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

Hudson DeYoe†‡, Robert I. Lonard§, Frank W. Judd†, Richard Stalter§, and Ilka Feller††

1School of Earth, Environmental and Marine Sciences
University of Texas Rio Grande Valley
Edinburg, TX 78539, U.S.A.

§Department of Biological Sciences
St. John’s University
Queens, NY 11439, U.S.A.

†Department of Biology
University of Texas Rio Grande Valley
Edinburg, TX 78539, U.S.A.

††Smithsonian Environmental Research Center
Smithsonian Institution
Edgewater, MD 21037, U.S.A.

**ABSTRACT**

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*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 (30.48810°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, Sereneshki de Lima et al. (2013) reported the following zonation sequence from the intertidal fringe to the high intertidal zone: *R. mangle* > *L. racemosa* > *Avicennia schauerniana*.

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, 1998).

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 depositionaly 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

Journal of Coastal Research, Vol. 00, No. 0, 0000
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


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 Hoehr.). 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 Millsapgh (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, mangliser 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.
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 anticinal 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;
Rhizophores and Roots

A prominent feature of *Rhizophora mangle* is an extensive network of rhizophores. Rhizophores have been referred to as still roots, aerial roots, prop roots, cable roots, and flying buttresses (Méndez-Alonso 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 substrate (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 stilllike 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-Alonso 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-Alonso 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. E. 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 son (1982) reported that chill resistance is based on the fatty freeze-induced xylem failure. Markley, McMillan, and Thomp-son (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. Profitt 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 sea-water 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., 1988). 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 CO₂ 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, 2011; Wier, Tattar, and Klekowski, 2000). Rodriguez-Rodriguez, Mancera-Pineda, and Rodriguez (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 CO₂ 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 ($^{15}$N, $^{13}$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 (Staller 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 *Rhizophora mangle*. *Avicennia germinans*, *B. maritima*, and *Sarcocornia* (Salticorna) 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, Rullköttö, 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-Rafi, Dood, 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 Ramirez (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 recycling 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. Ricardo 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 C₃ 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.

Détrès, Armstrong, and Connelly (2001) reported that ultraviolet (UV) radiation alters photosynthesis and protective 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 (Détrès, 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 CO₂ levels among R. mangle, A. germinans, L. racemosa, and C. erectus. They found no significant difference among the species in net primary production and instantaneous transpiration efficiency (ITE) at ambient CO₂; however, at higher CO₂ (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 (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 CO₂ assimilation rate than R. mangle or L. racemosa.

Salinity and CO₂ levels influence enzymatic activities that affect photosynthesis and respiration. Farnsworth and Ellison (1996) stated that elevated CO₂ levels increase biomass, total shoot length, branching, and leaf area. They found that doubling CO₂ levels decreased stomatal density as epidermal cells enlarged. Lin and da S.L. Sternberg (1992a) found that dwarf red mangroves have lower intercellular CO₂ concentrations and higher water-use efficiency than taller red mangroves. Photosynthetic gas exchange measurements showed 15% lower CO₂ assimilation, 6% lower intercellular CO₂ 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 (10²²) g year⁻¹ with 26 to 34 (10²¹) 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 mangroves 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
Biomass and Litter

Mangrove biomass is governed by the parent substrate and latitude, with productivity greatest near the equator (Caucaux, Allison, and Bianchi, 2012; Cuc and de Ruyter van Steveninck, 2015). Aboveground biomass is in part a reflection of productivity in a plant community (Olsland 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 kg dry weight m\(^{-2}\) at La Paz Bay, Baja California. 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 Fourquarean (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).

Bombin 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 (Bombin 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\(^{-1}\).
Mexico
At Veracruz, Mexico, Aki-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 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 Diel (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 pollinates, 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 Mancerra-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
Barthélemy 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-Gúmes, 1999; de Lima Nadija, Cerdeiro Morellato, and Machado, 2012; García-Hansen et al., 2002; Gill and Tomlinson, 1971b; Mehlig, 2006). In Brazil, de Lima Nadija, Cerdeiro 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 Mancerra-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, Cerdorio 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 conditions (Farnsworth and Ellison, 1997; Goo, 1993). Seedling establishment is a function of hypocotyl elongation (McKee, 1995b). Large propagules grow more rapidly and have lower mortality than smaller ones (Rabinowitz, 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

Journal of Coastal Research, Vol. 00, No. 0, 0000
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 anthropogenic 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) 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 alterniflora), Hibiscus tiliaeaceus, 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

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Journal of Coastal Research, Vol. 00, No. 0, 0000
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).

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 Lara-Dominguez et al., 2016); MEX = Mexico (Campeche and Yucatan) (Ake-Castillo, Vázquez, and López-Portillo, 2006; Day et al., 1996; Guerra-Santos et al., 2014; Lara-Domínguez 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 (Kowages et al., 2010); NCA = Nigeria and Cameroon (Ukpong, 1995).

Asquithia filamentososa and Spyridia filamentosa are common epiphytes (Rigonato et al., 2012). Rhizophora mangle 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 Caulerpa 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 Niestch (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 invertebrate epibionts (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, Diaz 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 Farnsworth, 1996a). The shallow intertidal zone dominated by R. mangle is a nursery for juvenile penaeid 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 (Cannici 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, Pulmanns 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 CO₂ may be released from burrows. They concluded that crab burrows are an important pathway for CO₂ export from mangrove sediments (Pulmanns 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 angulistera*), 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 Rafaelli, 2014).

*Isopods*

Isopods are 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; 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 (*Coccotreps rhizophorae = Pocelips 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 Klekowksi (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. Rayachchery 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 Volkman-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 Rosteu (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-Güemes (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 those normally phosphorus-limited sediments (Castañeda-Moya et al., 2010).

**REFORESTATION**

*Rhizophora mangle* seedling recruitment, growth, and survival can influence the rate and pathway of mangrove 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 rhizosphere 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 ephiphytic species on *R. mangle* roots (Rodriguez-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
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 (Centropomus 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, sawfish undergo early development in less than 90 cm of seawater in this zone (Norton et al., 2012). Alligators (Alligator mississippiensis) use red mangrove for nesting sites for birds, and Library Support Services at Rice University were helpful in obtaining red mangrove literature.

**LITERATURE CITED**


**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 antilucreorgenic 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.

Alarcón-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.


Red Mangrove Review


