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SAN SALVADOR MANGROVES: AN ECOSYSTEM UNDER CHRONIC STRESS

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Note from Conference Organizer: We are pleased that Dr. Ariel Lugo was kind enough to accept our invitation to be Keynote Speaker at this conference. The following paper, however, is not the presentation that was given as the Keynote Address. Normally we do not publish papers in these proceedings volumes that were not presented at the conference. However, because of Dr. Lugo's renowned international stature as a mangrove specialist and because of his astute observations concerning the mangroves on San Salvador Island, we considered it important that we make these observations available to other researchers. We thank Dr. Lugo for his contribution to this proceedings volume.

ABSTRACT

The mangrove forests of San Salvador are a good example of an ecosystem under stress. The red mangrove, *Rhizophora mangle*, appears to be the species most affected by the stressful conditions of this island. Short tree stature, small and rigid leaves, abundance of senescent leaves, vertical leaf orientation, thinned canopy, and high frequencies of occurrence of albino seedlings are indicators of stress. The stress factors are high salinity, low tidal energy, either short or long inundation periods, low soil fertility, and poor growth conditions. These stresses are the result of low rainfall, absence of rivers or freshwater discharges into the mangroves, poor geomorphological conditions, and low nutrient availability. These forests are optimal locations to study mangrove responses to chronic stress, the ecophysiology of stressed plants, the relationship between ecophysiology, species composition, and ecosystem function, particularly in terms of nutrient cycling.

INTRODUCTION

Mangroves appear to be simple ecosystems because they represent a small floristic group of trees capable of growing in sea water. No matter where one is in the tropical world, one can recognize a mangrove forest by their physiognomy, dominance of a few tree species growing in monospecific zone, their characteristic coastal location, and morphologic adaptations that include many types of gas exchange structures on roots and stems as well as viviparous seedlings. Mangroves are also naturally stressed ecosystems because they must overcome the effects of salinity, inundation, low soil oxygen, and many other stressors that converge on tropical coastlines (Lugo, 1990; Lugo *et al.*, 1990).

In spite of the common characteristics that typify world mangroves, there is always variation among stands and locations, and this variation is what makes this ecosystem such a complex and interesting subject of study. For example, the red mangrove (*Rhizophora mangle*) can reach maturity at one or fifty meters in height depending on the environmental conditions. In this note, I report my observations of the mangroves of San Salvador. I only visited the mangroves of this island for a few hours but was fascinated by what I saw. The mangroves of San Salvador grow in an environmental setting that places them on the highly stressed category of mangrove forests.

MANGROVES UNDER CHRONIC STRESS

The mangroves of San Salvador were described by Smith (1982, 1986), Godfrey and Klekowski (1989), Kass and Stephens (1990), Godfrey *et al.* (1993), and Kass *et al.* (this volume). These authors highlighted the non-classical zonation of the species. The black mangrove (*Avicennia germinans*) dominates the fringe of the forest, and the other mangrove species [red mangrove, white mangrove (*Laguncularia racemosa*), and buttonwood mangrove (*Conocarpus erectus*)] have a low abundance in this zone. In Osprey Pond, the black mangrove dominated the two most seaward of five topographic zones within the fringe (Godfrey *et al.*, 1993). The exceptions were *Manilkara sp*, a nonhalophytic species that delimits the end of the mangrove system; and the white mangrove, which dominated topographic high spots within the hypersaline pond. Kass and Stephens (1990) and Kass et al. (this volume) found uniformly low nutrient concentrations in soil along the mangrove zonation, but a higher soil salinity in inland locations. Open water salinity in the inland ponds studied by Godfrey *et al.* (1993) are all above 3.5% and range as high as almost 7.0% (twice normal sea water).

The physiognomy of the mangroves of San Salvador leaves no doubt of the stressed conditions of the trees. The trees are short in stature. Their canopies are open with much space between leaves. The leaves have mostly vertical orientation, they are small, thickened, and many (more than usual) of the red mangrove leaves are yellowing, suggesting a high level of senescence. Godfrey and Klekowski (1989) reported abundant numbers of albino red mangrove (*Rhizophora mangle*) seedlings in San Salvador. In addition, red mangrove seedlings are small and not abundant on trees of this island.

THE SOURCES OF STRESS

The climatic, geomorphic, edaphic, and hydrologic setting limit the development of mangroves in San Salvador. Climatically, the island is above the Tropic of Cancer and experiences low temperature events. Because the island has low relief, it receives low rainfall that causes drought and exacerbates salinity stress. The geomorphic setting lacks the best mangrove environment, the riverine condition. Mangroves occur on elevated shores, as scattered islands offshore, or in inland hypersaline lagoons. These are not optimal settings for mangrove growth. Hydroperiods under these extremes can be either too long or too short.

The absence of rivers, scarcity of freshwater springs, and low freshwater runoff to the mangrove ecosystem further exacerbate the stressful conditions for mangrove growth. The island soils are calcareous. Calcareous soils can fix phosphorus and thus limit its availability to vegetation. In addition, the island has many subterranean conduits under tidal influence. This expands the inland distribution of saline and hypersaline conditions. The result is that the mangroves of this island usually grow at high salinity, under drought conditions with low tidal energy, low periods of inundation (except those inside the inland hypersaline ponds that experience long hydroperiods), and on poor substrates with low fertility. Additional nutrient inputs into the system are low when they occur (by washouts during storms, dust, etc.).

FACTORS THAT MITIGATE STRESS

Microtopographic variability is important in these environments because it provides relief to high salt content by allowing leaching of salts to spots with lower topographic elevations. The white mangrove may take advantage of this feature of the topography as suggested by the profile published by Godfrey *et al.* (1993). The sandy soils with high shell contents described by Kass *et al.* (this volume) mitigates high salintiy conditions by allowing free passage of salts and promoting aeration of roots. This condition relieves salinity and anoxic stress and allows mangroves to grow in salt and hydroperiod conditions that would be inaccessible in clay soils. Kass *et al.* also reported soil organic matter accumulation in depressions. This mitigates low nutrient content as it represents an accumulation of nutrients above the lower fertility mineral soil. Locations with high water velocity flow also mitigate chronic hydroperiod and high salinity because they ventilate roots and allow conditions not to be as variable as they are without the water flux. Usually trees grow taller under these conditions of water flux.

While these mitigating conditions are common in San Salvador, they are not sufficient to overcome the overall stressful effect of climate, topography, geomorphology, hydrology, and edaphic conditions impinging on the mangroves. However, these mitigating conditions provide contrast to the overall conditions in the island, and are ideal for comparative studies that give a better understanding of species responses to the environment.

IMPLICATIONS TO MANGROVE FUNCTION

The mangroves of San Salvador are ideal ecosystems to study ecosystem response to chronic stress conditions. The key aspect to this environment is that it lacks a frequent relief from hypersalinity and low nutrient stress as it occurs in moist and wet coastal zones with freshwater flows. The role of species is important because previous studies have suggested that each of the four mangrove species in this island tolerates a particular range of conditions for each of the critical factors that regulate the growth and function of mangroves, i.e., salinity, temperature, hydroperiod, etc. (Lugo, 1980).

Salinity levels in San Salvador are not extreme, considering that black mangroves can grow at salinities in excess of 9.0% (Cintron *et al.*, 1978). However, taken in combination with poor soil fertility, long or short hydroperiods, low rainfall, and periodic cold weather, conditions in San Salvador can become quite stressful, particularly to the less tolerant red mangroves. Among the four mangrove species of this part of the world, red mangroves are the least tolerant to high salinity, long or short hydroperiods, low nutrient availability, and low temperature. In contrast, black mangroves appear to be the most tolerant as they extend into the higher latitudes and highest salinity conditions. It can also tolerate wide fluctations in hydroperiod or salinity. The response of white mangroves appears to be intermediate between the red and black mangroves. Buttonwood mangrove generally grows at the ecotone with non-halophytic vegetation at high topographic locations. Thus it appears that San Salvador conditions select against red mangroves and this results in altered species zonations and stressed red mangrove trees.

The ecophysiological responses of red mangrove trees to prevailing conditions provide an opportunity to study the relationship between ecophysiology, ecosystem level processes, and species tolerance to stress. For example, the abundance of yellowing leaves and albino and multipigmented seedlings may reflect high rates of retranslocation at the plant level. Is high retranslocation of nutrients and other chemicals necessary to maintain productivity in these environments? What effects do high rates of retranslocation have on the nutrient cycling and reproductive rate of the forest? Do leaves exhibit a shorter or longer life span under these stressful conditions? Extreme nutrient conservation mechanisms may occur in these mangroves. They also deserve study. Finally, the substitutions of black and white mangroves for red mangroves at the fringe provide an opportunity to learn more about the adaptations of these species. Knowledge gained here can help interpret their roles in less stressed and complex mangrove zonations elsewhere in the world.

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