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Rhizophora mangle, R. samoensis, R. racemosa, R. × harrisonii (Atlantic–East Pacific red mangrove)

Rhizophoraceae (mangrove family)

American mangrove (English, Australia); red mangrove (USA); *mangle rojo* (Central and Latin America, Pacific and Caribbean coasts); *tiri wai* (Fiji); *togo* (Samoa)

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IN BRIEF

Distribution Native to American west and east coasts and African west coast. One species, *Rhizophora mangle*, was introduced to the central Pacific, including Hawai'i and the Society Islands. Closely allied with Indo–West Pacific stilt mangroves whose ranges naturally overlap AEP mangroves only in the southern Pacific.

Size Can reach 30–50 m (100–160 ft) in height, although commonly attains 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 Commonly associated with other mangrove species.

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

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

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

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

Yields Timber volume was estimated at 100–150 m^3/ha/yr (1400–2100 ft^3/ac/yr).

Intercropping Recommended for planting together with other mangrove species.

Invasive potential These plants are ready colonizers of new mud banks, making them opportunistically invasive with a high potential to invade alien environments; generally not recommended for planting outside of their natural range.

Atlantic–East Pacific red mangrove *Rhizophora mangle* growing along an estuarine shoreline near Braganza, Amazonian Brazil.

INTRODUCTION

Atlantic–East Pacific red mangroves (AEP *Rhizophora* species) are the most important and dominant mangrove species of tropical coastal areas of the Atlantic Ocean, the American Pacific coast, and several islands in the southwestern Pacific Ocean. This species group is one of two that make up the genus *Rhizophora* and consists of three species (two being closely allied) and one hybrid: *R. mangle*, *R. samoensis*, *R. racemosa*, and *R.* × *harrisonii*, respectively.

Red mangroves, notably *R. mangle*, have also been introduced into new sites in the Indo–West Pacific (IWP) region during the past century. In the Hawaiian and Society Islands, no mangroves were present until introductions were made in the 1920s, since which time their presence has become quite noticeable. In the Hawaiian Islands, mangroves have reportedly overgrown channels, reduced tidal flows, and overgrown archeological sites. Red mangroves thrive under a range of intertidal wetland conditions, including high salinity levels from greater than full strength seawater to freshwater (Cintron et al. 1978), and they tolerate a range of flooding, soil types, and other physical site factors. Typically, they are most common in the middle to low intertidal zone above mean sea level, extending often along the seaward margin of mangrove stands.

Many of the values of red mangroves are difficult to separate from the larger role played by mangrove plants. As such, the roles of particular species of *Rhizophora* are often not distinguished from other members of the genus, including the IWP stilt mangroves. Because *Rhizophora* species dominate most tropical mangroves worldwide they are generally believed to play a vital role for mangrove ecosystems including shoreline protection, enhancement of water quality in near-shore environments (plus coral reef areas), and support of estuarine and marine food chains.

Red mangroves are generally considered non-native to the IWP, not withstanding the disjoint but natural occurrence of *R. samoensis* in New Caledonia, New Hebrides, Fiji, Tonga, and Samoa. However, where introductions of *R. mangle* have been made, the uses of such plants need to be weighed carefully against their effects as potentially invasive species. In Hawai'i, for example, several important negative effects have been documented, including reduction in the habitat quality for endangered water birds such as the Hawaiian stilt (*Himantopus mexicanus knudensi*), colonization of habitats to the detriment of native species (e.g., in anchialine pools), overgrowing native Hawaiian archaeological sites, and causing localized drainage problems by reducing the flow through tidal creeks or drainage channels.

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.

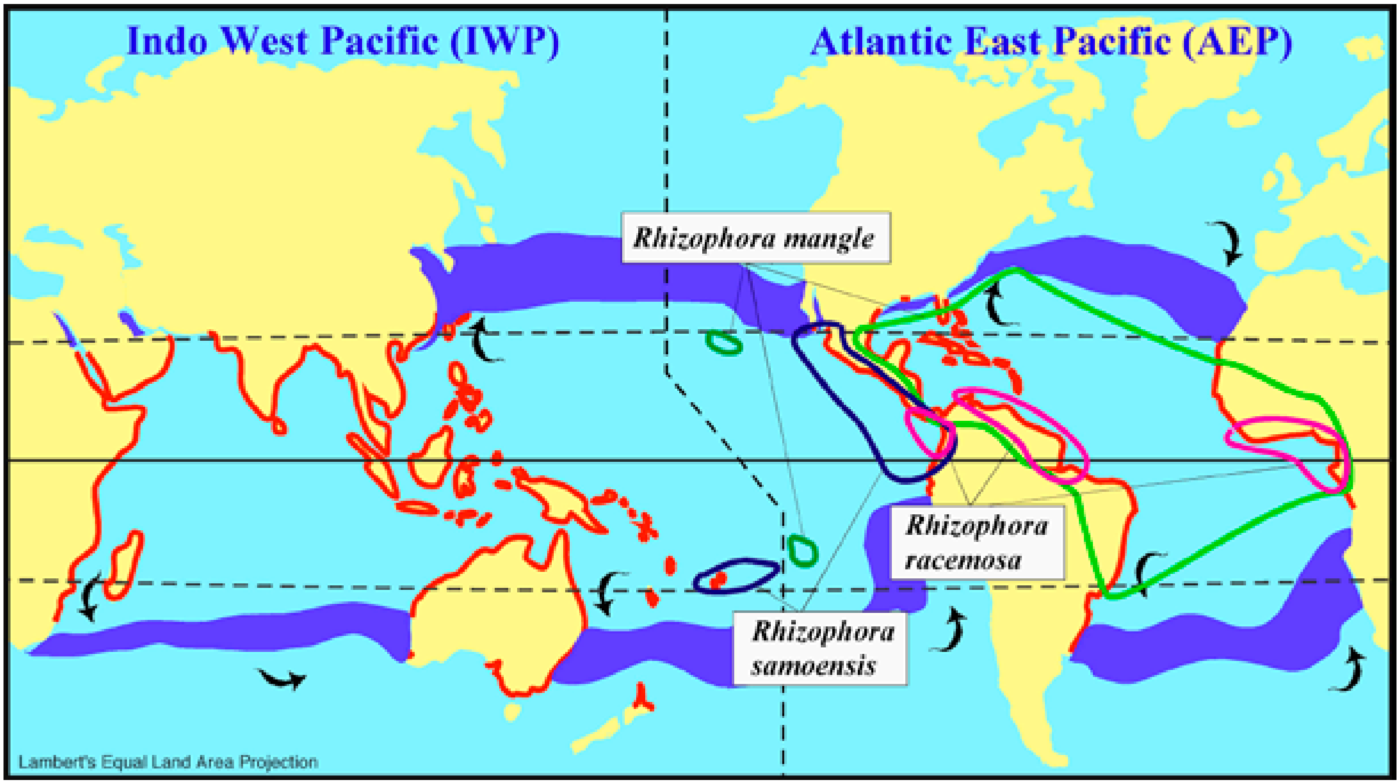
DISTRIBUTION

Native range

Atlantic–East Pacific red mangroves are native to tropical regions along the American east and west coasts to the African west coast, as well as in isolated occurrences in the southwestern Pacific islands.

Rhizophora mangle is the species that most characterizes AEP *Rhizophora*. It occurs naturally and dominates tropical tidal areas along both sides of the Atlantic. The closely related and almost identical "sibling species," *R. samoensis* (=*R. mangle sensu lato* Tomlinson 1986; =*R. mangle* var. *samoensis* Hochr.), is native to the American west coast and islands in the southwestern Pacific, notably New Caledonia, New Hebrides, Fiji, Tonga, and Samoa. The taxonomic status of these sibling taxa is arguable based on morphological data alone. The status of observed differences in like forms *R. mangle* and *R. samoensis,* however, will only be resolved in genetic studies and selected breeding programs.

Rhizophora racemosa is less common than *R. mangle* and *R. samoensis* but occurs as a distinct co-inhabitant of man-



World distribution of red mangroves, the AEP *Rhizophora* species. Given the apparent hybrid status of *R.* × *harrisonii*, its distribution is likely where the distributions *R. racemosa* and *R. mangle*/*R. samoensis* overlap. Coastlines marked in red indicate the distribution of all mangroves. IMAGE: N.C. DUKE

grove stands in wetter areas and larger catchment estuaries of the Atlantic. The species favors riverine estuaries, and it is restricted in the AEP to a few stands along the Pacific coast of the Americas and does not occur in the IWP. At least one other possible species, *R.* × *harrisonii*, occurs across the same range. Given this and its intermediate characters, the taxon is considered the putative hybrid of *R. mangle* and *R. racemosa*. The distribution of *R. racemosa* and the putative hybrid *R.* × *harrisonii* appears restricted mostly to equatorial estuaries of larger river systems with more continuous freshwater flows.

Of great interest also is the natural presence of red mangrove in the southwestern Pacific islands. Also occurring in this region is another hybrid taxon, *R. selala* (Salvoza) Tomlinson, whose putative parents include *R. samoensis* (=*R. mangle* var. *samoensis*) and *R. stylosa* (=*R. mucronata* var. *stylosa*). This hybrid taxon is special because *R. stylosa* is a dominant member of the IWP stilt mangroves. The occurrence of this hybrid means that there appears to be very little genetic separation between these defining and most divergent of *Rhizophora* species.

Current distribution

Because red mangroves are recognized as valuable timber producers, beneficial to shoreline stabilization and fisheries, it is feasible that their dispersal westward in the Pacific may have been assisted by aboriginal travelers in the past. However, there is no evidence for this happening, so currently there is no agreed explanation for the presence of *R. samoensis* in the southwestern Pacific. In the absence of human intervention, and accepting that long-distance dispersal was not possible, one explanation is island-hopping by natural dispersion across an ancient archipelago of seamounts that crossed the southeastern Pacific during early formation of the Pacific Plate in the Late Cretaceous period (Duke 1992, 1995). Any migration would have been westward, with distances between the putative ancient islands large enough to restrict all mangrove species except the dispersal-specialist red mangroves. In support of this theory, there are tantalizing similarities in cross-ocean linkages for several shallow-water reef fish.

Red mangroves extend notably beyond their native range. *Rhizophora mangle* has been introduced to the Hawaiian and Society Islands from Atlantic populations in Florida. In each case, founder populations have increased and expanded dramatically, especially in the Hawaiian Islands. Plants introduced in the early 1900s to Moloka‘i and O‘ahu now extend to most islands of the group, and the expectation is that they will spread further. Accordingly, *R. mangle* is treated as an invasive species in these islands.

Similar introductions of *R. mangle* elsewhere are apparently less invasive, possibly because other mangroves that already occupy the habitat reduce establishment opportunities for any new introductions. In the Townsville, Australia, area, local authorities were not prepared to take the risk, however, so when a small introduced stand of *R. mangle* was discovered in the upper part of Ross River, it was destroyed.

BOTANICAL DESCRIPTION

Preferred scientific names

Rhizophora mangle L.
Rhizophora samoensis (Hochr.) Salvoza (=*R. mangle* var. *samoensis* Hochr.)
Rhizophora racemosa G.F.W. Meyer
Rhizophora × *harrisonii* Leechman (=*R. mangle* × *R. racemosa*)

Family

Rhizophoraceae (mangrove family)

Common names

Atlantic–East Pacific red mangroves, American mangrove (English)
red mangrove (USA)
mangle rojo (Central and Latin America, Pacific and Caribbean coasts)
tiri wai (Fiji)
togo (Samoa)

Size

Atlantic–East Pacific red mangroves are medium to tall trees. They may reach 30–50 m (100–160 ft) in height, although they are commonly much shorter, around 5–8 m (16–26 ft). Stem diameters are about 15–35 cm (6–14 in) taken just above the highest prop root. This method of measurement differs fundamentally from the standard diameter at breast height (dbh) used for most forest surveys, as diameter height above the substrate varies from 0.5–7 m (1.5–23 ft) (consider the tree in the photo on the first page).

Form

Red mangroves are often multi-stemmed rambling to columnar trees with distinct aboveground prop roots. They tend to be of shorter stature and more spreading in shape on the seaward edge of stands or in sites of higher salinity. Taller, single-stemmed trees are often found just behind the seaward edge of stands downstream in major river estuaries. Multi-stemmed trees occur in frontal areas but are more common in upper intertidal regions. Prop roots are sturdy even when relatively thin.

Flowering

Flowers are perfect, containing both male and female parts. Inflorescences have few to many joints with 1,2,3,4–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. mangle*, *R.* × *harrisonii*, and *R. racemosa*, mature buds and flowers are located at 1–2, 3–5, and 7–9 nodes down from the apical shoot, respectively. The calyx is typically waxy yellow to creamy white and green at maturity, with four lobes. Buds elongate to ovate, green when immature to lighter colors as they mature, smooth, dimensions 1–2 cm (0.4–0.8 in) long, ~0.5 cm (0.2 in) wide. Petals, usually four, are lanceolate to linear, creamy white, with woolly to sparsely hairy margins, ~12 mm (0.5 in) long and ~4 mm (0.16 in) wide. Stamens number eight, pale yellow, to golden brown at maturity. Style is pale green, terete, filiform, 0.5–4 mm (0.02–0.16 in) above ovary base, 1.5–3 mm (0.06–0.12 in) wide, dichotomous tip, pale yellow. Bracts and bracteoles are distinct. Peduncle is 3–4 cm long (1.2–1.6 in), ~0.3 cm (0.01 in) wide. Flowering period is chiefly (but not exclusively) August–December in the southern hemisphere and February–June in the northern hemisphere.

Leaves

Leaves are opposite, simple, bright green, obovate, leathery, margins revolute, generally curved surface, obtuse blunt apex with a minute lip folded under. Cork wart spots occur on most species' leaf undersurfaces, scattered evenly, not raised, reddish brown (may be distinguished from infections and wounds by their uniform cover). Note that non-spotted leaves are found on an unusual form of *R. racemosa* in northern Brazil. Leaf emergence occurs chiefly during November–February in the southern hemisphere and May–August in the north. Leaf fall occurs chiefly over the wet summer period, October–February in the southern hemisphere and April–August in the northern hemisphere.

Fruit

Fruits, when mature, are pear-like, elongate, waist constriction, smooth brown surface, calyx lobes elongate spreading (when the hypocotyl is ready to emerge). For *R. mangle*, *R.* × *harrisonii*, and *R. racemosa* mature fruit located in leaf

Top left: The blunt apex of leaves is characteristic of all AEP red mangroves, as in this *R. samoensis* from Fiji. Top right: Leafy rosette of *Rhizophora mangle* (similar to *R. samoensis*) showing open flowers with elongate, reflexed calyx lobes. Bottom left: Open flower of *Rhizophora racemosa* showing flat, slightly hairy petals and stiff-erect, non-reflexed calyx lobes. Bottom right: Mature fruit of *Rhizophora mangle* (similar to *R. samoensis*) showing its elongate pear-shape, prior to emergence of the hypocotyl. Note the persistent style at the distil tip of the fruiting body. Atlantic Panama. PHOTOS: N.C. DUKE

axils 3, 7 (rare) and 10–11 nodes down from apical shoot, respectively.

Seeds/hypocotyls

Like all *Rhizophora* species, red mangroves are viviparous, meaning that they produce seeds hidden in the mature fruit, and these germinate while the fruit is still attached to the parent plant. 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 wider, distal tip pointed. *Rhizophora mangle* and *R. samoensis* both have distinct brown distal portions of otherwise green, relatively short hypocotyls (see photo). For *R. mangle*, *R.* × *harrisonii*, and *R. racemosa*, mature hypocotyls are located in leaf axils 3–8, ~8 (rarely observed), and 13–15 nodes down from the apical shoot, respectively.

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

Bark

Bark is smooth and red-brown in seaward and exposed locations (rocky and sandy substrates), to gray-fissured with smooth, red-brown prop roots in sheltered locations (mud substrates). There is total coverage of gray-fissured bark in some localities.

Mature hypocotyls of *Rhizophora mangle* (similar to *R. samoensis*), showing distinctive brown distal end, Hawai'i. PHOTO: N.C. DUKE

Expended fruits of *Rhizophora samoensis* (left) and *R. stylosa* (right), Fiji. PHOTO: N.C. DUKE

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 m) depth. This conforms to the anoxic conditions commonly observed in mangrove sediments.

Similar species

Red mangroves are distinguished from IWP stilt mangroves principally by the leaf apex: red mangroves have a blunt leaf apex and lack the spiked, mucronate leaf tip present in stilt mangroves.

Rhizophora mangle and *R. samoensis*, with mostly 0–3 inflorescence joints, are distinguished from *R. racemosa* and *R.* × *harrisonii*, which have 3–8 inflorescence joints.

Rhizophora racemosa is distinguished from *R.* × *harrisonii* by the node position of mature buds and flowers in leaf axils, down from the apical shoot, being 7–9 nodes and 3–5 respectively. The possible hybrid character is shown in *R.* × *harrisonii*, where it has characters intermediate between *R. racemosa* and *R. mangle*.

Rhizophora mangle and *R. samoensis*, the sibling species, are distinguished by minute/absent bracts on pedicles at the calyx base in *R. mangle*, while *R. samoensis* has bracts twice as wide as the pedicle. As noted, *R. mangle* and *R. samoensis* appear very closely related and are likely to be the same species. Discriminating between them reliably is not possible in many instances without detailed examination of key morphological and genetic characteristics.

GENETICS

Variability of species

Atlantic–East Pacific red mangroves are those *Rhizophora* species that occur naturally along the east and west coasts of the Americas, as well as along the west African coast and those island populations in the southwestern Pacific. In this group there appear to be four relatively distinct taxa, although at times their morphological and taxonomic differences are questionable. The uncertainty is chiefly based on: 1) the presence of one intermediate individual that is recognized as a distinct hybrid, namely *R.* × *harrisonii*, and 2) the occurrence of two sibling species, *R. mangle* and *R. samoensis*, which may, on closer examination, be shown to be the same species.

The relationship of *R. mangle* and *R. samoensis* is perhaps the most contentious. They appear very closely related, as they are distinguished by only a few morphological characters, as well as their distinct geographic ranges. The sibling species separate naturally across the American land barrier, with *R. mangle* in the Atlantic and *R. samoensis* in the Pacific. The situation became more complex during the 1900s when *R. mangle* (mostly from around Atlantic Florida) was introduced to the Pacific in several isolated instances, notably to Hawai'i, the Society Islands, and northeastern Australia. The Australian introduction was eradicated a few years ago, but in both other locations the spread of *R. mangle* has proceeded unchecked, and the species now dominates most intertidal wetland areas of each location. In Hawai'i changes in shoreline ecology have been dramatic, especially because no mangroves grew in this isolated location previously. A similar situation is expected in the Society Islands, but no detailed reports are available.

These introductions highlight the unexplained discontinuity of *R. samoensis* in the southwestern Pacific islands. This is the only example where AEP and IWP *Rhizophora* species naturally co-exist. Curiously, the human introductions of *R. mangle* demonstrate that island habitats without mangroves existed between Samoa and South America, and that these are suitable for mangrove colonization. The question raised by this natural discontinuity remains unresolved. This observation emphasizes the profound limitations of long-distance dispersal for this mangrove group of otherwise long-distance dispersal specialists.

Recognizing the morphological differences between *R. mangle* and *R. samoensis* is considered useful in distinguishing between introduced populations of *R. mangle* in the Hawaiian and Society Islands, as compared with natural populations of *R. samoensis* where they occur elsewhere in the Indo–West Pacific.

By contrast, *R. racemosa* is readily distinguished from *R. mangle* and *R. samoensis*. This species appears more common in estuaries influenced by larger and more continuous freshwater flows in equatorial regions of three distinct regions: the east Pacific (Costa Rica to Ecuador), west Atlantic (Venezuela to Brazil), and east Atlantic (western Africa). There are no reports of differences within this taxon between these areas, but recently (N.C. Duke, pers. obs.), two forms of *R. racemosa* were found to co-exist in northern Brazil. One fits the type description in every respect including the presence of cork wart spots on leaf undersurfaces, while the other form lacked these spots. This was particularly notable since all red mangroves until now have been reported to possess such spots on their leaf undersurfaces. This character is present in IWP stilt mangroves and in a similar way defines the two forms of *R. apiculata* occurring in Australasia and the northwestern Pacific.

Known varieties and hybrids

Rhizophora harrisonii is the apparent hybrid of *R. mangle* and *R. racemosa* based on its intermediate and shared morphological characteristics. Further investigations are needed to adequately describe *Rhizophora* taxa and their distributions throughout the AEP region. Current evidence indicates the situation may be more complex, with another possible hybrid where *R. racemosa* apparently occurs on the eastern Pacific coast of the Americas with *R. samoensis*, the allied partner to *R. mangle*.

Furthermore, as noted above, two forms of *R. racemosa* were observed in Brazil. The same recent investigation also discovered two intermediate forms, recognized as potential hybrids between the two *R. racemosa* forms and *R. mangle*. Key questions arise from these new observations including: what is the distribution of the two forms of *R. racemosa*, and how do these compare with populations in western Africa? There are clearly more questions than answers concerning genetic variation in red mangroves.

Aberrant individuals are reported to produce chlorophyll-deficient propagules, called albinos. This is particularly notable and common in *R. mangle* stands throughout the Caribbean area to northern Brazil. Yellow or red propagules can be observed hanging in affected trees alongside normal green propagules. Their relative numbers on an individual tree are believed to quantify the amount of outcrossing that occurs among neighboring normal trees. Other trees have also been observed with variegated foliage.

Culturally important related species

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

ASSOCIATED PLANT SPECIES

AEP red mangroves can be found growing with other mangrove species, preferably within intertidal wetland conditions above mean sea level elevations in tropical regions. *R. mangle* and *R. samoensis* grow in marine saline conditions, while *R. racemosa* forms and hybrid grow in proximity to a regular freshwater source. *R. racemosa* are commonly found in lower to middle tidal reaches of rivers and streams with regular, frequent freshwater runoff, while *R. mangle* and *R. samoensis* occur in coastal embayments and coral islands. In Fiji, however, *R. samoensis* occurs together with *R. stylosa* (a stilt mangrove). In this case, *R. samoensis* occurs more frequently in upstream locations of the freshwater dominated streams, while *R. stylosa* remains the marine specialist, preferring downstream and exposed coastal locations.

Red mangroves often extend up the tidal profile to the terrestrial fringe in areas of higher rainfall. In lower-rainfall areas, red mangroves occur on estuarine margins just above mean sea level. Best development has been observed in lower tidal reaches and on soft, fine, muddy sediment substrates.

Associated species commonly found

In Atlantic and east Pacific populations, red mangroves occur commonly with *Avicennia germinans* and *Laguncularia racemosa*. In the southwestern Pacific, *R. samoensis* is associated with IWP mangroves, including *R. stylosa* and *Bruguiera gymnorrhiza* predominantly. In other locations, red mangroves are associated with other mangrove species. The types of associated species are notably variable where this species has been introduced to the IWP region. In Hawai'i, while the species frequently occurs in nearly mono-specific stands, it does sometimes occur alongside a mangrove introduced from the IWP (*Bruguiera sexangula*) and species that typically occur in lower-salinity environments, such as *Hibiscus tiliaceus*.

ENVIRONMENTAL PREFERENCES AND TOLERANCES

Climate

Atlantic–East Pacific red mangroves thrive in tropical and subtropical environments characterized by moderately high and well distributed rainfall. Mangrove plants appear to depend on groundwater to sustain optimal growth, especially during drier months. In drier locations, such as the Baja Peninsula on the northern Pacific coast of Mexico, the stunted but dense thickets of *R. samoensis* (=*R. mangle*?) attest to the great adaptability of red 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

They grow in climates with summer or uniform rainfall patterns.

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

Because of access to groundwater, red mangroves grow in regions with up to 8 months of drought. 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

32–38°C (90–100°F) (estimate)

Mean minimum temperature of coldest month

0–5°C (0–41°F)

Minimum temperature tolerated

0°C (32°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. They are also anaerobic with high concentrations of sulfide. Trees also grow well in sites with aerobic sediments consisting of fine sands to coarse stones and rocks, and coral ramparts.

Soil texture

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

Soil drainage

The trees grow in soils with free and unimpeded drainage, as well as waterlogged soils.

Soil acidity

pH 6–8.5

Special soil tolerances

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

Tolerances

Drought

Red mangroves can tolerate drought periods well, although trees have apparently been killed by drought in some sites on Moloka'i, Hawai'i where groundwater sources appear to be limited. Drought conditions presumably cause soil salinity to increase in excess of tolerable limits for these plants.

Full sun

They grow best in full sun.

Shade

They appear to have low tolerance of shade. However, recent evidence shows this more likely due to weevils that infest and kill cooler, shaded seedlings (Brook 2001, Sousa et al. 2003).

Fire

Red mangroves have no tolerance of fire in close proximity.

Frost

Tolerance of sub-freezing temperatures is low to none.

Waterlogging

Red mangroves are tolerant of daily tidal flooding up to depths of up to 1.5 m (5 ft). While tolerating permanently saturated soils, they are intolerant of drying soils.

Salt spray

The trees are highly tolerant of salt spray.

Wind

Red mangroves are typically found in seaward areas subject to wind and salt spray but largely protected from waves. Planting in such highly wind-prone locations is recommended, but only where required and within the tree's native range.

Waves

In general, exposed, wave-prone coastlines are inhospitable to mangroves. In areas where wave action is infrequent, red mangroves are believed to provide significant buffering of coastal areas during storm and tsunami surge events (Dahdouh-Guebas 2005).

Abilities

Self-prune

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

Coppice

The trees have notably poor coppice ability. Generally, if 50% or more of the leaves are removed from a tree, it will die.

MANGROVES AND CLIMATE CHANGE

Atlantic–East Pacific red 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.

GROWTH AND DEVELOPMENT

Growth rates vary with age. They generally grow less than

1 m/yr (3.3 ft/yr) 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 seedlings. Growth rate slows when trees approach a site-specific maximum canopy height. When near maturity and maximum height, trees broaden their canopies and increase stem diameter rather than grow taller.

Flowering and fruiting

Flowering and fruiting periods of red mangroves are distinctly seasonal. Peak pheno-events are expected to shift into later months 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 *R. racemosa* with an expected period of around 30 months for each reproductive cycle.

Yields/growth rates

Growth rates vary with species, spatial position in the stand, competition, vigor, and age. For northern Pacific sites in Costa Rica, Jimenez (in Chong 1988) reported annual diameter growth increments for *R. mangle* and *R. racemosa* trees of 0.14–0.19 cm (0.06–0.07 in) for diameter size classes less than 10 cm (4 in), and 0.08–0.17 cm (0.03–0.07 in) for diameter size classes greater than 10 cm.

Chong (1988) provides information on potential yields from Playa Garza Pilot Area in an investigation of the feasibility of managing mangrove forests the Terraba-Sierpe Forest Reserve on the southern (wetter) Pacific coast of Costa Rica. The estimated mean annual increment (MAI) was 6 m^3/ha/yr (86 ft^3/ac/yr) with some stands as high as 11–14 m^3/ha/yr (157–200 ft^3/ac/yr).

Reaction to competition

Rapid early growth of red mangrove seedlings 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

Although natural regeneration is generally relied upon from Pacific to Atlantic regions, 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 20–60 cm (8–24 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 sufficient 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. Propagule maturation occurs later in relatively higher latitude locations north or south beyond the tropic zone (e.g., July–October in Hawai'i).

Mature propagules may be collected from the ground after they have fallen or picked directly from 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 are 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 red mangroves, although damaged and insect-infested individuals should be removed. The following pretreatment section gives 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 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

Mature hypocotyl of *Rhizophora racemosa* showing distinctive, slender, smooth propagule, Brazil. PHOTO: U. MEHLIG

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% were heavily infested (Brook 2001). Infested propagules were established under canopy-shaded areas. The study went further to find that pretreatment in a 50°C (122°F) water bath for 5 minutes killed the beetles and removed the risk of establishment losses 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.

Growing area

Red 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

Seedlings are ready for outplanting at the six-leaf (three-node) stage if grown up in nursery conditions, which can take up to 6 months to achieve. Older seedlings up to 0.5 m (1.5 ft) tall have also been successfully transplanted, but this is not recommended. Direct planting of large numbers of propagules is restricted by their peak seasonal availability, as propagules do not keep for extended periods.

Guidelines for outplanting

Outplanting anytime of the year is suitable. 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 reasonable 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) subjected to disturbance by grazing animals (e.g., goats, sheep, cattle, 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, red mangroves pose few significant disadvantages when planted within their native range. They are not especially susceptible to pests or pathogens and have not been reported to host major pests or pathogens of important crop species.

Potential for invasiveness

The very successful introduction and rapid spread of red mangroves in the Hawaiian Islands clearly demonstrates the potential for invasiveness of mangroves in areas where suitable habitat is available. The plants are readily opportunistic due to their relatively wide tolerance for salinity and soil conditions. Also, their floating propagules are spread widely by ocean currents over great distances.

The species *R. mangle* has unfortunately now taken on the public status of invasive weed and pest species in Hawai'i. To alleviate public concern, eradication efforts have been carried out in several locations on O'ahu and Hawai'i. It is not clear about the success or effectiveness of this campaign, as it appears to have been based on subjective information and no monitoring.

Pests and diseases

Susceptibility to pests and diseases is believed to be low, with the exception of insect borers and crabs that prey on propagules. For introduced stands in the Hawaiian islands, damage to propagules and leaves is notably lower than within the species' native range, and productivity (as expressed in litter fall) is higher.

Host to crop pests/pathogens

No reports are found of red mangroves serving as hosts for known major crop pests or pathogens. In Hawai'i, however, *R. mangle* stands have served as ideal sites for the non-native cattle egret (*Bubulcus ibis*) and also sometimes harbor significant populations of rats.

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

Red mangrove forests stabilize soils with their network of sturdy overlapping prop roots, which dampen water movement and promote sedimentation in areas that might otherwise be eroded. A major reason that red mangrove was introduced into Hawai'i was to stabilize mud flats that were expanding as a result of sugarcane production and resultant erosion. *Rhizophora mangle* has proven quite effective for this purpose and has been shown to improve water clarity in near-shore environments, presumably due to its role in sediment trapping and stabilization.

Fence posts

Red mangrove stems make good posts, as the wood is generally hard and resistant to insect borers.

Windbreaks

Red mangrove forests provide a windbreak along coastal margins generally, and places to seek sanctuary during typhoons and hurricanes.

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. Red mangrove timber is very useful for small construction and for fuel for cooking. Converting the wood 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

Red mangrove is a known source of native animal foods. Several observations demonstrate the diversity and quantity, and it is thought to be extremely important in mangrove ecosystems. Numerous insects, crabs, and mollusks graze on green leaves in the forest canopy and on fallen leaves on the forest floor. Where present, 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 (probably none in introduced Hawaiian stands) appear to use red mangrove as a major food source.

Wildlife habitat

In addition to aquatic marine organisms (see Fish/marine food chain), red mangroves serve as habitat for a wide range of terrestrial and arboreal wildlife. In various locations throughout the region, these mangrove forests provide shelter and food for a number of associated fauna, including birds, 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. Interestingly, one reason stated for the introduction of red mangrove to Hawai'i was as a "pasture plant for bees" (Cooke 1917). Clearly, it wasn't the best choice for this purpose!

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 red mangroves during part of their

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.

life cycles, as do species of shrimp and crabs. As mentioned above, senescent leaves that have fallen from *Rhizophora* trees are taken by grapsid (small mangrove) crabs into their burrows. In Hawaiian populations, there appears to be excessive leaf accumulation in some locations, suggesting that normal associated fauna and other decompositional biota are lacking.

Coastal protection

Red mangrove forests and mangroves in general play an important role in protection of coastlines, fishponds, and other coastal infrastructure. Red mangroves are planted for coastal or fishpond protection in some areas (e.g., in Terraba-Sierpe Forest Reserve, Costa Rica), and there are laws in many locations aimed at protecting mangroves in large part because of this important function.

USES AND PRODUCTS

Red 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 red mangroves is for wood used for a range of purposes from cooking fuel to construction of homes and canoe parts. Other uses of the tree include dyes, medicines, and tannin for tanning leather. It seems likely that red mangroves may have several other uses (e.g., as cattle feed) that to date have not been fully explored.

Staple food

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

Medicinal

Red 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 these cases.

Animal fodder

One report (Morton 1965) concluded that red mangrove leaves might serve as a valuable source of cattle feed, but this potential has yet to be realized.

Timber

The wood of red mangroves is widely used for structural components of traditional homes (e.g., poles, beams, flooring, wall-cladding, rafters) and other components including 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.

The heartwood of *R. mangle* is light red to dark red or reddish brown or purplish, with uniform or more or less striped grain. The sapwood is yellowish, grayish, or pinkish. The wood texture is fine to medium; grain straight to irregular; low-luster; without distinctive odor or taste. The specific gravity (oven-dry weight/green volume) is 0.89.

Fuelwood

Red mangrove wood is used for fuelwood in many places along the American Pacific coast (e.g., Panama, Costa Rica, Nicaragua). The wood is also made into charcoal in many Central American countries, including Panama and Costa Rica.

Canoe/boat/raft making

The wood has been used to make canoe parts.

Tannin/dye

The bark and hypocotyls are used to tan leather and to produce dyes ranging from red-brown to black (the latter with repeated dying). Tannin content of the bark is high for most *Rhizophora* species.

Top: Charcoal treatment plant established with the DANIDA Mangrove Project in Pacific Costa Rica, supported by IUCN and CATIE. Bottom: Typical earthen kiln used to convert stacked red mangrove poles into charcoal for local heating needs, Pacific Panama. PHOTOS: N.C. DUKE

COMMERCIAL CULTIVATION

Red mangrove timber is harvested commercially for charcoal production through much of its range, including Central and Latin America. The calorific value of the timber is significantly enhanced by converting it to charcoal. This is done with all local *Rhizophora* species, as well as *Pelliciera* and *Laguncularia*.

Rehabilitation and replanting

Projects to replant and rehabilitate mangrove forests have been conducted where they have been damaged in a significant way. For example, in Bahia las Minas, Atlantic Panama, a large oil spill killed around 50 ha (124 ac) of mangroves in 1986 (Duke et al. 1997), and Refineria Panama lead a project to replant the damaged areas. Because the soils were oiled it was decided to plant *R. mangle* seedlings using clean terrestrial sediments. Total plantings eventually amounted to in excess of 100,000 seedlings. A subsequent investigation (Duke 1996) found natural recruitment was 40 times greater than planted numbers, and natural seedlings grew equally as well as, or better than, planted seedlings. It was of great importance that naturally recruited sites recovered more quickly than planted sites, possibly because of site damage during planting. Furthermore, damage to exposed and damaged mangrove areas increased after 5–6 years when dead standing timber dramatically deteriorated and was moved by wave action with each tide and storm.

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 therefore 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 and design considerations

Some published guidelines for mangrove silviculture exist and are referenced below, but specific guidelines on thinning, fertilizing, etc., are lacking.

Growing in polycultures

Red mangroves naturally occur in mixed-species stands, and each species has its own ecological and economic values. It is also important to plant associated buffer areas, particularly along the shoreline where mangroves grow better adjacent to banks stabilized by shoreline upland plants. Together they will complement and enhance the richness and stability of the planted environment.

Estimated yield

For the southern (wetter) Pacific coast of Costa Rica, Chong (1988), in an FAO-sponsored project, provided information on potential yields from the 240 ha (590 ac) Playa Garza Pilot Area in an investigation of the feasibility of managing around 5200 ha (12,800 ac) of mangrove forests in the surrounding Terraba-Sierpe Forest Reserve. It was reported that yields resulting from uncontrolled felling of 100 ha/yr (250 ac/yr) could be achieved by felling just 10 ha/yr (25 ac/yr) if conducted more systematically.

Chong estimated that each hectare of mangrove in this reserve could produce US$619 ($250/ac) annually. A detailed management plan was proposed in the report. The average stand volume for red mangroves was 163 m^3/ha (2330 ft^3/ac), with a total mangrove forest stand volume around 280 m^3/ha (4000 ft^3/ac). Estimated yields of timber volume under bark were 100–150 m^3/ha/yr (1400–2100 ft^3/ac/yr) for red mangroves, and for the co-dominant mangrove *Pelliciera,* yields are estimated at 60 m^3/ha/yr (860 ft^3/ac/yr).

Markets

Markets for red mangrove products are local in nature, with little available except for firewood and charcoal in most places, other than indirect products such as mangrove crabs and fruit bats. In Central America, large quantities of red mangrove wood chips and charcoal may be moved greater distances and in greater volumes than other wood products. In Panama there is a strong trade in red mangrove poles around 3 m (10 ft) in length (around 10–15 years old) for construction of *bohio*, the locally popular outdoor recreation shelters for barbecues and parties.

INTERPLANTING

Some interplanting systems include:

Example 1—Bahia las Minas oil spill (Duke 1996, Duke et al. 1997)

Location

Bahia las Minas, Panama Atlantic coast

Description

Planting was undertaken in 1988 and 1989. Around 40 ha (100 ac) were planted with *Rhizophora mangle*, sponsored and implemented by Refineria Panama.

Crop/tree interactions

Not applicable.

Spacing/density of species

Spacing was about 1.5 m (5 ft).

Planting of red mangroves in an attempt to replace around 50 ha of tree loss following a major oil spill in Bahia las Minas, Atlantic Panama. PHOTO: N.C. DUKE

Example 2— Terraba-Sierpe Forest Reserve
(Chong 1988)

Location

Costa Rica, Terraba-Sierpe.

Description

Planned project. This project reached the planning stages only and was sponsored by FAO with IUCN and CATIE. The species to be planted included *R. racemosa*, *R. mangle*, and *Pelliciera rhizophorae*.

Crop/tree interactions

Not applicable, as there were no crops.

Spacing/density of species

Spacing was planned to be 1.5 m (5 ft) for all species.

PUBLIC ASSISTANCE

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Species Profiles for Pacific Island Agroforestry (www.traditionaltree.org)

Rhizophora mangle, R. samoensis, R. racemosa, R. × harrisonii (Atlantic–East Pacific red mangroves)

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