Rhizophora apiculata, R. mucronata, R. stylosa, R. × annamalai, R. × lamarckii (Indo–West Pacific stilt mangrove)

Rhizophoraceae (mangrove family)

***mangle hembra* (Guam: Chamorro); *tebechel*, *bngaol*, *agpat*, *apgal* (Palau); *raway*, *roway*, *ravey* (Yap Islands, FSM); *chia*, *cia* (Chuuk, FSM); *aak*, *akelel*, *akapah* (Pohnpei, FSM); *kahrak*, *suhkasrik*, *sakasrik* (Kosrae, FSM); *petu rogha*, *ngochango-chara* (Marovo, Solomon Islands); *tiri tambua* (Fiji); *koriki* (Daru and Kiwai, PNG); *totoa* (Motu, PNG); spotted leaved red mangrove (Western Australia); red mangrove, tall-stilted mangrove, prop root mangroves (Queensland)**

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IN BRIEF

Distribution Native to tropical and subtropical coastal areas from the African east coast, throughout Asia to Australia and to most islands of the eastern Pacific Ocean. Closely allied with Atlantic–East Pacific red mangroves whose ranges naturally overlap only in a small number of southern Pacific islands.

Size Can reach 30–40 m (100–130 ft) in height, although commonly reaches 5–8 m (16–26 ft).

Habitat Inhabits the intertidal wetland zone, 0–6 m (0–20 ft) elevation between mean sea level and highest tides, with variable rainfall.

Vegetation Mangrove communities.

Soils Adapted to a wide range but thrives best in fine mud sediments of downstream river estuaries.

Growth rate Grows <1 m/yr (3.3 ft/yr) in height.

Main agroforestry uses Soil stabilization, coastal protection, wildlife/marine habitat for marine fauna.

Main products Timber, fuelwood, charcoal, dyes, and traditional medicine.

Yields In Malaysia, the 30-year rotation harvested yield of green wood has been about 136–299 mt/ha (61–133 t/ac).

Intercropping Recommended for planting together with other mangrove species.

Invasive potential Has potential to invade new environments; not recommended for planting outside of the natural range. These plants are ready colonizers of new mud banks, making them opportunistically invasive.

***Rhizophora mucronata* trees showing stilt roots, Chuuk, Federated States of Micronesia.**

INTRODUCTION

Indo–West Pacific stilt mangroves (IWP *Rhizophora* species) are widespread throughout most tropical coastal areas of the western Pacific region to east Africa. This group is one of two that make up the genus *Rhizophora* and consists of three species (two being closely allied), *R. mucronata*, *R. stylosa*, and *R. apiculata*, and two hybrids, *R.* × *lamarckii* and *R.* × *annamalai*.

Stilt mangroves thrive under a range of intertidal conditions, including a range of salinity levels from near freshwater to full strength seawater. They tolerate a range of flooding regimes, soil types, and other physical site factors. Typically, these mangroves are common in the mid-intertidal zone, and particularly along the seaward margin of tropical mangrove stands.

Rhizophora are considered the most important of all mangrove genera across the Pacific tropical region. However, the benefits provided by stilt mangroves are difficult to separate from the larger role of mangroves and mangrove ecosystems in general. Mangroves are known to play a vital role in shoreline protection, enhancement of water quality in nearshore environments (including coral reefs), and in supporting estuarine and marine food chains. In most parts of the Pacific, trees are harvested for firewood, so the trunk is the main part of the tree considered for direct use.

DISTRIBUTION

Native range

Indo–West Pacific stilt mangroves occur widely throughout the western Pacific. Specifically, they occur in tropical and subtropical, intertidal wetlands from the east coast of Africa, through Asia to Micronesia extending east in the northwestern Pacific through the Federated States of Micronesia to the Marshall Islands, and south to northern Australia extending east in the southern Pacific as far as Samoa. Distributions appear continuous, but separate species have different preferred locations where they dominate:

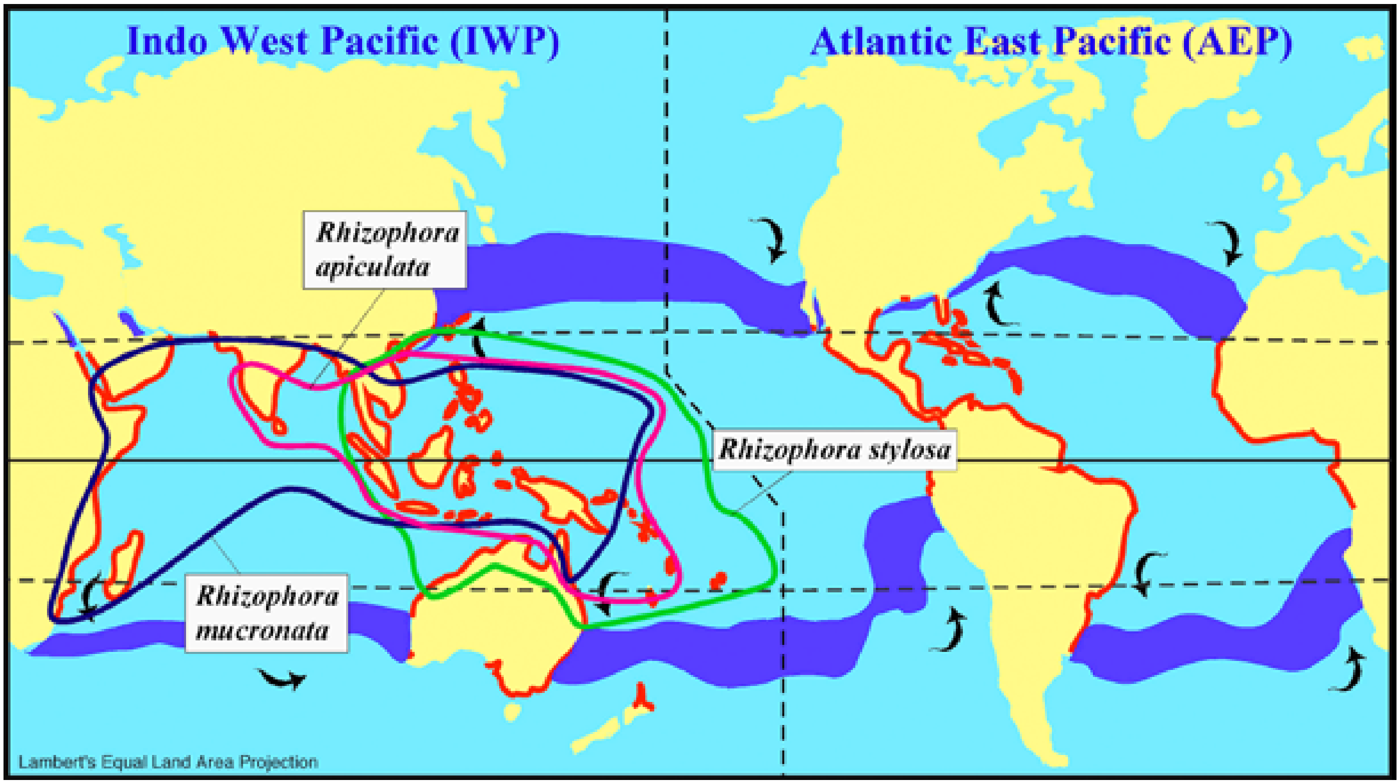
- *R. mucronata* occurs mostly in areas subject to regular freshwater flows (at least in the eastern part of its range)
- *R. stylosa* occurs in marine situations often preferring more exposed offshore sites
- *R. apiculata* is often found mid–lower estuary in larger riverine estuaries and embayments
- the hybrid *R.* × *lamarckii* is found downstream in middle to higher intertidal locations.

Rhizophora mucronata and *R. stylosa* are sibling species (i.e., possibly *R. stylosa* =*R. mucronata* var. *stylosa* (Griff.) Salvoza), and together they characterize most stands of IWP stilt mangroves. The range of *R. mucronata* is the widest of all IWP species, extending from east Africa, where it occurs as the sole *Rhizophora*, to the western Pacific, where it overlaps with all other IWP species. In contrast, *R. stylosa* extends exclusively east, notably into the southwestern Pacific. The range of *R. apiculata* also extends further east in the south Pacific than *R. mucronata*, but otherwise its range mostly fits within the ranges of other IWP *Rhizophora*. The status of observed differences in similar forms, *R. mucronata* and *R. stylosa,* will only be resolved in genetic studies and selected breeding programs.

The two hybrid taxa presumably have distributions in keeping with their hybrid status. As such, they are located wherever the ranges of their putative parents overlap. Confirmed records of hybrid distributions show *R.* × *lamarckii* to be widespread in the western Pacific, while *R.* × *annamalai* was found in India and Sri Lanka along the western limits of *R. apiculata*. However, considerable confusion is expected in the field distribution records, because these hybrids

WHAT IS A MANGROVE?

Mangroves form a unique and dominant ecosystem comprised of intertidal marine plants, mostly trees, predominantly bordering margins of tropical coastlines around the world. These halophytic (salt tolerant) plants thrive in saline conditions and daily inundation between mean sea level and highest astronomical tides, and they provide vital structure as habitat and food for similarly adapted resident and transient fauna. Mangrove plants exchange gases from exposed roots using special lenticels, while flooding tides allow uptake of river-borne nutrients and frequent dispersal by their buoyant propagules. The ecological limits defined by the diurnal tidal range explain the setting and why just 70 species around the world are considered to be mangroves (Tomlinson 1986, Duke et al. 1998), compared with adjacent rainforests that may have hundreds of tree species per hectare. Specialized morphological and physiological characteristics largely define and characterize mangrove plants, such as buttress trunks and roots providing support in soft sediments, aboveground roots allowing vital gas exchange in anaerobic sediments, and physiological adaptations for excluding or expelling salt. Fewer than 22 plant families have developed such essential attributes, representing independent instances of co-evolution over millions of years to form today's mangrove habitats.



World distributions of stilt mangroves, the IWP Rhizophora species. Given the hybrid status of *Rhizophora* × *lamarckii* (= *R. stylosa* × *R. apiculata*) and *R.* × *annamalai* (= *R. mucronata* × *R. apiculata*), their distribution is likely where the distributions of their respective parent trees overlap. Coastlines marked in red indicate the distribution of all mangroves. IMAGE: N.C. DUKE

are difficult to distinguish based on morphological characters alone.

Of great interest also in the southwestern Pacific islands is the only occurrence of another hybrid taxon, *R.* × *selala* (Salvoza) Tomlinson, derived from putative parents *R. samoensis* (=*R. mangle*?) and *R. stylosa* (=*R. mucronata* var. *stylosa*?). This hybrid taxon is special because *R. samoensis* is a key member of the AEP red mangrove *Rhizophora* species. The occurrence of this hybrid means there appears to be very little genetic separation between these defining and most divergent of *Rhizophora* species.

Current distribution

There are no reports of any stilt mangroves occurring outside their natural range. However, these species are recognized as valuable timber producers, so it is possible that their dispersal east in the Pacific and elsewhere may have been assisted by indigenous peoples in the past.

BOTANICAL DESCRIPTION

Preferred scientific names

Rhizophora mucronata Lamk.
Rhizophora stylosa Griff. (= *R. mucronata* var. *stylosa* (Griff.) Salvoza)
Rhizophora apiculata Bl.
Rhizophora × *lamarckii* Montr. (= *R. stylosa* × *R. apiculata)*
Rhizophora × *annamalai* K. Kathiresan. (= *R. mucronata* × *R. apiculata)*

Family

Rhizophoraceae (mangrove family)

Common names

aak, *akelel*, *akapah* (Pohnpei, FSM)
abat (Ceram, Indonesia)
ailave, *kailau* (Aru, Indonesia)
bakau (Malay Peninsula, Singapore, Borneo, Sumatra)
bakauan, *bakau, bakhaw* (Philippines)
bako (Java, Indonesia)
bangka (Acheh, Indonesia)
chia, *cia* (Chuuk, FSM)
Indo–West Pacific stilt mangroves (English)
kahrak, *suhkasrik*, *sakasrik* (Kosrae, FSM)
koriki (Daru and Kiwai, PNG)
lolaro, *belukap* (Sulawesi, Indonesia)
mangle hembra (Guam: Chamorro)
ngochangochara, petu rogha (Marovo, Solomon Islands)
prop root mangroves (northeastern Australia)

raway, *roway*, *ravey* (Yap Islands, FSM)
red, tall-stilted mangrove (Queensland)
spotted leaved red mangrove (Western Australia)
tebechel, *bngaol*, *agpat*, *apgal* (Palau)
tiri tambua (Fiji)
totoa (Motu, PNG)

Size

Indo–West Pacific stilt mangroves are medium to tall trees that may reach 30–40 m (100–130 ft) in height, although they are commonly much shorter, around 5–8 m (16–26 ft). Stem diameters are often about 15–35 cm (6–14 in) taken just above the highest prop root. This measure differs fundamentally from the standard diameter at breast height (dbh) used for most forest surveys, as diameter height above the substrate varies from 0.5 to 7 m (1.6–23 ft) (consider the tree in the photo on the first page).

Form

Stilt mangroves are rambling to columnar trees with distinct aboveground prop roots. Trees tend to be of shorter stature and more spreading in shape on the seaward edge of stands or in areas of higher salinity. Taller, single-stemmed trees are found most often just behind the water's edge of stands midstream in major riverine estuaries. Multi-stemmed trees are common in more arid or marginal habitats.

Flowering

Flowers are perfect. Inflorescences have few to many joints with 1,2-chotomous branching and one to many buds possible per inflorescence. Open flowers are located within or below leaf axils at leaf nodes below the apical shoot, depending on species. For *R. mucronata*, *R. stylosa*, *R.* × *annamalai*. *R.* × *lamarckii*, and *R. apiculata* mature buds and flowers are located at 1–3, 1–5, 3–5, 3–6, and 6–11 nodes down from apical shoot, respectively. Calyces are typically pale yellow at maturity with 4 lobes, rarely 3. Buds are obovate, green when immature to pale yellowish green as they mature, dimensions 1–2 cm (0.4–0.8 in) long and ~1 cm (0.4 in) wide. Petals, usually 4, are lanceolate to linear, creamy white, woolly to hairless, ~10 mm (0.4 in) long and ~2 mm (0.08 in) wide. Stamens number 7–12, pale yellow. Style is pale green, terete, 0.5–6 mm (0.02–0.24 in) above base, dichotomous tip. Bracts and bracteoles are variable depending on species. Mature bud bracts are slender green (*R. mucronata, R. stylosa*), swollen green (*R.* × *annamalai, R.* × *lamarckii*) and swollen corky green (*R. apiculata*). Peduncles are 1–7 cm (0.4–2.8 in) long, and ~3 mm (0.12 in) wide. Flowering period is chiefly during August–December in the southern hemisphere, and during February–June in the northern hemisphere.

Leaves

Leaves are opposite, simple, light or dark green, obovate, leathery, margins revolute, bluntly acute apex with a distinct mucronate tip, 1–7 mm (0.04–0.3 in) long. Upper leaf surface is smooth, shiny. Cork wart spots occur on undersurface, scattered evenly, not raised, present in most species in most locations, but absent only from *R. apiculata* and *R.* × *lamarckii* in southern New Guinea and Australia. Mature leaf dimensions are 6–19 cm (2.4–7.5 in) long, and 3–10 cm (1.2–3.9 in) wide. Petiole 1–4 mm (0.04–0.16 in) long.

Leaf emergence is mostly around November–February in the southern hemisphere and May–August in the northern hemisphere. Leaf fall occurs mostly during the wet summer period from October to February in the southern hemisphere and April–August in the northern hemisphere.

Fruit

Fruits, when mature, are pear-shaped, elongate, waist constriction, smooth brown surface, calyx lobes elongate spreading (when hypocotyl ready to emerge). For *R. mucronata*, *R. stylosa*, *R.* × *annamalai*, *R.* × *lamarckii*, and *R. apiculata* mature fruit located in leaf axils 3–5, 4–7, 5 (rare), 7 (rare), and 8 nodes down from apical shoot, respectively.

Seeds/hypocotyls

Like all *Rhizophora* species, stilt mangroves are viviparous, meaning that the trees produce seeds hidden in the mature fruit, and these germinate on the parent tree. The dispersal unit, a viviparous seedling, is called a hypocotyl. One hypocotyl is usually produced from each fruit, although on rare occasions twins may be observed.

Hypocotyls are narrowly cylindrical, elongate, green, smooth with irregular small brown lenticels, distal half is slightly wider, distal tip is pointed in most taxa, but rounded to blunt for *R. apiculata*. For *R. mucronata*, *R. stylosa*, *R.* × *annamalai*, *R.* × *lamarckii*, and *R. apiculata* mature hypocotyls are located in leaf axils 4–10, 4–9, none, 8–9 (rarely observed), and 9–13 nodes down from the apical shoot, respectively. Hypocotyl dimensions are variable and not consistently species-specific, 14–80 cm (6–31 in) long, 1–2 cm (0.4-0.8 in) at the widest point, and 0.5–1.5 cm (0.2–0.6 in) wide at the "collar," the fruiting structure that envelops the plumule (embryonic leaves).

"Fruiting," when mature hypocotyls fall, occurs chiefly (but not exclusively) from November to January in the southern hemisphere and May to July in the northern hemisphere.

Bark

The bark is gray to dark gray and heavily fissured, occa-

Top left: The distinct mucronate (abrupt, pointed) tip at the apex of leaves is characteristic of all IWP stilt *Rhizophora.* The coloration of the mucronate tip shown in this image of *R. stylosa* is variably red or green. Northeastern Australia. Top right: Inflorescence of *Rhizophora mucronata* (similar to *R. stylosa*) showing open flowers with distinctive woolly petals and slender smooth bract beneath the calyx. Bottom left: Inflorescence of *Rhizophora apiculata* showing open flowers with distinctive hairless petals, non-reflexed calyx lobes, and corky bract beneath the calyx. Bottom right: Leafy rosette of *Rhizophora mucronata* (similar to *R. stylosa*) showing mature buds and mature fruit. PHOTOS: N.C. DUKE

sionally red-brown and smooth. Prop roots are sturdy even when relatively thin.

Rooting habit

Mature trees have distinctive, sturdy, aboveground prop roots surrounding the stem base that anchor only shallowly in the sediments to 1–2 m (3.3–6.6 ft) depth. This conforms to the oxygen deficient (anoxic) conditions commonly measured in mangrove sediments.

Similar species

Stilt mangroves are distinguished from Atlantic–East Pacific red mangrove species principally by the spiked, mucronate tip at the leaf apex of stilt mangroves that is absent in red mangroves.

Rhizophora mucronata and *R. stylosa* have slender (i.e., length much greater than the width) bracts at the base of mature buds as distinguished from *R. apiculata, R.* × *lamarckii*, and *R.* × *annamalai* that have bracts almost as wide, or wider than the length.

Rhizophora apiculata is distinguished from *R.* × *lamarckii* and *R.* × *annamalai* plus other IWP species by swollen (wider than long), corky brown bracts, one inflorescence joint, and node position of mature buds and flowers in leaf axils at 6–11 nodes down from apical shoot, well below leaves in the leafy shoot.

Hybrid characteristics are shown in *R.* × *lamarckii* where

Mature hypocotyls of *Rhizophora stylosa* (similar to *R. mucronata*). Great Sandy Straits, NE Australia. PHOTO: N.C. DUKE

Left to right: Mature flower buds of *Rhizophora apiculata*, *R.* × *lamarckii*, *R. stylosa,* and *R. mucronata*. These samples were collected in NE Australia, where the four species grow side by side in several estuaries. PHOTO: N.C. DUKE

it has key characters intermediate between *R. apiculata* and *R. stylosa*. Similarly, hybrid characteristics are shown in *R.* × *annamalai*, which has key characters intermediate between *R. apiculata* and *R. mucronata*. Hybrids can often be larger and taller than neighboring parent trees.

Rhizophora × *lamarckii* is distinguished from *R.* × *annamalai* by style length <1.7 mm (0.07 in).

Rhizophora mucronata and *R. stylosa*, the sibling species, are distinguished by short styles (<2 mm [0.08 in] long) in *R. mucronata*, while *R. stylosa* has long styles (>2 mm [0.08 in] long). As noted, *R. mucronata* and *R. stylosa* appear closely related and are possibly the same species. If genetic studies show them to be the same, then *R. stylosa* would be renamed *R. mucronata* var. *stylosa*. Discriminating between them reliably is not possible in many instances without detailed examination of key morphological and genetic characteristics. Individuals with intermediate length styles occur in several locations.

GENETICS

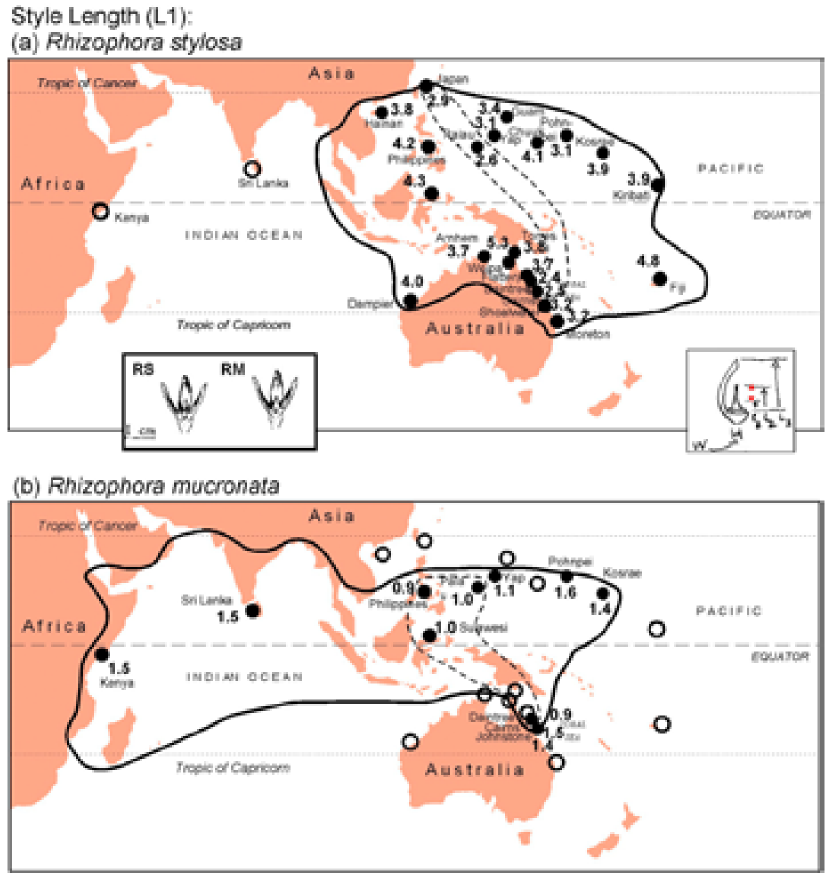
Variability of species

Indo–West Pacific stilt mangroves are those *Rhizophora* species that occur naturally from east Africa to the western Pacific Ocean (see the map). This group comprises five relatively distinct taxa, although at times their morphological and taxonomic differences appear questionable. The uncertainty is chiefly based on: 1) the presence of two intermediate individuals that are recognized as distinct hybrids, namely *R.* × *lamarckii* and *R.* × *annamalai*, and 2) the occurrence of two sibling species, *R. mucronata* and *R. stylosa*, which may, on closer examination, be shown to be the same species.

The relationship of *R. mucronata* and *R. stylosa* is perhaps the most contentious. They appear closely related because they are distinguished only by one key character, namely style length. The sibling species are largely not separated geographically, with a significant portion of the range of each overlapping the other. However, their ranges do include areas of exclusivity in the west and east, respectively. There are also indications that morphological and ecological characteristics vary for each taxon across their wide ranges. For instance, *R. mucronata* in east Africa has the same exposed water edge habit as *R. stylosa* in northern Australia. By contrast, *R. mucronata* in Australia and Asia occurs in upstream locations of freshwater dominated estuaries. There are also subtle but distinct differences in morphological characteristics in *R. mucronata* for bud shape, inflorescence structure, and leaf dimensions that may be related to differences in habitat. It is clear that *R. stylosa* is the taxon best adapted to marine exposed locations wherever it occurs.

It is of great interest to fully evaluate the relative and precise distributions of *R. mucronata* and *R. stylosa*, because these are likely to explain the way species have naturally evolved and dispersed. In some island groups to the north of Australia, for instance, there is a curious pattern in separate sympatric occurrences where these species are easily distinguished in some populations (Philippines, Sulawesi) while in others (Federated States of Micronesia, Palau) their style lengths overlap, making it impossible to always tell them apart using this character. This may be explained by a progressive lengthening of the style in *R. stylosa*, corresponding possibly with its more recent introduction in locations with longer styles. If this is correct, *R. stylosa* has spread from Australia and Federated States of Micronesia both westward and eastward; for example, in Sulawesi and Fiji where style lengths are the longest recorded. This idea concurs with the specialized marine habit of this species.

By contrast, *R. apiculata* is readily distinguished from *R. mucronata* and *R. stylosa*. This species appears more prevalent in estuaries influenced by larger and more continuous freshwater flows, and it is found in a continuous distributional range, from India to the western Pacific and northern Australia. Across this range there are also two forms of *R. apiculata*, and their occurrences do not overlap. One form, found north and west from the northern New Guinea coast, fits the type description in every respect including the presence of cork wart spots on leaf undersurfaces. The other form lacking these spots occurs south and east from the southern New Guinea coast. This character was thought to be unique to *R. apiculata* until recently, when trees of *R. racemosa* (an AEP red mangrove) without spots were discovered in Brazil. This character helps define two forms of *R. apiculata* in Australasia and the western Pacific.



Variation in style length of *Rhizophora stylosa* and *R. mucronata* in the IWP region. Note that for each species, but especially for *R. stylosa*, larger styles occur in eastern and western populations. IMAGES: N. C. DUKE

Known varieties and hybrids

Rhizophora mucronata and *R. stylosa* are both known to hybridize with *R. apiculata*, giving rise to morphologically distinct and geographically widespread hybrid forms, *R.* × *annamalai* and *R.* × *lamarckii*, respectively. Their hybrid status was initially based on intermediate morphological characters but has since been confirmed in genetic investigations.

As discussed above, *R. mucronata* and *R. stylosa* are sibling species with few diagnostic characters to separate them and a corresponding lack of genetic separation. This clearly makes it difficult to separate respective hybrid forms with *R. apiculata*, although this may be done by also using the style length character. The situation is more complex, however, when it must be considered further that there are the two forms of *R. apiculata*. These each have hybrids with *R. stylosa* based on occurrences north and south of New Guinea.

IWP stilt mangroves are also characterized by a number of notable genetic, morphological, and growth variants. Aberrant traits are observed in a small number of individuals throughout the range. Perhaps the most consistent aberrant trait, however, is "albino" hypocotyls (i.e., those lacking any green pigment, leaving them red or yellow) observed in Australia, Federated States of Micronesia, Palau, and other places. Yellow or red propagules can be observed hanging in affected trees alongside normal green propagules of all IWP species. Their relative number on an individual tree is thought to quantify the amount of outcrossing that occurs with neighboring normal trees. On rare occasions, other trees have also been observed with variegated foliage.

Culturally important related species

All *Rhizophora* species are closely similar in tree form, and different cultural groups in the Pacific region may not always distinguish between them. Other mangrove genera, like *Bruguiera*, are considered close in form and value also, and these are often used in similar ways by indigenous peoples.

ASSOCIATED PLANT SPECIES

IWP stilt mangroves are naturally associated with a number of other mangrove and non-mangrove species across their wide range of tidal and estuarine locations. Planting with other species is highly recommended, particularly terrestrial and beach strand associates growing naturally above mean sea level elevations. The idea is to establish and achieve whole-of-bank stabilization as soon as possible. Since stilt mangroves also occupy a range of substrate types, including coral, rocks, gravel, sand, and mud, it is important to choose associated species best suited to the particular local conditions.

Associated species commonly found

The associated species vary with geographic location, latitude, soil type, estuarine upstream location, and tidal position.

In frontal stands, IWP stilt mangroves may be associated with *Sonneratia alba* and *Avicennia marina* downstream. Where downstream stands of stilt mangroves are backed by sand ridges and beach margins, the associated species include *Calophyllum* spp., *Thespesia* spp., *Casuarina* spp., *Barringtonia asiatica,* and *Cocos nucifera*.

Upstream in riverine estuaries of tropical coastlines of larger islands and continental margins, associated species include *Sonneratia caseolaris*, *S. lanceolata*, and *Aegiceras corniculatum*. In such upstream locations, stilt mangroves are commonly backed by *Bruguiera* and other higher intertidal mangrove species, as well as associated upland species including *Barringtonia racemosa* and *Hibiscus tiliaceus*.

Foliage of *Rhizophora mucronata* showing a tree with a rare yellow "albino" form of hypocotyls among the normal green hypocotyls. Johnstone River, NE Australia. PHOTO: N. C. DUKE

ENVIRONMENTAL PREFERENCES AND TOLERANCES

Climate

IWP stilt mangroves thrive in tropical and subtropical environments characterized by moderately high and well distributed rainfall. However, in drier locations, like in northern areas of Western Australia, the stunted but dense thickets of *R. stylosa* attest to the great adaptability of stilt mangroves to a wide range of climatic types.

Elevation range

0–6 m (0–20 ft), in reference to mean sea level.

Mean annual rainfall

These mangroves grow in all rainfall conditions. Their extent, form, and biomass reflect the different rainfall conditions.

Rainfall pattern

Grows in climates with summer or uniform rainfall patterns.

Dry season duration (consecutive months with <40 mm [1.6 in] rainfall)

Mangrove plants appear to depend on groundwater to sustain optimal growth, especially during drier months. Across a wide variety of climatic regions, mangrove cover expands and contracts through time. This has been evident in correlations between El Niño events and reduced growth as possible causes of some damage to mangroves, presumably due to decreases in freshwater availability.

Mean annual temperature

20–30°C (68–86°F) (estimate)

Mean maximum temperature of hottest month

23–38°C (73–100°F) (estimate)

Mean minimum temperature of coldest month

13–18°C (55–64°F)

Minimum temperature tolerated

10°C (50°F) (estimate)

Soils

Trees develop greatest stature and columnar growth form in estuaries of larger tropical rivers, characterized by fine clay, black mud sediments with relatively high loads of organic carbon, and anaerobic soils with high concentrations of sulfide. Trees also grow well in sites with aerobic sediments consisting of fine sands to coarse stones and rocks, as well as coral ramparts.

Soil texture

Plants grow best in light, medium, and heavy texture soils (sands, sandy loams, loams, sandy clay loams, sandy clays, clay loams, and clays).

Soil drainage

Plants grow best in soils with free and un-impeded drainage, as well as waterlogged soils.

Soil acidity

pH 6–8.5

Special soil tolerances

Plants grow best in saline soils but can survive well in fresh water. The optimal salinity range is reported to be 8–26 ppt (parts per thousand), compared to approximately 34–36 ppt for seawater.

Tolerances

Drought

Stilt mangroves usually grow best in wetter conditions. However, *R. stylosa* and western range *R. mucronata* can tolerate drought periods well.

Full sun

They usually grow best in full sun.

Shade

Stilt mangroves are usually considered to have a very low tolerance of shade. However, in eastern Australia at its southern latitudinal limit, *R. stylosa* trees commonly grow under a closed canopy of *Avicennia marina*. This may be

MANGROVES AND CLIMATE CHANGE

Indo–West Pacific stilt mangroves, like other mangrove species, are affected by climate change. The unique physiological characteristics of each species define its capacity for survival in the face of change. Mangroves are expected to respond rapidly and decisively to shifts in key factors, like temperature, rainfall, and sea level, as each species has defined ranges of tolerance for each factor. For instance, because mangroves are characteristically restricted to elevations between mean sea level and highest tides, as sea level rises their communities must move upland to survive. Since mangroves have narrow optimal temperature ranges, rising temperatures will cause their distributions to shift north or south to areas where temperature conditions are most suitable, and they will die off in areas where they are not suited. Of course, their success in making these shifts depends on their successful dispersal and re-establishment, and the availability of suitable new space. Clearly, such changes have occurred throughout history, so the distribution of mangroves today represents the survivors of all past changes.

Key indicators of change can be identified and mapped as incremental shifts and responses of mangrove communities. These might be observed as shifts in vegetation, for example: 1) in the total tidal wetland habitat zone, as expected with changes in sea level; and 2) in the salt marsh–mangrove ecotone, as expected with changes in longer-term rainfall patterns as this affects moisture stress in saline environments. In both cases, the response zones will follow elevation contours. Changes along contours can be quantified from long-term spatial assessments over decade- and century-long time periods, depending on the rates of change. Knowledge of these changes and their causes allows better prediction of future change.

due to the absence of scolytid beetle larvae that usually infect shaded propagule-seedlings in the tropics (Brook 2001). If this is the case, it implies *Rhizophora* seedlings might be more shade tolerant than originally thought (Sousa et al. 2003). This is supported further by the observation that *Bruguiera* species, the apparent shade specialists of tropical areas, had few scolytid infections.

Trunk of *Rhizophora mucronata* showing distinctive stilt roots. Kenya, E Africa. PHOTO: N. C. DUKE

Fire

The trees have no tolerance of fire in close proximity.

Frost

They have low tolerance of sub-freezing temperatures.

Waterlogging

Stilt mangrove trees are tolerant of daily tidal flooding up to depths of 2.5 m (8 ft). While tolerating permanently saturated soils, they are intolerant of drying soils.

Salt spray

They are highly tolerant of salt spray.

Wind

Some species of stilt mangrove trees are typically found on the exposed water's edge of large riverine estuaries.

Abilities

Self-prune

Stilt mangroves self-prune well in dense stands, but they commonly maintain lower branches in more open locations.

Coppice

The trees have notably poor coppice ability. Generally, if greater than 50% or more of the leaves are removed from a tree, they will die. There appears to be a variant of *R. apiculata* in the Philippines and in some islands of the Federated States of Micronesia (Pohnpei and Kosrae) that is used by local people for sustainable firewood collection. These trees regrow from regular cutting, which keeps them stunted.

GROWTH AND DEVELOPMENT

Growth rates vary with age. The tree generally grows less than 1 m/yr in height but can exceed this in favorable circumstances. Height growth is rapid shortly after establishment while food reserves are taken up from the hypocotyls of established propagules. The growth rates appear to slow when trees approach a site maximal canopy height, dependant on specific site/location conditions. When near maturity, trees tend to spread and broaden their canopy and stem diameter rather than grow taller.

Flowering and fruiting

Flowering and fruiting periods of stilt mangroves are distinctly seasonal. Furthermore, peak pheno-events shift later with cooler temperatures and higher latitudes. Trees have notable and relatively long periods of reproductive development, taking 18–30 months from first emergence of flower bud primordia until maturation and drop of mature hypocotyls. The duration depends on species, with the longest being *Rhizophora apiculata*, with around 30 months for each reproductive cycle.

Yields/growth rates

Growth rates vary with species, spatial position in the stand, competition, vigor, and age. In the Matang Mangrove Forest Reserve in Malaysia, Putz and Chan (1986) reported that diameter growth rates of *R. apiculata* trees were 0.24–0.29 cm (0.09–0.11 in) for diameter size classes from 10 to 60 cm (4–24 in).

Watson (1928) estimated that under Malaysian conditions mean annual increment (MAI) of stilt mangroves culminated at around 10.6 m^3/ha/yr (152 ft^3/ac/yr) at 39–40 years.

Reaction to competition

Rapid early growth of seedlings of stilt mangroves in full sunlight ensures their success and dominance in preferred estuarine and intertidal conditions. Newly established seedlings grow best in close proximity with their same species cohort. This affords them maximal protection from physical damage by drift logs and erosive waves. Since competition is high between neighboring seedlings, slower plants die and decompose quickly, leaving faster competitors the benefit of not only the space they occupied but also their nutrients.

PROPAGATION

IWP stilt mangroves are readily propagated by direct planting of their propagules. Although natural regeneration is generally relied upon around the Pacific region, these species are relatively easy to propagate. Propagation is simple and relies on the special feature of the genus in having large viviparous propagules. Planting simply entails gently pushing the distal end of the 20–80 cm (8–31 in) long hypocotyl one third of its length into the sediment, spaced at about 1–1.5 m (3.3–5 ft) intervals. No holes need be dug, and neither nursery preparation nor stakes are needed. Low maintenance is generally required for maximizing seedling establishment success in sheltered areas. However, substantial protection is required in more exposed coastal locations during the first decade of establishment. Such protection methods may include encasement of individual seedlings in PVC piping (Riley and Kent 1999), or installation of temporary structures to dampen wave action and reduce debris drift across restoration sites as observed in Vietnam and China (Field 1996).

Propagule collection

Propagules may be available throughout the year, but peak production occurs around July–August in northern parts of the range and around January–February in the southern hemisphere. Mature propagules may be collected after they have fallen or been picked directly off trees. Only healthy looking propagules should be selected. Propagules that are shrunken or desiccated in appearance or that exhibit significant physical damage should be rejected. Although propagules with only minor borer damage may survive and grow, selection of propagules with no signs of borer or crab damage is strongly preferred. Propagules that already have some root or leaf development can be used in most cases but should not be stored for long.

Propagule processing

Processing of mature propagules is not required for stilt mangroves, although damaged and insect infested individuals should be removed. Also see the following pretreatment section for possible additional steps. Propagules can be sown in nursery beds, or preferably planted directly in the field soon after collection.

Propagule storage

Propagules can be kept viable for at least 6–7 days by storing them in brackish water or by wrapping them in wet

Left: Mature hypocotyl and fruits of *Rhizophora mucronata* showing distinctive collar on attached propagule and expended fruit. PHOTO: N. C. DUKE
Right: A sectioned wilting seedling of *Rhizophora stylosa* shows the extent of scolytid infection marked by brown frass. PHOTOS: B. M. BROOK

burlap bags and keeping them out of direct sunlight. Pretreatment is considered essential if considering such storage (see below). It is likely that propagules can be kept longer, but storage beyond 2 weeks is not recommended, and long-term storage is not feasible.

Propagule pretreatment

Pretreatment of propagules is generally considered unnecessary. However, a study of scolytid beetle larvae (*Coccotrypes fallax*) infections on *Rhizophora* propagules in Australia found at least 18% that were heavily infested (Brook 2001). Infested propagules were established under canopy-shaded areas. The study went further, finding that pretreatment in a 50°C (122°F) water bath for 5 minutes killed the beetles and removed the risk of establishment loses due to borer damage. Heat treatment might be easily achieved by leaving the collected propagules in the sun for a short period (a few hours) before planting.

New planting on seaward edge of *R. apiculata* at Ao Khung Krabaen Mangrove Forestry Center, Som Lek, Thailand. PHOTO: C. ELEVITCH

Growing area

Stilt mangroves should be grown in full sunlight.

Seedling establishment

Leaves and roots may begin to develop within a week or two of sowing.

Media

Although a wide variety of soil media are acceptable, a mix of sand and peat in equal parts has been recommended for mangrove nurseries.

Time to outplanting

Anytime during the year is suitable. Seedlings are ready for outplanting at the 6-leaf (=3 node) stage if grown up in nursery conditions. Older seedlings up to 0.5 m (20 in) tall have also been successfully transplanted, but this is not considered beneficial.

Direct planting of large numbers of propagules is restricted by their peak seasonal availability, as propagules do not keep for extended periods unless planted out in nursery conditions.

Guidelines for outplanting

Propagules or nursery-grown seedlings usually have excellent survival in sites correctly selected and, if appropriate, protected from disturbance. Survival rates of 90% or greater are not unreasonable in such circumstances.

On the other hand, survival may be zero on sites exposed to excessive wave action, on sites with inappropriate hydrologic or salinity regimes, or (rarely) disturbance by grazing animals (e.g., goats, sheep, cattle, and horses). A method of encasing propagules in PVC pipe has been used in Florida and the Caribbean to protect seedlings in places with a high likelihood of disturbance.

DISADVANTAGES

In general, the planting of stilt mangroves poses few significant disadvantages when planted within their native ranges. They are not especially susceptible to pests or pathogens and they have not been reported to host major pests or pathogens of important crop species.

Potential for invasiveness

Although the invasiveness of stilt mangroves has not been demonstrated, they are likely to be opportunistic due to their relatively wide tolerance for salinity and soil conditions. The spread of the closely allied AEP red mangrove species *R. mangle* when introduced into Hawai‘i has clearly demonstrated the potential for invasiveness of these mangroves. Although they were not native, suitable growing conditions existed, demonstrating that the global distribution of *Rhizophora* spp. is currently limited by their natural

BENEFITS OF MANGROVE TIDAL WETLAND

Benefits include, in no particular order (adapted from Tomlinson 1986):

- visual amenity and shoreline beautification
- nutrient uptake, fixation, trapping, and turnover
- habitat use by fauna
- mesoclimate, where forests moderate evapotranspiration to create a specialized niche climate
- nursery habitat for young fauna, where mangroves provide a source of food and physical protection from predation
- sanctuary niche for mature fauna, including migratory birds and fish, where mangroves provide protection and a food resource
- primary production based on photosynthesis, giving rise to forest growth and forest products, notably timber
- secondary production, including microbial and faunal production, as well as grazers, and via decomposition
- fishery products, including both estuarine and coastal
- shoreline protection, based on general mangrove tree and root structure, as well as edge trees, which reduce erosion and provide stand protection from waves and water movement
- carbon sequestration and a sink where carbon is bound within living plant biomass
- sediment trapping, based on mangroves being a depositional site for both water and airborne sediments, which in turn reduces turbidity of coastal waters.

dispersal range. This also means geographically isolated populations are vulnerable to introductions of genotypes from elsewhere.

Susceptibility to pests/pathogens

Susceptibility to pests and diseases is believed to be low, with the exception of insect borers and crabs that feed on propagules.

Host to crop pests/pathogens

No reports were found of stilt mangroves serving as hosts for known major crop pests or pathogens. The scolytid beetles are specific to the genus *Rhizophora*.

AGROFORESTRY/ ENVIRONMENTAL PRACTICES

Mulch/organic matter

Mulch in *Rhizophora* forests is hidden from view. If it were not for the small mangrove crabs, fallen leaves would be washed away with each tide. The crabs actively take leaves into underground burrows and chambers. The resulting mulch is rapidly colonized by bacteria and consumed by other burrowing fauna to release nutrients that appear to further enhance the forest.

Soil stabilization

Stilt mangrove forests stabilize soils with their network of sturdy overlapping prop roots dampening water movement and promoting sedimentation in areas that might otherwise be eroded.

Rhizophora mucronata **tree growing on the edge of an estuarine channel. While the stem leans out over the water to get the most light, the stilts both support the tree and stabilize the bank.** PHOTO: N. C. DUKE

Fence posts

Stilt mangrove stems make good posts since they are generally hard wood and resistant to insect borers.

Windbreaks

Rhizophora forests provide a windbreak along coastal margins, generally, and as places to seek sanctuary during typhoons and cyclones. Planting in highly wind-prone locations is not recommended unless the location has some history, or reasonable expectation, that mangrove survival is likely.

Woodlot

Mangroves adjacent to peoples' homes throughout the Pacific frequently serve as informal woodlots, particularly on islands with clear tenure systems that include mangrove areas. Stilt mangrove wood is very useful for small construction, and for cooking fuel. Converting it to charcoal can further enhance the timbers' calorific value. This is done commercially in SE Asia and Central America with various *Rhizophora* species.

Native animal/bird food

IWP stilt mangroves are largely an unknown source of native animal foods. However, several observations demonstrate that the diversity and quantity of the source is thought to be extremely important in mangrove ecosystems. Numerous insects, crabs, and mollusks graze on green leaves in the forest canopy. Sesarmid crabs consume a large quantity of fallen leaves and propagules. Organic matter processed by these herbivores is believed to broadly support aquatic food chains in coastal regions. Few mammals appear to use stilt mangroves as a major food source, although native rats often chew into the wood in search of boring insect larvae.

Wildlife habitat

In addition to aquatic marine organisms (see Fish/marine food chain), stilt mangroves serve as habitat for a wide range of terrestrial and arboreal wildlife. In various locations throughout the region, these forests provide shelter and food for a number of associated fauna, including birds, fruit bats, small mammals, shellfish, and other marine life.

Bee forage

Rhizophora species have no nectar, but they do produce copious pollen that is usually distributed by wind.

Fish/marine food chain

Mangroves in general are believed to play a vitally important role in protecting and supporting marine food chains. Many fish species use stilt mangroves during part of their life cycles, as do species of shrimp and crabs. Species such as the mangrove mud crab (*Scylla serrata*) are common in IWP mangroves, and these are important sources of food and income on many islands in the region. Populations of some smaller species may exceed 10 crabs/m^2 (1 crab/ft^2) in parts of the Pacific. Senescent leaves having fallen from *Rhizophora* trees are taken by grapsid (small mangrove) crabs into their burrows. Buried leaves decompose and contribute to nutrient recycling in mangrove forests. Nutrients also feed directly and indirectly to associated estuarine and marine food chains.

Rhizophora stylosa **sprouted propagules for sale in Iriomote, Japan.** PHOTO: N. C. DUKE

Coastal protection

Stilt mangrove forests, and mangroves in general, play an important role in protection of coastlines, fishponds, and other coastal infrastructure. Stilt mangroves are planted for coastal or fishpond protection in some areas (e.g., in Kalibo Bakhawan Eco Park, the Philippines) and there are laws in many locations aimed at protecting mangroves in large part because of this important function.

Ornamental

No significant ornamental trade is known. However, as an apparently isolated example, a small number of plants are sold as souvenirs to departing tourists from Iriomote and other southern islands of Japan. Sprouted hypocotyl seedlings are used to make bonsai "forest gardens."

USES AND PRODUCTS

IWP stilt mangroves are probably of greatest value for their environmental benefits, because they (and mangroves generally) are believed to play a vital role in supporting marine food chains, protecting coastal areas, and improving water quality.

In terms of direct benefits to people, the most widespread use of stilt mangroves is for wood for a range of purposes from cooking fuel to construction of homes and canoe parts. Other uses of the stilt mangroves include tannin and dyes. A less lauded benefit has been derived from some ecotourism ventures. The dual benefit in this practice comes from both a moderate economic return combined with a substantial longer-term educational value in raising environmental awareness in the community.

Staple food

Leaves and hypocotyls are edible but not widely used for food.

Medicinal

Stilt mangrove bark has reportedly been used to treat angina, boils, and fungal infections. The leaves and bark have been used as an antiseptic and to treat diarrhea, dysentery, fever, malaria, and leprosy, although it is not clear how effective the treatments have been in each of these cases.

Timber

The wood of stilt mangroves is widely used for structural components (e.g., poles, beams, flooring, wall-cladding, and rafters) of traditional homes and other structures like underground mine supports, fencing, cabinet works, tool handles, and boat anchors. The wood is also used for other purposes, ranging from traditional uses such as fishing stakes, spears, and copra-huskers to use as a source of chips for pulp production. However, pulp from *Rhizophora* species does not have good strength properties, so these species are not often sought after for this purpose (Percival and Womersley 1975).

Fuelwood

Stilt mangrove wood is used for fuelwood on many Pacific islands (e.g., Kosrae and Chuuk). The wood is also made into charcoal in countries such as the Philippines, Indonesia, and Malaysia (Ong et al. 1980, 1995).

Canoe/boat/raft making

The wood has been used to make canoe parts.

Top: Mangrove tourism in Hainan, China, complete with *Rhizophora* motifs on the jetty handrail panels. PHOTO: N. C. DUKE **Bottom: Boardwalk and signage for visitors (*R. mucronata* on left and *R. apiculata* on right), Ao Khung Krabaen Mangrove Forestry Center, Som Lek, Thailand.** PHOTO: C. ELEVITCH

Tannin/dye

The bark and hypocotyls are used to produce dyes ranging from red-brown to black (the latter with repeated dying). *Rhizophora* species are the best producers of tannins of all the mangroves with 20–25% of bark weight (Percival and Womersley 1975). Chopped bark is treated by continuous countercurrent extraction with first cold then warm water producing an extract called "cutch." The cutch can be exported for processing and final tannin extraction. Tannins were used extensively for preserving cotton ropes and netting. Mangrove tannins can be used to prepare tannin formaldehyde adhesives. These adhesives are recognized for their high moisture resistance and waterproof grades in plywood and particleboard production. *Rhizophora* tannins are also known to impart a red color to finished leather tanning, but this is considered undesirable since blending with other tannin extracts is needed.

Ecotourism

The mangrove environment is attractive and interesting to both local people and to visiting tourists. In China, for example, facilities have been provided to assist and regulate this form of ecotourism, including a dedicated hotel and restaurants. Simple boardwalks in other places (e.g., Australia, Thailand) are relatively low key but the intention is the same, to provide public access for those wanting to see and learn about this fascinating environment. The boardwalks are there to make the mangrove experience as effortless as possible while protecting the mangroves from direct damage. Walks are often also accompanied with informative and educational signage.

Eleven-year-old plantation of *Rhizophora apiculata* in the 63 ha (156 ac) Bakhawan Eco Park at Kalibo, northern Panay, Philippines. PHOTO: N. C. DUKE

COMMERCIAL CULTIVATION

Stilt mangrove timber is harvested commercially for charcoal production in SE Asia. The calorific value of the timber is significantly enhanced by converting it to charcoal. This is done with various *Rhizophora* species. Charcoal production has been conducted in a sustainable way on the Malay Peninsula for over 100 years using silvicultural practices developed for *Rhizophora* species, especially *R. apiculata* (Ong et al. 1980, 1995). In addition, forests in Malaysia, New Guinea, and the Solomon Islands have been clear-felled for wood chips using unsustainable harvesting practices.

Spacing

Mangrove plantations in general are typically planted at spacings of about 1.0–1.5 m (3.3–5 ft). Spacing wider than about 2.5 m (8 ft) tends to result in a high proportion of multiple-stemmed and/or shorter trees. Wider spacing and the resulting spreading trees may be desired for coastal protection projects, but not for timber production. In the absence of significant natural mortality timber plantations should be thinned to spacing of 2.5 to 3.5 m (8–11 ft) between trees as the stand develops and becomes crowded.

Management objectives

In areas where the mangrove fern (*Acrostichum speciosum*) is common, it may need to be controlled to promote early growth of stilt mangroves. Some published guidelines for mangrove silviculture exist and are referenced below, but specific guidelines on thinning, fertilizing, etc., are currently unavailable.

Growing in polycultures

Stilt mangroves naturally occur in mixed-species stands, and each species has its own ecological and economic values. Mixed-species plantings are recommended together with large-leaf mangrove, *Bruguiera gymnorrhiza*. It is also important to plant associated buffer areas, especially along the shoreline where mangroves grow better adjacent to banks stabilized by shoreline upland plants. Suitable upland tree genera include *Calophyllum*, *Casuarina*, *Hibiscus*, *Thespesia*, and *Barringtonia*. Within the mangrove forest, natural recruitment will often bring additional mangroves such as *Bruguiera* species, but these might be planted as well. Together they will complement and enhance the richness and stability of the planted environment.

Estimated yield

Snedaker and Brown (1982) state that mangrove forest products in Bangladesh have an annual value of US$36,000,000. Ong (1982) reports that the Matang Reserve in Malaysia with 35,000 ha (86,000 ac) of productive, almost monospecific, forests of *R. apiculata*, the value of mangrove wood alone is close to US$9,000,000 per year.

The Matang Mangrove Forest Reserve in Malaysia has been managed for timber production of chiefly *Rhizophora apiculata* since the beginning of the century and is reputedly the best managed mangrove forest in the world (Khoon and Ong 1995, Ong et al. 1995). The average stand volume for these stilt mangroves was 153 m^3/ha (2190 ft^3/ac). Stand volumes up to 226 m^3/ha (3230 ft^3/ac) have been reported from Thailand.

The present management plan for the Matang Reserve is a 30-year rotation period with two thinnings, at 15 and 20 years. The 30-year rotation harvested yields have been around 136–299 mt/ha (61–133 t/ac) of green wood. However, there has been a decline in yield from 299 mt/ha (133 t/ac) from virgin stands to the second-generation yields of 158 mt/ha (70 t/ac) in 1967–69 to an even lower 136 mt/ha (61 t/ac) in 1970–77. Because the standing biomass of the trees did not increase from 23 years (155 mt/ha [69 t/ac]) to 28 years (153 mt/ha [68 t/ac]), it was suggested that a rotation of 25 years be used instead of the previous recommendation of 30 years.

Markets

Markets on most Pacific islands are local in nature, with little in the way of stilt mangrove products (other than indirect products like mangrove crabs and fruit bats) being exported from one island to another. The exception is probably firewood and charcoal, which is available from local markets in most places. In Southeast Asia, large quantities of stilt mangrove wood chips and charcoal may be moved greater distances and in greater volumes than wood products on smaller islands.

INTERPLANTING/FARM APPLICATIONS

Some interplanting systems include:

Example 1—Bakhawan Eco Park (Primavera et al. 2004)

Location

Aklan, New Buswang, and Kalibo, Philippines

Description

Planting was undertaken in 1989 and 1993. Species planted included *R. apiculata* and *R. mucronata* on a total area planted of 63 ha (156 ac). Sponsors and implementers were DENR, PACAP AusAID, USWAG, and KASAMA.

Crop/tree interactions

Not known.

Spacing/density of species

Spacing was about 1.5 m (5 ft) for both species.

Example 2 (Primavera et al. 2004)

Location

Guimaras and Nueva Valencia, Philippines

Description

The planting was undertaken in 1994. Species planted included *R. apiculata* and *R. mucronata* on a total area of 149 ha (368 ac). Funding source and implementers were DENR-CEP.

Crop/tree interactions

Not known.

Spacing/density of species

Spacing was around 1.5 m (5 ft) for both species.

Example 3 (Primavera et al. 2004)

Location

Iloilo and Carles, Philippines

Description

The planting was done in 2001. Species planted included *R. apiculata* and *R. mucronata* on a total area of 530 ha (1300 ac). Funding source and implementers were DENR Forestry Sector Program: MACABATA-ARM Federated People's Organisation.

Crop/tree interactions

Not known.

Spacing/density of species

Spacing was around 1.5 m (5 ft) for both species.

PUBLIC ASSISTANCE

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Rhizophora apiculata, R. mucronata, R. stylosa, R. × *annamalai, R.* × *lamarckii* (Indo–West Pacific stilt mangroves)

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