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REVIEW ARTICLES

The Biological Flora of Coastal Dunes and Wetlands: *Avicennia germinans* (L.) L.

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ABSTRACT

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Avicennia germinans (L.) L. is a pantropical, subtropical, and occasionally warm-temperate mangrove species that occurs on shorelines that have a broad horizontal tidal range. Also known as black mangrove, stands typically develop under anoxic, water-logged conditions in substrates of silt or clay. Black mangrove can tolerate salinity values ranging from 0 to 90 parts per thousand. Salt is excreted from salt glands on both leaf epidermal surfaces, and aerosol salt spray and salt crystals are frequently observed on the upper leaf epidermis. *Avicennia germinans* is viviparous. The embryos have no dormancy requirements, and there is no seed bank. This mangrove species has the northernmost distributional range of any mangrove species in North America. It occurs in Louisiana and northern Florida. Color-infrared photography and airborne video imagery techniques have been used successfully to map stands of black mangrove on subtropical coastal shorelines. Reforestation efforts using seedlings and saplings have been successful in several areas of the tropics and subtropics. *Avicennia germinans* stands play an important role in ecosystem functions as a natural barrier to coastal erosion caused by tropical storms, as habitat for a wide range of organisms in intertidal food chains, and as a carbon repository.

ADDITIONAL INDEX WORDS: *Black mangrove, morphology, geographical distribution, habitats, communities, reproduction, physiological ecology, interaction with other species, geomorphological interactions, ecological restoration, economic importance.*

INTRODUCTION

The literature base for the broad topic of mangroves is immense. Rollet (1981) and Tomlinson (1986) listed more than 6000 articles and research reports published from 1600 to 1975. Tomlinson (1986) stated that, in his extensive review of the biology of mangroves, his biggest problem was what to exclude. A similar problem exists for the voluminous literature base for *Avicennia germinans* (black mangrove), particularly in the areas of physiological ecology and this species' expansion of its distributional range into higher latitudes in the temperate zone of the New World.

Mangroves rank second only to coral reefs in productivity in tropical marine ecosystems (Arreola-Lizárraga, Flores-Verdugo, and Ortega-Rubio, 2004). Globally mangroves are estimated to cover 2.4×10^5 km^2 of subtropical and tropical coastlines and had an economic value of U.S.$200,000 to U.S.$900,000 per hectare in 2006 (Alongi, 2008; Chen and Twilley, 1998). In the Caribbean alone, Lovelock *et al.* (2005) estimated mangrove-forested coastlines occupy 9800 km^2 of coastal vegetation zones. Murray *et al.* (2003) reported that mangroves occupy 78,511 ha of the Belize coastline and cover 3.4% of the land area of the country.

Mangrove ecosystems are one of the most threatened. An estimated 35% of mangroves have been lost globally from 1990 to 2010 (Fontalvo-Herazo *et al.*, 2011; Mumby *et al.*, 2004). Ellison and Farnsworth (1996) and Wang and Sousa (2009) stated that 1.4% to 1.7% of mangroves are lost annually in the Caribbean region. Ellison (1993) predicted that mangroves will experience further loss as sea levels rise due to climate change in this century. Farnsworth and Ellison (1997) have published an extensive review of conservation issues related to mangroves.

Avicennia is a pantropical and subtropical genus represented by eight species in East Africa, West Africa, the Indo-Pacific region, and the New World (Dodd, Rafii, and Bousquet-Mélou, 2000; Duke, 1992; Tomlinson, 1986). *Avicennia germinans* is one of the most important mangroves in the West African coastal zone and in the New World tropics and subtropics. This species has the most northern distribution of all mangrove species in Louisiana and Florida in the United States. (Pickens and Hester, 2010; Williams *et al.*, 2014). It is a facultative halophyte that tolerates salinities ranging from 0 ppt (parts per

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Table 1. *Synonyms of* Avicennia germinans. *(Adapted from Woodson, Schery, and Moldenke, 1973).*

Bontia germinans L.
Avicennia nitida Jacq.
Avicennia elliptica Holm *in* Thunb.
Avicennia tomentosa Jacq.
Avicennia floridana Raf.
Avicennia meyeri Miq.
Avicennia lamarckiana Presl
Avicennia oblongifolia Nutt. *ex* A.W. Chapm.
Avicennia officinalis α nitida (Jacq.) Kuntze
Avicennia officinalis β lanceolata Kuntze
Hilairanthus nitidus (Jacq.) van Tiegh.
Hilairanthus tomentosus (Jacq.) van Tiegh.

thousand) to 90 ppt (Alleman and Hester, 2011; Címtron *et al.*, 1978; Tomlinson, 1986).

Some ecosystem functions for *A. germinans* and other mangroves are coastal protection from storm tides, productivity, provision of habitat for fisheries and wildlife, and carbon sequestration (Mumby *et al.*, 2004; Pickens and Hester, 2010; Tomlinson, 1986). Herein, we review the biology of this important coastal-zone species.

TAXONOMY AND VARIATION

Avicennia germinans (L.) L. is a member of the family Acanthaceae, and is included in the subfamily Avicennioideae. This taxon has also been included in the family Verbenaceae and the monogeneric family Avicenniaceae. Synonyms or rejected names are listed in Table 1. Compére (1963) indicated that the parenthetical author citation, *A. germinans* (L.) Stearn, has been used incorrectly. Common names are numerous. They include black mangrove, honey mangrove, mangle negro, mangle blanco, salt bush, and mangle eguanero. The taxonomic description of *A. germinans* has been assembled from Correll and Correll (1972) and Tomlinson (1986).

Seed Morphology

The single seed has a thin, membranous seed coat (testa). The seed consists of a mature embryo with two fleshy cotyledons. Endosperm is absent. The primary root (radicle) is exserted, blunt, and has a terminal tuft of fine hairs.

Seedling Morphology

Seedling development is viviparous. The embryo emerges from the thin seed testa (seed coat) before fruit abscission from the parent plant. The fruit wall (pericarp) is shed after the seedling is released into seawater. The hypocotyl (embryonic stem below the cotyledons) extends from the cotyledons. This allows the radicle to anchor the seedling as the cotyledons extend vertically (Pickens and Hester, 2010). The seedling dispersal unit is referred to as a propagule by nearly all investigators (McKee, 1995a). Seedling development is epigeal. When the first true leaves develop, the seedling initiates formation of woody tissue (Pickens and Hester, 2010).

Root Morphology and Development

Avicennia germinans seedlings have the capacity to develop elongated roots and live for extended periods when floating in seawater. The root system consists of anchoring roots, horizontal (cable) roots, and aerial roots (pneumatophores). Anchoring roots, formed at the base of the trunk, usually alternate with pneumatophores and have a dense fibrous root system that increases absorption capacity. Anchoring roots usually do not exceed a depth of 1.0 m (Muller, Lambs, and Fromard, 2009; Schwendenmann, Riecke, and Lara, 2006). Pneumatophores are usually less than 30 cm tall, have a smooth surface, and contain chlorophyll (Figure 1a). The inner tissues are spongy and contain little secondary thickening. Pneumatophores serve in gas exchange with submerged roots (Tomlinson, 1986). Epiphytic green algae (Chlorophyta), red algae (Rhodophyta), and blue-green algae (Cyanobacteria) colonize pneumatophores (Dawes, Siar, and Marlett, 1999).

Shoot Morphology

The growth habit ranges from shrubs less than 1.0 m tall in higher latitudes and on arid coastlines to trees up to 30 m tall in northern South America (Dahouh-Guebas and Koedam, 2001; Pickens and Hester, 2010; Rosen and Zamirpour, 2014; Williams *et al.*, 2014) (Figure 1b). Black mangroves at higher latitudes are usually highly branched. Branches and twigs are round in cross section (terete). Bark is black, jointed, fissured, and has scattered nodes. Lenticels are usually abundant (Salas-Leiva, Mayor-Durán, and Toro-Perea, 2009).

Leaves

Leaves are simple, opposite, thick, and persistent. Petioles are 2.0 to 2.7 cm long and are often covered with a mealy, powdery substance. Stipules are absent. Blades are ovate, lanceolate, and elliptic or obovate, and they are 5.0 to 15 cm long and 2.0 to 4.5 cm wide. The lower epidermis is usually grayish with a mealy-pubescent surface. The upper epidermis is glabrous and is often covered with aerosol salt spray or salt crystals.

Inflorescence and Flowers

The inflorescence is up to 6.5 cm long and 1.5 cm wide and consists of axillary or terminal spicate clusters. Flowers are sessile and bisexual and have a superior ovary (Figure 1c). The calyx consists of 5 sepals slightly united at their bases. Sepals are ovate, overlapping, and subtended by small bracts. Sepals are 3 to 5 mm long and 2 to 3 mm wide. Sepals are densely pubescent on the outer surfaces and glabrous within. The corolla is white and ranges from 1.3 to 1.9 cm long and 1.0 to 1.3 cm wide. The corolla is irregular, and the petals are partially united and are parted above the middle. The corolla tube equals or is shorter than the calyx. The corolla lobes are spreading and are gray-pubescent outside and velvety-pubescent in the throat. Four stamens are attached in the corolla tube and are alternate with the corolla lobes. Filaments are about 0.5 mm long, are nearly equal in length, and are flattened near the bases. Stigmas are two-cleft with one lobe larger. The ovary is pubescent, and the placentation is axile.

Fruit

The fruit is an ovoid, elliptic, or obpyriform, leathery, one-seeded pubescent capsule that is beaked distally. The capsule is 2 to 3 cm long and about 1.2 cm wide (Figure 1d).

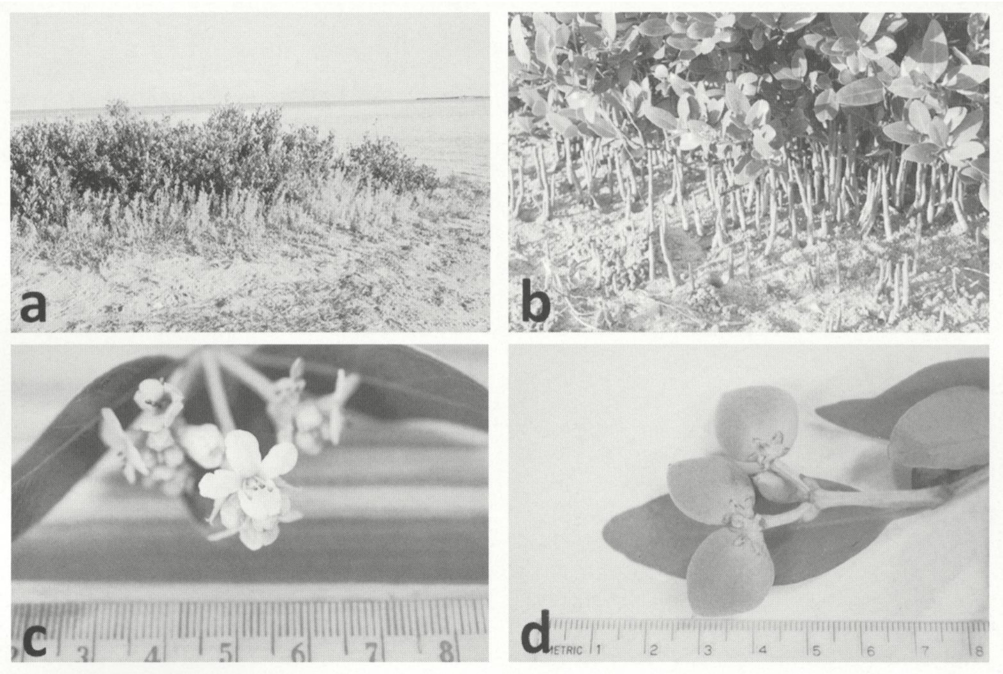

Figure 1. *Avicennia germinans* on the margin of the wind-tidal flats of South Padre Island, Texas: (a) shrubs associated with *Batis maritima*, (b) pneumatophores, (c) flower and inflorescence, and (d) mature fruit.

Variability

Little morphological variation in *A. germinans* populations has been noted over its pantropical and subtropical distributional range in the Old and New World (Compére, 1963; Dodd, Rafii, and Bousquet-Mélou, 2000). Nettel and Dodd (2007) reported that New World Pacific populations (Baja California to northern Peru) have greater genetic variability than West African and New World Atlantic and Caribbean populations. However, Moldenke (1960) recognized three varieties in the American tropics, including var. *guayaciliensis*, var. *cumanensis*, and var. *venezuelinesis*. He also recognized *A. africana* as a distinct species from *A. germinans* in West Africa. Moldenke (1960) based his designation on herbarium specimens. He stated that the leaves of the West African taxon are elongated and narrower than *A. germinans* specimens. However, most taxonomists have included *A. africana* with *A. germinans* (Compére, 1963).

McMillan (1986) noted a difference in isozyme patterns in black mangrove populations between the eastern and western regions of the Gulf of Mexico. Populations on the western Gulf of Mexico in Texas and Mexico showed patterns of phosphoglucose mutase and phosphoglucose isomerase that differed from those of populations found on the eastern side of Florida, Jamaica, and St. Croix. Populations in Belize and Panama had a mixture of isozyme patterns.

Two caffeic ester derivative iridoid compounds, 2′-cinnamoyl mussaenosidic acid and 2′-cinnamoyl mussaenosidic acid, have been identified as useful taxonomic markers to identify infraspecific *Avicennia* taxa. Bousquet-Mélou and Fauvel (1998) and Fauvel *et al.* (1995) suggested either a specific or subspecies designation for the West African taxon (*A. africana*, *cf.* Moldenke, 1960).

Dodd *et al.* (1998) examined aliphatic hydrocarbon and triterpenoid fractions of foliar waxes from *A. germinans* populations in French Guiana and Gabon. They found greater lipid-composition diversity and longer carbon chains in African populations than in New World populations. None of the authors listed above, with the exception of Moldenke (1960), published changes in nomenclature based on the results of their investigations.

Chromosome Number

Nettel, Rafii, and Dodd (2005) reported a chromosome number of $n = 15$ for populations of *A. germinans* from Bermuda and Baja California, Mexico.

GEOGRAPHIC DISTRIBUTION

Avicennia germinans, often referred to as *A. africana* in the Old World, occurs on tropical coastlines ranging from Mauritania to Angola (Dodd *et al.*, 2002; Nettel and Dodd, 2007). The northernmost distribution in North America is Bermuda (32°30′0.27″ N) (Johnston, 1983). Bermuda has warmer winter temperatures than Jacksonville and Daytona Beach, Florida. In the United States, *A. germinans* occurs from Florida on the Atlantic coast and from Florida to Louisiana and Texas on the Gulf of Mexico (Alleman and Hester, 2011; Everitt, Escobar, and Judd, 1991; Tomlinson, 1986). The northernmost distribution sites in the United States are Ponte Vedra Beach on the NE Atlantic coast in Florida (30°6′0.618″ N), at Ile de Chien (Dog Island) on the Gulf Coast of Florida (29°80′0.6″ N), and at Bay Champagne, Louisiana (29°6′0.35″ N) (Johnston, 1983;

Patterson, Mendelssohn, and Swenson, 1993; Williams *et al.*, 2014).

The range of black mangrove extends on the Mexican coastline from Tamaulipas to Quintana Roo (López-Portillo and Ezcurra, 1989; Sauer, 1967). It is widespread from Bermuda to the Caribbean, where it occurs on nearly all Caribbean islands (Ellison, 1993; Tomlinson, 1986). It is common in Central America and extends into northern Brazil (Tomlinson, 1986). Its distribution on the Pacific coast of the Americas ranges from Baja California, Mexico, to northern Peru (Clüsener and Breckle, 1987; Dodd *et al.*, 2002). Distribution in northern Peru is limited by topographic features, evapotranspiration, humidity, and the absence of a regular annual flow of rivers (Clüsener and Breckle, 1987).

RANGE OF HABITATS

Black mangrove occurs in the intertidal zone on tropical and subtropical shorelines. A broad horizontal intertidal range is an important topographic feature for the development of stands (Chapman, 1975). This habitat is influenced by periodic flooding and salinity (Muller, Lambs, and Fromard, 2009; Pezeshki, DeLaune, and Meeder, 1997). Mangroves outcompete salt marshes dominated by *Spartina alterniflora* in the absence of freezing conditions (Kangas and Lugo, 1990). At the latitudinal limits of the species in Louisiana, *A. germinans* has encroached on salt marshes dominated by *S. alterniflora* (Patterson, Mendelssohn, and Swenson, 1993). The ecotone in Louisiana salt marshes occurs on bay margins and is a transitional zone containing both species. The low marsh is dominated by *S. alterniflora* where *A. germinans* is absent. However, both species occur at higher elevations (Patterson, McKee, and Mendelssohn, 1997; Patterson, Mendelssohn, and Swenson, 1993).

Substrate Characteristics

Mangrove soils are virtually anoxic (Hogarth, 1999). *Avicennia germinans* stands develop on alluvium on deltaic coastlines and estuaries that are rich in organic matter and where the soil particles consist of fine silt and clay (Walsh, 1974). Granitic outcrops and quartz deposits are poor substrates (Walsh, 1974). However, in the Bahamas, dwarf *A. germinans* and *Rhizophora mangle* populations are found in the intertidal zone that has a sand substrate (Valentine-Rose and Layman, 2011). In Florida, McKee (1993) reported that zones supporting *A. germinans* as the dominant species have high sulfide concentrations and strongly reducing soils. Sulfide levels are much higher adjacent to pneumatophores (McKee, Mendelssohn, and Hester, 1988).

Black mangrove stands can occur in environments where salinity ranges from 0 ppt to 90 ppt (Twilley, Lugo, and Patterson-Zucca, 1986). In Nigeria, Chindah *et al.* (2011) reported that stands occur in salinities ranging from 0 ppt to 20 ppt. In Tabasco, Mexico, López-Portillo and Ezcurra (1985) and Thom (1967) reported that *A. germinans* occurs at salinities between 28 ppt to 65 ppt and 15.2 ppt to 35 ppt, respectively. Simpson, Feller, and Chapman (2013) found salinity ranging from 23 ppt to 43 ppt in Florida.

López-Portillo and Ezcurra (1985) reported that pH values range from 6 to 8 in the humid tropics of Tabsaco, Mexico. In Sierra Leone, Hesse (1961) noted a pH of 6.3 in nonfibrous mud under black mangrove stands. However, Amusan and Adeniyi (2005) found pH values as low as 3.3 to 4.8 on drying substrates in Nigeria.

Seedlings of *A. germinans* are sensitive to low soil-redox conditions. During inundation, oxygen cannot enter the root system through the pneumatophores. Thibodeau and Nickerson (1986) found that the surrounding substrate is reduced as much as the dense root system.

Some nitrogen fixation by *Desulfovibrio* sp. bacteria has been associated with black mangrove roots in Florida (Zuberer and Silver, 1975). Feller, Lovelock, and McKee (2007) examined the effects of adding supplemental nitrates and phosphates to nitrogen- and phosphorus-limited *A. germinans* stands in Florida and Belize, respectively. They found that supplemental nitrogen fertilizer added to nitrogen deficient sites stimulated an increase in growth of the stunted, shrub-like form by an elongation of the shoot system and reduction of lateral branching. In phosphorus-limited sites in Belize, supplemental phosphates increased leaf area, phosphorus uptake, and resorption of nitrogen (Feller, Lovelock, and McKee, 2007).

Climatic Requirements

Mangrove communities do not occur where seasonal temperatures exceed 50°C (Walsh, 1974). *Avicennia germinans* occurs at Daytona Beach and at Ponte Vedra Beach (near Jacksonville, Florida), where January temperatures typically fall below 0°C 4–6 nights per year, respectively. The mean January temperature at Ponte Vedra Beach is 12.6°C, and the mean January temperature at Daytona Beach is 14.4°C (Garwood, 1996). *Avicennia germinans* is a tropical species that has its northernmost distributional range in the United States. Its migration into more temperate sites is influenced by the severity and length of freezing conditions (Rosen and Zamirpour, 2014). At latitudes from 26° N to 30° N, *A. germinans* has greater chilling tolerance than other mangroves (Patterson, Mendelssohn, and Swenson, 1993). This species is a subshrub and is multistemmed at higher latitudes as a function of chilling temperatures (Osland *et al.*, 2014). At the latitudinal limits in coastal Louisiana, decreased survivorship occurs at –6.5°C or lower (Pickens and Hester, 2010). In northern Peru, *A. germinans* is found only in an area outside the cold waters of the Peruvian current (Clüsener and Breckle, 1987).

PLANT COMMUNITIES

Intertidal and adjacent tropical plant communities with black mangroves and associated plants form a discrete plant community referred to as a mangal (MacNae, 1968; Tomlinson, 1986). Species richness is low in the mangal. Undisturbed mature stands of *A. germinans* in New World tropics are noted for the absence of understory herbs, shrubs, and vines (Janzen, 1985; Snedaker and Lahmann, 1988). Snedaker and Lahmann (1988) advanced the hypothesis that the high metabolic expenditure for mangroves in tropical intertidal environments prevented the evolution of shade-tolerant terrestrial mangrove species.

Where black mangrove encroaches on the salt marsh in Louisiana, *S. alterniflora* is the dominant species (Perry and Mendelssohn, 2009). In southern Texas, understory species are often absent in the intertidal zone dominated by black

Table 2. *Representative species associated with* Avicennia germinans.

Species	MA	NG	GH	CO	FG	MX	FL	LA	TX
Achrostichum aureum		X		X	X	X			
Arthrocnemum macrostachyum	X								
Avicennia bicolor				X					
Batis maritima				X		X	X	X	X
Blutaparon vermiculare							X		
Borrichia frutescens							X		
Conocarpus erectus		X		X			X		
Cyperus articulatus			X						
Dalbergia brownei						X			
Distichlis spicata							X	X	
Euterpe oleracea					X				
Imperata cylindrica			X						
Laguncularia racemosa			X	X	X	X	X		
Mora oleifera				X					
Nypa fruticans		X							
Paspalum vaginatum		X	X						
Pellicieria rhizophora				X					
Pterocarpus officinalis					X				
Rhabdadenia biflora					X				
Rhizophora harrisonii	X								
Rhizophora mangle		X				X			X[a]
Rhizophora racemosa		X			X		X		
Salicornia perennis							X		
Salicornia depressa								X	
Sporobolus virginicus	X								
Salicornia senegalensis	X								
Sesuvium portulacastrum	X		X	X					
Sarcocornia ambigua									X
Spartina alterniflora							X	X	X
Spartina patens								X	
Suaeda sp.	X								
Tabebuia insignis					X				
Zygophyllum gaetulum subsp. *waterlottii*	X								

MA = Mauritania (Dahouh-Guebas and Koedam, 2001), NG = Nigeria (Chindah *et al.*, 2011), GH = Ghana (Gbogbo, 2007), CO = Colombia (Cerón-Souza, Toro-Perea, and Cárdenas-Henao, 2005; Elster *et al.*, 1999), FG = French Guiana (Fromard *et al.*, 1998); MX = Tabasco, Mexico (Thom, 1967), FL = Florida (Davis *et al.*, 2005; Simpson, Feller, and Chapman, 2013; Stalter *et al.*, 1999), LA = Louisiana (Guo *et al.*, 2013; Patterson, Mendelssohn, and Swenson, 1993), TX = Texas (Rosen and Zamirpour, 2014).

[a] F.W. Judd and R.I. Lonard, personal observations at the mouth of the Rio Grande.

mangrove. The succulent halophyte, *Batis maritima*, is often associated with *A. germinans* in slightly elevated conditions (F.W. Judd and R.I. Lonard, personal observations). Representative species associated with *A. germinans* are found in Table 2.

ANATOMY AND HISTOLOGY

Mature leaves are persistent, firm, and leathery in texture. Leaf venation patterns are not visible to the naked eye. The upper epidermis is glabrous and lacks stomata (Dschida, Platt-Aloia, and Thomson, 1992). The lower is usually grayish, scaly, and pubescent. The cuticle is thick and invested with waxes consisting of alkanes and triterpenoid compounds (Rafii, Dodd, and Fromard, 1996). Salt glands are present on both leaf surfaces and consist of two collecting cells, a stalk cell, and eight secretory cells (Balsamo and Thompson, 1993). Salt glands are scattered on the upper epidermis and dense and concentrated on the lower (Tomlinson, 1986). Aerosol salt spray and salt crystals are a conspicuous feature of the epidermis. Epidermal cell walls are straight, and sunken stomata are abundant on the lower epidermis. Turgor pressure in the guard cells allows the stomatal aperture to widen in the early morning hours, allowing greater photosynthetic activity contrasting with water loss (Naidoo and von Willert, 1995).

Anatomical features under the epidermis consist of a hypodermis, palisade tissue, and a mesophyll zone (Sobrado, 1999). Vascular bundles are surrounded by a single-layered sheath that is consistent with non–Kranz anatomy. A well-developed system of terminal tracheids are present at free xylem endings (Tomlinson, 1986).

Stems

Distinctive features characterize the anatomy of woody stems. The bark surface is thin and green when young and dark brown at maturity. Woody tissue is close grained and hard (Vines, 1960). Growth rings are anomalous. Each ring consists of xylem, phloem, and conjunctive tissue (Gill, 1971). Woody tissue is ring-porous, with vessels in the outermost growth layer (Gill, 1971; Kathiresan and Bingham, 2001). The vascular system contains included phloem with xylem tissue (Zamski, 1979). The alternating rings of xylem and phloem are separated by parenchyma cells. This anomalous arrangement has been considered in the past to be annual rings (Fromard *et al.*, 1998). Phloem cell walls are not crushed and may function in translocation for an extended period (Zamski, 1979). Growth rings are not correlated with age (Fromard *et al.*, 1998).

Roots

Root surfaces are smooth and the texture is spongy. Lenticels are present on pneumatophores (Chapman, 1947). Oxygen enters lenticels and moves by mass or bulk flow to submerged roots (Ball, 1988; McKee, Mendelssohn, and Hester, 1988; Scholander, van Dam, and Scholander, 1955). Cortical cells are lobed, and enlarged intercellular spaces (aerenchyma) characterize the middle cortex (Tomlinson, 1986).

PHYSIOLOGICAL ECOLOGY

Salinity affects primary productivity, root/shoot ratios, leaf area, leaf morphology, internode length, tree or shrub structure, and propagule size (Gonçalves-Alvim, Vaz dos Santos, and Fernandes, 2001). Plant height is inversely correlated with substrate salinity (Cintrón *et al.* 1978). Salinity and flooding influences numerous physiological processes, including enzymatic activity and stomatal activity, the latter which regulates photosynthesis and respiration (Pezeshki, DeLaune, and Meeder, 1997). *Avicennia germinans* is able to sustain growth ranging from freshwater to hypersaline conditions, but 95% mortality was noted at 55 ppt, and leaf area and growth were affected at salinities as low as 10 ppt (Suárez and Medina, 2005, 2006). Twilley, Lugo, and Patterson-Zucca (1986) reported that some plants survived at salinities as high as 90 ppt, but growth did not occur.

Osmotic adjustments are necessary to resist substrate salinity and to maintain constant turgor pressure in plant cells. Mizrachi, Pannier, and Pannier (1980) noted that *A. germinans* enhances internal chloride content. They found that high external salinity was accompanied by a decrease in root proteins and in a reduction in protein nitrogen levels. Salt is absorbed with water and transported to leaves, where it is secreted by salt glands in the blades (Muller, Lambs, and

Fromard, 2009). However, Hogarth (1999) and Sobrado and Greaves (2000) reported that most of the salt is excluded by roots, and only a small fraction reaches the leaves. Salinity tolerance is associated with high water-use efficiency and the development of greater root biomass.

Suárez and Medina (2005) reported that leaf half-life decreased from 425 days under freshwater conditions to only 75 days at 940 mm^{-3} NaCl. They noted that increasing salinity caused an increase in mortality and a decreased production of new leaves. Leaf growth of seedlings was affected more than root and stem growth (Taffouo *et al.*, 2007). Seedlings responded to salinity by increasing succulence and by decreasing cell elasticity (Suárez and Sobrado, 2000). Increased leaf succulence allowed leaves to store large amounts of solutes without increasing osmotic pressure (Suárez and Sobrado, 2000; Taffouo *et al.*, 2007). Oblong leaves were formed at low salinities, and round leaves developed under hypersaline conditions (Suárez and Medina, 2005). Rates of salt secretion in leaves increased during drought conditions. This results in greater salt concentration in the soil solution and lower soil water potential (Sobrado, 2002). Water transport at high salinity is balanced by stomatal guard cell regulation of water loss.

Avicennia germinans lowers xylem water below seawater concentrations. This factor allows water uptake by roots (Suárez, Sobrado, and Medina, 1998). Salt, transported by the xylem, enters leaves and is sequestered in salt glands in the hypodermal zone (Balsamo and Thompson, 1993; Dschida, Platt-Aloia, and Thomson, 1992). Salt is then expelled from vacuoles by the salt glands (Balsamo and Thompson, 1993; Sobrado, 1999). Salt secretion is coupled to changes in vacuole membrane ultrastructure and is apparently facilitated by an active-transport process controlled by hydrogen ions and ATPase enzymatic processes (Balsamo and Thompson, 1993). Dschida, Platt-Aloia, and Thomson (1992) noted that salt secretion was temperature dependent. They suggested that secretion was activated by mitochondria in salt gland cells.

Black mangrove is a C_3 halophyte in carbon fixation, with its light-independent reactions of photosynthesis (Kathiresan and Bingham, 2001). Decreasing photosynthetic activity is correlated with increasing salinity (Gonzalez-Mendoza *et al.*, 2011; Sobrado, 1999; Suárez and Medina, 2006). This may be related to stomatal closure and internal ion concentrations (Suárez and Medina, 2006). Sobrado (1999) reported that guard cell responses could be influenced by osmotic adjustment under hypersaline conditions or drought. Chloroplast thylakoids are apparently not affected by salinity (Ball, Taylor, and Terry, 1984). Gonzalez-Mendoza, Ceja-Moreno, *et al.* (2009) and Gonzalez-Mendoza, Espadas, *et al.* (2011) found that the primary targets of hypersalinity are reaction centers that inhibit electron transport at the acceptor side of photosystem II. Sobrado (2001) noted that *A. germinans* had significantly higher photosynthetic rates than other mangroves, including *R. mangle* and *Laguncularia racemosa*.

Mangrove communities may be either nitrogen or phosphorus limited (Lovelock *et al.*, 2006). Feller *et al.* (2003) reported that growth rates increased significantly with addition of nitrogen fertilizer. However, Lovelock *et al.* (2006) found that fertilization with nitrogen at nitrogen-limited sites had little effect on photosynthesis or hydraulic features. They found that phosphorus-limited populations were water deficient. *Spartina alterniflora–A. germinans* communities in Louisiana had significantly greater amounts of phosphates in the *A. germinans* habitats than in *S. alterniflora* segments of the community (Henry and Twilley, 2013).

Cold Tolerance

Mangroves are sensitive to extreme winter temperatures. However, *A. germinans* is the most cold-tolerant mangrove species (Saintilan *et al.*, 2014). The transition from mangals to salt marshes in higher latitudes is attributed to cold tolerance (Kangas and Lugo, 1990). McMillan and Sherrod (1986) found that seedlings were injured at 2°C to 3°C. They noted that Texas seedlings have more tolerance to low temperatures than seedlings from Florida and Belize (McMillan and Sherrod, 1986; Markely, McMillan, and Thompson, 1982). Cell membrane lipid composition, namely phosphatidylglycerol fractions, have been proposed as playing a role in chill resistance. However, Norman, McMillan, and Thompson (1984) found that chill-sensitive *A. germinans* populations in Belize had greater amounts of dipalmitoyl and 1-palmmitoyl-2-(trans-3-hexadecenoyl) phosphatidylglycerol fractions in leaves than in counterpart chill-resistant populations in Texas. Markely, McMillan, and Thompson (1982) found that Texas propagules had a lower percentage of oleic acid and a higher percentage of linoleic acid than propagules from Belize. They indicated that these differences in fatty acid compounds may contribute to cell membrane fluidity and, therefore, enhance chill resistance of northern populations of black mangrove.

At approximately 0300 on 24 December 1983, a cold front began moving through the Lower Rio Grande Valley of southernmost Texas, dropping air temperatures to –8.8°C at Edinburg, Texas, about 80 miles west of the Gulf of Mexico coast. Freezing or below-freezing temperatures were reported for 53 to 55 consecutive hours. During that time, temperatures of –6.7°C were recorded for 6 hours (Lonard and Judd, 1985). Lonard and Judd (1985) evaluated freeze damage to 75 woody species. Eight native woody species, including *A. germinans*, were damaged extensively. Most black mangrove were killed to ground level but resumed growth the following spring from the base of the plant or from subterranean perennating structures. Thus, freezing temperatures may "set back" black mangrove periodically and may be responsible for the short stature of the species on the Texas coast, but they do not appear to eliminate entire populations.

During 22–24 December 1989, two freezes occurred in the Lower Rio Grande Valley of Texas (Lonard and Judd, 1991). At Brownsville, Texas, at the southern tip of the state, the first episode had 33.75 consecutive hours at or below freezing, and the second had 16.75 consecutive hours at or below freezing. A temperature at or below –8.4°C occurred for 11.75 consecutive hours. This was the second-lowest temperature ever recorded at Brownsville (the lowest was –8.9°C). Black mangrove was again killed to ground level, but by March and April 1990 plants were recovering from subterranean structures.

Stuart *et al.* (2007) stated the hypotheses that the absence of mangroves at higher latitudes is due to freeze-induced xylem failure. Pickens and Hester (2010) reported that the duration and exposure of *A. germinans* decreased survivorship at –6.5°C. Lonard and Judd (1985, 1991) reported that catastrophic freezes in 1983 and 1989 killed black mangroves to the trunk bases. Recovery since 1989 has primarily been from freeze-damaged stem bases. Freeze-damaged shrubs resprouted by early spring 1990 (Lonard and Judd, 1991).

Comeaux, Allison, and Bianchi (2012) stated that mangroves are generally intolerant of freezing conditions as a result of xylem embolism and loss of hydraulic conductivity. Madrid, Armitage, and López-Portillo (2014) indicated that xylem vessel architecture affects chilling and salinity tolerance. Populations in cooler areas of Louisiana and Texas have narrow vessels, which may reduce the risk of freeze-induced embolisms but also decrease water conductance capacity.

Pollution

Mangroves in intertidal zones adjacent to urban centers are subject to a wide variety of heavy metals and petrochemical pollutants. Persistent petroleum pollutants cause defoliation, death of populations, and loss of animal populations (Ellison and Farnsworth, 1996). Chindah *et al.* (2011) reported that acute crude oil concentration treatments are more harmful than chronic oil spills over a longer duration. Petrochemicals disrupt salt extraction from root systems by disrupting the ability of roots to exclude ions. Crude oil may immobilize mineral-nitrogen activities by bacteria during degradation of crude oil. Crude oil alters substrate properties and reduces sediment porosity and gas exchange (Chindah *et al.*, 2011).

Avicennia germinans accumulates greater quantities of heavy metals compared with other species of mangroves. Black mangrove communities located close to urban development are also impacted by cadmium, nickel, and other heavy metals from industrial complexes. Roots have greater accumulation of cadmium compared with leaves (Gonzalez-Mendoza *et al.*, 2009).

Phenology

Flowering and fruiting phenophases in black mangrove are expected at any time of the year in tropical and subtropical zones. In northern Brazil, flowering occurs from August to January when temperatures are high, and fruiting takes place from October to April during the wet season (Fernandes, 1999). In Colombia, Sánchez-Núñez and Mancera-Pineda (2011) reported that when the water column height is below the surface level, flowering is initiated by water deficit conditions. They noted that pore salinity regulates flowering intensity and periodicity.

In Mauritania, on the northern distributional range in West Africa, flowering lasts only 5 days, and propagules are found on shrubs less than 1.0 m tall (Dahouh-Guebas and Koedam, 2001). These authors did not report flowering and fruiting on a seasonal basis.

In the United States, flowering and fruiting occur from July to September in Texas (Correll and Correll, 1972). Landry (2013) noted that flowering in Florida occurs from May to July, but he did not report months of fruiting.

Limited data are available on the age at which *A. germinans* reaches reproductive maturity. However, Stuart *et al.* (2007) indicated that it may take 3 to 5 years to initiate flowering. Marchand, Lallier-Vergés, and Baltzer (2003) and Marchand *et al.* (2006) stated that trees mature and become senescent between 30 to 50 years in French Guiana.

POPULATION BIOLOGY

Population dynamics in coastal habitats is controlled by biophysical factors and naturally occurring and anthropocentric disturbances. *Avicennia germinans* is a pioneer species that colonizes the upper intertidal fringe. In Cameroon, Din *et al.* (2002) stated that intraspecific competition is high, and the number of seedlings that reach maturity is less than 1.0%. Seedlings cluster around the parent plant at distances between 2 to 7 m. Only seedlings located outside the parent tree canopy develop. Therefore, the parent plant impacts development of its own progeny (Din *et al.*, 2002).

In the Amazon watershed, black mangrove colonizes unstable mud banks that may migrate as much as 1.0 km/y. These populations seldom survive more than 20 years, and understory vegetation is usually absent (Muller, Lambs, and Fromard, 2009).

PRODUCTIVITY

Aboveground biomass is an important parameter indicating productivity in a plant community (Osland *et al.*, 2014). Estimates of biomass are indicative of nutrient turnover and the potential to store carbon in the mangal ecosystem (Cuc and de Ruyter van Steveninck, 2015). Net primary productivity is used to elucidate the growth potential of mangroves. Productivity of *A. germinans* is a function of nutrients, light, salinity, sulfides, and frequency and duration of flooding (Twilley and Rivera-Monroy, 2005). Tree and shrub biomass is governed by latitude, with productivity greater near the equator (Comeaux, Allison, and Bianchi, 2012; Cuc and de Ruyter van Steveninck, 2015). Root biomass accounts for about 50% of the total biomass (Comeaux, Allison, and Bianchi, 2012).

Africa

In Guinea, Kovacs *et al.* (2010) estimated that *A. germinans* produced 2887 stems ha^{-1}. The mean height of trees was 3.0 m, and the mean diameter at breast height was 4.6 cm.

South America

Litter dynamics are important for the export of detritus as well as for nutrient cycling in the mangal. Litter degradation is much more rapid in the lower intertidal zone than in upper intertidal sites (Middleton and McKee, 2001). Chale (1996) reported litter production in a 12-month period in Guyana. Litter production included leaves (61.4%), propagules (24.8%), flowers (8.8%), and wood (4.9%). Chale (1996) stated that litter production is influenced by inflowing rivers rather than rainfall. He estimated litter production between 730 g m^{-2} y^{-1} and 910 g m^{-2} y^{-1}. At other sites in Guyana, he estimated litter production at 1771 g m^{-2} y^{-1}, which is greater than litter production for most tropical rainforests (Chale, 1996).

In northern Brazil, Mendoza *et al.* (2012) estimated stem density at 2875 stems ha^{-1}. Exportation of litter increases during spring tides (Schories *et al.*, 2003). Schories *et al.* (2003) indicated that tidal export accounts for less than 39% of annual litter fall. The remainder is consumed by crabs.

Mexico

In the Yucatán Peninsula, in Campeche, Mexico, Day *et al.* (1987) reported productivity for *A. germinans*, *L. racemosa*, *and R. mangle* in riverine and tidal fringing sites. They estimated total aboveground productivity for the combined species at 2458 g m^{-2} y^{-1} at the riverine site and 1607 g m^{-2} y^{-1} at the fringing tidal site. In the Campeche Basin, Utrera-López and Moreno-Casasola (2008) estimated litter production as follows: leaves, 5.09 t ha^{-1} y^{-1}; flowers and propagules, 0.49 t ha^{-1} y^{-1}; and woody material 0.56 t ha^{-1} y^{-1}, for a total litter production of 6.14 t ha^{-1} y^{-1}. Day *et al.* (1996) estimated total litter fall of 793 g m^{-2} y^{-1} in this region of SE Mexico.

In Tabasco, Mexico, López-Portillo and Ezcurra (1985) found that bark litter was shed 45 days after propagule dehiscence. Leaf fall occurred during periods of water stress. Propagules were shed during high-water conditions and lower salinity readings (López-Portillo and Ezcurra, 1985). Leaf production is common during summer (Utrera-López and Moreno-Casasola, 2008). López-Portillo and Ezcurra (1985) reported leaf litter production of 6.16 t ha^{-1} y^{-1}.

In more xeric regions of Mexico, such as Baja California and Sonora, annual leaf litter production is lower than expected. Félix-Pico *et al.* (2006) estimated an annual leaf litter production of 444 g m^{-2} y^{-1}, with maximum productivity in September and October at the end of the rainy season. Litter fall in Sonora was much lower than in Baja California. Arreola-Lizzáraga, Flores-Verdugo, and Ortega-Rubio (2004) estimated litter fall of 175 g m^{-2} y^{-1}. They noted that leaves accounted for 84% of the total litter, flowers and propagules 5%, and woody debris 11%.

U.S.A.—Florida and Puerto Rico

Productivity data are limited for *A. germinans* in the United States. In Florida, Henry and Twilley (2013) estimated net primary productivity for shrub forms of black mangrove ranging from 20 to 1630 g m^{-2} y^{-1}. Ross *et al.* (2001) estimated aboveground productivity in southern Florida. However, they pooled data for *A. germinans*, *L. racemosa*, and *R. mangle*.

Pool, Lugo, and Snedaker (1975) estimated pooled litter production for three sites in Florida and three sites in Puerto Rico for the mangrove species listed above. They estimated litter production for the two regions of 7967 g m^{-2} y^{-1}.

REPRODUCTION

Mangroves, including *A. germinans*, are adapted to generalized pollinators (Dodd, Rafii, and Bousquet-Mélou, 2000; Tomlinson, 1986). Tomlinson (1986) reported that black mangrove is usually pollinated by bees. Sánchez-Núñez and Mancera-Pineda (2011) reported unspecialized pollinators in the SW Caribbean, including bees (*Apis mellifera*, *Xylocopa* sp., and *Centris decolorata*), hoverflies (*Copestylum* sp.), and wasps (*Stictia signata*). Landry (2013) reported that bees (*A. mellifera*) were the most common pollinators in Florida. He also found that wasps (*Sphex jamaicensis*), flies (*Palpada albifrons*), and butterflies (*Junonia evarete*) were occasional pollinators.

Pollen

Tomlinson (1986) provided a generalized description of *A. germinans* pollen. Black mangrove pollen is produced as monads. Grains are tricolpate, are irregularly shaped, and have a reticulated surface. A small lumen is noted with deeply intruding colpi (Tomlinson, 1986). A more technical description has been reported by Magalhães e Silva and Ribeiro dos Santos (2009).

Propagules and Viability

Din *et al.* (2002) estimated that large black mangrove trees may produce up to 10,000 propagules per tree in the SW Caribbean. Sánchez-Núñez and Mancera-Pineda (2011) reported that propagules developed in 29% of black mangroves that were visited by pollinators.

Propagule Size and Seed Bank

McKee (1995b) reported that embryos do not have dormancy requirements and that there is no seed bank. Propagules remain viable for up to 2.5 years (Salas-Leiva, Mayor-Durán, and Toro-Perea, 2009). In Belize, propagules are leathery, ovoid, and beaked (McKee, 1995b). Propagules weigh only 1.05 ± 0.1 g per fresh biomass (McKee, 1995b). Rabinowitz (1978) found that propagules in Panama populations are 1.83 ± 0.05 cm in length and have a similar weight of 1.10 ± 0.11 g per fresh biomass. F.W. Judd (personal observations) noted that propagules on shrubs on South Padre Island and the lower Laguna Madre, Texas, varied in length between 2.9 and 3.2 cm and in width between 2.03 and 2.40 cm. He found that intact propagules with mature pericarps ranged in weight from 3.08 to 4.62 g.

Dispersal

The early life history of *A. germinans* consists of dispersal, stranding, and establishment of seedlings (Pickens and Hester, 2010). The actions of tides and currents play an important role as primary dispersal factors (Delgado *et al.*, 2001).

Gunn and Dennis (1999) estimated that less than 1.0% of tropical seeds and fruits drift in seawater for at least 1 month. The specific gravity of *A. germinans* is less than seawater. Buoyancy is attributed to the thinness of the propagule. Gunn and Dennis (1999) stated that propagules are buoyant for 1 year, but they did not suggest that propagules are viable. They reported that 5% of dredged samples from the ocean floor contain *A. germinans* propagules (Gunn and Dennis, 1999).

In Panama, McKee (1995b) noted that 92.3% of propagules were buoyant. Rabinowitz (1978) found that propagules were buoyant for 82 days. Propagules survived up to 110 days in saltwater and even longer in freshwater (Rabinowitz, 1978).

Duke *et al.* (1998) questioned long-distance dispersal of *A. germinans*. They found that fixed gene differences support specific status of *A. germinans* from Atlantic to east Pacific populations. They questioned the assumption of long-distance dispersal because gene flow among populations was low where populations were geographically continuous (Duke *et al.*, 1998).

Germination Ecology and Establishment of Seedlings

Avicennia germinans is viviparous. The embryo emerges from the seed coat but not the capsule before abscission (McKee, 1995a,b). The pericarp is shed after falling into seawater, and small roots are visible (Rabinowitz, 1978). Therefore, the propagule is technically a seedling (McKee, 1995a,b).

Seedling establishment includes interactions between nutrients, inundation, and salinity. McMillan (1971) indicated that salinity is not the primary factor in limiting seedling establishment. He found that seedlings rooted in distilled water and at a salinity two times greater than seawater. Turbulence inhibited seedling establishment, and seedlings did not develop in water depths greater than 5.0 cm (McMillan, 1974).

Many seedlings cluster around the parent plant at distances between 2 and 7 m, but only seedlings located outside the canopy reach maturity (Din *et al.*, 2002. Seedling establishment occurs in regularly flooded sites (Delgado *et al.*, 2001). In Costa Rica, Delgado *et al.* (2001) found that the half-life for seedlings was 17 days. Growth of seedlings was 4.8 mm d^{-1} under flooding conditions and only 1.1 mm d^{-1} at higher elevations (Delgado *et al.*, 2001). Propagules carried to dry sites and subjected to direct sunlight had mortality rates of 100% after 3 days of exposure (Elster, 2000).

Litter in the substrate can be an important factor in seedling establishment. Chapman and Feller (2011) found that seedlings grew rapidly in *R. mangle* and *A. germinans* litter in Florida.

Vegetative Reproduction

Avicennia germinans has a limited capacity for vegetative reproduction (McKee, 1995c; Tomlinson, 1986). Tomlinson (1986) stated that mangroves do not produce detachable vegetative structures that lead to vegetative reproduction. Limited vegetative reproduction may occur when lateral branches spread along the substrate. Adventitious roots may develop at the nodes. Baldwin *et al.* (2001) indicated that black mangroves survived a major hurricane in Florida by resprouting from stem bases that had been destroyed by hurricane-force winds and inundation.

GEOMORPHOLOGICAL INTERACTIONS

Mangroves are often the only species present in the intertidal zone of tropical shorelines that have fine-textured alluvium or where the substrate is soft mud or fine-textured silt clay (Walsh, 1974). These shorelines are free of strong waves or tidal action. Mangroves provide barriers to prevent shoreline erosion and for protection of inland areas during tropical storms and tidal waves (Everitt *et al.*, 2010; Vovides *et al.*, 2011). Roots, stems, and canopies attenuate waves and currents and contribute to greater sedimentation potential (Phan, van Thiel de Vries, and Stive, 2015).

In Tabasco, Mexico, Thom (1967) investigated sedimentation shifts on mudflats accompanied by discharge shifts from estuaries. These actions encouraged the spread of mangroves.

In coastal wetlands in Louisiana, where salt marshes are being invaded by *A. germinans*, *A. germinans* stands raise the surface topography (Bianchi *et al.*, 2013). The shift in topography may enhance protection from storms and may also increase the overall storage and sequestration of carbon (Bianchi *et al.*, 2013).

Deposition of silts and clays affect plants more adversely than deposition of larger-grained sands. Ellison (1993) noted that *A. germinans* is adapted to sediment deposition of 10 mm y^{-1}. Mature plants are killed when deposition exceeds the height of the pneumatophores (Ellison, 1993). Delgado *et al.* (2001) stated that 1.0% of buried propagules that were eventually exposed to the soil surface established seedlings. Alleman and Hester (2011) found that completely buried seedlings suffered 100% mortality. Partially covered seedlings survived 8 weeks (Alleman and Hester, 2011).

INTERACTION WITH OTHER SPECIES

Symbiotic relationships are common with *A. germinans* and other species. Epiphytic marine algae including diatoms and cyanobacteria are commensalistic on stems and pneumatophores. Maples (1983) found 109 species representing 27 genera of epiphytic diatoms associated with pneumatophores. The most abundant species were *Nitzschia brittonii*, *N. frustulum*, *Navicula diserta*, and *Amphora tenuissima*. Dawes, Siar, and Marlett (1999) found two species of green algae, *Boodleopsis pusilla*, and the filamentous *Cladophora coelothrix* on pneumatophores. Three species of red algae are common colonizers and include *Bostrychia binderi*, *B. moritzana*, and *B. radicans* (Dawes, Siar, and Marlett, 1999). Bashan *et al.* (1998) and Toledo, Bashan, and Soeldner (1995) found marine cyanobacteria including *Microcoleus chthonplastes*, *Anabaena* sp., *Lyngbya* sp., *Oscillatoria* sp., and *Aphanothece* sp. colonizing submerged roots and pneumatophores in Baja California, Mexico.

Competition

Competition in plant communities is more important in communities that have favorable conditions than it is in communities exposed to severe physical conditions (Bertness and Shumway, 1993). *Avicennia germinans* is a pioneer species. Populations are formed without succession and usually with no competing understory vegetation (Patterson and Mendelssohn, 1991). However, in Tabasco, Mexico, López-Portillo and Excurra (1989) found that as the *A. germinans* life-form changes from trees to shrubs, the presence of the understory *B. maritima* increases. Intraspecific competition is high, and the number of seedlings that reach maturity is less than 1.0% (Din *et al.*, 2002). Topographic and physical features may limit establishment of seedlings. High levels of sulfides and lower topographic features affect seedling establishment (Patterson and Mendelssohn, 1991).

Facilitation

Positive or facilitation interactions among species are more often a feature of unfavorable physical parameters. Neighboring individuals or adjacent species may serve as buffers from physical stress factors (Bertness and Shumway, 1993). Milbrandt and Tinsley (2006) found a greater number of black mangrove seedlings on sites occupied by the trailing succulent subshrub *B. maritima*, which alters abiotic conditions and allows *A. germinans* into previously intolerable habitats. *Batis maritima* stands promote a slight increase in elevation. Walsh (1974) reported that fibrous roots trap sediment and increase the rate of alluvium and litter deposition. These actions facilitate colonization of black mangrove.

Herbivores and Fungi

Avicennia germinans is often subjected to a wide variety of invertebrate herbivores. Fungi serve not only as agents of decomposition of litter but also as plant pathogens in the mangrove ecosystem (Elster *et al.*, 1999).

Crustaceans, mollusks, insects, and other larval forms feed on propagules and seedlings. In Colombia, Elster *et al.* (1999) reported that *Junonia evarete* (Lepidoptera) caterpillars defoliate black mangrove seedlings. The caterpillars and adult butterflies are abundant during the rainy season, which coincides with fruit production. *Junonia evarete* feeds exclusively on black mangroves due to the high nutritional values of the propagules. Vegetative features of mature trees escape herbivory (Elster *et al.*, 1999).

In Brazil, Gonçalves-Alvim, Vaz dos Santos, and Fernandes (2001) reported high densities of *Cecidomyia avicenniae* (Diptera: Cecidomyiidae, leaf-galling insect) larvae on stressed black mangroves growing under hypersaline conditions. They found that stressed plants were apparently attacked due to high levels of amino acids and for lack of inhibitory secondary metabolic products, including tannins, resins, and other compounds. In NE Brazil, Krause *et al.* (2001) reported that moth larvae (*Hyblae puera* complex) caused repeated severe leaf defoliation. Sousa and Mitchell (1999) and Sousa, Kennedy, and Mitchell (2003) stated that leaves lack phenolic compounds that deter insects. However, leaves contain alkaloid-related iridoid glycosides that serve as a defense against generalist herbivores (Sousa, Kennedy, and Mitchell, 2003).

In Belize, Farnsworth and Ellison (1991) noted damage by mangrove tree crabs (*Aratus pisonii*) and mangrove periwinkles (*Littorina angulifera*). Farnsworth and Ellison (1993) reported that 8% to 36% of black mangrove leaves were damaged by Lepidopteran and Coleopteran larvae, leaf miners (Homoptera: *Marmara* sp.), bag worms (*Oiketicus* sp.), and scale insects. Feller and McKee (1999) reported that mature trees were heavily damaged by *Elaphidion mimeticum* (wood-boring corymbycid beetles). McKee (1995a) also reported that snails cause extensive damage to seedlings in Belize.

Propagules are subject to extensive damage by crabs in Panama (Sousa and Mitchell, 1999). Propagules are consumed at higher rates in low intertidal sites where mature trees occur. Black mangrove propagules have higher nutritive value than other mangrove species in this zone. Major mangrove crab herbivores in Belize are *Goniopsis cruentata*, *Ucides cordatus*, and *Aratus pisonii* (Erickson, Bell, and Dawes, 2012; Erickson *et al.*, 2003; McKee, 1995a). The small size of black mangrove propagules facilitates burial in crab burrows (McKee, 1995a).

Mangroves have several defense mechanisms against fungal pathogens. Gilbert, Mejía-Chang, and Rojas (2002) stated that salt excretion in leaves may serve as an important defense mechanism. *Avicennia germinans* is less susceptible to fungal pathogens than *L. racemosa* and *R. mangle*. High salt concentrations on blades inhibit germination of spores and endophytic colonization (Gilbert, Mejía-Chang, and Rojas, 2002).

Propagules and young seedlings are most susceptible to fungal pathogens. Pickens and Hester (2010) tentatively identified *Collectotrichum* sp. (Ascomycota) on cotyledons in stranded propagules in Louisiana.

Decomposition of leaf litter and wood are facilitated by bacteria and fungi. Newell and Fell (1996) stated that marine (*Halophytophthora* sp. and *Pythium* sp. [Oomycota]) are probable decomposers of leaf litter. Schmit and Shearer (2004) reported a list of at least 32 species of fungi that are involved in decay of black mangrove woody detritus in the intertidal zone.

RESPONSE TO WATER LEVELS

In the Amazon floodplain of northern Brazil, black mangrove is a dominant species in the upper intertidal zone, where inundation occurs only 41 to 67 days per year (Mendoza *et al.*, 2012). Propagules cannot establish in flooded soils. Seedlings are sensitive to changes in water level, wind, waves, dry soil, and temperatures exceeding 45°C (Elster, Perdomo, and Schnetter, 1999). Ellison and Farnsworth (1993) found that seedlings did not survive in the highest or in the lowest water levels. Elster (2000) noted that optimal development of seedlings occurred at sites where water levels were near the surface and salinity was low. McKee (1993) stated that flooding under strongly reducing soils and highly toxic sulfide levels resulted in a decrease in seedling biomass. McMillan (1971, 1974) and West (1956) indicated that water turbulence inhibited root and seedling development, and that seedlings did not become established until the water depth was reduced to 5 cm or less. McKee and Mendelssohn (1987) suggested that metabolic adaptations to low oxygen levels during inundation may allow *A. germinans* to tolerate flooded conditions.

Krauss, McKee, and Hester (2014) found that *A. germinans* has lower water requirements than *S. alterniflora* in the black mangrove/salt marsh ecotone in Louisiana. They suggested that black mangrove has greater resistance to drought than *S. alterniflora*, and that this may play a role in future expansion of the species in the area.

REMOTE SENSING

Color infrared (CIR) aerial photography has been used to document the distribution and abundance of mangroves in several areas of the world (Reark, 1975; Ross, 1975; Saenger and Hopkins, 1975; Sherrod and McMillan, 1981). Everitt and Judd (1989) used CIR aerial photography and ground truthing to document the distribution and abundance of black mangrove along the Texas coast. They also provided the characteristics of spectral reflectance of black mangrove and developed a technique to quantify the abundance of black mangrove populations.

Everitt and Judd (1989) showed that in CIR images, black mangrove has a distinct red-image response compared with the lighter shades of magenta to pink of *B. maritima* and mixed herbaceous species that include *Distichlis littoralis* and *Prosopis reptans*. Dry, bare soil areas have a whitish-gray image tone, wet bare soil has a brown tone, mud has a black tone, and shallow water has a blue tone. The red image of *A. germinans* was primarily attributable to its low visible reflectance, but its generally high near-infrared reflectance also contributed to its image response.

Additional *A. germinans* populations could be easily identified in CIR photographs. Ground truthing of eight randomly selected CIR transparencies from the lower Texas coast gave 100% correct recognition of black mangrove. Black mangrove could be distinguished on 1:2000, 1:3000, and 1:5000 scale photos.

Everitt and Judd (1989) found that computer classification of percent area occupied by black mangrove in a CIR image was 17.5% and computer estimation of the photointerpreter's overlay map of the areas was 17.0%. Thus, computer analysis of CIR photographs can permit the quantification of black mangrove populations. This technique can permit area estimates that can be used to monitor the spread or contraction of populations over time.

Everitt, Escobar, and Judd (1991) evaluated airborne video imagery for distinguishing *A. germinans* stands on the lower Texas Gulf coast. Results showed that *A. germinans* populations had a distinct red signature on the CIR video imagery that could be separated from other vegetation, soil, and water. Computer-based analyses of the imagery showed that black mangrove populations could be quantified. Airborne video data provides a near–real-time tool for distinguishing and delineating black mangrove communities and should be useful for assessing damage to populations following catastrophic weather events, including freezing and tropical storms. Aerial surveys are also less costly to conduct with video than with photography.

Everitt, Escobar, and Judd (1992) reported that Satellite Pour l'Observation de la Terre (SPOT) imagery permitted the recognition of black mangrove and its mapping over extensive areas. They concluded that SPOT satellite imagery may be useful for preliminary mapping of large areas, such as the entire Texas coast or the Gulf coast of Mexico, but that the resolution is too coarse for accurate mapping.

REFORESTATION

Black mangrove forests, like those of other mangrove species, and tropical and subtropical woodlands in general, are threatened (Elster, 2000; Toledo, Rojas, and Bashan, 2001). Reasons for the decline in abundance and geographic distribution of black mangrove include harvesting the wood, converting the land to urban development, and converting the land to aquaculture.

McMillan (1971) studied the environmental factors affecting seedling establishment of black mangrove on the central Texas coast. He examined the effects of salinity, water turbulence, water depth, and temperature on seedling establishment. Seedlings showed a broad tolerance to salinity. In a 12-hour photoperiod with a day temperature of 30°C and a night temperature of 24°C, seedlings had 100% rooting in salt concentrations of 0 ppt to 57 ppt, 80% rooting at 65 ppt, and 10% rooting at 75 ppt. The continuous tumbling of seedlings by a stream of air in distilled water and synthetic seawater tested the effect of turbulence on rooting. This study was conducted at 22°C to 24°C. After 4 weeks of continuous agitation, most root development in the tumbled seedlings was slight compared with seedlings in still water. After 4, 7, and 12 weeks, tumbled seedlings showed rapid root elongations when the water was stabilized. Although the horizontal floating seedlings produced elaborate root systems at all water depths, they became established primarily at a water depth of 5 cm or less. Rooting occurred over a range of temperatures, but seedlings were damaged at high temperatures. Seedlings rooted at 18°C, 24°C, and 30°C, but they failed to root at 15°C or lower and showed inhibition of rooting at 37°C.

Most reforestation of mangroves has been carried out in the moist tropics. Indeed, in SE Asia, clear-cut mangrove forests have been replanted and managed since the early part of the 20th century. Despite the early beginning, knowledge of black mangrove reforestation is meager because most reforestation work has been done with species of the Rhizophoraceae, and the work was done by trial and error without scientific documentation.

Elster (2000) compared reforestation of *A. germinans*, *L. racemosa*, and *R. mangle* in a heavily damaged mangrove forest in the floodplain of the Ciénaga Grande de Santa Marta on the Caribbean coast of Colombia, where 60% of the original 51,000 ha of mangroves had died. The main reasons for mortality were hypersalinization, increased sedimentation rates, and lowering of the water level. Planting of the three species using propagules, seedlings, and saplings were carried out (Elster, 2000). Elster (2000) found that reforestation success depended mainly on site selection and preparation. The highest mortality rates were in propagules and seedlings of *A. germinans* and *L. racemosa*, and the best survival rates were in saplings of *L. racemosa* and propagules of *R. mangle*. Growth in the few surviving *A. germinans* was very slow and significantly less than in the other two species. Generally, all species developed best at sites with low salinities and a water level near the soil surface.

In greenhouse and transplant experiments in Louisiana, Patterson, Mendelssohn, and Swenson (1993) showed that *A. germinans* can grow in soils flooded for 13 months. *Spartina alterniflora* also survives permanently flooded conditions and may inhibit the growth of *A. germinans* under such conditions.

Most of Mexico's approximately 660,000 ha of mangroves occur in the humid tropics, but numerous populations are found in arid zones (Toledo, Rojas, and Bashan, 2001). Toledo, Rojas, and Bashan (2001) studied restoration of black mangrove in an arid coastal lagoon in Baja California Sur, Mexico. Propagules were collected from naturally growing individuals, planted in clusters of five plants, and grown in a terrestrial nursery for 3 months. Then they were transplanted to a clear-cut zone in a lagoon. Survival and development of the transplanted mangroves were monitored at 6-month intervals for 2 years. After 6 months 86% of the transplants were alive, after 1 year and 1.5 years 77% were alive, and at the close of the study at 2 years 74% were alive. After 4 years 74% were alive. Clearly the transplants survived and developed well under natural conditions.

ECONOMIC IMPORTANCE

Avicennia germinans stands play a significant role as natural barriers to coastal erosion caused by tropical storms, as habitat for a wide range of organisms in intertidal food webs, as carbon sequestration sources, and as a source of litter, detritus, and organic material that is exported to the sea (Schories *et al.*, 2003). Coastal fisheries and bird populations are supported by this species (Osland *et al.*, 2014; Vovides *et al.*, 2011).

Mangrove crabs are harvested in black mangrove communities in the Amazon River delta (Imbert, Rousteau, and Scherrer, 2000). Alvarez-Suarez *et al.* (2010) reported that *A.*

germinans contributes at least 45% of pollen in the production of Cuban coastal-zone honey. Bark has also been used in tanning in the tropics (Vines, 1960).

Wildlife Values

Avicennia germinans provides cover and nutrients for a wide variety of wildlife. Food and refuge are provided for fiddler crabs, periwinkles, clams, oysters, fish, and estuarine crocodilians (Davis *et al.*, 2005; Everitt *et al.*, 2010; Stevens, Fox, and Montague, 2006). In Puerto Rico, the green iguana (*Iguana iguana*) consumes large quantities of black mangrove leaves (Govender *et al.*, 2012).

Altenburg and van Spanje (1989) found that 10 species of birds—common sandpipers (*Actitis hypoleucos*), whimbrels (*Numenius phaeopus*), malachite kingfishers (*Aledo cristata*), blue-breasted kingfishers (*Halcyon malimbica*), Eurasian reed-warblers (*Acrocephalus scirpaceus*), melodious warblers (*Hippolais polyglotta*), subalpine warblers (*Sylvia cantillans*), Senegal eremomelas (*Eremomela pusilla*), beautiful sunbirds (*Nectarinia pulchella*), and village weavers (*Ploceus cucullatus*)—use *A. germinans* for roosting and feeding in Guinea-Bissau.

Snags of *A. germinans* and *R. mangle* trees provide nesting sites for bald eagles (*Haliacetus leucocephalus*) in Florida (Cornutt and Robertson, 1994). Nests were constructed in dead shrubs about 4.0 m tall and were occupied by bald eagles for about 4 years (Cornutt and Robertson, 1994). The endemic Florida prairie warbler (*Dendroica discolor paludicola*) and the Cuban yellow warbler (*D. petechial gundlachi*) nest in black mangrove shrubs that are about 2.5 m tall (Prather and Cruz, 1995).

Mangrove forests have some of the highest abundance of overwintering migratory birds in the Caribbean. Northern water thrushes (*Sciurus novaboracensis*) forage in black mangrove stands on woody debris and pneumatophores (Reitsma *et al.*, 2002). In the Yucatán Peninsula of Mexico, the endemic Yucatán wren (*Campylorhyncus yucatanensis*) nests in black mangrove trees (Vargas-Soriana, Ortiz, and Segura, 2010).

In the Galápagos Islands, Fessl *et al.* (2011) reported that one of Darwin's critically endangered finches (*Campylanychus heliobates*) nests in the outermost branches of the lower canopies of *A. germinans* and *L. racemosa*. These mangroves are often flooded at high tide.

Salt marshes on the Texas coast are the historic overwintering grounds for the critically endangered whooping crane (*Grus americana*) in North America. These salt marshes have been recently colonized by extensive stands of black mangrove. Black mangrove stands do not provide appropriate foraging sites for whooping cranes. However, *A. germinans* shrubs provide nesting sites for roseate spoonbills (*Platalea ajaja*) (Tresauge, 2012).

Medicinal Uses

To our knowledge little information is available about medical uses of *A. germinans*. However, Jones *et al.* (2005) found that extracts from leaves and twigs are cytotoxic to a panel of human cancer lines. They also reported isolation of two iridoid glycosides and phenylpropanoid and triterpenoid compounds that may have antitumor properties (Jones *et al.*, 2005).

Potential Control Agents

McMillan (1971) reported that the herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) in concentrations between 2.0% and 4.0% kill young seedlings. Older seedlings and young trees were more resistant. In June 2015, the International Agency for Research on Cancer confirmed its 1987 classification of 2,4-D as a possible carcinogen.

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