REVIEW ARTICLES

Biological Flora of the Tropical and Subtropical Intertidal Zone: Literature Review for *Rhizophora mangle* L.

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ABSTRACT ▮

DeYoe, H.; Lonard, R.I.; Judd, F.W.; Stalter, R., and Feller, I., 2020. Biological flora of the tropical and subtropical intertidal zone: Literature review for *Rhizophora mangle* L. *Journal of Coastal Research,* 36(4), 857–884. Coconut Creek (Florida), ISSN 0749-0208.

Rhizophora mangle L. is a tropical and subtropical mangrove species that occurs as a dominant tree species in the intertidal zone of low-energy shorelines. *Rhizophora mangle* plays an important role in coastal zones as habitat for a wide range of organisms of intertidal food webs, as a natural barrier to coastal erosion, and as carbon sequestration. A review of mangrove literature has been performed, but a review specifically on red mangroves has not. The approach was to cover a broad range of topics with a focus on topics that have seen significant work since the 1970s. This review includes a brief introduction to red mangroves and then focuses on the following topics: biogeography, habitats and zonation, geomorphological interactions, taxonomy, histology, anatomy, physiological ecology, productivity, biomass, litter, reproduction, population biology, plant communities, interactions with other species, impacts of storms, reforestation, remote sensing, modelling, and economic importance.

ADDITIONAL INDEX WORDS: *Red mangrove, taxonomy, morphology, biogeography, habitats, reproduction, physiological ecology, mangals, hurricanes, economic importance, climate change, coastal ecology.*

INTRODUCTION

Red mangrove (*Rhizophora mangle* L.) is a widely distributed intertidal mangrove and an ecologically and economically important coastal species in tropical areas of the world. The literature base on mangroves in general is immense. Rollett (1981) and Tomlinson (1994) listed more than 6000 articles published between 1600 to 1975. Peer-reviewed investigations related to mangroves increased exponentially in the late 20th century and in the first two decades of the 21st century. Tomlinson (1994), in an extensive review of mangroves, stated that his major difficulty was deciding what to exclude. A similar problem exists with the voluminous literature base for *R. mangle*.

The intent is to have an article that will be useful to coastal ecologists, natural resource managers, and parties interested in tropical coastal ecology and management. The approach is to summarize red mangrove literature with a focus on the period from 1970 to the present that was not covered by Rollett (1981) and Tomlinson (1994). Most of the references are from 2000 to the present, including references not covered by the previous investigators. These references will be of value to those interested in tropical coastal ecology and management.

BIOGEOGRAPHY

Rhizophora mangle occurs on tropical shorelines in West Africa from Mauritania to Angola (Keay, 1953; Tomlinson, 1994). The northernmost distribution in North America is on shorelines and in inland saltwater pools in Bermuda (32° N) (Thomas, 1993). In the United States, it occurs in the subtropics on the Atlantic coast of Florida as far north as 29.98° N, 81.33° W (Goldberg and Heine, 2017) and on the Gulf Coast of Florida as far north as Escambia County in the Florida Panhandle (30.49810° N) (Wunderlin *et al.*, 2018).

Red mangrove occurs on the southern Gulf of Mexico coast from Cameron County, Texas, at the mouth of the Rio Grande/ Rio Bravo (DeYoe, Lonard, and Judd, *personal observations*) and southward from Tamaulipas to Yucatan, Mexico (Britton and Morton, 1989). It is widespread in the Caribbean where it occurs on nearly all islands (Albrecht *et al.*, 2013; Berenguer *et al.,* 2006). It is common in intertidal sites in Central America where it extends from the Atlantic to Pacific coastlines. Its distribution in South America ranges from Guyana to northern Brazil (Tomlinson, 1994).

The distribution of *R. mangle* on the Pacific coast of the Americas extends from Baja California (29° N) and the Gulf of California (24° N) in Mexico to Ecuador, Peru, and northern Chile (Blanchard and Prado, 1995; Domínguez *et al.*, 1998; López-Medellín and Ezcurra, 2012; Sandoval-Castro *et al.*, 2012). Red mangrove also occurs on the Galapagos Islands (Fessl *et al.*, 2011; Song, White, and Heumann, 2011), has been introduced in Hawaii (Krauss and Allen, 2003), and is widely distributed on islands and atolls in the South Pacific (Graham, 1964).

HABITATS AND ZONATION

The typical habitat for *R. mangle* is the sheltered intertidal seaward fringe on tropical and subtropical shorelines where it is the dominant species. However, it may be found at the mouth of estuaries, on tidal creek banks, and in shaded and dry, stagnant hypersaline pools (Chen and Twilley, 1999; Farnsworth and Ellison, 1996). Chen and Twilley (1999) reported that red mangrove is the dominant species on the margins of the upper reaches of the Shark River Estuary in Florida.

Mangroves tend to develop where the elevation gradient is modest. The gradient is a product of physical and biological processes, including inorganic sedimentation, groundwater influx, and land movements. Biological processes of importance are root accumulation, leaf-fall and woody debris deposition, root accumulation, and sediment trapping by mangroves and algal mats (Kraus *et al.* 2014).

The biological zonation is a notable feature of the mangal plant community. Lugo and Snedaker (1974) conclude that the factors and forces responsible for zonation is complex, may not necessarily represent a successional sequence, and that zonation of mangroves may be a result of all the external sources acting on a locality. They observed that zonation is best developed where a steep topographic shoreline gradient occurs and that zonation may not be pronounced in areas with a very flat gradient (1 cm/km gradient), as exists in south Florida where mixtures of species can occur. In addition to zonation patterns, Lugo and Snedaker (1974) proposed a five-unit classification scheme: fringe forest, riverine forest, overwash forest, basin forest, and dwarf forest.

A common zonation pattern that occurs on shorelines is noted on Grand Cayman Island (Woodroffe, 1982). Zonation is expressed from the intertidal fringe to higher elevations landward as *R. mangle* > *Avicennia germinans* > *Laguncularia racemosa* > *Conocarpus erectus* (Woodroffe, 1982). *Conocarpus erectus* is a mangal-associated shrub in the landward transition zone. *Avicennia germinans* and *L. racemosa* tolerate higher levels of soil salinity and are found behind *R. mangle*, where flooding is less frequent (Atwell, Wuddivira, and Gobin, 2016).

In the Amazon region of northern Brazil, slightly different zonation patterns exist. One zonation sequence includes monotypic stands of *R. mangle* on the intertidal fringe and a mid-intertidal zone of *R. mangle* and *A. germinans* as co-dominants. *Avicennia germinans* is the dominant species in landward intertidal sites (Mendoza *et al.*, 2012). In southern Brazil, Sereneski de Lima *et al.* (2013) reported the following zonation sequence from the intertidal fringe to the high

intertidal zone: *R. mangle* > *L. racemosa* > *Avicennia schaueriana*.

Sousa *et al.* (2007) described a more complex mangal profile in Panama. *Rhizophora mangle* occurs in low velocity water and 10 to 20 m from the edge of the water. *Laguncularia racemosa* and *R. mangle* are co-dominants in the low intertidal belt, and *A. germinans* is the dominant species in the upper intertidal zone. *Laguncularia racemosa* reappears in the upland transition zone to tropical forest (Sousa *et al.*, 2007).

The mangal is circumscribed by a narrow zone of about 25 m in Bermuda. Red mangrove is present on the seaward margin, and *A. germinans* and *R. mangle* occur in the mid-intertidal zone. *Conocarpus erectus* and the invasive shrub *Schinus terebinthifolius* occur in the upland transition zone (Thomas, 1993).

Zonation in the mangal in Gambia, West Africa, is characterized by a tall gallery forest of *Rhizophora racemosa* at the low intertidal zone, a midlevel zone of *Rhizophora harrisonii*, and an upper inland zone of *R. mangle* shrubs about 3-m tall (Teas and McEwan, 1982).

GEOMORPHOLOGICAL INTERACTIONS

Mangal species are usually the only species present in the intertidal zone of tropical and subtropical shorelines that have fine-textured alluvium or where the substrate is soft mud or fine silt-clay (Walsh, 1974). These are low-energy coastlines that are free of strong waves and high tidal amplitudes (Lugo, 1980).

Davis (1940) stated that *R. mangle* is a pioneer in the classical Clementsian view of plant succession. In that interpretation, zonation is seral, and the stages of succession would in time proceed to climax vegetation. In the tropics, this would be a tropical forest.

Ball (1980), Farnsworth and Ellison (1996), Lugo (1980), and Thom (1967) stated that *R. mangle* does not fit categories of early or late succession. McKee and Faulkner (2000) indicated that mangroves are passive in shoreline changes and respond to geomorphological processes of sedimentation, erosion, and changing sea level.

Thom (1967) studied mangrove-dominated deltaic systems in Tabasco and Campeche, Mexico. He advanced the concept of microtopographic controls over mangrove zonation. He found that active sedimentation is an important ecological factor that sustains equilibrium in the mangal. *Rhizophora mangle* is dominant in fringe lagoons that are relatively stable where neither accretion nor erosion are occurring. Thom (1967) concluded that changes in habitat are attributed to geomorphic process rather than traditional successional concepts.

In Jalisco, Mexico, Méndez Linares *et al.* (2007) found that red mangrove is a pioneer species that dominates actively accreting frontal edges of deltaic fans. However, Cunha-Lignon *et al.* (2011) stated that fringe forests in Brazil dominated by *R. mangle* have significant structural development attributable to high flooding frequency in depositionally stable sites.

Alleng (1998) examined historical records of the Port Royal, Jamaica, mangal from 1692 to 1991. He concluded that the areal extent of the fringe mangrove community dominated by *R. mangle* has been stable. The horizontal extension of

Figure 1. Red mangrove habit with rhizophores.

Figure 2. Red mangrove shoot tip with leaves.

colonizers has not been significant. He stated that factors that promote equilibrium are a small tidal range, a lack of large sediment inputs, and episodic hurricanes. Ball (1980) made similar conclusions. She stated that zonation patterns of mangroves are consistent with geological data and these patterns have existed *in situ* for millennia.

TAXONOMY

Rhizophora mangle L. (red mangrove) is a member of the family Rhizophoraceae. The family is usually placed in the order Rhizophorales but has been referred to the orders Myrtales, Lecythidales, Cornales, and Celastrales (Tomlinson, 1994; Zomlefer, 1994). Taxonomists disagree on the number of species and hybrids in the genus. Mabberley (1997) stated that eight to nine taxa are included in the genus *Rhizophora*, and Arbeláez-Cortes *et al*. (2007) noted that the genus contains five species and several hybrids. Tomlinson (1994) lists the following species and putative hybrids: *R. mangle* L., *R.* x *harrisonii* Leechman, *R. racemosa* Meyer, *R. apiculata* BL., *R. samoensis* (Hochr.) Salvoza, *R. mucronata* Lamk., *R. stylosa* Griff., *R.* x *lamarckii* Montr., and *R. selala* (Salvoza) Tomlinson.

Breteler (1977) and Cornejo (2013) reported that the *R.* x *harrisonii* represents a morphotype produced by hybridization and introgression of sympatric populations of *R. mangle* and *R. racemosa*. Duke and Allen (2006) indicated that the *R. samoensis* taxon should be reduced to varietal status (*R. mangle* L. var. *samoensis* Hochr.). Tomlinson (1994) presents details of the hybrid taxa *R.* x *lamarckii* and *R. selala*. The latter taxon does not involve hybridization with *R. mangle*.

The following taxonomic description of the diagnostic features of *R. mangle* summarized below are from Britton and Millspaugh (1962), Graham (1964), Proctor (2012), and Tomlinson (1994). Common names for red mangrove in the Caribbean, Central America, and South America include mangle rojo, mangue vermelho, manglier rouge, and mangle rouge (Barker and Dardeau, 1930).

Growth Habit and Shoot Morphology

Red mangroves range in size from shrubs less than 1.0 m tall in nutrient-deficient sites to trees up to 50-m tall (Figure 1) (Golley *et al*., 1969). The growth habit or architectural model of *R. mangle* is considered to correspond with the Attims' model, *i.e.* the axes have continuous growth, differentiated into a monopodial trunk and equivalent branches (Hallé, Oldeman, and Tomlinson, 1978). Branching takes place either continuously or diffusely with branches having swollen nodes (Gill and Tomlinson, 1969).

Leaves

Leaves are simple, elliptical, entire, persistent, and leathery in texture (Figure 2). Each pair of opposite leaves is associated with interlocking stipules that form a terminal bud (Graham, 1964). Petioles are 0.5- to 2-cm long and extend into a prominent midvein. Stipules are 2.5- to 8-cm long, leaflike, convolute, and encompass the young leaf and open as the leaf expands. Blades are 5- to 15-cm long, elliptic, oblong to obovate, dark green and punctate on the lower epidermis. Occluded hydathodes, referred to as cork warts, are conspicuous on the leaves (Tomlinson, 1994).

Root Morphology and Development

Aerial roots, referred to as prop roots or rhizophores, are unbranched until they are anchored in the sediment or branch only after injury (Figure 1) (Gill and Tomlinson, 1977). Aerial roots above the high-tide mark have lenticels. Lenticels provide an aeration pathway to capillary roots in the typically anoxic sediment. The architecture of aerial roots facilitates anchorage and support of the shoot system. These roots usually form an extensive horizontal network that hinders human travel through the mangal community. Aerial roots have unique anatomical specializations that are similar to stem anatomy (discussed below). A reduction in root diameter and complexity is noted with each order of submerged roots. Capillary roots arise from mitotic activity in the root apical meristem. A root cap is present, but root hairs are absent.

Figure 3. Red mangrove flowers.

Figure 4. Red mangrove propagules.

Inflorescence and Flowers

The inflorescence is axillary, cymose, dichotomously branched, and usually bears two to three flowers. Occasionally only one flower is present; however, up to 16 flowers may be produced in the inflorescence. Peduncles on vigorous shoots are up to 6-cm long. Pedicels are 5- to 10-mm long. Flowers are actinomorphic and bisexual. The calyx comprises four persistent, leathery sepals and is adnate to the base of the ovary. Sepals are 7- to 8-mm long and have a longitudinal vein on the inner surface. The sepals are reflexed at maturity. The corolla is actinomorphic and comprises four distinct, white or yellowish petals that are about equal in length to the sepals (Figure 3). The margins are glabrous or pubescent. Eight stamens alternate with the petals. The filaments are about 5-mm long, and the anthers are grouped around the style. A single, two-celled ovary per flower is produced. The stigma is two-lobed, and the style is subtended by a semisuperior ovary. Flowers are usually wind pollinated, but insects may serve as occasional pollinators (Sánchez-Núñez and Mancera-Pineda, 2012b).

Fruit, Propagule, and Seedling Morphology

The fruit is a conical, indehiscent, one-celled, leathery structure that is 2.5- to 3.5-cm long and is attached to the base of the ovary.

The single propagule (a viviparous seed), when mature, is 15- to 20-cm long and has a thick, fleshy coat and two cotyledons (Figure 4). The cotyledons are exposed and expanded when germination is evident. The ovary has four ovules, but only one develops into an embryo. Endosperm development is free nuclear initially but becomes cellular in later stages of development. The cotyledons develop into a cylindrical structure that remains in the fruit at the time the propagule is released.

Seedling development is viviparous. The embryo is initially attached to the integuments at the micropylar end by an elongated suspensor. Later, the basal cells disintegrate. Expansion of the endosperm initiates germination and growth of the hypocotyl. Hypocotyl elongation extends the seedling beyond the developing fruit.

The hypocotyl of the viviparous seedling emerges from the seed coat and is now referred to as a propagule. After several months of maturation, the propagule is released from the parent plant. The mature propagule-seedling unit is about 10- to 50-cm long and is pencil shaped. When the first photosynthetic leaves develop, the propagule initiates formation of woody tissue.

Chromosome Number

Chromosome numbers reported for the family Rhizophoraceae are $2n = 36$ and $2n = 64$ (Graham, 1964). A chromosome number of $2n = 36$ for *R. mangle* was reported initially by Yoshioka *et al.* (1984) and confirmed by Tyagi (2002). Karyotype analysis suggested that five mangrove species (*R. mangle*, *Rhizophora mucronata*, *Kandelia candel*, *Bruguiera gymnorrhiza*, and *Ceriops tagal*) were closely related although they were taxonomically placed in different genera (Yoshioka *et al.*, 1984).

HISTOLOGY AND ANATOMY

Because of where they live, red mangroves have numerous structural and physiological adaptations to address the challenges of their environment, including variable salinity, frequent tropical storms, and low-energy shorelines with resultant fine-grained anoxic sediment. Leaf structure, roots, and rhizophores have features that enable red mangroves to grow in this kind of environment.

Leaves

Mature leaves are persistent, thick, fleshy, waxy, and shiny. They are bright green on the upper epidermis and light yellow on the lower. Leaf epidermal cells are polygonal and have straight and thickened anticlinal walls (Adenegan-Alakinde and Jayeola, 2015). The lower epidermis is characterized by a few randomly arranged, sunken stomata flanked by six or seven subsidiary cells (Adenegan-Alakinde and Jayeola, 2015;

Britton and Morton, 1989). Globular papillae 65 μm in diameter are present on the lower epidermis (Jayeola, Thorpe, and Adenegan, 2001). Cork warts are histological features of the lower epidermis and represent air entry sites (Evans and Bromberg, 2010; Evans, Okawa, and Searcy, 2005). Air is delivered to aerenchyma near the upper epidermis. For all mature leaves, aerenchyma composes 24% of the total leaf volume (Evans and Bromberg, 2010). Aerenchyma in leaves is linked to aerenchyma in stems and roots and ultimately to growing roots in the anoxic substrate.

A transverse section of the *R. mangle* leaf shows a one-to three–layered sclerified hypodermis, a three-layered palisade mesophyll, and a 10- to 12-celled spongy mesophyll and extensive aerenchyma. Vascular bundles are collateral and heavily sclerified (Adenegan-Alakinde and Jayeola, 2015).

Sclerophylly in the subepidermal hypodermis defines coriaceous and hard leaves and is a response to multiple environmental stresses (Sereneski de Lima *et al.*, 2013). Feller (1996) noted that sclerophylly decreased in the leaf anatomy of dwarf forms of red mangrove after addition of phosphorus fertilizer. Sclerophylly is viewed as protection for photosynthetic tissue when metabolic rates are limited because of macronutrient deficiencies and excess light intensity (Feller, 1996). Farnsworth and Ellison (1996) stated that leaf anatomy is insensitive to the light environment, but leaf length, width, leaf area, and summer photosynthetic rates vary among shade and sun leaves.

Red mangroves at sites of constant high salinity have a maximum leaf thickness of 2.4 mm, whereas leaves of plants growing in fluctuating salinity have a thickness of 0.9 mm (Camilleri and Ribi, 1983). They stated that thick leaves have more water-holding capacity than thin leaves, so they may play a role in osmoregulation.

A mass of colleters (secretory glands) occur at the base of the paired stipules that subtend the petiole. Colleters produce a viscous fluid that bathes the stipules (Lersten and Curtis, 1974). Primack and Tomlinson (1978) suggest that colleters may be a source of sugar secretions that attract pollinators.

Stems

Rhizophora mangle bark is light brown and contains tannins and calcium oxalate crystals. The wood is hard, and the stems have swollen trilacunar nodes (Zomlefer, 1994). Growth rates in brackish and frequently flooded saline sites have higher growth rates than trees in saline sites that are seldom inundated (Menezes, Berger, and Worbes, 2003). This species has annual rings that are the result of xylem pore density variations attributable to wet–dry seasons (Correa, Grajales, and Bernal Escobar, 2010). With increased rainfall and a reduction of salinity, pore density increases and wood density decreases. Cambial activity decreases when salinity is high resulting in smaller, more densely compacted secondary xylem (Correa, Grajales, and Bernal Escobar, 2010). Stem growth is rapid under optimal conditions. Rey (1994) reported stem growth increments of 1.1 m year^{-1} in Florida.

Stem galls produced by *Cylindrocarpum didymium* may occur on stems and rhizophores. Some sites in Florida have infection rates of 100% for red mangrove (Olexa and Freeman, 1978).

Rhizophores and Roots

A prominent feature of *R. mangle* is an extensive network of rhizophores. Rhizophores have been referred to as stilt roots, aerial roots, prop roots, cable roots, and flying buttresses (Méndez-Alonzo *et al.*, 2015; Tomlinson, 1994). Rhizophores are formed adventitiously from stems and do not form lateral branches unless they are anchored in loose sediment or are injured (Gill and Tomlinson, 1969). These specialized plant features combine anatomical properties of roots and stems. Conspicuous white lenticels are present on rhizophores above the water level and are sites of aeration from aerial parts of the plant to the fine root mass in the anoxic sediment (Zomlefer, 1994). Respiration-derived carbon dioxide is released from lenticels on the rhizophores (Evans, Okawa, and Searcy, 2005). A reduction in diameter of rhizophores and anatomical features of true roots are found in the ultimate absorptive capillary roots in the substrate (Gill and Tomlinson, 1971a). Capillary roots lack root hairs and have a root cap covering the apical meristem.

True roots in the sediment have a cortex with a loose arrangement of parenchyma tissue and a narrow vascular cylinder. Trichosclereids are absent. A periderm (lignified cork layer) is present, and an extensive aerenchyma network typical of wetland species is noted (da Costa Souza *et al.*, 2014; de Menezes, 2006).

Lin and da S.L. Sternberg (1994) reported that most of the fine root mass is located 0- to 50-cm deep in the sediment, and root biomass increases with lower salinity. Capillary roots lengthen 3 to 9 mm day^{-1} (Gill and Tomlinson, 1971a). McKee (1995a, 2001) and McKee, Cahoon, and Feller (2007) found that low macronutrient levels combined with high light levels stimulate an increase in root biomass.

de Menezes (2006) discussed the unique stemlike features of *R. mangle* rhizophores. Morphological features include positive geotropism and sympodial branching. Anatomical features are a slightly thickened cortex, a polyarch vascular cylinder, collateral vascular bundles, and an endarch protoxylem.

Trichosclereids are in the parenchyma of the cortex. This represents a stemlike feature (Gill and Tomlinson, 1971a). Trichosclereids are absent in the capillary root mass in the sediment, and few tannin cells are produced (Gill and Tomlinson, 1977).

The stiltlike flying buttress appearance of the rhizophores present an almost impenetrable thicket in the *R. mangle* low intertidal zone. Rhizophores play a crucial role in stabilizing the slender tree canopy (Méndez-Alonzo *et al.*, 2015). Dynamic loads are supported from the top of the tree to the unstable substrate. The specialized anatomy of rhizophores is related to mechanical stress attributable to canopy orientation and prevailing winds. Therefore, red mangrove trees are well suited to withstand frequent tropical storms (Méndez-Alonzo *et al.*, 2015).

PHYSIOLOGICAL ECOLOGY

Physiological stress, which is a near constant where red mangroves live, includes variable salinity and nutrient availability, tropical heat, high light intensity, anoxic sediments, and coastal pollution. This species, as well as other mangrove species, has developed various physiological strate-

gies to survive and grow in this environment. Acquisition of water, although not in short supply, requires significant energy expenditure of metabolic processes that cope with the salt in it.

Temperature

Climatic conditions suitable for *R. mangle* are found in tropical-megathermal and humid to subhumid zones (Souza-Santos *et al.*, 2016). Mangroves can tolerate seasonal temperatures that exceed 50°C (Feller, *personal observation*) despite earlier observations that they cannot (Walsh, 1974). The latitudinal limit for this species is a 16°C isotherm where the distributional range is not limited by physiographic features (J. Ellison, 2000).

Frequency, duration, and/or severity of freezing conditions affect distribution and abundance of red mangrove. Mehlig (2006) noted that low temperature usually reduces floral production, but a minimal temperature was not reported. A temperature of −6.11°C for three hours or freezing conditions at or slightly below 0°C for 54 consecutive hours killed *R. mangle* shrubs at South Padre Island, Texas (Sherrod, Hockaday, and McMillan, 1986).

Stuart *et al.* (2007) advanced the hypothesis that the absence of mangroves in general at higher latitudes is attributable to a freeze-induced xylem failure. Markley, McMillan, and Thompson (1982) reported that chill resistance is based on the fatty acid content and subsequent fluidity of cell membranes. They found that seven- to 12-month-old red mangrove saplings exposed to 2°C to 4°C for 144 hours showed leaf injury that correlated with latitudinal origin of the seedlings. Proffitt and Travis (2014) noted that cold stress conditions reduced mutation rates in red mangroves and increased reproductive output along a latitudinal gradient.

Salinity

Rhizophora mangle is a facultative halophyte and can occur in environments where salinity ranges from 0 to 90 ppt (Orihuela, Diaz, and Conde, 1991; Stern and Voigt, 1959) but typically occurs where the range of salinities is close to seawater conditions (Pezeshki, DeLaune, and Patrick, 1989). In the short term, high soil salinity (90 ppt) limits growth, whereas in the long term it can lead to mortality (Cintron *et al.*, 1978). They proposed that cyclic rainfall patterns and hurricanes act as regulators of speed and direction of succession. Rainy periods are associated with lower soil salinities and expansion of the red mangroves. Drought periods result in high soil salinities and mangrove mortality. Salinity, in combination with water logging, influences enzymatic functions, stomatal activity, carbon fixation, and water-use efficiency (Pezeshki, DeLaune, and Meeder, 1997). High salinity, low nutrient level, and high sediment sulfide concentration all significantly decreased CO_2 assimilation, stomatal conductance, and plant growth (Lin and da S.L. Sternberg, 1992b). High nutrient levels can partially alleviate growth depression because of high salinity (Lin and da S.L. Sternberg, 1992b). Hyperspectral remote sensing can be used to assess large-scale salinity stress of mangroves (Song, White, and Heumann, 2011).

Salinity affects enzymatic reactions, stomatal functions, carbon assimilation, and water-use efficiency and regulates photosynthesis and respiration (Lovelock *et al.*, 2006; Pezeshki, DeLaune, and Meeder, 1997). Hypersalinity is a primary factor in limiting the distribution of *R. mangle* (Chen and Twilley, 1999; Song, White, and Heumann, 201l; Wier, Tattar, and Klekowski, 2000). Rodríguez-Rodríguez, Mancera-Pineda, and Rodríguez (2016) reported a die-off of *R. mangle* in Colombia attributable to hypersalinity.

In well-developed stands of red mangrove in Florida, optimal conditions for growth occur in salinities ranging from 24.5 after heavy rain to normal sea-water salinity of 33.5 (Maybruck and Rogerson, 2004). In Puerto Rico, Cintron *et al.* (1978) reported rainy periods associated with lower sediment salinity that resulted in the expansion of the red mangrove zone. Monotypic stands of red mangrove occur in Hawaii in salinities ranging from 15 to 55. Lin and da S.L. Sternberg (1994) found that fine root mass in dwarf forms increased and that overall root biomass increased during the wet season presumably as a result of lower salinities. In general, Guanghui and Sternberg (1993) found that fluctuating salinity has significant negative effects on photosynthesis and plant growth relative to constant salinity of the same mean.

Hao *et al.* (2009) found that dwarf forms of red mangrove have lower stem vessel diameters and lower sapwood-specific hydraulic conductivity than tall trees. Dwarf forms have smaller leaf sizes, lower CO_2 assimilation rates, and lower stomatal conductance than tall trees. Hao *et al.* (2009) suggested that the lower water transport efficiency of dwarfs may be caused by high salinity in the surface soils, notably in the dry season. Melcher *et al.* (2001) found that *R. mangle* adjusts hydraulic properties of its water-transport system, as well as the leaf osmotic potential, in concert with the environmental growing conditions.

Metabolic processes in roots counteract the admission of salts into the vascular system. Gilbert, Mejia-Chang, and Rojas (2002) found that via ultrafiltration in the roots, salt is largely prevented from entering the vascular tissue, but a small amount is ultimately found in leaves. Red mangrove does not actively secrete salt from leaves by salt glands as *A. germinans* does.

Smith and Snedaker (1995) stated that red mangrove maintains a high negative internal osmotic pressure while permitting an intake of freshwater; therefore, hydraulic properties of water and cellular osmotic potential are maintained. Sperry, Tyree, and Donnelly (1988) reported that red mangrove loses 80% of its hydraulic conductivity in the range of −6.0 to −7.0 MPa (Pascal metric units). Field populations of *R. mangle* typically have xylem pressures ranging between −2.5 and 4.0 MPa (Sperry, Tyree, and Donnelly, 1988). They found that water-column breakage occurs when air enters water-filled vessels from a neighboring air-filled one via pores in the shared pit membranes. Embolism follows breakage of the water column (Sperry, Tyree and Donnelly, 1988).

Nutrient Limitation

Nitrogen-use efficiency in mangroves and nutrient reabsorption are among the highest in angiosperms (Feller *et al.*, 1999), but macronutrient limitation (nitrogen and phosphorus) is still one of a variety of factors that influence red mangrove growth and biomass (Feller *et al.*, 2002). Patterns of nutrient limitation are complex. The few tropical and subtropical mangrove wetlands that have been studied seem to be either nitrogen

or phosphorus limited (Boto and Wellington, 1983; Feller, 1995; Feller *et al.*, 1999). Phosphorus deficiency has been shown to be a major factor limiting plant growth in some dwarf mangrove forests (Feller, 1995). In mesocosm studies in Florida, Koch and Snedaker (1997) found that phosphorus limitation in sediment is a more important limiting factor than nitrogen availability. Feller *et al.* (2003) found in Florida that growth rates where dwarf mangroves occur increased significantly after nitrogen fertilization, indicating nitrogen limitation. They found that dwarfs resembled vigorously growing saplings two years after nitrogen fertilization. Feller, Lovelock, and Piou (2009) studied the effects of macronutrient deficiencies on red mangrove in Florida, Belize, and Panama. They reported that fringe intertidal and inland dwarf zones of *R. mangle* on siliciclastic/carbonate sediments in Florida are deficient in nitrogen. In Belize, where substrates comprise peat and limestone, the intertidal fringe was nitrogen deficient whereas the dwarf zone was phosphorus deficient. In Panama, where substrates comprised peat and limestone, plants of the intertidal fringe responded to the addition of nitrogen whereas in the adjacent dwarf stands plants were phosphorus deficient (Feller, 1996; Feller, Lovelock, Piou, 2009).

In a field experiment Feller (1995) and in a greenhouse experiment Koch and Snedaker (1997) examined the effects of adding fertilizers of nitrogen, phosphorus, and potassium to dwarf red mangroves. They found slow growth rates in controls and in nitrogen-fertilized dwarfs. Growth in leaf area and woody shoots of dwarf forms was stimulated by the addition of the three macronutrients in combination and in the addition of only phosphorus. They concluded that phosphorus enhances stem elongation and leaf area expansion and was the most important macronutrient.

Nutrients

Lovelock *et al.* (2006) found that the addition of phosphorus to dwarf *R. mangle* stimulates the expansion of xylem vessel diameters and leaf area indices. They concluded that hydraulic properties are a key to controlling growth. Zimmermann *et al.* (1994) reported the occurrence of a viscous protein in xylem sap that enhances long distance water transport. Lovelock *et al.* (2004) noted that stem hydraulic conductance in dwarf red mangrove increased six times after the addition of phosphorus and 2.5 times after the addition of nitrogen compared to controls. Overall shoot growth increased 10-fold with the addition of phosphorus and twofold over controls after the addition of nitrogen fertilizer.

Potential for nitrogen to be supplied by nitrogen-fixation occurs in the aged leaf litter of the sediment (Gotto and Taylor, 1976; Peligri, Rivera-Monroy, and Twilley, 1997). Birds of numerous species are common to red mangroves and are potentially abundant enough to be another nutrient source for mangroves (Walsh, 1974). Fry and Cormier (2011) used a combination of chemical markers ($^{15}\delta$N, $^{13}\delta$C, C, N, P, B, Cu, Mg, K, and Ca) as indicators of nitrogen loading in red mangrove habitat.

Substrate Characteristics

Mangrove soils are essentially anoxic and are usually characterized by having high sulfide levels (Jacinthe and Groffman, 2006; Lacerda *et al.*, 1993; McKee, 1993, 1995c).

McKee (1996) found that anoxic sediment conditions modify physiological and morphological growth patterns. Maintenance of root oxygen concentrations, root respiration rates, and root extension rates by *R. mangle* demonstrated an ability to reduce low oxygen stress, unlike *A. germinans* with minimal changes in root morphology and physiology.

Mangals occur in substrates that range from hypo- to hypersaline conditions and low- to high-nutrient levels. Optimal conditions for the development of red mangrove stands are on alluvial substrates on coastlines that are rich in organic matter and where soil particles comprise fine silt and clay (Demopoulos and Smith, 2010; Walsh, 1974). In Hawaii, where red mangrove has been introduced, this species has colonized saline sands overlain by silty, alluvial sediments (Cox and Allen, 1999). Sheridan (1997) also reported this species in sandy clay substrates rich in organic content in Rookery Bay, Florida. In Nigeria, Asuquo and Ewa-Oboho (2005) noted an enriched development of the mangal in sediments comprising sandy clays, silty clays, and fine sediment muddy flats.

Sediment/Nutrient

Substrate characteristics affect nutrient availability. Sauer (1982) reported that *R. mangle* occurs on unconsolidated calcareous sands in the Cayman Islands. Calcareous substrates, typically deficient in phosphorus, are not conducive to the development of a tall forest canopy of red mangrove (Cordeiro da Cruz *et al.*, 2013). Dwarf forms of red mangrove, usually less than 5-m tall, characterized these substrate conditions in Puerto Rico, the Florida Everglades, and sites in Belize (Feller, 1995; Koch and Snedaker, 1997; Medina, Cuevas, and Lugo, 2010). Medina, Cuevas, and Lugo (2010) emphasized that the stunted growth of *R. mangle* in Puerto Rico is a result of the combination of a calcareous substrate, phosphorus deficiency, and seasonal water stress.

Water-Level Change

Global mean sea-level rise in the 21st century is 3.2 mm year^{-1} (Kraus *et al.*, 2014). Carbon dioxide and methane are the principal players, and these gases are predicted to increase in the earth's atmosphere, accelerating the rate of sea-level rise. Local disturbances such as hurricanes and tsunamis may also affect sea level, causing a rise in sea level (at times) relative to mean sea-level rise by soil and debris deposition (Stalter and Baden, 1994) or elevation loss by peat collapse. Oil extraction in the Gulf of Mexico may also cause the land there to sink, exacerbating sea-level rise. Rates of sea-level elevation change are variable, but all will affect mangrove distribution (Kraus *et al.*, 2014). Mangroves may contribute to accretion and positive elevation change by aerial roots and sedimentation, subsurface root accumulation, litter and root debris accumulation, and benthic mat formation (Kraus *et al.*, 2014).

Hydraulic properties of *R. mangle* are a key in promoting growth. Dwarf and canopy tree heights are associated with flooding, nutrient availability, and the absence of a salinity gradient (Koch and Snedaker, 1997; Lovelock *et al.*, 2006). Mendoza *et al.* (2012) confirmed that water logging, pore water salinity, and nutrient availability influence red mangrove forest structure.

Flooding in conjunction with salinity influences enzyme systems, stomatal function, carbon fixation, and water-use

efficiency (Pezeshki, DeLaune, and Meeder, 1997). Ellison and Farnsworth (1996b) indicated that mangroves are sensitive to increasing water depth and seasonal variations in insolation. They predicted that mangroves in coral cays in Belize will not survive rising sea levels.

High water levels result in the loss of potential competitors of *R. mangle*. *Avicennia germinans*, *B. maritima*, and *Sarcocornia* (*Salicornia*) sp. do not survive long-term inundation (Vogt *et al*., 2012). *Rhizophora mangle* saplings grow faster than *L. racemosa* seedlings in reforested sites under higher water levels. Red mangrove seedlings are highly resistant to total flooding and survive for six months or longer (Elster, 2000).

Rising sea level that is attributable to global warming may pose an additional threat to mangroves (Ellison and Farnsworth, 1997) in the future if sea-level rise outpaces colonization. Following the late Holocene, which was a period of greater sea-level stability, a period of more rapid sea-level rise started in the mid to late 19th century. The latest estimates for sea-level rise are 3.2 mm year^{-1} although there are lower (1.9 mm year^{-1} in the Caribbean) and higher (7.5 mm year^{-1} in Indonesia) estimates (Kraus *et al*. 2014).

Ellison and Farnsworth (1997) evaluated reproduction, physiology, growth, and anatomical changes in *R. mangle* subjected to simulated rising sea level. They found that red mangrove seedlings initially grew more rapidly in experimental higher water levels than under current (control) sea-level conditions. However, at the conclusion of the experiment, saplings under control conditions were 10 to 20% larger than those that were placed in simulated sea-level rise conditions (Ellison and Farnsworth, 1997).

Secondary Metabolites

A wide variety of carbon-based secondary metabolites have been identified from red mangrove leaves and wood. Kandil *et al*. (2004) reported that most of these compounds play a role as deterrents to herbivory. Aromatic polyphenols such as tannins may have astringent properties. These compounds comprise 23% of the leaf dry weight (Kandil *et al*., 2004). Koch, Rullkötter, and Lara (2003) indicated that leaves have high amounts of triterpenoids, including β-amyrin, germanicol, taraxerol, and leucol, whereas tannins are also found especially in the bark (Drabble, 1908). Barr *et al*. (2003) reported that red mangroves periodically release low amounts of volatile isoprene and monoterpenes that contribute to ozone concentrations and biogenic aerosol formation. Afzal-Rafii, Dodd, and Fauvel (1999) found that long-chain alkanes lend biophysical properties to cuticular properties of waxes produced by the leaf epidermis, such as increased impermeability of the epidermal layer.

Pollution

Rhizophora mangle in the intertidal zone adjacent to urban centers is vulnerable to a wide variety of pollutants. Persistent petroleum pollutants cause seedling mutations, defoliation, death of populations, and loss of epibionts and motile animals (Ellison and Farnsworth, 1996a). Proffitt, Devlin, and Lindsey (1995) found that red mangrove mortality was greatest and growth was lowest after a one-time oil spill under full sunlight and hot conditions. Motor oil accounts for 40% of oil in harbors,

estuaries, and other coastal waterways (Proffitt, Devlin, and Lindsey, 1995).

Proffitt and Devlin (1998) monitored effects of multiple oilings of seedlings and saplings. They found no significant effects on seedlings and saplings exposed to number-6 oil after 10 months of exposure over controls. A second oiling 32 months later with number-6 oil resulted in reduced lateral stem growth, fewer lateral stems, and fewer leaves than controls. A combination of number-6 oil and crude oil was administered in a second experiment. They found significant detrimental effects on seedling and sapling survival, stem growth, number of leaves, and leaf production after the first addition of crude oil and number-6 oil over controls (Proffitt and Devlin, 1998). Chindah *et al*. (2011) implied that crude oil may immobilize mineral-nitrogen activities by bacteria during degradation of crude oil. Crude oil also alters substrate properties and reduces sediment porosity and gas exchange (Chindah *et al*., 2011).

Proffitt and Travis (2005) noted that contaminated sites have higher levels of mutagenic stress. They reported higher frequencies of propagules heterozygous for albinism in contaminated sites than in uncontaminated areas.

Burns *et al*. (1994) monitored the effects of the largest crude oil spill in Panama that occurred in an area east of the Panama Canal. They reported aromatic residues of crude oil in anoxic sediments 5 years after the spill. They noted an increased number of dead red mangrove rhizophores. They predicted a 20-year minimum recovery time for the loss of toxicity of trapped crude oil in the sediment (Burns *et al*., 1994). Levings and Garrity (1994) found that 13% of red mangroves were lost in a crude oil spill. They found 10 to 51% fewer submerged roots and shorter submerged roots at oiled locations.

Organochlorides pose a long-term major pollution problem in the mangal. Espinosa, Campos, and Ramírez (1998) reported high levels of toxic residues of lindane, heptachlor, aldrin, DDE, and DDT in an estuary in Colombia. Lindane was more common in the dry season. The effects of organochlorides on the mangal ecosystem are largely unexplored.

The red mangrove community located close to urban development and industry are subject to a wide variety of heavy metal contaminants (Martins de Oliveira *et al*., 2015; Ramos e Silva, da Silva, and de Oliveira, 2006; Vilhena, Costa, and Berredo, 2013). Ramos e Silva, da Silva, and de Oliveira (2006) and Silva, Lacerda, and Rezende (1990) stated that mangroves, including *R. mangle*, provide efficient biogeochemical transport. They suggested that the red mangrove community contributes to cycling of pollutants. Reducing conditions in mangrove sediments favors heavy metal preservation and immobilization as sulfides (Silva, Lacerda, and Rezende, 1990).

Iron, zinc, and lead primarily remain concentrated below the sediment surface in the root zone. Aluminum is concentrated in rhizophores, cadmium in lateral branches, and nickel in large trunks (Ramos e Silva, da Silva, and de Oliveira, 2006). Walsh, Ainsworth, and Rigby (1979) confirmed that lead is not translocated, but cadmium and mercury are. Methyl mercury is highly toxic and tends to become more concentrated with increasing salinity (Martins de Oliveira *et al*., 2015). Ruelas-Inzunza and Páez-Osuna (2006) found cadmium and manganese translocated to twigs and copper and zinc to leaves.

Vilhena, Costa, and Berredo (2013) found zinc, strontium, arsenic, and selenium concentrated in red mangrove leaves. These heavy metals enter the food chain when crabs (*Ucides cordatus*) consume contaminated leaves. They indicated that selenium was concentrated in crab muscle tissue and in the hepatopancreas. Iron plaques (metal-rich deposits on roots) may moderate uptake of heavy metals by roots. Machado *et al.* (2005) found that seedlings exclude iron, manganese, and zinc by iron plaque formation.

Studies of the impacts of sewage outflow, air pollution, and long-term effects of plastic flotsam on red mangroves are limited. Ricarda Boehm *et al.* (2016) reported that sewage outflow reduces crab herbivory of *R. mangle* propagules. They found that herbivory was significantly lower in contaminated than in uncontaminated sites. Pereira Arrivabene *et al.* (2015) reported that air pollution by particulate iron from mining operations had no evident morphological or structural damage to highly exposed leaves. Ivar do Sol *et al.* (2014) noted that plastic debris is trapped and retained by rhizophores for months to years. They did not indicate the long-term effects of plastics degradation on the ecosystem.

Photosynthesis

Rhizophora mangle is a C_3 facultative halophyte in carbon fixation with its light independent reaction of photosynthesis (Kathiresan and Bingham, 2001). Suárez (2003) stated that chlorophyll *a* and *b* levels are highest in adult leaves but that chlorophylls decline with age. Flores-de-Santiago, Kovacs, and Flores-Verdugo (2012) found no seasonal differences in leaf chlorophyll *a* content. They reported higher levels of chlorophyll *a* in the upper canopy than in shade leaves in the middle and lower canopies. Farnsworth and Ellison (1996) noted that photosynthesis rates did not differ between summer and winter. Demmig-Adams *et al.* (1989) found that red mangrove leaves exposed to 5°C and high light intensities affected photosystem II and enzyme-influenced carbon fixation pathways, *i.e.*, zeaxanthin synthesis and non-photochemical fluorescence quenching were reduced. They found that zeaxanthin synthesis and nonphotochemical fluorescence quenching were reduced under the previous conditions.

Detrés, Armstrong, and Connelly (2001) reported that ultraviolet (UV) radiation alters photosynthesis and photoprotective UV pigments. The UV radiation reduces chlorophyll content and affects the protective role of flavonoids. Full solar radiation showed lower red mangrove leaf reflectance and a shift of 5 nm in the inflection point at the red edge of the visible spectrum (Detrés, Armstrong, and Connelly, 2001). They noted that even minor shifts of UV radiation could have significant effects on pigments.

Snedaker and Araújo (1998) compared net primary production and stomatal conductance under ambient and elevated CO_2 levels among *R. mangle*, *A. germinans*, *L. racemosa*, and *C. erectus*. They found no significant difference among the species in net primary conduction and instantaneous transpiration efficiency (ITE) at ambient CO_2; however, at higher CO_2 (361–485 ppm) ITE increased 2.7-fold in *Rhizophora*, 1.9-fold in *Avicennia*, and 1.5-fold in *Laguncularia* and *Conocarpus*. They concluded that the ITE pattern was consistent with the classical zonation pattern of these species. Sobrado

Table 1. *Gross and net primary production (g C m^{-2} day) of red mangroves at four sites in Florida.*

Location	GPP	NPP
Rookery Bay	6.3	4.4
Key Largo	5.3	0
Hammock Forest	1.9	1.3
Scrub Forest	1.4	0

Note: From Lugo and Snedaker (1974).

(2000) looked experimentally at gas exchange and hydraulic properties of three mangrove species: *R. mangle* L., *L. racemosa* (L.) Gaertn.f, and *A. germinans* (L.).L. He found that *A. germinans* had a higher CO_2 assimilation rate than *R. mangle* or *L. racemosa*.

Salinity and CO_2 levels influence enzymatic activities that affect photosynthesis and respiration. Farnsworth and Ellison (1996) stated that elevated CO_2 levels increase biomass, total shoot length, branching, and leaf area. They found that doubling CO_2 levels decreased stomatal density as epidermal cells enlarged. Lin and da S.L. Sternberg (1992a) found that dwarf red mangroves have lower intercellular CO_2 concentrations and higher water-use efficiency than taller red mangroves. Photosynthetic gas exchange measurements showed 15% lower CO_2 assimilation, 6% lower intercellular CO_2 concentrations, and almost 12% higher water-use efficiency in dwarfs than in tall canopy trees (Lin and da S.L. Sternberg, 1992a).

PRODUCTIVITY, BIOMASS, AND LITTER

Mangroves rank second only to coral reefs in gross productivity in tropical marine ecosystems (Arreola-Lizárraga, Flores-Verdugo, and Ortega-Rubio, 2004). In general, mangrove primary productivity is a function of salinity, light, nutrients, sulfides, and duration of flooding (Twilley and Rivera-Monroy, 2005). Net global primary productivity of mangroves is estimated at 218 (10^{22}) g year^{-1} with 26 to 34 (10^{22}) g year^{-1} subject to burial (Smoak *et al.*, 2013). Data for net global primary production for red mangroves are lacking.

Productivity

Lugo and Snedaker (1974) measured primary production at several sites in Florida and concluded that gross primary productivity (GPP) of red mangrove decreased with increased salinity (Table 1). In areas of low salinity and under similar light intensity, GPP of *R. mangle* was four times as great as that of *A. germinans*. In sites of intermediate salinity, *Laguncularia racemosa* exhibited twice the GPP of *R. mangle* (Lugo and Snedaker, 1974). In Florida, Koch (1997) indicated that productivity of *R. mangle* in riverine sites is usually highest and lowest in dwarf forests.

In Brazil, Silva, Mozeto, and Ovalle (1998) estimated red mangrove root biomass production at 7439 kg ha^{-1} year^{-1}, and the sediment sequestered 452 kg of phosphorus ha^{-1} year^{-1}. Imbert and Menard (1997) reported productivity values for *A. germinans* and *R. mangle* at Fort-de-France Bay, Martinique. They estimated biomass of the combined species of 19 tons ha^{-1} year^{-1}. They found that red mangrove populations produced 2.5 times more leaves than *A. germinans*. For Hawaii, Cox and Allen (1999) estimate of the average net daytime canopy

Table 2. *Biomass of* Rhizophora mangle *in Brazil, Puerto Rico, Mexico, Florida, Hawaii and Martinique.*

Country	Biomass (kg ha^{-1} year^{-1})	Source
Brazil	7939 (including roots)	Silva, Mozeto, and Ovalle (1998)
Puerto Rico	7780	Golley, Odum, and Wilson (1962)
Mexico	1653	Guerra-Santos *et al.* (2014)
Florida	2317–4673 (including roots)	Castañeda-Moya *et al.* (2011); Ross *et al.* (2001)
Hawaii	8065	Cox and Allen (1999)
Martinique	17,442	Imbert and Menard (1997)

primary production was 10.5 g m^2 day^{-1} or 76.6 t ha year^{-1}. Ross *et al.* (2001) provided estimates of above-ground biomass production in the mangrove fringe and adjacent dwarf forests at Biscayne National Park in Florida. They found that above-ground productivity in the tall canopy forest was about three times higher than that in the dwarf forest, 26.1 versus 8.1 Mg ha^{-1} yr^1, respectively. Félix-Pico *et al.* (2006) estimated annual primary productivity of *R. mangle* (509 g dry wt m^{-2}), *L. racemosa* (805 g dry wt m^{-2}), and *A. germinans* (444 g dry wt m^{-2}) at La Paz Bay, Baja California.

Biomass and Litter

Mangrove biomass is governed by the parent substrate and latitude, with productivity greatest near the equator (Comeaux, Allison, and Bianchi, 2012; Cuc and de Ruyter van Steveninck, 2015). Aboveground biomass is in part a reflection of productivity in a plant community (Osland *et al.*, 2014) and the potential to store carbon in the mangal zone (Cuc and de Ruyter van Steveninck, 2015). Biomass is usually given as aboveground biomass with a range from 1653 to 17,442 kg ha^{-1} year^{-1} (Table 2). Feliciano, Wdowinski, and Potts (2014) assessed mangrove above-ground biomass and structure using terrestrial laser scanning.

Belowground biomass is not often quantified, but because of its role in carbon storage it is gaining attention. For example, Ochoa-Gómez *et al.* (2019) found 209.2 ± 144.6 Mg C ha^{-1} in red mangrove sediment in La Paz Bay, Mexico. In a typical fringe forest in Brazil with tree density of 4510 stems ha^{-1}, aboveground biomass was 65 t ha^{-1} (80% of total biomass), whereas belowground biomass was 16 t ha^{-1} (Silva *et al.*, 1991). Aerial and belowground roots accounted for 40% of the total biomass, confirming the importance of such structures to mangrove forests.

Rhizophora mangle has the highest rate of litter decomposition of all other mangrove species that occur in the regularly inundated intertidal fringe. Litter dynamics are important for the export of detritus as well as for nutrient cycling. Litter degradation is more rapid in the lower intertidal fringe because of frequent inundation. Leaves contribute about 90% of litter, litter decomposition is rapid, and initial rapid decomposition is followed by deceleration and slow weight loss (Bomfin de Oliveira, Rizzo, and da Conceição Cuerreiro Couto, 2013). Immobilization of nutrients in leaf litter during decomposition and high root-shoot ratios contribute to nutrient-conserving processes (Feller, Lovelock, and Piou, 2009; Reef, Feller, and Lovelock, 2010). As in most mangle ecosystems, decomposition and export of litter is dependent on the magnitude of tidal flooding (Twilley, Lugo, and Patterson-Zucca, 1986).

Rapid weight loss of leaf litter is attributable to leaching and degradation of soluble sugars and highly soluble polyphenolic tannins (Bomfin de Oliveira, Rizzo, and da Conceição Cuerreiro Couto, 2013; Lima de Colpo and Colpo, 2014). Little data are available for the decomposition of *R. mangle* wood. Romero, Smith, and Fourqurean (2005) found that wood decomposed faster on the sediment surface than wood buried in the sediment. They noted that 17 to 68% of phosphorus in wood litter was leached during the first two months of decomposition. Anaerobic rates of leachable lignocellulosic compounds are 10 to 30 times slower than in aerobic conditions (Benner and Hodson, 1985). The polysaccharide fraction of lignocellulose is mineralized twice as quickly as mineralization of the lignin fraction. Lignocellulose and hemicellulose are resistant to decomposition, and lignin is most resistant (Benner and Hodson, 1985).

Bomfin de Oliveira, Rizzo, and da Conceição Cuerreiro Couto (2013) found that 95% of red mangrove leaves decayed within 35 days. Benthic macrofauna play an important role in litter decomposition (Bomfin de Oliveira, Rizzo, and Conceição Guerreiro Couto, 2012; Proffitt and Devlin, 2005; Proffitt *et al.*, 1993). Proffitt *et al.* (1993) found that snails (*Melampus coffeus*) consumed 80% of brown *R. mangle* leaves within six weeks and 90% of all leaves within seven weeks.

Florida

Castañeda-Moya *et al.* (2011) found belowground biomass of roots ranged from 2317 to 4673 g m^2 in the Everglades. The root zone from 0- to 45-cm deep had 62% to 85% of the root biomass.

Davis *et al.* (2003) found that leaching accounted for 33% of leaf decomposition after three weeks. Leaching losses peaked the second day after leaf fall. They found that 60% of the leaf mass was retained after 1 year of decomposition. Davis *et al.* (2003) concluded that litter may be a substantial reservoir of phosphorus in the ecosystem.

Ellis and Bell (2004) studied the effects of creating canopy gaps in mangrove stands relative to complete canopies. They found no difference between the biomass of standing litter on the forest floor beneath the trimmed canopy and the undisturbed intact canopy.

Hawaii

In Hawaii, where *R. mangle* was introduced in 1902, high levels of tree densities and productivity have been reported (Allen, 1998; Cox and Allen, 1999). Cox and Allen (1999) recorded greater than 24,000 trees ha^1 and 121 seedlings m^2. Because of very high rates of propagule production and low predation, densities are high and are comparable or higher than productivity values for the Gulf of Mexico and for mangal stands in southeast Asia (Allen, 1998; Cox and Allen, 1999). Aboveground biomass ranged from 266 tons ha^{-1} to 279 tons ha^1.

Caribbean

Juman (2005) reported aboveground biomass of red mangrove at Bon Accord Lagoon, Tobago, ranging from 20 to 25.9 kg dry weight m^2. Decomposition of leaf litter was estimated as 12 kg dry weight day^{-1}.

Golley, Odum, and Wilson (1962) estimated *R. mangle* biomass of 778 g m^2, wood dry weight of 5507 g m^2, and peat and root biomass of 45 kg m^2 in Puerto Rico.

Mexico

At Veracruz, Mexico, Aké-Castillo, Vázquez, and López-Portillo (2006) estimated litter production of 1116 g m^2 year^1 and total leaf litter fall ranging from 3.4 to 17 tons ha^{-1} year^1. They noted that leaching and microbial degradation accounted for 50% of litter loss. In the rainy season, the snail *Nerita reclivata* increased the rate of decomposition. Utrera-López and Moreno-Casasola (2008) reported productivity of *A. germinans*, *L. racemosa*, and *R. mangle* at two basins at La Mancha Lagoon, Veracruz. The estimated litter fall ranged from 2.35 g m^2 day^1 (Utrera-López and Moreno-Casasola, 2008).

In Campeche, Guerra-Santos *et al.* (2014) included *C. erectus*, a mangal associate, with *A. germinans, L. racemosa,* and *R. mangle* in aboveground biomass estimates. They found that aboveground biomass was 182 tons ha^{-1}. Carbon sequestration ranged from 34 to 480 tons ha^{-1}.

In arid environments on the shorelines of the Sonoran Desert in Sinoloa, Sonora, and Baja California, mangroves produce surprisingly high amounts of organic matter. Félix-Pico *et al.* (2006) estimated biomass of *R. mangle*, *L. racemosa*, and *A. germinans* at La Paz Bay, Baja California. They found 2960 individuals ha^{-1} with a mean height of 3.1 m. Litter fall was 509 g dry weight m^2. López-Medellín and Ezcurra (2012) stated that litter fall production was associated with latitude on the Mexican Pacific coast and estimated litter fall of 1053 g ha^{-1} year^1. Adame and Fry (2016) examined century-old sediment cores on the Mexican Pacific coastline. They concluded that buried carbon reserves have changed little over the past century. Productivity had been constant and decomposition rates were slow.

Belize

In Belize, Middleton and McKee (2001) and Koltes, Tschirky, and Feller (1998) found that amphipods and crabs triple the overall rate of leaf litter decomposition. These invertebrates consumed all unbagged leaf litter within 23 days. Twigs and roots required 540 and 584 days for decomposition, respectively.

Brazil

In southern Brazil, Cunha, Tongella-de-Rosa, and Costa (2005) estimated *R. mangle* tree density of 4700 trees ha^{-1} and litter production of 214,095 kg ha^{-1} year^{-1}. They related that the ecosystem is highly productive because of high carbon concentrations in stems and roots. Silva, Mozeto, and Ovalle (1998) reported fluctuations of phosphorus in detritus in Sepetiba Bay. They reported the addition of 3.9 kg m^2 of phosphorus to the substrate, of which 63% of the phosphorus is incorporated into leaf biomass.

In northern Brazil, Schories *et al.* (2003) found that litter was exported from the *R. mangle* intertidal fringe 10 to 17 times faster in spring tides than in neap tides. They estimated that tidal export and decomposition account for 39% of annual litter production and crabs (*U. cordatus*) consume the bulk of the litter. Nordhaus, Wolff, and Diele (2006) estimated that leaf litter and propagule biomass of 16.4 tons ha^{-1} year^{-1} in nutrient-poor mangal in the dry season.

At a polluted mangrove site at Natal, Brazil, Ramos e Silva, da Silva, and de Oliveira (2006) reported leaf fall of 11,158 kg ha^{-1} year^{-1}, and of that total, 8618 kg ha^{-1} year^1 were branches.

REPRODUCTION

Rhizophora mangle lacks the capacity for vegetative reproduction. Red mangrove stems are too dense to float after tropical storms disrupt the intertidal fringe (Rumbold and Snedaker, 1994). Both green and dry wood have a greater density than sea water; therefore, rafting and establishment of stem fragments are unlikely (Rumbold and Snedaker, 1994). Elster and Perdomo (1999) further noted that no red mangrove vegetative cuttings survived after 110 days of planting trials.

Nadia and Machado (2014) and Tomlinson (1994) reported that *R. mangle* is wind pollinated, but Tomlinson (1994) noted that the stigma shape is not conducive to catching wind-born pollen and that bees are frequent visitors to *Rhizophora* flowers. Although it can self-pollinate, Nadia and Machado (2014) noted that its fruit production rate by spontaneous self-pollination is low (2.56%) compared with wind pollination (19.44%). *Rhizophora mangle* exhibited ambophilous pollination with a fruit set of 7.2% and a highly effective pollinator, the hoverfly *Copestylum* sp. (Sánchez-Núñez and Mancera-Pineda, 2012b). Reproduction of *R. mangle* appears to be favored by self-pollination, but cross-pollination does occur (Lowenfeld and Klekowski, 1992; Menezes, Oliveira, and Mello, 1997).

Phenology

Barthélémy and Caraglio (2007) found that vegetative growth of red mangrove is continuous. Mehlig (2006) noted that there is no distinctive growth cycle. Gill and Tomlinson (1971b) indicated that the rate of leaf expansion and leaf fall peaks in summer. Leaf fall is correlated with leaf expansion. In Belize, Ellison and Farnsworth (1996b) found that the relative rates of change in the number of shoot meristems and stem length peaked 1 month after solar insolation peaked in May.

In Martinique, Mehlig (2006) reported that flowering and leaf production are linked and that low temperatures reduce flower production. Leaf production declines slightly at the end of the dry season, and the maximum life span of a leaf is about 1 year. Davis (1940) stated that *R. mangle* reaches sexual maturity in 4 to 5 years, but precocious reproduction (plants <2 years old) has been found in Florida at the northern edge of their distribution (Dangremond and Feller, 2016).

Flowering in red mangrove is expected at any time of the year in tropical regions (Agraz-Hernández *et al.,* 2011; Barreiro-Gümes, 1999; de Lima Nadia, Cerdeiro Morellato, and Machado, 2012; García-Hansen *et al.*, 2002; Gill and Tomlinson, 1971b; Mehlig, 2006). In Brazil, de Lima Nadia, Cerderio Morellato, and Machado (2012) noted a flowering peak in April to June that corresponds to the rainy season. Precipitation plays an important role in the intensity of flowering and subsequent production of propagules.

In the Amazon region of Brazil, Fernandes (1999) found significant variation in the flowering phenophase. Flowering peaks were noted from August to January when temperatures are high. Fruiting peaks and propagule dispersal are from October to April during the wet period.

In a study on San Andrés Island in the Caribbean off the coast of Colombia, Sánchez-Núñez and Mancera-Pineda

(2012a) noted that flowering is dependent on seasonally contrasting salinity conditions. They found that flowering intensity is regulated by pore water salinity and energetic balance and that flower and floral bud maturation depends on the amount of resources available after water and salinity regulation.

Fruit development requires 4 to 7 months after flowering, and the largest production of propagules is 4 to 6 months later (Gill and Tomlinson, 1971b). Propagules are produced after the highest intensity of fruiting. Gill and Tomlinson (1971b) found peak propagule production in January at the end of the dry season. In Martinique, Mehlig (2006) reported that propagules mature and are dispersed in the wet season. Timing of the release and dispersal of propagules is dependent on day length (de Lima Nadia, Cerderio Morellato, and Machado, 2012). Release of propagules is nearly aseasonal near the equator but becomes more seasonal the farther away from the equator (Van der Stocken, López-Portillo, and Koedam, 2017).

Pollen

Bertrand (1983) provided a detailed description of *R. mangle* pollen. The pollen is zonocolporate and equatorially broad with a continuous band. The exine is thick with pits evenly distributed over the surface. The outline of the grain is irregularly circular in the equatorial view and semi-angular in the polar view. The grain axis is 22 μm to 24 μm, and the equatorial diameter is 20 μm to 22 μm (Bertrand, 1983).

Mangrove pollen is a good indicator of sea-level change and is used to describe transgressions and regressions of Quaternary coastal deposits (Bertrand, 1983). *Rhizophora mangle* pollen dominated sediment cores from 6200 to 3400 BP in mid-Holocene deposits in Chiapas, Mexico (Joo-Chang, Islebe, and Torrescano-Valle, 2015). Torrescano and Islebe (2006) found that *R. mangle* and *C. erectus* pollen dominates mid-Holocene deposits from 4600 to 4000 BP at the Yucatan Peninsula, Mexico.

Propagules and Viability

Red mangrove seeds are viviparous, and the seedling unit is termed a propagule (Gill and Tomlinson, 1969). Vivipary is best described as precocious growth of the embryo with no dormancy period while the seedling is still attached to the parent plant (Farnsworth and Ellison, 1997). Seedling development requires four to eight months before it is detached as a propagule (Farnsworth and Ellison, 1997; McKee, 1995b; Mehlig, 2006). At maturity the cotyledons remain on the tree and propagules can persist for a year or more under forest canopies (Rabinowitz, 1978b).

Propagule predation by herbivores is high. Longonje and Rafaelli (2014) found that two-thirds of *R. mangle* propagules are consumed by mangrove crabs in Cameroon. Farnsworth and Ellison (1997) noted that a host of herbivores nearly doubled the abscission rate of immature propagules.

No seed bank is available for *R. mangle*; however, propagules are viable for a year or more (Arbeláez-Cortes *et al.*, 2007; Davis, 1940; Sauer, 1982; Sengupta *et al.*, 2015). Davis (1940) found that propagules have continuous development of roots while floating in cages.

Mature propagules range in length from 12 to 40 cm (Allen and Krauss, 2006; McKee, 1995b; Smith and Snedaker, 2000;

Sussex, 1975). Propagule length is a function of hypocotyl elongation (McKee, 1995b). Large propagules grow more rapidly and have lower mortality than smaller ones (Rabino-witz, 1978a; Sousa, Kennedy, and Mitchell, 2003). Stomata are absent, but lenticels bearing chloroplasts are conspicuous (Smith and Snedaker, 2000). Allen and Krauss (2006) and Smith and Snedaker (2000) reported that large propagules weigh 20 g or more.

Dispersal

The early life history of *R. mangle* comprises dispersal, stranding, and establishment of the seedling-propagule unit. In Martinique, primary release of propagules occurs during the wet season (Mehlig, 2006). The action of tides and oceanic currents plays an important role in dispersal (Gunn and Dennis, 1999). Sengupta *et al.* (2005) found that propagules are buoyant for 20 to 100 days.

Dispersal is usually highly localized. Most propagules are stranded within 2 to 5 km from parent trees (Blanchard and Prado, 1995; Sengupta *et al.*, 2005). However, Gunn and Dennis (1972) found live seedlings stranded on North Carolina beaches 805 km from the nearest source in Florida.

Germination Ecology and Establishment of Seedlings

Sousa, Kennedy, and Mitchell (2003) found that seedlings established regardless of propagule size, but large propagules grew more rapidly. In Florida, Rey (1994) reported that seedling mortality was less than 10% yr⁻¹. Predation by herbivores and desiccation are the major causes of seedling failure (McKee, 1995c). Rey (1994) stated that moderate salinities and a lack of competition from canopy trees are largely responsible for low mortality and high growth rates. Ellison and Farnsworth (1993) found that seedlings planted in open canopy sites had greater survivorship, grew twice as fast, produced more leaves, and had less damage by herbivores than seedlings growing beneath the intact canopy. Litter in the substrate can be an important factor in seedling establishment. Chapman and Feller (2011) found that seedlings grew rapidly in the *A. germinans* litter.

A long-held assumption of propagule-seedling establishment was that propagules planted themselves by a "dartlike" process where the elongated propagule drops at the distal root end into the muddy sediment and assumes an upright position. This may be true in a limited sense, but propagule dispersal at more distant sites usually deposits propagules in a horizontal position.

Cheeseman (2012) and Tomlinson and Cox (2000) discussed the anatomical adaptations of *R. mangle* for vertical orientation of the propagule, but Fisher and Tomlinson (2012) stated that Cheeseman (2012) did not make a comprehensive review of the literature on the topic. Tension wood fibers produced by the secondary xylem at the distal end of the propagule seedling form a hook that aids in the righting of the seedling. Fisher and Tomlinson (2002, 2012) stated that extreme bending occurs in the hook region above the basal 1.0 cm of the hypocotyl where roots are formed. The morphological result of wood tension fiber action and the hook is that the shoot is raised above the tidal level. The process takes several months, and the elevation of the seedling is related to production of additional secondary xylem and the abundance

of tension wood fibers on the adaxial side of the hook region. Cheeseman (2012) stated that this developmental phenomenon improves chances of establishment of *R. mangle* in unpredictable fluctuating sediments.

POPULATION BIOLOGY

As might be expected from a widely distributed pantropical species with propagules often dispersed by oceanic currents, genetically distinct populations of *R. mangle* have evolved. Colonization or recolonization by a few individuals followed by selfing may produce morphological distinctions among populations. Kennedy *et al.* (2016, 2012) found genetically distinct populations of red mangrove in the Caribbean and Florida with a genetic relationship with *R. mangle* populations on the Caribbean mainland. Albrecht *et al.* (2013) reported that small red mangrove populations in Florida and on Caribbean islands are genetically isolated but may not be morphologically distinct.

The isthmus of Central America serves as a barrier to gene flow from the Atlantic to the Pacific (Cerón-Souza *et al.*, 2012, 2010). Takayama *et al.* (2013) further stated that the Central American isthmus is a barrier to gene flow and that clear genetic distinctions occur in *R. mangle* between Atlantic and Pacific populations. They noted that the trans-Pacific dispersal of *R. mangle* propagules has given rise to the taxon *R. mangle* var. *samoensis*.

In Baja California and the Gulf of California in NW Mexico, Sandoval-Castro *et al.* (2012) found two genetically distinct populations. They indicated that genetic diversity is reduced in northern populations because of small population sizes, inbreeding, and by harsh environmental conditions.

Domínguez *et al.* (1998) studied floral variation of red mangrove from 12 populations in Mexico—seven from the east coast and five from the west coast. Through principal component analysis, they found that floral morphology variation was strongly linked to calyx and corolla size and gynoecium size. They suggested that frequent events of extinction and recolonization by a few individuals, followed by selfing, produced differentiation among red mangrove populations in Mexico.

Population dynamics in coastal habitats are controlled by biophysical factors and naturally occurring and anthropocentric disturbances. *Rhizophora mangle* stands colonize the lower intertidal fringe. In Panama, Rabinowitz (1978b) stated that intraspecific competition is high. However, she reported that greater than 50% of seedlings survive the first year. In Ecuador, Blanchard and Prado (1995) found that seedling densities are high within 5 m of large canopy red mangrove trees of 25 cm diameter at breast height (dbh) or greater. Seedlings were in frequently flooded sites with soil salinities ranging from 23 to 26 ppt (Blanchard and Prado, 1995).

PLANT COMMUNITIES

Intertidal and adjacent tropical and subtropical communities with *R. mangle* and associated species form a discrete plant community referred to as a mangal (Tomlinson, 1994). Species richness is low in the mangal (Table 3) because of the harsh environment. Undisturbed mature stands of *R. mangle* in the New World tropics and subtropics are noted for the paucity of understory herbs, shrubs, and vines (Janzen, 1985). Snedaker and Lahmann (1988) stated the hypothesis that the high metabolic expenditure in intertidal environments prevents the evolution of tolerant terrestrial species.

Mangrove forest patterns are the result of the interplay of species-specific responses to abiotic stress factors, disturbance, dispersal, and competition resulting in species zonation (Ball, 1988; Jiménez and Sauter, 1991; McKee, 1993; Snedaker, 1982). Structural patterns as a result of succession have been discussed (Ball, 1980; Fromard *et al.*, 1998; Smith, 1992), but there is no consensus about the nature and outcome of mangrove succession. Berger *et al.* (2006) used a spatially explicit, individual-based model, KiWi (Berger and Hildenbrandt, 2000), to test different hypotheses about the effect of nutrient availability on species-specific growth rates. They modelled secondary succession of mangroves (*R. mangle*, *L. racemosa*, and *A. germinans*) and determined that the initially dominating species were gradually replaced in the canopy and that high growth rate of the pioneer species slows down relative to those of later species. They excluded shade tolerance as a factor and concluded that the height growth rate of the pioneer species slowed down relative to those of later species. They attributed slower growth to a decrease in nutrient availability, which might be explained by species-specific differences in nutrient-uptake efficiency. They concluded that a disproportionate change occurs in growth rates between *L. racemosa* and *A. germinans* during early secondary succession in abandoned Brazilian rice fields. Although nutrient availability was deemed important, the extent to which this process contributes to the observed successional process is not known (Berger *et al.*, 2006).

In Ecuador, Blanchard and Prado (1995) reported that the red mangrove community has a limited number of associated species including *R. harrisonii*, *Pelliciera rhizophorae*, and the fern *Acrostichum aureum*. In Colombia, Urrego *et al.* (2009) also noted a paucity of species in the red mangrove community, including *L. racemosa*, *A. germinans*, *C. erectus*, and *A. aureum*. The northernmost stand of *R. mangle* in Texas occurs in the tidal segment of the Rio Grande, the border with Mexico. This small population occurs with *A. germinans* (the dominant) and *Batis maritima* adjacent to a shallow tidal inlet (DeYoe, Lonard, and Judd, *personal observations*).

Rhizophora mangle as an Invasive Species

Red mangrove was introduced to Oahu, Hawaii, from stock from Florida in 1902 to stabilize mudflats and now is recognized as an invasive species (Allen, 1998). It is associated with *B. maritima*, *Spartina alterniflora* (=*Sporobolus alterniflorus*), *Hibiscus tiliaceus*, *Paspalum vaginatum*, and *Thespesia populnea*. Red mangrove currently occurs on nearly all Hawaiian Islands and has negative economic and ecological impacts. It has altered drainage patterns, reduced habitat for the endangered Hawaiian stilt (*Himantopus mexicanus*), and has posed aesthetic problems for shorelines (Allen, 1998). Red mangroves have colonized fishponds, riparian zones, tidal flats, reefs, embayments, lagoons, and 70% of the area around Pearl Harbor (Chimner *et al.*, 2006). Both *R. mangle* and the Old World mangrove *Bruguiera sexangula* are naturalized in

Table 3. *Representative species associated with* Rhizophora mangle.

Species	BRZ	MEX	PUE	COR	PAN	NIC	BER	FLA	GUI	NCA
Acrostichum aureum	X				X				X	
Asparagus sprengeri							X			
Avicennia bicolor				X						
Avicennia germinans	X	X	X	X	X	X	X	X	X	X
Avicennia schaueriana	X									
Cyperus articulatus										X
Batis maritima								X		
Borrichia frutescens							X			
Casuarina equisetifolia								X		
Cladium jamaicense		X								
Clusia sp.					X					
Conocarpus erectus		X					X			X
Distichlis spicata								X		
Hibiscus tiliaceus										X
Laguncularia racemosa	X	X	X	X	X	X	X	X		X
Nypa fruticans										X
Pachira aquatiaca		X								
Pandanus spp.										X
Pelliciera rhizophorae					X	X	X			
Phoenix reclinata										X
Raphia taedigera					X					
Rhizophora harrisonii									X	X
Rhizophora racemosa									X	X
Sarcocornia perennis								X		
Schinus terebinthifolius							X	X		
Sesuvium portulacastrum							X			

BRZ = Brazil (Bomfin de Oliveira, Rizzo, and da Conceição Guerreiro Couto, 2013; Calegarío et al., 2015; Castellanos-Galindo and Krumme, 2014; Souza-Santos et al., 2016); MEX = Mexico (Campeche and Yucatan) (Aké-Castillo, Vázquez, and López-Portillo, 2006; Day et al., 1996; Guerra-Santos et al., 2014; Lara-Dominguez et al., 2005); PUE = Puerto Rico (Medina, Cuevas, and Lugo, 2010); COR = Costa Rica (Zamora-Trejos and Cortés, 2009); PAN = Panama (Phillips, Rouse, and Bustin, 1997); NIC = Nicaragua (Roth, 1992); BER = Bermuda (Thomas, 1993); FLA = Florida (Simpson, Feller, and Chapman, 2013); GUI = Guinea (Kovacs et al., 2010); NCA = Nigeria and Cameroon (Ukpong, 1995).

Hawaii, but *B. sexangula* occurs only on Oahu (Allen and Krauss, 2006).

INTERACTIONS WITH OTHER SPECIES

Rhizophora mangle is a pioneer species in the inundated intertidal fringe, a habitat unsuitable for many plant species. Populations are established without succession. Interspecific competition may occur, but there are few competitors. Intraspecific competition between sapling and neighboring canopy trees may be important. On the other hand, neighboring individuals may also serve as buffers (facilitation) from physical stress factors such as storms (Bertness and Shumway, 1993).

In Florida, Donnelly and Walters (2014) found that succulent halophytic ground cover, including *B. maritima* and *Sarcocornia perennis*, act as traps for the capture and retention of rafted *R. mangle* propagules. They concluded that for red mangrove revegetation efforts, the first step is to establish perennial species, as listed previously, into disturbed sites before planting.

Micro- and Macroflora

Rhizophora mangle is a foundation species that facilitates the establishment and persistence of an abundance of micro- and macroflora and fauna (Demopoulos and Smith, 2010). The distribution of the microbial communities in *Rhizophora* forest soil is influenced by the silt-clay percentages for both Bacteria and Archaea and organic matter content significantly influences the distribution of Archaea (Barquil Colares and Macial Melo, 2013). Symbiotic relationships are common with *R.*

mangle and other species. Epiphytic cyanobacteria (blue-green algae) and marine algae are commensalistic on rhizophores and submerged roots. Epiphytic benthic diatoms are primary producers associated with submerged rhizophores and serve as a food source for grazing invertebrates. Siqueiros Beltrones *et al*. (2005) reported the occurrence of 171 diatom taxa on red mangrove rhizophores on the west coast of Baja California, Mexico. They stated that diatom population estimates are among the highest ever inventoried for benthic species. In Florida, Maybruck and Rogerson (2004) estimated that pennate diatoms accounted for 2.4×10^6 cells g^{-1} dry weight and were exceeded only by bacteria (6.9×10^9 cells g^{-1} dry weight).

Rigonato *et al*. (2012) documented the occurrence of 19 genera of cyanobacteria as epibionts on *R. mangle* in Brazil. The orders Oscillatoriales and Nostocales constituted most of the species. The genera *Symphyonemopsis* and *Brasilomema* are common epiphytes (Rigonato *et al*., 2012).

Red mangrove rhizophores provide a stable substrate for the attachment of epiphytic green and red algae. No data exist for brown algae associated with rhizophores. Farnsworth and Ellison (1996) found that epiphytic macroalgae were abundant in well-lit windward sites in the mangal. In southern Belize, Taylor, Littler, and Littler (1986) reported that fleshy submerged marine algae are dominant on submerged rhizophores that do not contact the sediment. Calcifying green algae dominate roots that penetrate the sediment. Dominants on hanging rhizophores are the red algae *Acanthophora spicifera* and *Spyridia filamentosa* and the green alga *Caulpera race-*

mosa var. *occidentalis*. Calcified green algae *Halimeda opuntia* and *H. monile* are confined to the root-sediment interface (Taylor, Littler, and Littler, 1986).

In another site in Belize, Farnsworth and Ellison (1996) indicated that the dominant taxa of the rhizophore zone were the green algae *Bryopsis pennata* and *H. opuntia*; in Colombia, Pena, Zingmark, and Nietch (1998) reported that the red algae *Bostrychia calliptera* and *Caloglossa leprieurii* are common on rhizophores. In Panama, Levings and Garrity (1994) indicated that submerged rhizophore surfaces are covered with 27 species of foliose red algae.

Microfauna

An immense diversity of microfauna are epibionts on red mangrove rhizophores or are early colonizers on red mangrove leaf litter. Leaf litter has a thin film of microorganisms that increases the nutritive value of debris and attracts benthic invertebrates (Bomfim de Oliveira *et al.*, 2012). Laurent *et al.* (2013) indicated that sulfide-tolerant nematodes, flatworms, and ciliated protozoans and amoebae are the initial colonizers on leaf litter. Heterotrophic flagellates (2.7×10^{-3} g^{-1} in dry film), amoebae (7×10^{-3} g^{-1} in dry film), and ciliated protozoans (4.8×10^{-3} g^{-1} in dry film) occur as epibionts on rhizophores or in leaf detritus (Maybruck and Rogerson, 2004).

Marine nematodes are the most abundant metazoans inhabiting decaying leaves (Hopper, Fell, and Cefalu, 1973). Copepods, foraminifera, rotifers, gastrotrichs, tardigrades, turbellarians, phoronids, and tanaeids inhabit detritus and serve as food sources for larger invertebrates in the ecosystem (Hopper, Fell, and Cefalu, 1973; Sheridan, 1997). Fleck and Fitt (1999) found that the planula stage of the upside-down jellyfish *Cassiopea xamachana* settles on decomposing *R. mangle* leaf litter and undergoes metamorphosis on the litter substrate.

Epiphytic Animals

Slightly larger macroscopic epibionts use benthic rhizophores and roots as substrates. Sponges, ascidians, cnidarians, bryozoans, hydroids, amphipods, coelenterates, tunicates, urochordates, ectoprocts, and endoprocts are common commensalistic organisms associated with *R. mangle*.

Rhizophore and root-fouling invertebrates include bivalves, sponges, and tunicates (Sutherland, 1980). Hunting *et al.* (2010) stated that a positive correlation of tannins in red mangrove bark provides a chemical stimulus for the attachment of epiphytic sponges. In southern Belize, Díaz and Rützler (2009) found that sponges comprise 10 to 70% of the epiphytic diversity of meiofauna on rhizophores and roots. In Florida, Engel and Pawlik (2005) reported that 74% of benthic rhizophore and root surfaces were covered by 1200 sponges represented by 10 species. Ellison, Farnsworth, and Twilley (1996) found that sponges protect rhizophores from isopod attack.

Creary (2003a) identified 18 epiphytic species of bryozoans associated with rhizophores and roots of *R. mangle* in Kingston Harbor, Jamaica. Creary (2003b) noted that the preponderance of sponges and ascidians can smother bryozoans.

Macrofauna

Mangrove forests in the Caribbean host the earth's richest mangrove-associated invertebrate fauna (Ellison and Farns-

worth, 1996a). The shallow intertidal zone dominated by *R. mangle* is a nursery for juvenile penaid shrimp and lobsters and is a critical habitat for keystone crab species and other crustaceans. *Rhizophora mangle* provides a habitat for macrofaunal invertebrates including oysters, crabs, annelids, mussels, arthropods, and snails. Snails forage on fungal mycelia on the surface of rhizophores in the narrow interface at and above the mean high tide mark (Kohlmeyer and Bebout, 1986). Snails also browse leaf litter at low tide and move to higher branches during inundation (Proffitt and Devlin, 2005).

Colonies of ants and termites utilize aerial shoots. Dejean *et al.* (2003) identified one species of termite and 37 species of arboreal ants that populate shoots of red mangrove in Quintana Roo, Mexico. Adams and Levings (1987) found that rhizophores provide connections between trees in the canopy for termite migrations.

Many mosquito species use red mangrove for depositing eggs. Ritchie and Johnson (1991) found that *Aedes taeniorhynchus* exclusively selected stands of *R. mangle* in an *A. germinans* forest to lay eggs.

Crabs

Crabs (Order: Decapoda) play an important ecological role in the functioning of mangrove ecosystems. They are among the most common and abundant large invertebrates in the mangal (Cannicci *et al.*, 2008). They perform vital biogeochemical functions, influence seedling recruitment, and provide an important human food source (Longonje and Rafaelli, 2014).

Ucides cordatus (mangrove crab or hairy crab) is a keystone species of subtropical and neotropical mangrove forests and is an important source of human food in developing countries (de Cássia Conti and Cunha Nalesso, 2010). It is a wide-spread, semiterrestrial species in the western Atlantic from Florida to the Gulf of Mexico, Central America, the Caribbean, and northern South America from Brazil to Uruguay.

Ucides cordatus is a leaf-removing species and acts as an ecological engineer (Piou, Berger, and Feller, 2009). The species is abundant in the intertidal fringe in Brazil where it has densities ranging from 1.38 to 4.75 crabs m^{-2} (de Cássia Conti and Cunha Nalesso, 2010; Schories *et al.*, 2003). It is estimated that each crab ingests 1.30 g dry weight of *R. mangle* leaves day^{-1} (Schories *et al.*, 2003). Christofoletti, Hattori, and Pinheiro (2013) stated that the preferred food of *U. cordatus* is *R. mangle* leaves and that they consume 81% of leaf litter. They also reported that senescent leaves with high polyphenol levels were rejected as a food source. In northern Brazil, Pülmanns *et al.* (2014, 2016) found that this species consumes 70% of the total leaf litter and propagules and is the primary modifier of sediments where it burrows 2-m deep. Sediment around burrows may oxidize during low tides, and significant amounts of CO_2 may be released from burrows. They concluded that crab burrows are an important pathway for CO_2 export from mangrove sediments (Pülmanns *et al.*, 2014).

Mangrove crabs are continuous feeders (Nordhaus, Wolff, and Diele, 2006). They estimated food intake of *U. cordatus* at 4.1 g dry weight m^2 day^{-1}. Rates of propagule consumption in Brazil is highest in the intertidal fringe where *R. mangle* is the dominant species (Ferreira *et al.*, 2013; Sousa and Mitchell, 1999). Litter processing by *U. cordatus* is important in the

mangal for retaining energy and nutrients in nutrient-deprived mangrove ecosystems (Nordhaus, Wolff, and Diele, 2006).

Aratus pisonii (mangrove tree crab) is an arboreal species that lives in *R. mangle* trees in Florida and the Caribbean. Its distribution ranges from Nicaragua to Peru (Beever, Simberloff, and King, 1979). It feeds mostly on red mangrove leaves and is found on roots, branches, and in the canopy of *R. mangle* (Diaz and Conde, 1989; Erickson, Bell, and Dawes, 2012). Mangrove tree crabs feed on fresh and senescent leaves while they are attached to the parent plant (Miranda *et al.*, 2017). *Aratus pisonii* consumes the leaf epidermis and leaves distinctive scraping marks where they have fed. Damage may range from 4 to 25% of the leaf area and may be attributed not only to *A. pisonii*, but also to mangrove periwinkles (*Littorina angulifera*), insects, and aphids (Farnsworth and Ellison, 1991).

Rhizophora mangle and *A. germinans* typically do not share *A. pisonii* as a herbivore (López and Conde, 2013). Erickson, Bell, and Dawes (2012) found by gut analysis that *A. pisonii* preferred red mangrove leaves more than *A. germinans* and *L. racemosa* in Tampa Bay, Florida.

Goniopsis cruentata (mangrove root crab) is also a widespread species that ranges from south Florida to southern Brazil, throughout the Caribbean, and in West Africa from Senegal to Angola. It is a common semiterrestrial crab in Brazil and is an important human food source. It serves the role as a keystone species and affects sediment biogeochemistry, rates of litter decomposition, and nutrient recycling. This species like *U. cordatus* and *A. pisonii* consumes leaf litter adjacent to red mangrove and other mangrove roots and *R. mangle* seedlings (Mohammed, 2016; Reis, Taddei, and Cobo, 2015).

Goniopsis cruentata and *U. cordatus* are the most important consumers of red mangrove propagules in Brazil. They affect establishment of seedlings and saplings; therefore, they are crucial to mangrove conservation (Ferreira *et al.*, 2013; Ricarda Boehm *et al.*, 2016). In Costa Rica, Perry (1988) found that colonization of red mangrove was reduced by predation of hermit crabs (*Clibanarius panamensis*).

In Cameroon, predation of *R. mangle* propagules is estimated at 66.7% (Longonje and Rafaelli, 2014). Leaf-eating crabs are dependent on litter, and they supplement their diet from other sources. Important species of crabs in estuaries and intertidal sites in Cameroon include *Metagrapsus curvatus*, *Sesarma huzardi*, *S. elegans*, *S. alberti*, *Goniopsis selii*, and *Grapsus grapsus* (Longonje and Raefaelli, 2014).

Isopods

Isopoda is an order of crustaceans with 10,000 species represented in terrestrial, fresh water, and marine environments (King, 2004). Two species, *Sphaeroma terebrans* and *S. peruvianum*, are wood-boring crustaceans that burrow into hanging aerial roots of *R. mangle*. These marine isopods feed on wood, cause extensive damage to manmade structures, and have enzymes that digest cellulose (Benson, Rice, and Johnson, 1999). *Sphaeroma terebrans* was introduced in Florida in 1897 from Atlantic and Caribbean sources. It possibly arrived via wooden-hulled boats (Perry and Brusca, 1989). *Sphaeroma peruvianum* was introduced into the New World from the eastern Pacific into the *R. mangle* intertidal zone on the Pacific coast of Costa Rica (Perry and Brusca, 1989).

Brooks and Bell (2005a) found *S. terebrans* activity in all seasons in Tampa Bay, Florida, and found that 60% of all aerial rhizophores were occupied by burrows. Thiel (2000) noted that juvenile forms of *Sphaeroma quadridentatum* may be found in burrows unoccupied and occupied by *S. terebrans*. Isopods cannot burrow in older roots (Perry, 1988). Isopod-infected aerial rhizophores die and tend to break off at the highwater mark (Brooks and Bell, 2001, 2005a,b; Perry and Brusca, 1989; Thiel, 2000).

Brooks (2004) and Brooks and Bell (2001, 2005a) found that *S. terebrans* caused root death, aerial rhizophore breakage, reduced root production, reduced growth rates, and decreased plant survivorship. Brooks and Bell (2001) reported that epiphytic sponges have an indirect effect by preventing colonization of *S. terebrans*.

A difference of opinion exists over the detrimental and beneficial effects of wood-boring isopods. Simberloff, Brown, and Lowrie (1978) found that damage caused by isopod and insect borers stimulate root initiation. They found that for every rhizophore damaged, 1.4 new roots reach the sediment; however, Brooks and Bell (2002) found that the most common response was repair of abandoned isopod burrows and that lateral root production occurred at a lower frequency. Their conclusion was that the most common response to damage is root tissue replacement of the wound rather than initiation of new root tissue.

Gastropods

The mollusk *M. coffeus* is an important invertebrate in the decomposition of *R. mangle* leaf litter in Florida (Proffitt and Devlin, 2005; Proffitt *et al.*, 1993). Snails forage on leaf litter at low tide and climb into the canopy during inundation at high tide. Leaf litter ingestion estimates ranged from 70 to 90% of individual leaves within 6 weeks of initial feeding, and 80% of all brown leaves were completely consumed by the end of the experiment (Proffitt and Devlin, 2005; Proffitt *et al.*, 1993).

Insects

Wood-boring insects, such as some isopods (see previous information), play an important role in structuring the mangal. Wood borers include longhorn beetles, weevils, moths, and other beetles (Feller and Mathis, 1997). Feller (2002) reported that wood-boring insects killed 50% of the mangrove canopy at a site in Belize. She also reported that wood-borer injury promotes adventitious stem growth and floral initiation after 50% of the branches were girdled.

Larvae of the cerambycid beetle (*Elaphidion mimeticum*) feeding on live wood is responsible for killing red mangroves in Belize. Beetle predation produces small light gaps in the forest canopy (Feller and McKee, 1999). *Avicennia germinans* is not attacked by this species. Sousa, Kennedy, and Mitchell (2003) reported that 86% of red mangrove propagules were girdled by scolytid beetle larvae (*Coccotrypes rhizophorae* = *Poecilips rhizophorae*). The obligate parasite attacks the hypocotyl of the propagule and causes mortality. However, if girdling is not complete, seedlings may survive and grow at a slower rate (Sousa, Kennedy, and Mitchell, 2003). Crickets and moth larvae are generalist feeders. Feller (1995) found that 1% to 4%

of red mangrove leaves were damaged by the leaf-mining microlepidopteran (*Marmara* sp.) within a 6-month experiment.

Fungi

Fungi serve not only as agents of decomposition of litter but also as plant pathogens in the mangal (Elster, Perdomo, and Schnetter, 1999). Wier, Tattar, and Klekowski (2000) found that the imperfect fungus (*Cytospora rhizophorae*) causes dieback and mortality of red mangroves in Puerto Rico. *Cytospora rhizophorae* is a facultative pathogen that usually enters stems through a wound and produces a gall that leads to slow stem-diameter growth and causes further stem and rhizophore wounds that may result in mortality. Rayachhetry *et al.* (1996) reported the occurrence of branch and stem galls in *R. mangle* produced by the parasitic imperfect fungus *Botryosphaeria ribis* in south Florida.

Myxomycota, Ascomycota, Basidiomycota, and anamorphic fungi play an important role in the decomposition of litter. Cavalcanti *et al.* (2016) reported the occurrence of eight species of slime molds in Brazilian mangal that are active on aerial red mangrove leaf litter.

Numerous ascomycetes and anamorphic fungi are involved in the decomposition of leaf litter and wood. These taxa are obligate marine species that work optimally on submerged dead branches (Kohlmeyer, 1981, 1986; Kohlmeyer and Kohlmeyer, 1977; Kohlmeyer and Volkmann-Kohlmeyer, 1988).

Basidiomycetes species are less common and usually occur on advanced stages of decaying red mangrove wood (Gilbert and Sousa, 2002). Nogueria-Melo, Parreira Santos, and Baptista-Gillertoni (2014) documented 13 species of basidiomycetes in Brazilian mangals. They noted that their occurrence was primarily in the rainy season.

IMPACTS OF STORMS

Hurricanes and tropical storms play an important role in controlling structure of the mangal (Alongi, 2008; Lara-Dominguez *et al.*, 2005), but it is difficult to generalize about the impacts. Mangroves act as buffers to the destructive effects of tropical storms and storm surges and serve to protect human life and property (Vogt *et al.*, 2012). For Hurricane Andrew in Florida, damage to the coastal forest was primarily confined to within 200 to 300 m of the coasts with 94% mortality with survivors being small trees or sprouts (Ross *et al.*, 2006). In the coastal fringe forest, *R. mangle* regained dominance after the hurricane partly due to its shade tolerance (Ross *et al.*, 2006).

Vogt *et al.* (2012) and Roth (1992) found that larger trees with lower densities were more susceptible to hurricane damage and that *R. mangle* became the dominant species in the mangal that repopulated open gaps in the forest. Delays in mangrove forest recovery may occur in severely impacted areas if delivery of propagules is reduced or production of seedlings is reduced by habitat fragmentation (Milbrandt *et al.,* 2006).

Kovacs, Blanco-Correa, and Flores-Verdugo (2001) found that *R. mangle* was less affected by a hurricane on the Mexican Pacific coast than either *L. racemosa* or *A. germinans*. *Rhizophora mangle* seedlings and saplings are more shade tolerant than *L. racemosa*. On the other hand, Imbert, Labbé,

and Rosteau (1996) reported that red mangrove trees were more heavily damaged than either *L. racemosa* or *A. germinans* in the Caribbean. *Laguncularia racemosa* is better represented in interior sites where canopy closing is delayed (Ross *et al.*, 2006). Roberts, Hedgepeth, and Gross (2011) found that tall *L. racemosa* trees were heavily damaged by Category 2 and 3 hurricanes in Florida, but red mangrove trees were only defoliated and marginally impacted. After leaf defoliation of *R. mangle*, Barreiro-Gümes (1999) noted that leaf renewal occurred 129 to 392 days after a major hurricane in Campeche, Mexico.

Several investigators have found significant hurricane damage to red mangrove stands. Proffitt, Milbrandt, and Travis (2006) reported that the number of reproducing *R. mangle* trees 1 km from the shoreline in Charlotte Harbor and Tampa Bay, Florida, was significantly reduced after a hurricane. More recruits of red mangrove were found at sites that had higher densities of prestorm seedlings and greater dominance by *R. mangle*.

In early 1992, Hurricane Andrew (Category 5 hurricane) caused major damage to mangroves and property in Florida. Smith *et al.* (1994) noted that red mangroves with diameter at breast height (DBH) greater than 5 cm had significant initial mortality and those with a DBH less than 5 cm DBH had 10% mortality. Maximum mortality occurred in trees in the 15- to 20-cm size class. Mortality decreased for trees greater than 30 cm DBH. Baldwin *et al.* (2001) found high densities of seedlings, seedling growth, recruitment, and resprouting of red mangroves after Hurricane Andrew. Recruitment of red mangrove propagules led to a monotypic stand of the species.

Bologna *et al.* (2019) looked at red mangrove genetic diversity and to ascertain potential population bottlenecks two decades after Hurricane Hugo. Two fringing red mangrove populations had low observed heterozygosity and high inbreeding coefficients, whereas the fully forested sites showed higher heterozygosity and lower inbreeding frequencies. The effective population size of one site places it in risk of genetic dysfunction, but future rehabilitation of the site may be possible by the introduction of propagules from other regions.

Lightning, hurricanes, and tropical storms create gaps in the mangal that allow rapid colonization of *R. mangle*. Sherman, Fahey, and Battles (2000) noted greater sapling densities and sapling growth rates in canopy gaps than in closed canopies in the Dominican Republic. Annual mortality of red mangrove saplings in the lightning-created gaps was only 9% compared to mortality rates for *L. racemosa* and *A. germinans* in the gaps as 32 and 56%, respectively (Sherman, Fahey, and Battles, 2000).

Hurricanes and tropical storms may bring positive benefits to the mangal, *i.e.* hurricanes may play an important role in the distribution of mangrove propagules. Hurricane Donna (1960) savaged the coast of Florida toppling, uprooting, and defoliating mangroves. Mangrove mortality ranged from 25 to 75% over approximately 100,000 acres, with the black mangrove having the highest mortality (Lugo and Snedaker, 1974). Whereas propagules of both the red and black mangrove were widely distributed, it was the red mangrove that formed the greatest proportion of new mangrove community. Phosphorus can be a limiting nutrient for red mangrove growth and development. In phosphorus-limited, carbonate-dominated

sites in southern Florida, storm-derived sediments had twice the average phosphorus level than these normally phosphorus-limited sediments (Castañeda-Moya *et al.*, 2010).

REFORESTATION

Rhizophora mangle seedling recruitment, growth, and survival can influence the rate and pathway of mangal reforestation following disturbances (Sousa, Kennedy, and Mitchell, 2003). Reforestation is enhanced by sufficient water levels and optimal salinities and temperatures. A.M. Ellison (2000) reviews mangrove reforestation from a global perspective. High light availability in forest gaps increases survival and growth rates (Elster, Perdomo, and Schnetter, 1999). Red mangrove and other mangroves may be slow to grow in hypersaline sites hampering recovery (McKee, Rooth, and Feller, 2007).

Artificial flooding often promotes reforestation (Vogt *et al.*, 2012). Die-offs in the mangal may be caused by hypersalinity, and channeling may be required to reduce salinity. In Venezuela, reforestation requiring this type of habitat enhancement may require more than 10 years to restore the mangal (Rodríguez-Rodríguez *et al.*, 2016).

Forest regeneration depends on habitat conditions adjacent to cleared sites. Natural red mangrove reforestation in strip-cleared cutting sites in Ecuador was enhanced by soil salinities ranging from 23.3 to 26.3 ppt (Blanchard and Prado, 1995). They found high *R. mangle* seedlings density within 5 m of trees with a DBH of 25 cm or greater. Seedlings that develop from large propagules grow more rapidly (Sousa, Kennedy, and Mitchell, 2003). Rivera-Monroy *et al.* (2004) reported that clear-cutting did not have a major effect on modifying soil-nutrient concentrations. They predicted that preforest disturbance nutrient distributions would be reestablished 15 to 25 years following clear-cutting.

Shoreline stabilization using red mangroves has been successful in Florida. Revegetation of red mangrove stands has been successful in areas with low-velocity currents and low wave-energy sites by placing saplings in full-length PVC pipes (Salgado Kent, 1999). By using this procedure, they reported seedling establishment success of 87% to 94% based on seasonal plantings. Donnelly and Walters (2014) reported that seedling establishment can be facilitated by planting seedlings in perennial, halophytic ground cover of *B. maritima* and *S. perennis*.

REMOTE SENSING AND MODELLING

Remote sensing technology has proven to be effective in mapping and monitoring mangal vegetation. Wang *et al.* (2019) provide a review of mangrove remote sensing literature. Kovacs, Wang, and Flores-Verdugo (2005) used commercially available high-resolution satellite imagery (IKONOS) and LI-2000 plant canopy sensors to map mangrove vegetation. They found that the combination of these technologies easily discriminates between *R. mangle* and *L. racemosa*. Both species were present in almost equal amounts on the coastline of Baja California, Mexico. Visible infrared imaging spectrometer data showed 40% accuracy for mapping *R. mangle* in the Florida Everglades and 100% accuracy for mapping the wetland sedge (*Eleocharis cellulosa*) in Florida marshes (Hirano, Madden, and Welch, 2003). LIDAR shows promise in nondestructive estimation of mangrove above-ground biomass but has not yet been applied to red mangroves (Olagoke *et al.*, 2016).

Models are being used to estimate mangrove aboveground biomass, but little modeling effort occurs for belowground biomass. Various regression models were evaluated for estimation of the aboveground biomass of *R. mangle* and *L. racemosa* (Gomes Soares and Schaeffer-Novelli, 2005). Greuters *et al.* (2014) developed an individual-based mangrove dynamics model based on canopy plasticity and lateral stem and rhizophore data. Smith and Whelan (2006) developed allometric equations for *R. mangle* to estimate total biomass and components of biomass. Their equations explained ≥93% of the variance in total dry weight. The DBH was a better predictor of dry weight than stem height.

ECONOMIC IMPORTANCE

Rhizophora mangle stands play an important role in shoreline stabilization (Salgado Kent, 1999). Red mangrove populations serve as natural barriers to coastal erosion caused by tropical storms (Vanegas *et al.*, 2019); as habitat for a wide range of organisms in intertidal food webs; as carbon sequestration reservoirs; and as a source of litter, detritus, and organic material that is exported to neighboring ecosystems (Schories *et al.*, 2003). Coastal fisheries and wildlife populations are supported by this species (Mumby *et al.*, 2004; Osland *et al.*, 2014; Vovides *et al.*, 2011).

Red mangrove bark and wood are valuable resources. Tannins are extracted from the bark and are a source of dyes that are used for tanning leather (Blanchard and Prado, 1995; Mabberley, 1997; Proctor, 2012; Satyanarayna *et al.*, 2012; Zomlefer, 1994). The hard, durable wood is used for posts, pilings, railroad ties, and other construction projects. In Gambia, Satyanarayna *et al.* (2012) noted that wood is used for constructing fish-drying racks and for conversion to charcoal. Williams (1999) found that triterpinoids (taraxerol and cinnamyoyl-lupeol) extracted from bark are effective as an insecticide to control potato weevils (*Cylas formicarius*).

Wildlife Values

Red mangrove provides cover and nutrients for a wide variety of wildlife and commercially important invertebrates and vertebrates. Food, reproductive sites, and refuge are provided for oysters, crabs, fish, reptiles, and birds (Freitas *et al.*, 2002). In the Caribbean, the mangal dominated by *R. mangle* is the ecosystem that supports juvenile shrimp, spiny lobsters, and over 200 species of fish (Ellison and Farnsworth, 1996b). In particular, the mangrove oyster, *Crassostrea rhizophorae*, is of importance in the Caribbean as it is an epiphytic species on *R. mangle* roots (Rodríguez-Romero and Gasca-Montes de Oca, 1998).

Aburto-Oropeza *et al.* (2009) reported that juvenile yellow snappers (*Lutjanus argentiventris*) spend at least 300 days among benthic rhizophores and roots of red mangrove prior to migration to open water. MacDonald, Shahrestani, and Weis (2009) found that juvenile school masters (*Lutjanus apodus*) use the same habitat listed above as a refuge. As this species increases in size, less time is spent in the *R. mangle* zone. In

Table 4. *Water birds that use* Rhizophora mangle *as nesting sites in Florida.*

Ardea alba	Great Egret
Ardea herodias occidentalis	Great White Heron
Ardea herodias wardi	Great Blue Heron
Bulbulcus ibis	Cattle Egret
Coccyzus minor	Mangrove Cuckoo
Dendrioca petechia grundlachi	Cuban Yellow Warbler
Egretta caerulea	Little Blue Heron
Egretta thula	Snowy Egret
Eucocimus albus	Reddish Egret
Haliaectus leucocephalus	Bald Eagle
Melanerpes carolinensis	Red Bellied Woodpecker
Pandion haliaetus	Osprey
Patagioenas leucocephala	White-Crowned Pigeon
Pelecanus occidentalis	Brown Pelican
Phalacrorax auratus	Double-Crested Cormorant
Platalea ajaja	Roseate Spoonbill
*Rostrhamus sociabilis**	Snail Kite
Vireo altiloquus	Black-Whiskered Vireo

Endangered (Curnutt and Robertson, 1994; Drietz and Duberstein, 2001; Lloyd and Doyle, 2001; Mackenzie, Schaeffner, and Swartz, 2015; Onuf, Teal, and Valiela, 1977).

Bonaire, mangroves, seagrass beds, and the shallow coral reef serve as a nursery and as a refuge for juvenile schoolmaster, mangrove snappers (*Lutjanus griseus*), and barracudas (*Sphyraena barracuda*) (Nagelkerken *et al.*, 2000).

In Florida, juvenile snook (*Centropomis undecimalis*) and sawfish (*Pristis pectinata*) are common in the shallow intertidal fringe (Barbour *et al.*, 2012; Norton *et al.*, 2012). Juvenile sawfish undergo early development in less than 90 cm of seawater in this zone (Norton *et al.*, 2012).

The red mangrove community provides habitat for reptiles including the endangered green sea turtle (*Chelonia mydas*). Gut analysis showed that this species consumes propagules, leaves, and marine algae in the Galapagos Islands and Colombia (Amorocho and Reina, 2008; Carrión-Cortez, Zárate, and Seminoff, 2010). Alligators (*Alligator mississippiensis*) and crocodiles (*Crocodylus acutus*) use *R. mangle* sites for nesting in Florida and elsewhere (LeBuff, 2014). Rosenblatt *et al.* (2013) found that the mangrove salt marsh snake (*Nerodia clarkia compressicauda*) forages on rhizophores but spends most of its time in water (Mullin and Mushinsky, 1995).

The red mangrove canopy provides breeding, nesting, and resting sites for water birds and migratory birds. In Florida, red mangrove provides nesting sites for birds listed in Table 4. Numerous overwintering nonbreeding migratory birds use the red mangrove rookery. In Puerto Rico, Northern Water Thrushes (*Parkesia noveboracensis*) forage on leaf litter and *R. mangle* roots (Reitsma *et al.*, 2002; Smith, Reitsma, and Marra, 2011a,b).

Nearctic overwintering Blue-Winged Teal (*Anas acuta*) and American Widgeons (*Anas americana*) use red mangrove for resting and preening in Yucatan, Mexico (Thompson and Baldassarre, 1991). Resident Scarlet Macaws (*Ara cacao*) nest in trunk cavities in Costa Rica (Vaughn, Nemeth, and Marineros, 2003), and Scarlet Ibis (*Eudocimus ruber*) use the canopy as breeding sites in southern Brazil (Olmos and Silva e Silva, 2002).

Medicinal Uses

Aqueous decoctions of *R. mangle* bark and leaves have been used in a wide variety of traditional folk medical practices in the tropics to treat eye ailments, diarrhea, leprosy, digestive disorders, respiratory ailments, tuberculosis, venereal disease, and sore throat (Berenguer *et al.*, 2006; Melchor *et al.*, 2001). In Cuba, aqueous polyphenolic tannins extracted from bark have been used as an antiseptic, astringent, haemostatic agent, antibiotic, and as a treatment for gastric ulcers (Berenguer *et al.*, 2006; Melchor *et al.*, 2001).

Sánchez Perera, Ruedas, and Gómez (2001) and Sánchez Perera *et al.* (2004) used bark extracts to test tannins for antiulcerogenic properties in rats. They found that these polyphenolic compounds reduced gastric lesions in laboratory animals. Cáceres *et al.* (1993) reported that decoctions of leaves show promise as an antifungal agent to treat imperfect fungi that include *Candida albicans*, *C. krusei*, and *C. parapsilosis*. Melchor *et al.* (2001) reported antibiotic properties of red mangrove decoctions. They found that seven species of bacteria associated with wounds are inhibited by bark extracts. They indicated that polyphenolic compounds probably confer antibiotic properties.

Alarcon-Aguilara *et al.* (1998) noted that aqueous bark decoctions show promise in treatment of diabetes. They stated that *R. mangle* compounds decreased the hyperglycemic peak associated with diabetes and decreased the area under the glucose tolerance curve in laboratory animals.

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