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

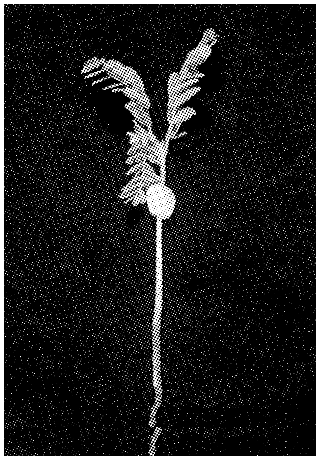


Fig. 122.

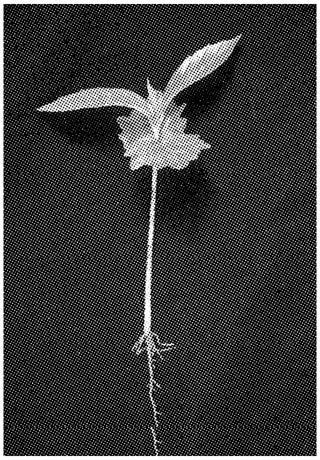


Fig. 124.

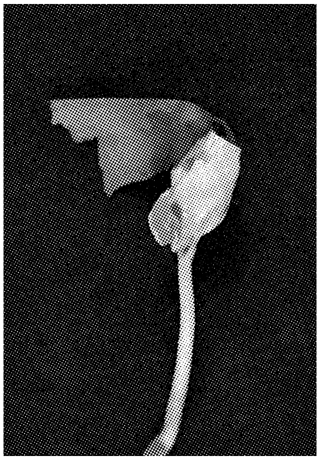


Fig. 125.

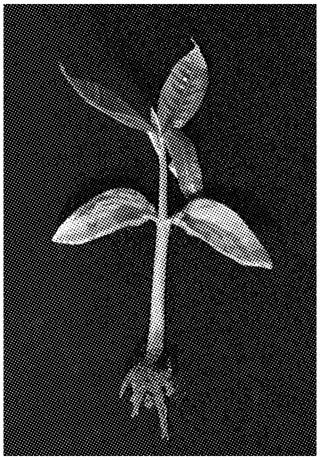


Fig. 126.


Fig. 123.

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

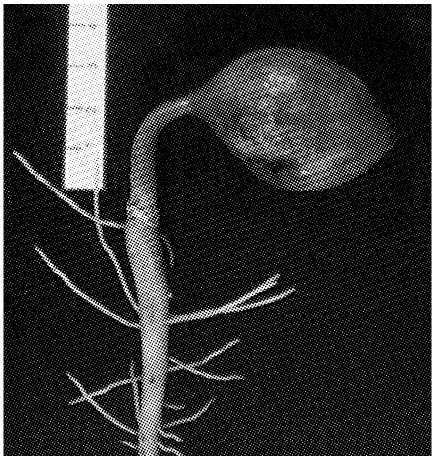


Fig. 127.

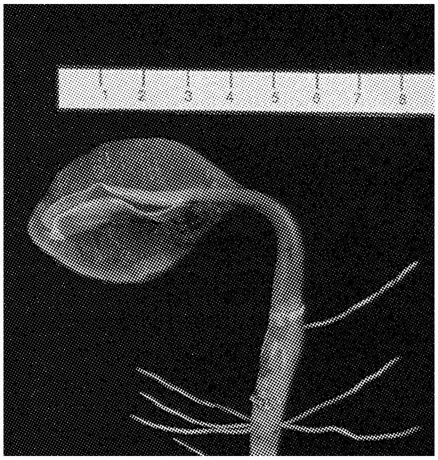


Fig. 128.

Fig. 129.

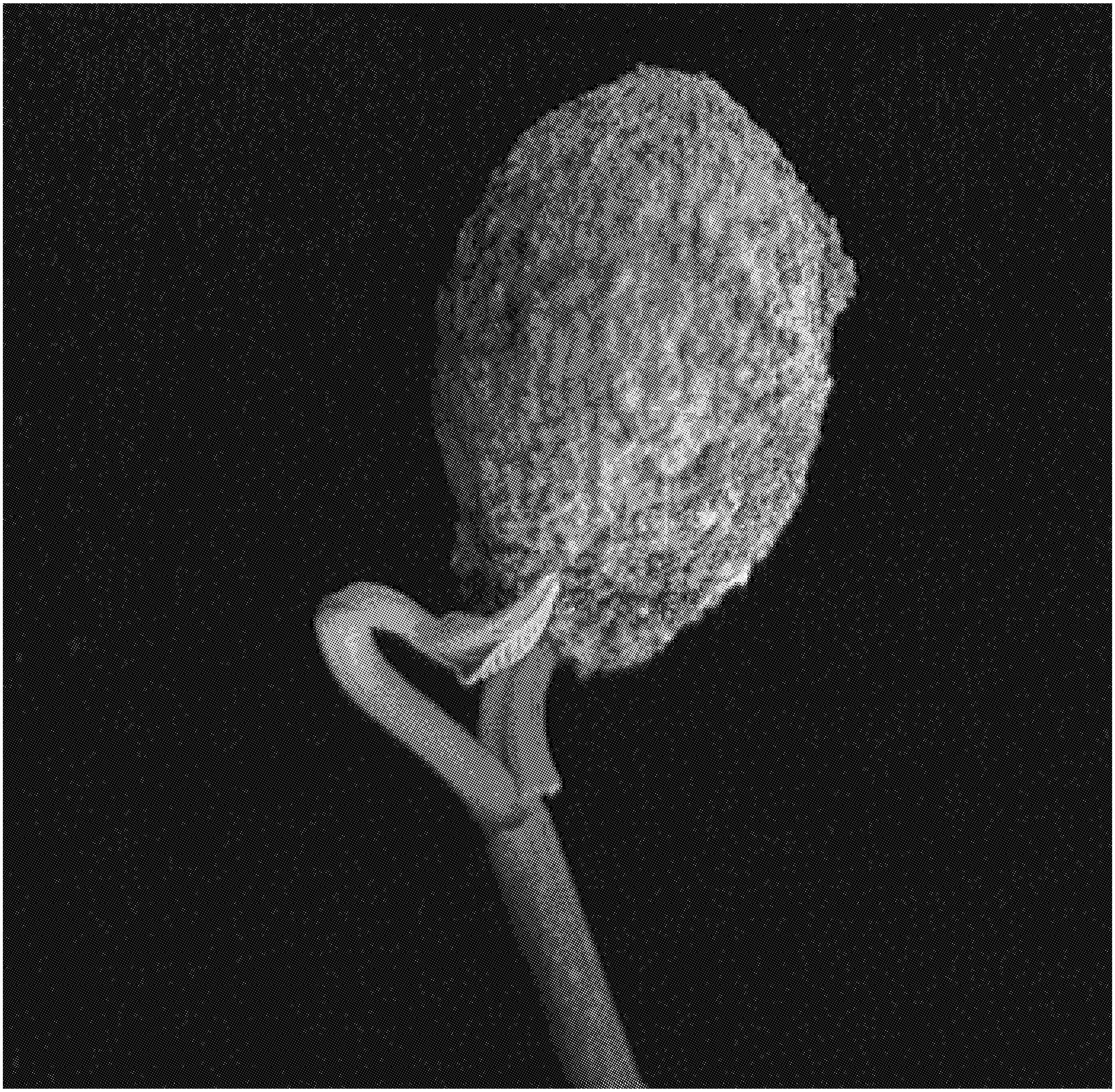


Fig. 131.

Fig. 130.

Fig. 132.

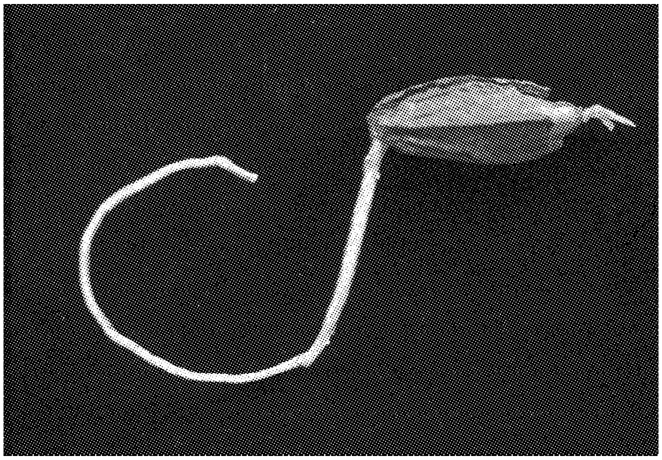


Fig. 133.

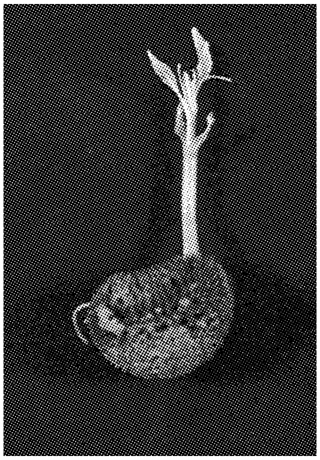


Fig. 134.

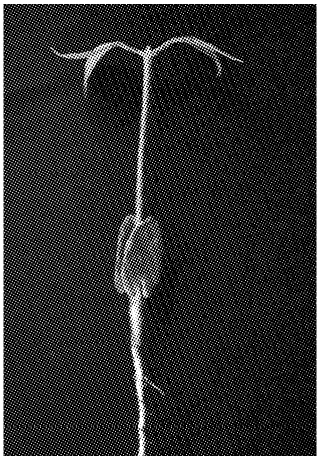


Fig. 135.

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).

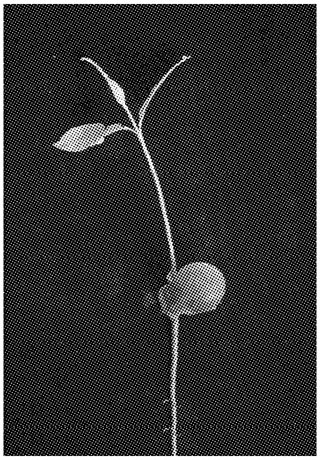
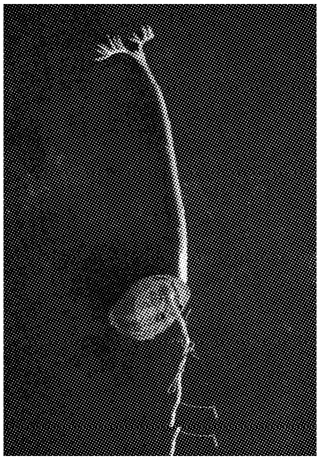


Fig. 136.



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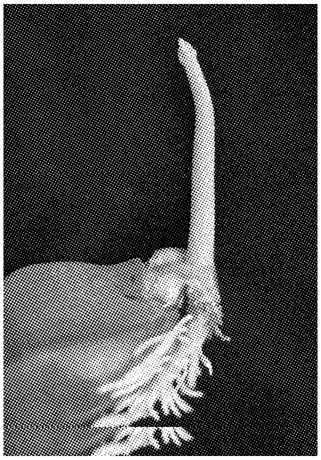


Fig. 139.

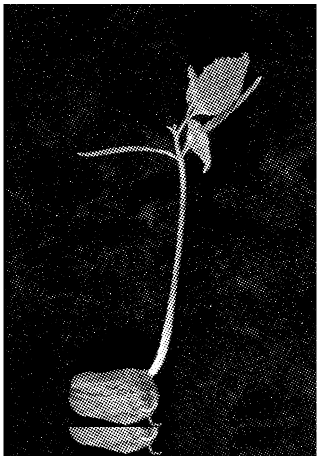


Fig. 140.

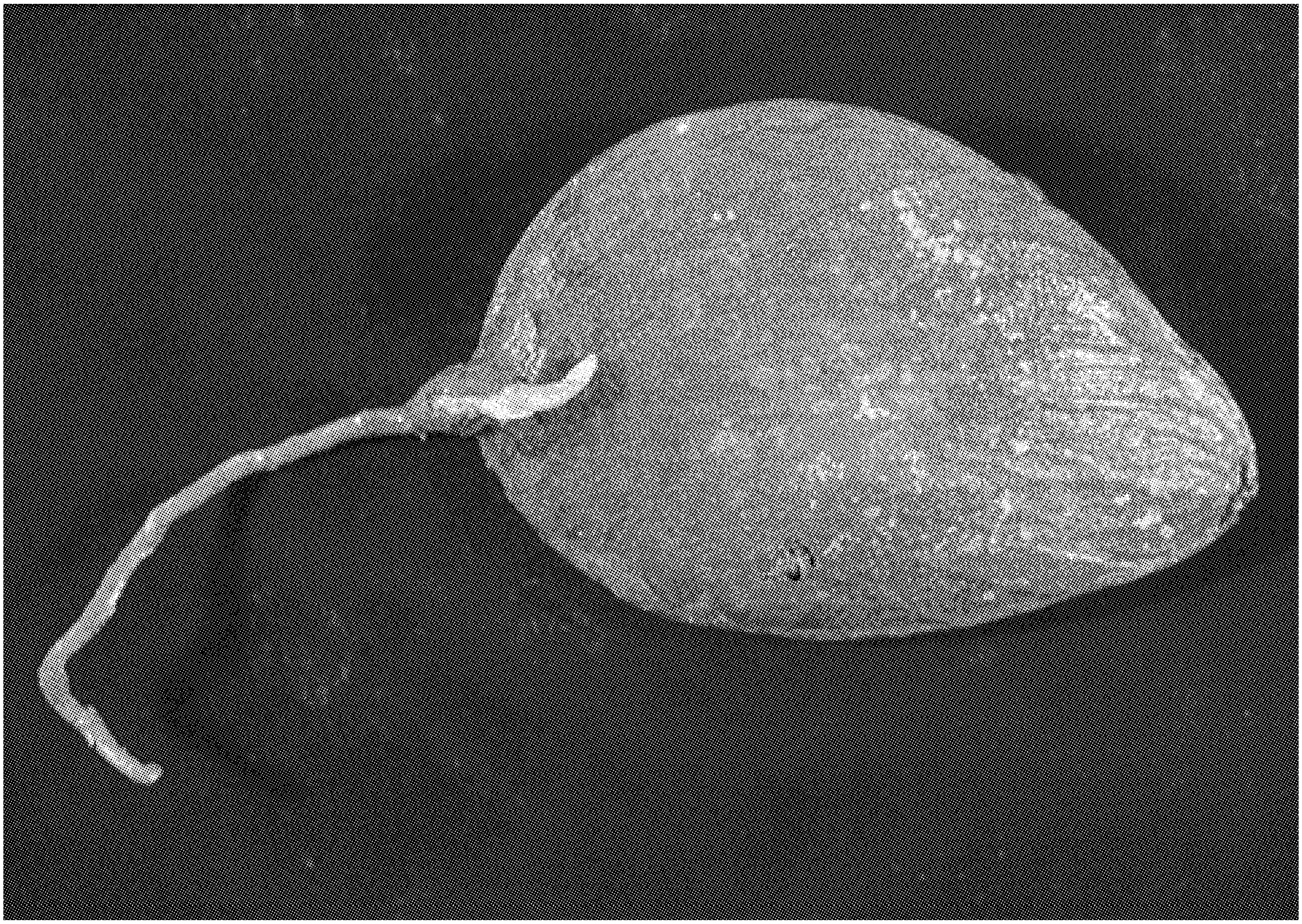


Fig. 138.

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).

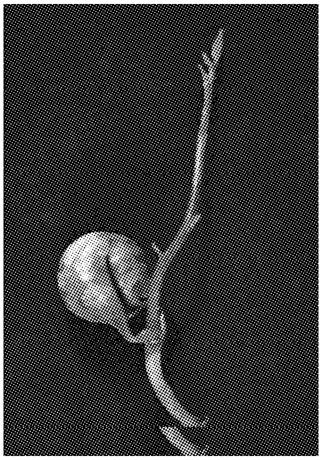
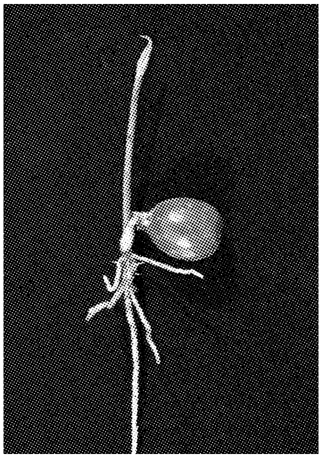


Fig. 141.



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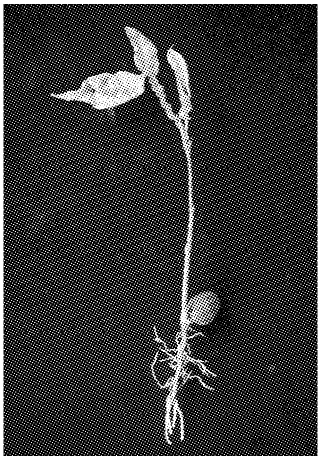

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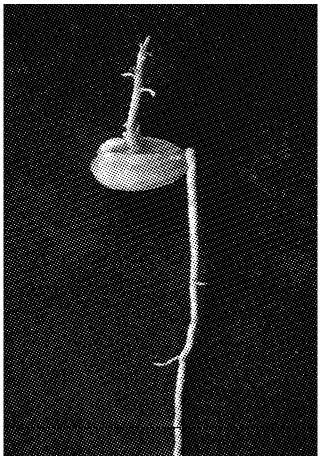
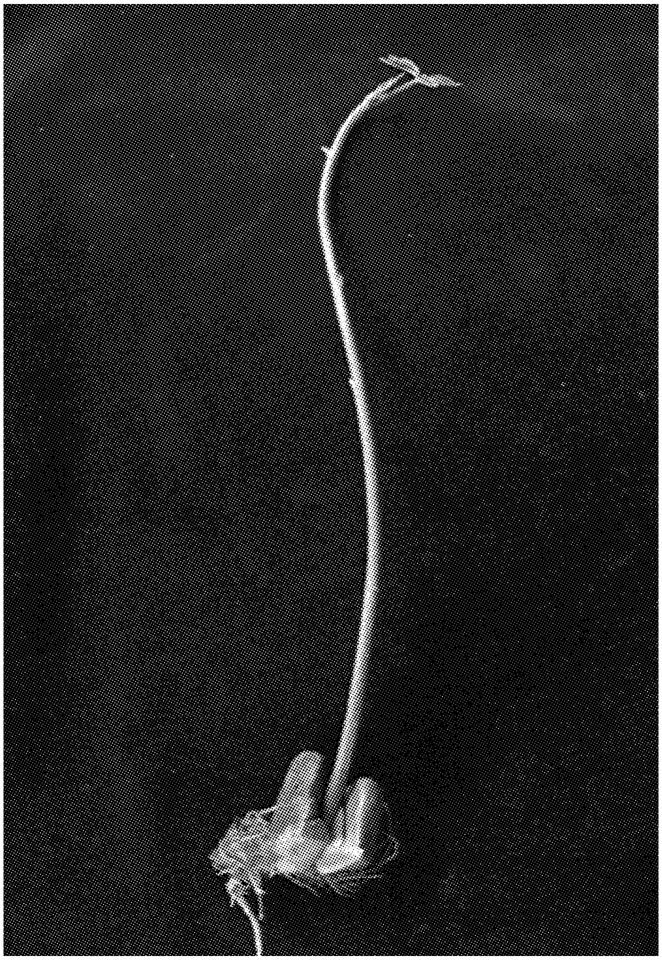


Fig. 146.



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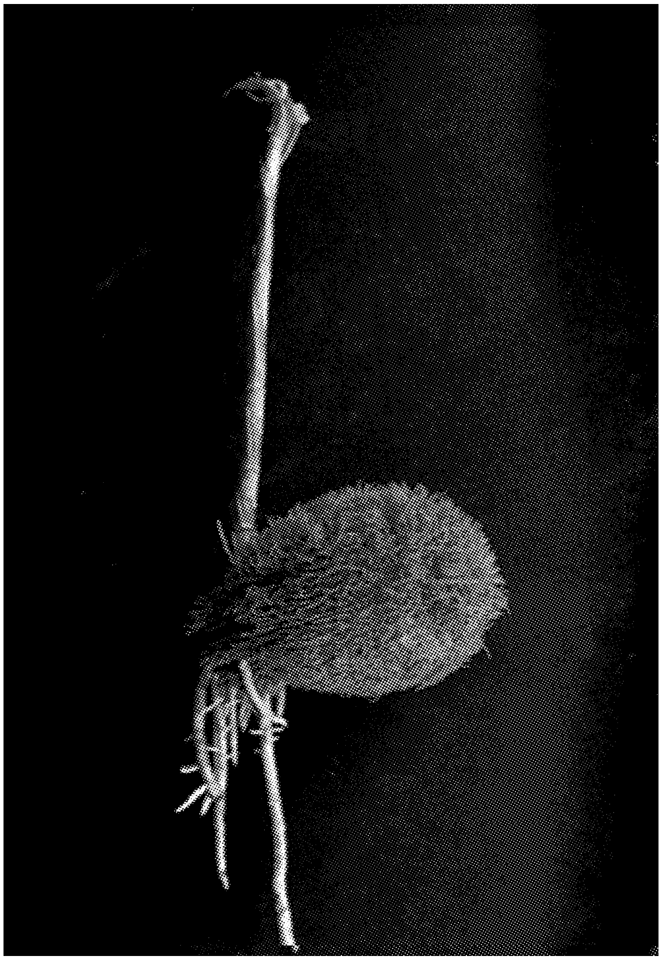

Fig. 143.

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.

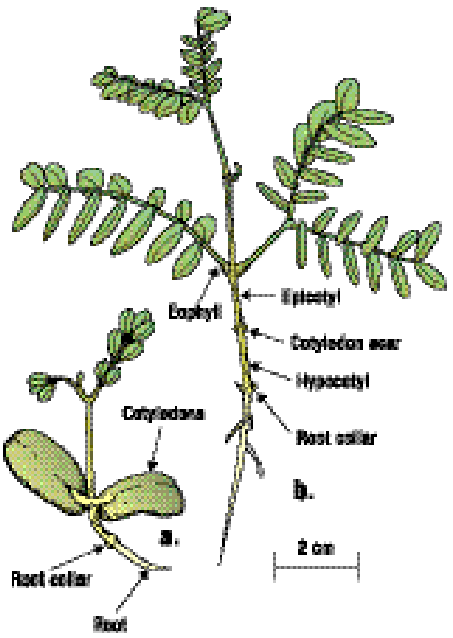

Fig. 147. *Stryphnodendron microstachyum* seedlings.

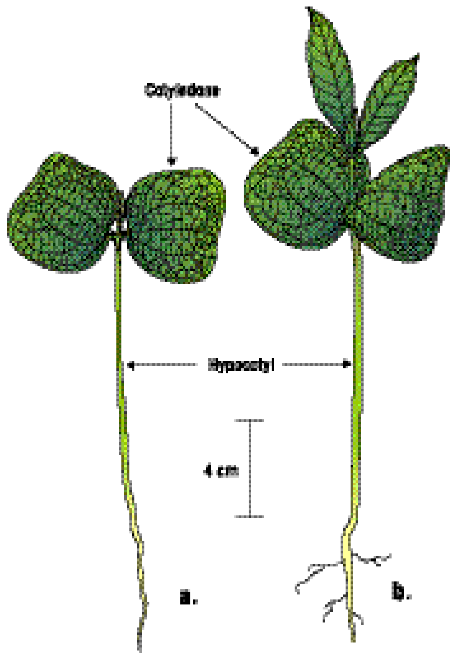

Fig. 148. *Vochysia guatemalensis* seedlings.

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

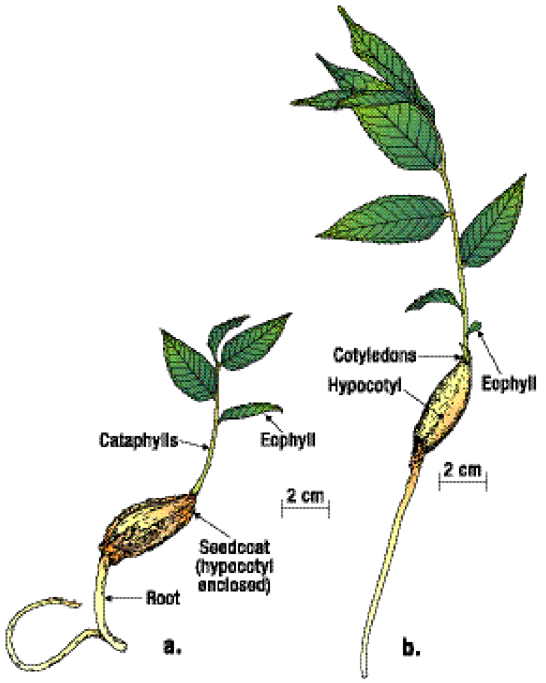

Fig. 151. *Lecythis ampla* seedlings.

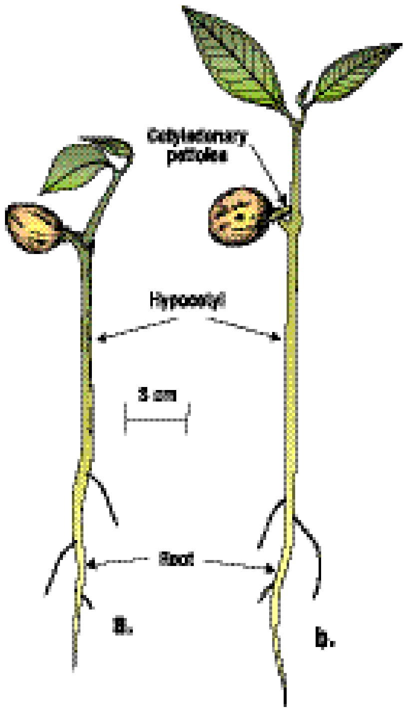

Fig. 149. *Virola koschnyi* seedlings.

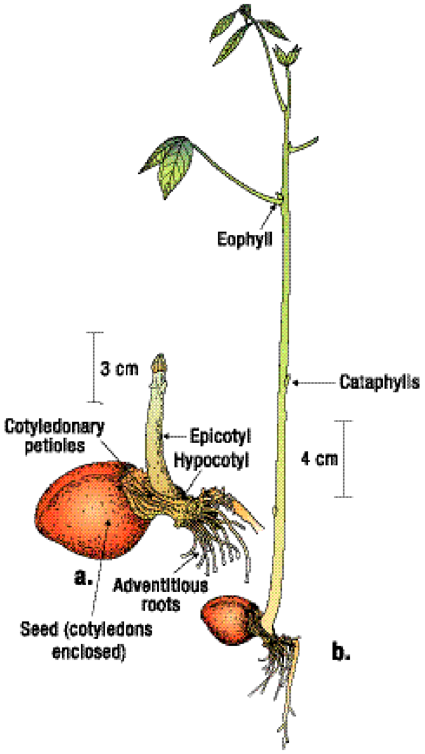

Fig. 150. *Carapa guianensis* seedlings.

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*

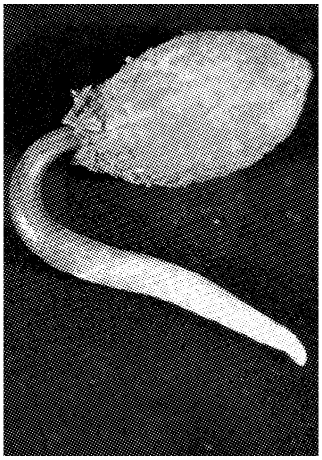

Fig. 154.

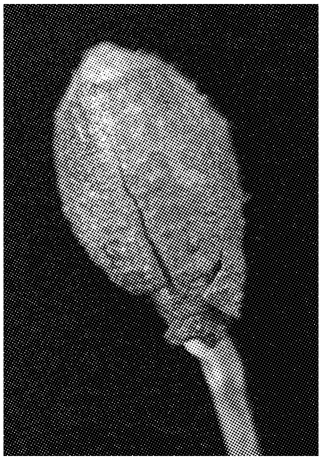

Fig. 155.

Fig. 156.

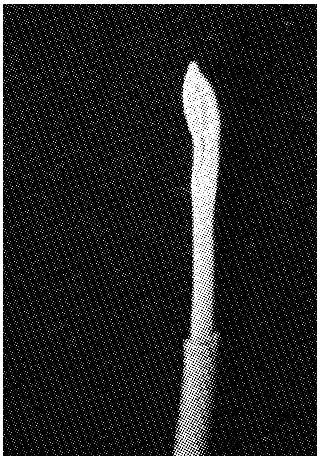

Fig. 158.

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.

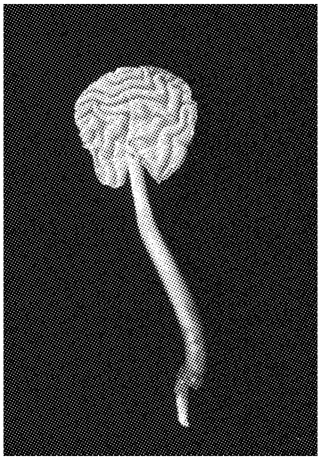

Fig. 153.

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,

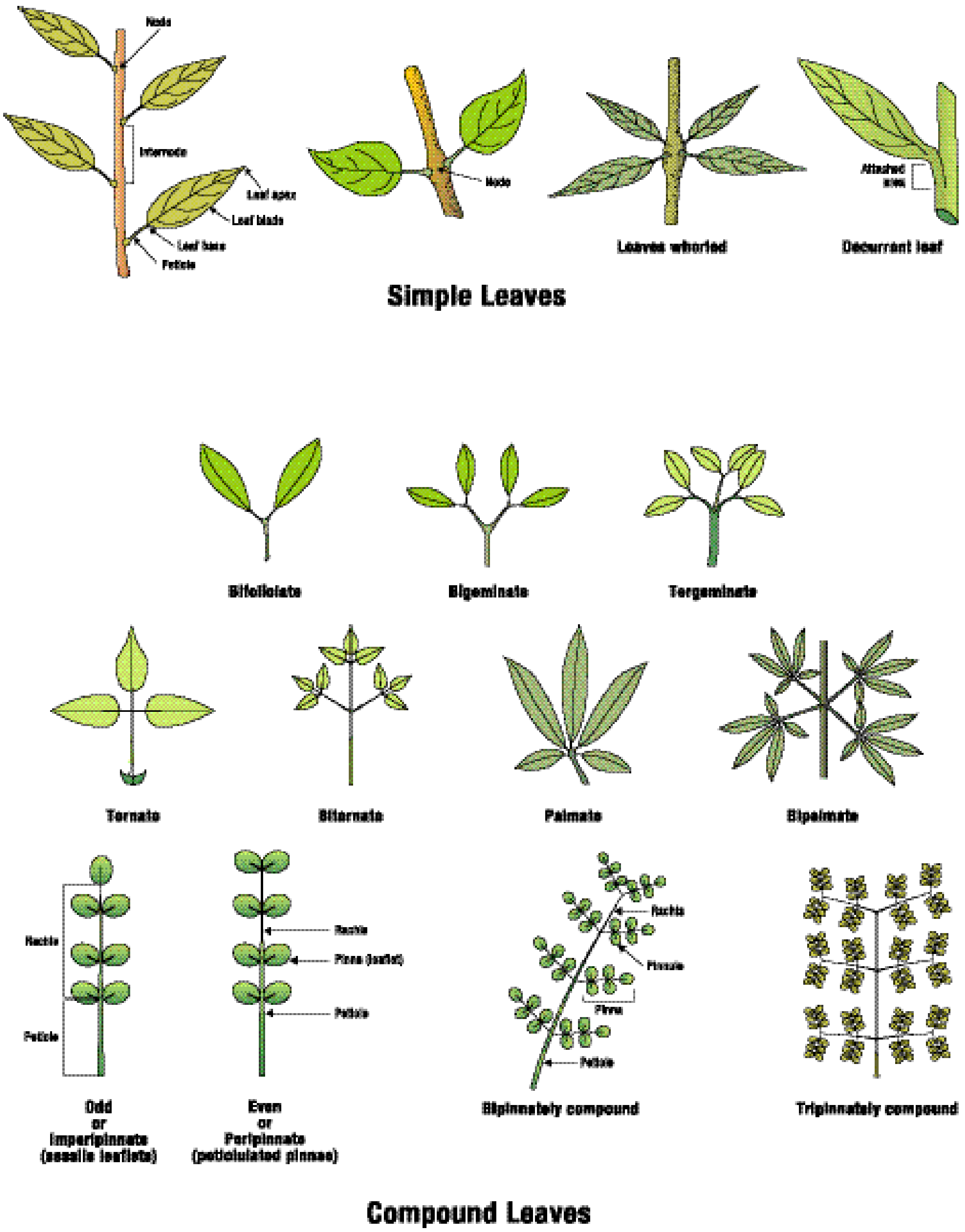

Fig. 159. Simple and compound leaves.

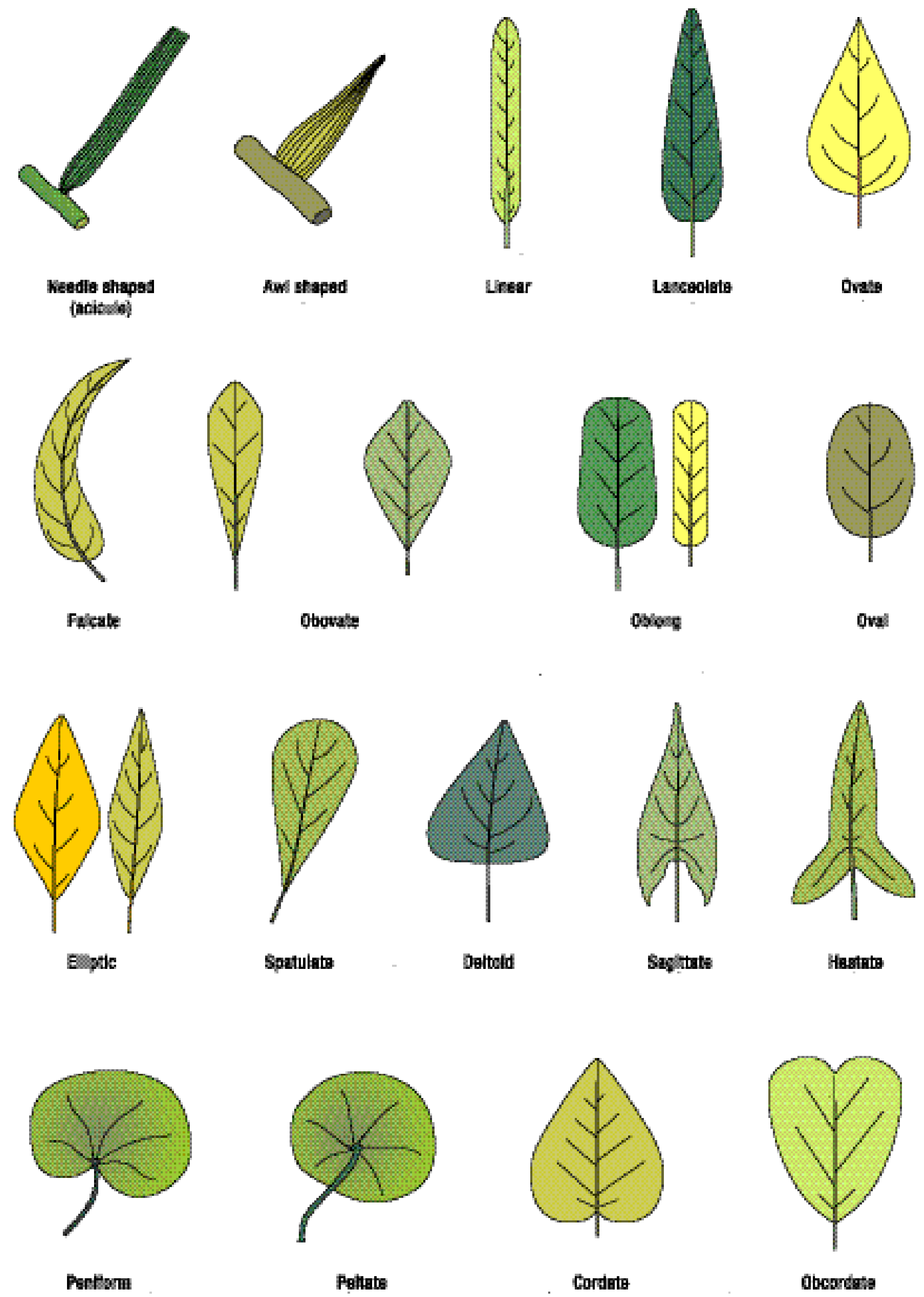

Fig. 160. Leaf shapes.

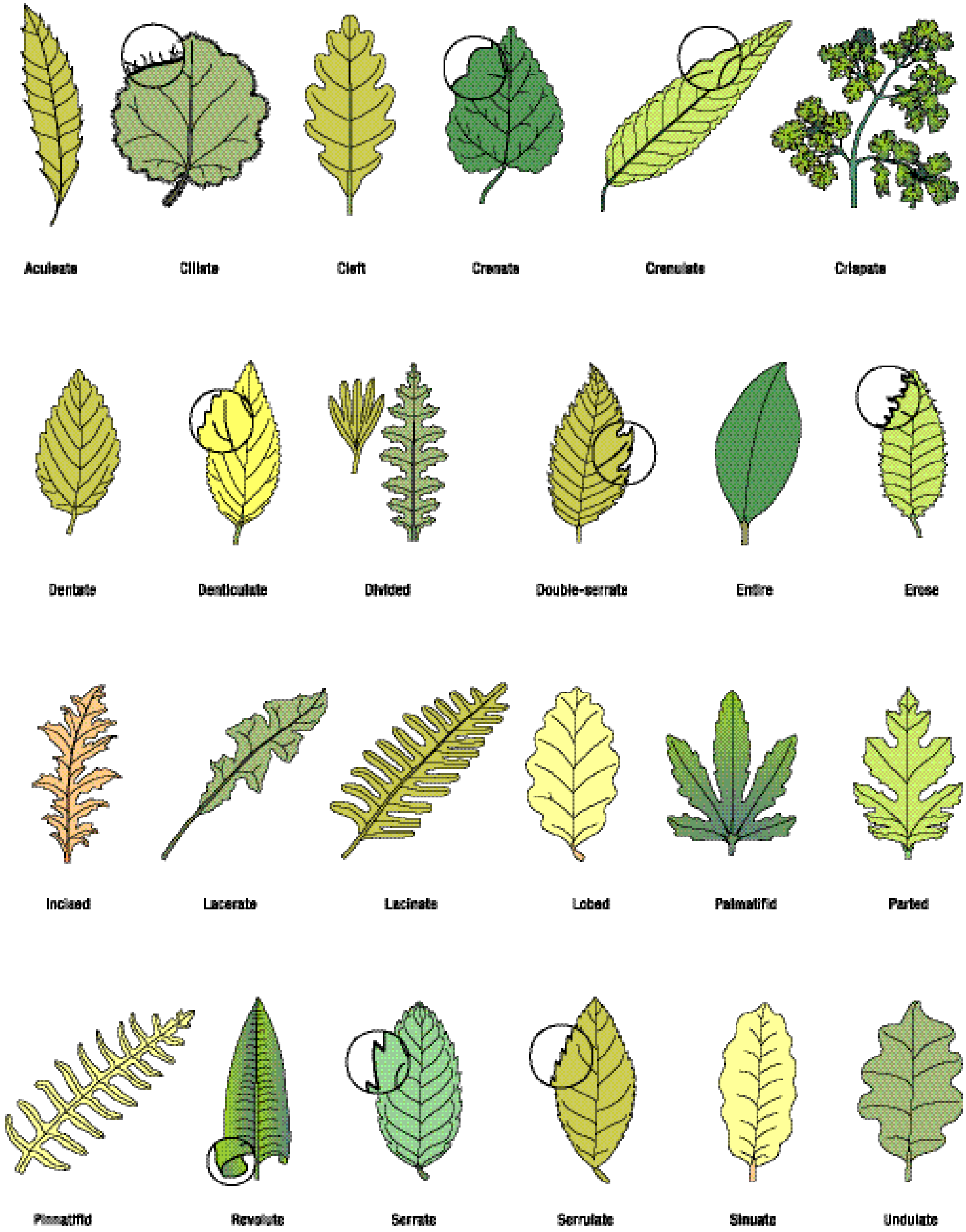

Fig. 161. Leaf margins.

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.

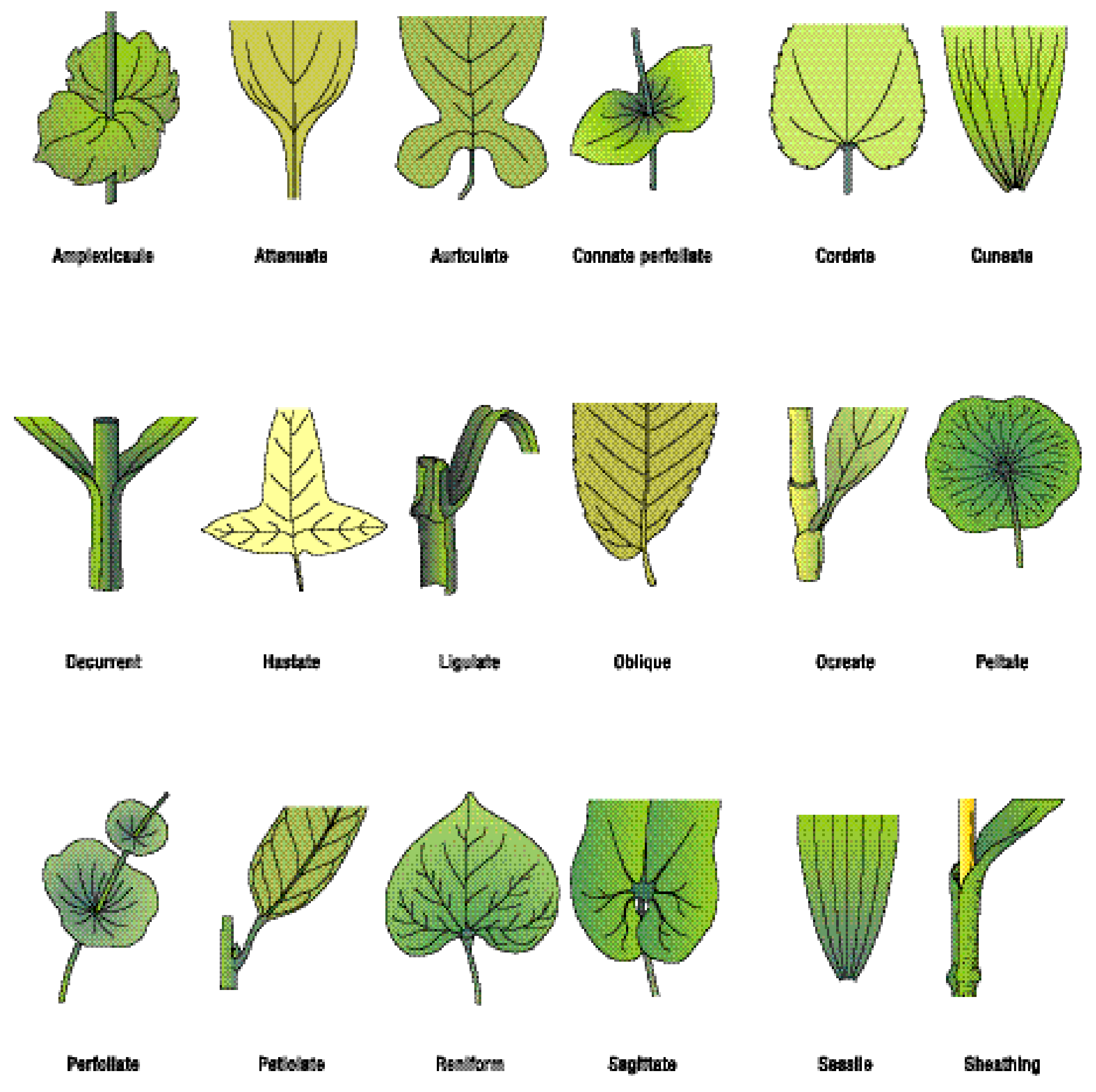

Fig. 162. Leaf bases and attachments. (Redrawn from Bradford *et al.* 1974).

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

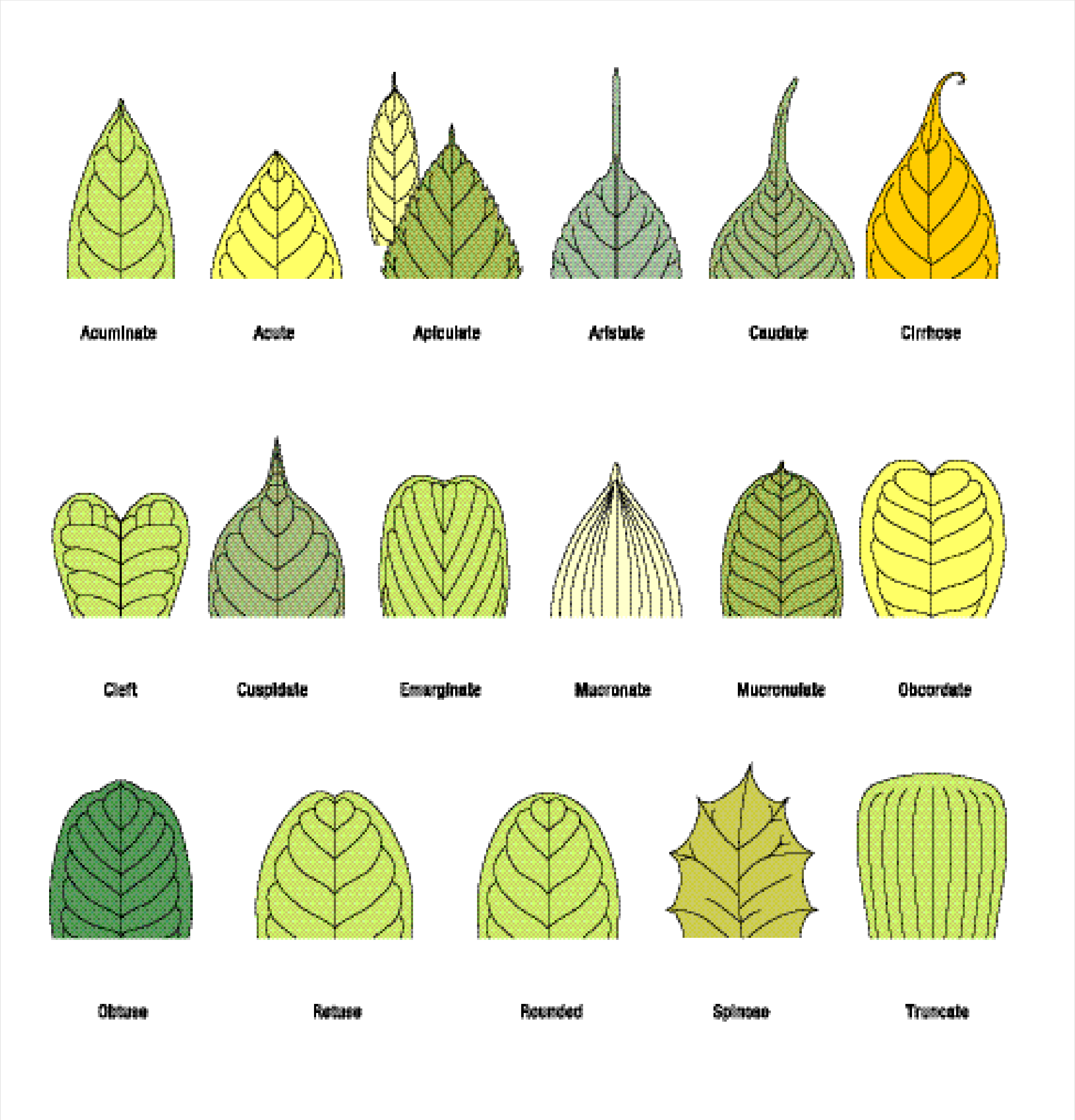

Fig. 163. Leaf apices. (Redrawn from Bradford *et al.* 1974).

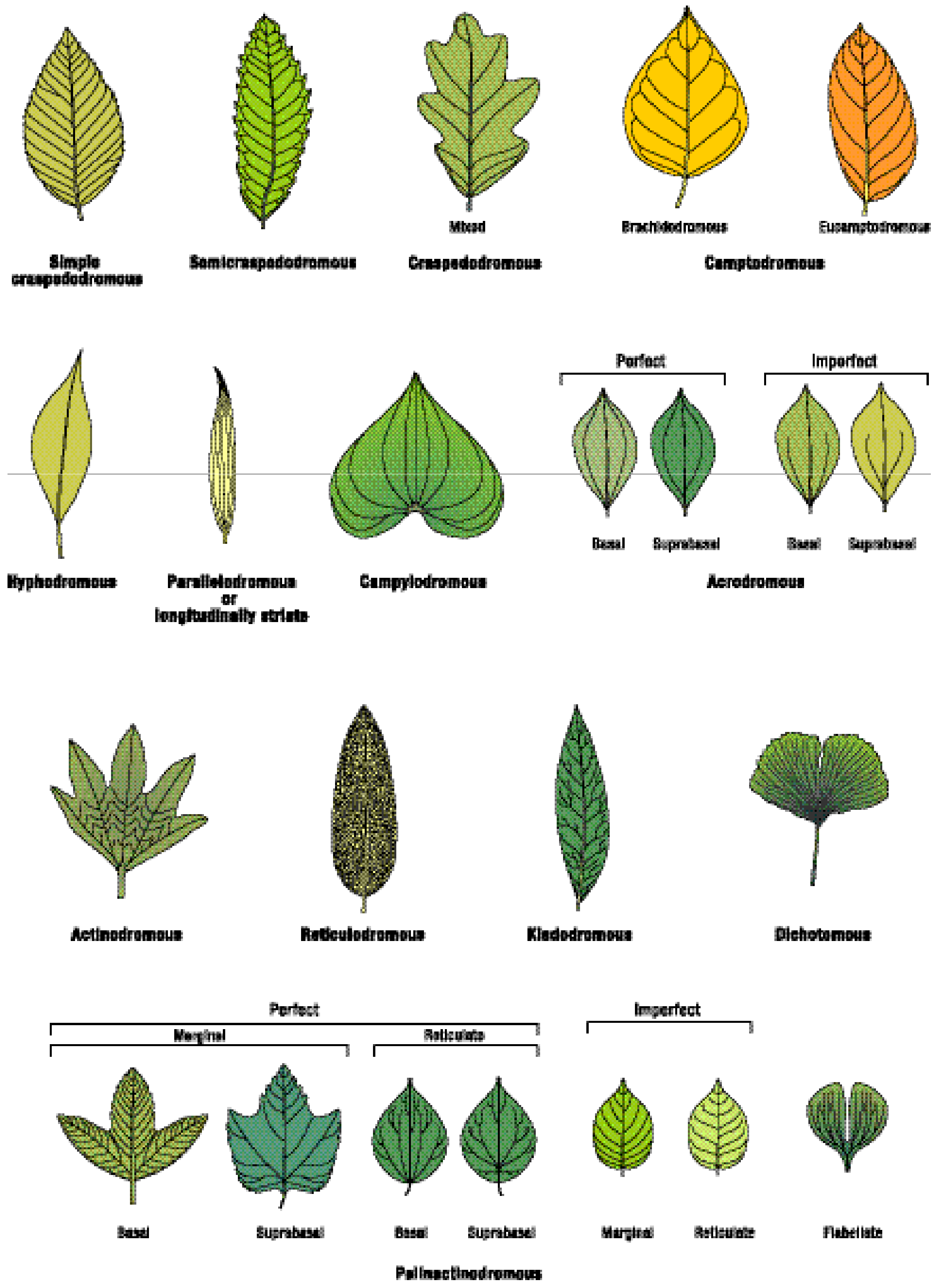

Fig. 164. Venation patterns in dicotyledons. (Redrawn from Hickey, 1974).

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.

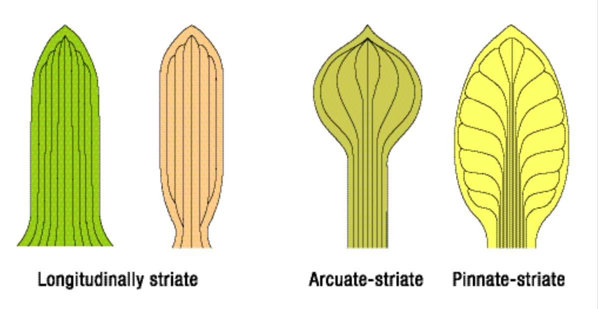

Fig. 165. Types of striate venatin in the leaves of monocotyledons.

(Redrawn from Foster & Gifford 1974).

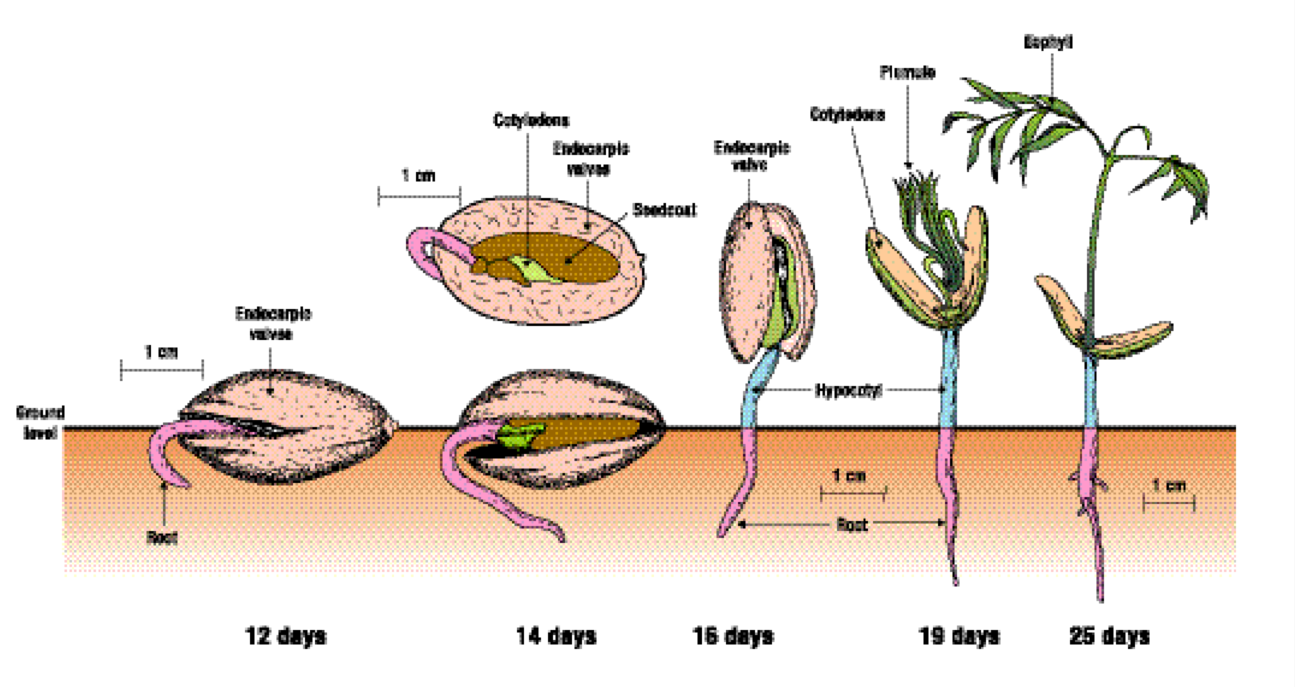

Fig. 166. Seedling development in *Dipteryx panamensis*.
Germination in epigeal; the seedling is phanerocotylar.

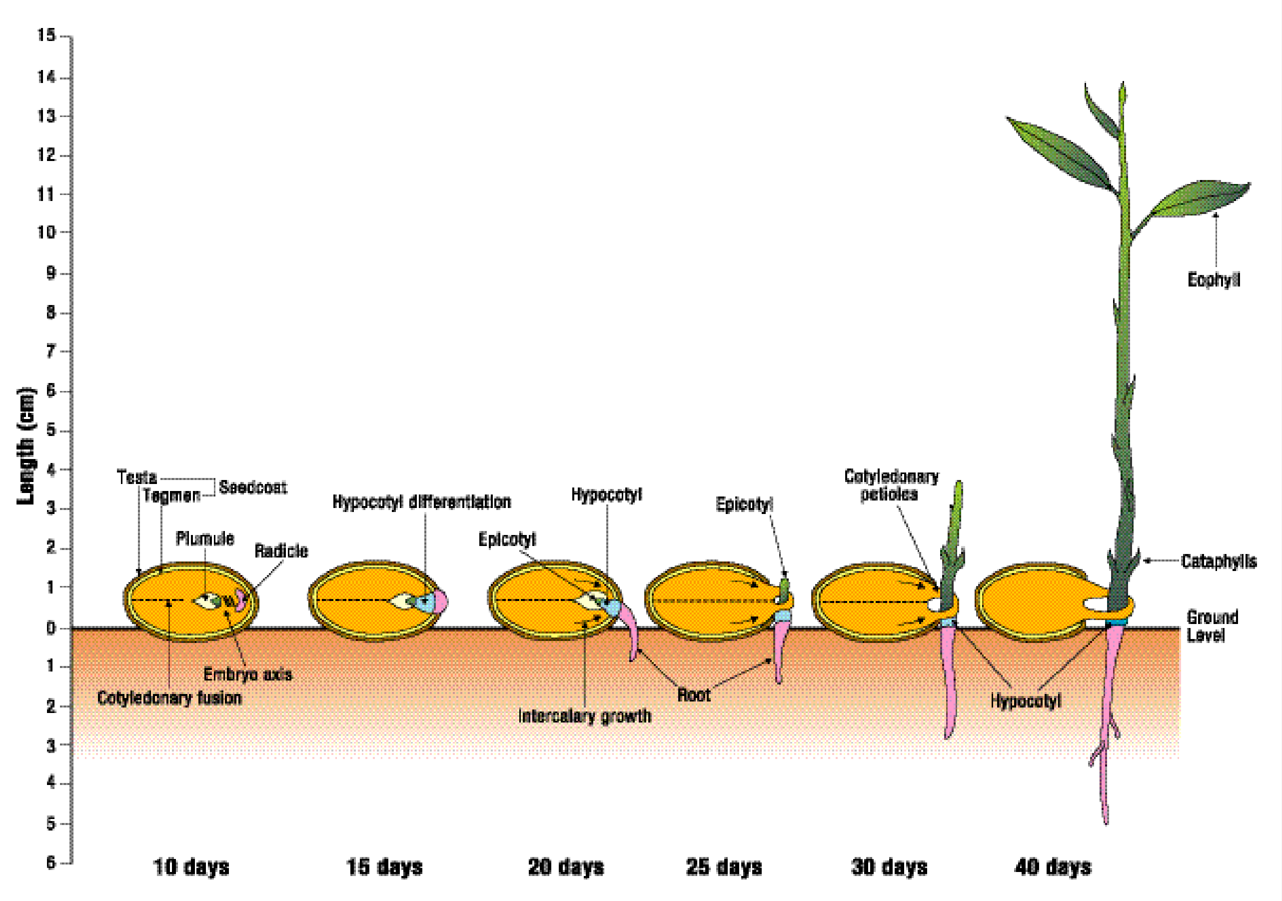

Fig. 167. Seedling development in *Calophyllum brasiliense*.
Germination is hypogeal; the seedling is cryptocotylar.

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-

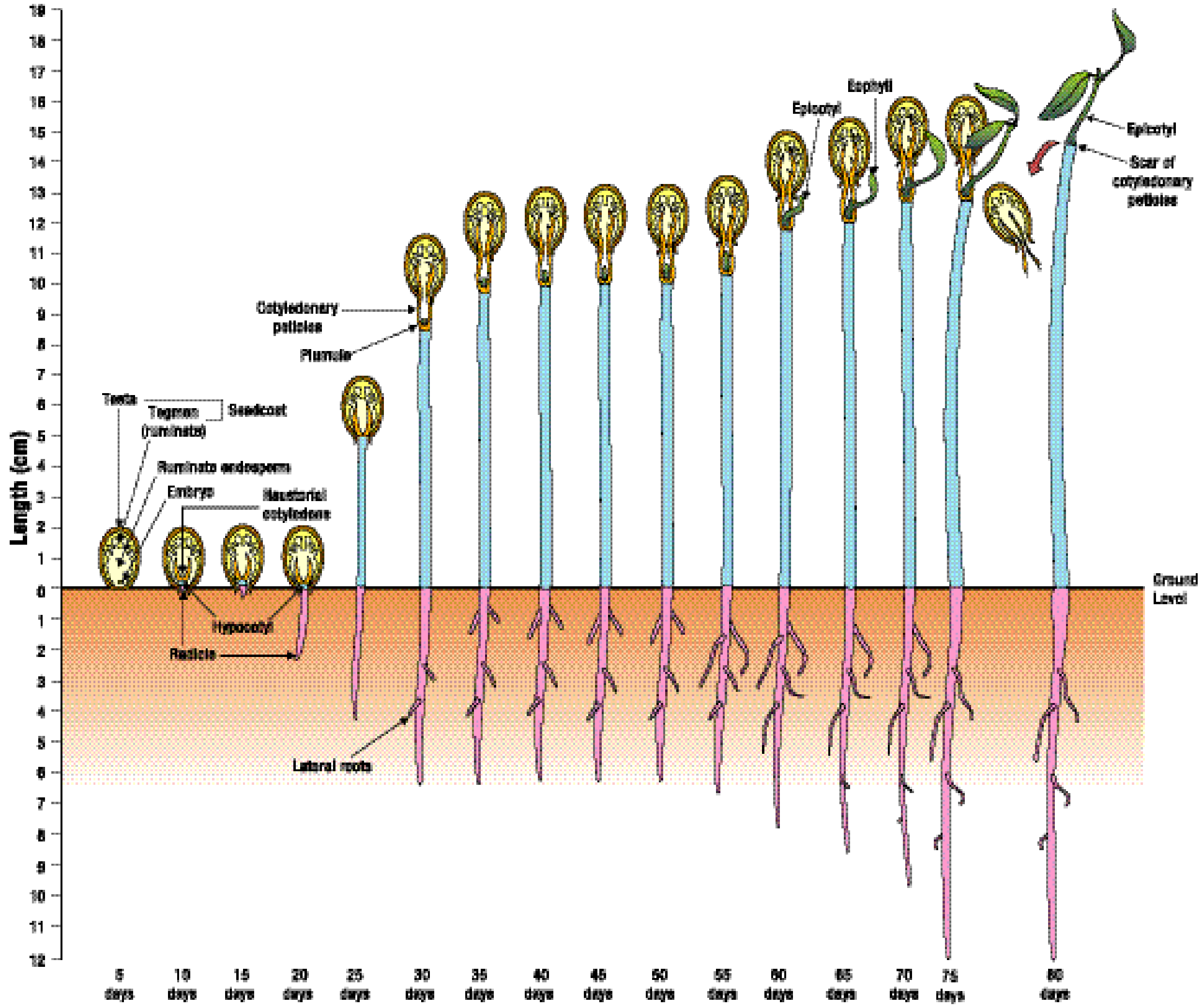

Fig. 168. Seedling development in *Virola* spp. Germination is epigeal; seedling cryptocotylar. (Most Myristicaceae studied share this pattern.)

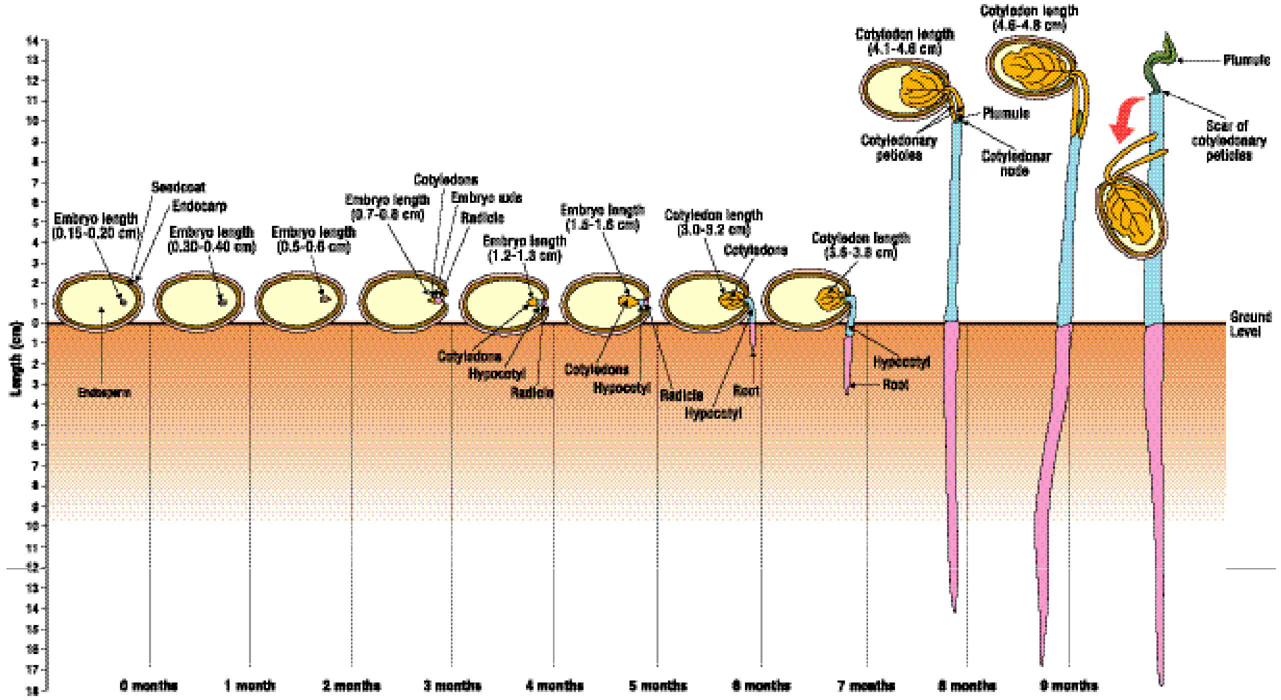

Fig. 169. Seedling development in *Minquartia guianensis*. Germination is epigeal; the seedling is cryptocotylar.

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

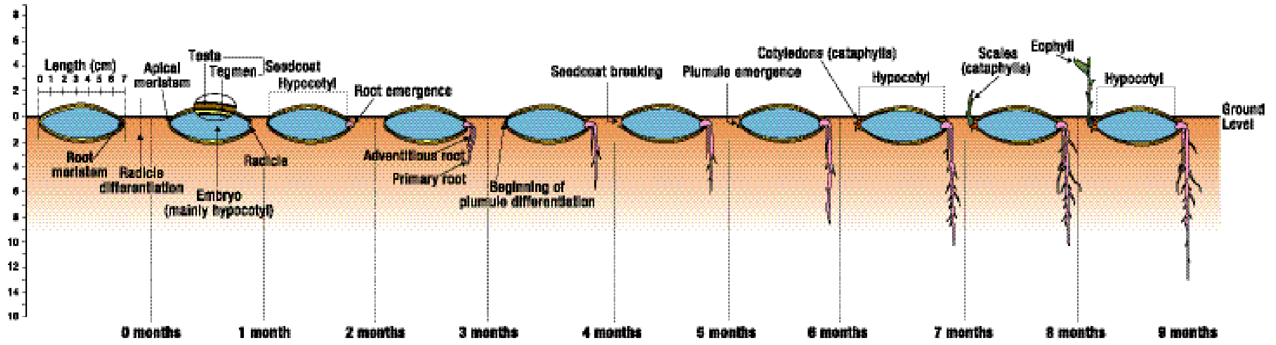

Fig. 170. Seedling development in *Lecythis* spp.. Germination is hypogeal; the seedling is phanerocotylar although the hypocotyl remains inside the seedcoat.

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.