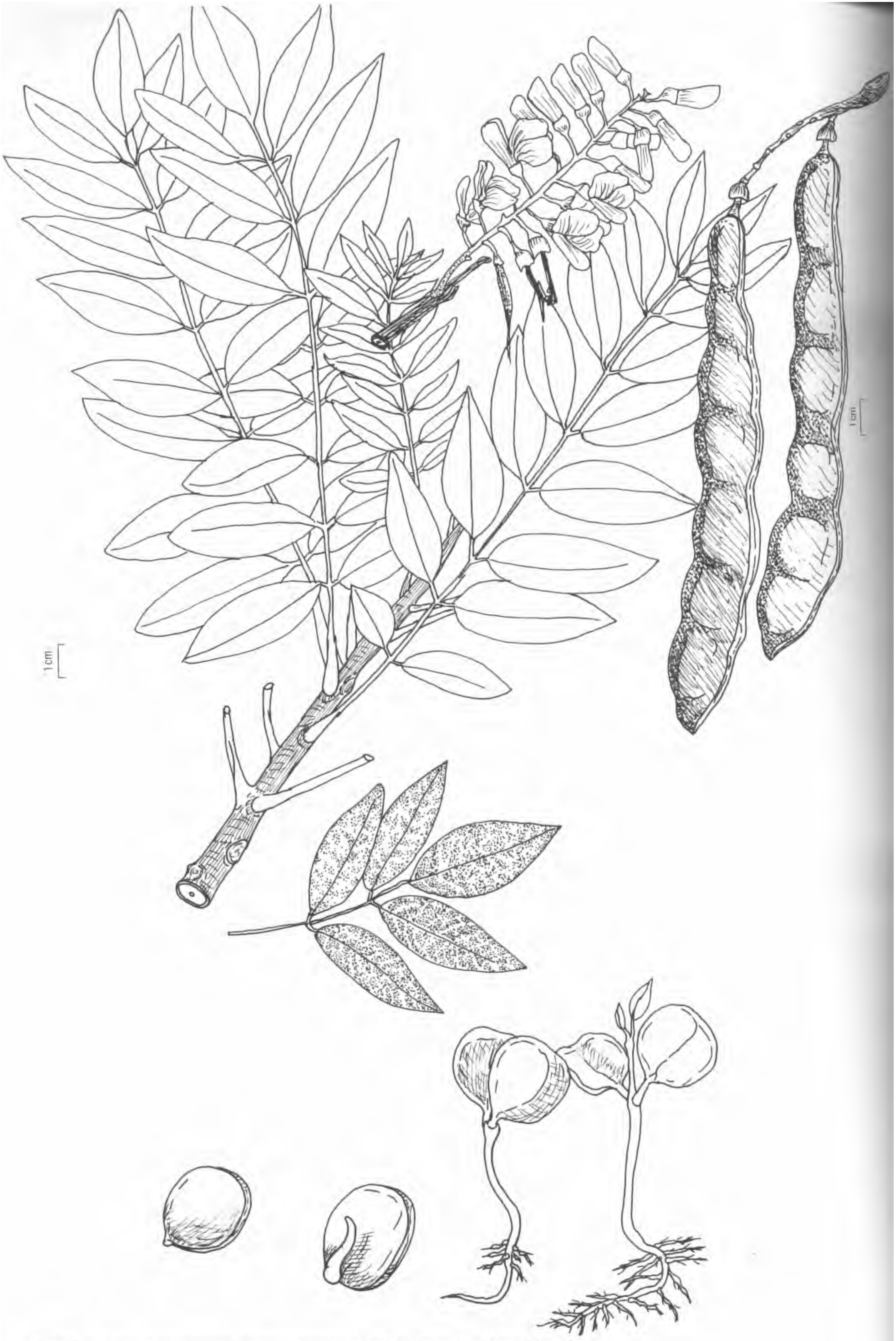

Gliricidia sepium (Jacq.) Steud.


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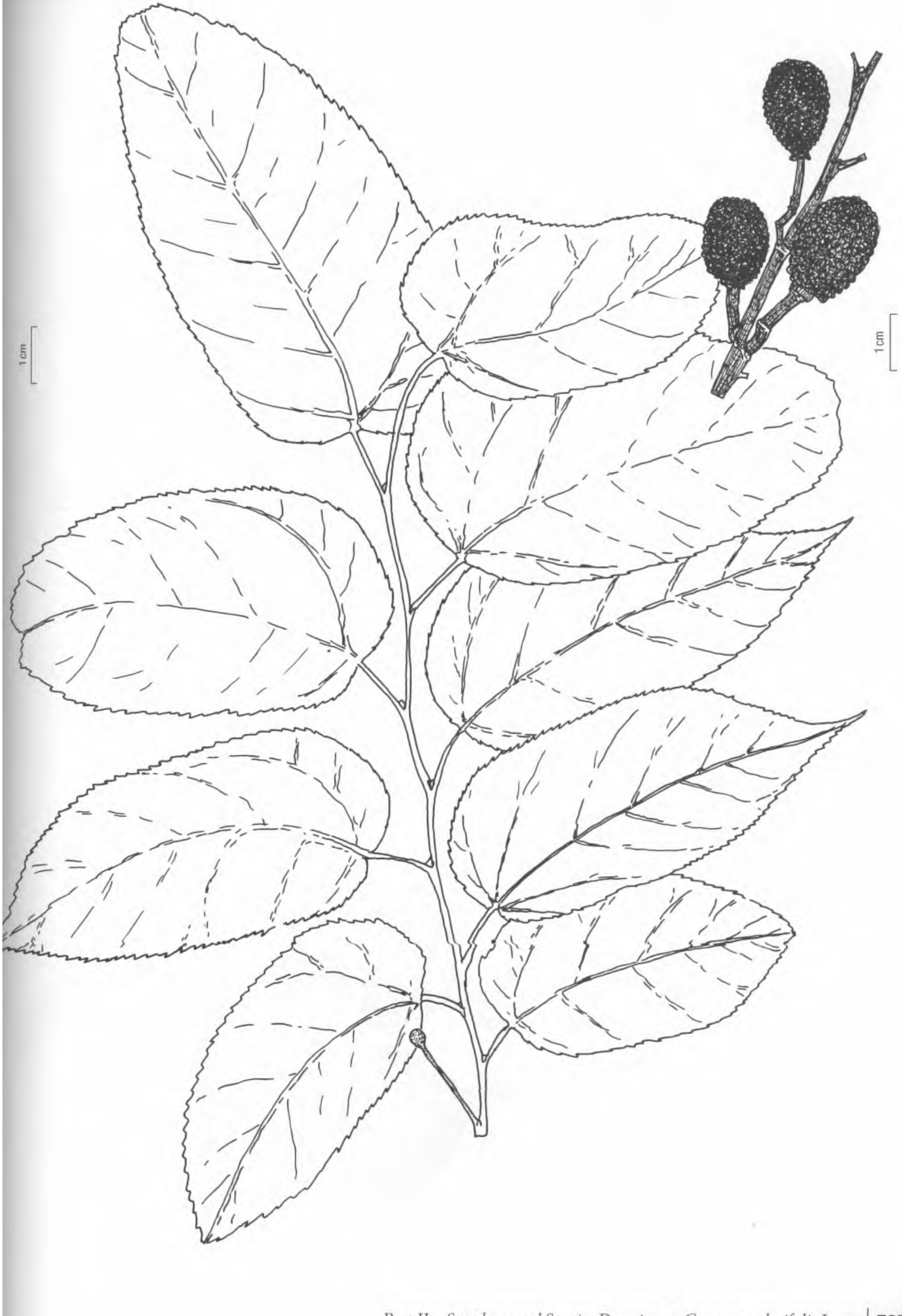
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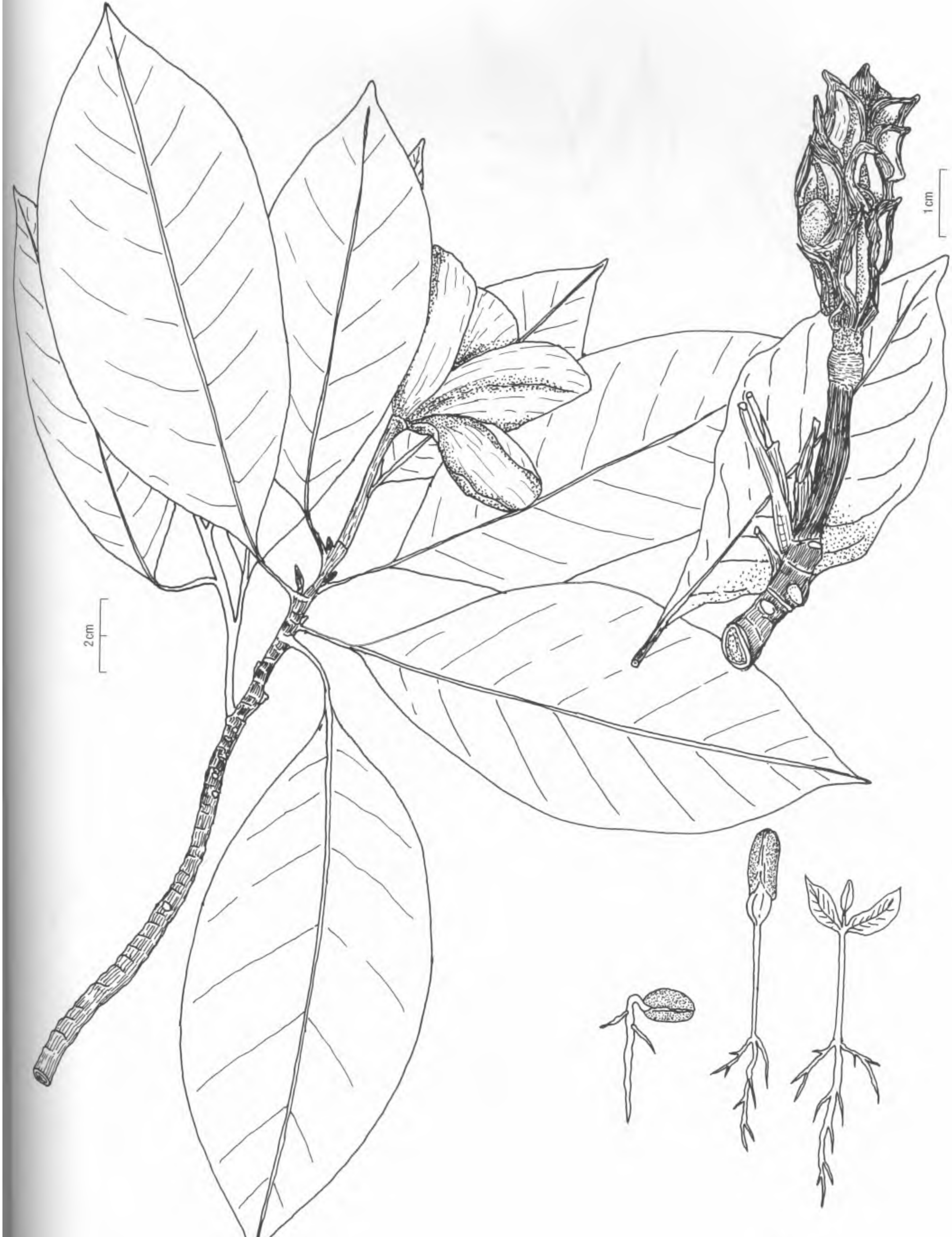

Part II—Supplemental Species Drawings • *Magnolia poasana* (Pittier) Dandy


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GLOSSARY OF TERMS

E.M. FLORES, ANÍBAL NIEMBRO ROCAS,
RAFAELA CARVAJAL, J. A. VOZZO

Abiotic: characterized by the absence of life or living organisms, 35, 80, 87, 181, 183, 207

Abscission: normal separation of flowers, fruit, and leaves from plants, 26, 48–49, 94, 139, 149, 161, 311, 391, 424, 540–541, 590, 691, 750, 753, 757

Acarus: a mite, especially one of the genus Acarus, 535

Achene: small dry fruit containing a single seed, not stuck to the pericarp, 16, 51, 233, 397

Acicular: needle-shaped, 113, 375, 609

Acrodrome: apical point on structure, 285, 395

Acropetally: developing upward, toward the apex, 321, 349

Actinomorphic: divisible vertically into similar halves by each of a number of planes passing through the axis, 15, 17, 38, 312, 354, 390, 403, 587, 589, 593, 606, 719, 749, 756, 773

Acuminate: tapering gradually to a long, thin point; compare with Acute, 111, 232, 285, 289, 311, 342, 360, 386, 391, 395, 408, 420, 429, 446, 452, 456, 464, 491, 493, 503, 514, 531, 541, 548, 553, 572, 575, 582–583, 587, 589, 592, 599, 643, 693, 722, 732, 735, 737, 748, 752, 755, 772, 781

Acute: applied to tips and bases of structures ending in a point less than right angle; compare with Acuminate and Obtuse, 111, 232, 264, 278, 289, 342–343, 355, 360, 391–392, 402, 409, 429, 470, 481, 486, 490–491, 493, 497, 541, 558, 575–576, 582, 587, 593, 602, 606, 651, 676, 683, 685, 687, 693, 701, 722, 737, 750, 753, 756

Adobe: clay-soil composition, 354, 515, 703, 750, 753, 756

Adventitious buds: buds formed along a stem, usually after the stem has been injured

Aerenchyma: parenchyma cells associated with an air space or surrounded by open canals, 69, 90, 440

Air chambers: open chambers in the thallus of Marchantia and other liverworts; located in the upper portion of the thallus, which has a pore at the top for gas exchange, 54, 440

Alate: having wings; winged, 264, 266

Aleta: misplaced

Aleurone layer: layer of high-protein cells surrounding the storage cells of the endosperm

Aliform: wing-shaped, 547

Alternate: one leaf, bud, or branch per node, 15, 18, 20, 156, 164, 231, 241, 272, 277, 287, 292, 297, 303, 311, 318, 335, 363, 384, 391–392, 405–406, 408, 415, 423, 429, 439, 442, 446, 464, 466, 468, 470, 473, 481, 505, 514, 528, 540, 553, 555, 558–559, 561, 568, 573, 575, 582, 585, 595, 597, 599, 603, 645, 649, 651, 676, 678, 680, 687, 693, 701, 708, 719, 767, 772, 781

Ambient: when used with temperature, 24 to 30°C, 126–129, 141, 144, 181, 244, 247, 257, 278, 309, 312, 336, 375, 379, 387, 397, 415, 436, 440, 449–450, 487, 518–519, 538, 545, 550, 565, 602, 649, 667, 691, 696, 702, 713–714, 717, 723, 738, 740

Ament: spike of unisexual, apetalous flowers having scaly, usually deciduous, bracts; a catkin, 28–29

Amyloplastic: containing a large amount of starch, but no chlorophyll; specialized for storage

Anaerobic: living in the absence of air or free oxygen, 93, 315, 538, 691

Anastomosed: joined, 395

Anatropous: inverted at an early stage of growth, so that the micropyle is turned toward the funicle, with thechalaza situated at the opposite end, 33, 69, 278, 312, 354, 391, 403, 424, 491, 494, 516, 541, 577, 587, 593, 603, 667, 749, 753, 756, 773

Androecium: the collective stamens of a flower, 15, 18, 20, 23–24, 59, 87, 232, 312, 354, 391, 405, 409, 424, 439, 487, 494, 512, 516, 541, 576–577, 587, 589, 593, 654, 667, 702, 738, 749, 753, 756

Androgynophore: a stalk bearing both stamens and pistil above the point of perianth attachment, 424, 541

Anemochorous: wind–dispersed pollination, 72, 391, 430, 439, 583, 738, 778

Angiosperm: flowering plant; plant with ovules enclosed in an ovary, 29, 36, 48, 62, 198, 230

Angulous: pertaining to angles, 514

Anther: pollen–bearing part of a stamen, 16, 18, 20, 24, 26, 30, 32, 36–39, 41, 45, 232, 278, 298, 312, 318, 343, 350, 354, 391, 403, 405, 409, 487, 494, 512, 516, 541, 577, 583, 587, 603, 606, 655, 667, 683, 687, 695, 698, 716, 738, 750, 753, 756, 773

Antheridial head: umbrella-like structure containing antheridia; grows attached to the upper surface of the thallus of Marchantia and other members of the liverwort family

Antheridium: male gametangium where the sperm is produced and housed

Anthesis: period or act of expansion in flowers, especially the maturing of the stamens, 35–37, 39–40, 43, 350, 390, 424, 494, 515–516, 541, 772

Anthocyanin: water-soluble red, blue, or purple pigments, 36

Anthotaxia: distribution of the floral parts on the receptacle

Anticlinal: perpendicular to the surface; dividing away in opposite directions, 31, 69

Antihelmintic: worm preventative, 298

Antipodes: three haploid nuclei that are formed during megasporogenesis in plants, all located opposite the micropyle end of an ovule

Antiraphe: part of the ovule or seed, located between the chalaza and the micropyle

Apetalous: without petals, 15, 29, 405, 409, 512, 654

Apical: of, at, or forming the apex, 43, 64, 66, 70, 78–79, 100, 103–104, 360, 363, 408, 562, 583, 606, 619

Apical buds: buds that produce stems and are located at the tip of the stem

Apical meristem: meristem located at the tip of the stem, 64, 77, 79, 100, 103

Apiculate: ending with a short, sharp, abrupt, point, 111, 354, 391, 655, 687

Apocarpous: having the carpels separate, 20

Apogamy: a type of apomixis involving the suppression of gametophyte formation so that seeds are formed directly from somatic (body) cells of the parent tissue, 68

Apomixis: reproduction without fertilization or formation of gametes, 68

Appressed: lying flat against, 106, 110, 486, 494

Arachnoid: formed of or covered with delicate hairs or fibers, 553

Archegonium: multicellular female gametophyte; also, flask-shaped female reproductive organs on the prothallium in higher cryptogams; correspond to a pistil in the flowering plants and contain the egg which becomes the sporophyte, 46–48

Archesporial cell: cell of the nucellus that differentiates and gives rise to the cell that is ultimately destined to undergo meiosis and produce the megaspore mother cell, 35

Areolas: small mesophyll areas delimited by minor veins, 113, 667

Aril: fleshy or pulpy covering or appendage arising from the base of a seed, 50, 60, 69–71, 74, 77, 81–83, 136, 154–155, 188, 264, 266, 269, 278, 403, 406, 409, 483, 487, 523, 541, 555, 593, 667, 740, 773

Arillate: having an aril or arils, 83, 136, 593

Aristate: awned, 111, 687

Attenuate: tapering gradually to a narrow extremity, 110, 395, 426, 491, 493, 514, 592, 738, 748, 752, 755, 772

Auricle: small fingers of tissue at the base of the leaf blade of a grass that extend partially around the stem

Auriculate: eared, 103, 110, 370, 427, 603, 714

Axial: located in the axis, 66, 139, 452, 658, 660

Axial parenchyma: parenchyma cells of the axial system; located in the secondary vascular tissue

Axial system: vascular transport system in a stem that runs vertically (up and down) in contrast to the lateral system, which runs right and left, or out to the margin of the stem); carries water and raw minerals up the stem in the xylem and carries glucose in the phloem up and down the stem; composed of fibers for strength, sieve-tube members and companion cells in the phloem, and fibers, vessels, and tracheids in the xylem; fusiform initials produce the axial system

Axial: located in the axis, 66, 139, 452, 658, 660

Axil: space between any two adjoining organs, such as stem and leaf, 27, 593, 603, 605, 749, 752

Axillary: located in an axil, 104, 152, 158, 231–232, 253, 266, 285, 308, 321, 329, 354, 357, 360, 382, 403, 423, 429, 439, 464, 474, 479, 481, 490, 494, 503, 505, 515, 547, 553, 555, 580, 583, 587, 589, 605, 643, 646, 649, 690, 693, 702, 752, 756, 773, 778, 781

Barbascous: poisonous to fish

Basitonia: having more growth of branches in the basal part of the stem

Bast: phloem, 301

Berry: fleshy or pulpy indehiscent fruit with one or more seeds embedded in the fleshy tissue of the pericarp; may be formed from either a superior or an inferior ovary, 13, 59–60, 77–78, 81, 83, 136, 152–155, 157, 159, 233, 297, 335, 354, 408, 564, 649, 651, 740

Beveled: inclined at an angle, 293

Bifid: cleft, 516, 738

Bilateral symmetry: being divided into two equal, mirror-image parts

Bisexual: having both sexes present and functional in the same individual, 24, 26, 42, 354, 589, 602, 732, 756

Blade: the flattened and expanded part of a leaf or parts of a compound leaf, 74, 103–104, 106, 110–111, 164, 231–232, 289, 297, 311, 329, 353, 360, 382, 391–392, 397, 405, 408, 420, 491, 511–512, 514, 553, 576–577, 587, 592, 599, 603, 616, 629, 633, 640, 667, 687, 695, 698, 703, 732, 778, 781

Brackish: somewhat salty, 357, 399, 418, 470, 500, 538, 691

Bract: reduced leaf, particularly at base of flower or flower stalk, 27, 29, 36–37, 43, 59, 62, 123, 156, 241, 305, 312, 315, 343, 363, 375, 397, 405, 408, 420, 424, 429, 476, 512, 516, 558, 561, 576, 583, 593, 605–606, 660, 678, 735, 738, 756, 773

Branchlet: small or secondary branch, 297, 360, 378–380, 390, 420, 452, 576, 589, 693, 781

Braquibrast: branches having short internodes in which the leaves and cones grow close together

Bristle: still, hairlike structure, 18

Bud primordium: meristem tissue that gives rise to a lateral bud

Bulbil: small bulb formed in the axil of a leaf or bract functioning to propagate the plant vegetatively

Bundle scar: scar within a leaf scar where the vein system broke as the leaf dropped

Caducifolio: dropping off or shedding of leaves at an early stage of development

Caducous: having a tendency to fall; dropping off very early, as leaves; deciduous, 297, 555, 558, 561, 683, 685, 687, 735

Calcareous: containing calcium carbonate, 264, 266, 321, 335, 386, 415, 436, 449, 464, 466, 476, 528, 550, 564, 567, 615, 636, 649, 651, 740, 770

Callosa: polysaccharide present in some cell walls, composed of glucose residues

Callus: a small hard protrusion, e.g. on the labellum of some Orchidaceae; a hard point below the lemma, in spikelets of Poaceae; a protective layer of tissue formed over an injury

Calyptra: mass of cells that covers the apical meristem of the root

Calyx: collective term for all the sepals of a flower, whether separate or united; the outer series of flower parts and the perianth, 15, 17–18, 36, 39, 59, 89, 152–155, 157, 230, 232, 278, 298, 312, 315, 324, 327, 329, 332, 354, 363, 384, 391, 403, 405, 409, 412–413, 418, 424, 429, 433, 439, 444, 452, 490, 494, 508, 512, 516, 541, 576, 583, 587, 589, 593, 603, 606, 654, 666, 702–703, 719, 735, 738, 749, 752–753, 756, 767, 770, 773

Cambium: internal layer of living cells between the inner bark and the sapwood where growth takes place, producing secondary xylem and phloem

Campanulate: order of angiosperms, 17, 40, 298, 429, 439, 452, 576, 583, 703, 735

Camptodrome: bent structure, 395, 503, 548, 555, 558, 562

Capitular: having a globular head; collected in a head

Capsule: dry dehiscent fruit derived from two or more carpels, 51–52, 54, 56, 58, 78, 83, 123, 136, 151–152, 154–157, 159, 186, 233, 285, 303, 315, 340, 361, 384, 391, 394, 418, 426, 471, 483, 487, 490, 494, 505, 508, 512, 532, 535, 541, 553, 558, 561, 568–570, 585, 587, 664, 726–727, 729–730, 734–735, 738, 762, 765, 775–776, 778

Carnose: fleshy, 426, 452

Carpel: simple pistil or unit of a compound pistil, 15–16, 20–21, 23, 43, 49, 51, 54, 56, 58–59, 151–157, 232–233, 318, 363, 487, 500–501

Cartaceous: furrowed or grooved, 266, 366, 369, 372, 386, 449, 713, 723

Caruncle: appendage of a seed, near the hilum (scar), 70–71, 74, 558, 561

Casparian strip: band of suberin within the anticlinal walls of endodermal and exodermal cells

Cauliforous: stalk-like, 308

Cellulose: long chain of complex carbohydrate compounds, (polysaccharides); chief substance forming the cell wall and woody parts of plants, 70, 174, 481, 585

Chalaza: point of an ovule or seed where the integuments are united to the nucellus opposite the micropyle, to which the funiculus is attached, 32, 43, 46, 68–69, 73, 77, 163, 723

Chalazal: in direction to the chalaza, 33, 35, 64, 68–70, 73–74, 79, 162–164, 392

Chamfer: cut at an angle, 503

Chartaceous: papery, 106, 278, 312, 430, 493, 511, 540, 575, 587, 592, 667, 676, 687, 748, 755

Chlorenchyma: plant parenchyma cells that contain chloroplast in their cytoplasm, 69, 623

Chloroplast: microscopic body within the cell; contains chlorophyll

Chromoplast: chloroplast in which other pigments mask the green color

Ciliate: fringed with hairs, 109, 773

Clavate: club-shaped, gradually thickened upward, 309

Coleoptile: in monocots, a sheath that covers the plumule

Coleorhiza: in monocots, a sheath that covers the radicle

Collenchyma: tissues composed of cells with unevenly thickened primary cell walls that strengthen growing organs, 69–70

Columella: The persistent axis of certain capsules, 391

Commensal: sharing of nutrients by two organisms

Comose: hairy, 386, 722

Companion cells: phloem cell connected to a sieve-tube member by numerous plasmodesmata

Complete flower: having all the components: pistils, stamens, petals, and sepals, 232

Compound leaf: divided into two or more blades (leaflets); palmately compound leaves have three or more leaflets arising from a common point, while pinnately compound leaves have leaflets arranged along a common axis, 106, 231

Cone: mass of ovule-bearing or pollen-bearing bracts or scales arranged spirally on a cylindrical or globose axis; common to most conifers, 43, 45–46, 120, 122, 177, 179–182, 239, 241, 290, 292, 305–306, 375, 609, 612–613, 615–616, 618–620, 622–623, 625–626, 628–629, 633, 636–637, 639–640, 645

Conic: cone-shaped, 70

Conifer: plants with cones and naked ovules; any of an order of trees and shrubs bearing true cones or with arillate seeds, 46, 48, 79, 177–183

Conspecific: of the same species, 42

Coppice: cut-over area, 212, 501

Cordate: heart-shaped in outline; descriptive of an ovate organ (such as a leaf) with two rounded basal lobes, 103, 108, 110, 264, 397, 511, 514, 587

Coriaceous: having a stiff leathery texture, 52, 58, 79, 81, 106, 294, 300, 309, 353–354, 360, 391, 397, 403, 408–409, 423, 426, 458, 464, 493, 497, 503, 548, 550, 555, 557–558, 575, 587, 602, 645, 678, 680, 713, 748, 752–753, 772–773, 778

Corm: enlarged fleshy base of a stem, bulb-like but solid

Cornaceous: belonging to the Cornaceae family, 266, 367, 370, 373, 714

Corolla: collective term for all the petals of a flower, whether separate or united; inner series of the perianth, 15, 17–18, 37, 39–40, 48, 151, 157, 230, 232, 278, 298, 301, 312, 315, 354, 391, 403, 412–413, 418, 424, 429, 439, 490, 494, 541, 576–577, 587, 657, 667, 695, 698, 702–703, 735, 738, 756

Corymb: flat- or round-topped flower cluster in which the outer pedicels are longer than the inner ones, the outer flowers opening before the center ones, 27–28, 329, 569

Costa: rib, 13, 27, 104, 117, 121, 151, 203, 210, 212, 269, 272, 277, 287, 289, 294, 297, 301, 311–312, 338, 340, 344, 348, 353, 355, 360, 382, 390–391, 402, 405–406, 408, 412–413, 420, 423, 429, 436, 439, 446, 450, 452, 458, 461, 474, 476, 479, 481, 486–487, 489, 493, 503, 511, 514–515, 540, 553, 564, 575, 582, 586, 589, 592, 597, 599, 601–602, 640, 643, 654, 660, 662, 666–667, 676, 678, 683, 685, 687–688, 693, 695, 701–703, 716, 719–720, 732, 735, 737–738, 748, 750, 752, 755, 767, 770, 772, 775–776, 778–779, 781

Cotyledon: primary or rudimentary leaf of the embryo of seed plants, 47, 64, 66, 70, 73–79, 91, 93–95, 97, 100, 103–104, 106, 110, 113–117, 151, 153, 158, 178, 183, 216, 264, 267, 270, 278, 301, 309, 315, 318, 336, 355, 363, 367, 370, 373, 376, 387, 392, 403, 406, 413, 416, 424, 427, 437, 450, 456, 491, 495, 498, 501, 512, 515–516, 521, 541–542, 550, 559, 565, 577, 579, 587, 590, 593, 602–603, 605, 649, 651, 655, 668, 680, 703, 714, 723, 740, 743, 750, 753, 757, 759, 767–768, 773

Crassinucelate: nucellar condition in which the embryo sac originates and develops deep (several cell layers) beneath the nucellar epidermis

Crassula: swelling of intercellular material and primary wall in the edges of the punctuated pair in the tracheid

Crenate: having margins scalloped with shallow rounded teeth, 109, 541, 773

Crenatures: notches or indentations

Crenelate: minutely crenate, 109

Crustaceous: having a hard covering or crust, 106, 416, 436, 553, 564, 740

Cryptocotilar germination: keeping the cotyledons inside the seed; germination can be epigeal or hypogeal

Cuneate: wedge-shaped; triangular and tapering to a point at the base, 110, 241, 420, 452, 491, 493, 514, 531, 555, 676, 683, 693, 732, 781

Cupola: domelike structure

Cutaneous: of, pertaining to, or affecting the skin, 412, 443

Cuticle: waxy covering on the surface of stems and leaves that acts as an adaptation to prevent desiccation in terrestrial plants, 42–43, 70, 90, 163

Cutin: complex fatty or waxy substance found on the surface of certain seeds or leaves, often making them impermeable to water, 43

Cyme: inflorescence in which the primary axis bears a single terminal flower which develops first, 27, 151, 156–157, 233, 418, 479, 490, 503, 690, 705

Cyme scorpioid: determinate inflorescence in which the lateral buds on one side are suppressed during growth, resulting in a curved or coiled arrangement

Cytokinesis: division of the cytoplasm to form two separate daughter cells immediately after mitosis

Cytoplasm: living portion of a cell excluding the nucleus, 31, 140, 144

Daughter cells: separate cells resulting from cytokinesis, 64

D.b.h.: diameter at breast height; generally accepted standard for measuring trees at 137 cm above the ground, 192, 211, 222, 241, 244, 247, 250, 253, 259, 262, 264, 266, 269, 272, 274, 277, 282, 287, 289, 292, 294, 297, 300, 303, 305, 308, 311, 315, 318, 321, 335, 338, 340, 342, 346, 353–354, 357, 360, 363, 366, 369, 372, 375, 378, 382, 384, 386–387, 390, 397, 399, 402, 405, 408, 411, 415, 418, 420, 423, 426, 429–430, 432–433, 436, 439, 442–443, 446, 449–450, 452, 455, 461, 466, 468, 473, 476, 479, 483, 486, 490, 497, 500, 505, 508, 511, 514, 521, 523, 526, 528, 532, 535, 537, 540, 544, 550, 553, 557–558, 561, 564, 567, 569, 575, 579, 582, 585–586, 589, 592, 595, 597, 599, 601, 609, 612, 615, 618–619, 622, 625, 628, 632, 636, 639, 643, 645–646, 649, 651, 654, 657, 660, 662, 664, 666–667, 670, 673, 676, 678, 680–681, 683, 685, 687–688, 690, 693, 701, 703, 705, 708, 713, 716, 719–720, 722, 729, 732, 735, 737–738, 740, 742, 752, 755, 759, 762, 765, 770, 772, 775, 778, 781

Deciduous: detaching or falling off very early; usually in reference to leaves, leaf tips, or perianths; caducous, 111, 150, 212, 231, 234–236, 269, 274, 278, 280, 282, 289, 300, 305, 311–312, 332, 340, 343, 360, 366, 369, 386, 411, 413, 415, 420, 423–424, 433, 439, 442–443, 449, 452, 458, 474, 476, 511, 540–541, 544, 550, 573, 576, 580, 586–587, 593, 595, 597, 599, 605, 613, 622, 636, 643, 651, 657, 664, 673, 676, 701, 716, 722, 734, 737, 740, 742, 745, 752, 773

Decurrent: extending down and attached to the stem, forming a ridge or wing, 110, 541, 589, 693, 778

Decussate: arranged along the stem in pairs, each pair at right angles to the pair immediately above or below, as leaves, 315, 353–354, 737, 778

Dehiscence: opening regularly to let seeds or spores escape through valves, slits, etc., as a capsule or anther, 20, 24, 32, 37, 45, 48–51, 54, 56, 58, 63–64, 66, 74, 94, 133, 278, 290, 315, 349–350, 361, 386, 391, 405, 409, 424, 464, 490, 494, 512, 516, 541, 545, 561, 587, 602–603, 667, 693, 722, 738, 750, 753, 756, 773, 778, 781

Dehiscent dry fruit: mature fruit that has dry pericarp that opens to let seeds escape

Dentate: toothed; having sharp, spreading, coarse teeth that are perpendicular to the margin, 106, 109, 491

Denticulate: finely dentate, 109

Dichasium: cyme in which branches appear in regular opposite pairs, 27, 29, 690

Dicotyledons: major group of angiosperms (flowering plants) characterized by the embryo having two cotyledons, 15, 43, 66, 68, 74–75, 101, 103, 111–113, 225

Dioecious: having male and female organs in separate and distinct individuals; also dioicious, 24, 27, 42–43, 312, 340, 363, 375, 382, 474, 490, 494, 515, 537, 592, 645, 740, 767

Diploid (2 n): refers to two sets of chromosomes; germ cells have one set and are haploid; somatic cells have two sets of chromosomes and are diploid (except for polyploid plants), 27, 43, 49, 68, 79, 244, 762

Discoidal: consisting of a disk only, without rays, 678

Distal: Opposite the point of attachment; apical; away from the axis, 424

Drupe: fleshy indehiscent fruit having a single seed encased in a hard stony covering; sometimes having more than one encased seed, 49, 59–60, 77–78, 81, 83, 89, 100, 136, 151–153, 155, 157, 233, 294, 321, 343, 357, 420, 476, 503, 537, 576, 662, 705, 708, 710

Druse: star-shaped crystal, 678

Duramen: internal layers of secondary xylem that have lost their conduction and storage function, 285, 394, 530, 547, 555

Eared: having an ear-like process or appendage, usually at the base of an organ; frequently applied to leaves and petals

Ecophene: modified by specific adaptive response to environmental factors, 360

Egg cell: nonmotile female sex cell (gamete); cell of the embryonic sac (megametophyte), 35, 43, 47–48, 68, 79, 660

Elaioplast: type of plastid containing essential oils or protein and lipid combinations

Ellipsoid: three-dimensional body whose plane sections are all either ellipses or circles, 41, 312, 386, 487, 494, 503, 593, 651, 732, 740

Elliptic: oblong with the ends equally or almost equally rounded, 75, 103, 108, 231, 264, 269, 285, 289, 312, 318, 324, 329, 335, 342, 353, 360, 369–370, 372, 375, 387, 397, 409, 415, 423–424, 427, 436, 452, 486, 491, 493, 521, 540–541, 550, 553, 564, 567, 575, 582, 592, 595, 603, 643, 676, 683, 685, 687, 695, 701, 713, 740, 755, 767, 773, 781

Emarginate: notched at the apex, as a petal or leaf, 111, 397, 408, 426–427, 429, 667, 683

Embryo: generative part of the seed that develops from the union of the egg and sperm cells and during germination becomes the young plant, 14, 26–27, 29, 33–35, 43, 46, 48–49, 62–64, 66–68, 70, 73–81, 85, 90–91, 93–94, 100, 103–104, 115–116, 127, 142, 149, 152, 155–156, 160, 162–163, 165, 168–172, 176, 178, 232, 264, 266–267, 269, 278, 305, 312, 318, 335–336, 355, 363, 367, 370, 373, 376, 387, 391–392, 394, 406, 412–413, 416, 424, 427, 430, 437, 444, 450, 456, 479, 491, 495, 498, 512, 516, 521, 523, 541–542, 550, 553, 565, 576–577, 587, 593, 603, 605, 649, 651, 655, 667–668, 678, 703, 714, 723, 740, 750, 753, 756, 773

Embryo sac: female gametophyte of angiosperms, formed from the growth and division of the megaspore into a multicellular structure with eight haploid nuclei, 26–27, 29, 33–35, 43, 62, 64, 424, 541

Embryogenesis: formation and subsequent development of plumule, radicle, and cotyledons in a plant, 62–64, 66–67, 79, 456

Endarch xylem: inner position of the protoxylem

Endocarp: inner layer of a pericarp, 48, 59–60, 70, 77–78, 81–83, 86, 93–95, 100, 103, 116, 153, 168, 278, 298, 312, 354, 391, 399, 403, 406, 420, 430, 490, 494, 515, 558, 576–577, 602, 667, 702, 719, 749, 753, 756

Endodermis: thin sheath of cells bounding the stele and separating it from the cortex

Endosperm: in angiosperms, an embryonic nutritive tissue formed during double fertilization by the fusion of a sperm with the polar nuclei; in gymnosperms, a food reserve derived from the megagametophyte; the nutritive material in plant seeds which is triploid (3n), resulting from the fusion of three nuclei during double fertilization, 29, 35, 43, 48–49, 62–63, 66, 68, 70, 73–79, 85, 91, 93, 95, 115, 127, 149, 151–157, 264, 266, 269, 278, 355, 363, 367, 370, 373, 387, 392, 399, 403, 427, 437, 450, 497, 512, 516, 521, 542, 565, 576–577, 593, 603, 605, 668, 703, 714, 723, 750, 753, 756, 773, 775

Endothecium: tissue layer under the epidermis of the anther, 30–32

Endothelium: innermost tegument layer which covers the embryonic sac in some taxa, 541

Entire: smooth, without teeth or indentations; applied to margins, edges, 29, 63, 91, 109, 116, 122, 225, 232, 294, 311, 353, 360, 391–392, 402, 405, 408, 423, 439, 446, 473, 486, 493, 512, 514, 523, 567, 575, 582, 587, 592, 602–603, 685, 687, 701, 719, 735, 737, 748, 752, 755, 772, 778, 781

Entomophilous: insect related, 36, 48, 355, 390, 403, 490, 494, 512, 583, 593, 702, 738, 749, 756, 773

Eophyll: first leaf above the cotyledons, 278, 406, 593, 667, 749, 753, 756

Epicarp: outer layer of the pericarp or matured ovary, 48, 406, 440, 558, 702, 743, 746

Epicotyl: portion of the embryo or seedling above the cotyledons, 64, 66, 78, 100–104, 106, 114–115, 158, 361, 403, 456, 500, 559, 723

Epidermis: outer layer of cells, 30, 70, 162–163, 343, 542, 561

Epigeal: growing on or close to the ground, 94–95, 97, 102–103, 114–116, 157–158, 266, 275, 278, 283, 313, 384, 387, 391, 406, 409, 424, 430, 440, 487, 512, 515, 545, 576, 587, 593, 645, 660, 667, 703, 738, 746, 749, 756, 760, 763, 773, 779

Epigeal germination: of or relating to the emergence of cotyledons above the surface of the ground, 95, 102, 157–158, 645

Epigynous: growing on the summit of the ovary, or apparently so, 23, 354, 749, 752, 756

Ergastic substance: nonliving cellular material

Ester: chemical compound formed between an acid and alcohol while eliminating water, 343

Etiolate: elongated due to lack of chlorophyll

Etiolation: elongation, discoloration, and poor plant growth due to the lack of chlorophyll

Eukaryotic: having a true nucleus

Evergreen: plants with live leaves persisting through one or more winter seasons, 136, 150, 212, 231, 236, 241, 256, 264, 266, 285, 297, 300, 305, 308, 315, 324, 329, 332, 335, 342, 353, 357, 360, 375, 378, 405, 408, 418, 426, 436, 443, 458, 474, 481, 490, 497, 500, 503, 508, 511, 514, 521, 532, 537, 550, 555, 564, 567, 569, 572, 582, 586, 645–646, 649, 662, 676, 683, 685, 701, 705, 713, 722, 732, 742, 748, 781

Exarch xylem: outer position of the protoxylem

Excrescence: abnormal, disfiguring outgrowth or enlargement

Exine: outer wall of angiosperm microspore, 31–32, 36, 40–43, 278, 577, 603, 667, 750

Exocarp: outermost layer of the fruit wall (pericarp), 48, 51, 77, 81–83, 298, 312, 354, 363, 391, 403, 406, 424, 430, 446, 515, 541, 577, 602, 662, 749, 753, 756, 773

Exoderm: outer layer of one or more layers of thickness in the cortex of some roots

Exostome: opening of the outer integument of an ovule that has two integuments, 68–70, 100, 541

Exothecium: epidermis of the anther with fibrous strands, such as that of the endothecium

Falcate: crescent-shaped, 108

Fanerocotylar germination: having cotyledons free and conspicuous

Fascicular cambium: vascular cambium that arises within vascular bundles

Fat: ester of fatty acid and glycerol (or another alcohol) found in plants and animals; in liquid form, called oils, 216, 605

Ferruginous: containing or similar to iron; having the color of iron; rust, 110, 259, 403, 408–409, 555, 576, 586, 601, 666–667, 703, 749–750, 773

Fertilization: fusion of nuclei of egg and sperm, 24, 26, 32–33, 35, 43, 47–48, 60, 64, 69, 71, 79, 89, 211, 232, 312, 363, 379, 384, 691, 749, 753, 756, 773, 779

Fiber: one of the types of sclerenchyma that is long, straight, and thin; often occurring in bundles, 13, 70, 84, 151, 354, 390–391, 423, 446, 494, 515, 540, 585, 587, 595, 602, 605, 607, 664

Filament: stalk-like portion of a stamen, supporting the anther, 18, 20, 31, 39, 41, 140, 232, 312, 343, 349, 354, 391–392, 403, 409, 424, 446, 541, 577, 583, 587, 593, 603, 606, 683, 750, 753, 756

Fimbriate: margin divided into narrow or filiform segments, often of irregular sizes

Flagellum: long cellular appendage specialized for locomotion, unsheathed in an extension of plasma membrane

Florigen: universal hormone that supposedly causes plants to change from the vegetative to the reproductive state

Floury perisperm: a type of perisperm of some seeds; has the consistency of flour

Foliaceous: leaflike, 74, 76, 104, 110, 267, 387, 392, 408, 424, 498, 516, 565, 723, 750, 753, 757

Foliole: leaflet

Follicle: dry, one-celled fruit with a single placenta and splitting along the opposite edge, 58, 60, 81, 83, 136, 151, 156, 159, 233, 338, 555, 693, 781

Fresh fruit: fruit with succulent pericarp

Funicular: having the form of or associated with a cord, 33, 69, 71, 73–74, 266, 269, 278, 367, 370, 372, 387, 403, 427, 497, 541, 550, 667, 723, 773

Funiculus: basal stalk of an ovule arising from the placenta, as in the angiosperms, 32–33, 50, 69, 259, 278, 391, 403, 406, 409, 424, 440, 516, 521, 541, 603, 667, 749, 753, 756

Fusiform ray: cigar-shaped ray cell

Galea: in Orchidaceae, a perianth segment or group of perianth segments shaped like a helmet

Gamete: reproductive cell, a cell or nucleus that fuses with another in sexual reproduction, 46

Gametophyte: body that bears gametes; produced by the germinating spore, 26–27, 29, 45, 48, 68

Gamophyllous: having the bases of opposite leaves fused around the stem, 106

Generative cell: one of two haploid nuclei found within pollen grains of flowering plants; enters the pollen tube when it is produced, divides by mitosis, and becomes the male gamete nucleus that fuses with the female egg cell at fertilization, 31, 46

Geotropism: growth determined by gravity, 174

Gibberellin: any class of compound—found in certain mold fungi—that regulates plant growth

Glabrescent: smooth, 303, 486, 553, 572, 592, 693

Glabrous: without hairs, bristles, or stalked glands, 106, 174, 272, 277–278, 285, 289, 294, 300–301, 312, 342–343, 346, 353–354, 363, 391, 395, 403, 405–406, 408–409, 420, 423, 429, 439, 446, 452, 464, 470, 481, 486, 490–491, 494, 503, 511–512, 515, 531, 540, 547–548, 558, 561–562, 572, 576–577, 582, 587, 590, 592–593, 602, 643, 676, 687, 693, 703, 732, 735, 737, 742, 750, 753, 756, 767, 781

Gland: depression, protuberance, or appendage on the surface of an organ that secretes a usually sticky fluid; any structure resembling such a gland, 16, 18, 36, 110, 285, 316, 342–343, 403, 405, 408, 461, 487, 505, 511, 557, 576, 603, 606–607, 735

Gland of salt: hydatode that excretes water with a high salt and mineral proportion

Glaucous: surface with a fine white substance (bloom) that will rub off, 390, 452, 592

Globose: globe-shaped, spherical, 282, 335, 354, 391, 426–427, 436, 490, 564, 576–577, 590, 606, 645, 649, 651, 680, 710, 723, 732, 740, 781

Glomerule: small, compact cluster, 29

Glucogenesis: formation of glucose or glycogen from sources other than carbohydrates

Glume: a bract in the inflorescence of some monocots; one of the two bracts at the base of the grass spikelet; also used for Cyperaceae and Restionacae to refer to the small bracts on the spikelet in which the flower is subtended

Glutinous: sticky, gummy, having the quality of glue

Glyoxysome: microbodies found in seeds

Gramineous: of, pertaining to, or characteristic of grass

Guard cell: specialized epidermal plant; cell that forms the boundaries of the stomata

Gummosis: any of various viscous substances that are exuded by certain plants and trees, then dry into water-soluble, noncrystalline, brittle solids, 260

Gutation: process by which water passes from inside the leaf and is deposited on the outer surface

Gymnosperm: plant, such as a conifer or cycad, whose seeds are naked; the ovules not being enclosed in an ovary, 43, 45, 47, 60, 79, 241

Gymnospermous: bearing naked seeds, without an ovary

Gynobase: enlargement or prolongation of the receptacle bearing the ovary

Gynoecium: whorl or group of carpels in the center or at the top of the flower; all the carpels in a flower, 15, 18, 20–21, 23–24, 36–37, 48, 51, 58–59, 278, 312, 439, 491, 494, 512, 587, 589, 603, 654–655, 667, 702–703, 738, 749, 753, 756, 773

Halophyte: plant with the capability to grow in calcareous soil, 234, 315

Haploid (1n): one-half the normal diploid complement of chromosomes, 27, 31, 35, 49, 68, 142

Haulm: plant stem after removing edible fruit or seed, 723

Haustorium: absorbing organ of some parasitic plants through which substances pass from the host to the parasite

Heteromorphic: having different forms at different periods of the life cycle, 26, 278, 693

Heterosis: increased vigor or other superior qualities arising from the crossbreeding of genetically different plants

Hilar: of, relating to, or located near a hilum, 69, 71, 100, 163, 264, 269, 278, 335

Hilum: mark or scar on a seed produced by separation from the funicle or placenta, 35, 68–69, 77, 100, 162–164, 264, 266, 269, 278, 285, 321, 336, 355, 367, 370, 372–373, 387, 392, 394, 403, 416, 427, 437, 450, 452, 456, 497, 503, 521, 530, 533, 547, 550, 564–565, 649, 651, 667, 714, 723, 740

Horny perisperm: type of perisperm of some seeds; has a hard consistency

Hydathode: structure that secretes water; found in the margins of leaves

Hydrochorous: water environment, 70, 430

Hypanthium: floral tube formed by the fusion of the basal portions of the sepals, petals, and stamens from which the rest of the floral parts emanate, 23, 59, 397, 405, 541, 576–577, 589, 690

Hypocotyl: portion of the axis of a plant embryo below the point of attachment of the cotyledons; forms the base of the shoot and the root, 64, 73, 75–79, 93, 95, 97, 100–104, 114–116, 145, 158, 301, 387, 392, 456, 500, 512, 542, 559, 577, 603, 691, 750, 753, 757

Hypogeal: underground; subterranean, 94–95, 97–98, 102–104, 114–117, 157–158, 212, 287, 298, 354, 361, 403, 490, 494, 541, 583, 590, 602, 655, 680, 723, 730, 753

Hypogeal germination: of or relating to the emergence of cotyledons below the surface of the ground, 95, 102–103, 157–158, 490

Hypogynous: situated on the receptacle beneath the ovary and free from it and from the calyx; having the petals and stamens so situated, 23, 593, 773

Hypostase: condition in which the action of one gene conceals or suppresses the action of another gene that is not an allele but that affects the same organ, part, or state of the body, 33, 354

Imbricate: having the edges overlapping in a regular arrangement, as tiles on a roof, in the bracts or sepal of a plant, 18, 43, 312, 391, 405, 408–409, 490, 587, 589, 603, 654

Imperfect flower: unisexual flower; flower lacking either male or female parts, 24

Incomplete flower: flower acking at least one of the four basic parts; pistils, sepals, stamens, or petals

Incumbent: describing cotyledons lying with the back of one against the radicle, 75

Indehiscent: not opening naturally at or after maturity, 49, 51–52, 54, 64, 70, 85, 100, 152–153, 156, 160, 233, 264, 346, 366, 369, 372, 415, 426, 430, 436, 440, 442, 449, 479, 491, 494, 523, 550–551, 557, 583, 643, 654, 702

Indumentum: general term for the hairy or scaly covering of plants, 102, 342, 514, 516

Inferior ovary: one with the flower-parts growing from above; one that is adnate to the calyx., 52, 59, 232

Inflorescence: any complete flower cluster including branches and bracts; clusters separated by leaves are separate inflorescences, 15, 24–25, 27–29, 36, 51, 153, 157, 232–233, 308, 312, 321, 349, 386, 390, 397, 399, 413, 424, 456, 459, 479, 505, 516, 541, 553, 558, 561, 569, 576, 589, 593, 602, 695, 699, 708, 710, 722, 729, 735, 770

Infundibuliform: funnel-shaped, 415, 587

Infusion: liquid derived from seeping or soaking (leaves, bark, roots, etc.); extraction of soluble properties or ingredients, 308, 343–344, 366, 382, 386, 415, 436, 449, 497, 550, 597, 722

Integument: natural covering, as skin, shell, rind, etc.; also tegument, 32–33, 46, 48, 62, 68–70, 73, 79, 354, 541

Intercalary: meristem situated between the apex and the base, 103

Intine: inner wall of angiosperm microspore, 32, 42

Intrusive growth: growth of a cell into another cell

Involucre: collection or rosette of bracts subtending a flower cluster, umbel, or the like, 27, 29, 52, 508, 745

Jaspé (Jasper): having a mottled, variegated appearance imitating jasper

Jugate: yoked, 272

Kraft: strong, usually brown paper processed from wood pulp and used for bags and wrapping paper, 568, 640

Lamina: blade or expanded portion of a leaf, 140, 342, 395, 461, 503, 531, 547, 555, 558, 562, 606, 676, 687

Lanceolate: much longer than wide, widest below the middle, tapering toward the apex, or both apex and base; resembling a lance head, 103, 106, 108, 231, 244, 272, 311, 360, 366–367, 386, 391, 395, 415, 424, 464, 466, 468, 470, 473, 481, 494, 511, 521, 572, 575, 582, 687, 713, 722, 732, 735, 772

Laticifer: cell or series of longitudinal cells that contain a specific fluid called latex, 355

Leaf primordium: lateral outgrowth from the apical meristem that develops into a leaf

Leaf scar: mark left on a twig when a leaf falls, 294, 315, 474, 708

Leaflet: single segment (blade) of a compound leaf, 231, 297, 311, 360, 391–392, 408, 429, 446, 493, 695, 735, 737

Legume: member of the family Fabaceae with a dry, dehiscent fruit formed from one carpel and having two longitudinal lines of dehiscence, 58–59, 73, 152, 160, 162–164, 233, 272, 301, 366, 369, 372, 409

Lens: biconvex-lens shaped, 70, 163–164, 228, 264, 266, 269, 367, 370, 372, 450, 497, 550

Lenticel: corky spot on the surface of a twig; sometimes persists on the bark of a branch to admit air into the interior, 503

Ligneous: resembling wood; woody, 298, 363, 366, 372, 384, 394, 406, 449, 455, 607

Lignin: hard material embedded in the cellulose matrix of vascular plant cell walls; functions as an important adaptation for support in terrestrial species, 70

Lignotuber: woody underground stem

Ligule: strap-shaped corolla, as in the rayflowers of Asteraceae; a thin, often scarious projection from the summit of the sheath in grasses, 424, 541

Linear: narrow and elongated with sides parallel or nearly parallel, 42, 47, 64, 74–75, 79, 93, 103, 106, 108, 231, 241, 278, 327, 369–370, 373, 387, 586, 597, 602, 703, 713, 738

Littoral: shoreline environment, 236, 752

Lobe: segment of a leaf between indentations that do not extend to the midrib or base of the leaf, 151–152, 156, 232, 301, 324, 327, 329, 332, 354, 382, 391, 397, 403, 429, 436, 439, 444, 481, 490, 494, 516, 550, 558, 561–562, 583, 587, 603, 738, 749, 753, 756, 767

Locule: compartment or cavity of an ovary, anther, or fruit, 20–21, 51–52, 56, 151–153, 156–157, 391, 490–491, 494, 516, 541, 577, 587, 667, 738, 773, 778

Loculicidal: dehiscing lengthwise, dividing each loculus into two parts, 51, 56, 151, 154, 778

Loculus: cell of a carpel in which the seed is located; cell of an anther in which the pollen is located, 51

Lysosome: simple wall cell organelle containing enzymes to hydrolyze proteins and other organic macromolecules

Macrofibril: package of microfibrils found in the cell wall

Medium plane: plane that divides the seed into two equal parts

Medulla: tissue located in the center of the stem or root, 364

Megagametogenesis: development of the female gametophyte (megagametophyte) from a functional megaspore

Megagametophyte: female gametophyte; formed by vegetative growth of the megaspore of a heterosporous plant, 33, 35, 46–47, 79, 93

Megophyll: well-developed leaf

Megasporangium: female sporangium containing the megaspores, 32, 46

Megaspore: spore in heterosporous plants that gives rise to a female gametophyte and is generally larger than the microspore; the spore usually not shed but remaining on the parent plant and developing in situ, 29, 35, 45–48, 79

Megasporogenesis: the development of the megaspore from the archesporial cell., 35

Megasporophyll: the leaf bearing the megasporangia, 44–45

Meiosis: two-stage division of a diploid nucleus in which genetic recombination occurs and the number of chromosomes characteristic of the species is halved prior to the production of the sexual gametes, 29, 31, 35, 46–47, 68

Membranous: thin and translucent, 106, 153, 312, 318, 363, 375, 427, 430, 437, 497, 555, 558, 577, 667, 716, 775

Mericarp: portion of fruit that seemingly matured as a separate fruit, 59

Meristem: undifferentiated tissue from which new cells are formed, 64, 79, 91, 100, 103

Mesarch xylem: middle position of the protoxylem

Mesocarp: fleshy part of the wall of a succulent fruit; the middle layer of the pericarp in a drupe, 48, 51, 77, 81, 83–85, 208, 278, 298, 312, 354, 391, 403, 406, 430, 440, 446, 494, 515, 558, 577, 590, 602, 605, 658, 662, 667, 702, 746, 749, 753, 756

Mesocotyl: internode formed between the scutellum node and the coleoptile of the grass embryo or seedling

Mesomorphic: soft and with little fibrous tissue, but not succulent

Mesophyll: middle and photosynthetic tissue of a leaf, 111, 113, 163–164, 183, 521, 750, 756

Microbodies: small organelles containing enzymes, having a specialized role in a specific metabolic pathway

Microfilaments: fibrous elements with high protein content that are involved in generating cytoplasma movement, 140

Microgametogenesis: the development of the microgametophyte (pollen grain) from a microspore

Microphyllous: having small leaves that are usually hard and narrow

Micropyle: integumentary opening of the ovule through which pollen enters prior to fertilization, 32–33, 35, 43, 46–48, 68–69, 71, 77, 100, 162–163, 264, 266, 269, 278, 336, 355, 367, 370, 372–373, 387, 416, 427, 437, 450, 491, 494, 497, 521, 541, 550, 565, 649, 651, 667, 714, 723, 740

Microspecies: segregated species of a larger species or species-aggregate, 247

Microspophyte: mother cell of the pollen

Microsporangios: sporangia in which the spores are formed

Microsporangium: sporangium from which the microspores are formed, which in higher plants is the pollen sac, 30–31, 45–46

Microspore: smaller of the two types of spores produced by ferns and higher plants, giving rise to the male gametophyte; in Tracheophytes, the microspore is the pollen grain, 31–32, 46

Microsporocarp: a body containing the microsporangium

Microsporogenesis: development of microspores from the microspore mother cell, 31

Midrib: central or main vein of a leaf or leaf-like part, 232, 355, 491, 516, 750, 753, 756, 781

Mitochondrion: organelle in eukaryotic cells that serves as the site of cellular respiration

Mitosis: normal cell division in which each daughter cell has exactly the same chromosome number as the mother cell, 64, 68–69, 142

Monocotyledons: plants with single seed-leaves (cotyledons), 15, 66, 68, 74–75, 100–101, 111, 113

Monoecious: having stamens and pistils in separate flowers on the same plant, 24, 27, 43, 241, 335, 386, 390, 505, 530, 558, 561, 729

Monotypic: having only one representative, 399, 537, 575, 646–647, 654

Morphology: study of the form and structure of an organism, 14, 23–24, 35–36, 62, 70, 80, 89, 94, 102, 195, 225–226, 230, 615, 673, 723, 756

Mother cells: special cells in the anther and ovule that give rise to pollen or egg cells, 31, 46, 48

Mucilage: any of various gummy secretions or gelatinous substances, 41–42, 69–70, 79, 81, 163, 336, 439

Mucronate: having an abruptly projecting point, 111, 264, 548

Muller body: multicelled body in which glycogen is accumulated

Mycorrhiza: symbiotic association of fungus and root, 102, 118, 151–157

Naked flower: having no perianth

Nectary: gland that secretes nectar, 272, 278, 491, 606, 667, 738

Needle: narrow, usually stiff leaf, as in pines, firs, and hemlocks, 106, 230, 615, 629, 632

Nervation: arrangement of veins, as in a leaf; venation, 264, 285, 426, 468, 505, 535, 553, 585

Node: the narrow region on a stem where a leaf or leaves are or were attached, 95, 100, 102–103, 107, 231, 477

Nodose: having nodules, 420

Nucellus: central cellular mass of the body of the ovule, containing the embryo sac; equivalent to the megasporangium, 32, 35, 46, 70

Nucleolus: small, generally spherical body found within the nucleus of eukaryotic cells; site of ribosomal RNA synthesis

Nucleoplasm: granular substance of the nucleus

Nut: dry, hard, indehiscent, one-celled and one-seeded fruit; usually resulting from a compound ovary, 53, 73, 87, 89, 152–156, 233, 335, 375, 400, 745, 767

Ob–: prefix signifying an inversion such as obcordate, the opposite of cordate

Oblong: elongate in form with sides parallel or nearly parallel, the ends blunted and not tapering; wider than long, 75, 103, 108, 232, 264, 269, 275, 278, 297–298, 301, 308–309, 312, 318, 353–354, 369, 372, 386–387, 391, 406, 408–409, 415, 420, 423, 429–430, 436–437, 439, 442, 452, 476, 486, 491, 494, 497–498, 521, 541, 547, 550, 553, 562, 564, 575, 589, 597, 643, 667, 676, 683, 687, 701–703, 708, 713, 719, 722, 732, 750, 753, 755–756, 775, 778, 781

Obovate: ovate with a narrow end at the base; inversely ovate, 103, 108, 231, 241, 280, 342, 353, 369, 372, 375, 426, 487, 514, 558, 564, 583, 592, 602, 651, 667, 676, 683, 685, 687, 713, 723, 737, 740, 748, 752, 755, 772, 775, 778, 781

Obtuse: blunt point, the angle of the point greater than 90 degrees, 111, 232, 264, 278, 285, 289, 298, 311, 342, 354–355, 360, 369, 391–392, 405, 426, 429, 486, 491, 493, 497, 503, 514, 531, 541, 555, 561, 565, 575, 582, 587, 589, 602, 676, 683, 687, 693, 701, 719, 735, 737, 748, 756, 778

Oligosaccharine: small molecules produced by enzymatic process in the cell wall; thought to affect the growth, morphogenesis, reproduction, and defense mechanisms

Ontogeny: development of an individual organism; for example, human embryonic development from a unicellular zygote to an adult, 16, 69, 100

Oosphere: egg

Opposite: growing in pairs, one on each side of the axis and 180 degrees from each other, 15, 20, 46, 49, 66, 100, 103, 110–111, 116, 213, 230–231, 264, 269, 277, 297, 300, 303, 311, 315, 318, 342, 360, 367, 370, 373, 390–392, 402, 406, 408, 420, 432, 446, 450, 456, 464, 468, 470, 474, 486–487, 491, 497, 531, 535, 542, 547, 550, 603, 643, 666–667, 701, 719, 723, 732, 735, 749, 753, 756, 765, 778, 781

Orbicular: circular in outline, 232, 282, 312, 397, 430, 439, 512, 583, 593, 654

Organelle: specific part and function of a cell

Organogenesis: early period of rapid embryonic development in which the organs take form from the primary germ layers, 64

Ovary: part of the pistil containing the ovules; produces seeds and matures into a fruit, 20–21, 23, 48–49, 51–54, 59, 151, 154–157, 231–233, 298, 312, 318, 342–343, 354, 361, 380, 391, 403, 405, 409, 412, 424, 430, 439, 452, 487, 491, 494, 512, 516, 541, 557–558, 561, 576–577, 583, 587, 590, 593, 603, 606, 738, 750, 752–753, 757, 767, 781

Ovate: two-dimensional structure having the outline of an egg with the wider half below the middle, 108, 231, 264, 266, 269, 272, 278, 285, 289, 300, 312, 335, 342–343, 354, 366, 397, 403, 415, 420, 424, 430, 436–437, 446, 449, 452, 458, 503, 511, 514, 521, 541, 550, 561, 565, 572, 576, 586–587, 602, 667–668, 693, 698, 703, 722, 735, 773

Ovoid: three-dimensional structure having the shape of an egg with the broader half below the middle, 308, 311, 315, 321, 354, 375, 387, 391–392, 394, 403, 409, 430, 432, 468, 505, 516, 541, 564, 576, 590, 593, 605–606, 609, 619, 625, 636, 649, 651, 680, 687, 722, 740

Ovule: structure found in higher plants that contains an egg cell and develops into a seed after fertilization, 16, 20–21, 24, 29, 32–35, 37, 43, 45–46, 48–49, 52, 62, 68–69, 73, 151, 153–157, 159, 230, 232, 241, 278, 298, 312, 351, 354, 361, 391, 403, 405, 409, 412–413, 424, 430, 439, 491, 494–495, 512, 516, 541, 577, 583, 587, 593, 603, 667, 703, 738, 749–750, 753, 756–757, 767, 773

Palmate: radiately arranged, ribbed, or lobed, as fingers of a hand, 107, 231, 708, 735

Palminerved: having lobes radiating from a common point, 553

Panicle: inflorescence in which the lateral branches arising from the peduncle produce flower-bearing branches instead of single flowers, 27, 28, 152, 154, 233, 264, 280, 294, 298, 312, 315, 318, 321, 327, 346, 354, 366, 386, 390, 399, 405, 408, 415, 418, 423, 429, 446, 474, 476, 490, 500, 505, 508, 515–516, 532, 537, 547, 561, 580, 593, 597, 599, 605, 670, 673, 695–696, 698, 710, 713, 722, 726, 734–735, 740, 745, 767, 773, 775, 778, 781

Papilla(–ae): A minute nipple-shaped projection, 391

Parenchyma cell: relatively unspecialized plant cell type that performs most of the metabolism, synthesizes and stores organic products, and develops into more differentiated cell types

Pari–: prefix meaning equal

Parthenocarpy: production of fruit without seeds, as in bananas and some grapes, 48

Parthenogenesis: type of reproduction in which females produce offspring from unfertilized eggs, 68

Pedicel: stalk of a single flower, 15, 27, 29, 40, 49, 53, 232–233, 312, 343, 363, 397, 400, 409, 424, 456, 464, 471, 540–541, 561, 589, 593, 602, 606, 743, 745, 762

Peduncle: main flower stalk of the inflorescence supporting either a cluster of flowers or the only flower of a single-flowered inflorescence, 27, 29, 59, 232–233, 301, 315, 408–409, 424, 447, 464, 481, 487, 516, 540, 558, 561, 589, 607, 612–613, 618–619, 622, 625, 628, 636, 639, 645, 660, 666, 683, 687, 749

Pellucid: translucent, 781

Peltate: having the stalk of a leaf attached to the lower surface of the blade somewhere within the margin, rather than on the margin, 108, 110, 289, 382, 516

Pendulous: drooping or hanging loosely, 154, 289–290, 391, 394, 516, 580

Pentamerous: grouped in fives, 15, 278, 312, 390–391, 409, 576, 602, 657, 666, 702, 749, 752, 756

Perennial: plant that lives for more than 2 years, 43, 196–197, 222, 379, 461, 501, 606

Perfect: flowers having both functional stamens and pistils, 15, 24, 42, 113, 223, 230, 315, 348, 537, 576, 745, 752

Perianth: calyx and corolla collectively, or the calyx alone if the corolla is absent, 15–18, 23, 27, 36–37, 41, 48, 59, 80, 83, 87, 89, 100, 153, 156, 382, 397, 424, 541, 576–577, 589, 593, 606, 678, 770, 773

Pericarp: walls of a ripe ovule or fruit, 48–49, 51–54, 59–60, 64, 78, 81, 83, 85–87, 93–95, 100, 104, 264, 269, 278, 287, 294, 309, 354, 363, 366, 369, 372, 391–392, 420, 424, 426, 430, 440, 444, 449, 476, 487, 490, 494, 497, 512, 537, 541, 576, 583, 593, 605, 655, 667, 678, 680, 691, 698, 702, 722, 750, 757

Periclinal: parallel to the surface, 31, 69

Perigynium: inflated sac that encloses the ovary in Carex

Perigynous: adnate to the perianth; therefore around the ovary and not at its base, 23, 153

Periodicity: the tendency to occur regularly, 43, 500

Perisperm: food reserve tissue found in the seeds of certain plants; derived from a diploid nucellus, e.g. coffee, beets, spinach; unlike endosperm, formed outside the embryo sac, 49, 68, 73–75, 78, 149, 155, 278, 355, 403, 593, 603, 668, 703, 750, 753, 756, 773

Peroxisomes: microbodies containing large amounts of catalase enzyme used to remove often harmful metabolic byproducts

Persistent: remaining attached past the expected time for dropping, 35, 79, 89, 156, 195, 197, 201, 259, 294, 301, 312, 315, 375, 412–413, 429, 618–619, 667, 690, 732, 738

Petal: one of the parts of the corolla, the inner set of the perianth; may be separate or united to another petal, 15–18, 20, 39, 89, 151–157, 232, 312, 318, 324, 327, 329, 332, 338, 342, 354, 360, 391, 412, 420, 424, 429, 439, 461, 487, 490, 494, 508, 532, 541, 555, 557, 580, 583, 587, 595, 603, 606, 646, 678, 690, 695, 698, 713, 759, 767

Petaloid: sepal having color and texture similar to that of the petal, 452, 654

Petiole: attaching stalk of a leaf; sometimes absent, 101, 103, 106–107, 115–116, 229, 231, 244, 254, 272, 278, 285, 311, 315, 324, 327, 329, 343, 363, 382, 390, 395, 397, 403, 405, 432, 452, 456, 461, 468, 486, 491, 500–501, 503, 505–506, 511–512, 514, 531, 535, 541, 547, 555, 558, 562, 572, 575, 577, 582, 585, 587, 603, 667, 680, 687, 693, 695, 698, 703, 708, 723, 732, 737, 750, 753, 757, 759, 767, 773, 778, 781

Phelloderm: tissue similar to the cortical parenchyma produced centripetally by the phellogen (cork cambium) as part of the periderm

Phellogen: sheet-like meristem that produces cork

Phellum: protecting tissue on the outer surface, derived from a cork cambium or phellogen

Phloem: part of the vascular bundle consisting of sieve tubes, companion cells, parenchyma, and fibers and forming the food-conducting tissue of the plant; the photosynthate-conducting tissue of plants, 49, 102, 423, 540, 667

Photoperiodism: response (e.g., flowering, germination) of organisms to the relative length of the daily periods of light and darkness

Phyllode: expanded petiole resembling and having the function of a leaf, 106, 251

Phylotaxy: arrangement of leaf order

Pilose: covered with hair, especially soft hair, 106, 297, 391, 397, 767

Pinnate: having lobes or blades of a leaf arranged along the sides of a common axis; also applies to major lateral veins of a leaf, 106, 113, 115, 231, 278, 355, 360, 390, 408, 490, 493, 511, 516, 521, 541, 576, 597, 599, 667, 695, 698, 713, 772, 778

Pinnule: foliole of second or third order, 403

Piscicidal: poisonous to fish, 282, 512

Pistil: female, ovule-bearing organ of a flower, composed of stigma(s) and ovary, usually with a style or styles between; consists of a single carpel or two or more fused carpels, 230–233, 380, 452, 487, 606, 698

Pit: hard endocarp that encloses the seed of a drupe, 363, 533, 580

Placenta: ovule-bearing surface in the ovary and seed-bearing surface in the fruit, 20, 33, 59, 344, 603

Placentation: method of attachment of the seeds within the ovary, 20–22, 278, 391, 409, 424, 512, 541, 603, 667, 702, 749, 753, 756, 773

Plagiotropic: attracted to one side, 748, 750, 752–753, 755, 757

Plasmalemma: membrane that surrounds the cytoplasm, 35, 43

Plasmodesma: cytoplasmic channels lined with a plasma membrane connecting the protoplasts of adjacent cells across the cell wall

Plasmolysis: disruption of the protoplasm due to a lack of water in the osmosis process

Plastid: any of various cytoplasmic organelles of photosynthetic cells that serve in many cases as centers of special metabolic activities, e.g., chloroplasts, 139, 146

Plumule: shoot of the embryo, 64, 66, 77, 95, 100, 103, 114–117, 158, 163, 264, 267, 270, 278, 336, 354–355, 361, 367, 370, 373, 376, 387, 403, 406, 416, 424, 427, 437, 450, 456, 490–491, 494–495, 498, 501, 512, 541–542, 550, 559, 565, 577, 602–603, 649, 652, 668, 703, 714, 723, 740

Pneumatophor: specialized roots for aeration

Pod: any dry, dehiscent fruit, 53–54, 58–59, 81, 120, 123, 136, 152, 154–156, 159, 233, 244, 247, 250, 253, 256, 274–275, 278, 280, 282–283, 324, 327, 329, 332, 346, 349, 351, 403, 405, 409, 430, 433, 440, 442, 446, 452, 459, 461, 518, 523, 545, 547, 551, 579–580, 583, 593, 597, 599, 602, 643, 654–655, 657–658, 667–668, 670–671, 673–674, 701–703, 716, 719, 738, 742–743

Polar nuclei: two nuclei formed at each pole of the angiosperm embryo sac; they will fuse with a male nucleus to form a primary endosperm nucleus, 35, 43

Polarity: structural and/or physiological difference established in the plant, embryo, organ, tissue, cell, 64, 66

Pollarded: cut back nearly to the trunk to produce a dense mass of branches, 274

Pollen: male spore-like structures produced by anthers in flowers and by male cones, 18, 20, 23–24, 26–27, 29–33, 35–43, 45–48, 144, 230, 232, 278, 330, 343, 405, 424, 470, 491, 512, 516, 541, 577, 603, 606, 625, 667, 691, 750, 753, 756

Pollen grain: small structure of higher plants that contains haploid male gamete nuclei and is surrounded by a double wall, the exina and intina; transported from the male stamen to the female stigma in a process called pollination, 23, 26–27, 29–32, 36, 39–41, 43, 46–47, 232, 405, 516, 603, 750

Pollen sac: locus in the anther that contains the pollen grains, 18, 32, 45–47, 232

Pollen tube: microscopic tube that grows down the stigma from the pollen grain; through it the sperm cells are deposited into the embryo sac, 23, 26, 29, 31–33, 42–43, 46–48, 232

Pollination: process by which pollen is transferred from the anther where it is produced, to the stigma of a flower, 23–24, 26, 32–33, 35–36, 38–43, 46–49, 159, 202, 208–209, 232, 346, 349–350, 355, 379, 390, 400, 403, 412–413, 424, 494, 508, 512, 541, 576, 590, 593, 606, 616, 633, 702, 726, 738, 749, 756, 773

Pollinium: mass of pollen grains

Polymorphic: having, assuming, or passing through many or various forms or stages; polymorphous, 160, 508

Polysome: ribosome associated with protein syntheses

Pome: fruit in which the floral cup forms a thick outer fleshy layer and has a papery inner pericarp layer (endocarp) forming a multiseeded core (e.g., apple, pear), 59, 159

Poricidal: anther opening by pores, 56, 516

Prick: transplant into a container that provides more room for growth

Primary cell wall: cell wall layer deposited while a cell is growing; typically extensible

Primordium: organs in their earliest stages of development, as a leaf primordia or meristem

Procambium: meristem that develops into the vascular tissue

Proembryo: young embryo in its early stages of development, 64, 68

Propagule: propagative part, as a bud or shoot, 80, 212, 538, 691

Proteoplastid: plastid that stores protein

Protocorm: fleshy tissue with few cells, formed from the rudimentary embryo in the orchidaceous seeds

Protoderm: develops into the dermal tissue system

Protofila: first leaf-pair in the plant, after the cotyledons

Protoplast: organized, living portion of cell

Pseudocarp: fruit that develops not only from the ripened ovary, or ovaries, but from nonovarian tissue as well

Puberulent: minutely pubescent, 41, 106, 391, 397, 424, 452, 486–487, 540, 589, 676, 683, 687, 781

Pubescent: covered with fine, short hairs, 87, 106, 174, 289, 300, 327, 343, 390–391, 403, 405, 409, 423, 446, 490–491, 494, 572, 576, 582–583, 587, 592–593, 603, 605–607, 658, 666–667, 687, 703, 735, 748–749, 753, 755–756, 767, 775

Pulvinule: pulvinus at the base of a petiole

Pulvinus: swelling at the base of the petiole; related to leaf movement, 106, 278, 667, 703

Punctate: spotted with colored or translucent dots or depressions, usually due to glands, 72, 397, 406, 781

Puntiform: rod-like, 264, 269, 336, 367, 372, 450, 550, 649, 652, 723

Pyrene: hard or stony endocarp; nutlet, 415, 437

Pyriform: pear-shaped, 479, 577, 587, 649

Raceme: type of inflorescence in which the single-flowered pedicels are arranged along the sides of a flower-shoot axis, 27–29, 153–154, 156–157, 253, 266, 282, 324, 327, 332, 349, 369, 372, 405, 423, 433, 436, 439, 442, 444, 456, 459, 461, 470, 490, 497, 518, 530, 532, 540, 550–551, 583, 593, 602, 643, 646, 662, 670, 673, 693, 708, 710, 713, 716, 742, 749, 756, 767, 770

Rachis: main axis of a spike or of a pinnately compound leaf, excluding the petiole, 106, 278, 397, 403, 424, 446, 452, 486, 491, 512, 531, 540, 547, 576, 582, 589, 599, 602–603, 667, 676, 683, 685, 687, 693, 695, 698, 703, 749, 781

Radial symmetry: when cut through the center along any plane, produces similar halves, 15

Radicle: portion of the embryo below the cotyledons that will form the roots, more properly called the caudicle, 75–79, 90–91, 93–94, 100–101, 104, 115–116, 149, 158, 163, 168, 170, 172, 174, 176, 178, 259, 264, 267, 270, 278, 301, 315, 336, 355, 361, 363, 367, 370, 373, 376, 387, 392, 397, 403, 406, 413, 416, 424, 427, 437, 450, 456, 481, 491, 494–495, 498, 512, 516, 521, 538, 542, 550, 565, 593, 602–603, 649, 652, 657, 667–668, 691, 696, 703, 714, 723, 740, 749, 753, 756, 759, 773

Raphe: ridge connecting the hilum with the chalaza, 32, 69, 71, 558, 561

Receptacle: portion of the axis of a flower stalk on which the flower is borne, 15–16, 20, 27, 59–60, 80, 83, 87, 232, 590, 660, 667, 703, 756

Reflexed: abruptly turned or bent toward the base, 342, 439, 580, 619, 636, 668

Refracted: bent sharply backward

Regular flower: flower that is radially symmetrical: petals and sepals are of similar size and shape

Reniform: kidney shaped, 103, 110, 397, 440, 550, 750, 753, 757

Reticulate: having the veins or nerves disposed like the threads of a net, 41, 70–71, 75, 113, 264, 311, 397, 405, 429, 497, 558

Retrorse: directed backward and downward

Revolute: rolled under at the margin, i.e. toward the underside, 109, 429, 555, 589, 687, 781

Rhizome: underground stem usually growing horizontally

Rhizosphere: soil surrounding the root, 102

Ribosomes: protein synthesis structures, 64

RNA: ribose nucleic acid (ribonucleic acid), 49, 91

Rugose: rough and wrinkled; applied to leaves on which the reticulate venation is very prominent underneath, 41, 369, 386, 406, 409, 415, 486, 592, 652, 680

Sagittate: shaped like an arrowhead, 108, 110

Samara: indehiscent, winged fruit in which the seedcoat is loose inside the pericarp (e.g., maple, ash), 51, 53, 89, 152, 379, 430, 474, 749, 756, 770

Samaroid: having the shape of the samara, 53, 152, 375, 386, 583, 722

Sarcotesta: fleshy testa, 69, 83, 85–86, 97, 154, 491, 494–495

Scabrous: rough or harsh to the touch due to minute stiff hairs or other projections, 41

Scale: applied to many kinds of small, thin, flat, appressed, usually dry leaves or bracts, often vestigial; sometimes epidermal outgrowths, if disclike or flattened, 45, 62, 123, 134, 184, 241, 392, 567, 603, 612, 616, 622, 640, 660

Scape: long stem that finishes in a flower or inflorescence, 29

Scion: part of plant inserted into a stalk for grafting

Sclereids: type of sclerenchymatic cells, variable in shape but typically not long, with thick and lignified secondary walls, 70

Sclerenchyma: tissues composed of cells with thick, secondary cell walls that are usually lignified, 69–70, 79, 605

Scutellum: shield-shaped organ of the embryo of grass; often viewed as a highly modified cotyledon in monocotyledons

Seedcoat: outer protective layer of a seed that develops from the integument of the ovule; testa, 32, 47, 54, 62–63, 68–70, 73–75, 77–79, 81–82, 86–87, 91, 93–95, 97, 100, 103–104, 114–116, 149, 158–160, 162, 164–166, 169, 172, 178–179, 182, 250, 266, 269, 312, 318, 335, 350, 354, 361, 366–367, 369, 372, 375, 386, 391, 416, 426, 430, 437, 449, 452, 459, 494, 497, 515, 521, 541, 545, 564, 576, 583, 590, 593, 595, 602, 646, 649, 651, 667, 705, 713, 722, 749–750, 753, 756–757, 773

Seminal rudiment: ovoid structure formed above the placenta or carpellary leaf; composed of the nucellus and one or two teguments surrounding it

Senescence: aging, a progression of irreversible change in a living organism, eventually leading to death, 48–49, 193, 200, 207–208

Sepal: one of the parts of a calyx or outer set of flower parts; may be separate or united to another sepal, 15–17, 151–157, 232, 312, 338, 342–343, 354, 363, 380, 405, 409, 424, 487, 532, 541, 561, 580, 603, 606, 678, 690, 695, 698, 749, 753, 756, 773

Septate: divided by a septum or septa, 278, 366, 369, 372, 403, 602, 702, 719, 767

Septum: dividing wall or membrane in a plant, 50, 366, 369, 372, 424, 516, 541

Sericeous: covered with silky down, 110, 420, 494

Serotinous: late in occurring, developing, and flowering, 616, 618

Serrate: having sharp, sawlike teeth pointed upward or forward, 109, 289, 311, 511, 693

Serrulate: finely or minutely serrate, 109, 474, 735

Sessile: lacking any kind of stalk, 27, 29, 103, 106, 110, 231, 280, 308, 363, 395, 402, 486, 516, 568, 587, 593, 602, 645, 651, 654, 701, 719, 773

Sessile leaf: leaf that has no petiole, 106

Setiform: bristle-like, 278

Sheath: tubular structure surrounding an organ or part, such as the basal part of a leaf; the circle of scales around the base of pine needles, 110, 145, 298, 309, 695, 698

Shrub: woody plant less than tree size, frequently with several branches at or near the base, 157–158, 184, 197, 222, 228, 247, 324, 346, 348, 397, 561, 569, 579, 595, 646, 657

Sieve: transverse partition with holes, 568

Sieve element: conducting elements involving sieve cell and sieve tube member

Silique: dry, dehiscent, elongated fruit formed from a superior ovary of two carpels, with two parietal placentas, and divided into two loci by a false septum between the placentas; occurs in plants of the family Cruciferae

Simple fruit: fruit developed from a single ovary, 51, 233

Sincarpica flower: flower with its carpels fused

Sinus: cleft or recess between two lobes of an expanded organ such as a leaf, 762

Sode: supporting structure

Spadix: spike with a thickened, fleshy axis, usually enveloped by a conspicuous or colored bract called a spathe., 27–29

Spathe: large bract at the base of a spadix, which it encloses (at least initially) as a sheath, 27, 29

Spatulate: shaped like a spatula; somewhat widened toward a rounded end, 74–76, 79, 104, 108, 308, 376, 426, 565, 583, 714

Spike: type of inflorescence in which stalkless flowers are attached along the sides of an elongated common axis, 27–29, 156, 233, 250, 568, 676

Spoil: material excavated; usually in mining or dredging

Sporophyll: specialized leaves for housing spores

Sporophyte: diploid plant producing meiospores after meiosis; occurs within alternating generations, 24, 26–27, 29, 33, 47, 49, 62, 90, 94

Squamiform: scale-like, 106, 111, 117, 424, 541–542

Stamen: male sporophyll within the flower; in angiosperms, the floral organ that bears pollen, 16, 18–20, 29, 48, 59, 232, 298, 324, 380, 452, 587, 750, 753, 756

Staminode: stamen in which the microsporangium of the anther remains reduced and sterile, 738

Starch: water-insoluble polysaccharide found as common carbohydrate storage, 31, 49, 73, 91, 127, 139, 335, 462, 577, 605, 696, 776

Stellate: star-shaped; applicable where several similar parts spread out from a common center, as with clustered hairs, 285, 587, 683, 734–735, 773

Stigma: pollen-receptive part of a pistil, often enlarged, usually at the tip of the style, 20, 23–24, 26–27, 32, 37, 43, 232, 298, 312, 318, 350, 354, 391, 403, 405, 409, 430, 439, 452, 494, 516, 576, 583, 587, 590, 593, 603, 606, 655, 738, 750, 753, 756

Stipe: stalk of a pistil; not the pedicel; stalk under elevated glands, 403, 452, 487, 491, 494, 687

Stipitate: having a stipe or borne on a stipe, 39, 298, 405–406, 409, 430, 439, 583

Stipule: one of a pair of lateral appendages at the base of a leaf petiole, 110, 315, 586

Stolon: large, indeterminate, underground stem that is capable of giving rise to a new plant

Stoma: small pore in leaf epidermis; used for gas exchange

Stone: drupe, 229, 233, 321, 340, 366, 476, 521, 745

Stool: cluster of shoots or stems springing up from a base or root, 641

Stratification: moist, cold storage, 139, 142, 153, 168–169, 179, 182, 242, 464, 471, 473, 568, 616, 629, 633

Strobile: cone-like structure, 43, 45, 62

Strophile: appendage at the hilum of certain seeds

Style: usually attenuated portion of the pistil connecting the stigma and ovary, 20, 23, 26–27, 32, 39, 43, 59, 136, 156, 224, 232, 285, 298, 308, 312, 321, 343, 354, 380, 387, 391, 403, 409, 424, 429–430, 439, 452, 487, 490–491, 493–494, 516, 541, 576, 583, 587, 590, 593, 603, 606, 612, 622, 636, 639, 655, 698, 723, 729, 732, 738, 749–750, 753, 756

Sub–: prefix signifying almost, less than completely, somewhat, under

Subbasal: related to, situated at, or forming the base, 264, 266, 367, 370, 372–373, 437, 565, 649, 651, 714

Suberin: complex of fatty substances present in the wall of cork tissue that waterproofs it and makes it resistant to decay, 70, 163

Suberize: convert to corky tissue, 102

Substrate: base on which an organism lives, 14, 36, 169, 174, 207, 259, 262, 287, 292, 303, 336, 361, 382, 384, 394, 464, 466, 468, 471, 473, 481, 490, 508, 515, 526, 528, 530, 562, 587, 602, 662, 678, 711, 770, 773, 776, 782

Subterete: positioned underneath, 514

Superior ovary: ovary with the flower-parts growing from below it, 51, 151, 232, 767

Suspensor: group or chain of cells produced from the zygote that pushes the developing proembryo toward the center of the ovule and its nutrient supply, 64, 67–68, 79

Sward: grassy surface of land; turf, 256–257

Sympodial: an axis made up of multiple bases, 595, 737, 748, 752, 755

Syncarpous: having the carpels of the gynoecium united in a compound ovary, 20–21, 308

Synergid nuclei: two of the eight cells of the embryo sac, usually remaining nonfunctional

Synpetalous: without petals, 278

Synsepalous: without sepals, 278, 390

Tapetum: layer of nutritive cells that lines the pollen sac, 31, 46, 48

Tegmen: part of the seminal cover, derived from the tegument, 33, 68, 70, 73, 77–78, 114–115, 354, 391, 427, 494, 516, 541, 576–577, 590, 593, 602, 722–723, 750, 753, 756, 773

Tegument: covering; integument, 363

Tepal: perianth member or segment; term used for perianth parts undifferentiated into distinct sepals and petals

Terete: circular in cross section, 289, 390, 403, 415, 491, 516, 582, 649, 651, 693

Terminal bud: apex of the leaf is at the tip end opposite the petiole, 231, 456, 490, 493, 538, 606

Testa: outer covering of the seed; the seedcoat, 33, 68–71, 77–78, 81, 83, 114–115, 156, 164, 181–182, 275, 278, 282, 301, 309, 321, 354, 363, 391, 403, 406, 432, 456, 512, 516, 530, 553, 559, 576–577, 590, 593, 651, 655, 667, 703, 719, 722–723, 750, 753, 756, 773, 775

Tetramerous: relating to groups of four, 15, 354, 516

Thorn: hard, sharp-pointed stem, 106, 110, 235–236, 303, 394, 452, 456, 458, 461, 657–658

Tomentose: densely covered with soft, fine, matted, wooly, relatively short hairs, 110, 342–343, 391, 420, 494, 553, 666–667, 685, 693, 703

Tonoplast: membrane surrounding the vacuole

Torose: cylindrical with alternate swellings and contractions

Torulose: somewhat torose, 597

Tracheary element (xylem): conducting cell of the xylem, characterized by an elongated shape and lignified secondary cell wall; involves tracheids and vessel members

Transmedium plane: plane perpendicular to the medium plane

Transpiration: passage of water through the stomas or cuticle

Transverse plane: plane perpendicular to the medium and transmedium planes

Trichome: hair, bristle, scale, or other such outgrowth of the epidermis, 110, 756

Truncate: having an apex or base that is almost or quite straight across, if cut off, 111, 355, 397, 408–409, 493–494, 512, 587, 603, 750, 753, 756

Tuber: underground stem in which carbohydrates are stored

Tuff: cluster of short-stalked flowers, leaves, etc., growing from a common point

Turbinate: top-shaped; a solid having a tapering base and a broad, rounded apex, 74, 439

Umbel: inflorescence on which a number of flower stalks or pedicels, nearly equal in length, spread from a common center, 27–29, 233, 436, 464, 470, 589, 703, 708, 770

Unguiculate: having a small hook, 17, 342

Vacuole: a small cavity, 69, 139

Valvate: opening by valves, as certain capsules and anthers; meeting without overlapping, as the parts of certain buds, 18, 278, 403, 409, 490, 494, 603, 666–667, 702–703

Valve: one of the segments into which a capsule dehisces; flap or lid-like part of certain anthers, 32, 50, 95, 104, 115, 155, 163, 269, 285, 361, 366, 372, 379, 386, 391, 394, 403, 406, 464, 468, 490, 494, 521, 580, 587, 593, 595, 602, 667, 702, 722, 753

Vestigial: of or pertaining to a degenerate or imperfectly developed organ or structure having little or no utility, but which in an earlier stage of the individual or in preceding organisms performed a useful function, 17, 95, 103, 115, 361, 391, 516, 603, 749, 756, 773

Villous: densely covered with soft, fine, unmatted, relatively long hairs, 516, 583, 585, 765

Viscid: sticky

Whorl: three or more structures (leaves, stems, etc.) in a circle, not spiraled, 18, 20, 27, 29, 79, 151, 156, 232, 378, 424, 512, 589, 749, 753, 756

Wing: membrane; or thin, dry expansion or appendage of a seed or fruit, 46, 72, 79, 89, 123, 152–153, 161, 241, 298, 303, 324, 375, 386–387, 391, 412, 424, 430, 439, 444, 452, 474, 553, 558, 580, 583, 609, 613, 618–619, 622, 625, 636, 646, 670, 673, 716, 722–723, 735, 738, 749, 756, 767, 776

Xylem: vascular tissue; wood, 102, 164

Zygomorphic: having bilateral symmetry, 15–16, 20, 38, 424, 429, 446, 456, 541, 738, 775, 778

Zygote: fertilized egg, 29, 43, 45, 47–48, 64, 79

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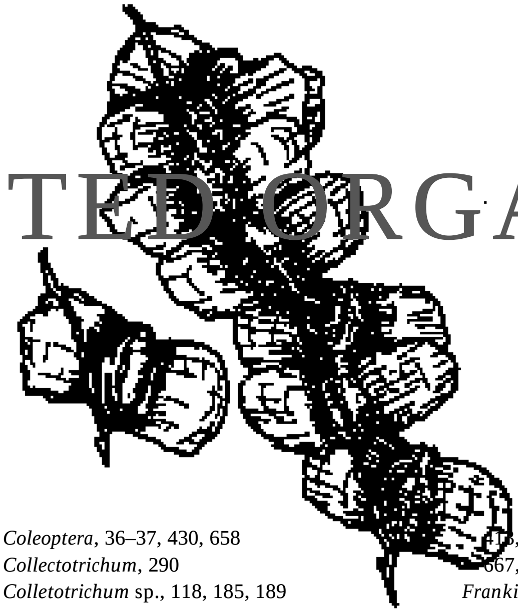
INDICES

COMMON NAMES

GENUS/SPECIES NAMES

FAMILY NAMES

ASSOCIATED ORGANISMS



CONVERSION FACTORS

TTSM lists descriptive units according to the metric system with standard abbreviations:

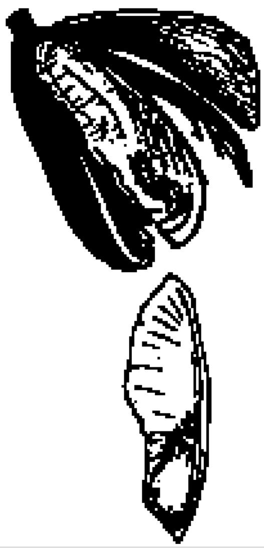
cal	calorie
cm	centimeter
cm^2	square centimeter
cm^3	cubic centimeter
°C	Centigrade
g	gram
ha	hectare
hl	hectoliter
kg	kilogram
km	kilometer
l	liter
m	meter
m^2	square meter
m^3	cubic meter
mb	millibar
mm	millimeter
mm^2	square millimeter
mm^3	cubic millimeter
MPa	megapascal

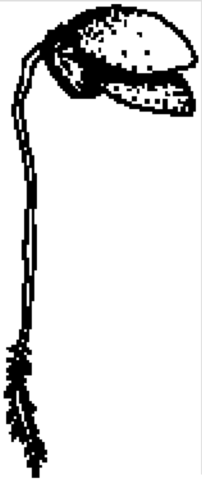
The following selected conversions are for the convenience of users to convert from metric to English units:

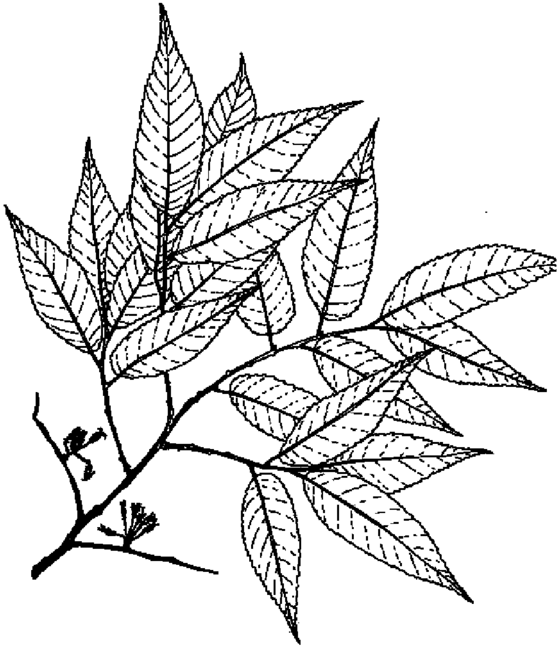
Table 1

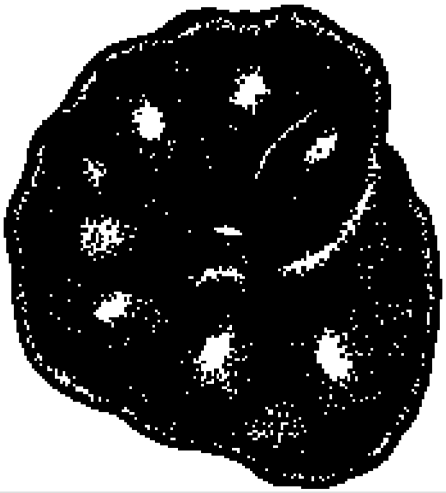
Metric to English Conversions

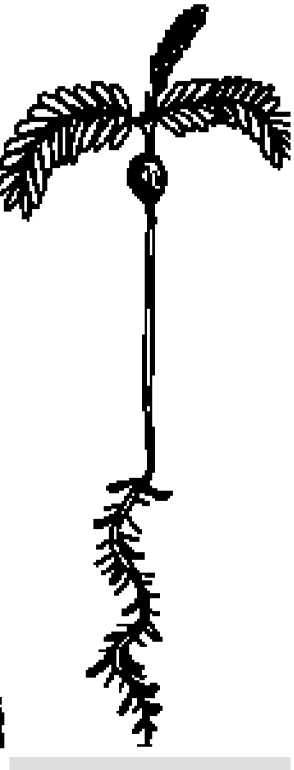
From	To	Multiply By
calories/ gram	foot-pounds	3090.4
Centigrade	Fahrenheit	1.800(°C) + 32
centimeters	inches	0.3937
centimeters	feet	0.0328
cubic centimeters	cubic inches	0.06102
cubic meters	cubic feet	35.314
cubic meters	cubic yards	1.307
cubic meters	cubic inches	61023.7
cubic millimeters	cubic inches	6.10237×10^{-5}
grams	ounces	0.035
grams	pounds	0.0022
grams/cubic centimeter	pounds/gallon	8.345
hectares	acres	2.47
hectares	square feet	107639.1
hectares	square miles	0.00386
hectoliters	bushels	2.838
joules/gram	B.T.U./(pounds x °F)	0.239
kilograms	pounds	2.205
kilograms/cubic meter	pounds/cubic inch	3.6×10^{5}
kilograms/hectare	pounds/acre	0.89
kilometers	miles	0.6214
liters	ounces	33.814
liters	pints	2.113
liters	quarts	1.056
liters	gallons	0.264
liters/minute	gallons/minute	0.2642
megapascals	pounds/square inch	145.0
meters	inches	39.37
meters	feet	3.28
meters	yards	1.094
millibars	pounds/square inch	0.0145
millimeters	feet	0.00328
millimeters	inches	0.0393
square centimeters	square feet	0.0010
square centimers	square inches	0.1550
square meters	square yards	1.196
square meters	acres	0.00024
square meters	square feet	10.763
square millimeters	square inches	0.00155

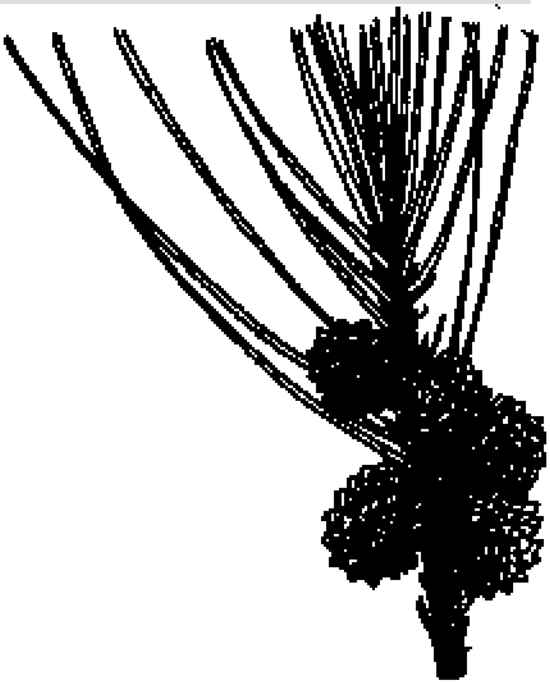












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