Mangrove Forests

Ariel E. Lugo
International Institute of Tropical Forestry, Forest Service, U.S. Department of Agriculture (USDA-FS), Río Piedras, Puerto Rico
Ernesto Medina
International Institute of Tropical Forestry, Forest Service, U.S. Department of Agriculture (USDA-FS), Río Piedras, Puerto Rico, and Center for Ecology, Venezuelan Institute for Scientific Research, Caracas, Venezuela

Abstract

The mangrove environment is not globally homogeneous, but involves many environmental gradients to which mangrove species must adapt and overcome to maintain the familiar structure and physiognomy associated with the mangrove ecosystem. The stature of mangroves, measured by tree height, decreases along the following environmental gradients from low to high salinity, low to high wind speed, high to low air temperature, high to low nutrient availability, and high to low rainfall. Litterfall, an indirect measure of mangrove productivity, decreases along the same environmental gradients. Mangrove stature is low at the two extremes of the inundation period (hydroperiod) and peaks at intermediate levels of inundation. The main factors that control mangrove structure and function are the latitudinal temperature gradient, regional presence/absence of hurricanes, nutritional status of mangrove substrates, and local salinity gradients.

INTRODUCTION

Mangroves are woody plants that grow in saline soils. Tomlinson[1] considered 20 genera with 54 species as mangrove species of which 9 genera and 34 species constituted "true mangroves." He established five criteria to typify a true mangrove, including the ecophysiological capacity for excluding salinity. The other four criteria were the following: complete fidelity to the mangrove environment, a major role in the structure of the community and capacity to form pure stands, morphological specialization that adapts them to their environment, and taxonomic isolation. Tomlinson also listed 46 genera and 60 woody species as mangrove associates and was emphatic that the number of mangrove associates is a potentially large list of species, given the many habitats that converge with the mangrove environments:

> *The ecological literature seems incapable of being reduced to a simple set of rules to account for the diversity of vegetation types within the broad generic concept of mangal. Lack of uniformity is… a measure of the plasticity of mangroves and their ability to colonize such an enormous range of habitats.*
>
> Tomlinson, p. 5[1]

In 2005, mangrove forests covered about 15 to 17 million hectares worldwide.[2,3] They occur on low-latitude coastal zones where waters with different levels of salinity flood forests at different frequencies and depths. The mangrove environment is diverse, and we use the many environmental gradients under which mangroves grow to organize this review. At the extremes of any of the environmental gradients that we discuss, mangroves not only function differently, but also may appear to be exceptions to generalities. For example, some mangroves appear to grow in freshwater, whereas others appear never to flood. In both cases, the incursion of seawater or floods occurs but at very low frequencies that require long-term observation. In spite of the complexity of gradient space under which mangroves occur, they are all forested and tidal wetlands in estuarine environments. Mangroves have global importance because their carbon sequestration and dynamics are in the same order as the unaccounted global carbon sink.[4] The term "blue carbon" is used to depict the carbon sink function associated with sediment burial in coastal vegetation, particularly mangroves.[5] Mangroves are also important to the functioning of coastal ecosystems, and have economic and cultural importance to people.[6] However, between 1980 and 2005, there was a 20% to 30% loss in the global mangrove area.[2,3] Fortunately, mangroves can recover from deforestation if socioeconomic and environmental conditions are favorable.[7] We focus only on natural environmental gradients and ignore anthropogenic gradients, which are reviewed in Lugo et al.[8] and Cintrón and Schaeffer Novelli.[9]

Encyclopedia of Natural Resources DOI: 10.1081/E-ENRL-120047500

THE ECOPHYSIOLOGICAL CHALLENGE OF THE MANGROVE ENVIRONMENT

Growing on saline, periodically flooded, and low-oxygen environments imposes severe restrictions on plant growth. The effects of other environmental variables are exerted through salinity stress and oxygen supply at the root level. Salt exclusion from roots has high energy cost and effects on plant structure and nutrient uptake such that for plants in saline environments, the salt balance is more critical than the water balance. For example, restricted water uptake in halophytes prevents excess accumulation of salt in their tissues. Thus, in contrast to non-halophytes, high atmospheric evaporative demand (as a result of high temperature and irradiation) cannot be compensated in halophytes by high transpiration because of the resulting salt accumulation inside the plant. Restriction of freshwater supply to mangroves primarily affects salt concentration at the root level, thus affecting water and nutrient uptake. In the high-radiation environment where mangroves grow, maintenance of leaf temperature within physiological limits is strongly dependent on evaporative cooling provided by transpiration. However, because salinity restricts water uptake and transpiration, mangroves maintain leaf temperature and optimize water-use efficiency through variations in leaf inclination, leaf area, and succulence.[10]

The hypoxia factor in mangrove wetlands is counteracted mainly through structural devices allowing oxygen to reach waterlogged roots. Mangroves do not tolerate deep flooding for prolonged periods although in true mangroves, tolerance to periodic flooding is high. Finally, the gradient analysis that we undertake here is complex, particularly in the case of nutrients where actual gradients in the field are difficult to establish. Although there are certainly nutrient-rich (estuarine, high-runoff, high-rainfall) and nutrient-poor (calcareous islands in semiarid areas) sites, an actual nutrient availability gradient is observed only in connection with salinity gradients, as salinity interferes with nutrient uptake.

Temperature

Mangroves are considered a lowland tropical ecosystem, where normally tree species do not tolerate frost. However, mangrove forests occur over a wide range of temperature and a wide latitudinal range that extends from the equator to 30° and 38° north and south, respectively, for *Avicennia marina*.[11] Similar latitudinal range is observed for *Avicennia* spp. and *Laguncularia racemosa* in the Neotropics.[12] These high-latitude mangroves are clearly no longer tropical forests *sensu stricto*, as they may reproduce and regenerate in lowlands with frost, i.e., in warm temperate and temperate life zones.

Woody vegetation on coastal systems is completely replaced by herbaceous vegetation above 32° and 40° north and south, respectively.[12,13] In Florida, *Spartina alterniflora* salt marshes compete with mangroves for space at the coastal fringe, a competition that is mediated by freezing events,[14] with mangroves losing ground with increased freezing frequency or intensity or both.[15] *Spartina brasiliensis* and *S. alterniflora* co-occur with mangroves in the Neotropics,[16,17] but their competition outcome depends on a different ecological constraint, possibly depth of flooding and sediment erosion and deposition dynamics.

Mangroves cope with the latitudinal temperature gradient with a change of species. In Florida, for example, four mangrove species occur in the keys and Everglades, but as frost frequency increases northward, all species but *A. germinans* drop out.[18] In the Brazilian coast, two species of mangroves reach the same latitudinal limit (28°30′S), but only *A. schaueriana* grows as a large tree, *L. racemosa* grows stunted as a shrub.[12] Among mangrove species, *A. marina*, *A. schaueriana, A. germinans,* and *L. racemosa* are the most tolerant to lower temperatures. Duke[11] found that as the temperature decreases, *A. marina* undergoes significant phenological changes involving leaf production, flowering, and fruiting, such that with lower temperatures, growth rates and reproductive potential diminish. Distributional limits for this species coincide with trends toward zero reproductive success. For each 10°C increase, growth increased by a factor of two or three. Stuart et al.[13] found that at freezing temperatures, water deficits cause freeze-induced xylem failure (xylem embolism). Species with wider vessels experienced 60% to 100% loss of hydraulic conductivity after freezing and thawing under tension, whereas species with narrower vessels lost as little as 13% to 40% of hydraulic conductivity. They suggest that freeze-induced embolism may play a role in limiting latitudinal distribution of mangroves either through massive embolism or through constraints on water transport as a result of vessel size. For canopy leaves of *Rhizophora stylosa* at its northern limit in Japan (26°11′N), light-saturated maximum photosynthesis rate decreased with decreasing temperature reaching minimum values in January and maximum in June.[19]

Our observations of mangroves at high latitudes along the coasts of Florida, Brazil, and Australia show that trees become shrubby and leaves turn yellowish at the extremes. Multiple sprouting increases as well. However, in global-warming scenarios for the future, mangrove species are expected to move to higher latitudes in both hemispheres and establish closed-canopy mangrove forests where *Spartina* marshes grow today.

The effects of high insolation and its influence on photoinhibition confound the determination of high-temperature tolerance of mangroves. However, Biebl[20] found species differences in the temperature range of tolerance of four mangrove species in Puerto Rico: *Conocarpus erectus* −3°C to 54°C, *L. racemosa* −1°C to 51°C, *R. mangle* −3°C to 50°C, and *A. germinans* −3°C to 48°C. Notably, the high-temperature tolerance is higher than temperatures normally encountered by mangroves under natural conditions.

Rainfall

Mangroves occur from rain forest to very dry forest life zones, which cover a gradient from 500 to about 8000 mm annual rainfall. This wide rainfall gradient influences soil salinity and forest structure. In Mexico, for example, Méndez Alonzo et al.[21] found that average tree height, average tree dbh (diameter at breast height), and leaf mass per unit area of *Avicennia* trees increased with both precipitation (500 to 3000 mm/yr) and minimum annual temperature (−2°C to 14°C). High-rainfall areas also increase the likelihood of coupling mangroves to terrestrial nutrient sources through runoff. Those mangroves that receive both high rainfall and runoff are usually the most complex and productive mangroves of all, particularly those growing under riverine conditions.

Many mangroves, however, are isolated from significant terrestrial runoff and thus depend on rainfall for sustaining their primary productivity. In these cases, their development is proportional to rainfall. Those that receive terrestrial runoff (including groundwater) are less dependent on rainfall for sustaining primary productivity. Mangroves in dry life zones sometimes receive riverine runoff that originates in upland moist, wet, or rain forest life zones as happens with the mangroves at Tumbes in Peru[9] and those in the strait connecting Lake Maracaibo with the Caribbean Sea in western Venezuela, which receive runoff from Río Limón.[22,23] However, mangroves in dry life zones are generally exposed to drought and high soil salinity. *A. germinans* exhibits reduced photosynthetic rates when exposed to drought, irrespective of salinity,[24] although the reduction was stronger in plants grown at lower salinities. Coincidentally, plants under higher salinity have a higher osmotic potential in their leaves, which allows them to be more effective in water uptake as we discuss in the following text.

Salinity

Mangroves *sensu stricto* are halophytes with elevated salt concentration in their cells. They require a higher level of sodium (Na) than non-halophytes for optimum growth, achieved under controlled conditions at salinity equivalent to 25% of seawater.[25–27] The salinity gradient under which mangroves grow ranges from freshwater to about three times the salinity of seawater.[28] For a given species, such as *Rhizophora mangle*, mangrove height [28] and leaf size decreases,[29,30] whereas leaf thickness increases[31] with increasing salinity. Osmolality (concentration of osmotically active solutes) of leaf sap in mangroves increases with soil salinity.[32] Leaf area decreases linearly as osmolality increases with *R. mangle* appearing to be more sensitive than *A. germinans* and *L. racemosa.* Also, as salinity increases along a spatial gradient, mangrove species respond by forming monospecific zones according to their salinity tolerance.[33] The changes in species along a salinity gradient are usually accompanied by changes in photosynthetic rates and nutrient-use efficiency,[29] and when exposed to hypersaline conditions (>100‰), quick and massive mangrove mortalities ensue.[34,35]

Tolerance to high levels of salt in the vacuoles of mangroves requires the accumulation of "compatible solutes" in the cytoplasm to prevent dehydration of proteins. Those compatible solutes, which accumulate in the cytoplasm without toxic effects, counteract the osmotic effect of ions in the vacuoles. Among the most common are cyclitols such as mannitol in the species of *Aegiceras* and *Sonneratia*, pinitol in the species of *Bruguiera* and *Aegialitis*, methyl-muco-inositol in *Rhizophora* spp., nitrogen-containing glycinbetaine in *Avicennia* spp., and proline in the species of *Aegialitis* and *Xylocarpus*.[36,37] Mangroves accumulating betaines and proline as compatible solutes also have higher total nitrogen (N) concentration in their leaves than mangroves accumulating cyclitols.[22,29,32]

Although under natural conditions mangroves can grow in freshwater, at some point in their life cycle, they have to be exposed to seawater, as they are not effective competitors with non-halophytic species. Ball and Pidsley[38] showed that the distribution of *Sonneratia alba* and *S. lanceolata*, two species that grow at low salinities and freshwater, followed the temporal distribution of salt incursion nicely. Neither species grew under conditions where salinity was always absent, reaching just as far into the salinity gradient as was seasonally present. Biomass accumulation in *S. lanceolata* peaked at very low salinities and rapidly decreased with increasing salinity.[39] Mangrove trees grow to the largest sizes and biomass in estuaries with salinities well below sea water. Some species of mangroves such as *A. germinans* behave as euryhaline species with a wide tolerance to salinity. They tend to grow in basins where salinity can range through the whole range of tolerance of mangroves.[40] In contrast, species such as *R. mangle* behave as a stenohaline species with a narrower range of salinity tolerance. They occur mostly on fringes where salinities range narrowly and their range is from almost freshwater to salinities in the order of twice seawater.[41]

The salinity gradient in mangroves develops with distance from the ocean (higher-salinity inland in dry and moist environments and lower-salinity inland in wet and rainy environments), with distance from freshwater runoff (higher salinity toward the ocean), or seasonally depending on rainfall and runoff events or periodic droughts. Salinity gradients are sharper in arid coastlines where differences between seawater and inland hypersaline soils can span the range of tolerance of all mangroves. Interstitial soil water also exhibits a vertical salinity gradient from surface waters (usually lower salinity) to deep-soil water (salinity increases with depth).[42] However, freshwater discharges of aquifers can reverse the gradient and make soil water less saline than surface water, if the surface water is fed by tides.

The photosynthetic rate of mangrove species decreases with increasing salinity.[24,40,43,44,46] In *L. racemosa* and *A. germinans*, net photosynthesis and leaf conductance decrease in parallel as the salt concentration of the nutrient solution increases from 0‰ to 30‰ and 55‰, respectively.[43,45] In contrast to reports on other *Avicennia* species under natural conditions,[44,47] *A. germinans* grows well and shows higher photosynthetic rates in nutrient solutions without added salt than those grown at salinities above 10‰. Potassium (K) is the main ion accumulated in the leaves under those conditions.[45] Measurements of gas exchange during rainy and dry seasons showed that *A. germinans* and *C. erectus* maintain much higher photosynthetic rates and lower salinities of leaf sap during the rainy season.[40]

At intermediate to high salinities (30‰ to 55‰), fertilization with N or phosphorus (P) slightly increases photosynthetic rates of *Avicennia* and *Rhizophora*, but not over the levels of control trees,[48] i.e., fertilization is less effective in overcoming the effects of high salinity.

Mangrove associates are species that are either tolerant to salinity to a certain degree or that are present at those stages in their life cycle that are tolerant to high salt concentrations. *Pterocarpus officinalis* belongs to the first group. It is a mangrove associate throughout the Caribbean and northern South America in areas with high rainfall or surface runoff.[49,50] This species coexists with species of *Rhizophora* and *Laguncularia*, is able to restrict Na input to leaves, and appears to have a high affinity for K. The fern *Acrostichum aureum* is in the second group of mangrove associates, a species found throughout the tropics and that at times competes with mangrove establishment. The sporophytic phase of this fern has a salt tolerance similar to that of coexisting mangrove species,[51] but the gametophytic phase cannot survive under saline conditions; therefore, the distribution of the mangrove fern is restricted to areas with high rainfall or low salinities that allow the sexual reproduction of the species.

Hydroperiod

The importance of hydroperiod to mangrove structure and species zonation was first recognized by Watson,[52] who estimated the hydroperiod based on the number of tidal events that flooded particular areas of mangroves. Mangroves that grow over patches of coral reef or are located on off-coast overwash islands, or on fringes below low tide, are usually continuously flooded or experience a long hydroperiod. In contrast, some inland mangroves appear to always grow on dry land, except perhaps during the highest tidal events, storm tides, or excessive rainfall or runoff events; their hydroperiod is short. These extreme points in the hydroperiod gradient create numerous ecophysiological challenges to mangroves. Krauss et al.[53] found little effect of hydroperiod on gas exchange of seedlings and saplings of three mangrove species from south Florida, confirming studies that showed that the flooding regime affected mostly the maintenance of leaf area and biomass partitioning.[54]

Oxygen availability to roots can become limiting under long hydroperiods. Mangroves exposed to long hydroperiods or to abnormally high water depth develop adventitious roots on the water surface, which supplement oxygen supply to below-water parts. Water movement by tidal or runoff forces also mitigate low-oxygen conditions during chronic inundation. Low root respiration in mangroves[55] is another mitigating effect to low oxygen supply. In contrast to the long hydroperiod, mangroves with a short hydroperiod can experience excessive soil salinity or drought. Between these two extremes grow most of the mangroves with different degrees of soil oxygenation and salinity. Both long and short hydroperiods inhibit understory development and mangrove regeneration and reduce mangrove height.

As sea level rises, some coastal zones flood beyond the tolerance of mangroves. On the other hand, the saline wedge penetrates much further inland into estuaries and provides an opportunity for mangrove expansion. An example of how this phenomenon may proceed has been observed in one of the main tributaries of the Orinoco River, from which a large fraction of its freshwater supply was reduced due to the damming upriver. The consequence of the change in hydrology was that mangroves moved hundreds of kilometers inland.[56] In south Florida, mangroves expanded 3.3 km inland with a sea-level rise of 10 cm between 1940 and 1994.[57]

Hydrologic Energy

In general, mangroves occupy low-energy coastlines. In high-energy coastlines, mangroves grow behind sand dunes where waters are calm. However, fringe mangrove forests on different sections of low-energy coastlines face different levels of wave energy. This energy gradient is poorly studied but is now relevant to understanding mangrove responses to increased sea level[58] and tsunamis. Nevertheless, mangrove response to sea-level rise will depend not only on the amount of area with saline soils but also on air temperature (greater frost frequency at higher latitudes), competition with salt marshes[14] and other vegetation,[58] and the balance between the rate of sea-level rise, input of allochthonous sediments, and mangrove production of peat.[59]

Usually, mangrove peat and root systems are undercut by rising sea level, and it is common to see overturned mangroves in places where this process occurs. Mangrove stems and prop roots offer resistance to incoming tides and waves and in so doing, reduce the hydrologic energy dissipated on coastlines. Under high-energy conditions, prop root and stem density increase, allowing mangroves to perform this ecological service of coastline protection. However, this process occurs within a limited range of tolerance to high-wave or tidal energy. In the tropical Atlantic Brazilian coast, *Avicennia* is frequently at the fringe, and this species is less tolerant to the erosive force of tides, coastal currents, and strong winds.[42]

In locations affected by macrotides, where large rivers discharge, as in the Atlantic coast of Brazil north of the mouth of the Amazon river, mangroves face strong effects from erosion and sediment deposition. Batista et al.[60] used remote sensing to show that along the coast of Amapa, Brazil, during the period 1980–2003, large erosion rates caused the disappearance of 1.37 km^2/year of mangroves on one location, whereas in another location, progradation added 56 km^2 of mangrove areas to the shoreline. Such dramatic shifts in erosive and sedimentary forces maintain mangrove vegetation in a constant state of successional change.

When mangroves are massively killed by drought, hurricanes, or other disturbances, the organic peat on which they grow, collapses under the erosive power of tides and waves and because the production of organic matter by the forest ceases. This collapse of the forest floor causes the intrusion of seawater and converts the forest into a lagoon.[28,61] This sets succession back by many decades as it takes time for the mangroves to reverse a lagoon environment back to forest growing at the higher elevation afforded by the accumulation of peat and roots. McKee et al.[62] increased the rate of mangrove root accumulation, and therefore the rate of peat accretion by fertilizing mangroves in the Caribbean coast of Belize.

Mangroves are overtaken by tsunamis and are exposed to significant structural effects.[63,64] However, behind the mangroves, there is less destruction of property because of the energy dissipation involved in overcoming mangrove resistance to wave energy (search for mangroves and tsunamis in http://www.fao.org).

Nutrients

The levels of nutrient availability experienced by mangroves range from oligotrophic with extreme P limitation to highly eutrophic. Oligotrophy occurs in carbonate environments[65,66] or over acid peat soils.[67] The area covered by nutrient-limited mangroves is large and mostly in the wider Caribbean (including the Everglades of Florida) and many Pacific atolls. Nevertheless, mangroves in general are eutrophic systems and without nutrient limitation. Eutrophy occurs on alluvial floodplains and riverine fringes. Polluted coastlines also provide eutrophic conditions for mangrove growth. Within this generally favorable nutrient availability, conditions may vary with the type of water entering the mangroves (nutrient rich from land, nutrient poor from the ocean). For example, Chen and Twilley[68] found a gradient of mangrove structure and productivity from the mouth of the Shark River to inland sites in south Florida. The biotic gradient was not responding to salinity or sulfide concentration but to N and P concentrations in soil pore water. Fertile sites were dominated by *L. racemosa*, whereas *R. mangle* grew in the less fertile sites. These forests exhibited seasonal changes in photosynthetic rates in response to changes in air temperature and light intensity.[69]

Oligotrophy leads to the formation of dwarf mangroves, which are low-height trees (no more than 1 m) with normal leaf sizes and reduced leaf-turnover rates. Fertilization experiments with mangroves in Belize, Florida, and Panama illustrate some of the complexities associated with nutrient limitations in mangroves.[70–73] Dwarf *R. mangle* and *A. germinans* mangroves in carbonate environments always respond to P fertilization, but surrounding fringing *R. mangle* mangroves respond only to N fertilization, and mangroves under intermediate conditions responded to both N and P fertilization.[70] In a disturbed mangrove forest in the Indian River Lagoon, both *R. mangle* and *A. germinans* responded to N fertilization but not to P fertilization along a tree-height gradient.[71] Contrasting responses to nutrient fertilization by the same species under different environments differentially affected ecological process of the species.[72] Among the biotic responses affected by fertilization were changes in plant habit from stunted to larger-sized individuals, which were accomplished by increasing wood relative to leaf biomass and changes in leaf-specific area, nutrient uptake, and leaf herbivory.

Feller et al.[73] also observed changes in the cycling of nutrients at a stand level through leaf fall and within-stand cycling. They found that in P-limited environments, retranslocation (or resorption) of P by *R. mangle* is much higher (≈70%) than that of N (≈45%). Nitrogen fertilization did not change those percentages, but P fertilization decreased P resorption efficiency (<50%) but increased N resorption (≈70%). Studies of dwarf mangroves on P-deficient peats in Puerto Rico [67] and stunted mangroves under hypersaline conditions[29] confirmed larger resorption values for P than for N. It appears that under conditions of P limitation, resorption of P is greater than that of N and that a sufficient supply of P reduces its resorption levels below those of N.

In Panama, Lovelock et al.[74] found that fertilized dwarf mangroves responded to N and P fertilization by increasing hydraulic conductance sixfold by P and 2.5-fold by N. The response of the hydraulic conductivity, more than the photosynthetic response per unit leaf area, accounted for the increased in size of the fertilized mangroves.

Lovelock et al.[55] found that *R. mangle* root respiration per unit mass was low in Belize compared to temperate tree species at the same temperature. Root respiration did not differ significantly between zones (fringe vs. dwarf) and fertilization treatments (N or P), although rates were consistently higher after fertilization, particularly in dwarf mangroves. The fine roots fertilized with P responded to fertilization with increased P concentrations.

Wind

Coastal zones are usually windy mostly due to sea breezes, which favor gas exchange through their influence on gaseous gradients across leaf surfaces. Sea breezes ventilate the forest and moderate air temperatures. A significant fraction of mangroves occur in the hurricane belt, which results in periodic exposures to extreme wind events (velocities >100 km h^{-1} are common and can exceed 250 km h^{-1}). In the process, hurricanes dissipate high levels of energy over forests, as it happened when Hurricane Hugo dissipated about 210 J m^{-2} s^{-1} over the northeastern mangroves of Puerto Rico.[75] Cintrón and Schaeffer Novelli[76] found that for Neotropical mangroves, the maximum canopy height decreased with increasing latitude, where winds (Caribbean) and frost (Florida and Brazil) become significant factors affecting forest structure. The large tree sizes in the Pacific Island of Kosrae vs. Pohnpei,[77] or San Juan River mangroves in Venezuela[78] vs. mangroves in nearby Caribbean Islands are examples of wind effects on mangrove stature. Hurricane winds exert selective pressure on forests by periodically trimming or overturning taller trees, which are usually the ones most affected by wind energy.[75] As a result, hurricane-affected forests have lower stature and wind-sculptured canopies.

Redox

Redox gradients occur in mangroves in association with anoxic conditions in mud and the relatively high concentration of sulfate in seawater. Sulfur is the fourth-most abundant element in seawater after chlorine (Cl), Na, and magnesium (Mg). Under reduced conditions (no oxygen), sulfur is present as sulfide, which is toxic for mangroves and reduces photosynthesis and growth.[79] Mangroves mitigate sulfide accumulation around the roots by the transport of oxygen through aerenchyma cells.[80,81] The ecological significance of the redox gradient in soils is expressed by its effects on the rates of microbial decomposition processes as well as in the diversity of both microbial communities and metabolic pathways associated with increasingly reducing conditions with soil depth (Fig. 5.5 and Table 5.6 in Alongi).[82]

Other Organisms

In addition to mangrove trees, other groups of organisms respond to environmental gradients within the mangroves and in some cases, affect mangrove trees and ecosystem functioning. For example, gastropods respond to sediment metal concentration.[83] Crabs respond to tidal range, and epibionts increase with light availability but decrease with tidal energy. In the case of crabs, they act as ecosystem engineers, not only facilitating mangrove regeneration but also influencing soil aeration and transport of oxygen to anaerobic soil layers.[82]

A. germinans mangrove forests in Panama growing under different environmental conditions (Caribbean and Pacific coasts with different rainfall, hydroperiod, and soil salinity) differed in phenology, and invertebrate and bird composition.[84] Although the coastal zones shared 95% of the bird species, the mangroves only shared 34%, and each forest had a different feeding guild assemblage in the bird community. The results suggest that in spite of being the same mangrove species, the different environmental conditions along the environmental gradients ripple through the food chain and result in different community composition.

Integration and Spatial Scales of Mangroves

There is no mangrove model that considers all the gradients discussed here and uses the responses of mangrove organisms to these gradients to holistically explain mangrove structure and productivity (but see Lugo[33] for a zonation/succession diagram with many of the gradients included). Such a model would be extremely useful to mangrove conservation actions, including restoration and rehabilitation of mangrove sites. However, there have been several efforts to model or conceptualize mangrove functioning. Odum[85] developed trophic-level models of mangroves for south Florida, and Lugo et al.[86] used energy flow to simulate mangrove productivity and response to hurricanes. Cintrón et al.[28] developed a model of the effects of salinity on mangrove functioning, and Twilley et al.[87] modeled mangrove succession and applied it to restoration. Kangas[88] developed an energy theory for the landscape classification of wetlands, which dovetails with the stand classification of mangrove ecosystem types of Lugo and Snedaker.[89]

Thom[90–92] was the first to relate mangrove ecosystem structure and function with the geomorphology of coastlines. Twilley et al.[93] developed a spatial and functional hierarchy for assessing mangrove forests (Fig. 13.3 in Twilley et al.).[93] Their concept included the latitudinal or global distribution of mangroves at the top of the hierarchy. Within the latitudes, they included the environmental settings, which were based on Thom's geomorphological types. Geomorphologic conditions expose mangroves to different energy conditions such as direction and force of hydrological fluxes and origin and quality of waters interacting with the mangroves, i.e., coastal vs. inland waters. Inside these environmental settings, Twilley et al. included the ecological types of Lugo and Snedaker, which function in relation to topography and hydrology. Mangrove stands occur within any of the ecological types, and within a stand, both above and belowground processes take place. Twilley and Rivera Monroy[94] modified and refined their 1996 model and compiled what they called five ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. These models represent the state of understanding of the whole mangrove ecosystem functioning, taking into consideration the effects of multiple environmental gradients on these ecosystems.

CONCLUSION

Mangrove ecosystem function results in different rates of ecological processes and structural development depending on whether the mangroves are above or below the frost line, exposed or not to hurricanes, and in dry or rain forest climates. These overarching environmental extremes (temperature, rainfall, and wind disturbances) have controlling effects on how mangroves respond to environmental gradients and which species might predominate at the environmental extremes.

ACKNOWLEDGMENTS

This work was done in collaboration with the University of Puerto Rico. Mildred Alayón edited the manuscript. We received useful comments from Gilberto Cintrón, Frank Wadsworth, Blanca Ruiz, and two anonymous reviewers.

REFERENCES

1. Tomlinson, P.B. *The Botany of Mangroves*; Cambridge University Press: Cambridge, England, 1986.
2. Valiela, I.; Bowen, J.L.; York, J.K. Mangrove forests: one of the world's threatened major tropical environments. BioScience **2001,** *51*, 807–815.
3. FAO. *The World's Mangroves 1980–2005*; The Food and Agriculture Organization of the United Nations: Rome, Italy, 2007.
4. Bouillon, S.; Borges, A.V.; Castañeda-Moya, E.; Diele, K.; Dittmar, T.; Duke, N.C.; Kristensen, E.; Lee, S.Y.; Marchand, C.; Middleburg, J.J.; Rivera-Monroy, V.H.; Smith III, T.J.; Twilley, R.R. Mangrove production and carbon sinks: a revision of global budget estimates. Global Biogeochem. Cycles **2008,** *22*, GB2013. doi:2010.1029/2007GB003052.
5. Mcleod, E.L.; Chmura, G.L.; Bouillon, S.; Salm, R.; Björk, M.; Duarte, C.M.; Lovelock, C.E.; Schlesinger, W.; H. Silliman, B.R. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. **2011**, *9*, 552–560.
6. FAO. *Mangrove Forest Management Guidelines*; Food and Agriculture Organization of the United Nations: Rome, Italy, 1994.
7. Martinuzzi, S.; Gould, W.A.; Lugo, A.E.; Medina, E. Conversion and recovery of Puerto Rican mangroves: 200 years of change. Forest Ecol. Manag. **2009**, *257*, 75–84.
8. Lugo, A.E.; Cintrón, G.; Goenaga C. Mangrove ecosystems under stress. In *Stress Effects on Natural Ecosystems*; Barret, W.G.; Rosenberg, R., Eds.; John Wiley and Sons Limited: Sussex, England, 1981; 129–153.
9. Cintrón Molero, G.; Schaeffer Novelli, Y. Ecology and management of new world mangroves. In *Coastal Plant Communities of Latin America*; Seeliger, E., Ed.; Academic Press, Inc.: San Diego, CA, 1992; 233–258.
10. Ball, M.C.; Cowan, I.R.; Farquhar, G.D. Maintenance of leaf temperature and the optimization of carbon gain in relation to water loss in a tropical mangrove forest. Aust. J. Plant Physiol. **1988**, *15*, 262–276.
11. Duke, N.C. Phenological trends with latitude in the mangrove tree *Avicennia marina*. J. Ecol. **1990**, *78*, 113–133.
12. Schaeffer Novelli, Y.; Cintrón Molero, G.; Rothleder Adaime, R.; de Camargo, T.M. Variability of mangrove ecosystems along the Brazilian coast. Estuaries **1990**, *13*, 204–218.
13. Stuart, S.A.; Choat, B.; Martin, K.C.; Holbrook, N.M.; Ball, M.C. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytol. **2007**, *173*, 576–583.
14. Kangas, P. C.; Lugo, A. E. The distribution of mangroves and saltmarshes in Florida. Trop. Ecol. **1990**, *31*, 32–39.
15. Lugo, A.E.; Patterson Zucca, C. The impact of low temperature stress on mangrove structure and growth. Trop. Ecol. **1977**, *18*, 149–161.
16. Braga, C.F.; Beasley C.R.; Isaac V.J. Effects of plant cover on the macrofauna of *Spartina* marshes in northern Brazil. Braz. Archi. Biol. Technol. **2009,** *52*, 1409–1420.
17. Colonnello, G. *Spartina alterniflora* Loisel, primer registro para Venezuela. Memorias Fundación La Salle de Ciencias Naturales **2001**, *59*, 29–33.
18. Odum, W.E.; McIvor, C.C. Mangroves. In *Ecosystems of Florida*; Myers, R.L.; Ewel, J.J., Eds.; University of Central Florida Press: Orlando, FL, 1990; 517–548.
19. Suwa, R.; Hagihara K.C. Seasonal changes in canopy photosynthesis and foliage respiration in a *Rhizophora stylosa* stand at the northern limit of its natural distribution. Wetlands Ecol. Manag. **2008**, *16*, 313–321.
20. Biebl, R. Temperaturresistenz tropischer Pflanzen auf Puerto Rico (Verglichen mit jener von Pflanzen der gemässigten Zone). Protoplasma **1965,** *59*, 133–156.
21. Méndez Alonzo, R.; López Portillo, J.; Rivera Monroy, V.H. Latitudinal variation in leaf and tree traits of the mangrove *Avicennia germinans* (Avicenniaceae) in the central region of the Gulf of Mexico. Biotropica **2008**, *40*, 449–456.
22. Medina, E.; Fonseca, H.; Barboza, F.; Francisco, M. Natural and man-induced changes in a tidal channel mangrove system under tropical semiarid climate at the entrance of the Maracaibo lake (Western Venezuela). Wetlands Ecol. Manag. **2001**, *9*, 243–253.
23. Barboza, F.; Barreto, M.B.; Figueroa, V.; Francisco, M.; González , A.; Lucena, M.; Mata, K.Y.; Narváez, E.; Ochoa, E.; Parra, L.; Romero, D.; Sánchez, J.; Soto, M.N.; Vera, A.J.; Villarreal, A.L.; Yabroudi, S.C.; Medina, E. Desarrollo estructural y relaciones nutricionales de un manglar ribereño bajo clima semi-árido. Ecotropic. **2006,** *19*, 13–29.

24. Sobrado, M.A. Drought effects on photosynthesis of the mangrove, *Avicennia germinans*, under contrasting salinities. Trees **1999**, *13*, 125–130.
25. Pannier, F. El efecto de distintas concentraciones salinas sobre el desarrollo de *Rhizophora mangle* L. Acta Científica Venezolana **1959**, *10*, 68–78.
26. Downton, W.J.S. Growth and osmotic relations of the mangrove *Avicennia marina,* as influenced by salinity. Aust. J. Plant Physiol. **1982**, *9*, 519–528.
27. Clough, B.F. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. Aust. J. Plant Physiol. **1984**, *11,* 419–430.
28. Cintrón, G.; Lugo, A. E.; Pool, D. J.; Morris, G. Mangroves of arid environments in Puerto Rico and adjacent islands. Biotropica **1978**, *10*, 110–121.
29. Lugo, A. E.; Medina, E.; Cuevas, E.; Cintron, G.; Laboy Nieves, E.N.; Novelli, Y.S. Ecophysiology of a mangrove forest in Jobos Bay, Puerto Rico. Caribbean J. Sci. **2007**, *43*, 200–219.
30. Duke, N. C. Morphological variation in the mangrove genus *Avicennia* in Australasia: systematic and ecological consideration. Aust. Syst. Bot. **1990b**, *3*, 221–239.
31. Camilleri, J. C.; Ribi, G. Leaf thickness of mangroves (*Rhizophora mangle*) growing in different salinities. Biotropica **1983**, *15*, 139–141.
32. Medina, E.; Francisco, M. Osmolality and δ13C of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. Estuar. Coast. Shelf S. **1997**, *45*, 337–344.
33. Lugo, A. E. Mangrove ecosystems: Successional or steady state? Biotropica **1980**, *12* (supplement 2), 65–72.
34. Botero, L. Massive mangrove mortality on the Caribbean coast of Colombia. Vida Silvestre Neotrop. **1990**, *2*, 77–78.
35. Jiménez, J. A.; Lugo, A. E.; Cintrón, Tree mortality in mangrove forests. Biotropica **1985**, *17*, 177–185.
36. Stewart, G. R.; Popp, M. The ecophysiology of mangroves. In *Plant Life in Aquatic and Amphibious Habitats*; Crawford, R.M.M., Ed.; Blackwell Science Publishers: Oxford, 1987; 333–345.
37. Popp, M.; Polania, J. Compatible solutes in different organs of mangrove trees. Annales des Sci. Forest. **1989**, *46*(suppl.), 842–844.
38. Ball, M.C.; Pidsley, S.M. Growth responses to salinity in relation to distribution of two mangrove species, *Sonneratia alba* and *S. lanceolata*, in Northern Australia. Funct. Ecol. **1995**, *9*, 77–85.
39. Ball, M.C.; Sobrado, M.A. Ecophysiology of mangroves: challenges in linking physiological processes with patterns in forest structure. In *Physiological Plant Ecology*; Press, M.C.; Scholes, J.D.; Barker, M.G., Eds.; Blackwell Science: Oxford, England, 1999; 331–346.
40. Smith, J.A.C.; Popp, M.; Lüttge, U.; Cram, W.J.; Diaz, M.; Griffiths, H.; Lee, H.S.J.; Medina, E.; Schäfer, C.; Stimmel, K.-H.; Thonke, B. Water relations and gas exchange of mangroves. New Phytol. **1989**, *111*, 293–307.
41. Lugo, A.E. Fringe wetlands. In *Forested Wetlands*; Lugo, A.E.; Brinson, M.M.; Brown, S.; Eds.; Elsevier: Amsterdam, the Netherlands 1990; 143–169.
42. Mehlig, U.; Menezes, M.P.M.; Reise, A.; Schories, D.; Medina, E. Mangrove vegetation of the Caeté Estuary. In Mangrove dynamics and management in north Brazil; Saint-Paul, U; Schneider, H., Eds.; Springer: Berlin, 2010; 71–108.
43. Sobrado, M. A. Leaf characteristics and gas exchange of the mangrove *Laguncularia racemosa* as affected by salinity. Photosynthetica **2005**, *43*, 217–221.
44. Naidoo, G.; Tuffers, A.V.; von Willert, D.J. Changes in gas exchange and chlorophyll fluorescence characteristics of two mangroves and a mangrove associate in response to salinity in the natural environment. Trees **2002**, *16*, 140–146.
45. Suárez, N.; Medina, E. Influence of salinity on Na+ and K+ accumulation, and gas exchange in *Avicennia germinans*. Photosynthetica **2006**, *44*, 268–274.
46. Nandy (Datta), P.; Sauren Das, S.; Ghose, M.; Spooner-Hart, R. Effects of salinity on photosynthesis, leaf anatomy, ion accumulation and photosynthetic nitrogen use efficiency in five Indian mangroves. Wetlands Ecol. Manag. **2007**, *15*, 347–357.
47. Tuffers, A.; Naidoo, G.; von Willert, D. J. Low salinities adversely affect photosynthetic performance of the mangrove, *Avicennia marina.* Wetlands Ecol. Manag. **2001**, *9*, 235–242.
48. Lovelock, C. E.; Feller, I.C. Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest. Oecologia **2003**, *134*, 455–462.
49. Medina, E.; Cuevas, E.; Lugo, A.E. Nutrient and salt relations of *Pterocarpus officinalis* L. in coastal wetlands of the Caribbean: assessment through leaf and soil analyses. Trees: Struct. Func. **2007**, *21*, 321–327.
50. Medina, E.; Francisco, M.; Quilice, A. Isotopic signatures and nutrient relations of plants inhabiting brackish wetlands in the northeastern coastal plain of Venezuela. Wetlands Ecol. Manag. **2008**, *16*, 51–64.
51. Medina, E.; Cuevas, E.; Popp, M.; Luga, A.E. Soil salinity, sun exposure, and growth of *Acrostichum aureum*, the mangrove fern. Botanical Gazette **1990**, *151*, 41–49.
52. Watson, J. G. Mangrove forests of the Malay Peninsula. Malayan Forest R. **1928**, *6*, 1–274.
53. Krauss, K.W.; Twilley, R.R.; Doyle, T.W.; Gardiner, E.S. Leaf gas exchange characteristics of three neotropical mangrove species in response to varying hydroperiod. Tree Physiol. **2006**, *26*, 959–968.
54. Pezeshki, S.R.; DeLaune, R.D.; Patrick Jr., W.H. Differential response of selected mangroves to soil flooding and salinity: gas exchange and biomass partitioning. Can. J. Forest Res. **1990**, *20*, 869–874.
55. Lovelock, C.E.; Ruess, R.W.; Feller I., C. Fine root respiration in the mangrove *Rhizophora mangle* over variation in forest stature and nutrient availability. Tree Physiol. **2006**, *26*, 1601–1606.
56. Colonnello, G.; Medina, E. Vegetation changes induced by dam construction in a tropical estuary: The case of the Mánamo River, Orinoco delta (Venezuela). Plant Ecol. **1998**, *139*, 145–154.
57. Ross, M.S.; Meeder, J.F.; Sah, J.P.; Ruiz, P.L.; Telesnicki, G.J. The southeast saline everglades revisited: 50 years of coastal vegetation change. J. Veg. Sci. **2000**, *11*, 101–112.
58. Doyle, T.W.; Krauss, K.W.; Conner, W.H.; From, A.S. Predicting the retreat and migration of tidal forests along the

northern Gulf of Mexico under sea-level rise. Forest Ecol. Manag. **2010**, *259*, 770–777.

59. Ellison, J.C.; Stoddart, D.R. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. J. Coast. Res. **1991**, *7*, 151–165.
60. Batista, E.D.M.; Souza Filho, P.W.M.; Machado da Silveira, O.F.Avaliação de áreas deposicionais e erosivas em cabos lamosos da zona costeira Amazônica através da análise multitemporal de imagens de sensores remotos. Revista Brasileira de Geofísica **2009**, *27*. doi: 10.1590/S0102-261X2009000500007.
61. Cahoon, D.R.; Hensel, P.; Rybczyk, J.; McKee, K.L.;Proffitt, C.E.; Perez, B.C. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. J. Ecol. **2003**, *91*, 1093–1105.
62. McKee, K.L.; Cahoon, D.R.; Feller, I.C. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecol. Biogeogr. **2007**, *16*, 545–556.
63. Baird, A.H.; Kerr, A.M. Landscape analysis and tsunami damage in Aceh: comment on Iverson and Prasad (2007). Landscape Ecology **2008**, *23*, 3–5.
64. Iverson, L.R.; Prasad, A.M. Modeling tsunami damage in Aceh: a reply. Landscape Ecol. **2008**, *23*, 7–10.
65. Feller, I.C. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecol. Monogr. **1995**, *65*, 477–505.
66. Cheeseman, J.M.; Lovelock, C.E. Photosynthetic characteristics of dwarf and fringe *Rhizophora mangle* L. in a Belizean mangrove. Plant, Cell Environ. **2004**, *27*, 769–780.
67. Medina, E.; Cuevas, E.; Lugo, A.E. Nutrient relations of dwarf *Rhizophora mangle* L. mangroves on peat in eastern Puerto Rico. Plant Ecol. **2010**, *207*, 13–24.
68. Chen, R.; Twilley, R.R. Patterns of mangrove forest structure and soil dynamics along the Shark River estuary, Flo. Estuaries **1999**, 22, 955–970.
69. Barr, J.G.; Jose, D.; Fuentes, J.D.; Engel, Vic.; Zieman, J.C. Physiological responses of red mangroves to the climate in the Florida Everglades. J. Geophys. Res. **2009,** *114*, G02008. doi:10.1029/2008JG000843.
70. Feller, I.C.; McKee, K.L.; Whigham, D.F.; O'Neill, J.P. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry **2002**, *62*, 145–175.
71. Feller, I.C.; Whigham, D.F.; McKee, K.L.; Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia **2003**, 134:405-414.
72. Feller, I.C.; Lovelock, C.E.; McKee, K.L. Lovelock, C.E. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen vs. phosphorus limited mangrove ecosystems. Ecosystems **2007**, 10, 347–359.
73. Feller, I.C.; Whigham, D.F.; O'Neill, J.P.; McKee, K.L. Effects of nutrient enrichment on within-stand cycling in a mangrove forest. Ecology **1999**, *80*, 2193–2205.
74. Lovelock, C.E.; Feller, I.C.; Mckee, K.L., The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panamá. Funct. Ecol. **2004**, *18*, 25–33.
75. Lugo, A.E. Visible and invisible effects of hurricanes on forest ecosystems: An international review. Aust. Ecol. **2008**, *33*, 368–398.
76. Cintrón, G.; Schaeffer Novelli, Y. Los manglares de la costa brasileña: revisión preliminar de la literatura. Oficina Regional de Ciencia y Tecnología de UNESCO para América Latina y el Caribe y Universidad Federal de Santa Catalina, Santa Catarina, 1981.
77. Allen, J.A.; Ewel, K.C.; Jack, J. Patterns of natural and anthropogenic disturbance of mangroves on the Pacific Island of Kosrae. Wetlands Ecol. Manag. **2001**, *9*, 279–289.
78. Twilley, R.R.; Medina, E. Forest dynamics and soil characteristics of mangrove plantations in the San Juan River estuary, Venezuela. In Annu. Lett.; Lugo, A.E., Ed.; International Institute of Tropical Forestry, USDA Forest Service: Río Piedras, PR, **1997**; 87–94.
79. Lin, G.H.; Sternberg; L.D.S.L. Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Australian J. Plant Physiol. **1992**, *19*, 509–517.
80. McKee, K.L.; Mendelssohn, I.A.; Hester, M.K.A reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. Am. J. Bot. **1988**, *75*, 1352–1359.
81. McKee, K.L. Soil physicochemical patterns and mangrove species distribution - reciprocal effects? J. Ecol. **1993**, *81*, 477–487.
82. Alongi, D.M. *The Energetics of Mangrove Forests*; Springer: New York, NY, 2009.
83. Amin, B.; Ismail, A.; Arshad, A.; Yap, C.H.; Kamarudin, M.S. Gastropod assemblages as indicators of sediment metal contamination in mangroves. Water Air Soil Pollut. **2009**, *201*, 9–18.
84. Lefebvre, G.; Poulin, B. Bird communities in Panamanian black mangroves: potential effects of physical and biotic factors. J. Trop. Ecol. **1997**, *13*, 97–113.
85. Odum, W.E. Pathways of energy flow in a south Florida estuary; Sea Grant Technical Bulletin 7; University of Miami: Miami, FL, 1971.
86. Lugo, A.E.; Sell, M.; Snedaker, S.C. Mangrove ecosystem analysis. In *Systems Analysis and Simulation Ecology*; Patten, B.C., Ed.; Academic Press: New York, 1976; 13–145.
87. Twilley, R.R.; Rivera Monroy, V.H.; Chen, R.; Botero, L. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. Mar. Pollut Bull. **1999**, *37*, 404–419.
88. Kangas, P.C. An energy theory of landscape for classifying wetlands. In *Forested Wetlands*; A.E.; Brinson, M.; Brown, S., Eds.; Elsevier: Amsterdam, 1990; 15–23.
89. Lugo, A.E.; Snedaker, S.C. The ecology of mangroves. Annu. Rev. Ecol. Syst. **1974**, *5*, 39–64.
90. Thom, B.G. Mangrove ecology and deltaic geomorphology, Tabasco, Mexico. J. Ecol. **1967**, *55*, 301–343.
91. Thom, B.G. Mangrove ecology from a geomorphic viewpoint. In *Proceedings of the International Symposium on Biology and Management of Mangroves*. Walsh, G; Snedaker, S.; Teas, H., Eds.; Institute of Food and Agricultural

Sciences, University of Florida: Gainesville, FL, 1974; 469–481.

92. Thom, B.G. 1982. Mangrove ecology-a geomorhological perspective. In *Mangrove Ecosystems in Australia: Structure, Function and Management*; Clough, B.F., Ed.; Australian Institute of Marine Sciences: Canberra, Australia, 1982; 3–17.
93. Twilley, R.R.; Snedaker, S.C.; Yáñez Arancibia, A.; Medina, E. Biodiversity and ecosystem processes in tropical estuaries: perspectives of mangrove ecosystems. In *Functional Role of Biodiversity: A Global Perspective*; Mooney, H.A.; Cushman, J.H.; Medina, E.; Sala, O.E. Schulza, E.-D., Eds.; John Wiley & Sons: New York, 1996; 327–370.
94. Twilley, R.R.; Rivera Monroy, V.H. Ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. In *Coastal Wetlands: An Integrated Approach.*; Perillo, G.M.E.; Wolanski, E.; Cahoon, D.R.; Ironson, M.M. Eds.; Elsevier: Amsterdam, 2009; 641–683.

To cite this article: Lugo, Ariel E. and Medina, Ernesto. Published online: 21 Oct 2014. Mangrove Forests. Pages 343-352 in Encyclopedia of Natural Resources. New York: Land. Taylor and Francis.