Coral Reef, Seagrass Beds and
Mangroves: Their interaction in
the coastal zones of the Caribbean.
Workshop.
West Indies Laboratory, Fairleigh
Dickinson University
St. Croix, U.S.V.I.
24-30 May 1982

Working paper
UNESCO/W.I.L.-F.D.U./
IOCARIBE

MANGROVE FORESTS: ECOLOGY AND RESPONSE TO NATURAL AND MAN INDUCED STRESSORS

Document prepared by Gilberto Cintrón, Director of the Marine Resources Division, Department of Natural Resources of the Commonwealth of Puerto Rico, and Yara Schaeffer-Novelli, Instituto Oceanografico Universidade de Sao Paulo, Brasil. Document prepared for use by workshop participants.

CONTENTS

Contents (Cont.)

1. INTRODUCTION

Until very recently, mangrove swamps were seen as mosquito-infested wastelands, unfit for most uses, but convenient sites for open dumps and sewage discharges. Mangrove management meant "reclamation," either for agricultural purposes or housing developments. Mangrove forests are, however, among the most productive ecosystems on the planet. Their daily rate of organic matter fixation ($\sim$ 20 g.O.M./$m^2 \cdot$day) is about 70 times the maximum value reported for tropical oceanic waters and 6 times the mean for the rates reported for marine flagellate blooms in neritic waters in the Caribbean (Ryther, 1969; Burkholder et al., 1967). Because of this high rate of production of organic matter, they are able to sustain important and valuable populations of fish, shellfish and wildlife and are prime breeding and nursery grounds for many species.

The main reason that mangroves have been consistently undervalued and poorly managed in our region is the lack of available information about the resource, its role and vulnerability. In this paper, we summarize some basic information about the ecology of these forests in our geographic region.

2. DEFINITION

The word mangrove is employed to describe a group of plants adapted to colonize waterlogged anaerobic and saline soils. They grow as trees or shrubs along most tropical estuaries and sheltered shores. The term is also used to describe the complex assamblage of animals and other plants associated with this forest type.

3. DISTRIBUTION

Mangroves are limited on a global scale by temperature and their lack of tolerance to frost. They extend latitudinally beyond the tropics, reaching in places to 29-30° in both hemispheres. At these latitudes, the mean monthly temperature for the coldest month is between 15 and 16° C, the mean annual temperature is 20-22° C and the annual temperature amplitudes range from 8-13° C. Frosts occur periodically at these areas and at the latitudinal limits the mangrove forests are poorly developed and grade into salt marshes dominated by herbaceous vegetation. Black mangroves (*Avicennia* sp.) are most frost tolerant and have the widest latitudinal range. Within the warmer portion of their range temperature is not limiting but the following other factors remain to be determinants or modifiers of their degree of development and areal coverage.

Suitable physiography: Mangroves develop in low lying areas subjected to saline intrusions. They develop best where topographic gradients are very small and saline intrusions penetrate far inland, for example on broad coastal plains.

Presence of salt water: Mangroves are not obligate halophytes but salt water removes the competition from plants that lack adaptations to deal with salt.

Large tidal amplitude: Tidal intrusions force salt wedges into the low lying areas. Where the tidal amplitude is large and the topographic gradient small, the mangrove belt may reach several kilometers in thickness.

Precipitation in excess of evapotranspiration ($P > PET$): Mangroves develop best in moist regions where there are fresh water surpluses. This results in abundant land drainage and extensive development of forests in the areas subjected to saline intrusions.

River discharge: Rivers are important geomorphic agents that shape the earth's surface and create deltaic features over which mangroves develop. In some regions their discharge may allow mangroves to develop in very dry regions where evapotranspiration greatly exceeds precipitation. In these areas, mangroves develop as riverine forests backed by extensive salt flats. Mangroves may develop in areas where there are no permanent river discharges (coastal fringes), but their development in these areas is limited. The absence of river discharges can be mitigated by the availability of runoff or fresh water upwellings.

Shelter: Mangrove seedlings and mature trees are vulnerable to uprooting by waves and current scour. They therefore develop best in low energy environments. They reach the sea only on protected segments of the coast, on the lee of offshore reefs, shoals or other protective structures. They line sheltered estuaries and coastal lagoons.

Availability of allocthonous sediments: Sediments from outside areas are essential for land building and encroachment. Terrestrially derived sediments bring nutrients that are incorporated by the plants. Although mangroves may develop in areas where there are very low allocthonous sediment inputs, the best developed forests are those of riverine environments that are subjected to periodic deposition of silts.

4. SPECIES

In contrast to the Indo-Pacific region, where mangroves are thought to have originated, and where there are some 44 species, in the Caribbean region only seven species are present. These are the red mangroves Rhizophora mangle, R. harrisonni, and R. racemosa; the black mangroves Avicennia germinans and A. schaueriana; the white mangrove Laguncularia racemosa; and the buttonwood Conocarpus erecta. Of the red and black mangroves, only R. mangle and A. germinans are widely distributed in the Caribbean. The last two species, L. racemosa (white mangrove) and C. erecta (buttonwood) are found throughout the region. The buttonwood is considered a peripheral species and quite often is found in coastal nonmangrove associations.

5. ADAPTATIONS AND ZONATION

Several environmental factors determine the position of individual species in a forest. For instance, in a fringe one may observe variations in terms of tidal exposure, salinity gradients and different soil types and textures with distance inland. Each species has adaptations that allow it to cope best with the site's factors with the least metabolic cost. This means that more energy can be alloted for growth and reproduction allowing that species to become highly competitive and ultimately dominant. This may lead to an observable zonation of species in a mangrove stand.

Red mangroves are usually found at the outer edges of a fringe or bordering tidal creeks and channels. This species has a large propagule (seed) that can reach some 30 cm long and weigh 30-40 g. Upon settlement the sapling quickly develops supporting roots that protect the young plant from washout. This prop root system is surprisingly responsive to the environment (Gill and Tomlinson 1977). Very complex prop root mazes develop in some fringe forests, possibly as a response to wind and wave stresses. The trees growing on more stable substrates often develop very erect boles and have proportionately fewer prop roots. These characteristics: the ability to become implanted in deeper water (up to 30 cm), and to windstand dislodgement by water movement, contribute to allow this species to become dominant in the outer fringes. Red mangrove has a low tolerance to high salinities. It actually develops best at low salinities (10-20‰) but will form forests, even where salinities reach 50-55‰. These salinity levels are very close to the limits of its tolerance, and growth and development are poor under hypersaline conditions.

Black and white mangroves tolerate higher salinity levels and thrive in higher salinity substrates with a greater metabolic efficiency (Carter et al. 1973). These species are typical of the inner swamp where tidal flooding is less frequent and evapotranspiration contributes to accumulate salts. Black mangroves are the most salinity tolerant. Scrub forests are found in soils with interstitial salinities of 90‰. Well developed forests are found where interstitial salinities are 60-65‰. Although white mangroves are also fairly tolerant of high salinities, they seem to do best where these are not so high.

In general, in tropical areas, where there are ample fresh water flows and interstitial salinities are low, the white mangrove dominates. In areas where there are pronounced drought periods and salinities are high, black mangroves may be dominant.

The relative stagnation of water in basin forests requires special adaptations to allow ventilation of the root system. Black and white mangroves have adaptations to overcome this problem. They ventilate their root system by producing networks of chimney-like organs (pneumatophores). These arise from the root and project from the soil and the stagnant water surface. The surface of the pneumatophore has minute pores through which gas exchange takes place. In this way oxygen diffuses down to the root and carbon dioxide is vented out. These pneumatophores reach 10-30 cm in length depending on the site's flooding levels. They are never totally flooded for extended time periods since this would result in the eventual death of the tree.

These species also have small seeds. This is advantageous since the floating propagules can be disseminated by the weak water flows typical of these areas. The movement of small seeds is not as easily hampered by the profuse growth of pneumathophores.

Because of the smaller size of the propagule, the implantation depth is more restricted (10-15 cm). In general black mangroves appear to tolerate deeper and longer flooding than white mangrove. In this respect, black mangroves may be dominant in low salinity environments subjected to large seasonal changes in water level.

The buttonwood is a peripheral species. It has a low tolerance to salinity but can stand flooding by very brackish waters, usually where the salinity is less than 5‰. It does well in sandy or rocky substrates and may be found in areas that are not flooded. A few pure stands of Conocarpus occur in Puerto Rico in permanently flooded basins where salinity is less than 5‰.

6. ZONATION AND SUCCESSION

It has been suggested that the zonation observed in a mangrove swamp is the result of a succession of species (Davis 1940, Macnae 1968). According to Davis, the red mangrove is the pioneer species that prepares the way for the others. As this species progressively grows toward the sea, accretion takes place, and in the inner parts of the prograding fringe it is replaced by the black mangrove. Eventually, black mangrove is also replaced by the white mangrove, which gives way to buttonwood or fresh water swamps. This scheme suggests that mangroves are the 'causal' agent of coastal progradation. It now appears that mangroves are not the cause of the rapid accretion but that they are responding to coastal accretionary patterns. In this sense they contribute to stabilize rapidly accreting banks and shoals but the extent to which they promote accretion is uncertain (Bird 1976).

Davis' scheme is applicable only in some instances where sediment inputs are high and there is active coastal progradation and freshwater runoff, since in some areas the landward succession could be arrested by dry conditions. In areas where there are no large freshwater and sediment inputs, as in most of the dry portions of the Caribbean islands, mangroves develop over autocthonous peats. Progradation under these circumstances is very slow and may be surpassed by the known rise in sea level which is estimated to be some 3 mm/yr (Emery 1980 as cited by Etkins and Epstein 1982). In most instances, mangroves have retreated landwards due to the submergence of land masses during the Holocene transgression. Zonation patterns in these sediment starved areas are a response of the various species to environmental factors and do not necessarily 'recapitulate' successional patterns.

An analysis of old aerial photography (1936) to ascertain the patterns of establishment after a hurricane in southwest Puerto Rico (Cintrón et al. 1980a) shows that there has been little or no peripheral accretion.

Suitable areas were immediately recolonized and the present zonation pattern did not result from a successional of species.

7. PHYSIOGRAPHIC TYPES

Mangrove forests vary greatly in their structural development. This structural variability is the response of the trees to the sum total of particular environmental factors, each of which can vary both in intensity and in frequency of recurrence. Individual forcing functions, or environmental factors, that control mangrove structure include tidal fluctuations (with daily, monthly and annual cycles), runoff and groundwater periodicity (usually over annual or longer cycles), nutrient inputs (usually tied to runoff hydroperiods), droughts (sometimes over periods of several years), soil salinity, etc. It is not usually possible to quantify all these factors to describe the so-called "energy signature" of each stand. Snedaker and Pool (1973) and Lugo and Snedaker (1974) developed a classification scheme that grouped mangrove forest types in units in which the major forcing functions operate at similar levels within each unit. Because of this, forest types within each unit share similar structural characteristics. Originally these authors recognized five types: (1) fringe forests, (2) riverine forests, (3) overwash forests, (4) basin forests (including hammocks) and (5) dwarf forests (Lugo and Snedaker 1974). More recently, after a review of all the available quantitative structural data available, we simplified the previous scheme by incorporating overwash forests as a type of fringe and considering dwarf forests a type of basin. The description of these forest types, taken from Cintrón et al. (1980) and Cintrón and Novelli (1981), follows:

7.1. Riverine forests

Riverine forests develop along the edges of river estuaries, often as far inland the toe of the saline intrusion. In this environment water flows and nutrient inputs are high. Flood waters bring in silts and mineral nutrients and these are rapidly incorporated into plant tissue. On the periphery of the forest, an area of high kinetic energy due to tidal motion and river discharge, the dominant species is *Rhizophora* sp., which develops a complex maze of adventitious roots. This root maze allows the establishment of well developed trees in spite of the strong water flows. Inland from the fringe one finds stands of *Laguncularia* sp. and *Avicennia* sp. Usually, riverine forests are most luxuriant in the lower and middle part of the estuary. Generally, interstitial salinities in these forests are lower than in the other types. They are lowest at times of flood when the salt wedge is driven seaward. During times of low flow, salt intrudes into the innermost parts of the estuary, raising the salinity temporarily. Usually interstitial salinities are in the range of 10-20‰ or less.

7.2. Fringe forests

Fringing mangroves develop along protected shores, over shoals or spits, often forming overwash islands. Fringes usually have pronounced gradients in topography, turbulence and tidal amplitude. Damping of the variation in tidal amplitude and turbulence inside the stand may result in high interstitial salinities in the inner parts of the fringe. There, the soil elevations are high and the terrain is less often flooded. In these inner portions Avicennia sp. may become dominant. On the outer edge where the levels of kinetic energy are high Rhizophora sp. dominates. Interstitial salinities in the outer fringe are just above ambient sea water (39 ± 1.3‰), but increase to higher levels (59 ± 4‰) in the Avicennia sp. zone (Cintrón et al. 1980a).

7.3. Basin forests

Basin mangroves are characterized by sluggish laminar water flows over wide areas of very small topographic gradients. The water turnover rate is slow. Basins receive and store water seasonally. Because of the uniform sheet flows strong salinity gradients do not develop within the basin. Basin forests may be dominated by either Laguncularia sp. or Avicennia sp., although mixed stands may be found. Tidal creeks and drainage channels within the basin are often lined with Rhizophora sp. Avicennia sp. dominates in basin forests where high salinities prevail (> 50‰), whereas Laguncularia sp. dominates in low salinity basins. Mixed forests are found at intermediate salinities (30-40‰).

The structural characteristics of basin forests depend on the hydroperiod. Where flows are weak but constant, forests develop well. In stagnant basins there may be oxygen depletion, slow nutrient recycling and reduced growth.

7.4. Dwarf forests

Dwarf forests occur where growth is limited by edaphic factors. Stands of dwarf Rhizophora mangle develop in some areas of the Caribbean over peat substrates in basins that do not receive substantial amounts of terrestrial runoff. Mature red mangrove trees in these basins are usually less than 2 m tall and often are about 1-1 1/2 m in the inner parts of the stand. Dwarf stands of R. mangle develop over marl in Florida, USA. It appears that in both instances (growth over peat and marl) the plants are being subjected to nutrient deficient (oligrotrophic) conditions.

Dwarf stands of Rhizophora are known from Puerto Rico, St. Thomas (U.S.V.I.), and Paso de Catúan in the Dominican Republic.

Dwarfed black mangroves are often found on the landward side of fringes and basins in seasonally dry areas, immediately adjacent to salt flats or hypersaline lagoons. The dwarfing factor here is extremely high levels of salt in the soil.

8. PRODUCTIVITY

Table 1 is a summary of productivity data from Lugo and Snedaker's (1974) review. The data have been converted from $gC/m^2 \cdot day$ to grams of organic matter/$m^2 \cdot$day and presented by forest type. These numbers were obtained from gas exchange studies and represent total community metabolism. Riverine forests show very high rates of gross production (24g O.M./$m^2 \cdot$day), followed by basins (18g O.M./$m^2 \cdot$day), and fringes (13.2g O.M./$m^2 \cdot$day). Net production is the amount of organic matter left after metabolic losses are accounted for. This is the amount of organic matter available for growth, foliage and seed production. These rates are also high. Between 20 and 40% of net production is partitioned for the production of leaves, flowers, fruits and stipules, which constantly fall to the forest floor.

Litterfall rates (dry weight) are highest in riverine forests ($2.94 - 3.96$ g/m^2·day), slightly less in fringe forests (2.0 g/m^2·day) and intermediate in value in basins ($1.9 - 2.3$ g/m^2·day) (Pool et al. 1975). Well developed riverine forests in Puerto Rico have litterfall rates averaging 4.12 g/m^2·day (Negrón 1980). A monospecific black mangrove basin in Puerto Rico averaged 2.29 ± 0.30 g/m^2·day (Negrón and Cintrón 1981). Litterfall rates in *Avicennia* sp., *Rhizophora* sp., and *Laguncularia* sp. stands in Guadeloupe were 3.56, 4.33 and 2.74 g/m^2·day, respectively (Febvay and Kermarrec 1978).

9. DECOMPOSITION AND UTILIZATION OF LITTERFALL

It is now recognized that one of the primary reasons mangrove areas are so important is because of their high rates of productivity of organic matter as litter. This material falls to the forest floor where it starts to decompose. During this time soluble organics are leached out and the leaf surfaces are colonized by fungi and bacteria. In time a complex meiofaunal assemblage develops, grazing on the decomposers. The decomposing material, originally high in carbohydrates and low in proteins, becomes enriched with microbial protein. The C:N ratio of the plant material decreases during decomposition. In R. mangle the C:N ratio decreases from 90.6 to 40.7 during the first 70 days of the decomposition process (Cundell et al. 1979). These low C:N ratios indicate the greater nutritional value of the decomposing material. As a result of decomposition and the intense activity of grazing organisms the plant material is gradually reduced to very small particles. These detrital particles, enriched with microbial tissue, are consumed by detritivores. These derive their nutrition primarily from the microbial and meiofaunal assamblage associated with the detrital particle. Once consumed, the particle is stripped of its microbial and meiofaunal cover and egested. The undigested stripped particles may become recolonized by microbes, repeating the cycle anew until all the digestible components are utilized.

As stated earlier, the initial autolysis of the plant material releases large amounts of dissolved organic matter to the water. This DOM is an important component of the outflux from mangrove areas, especially from basins where tidal and freshwater flows are too weak to export particulate matter. Bacteria are known to be important in the uptake and utilization of DOM.

Prackash (1971) has shown that blooms of the bioluminescent dinoglagellate Pyrodinium bahamense are stimulated by humic substances from mangrove areas. These humic substances also enhance the productivity of other neritic diatoms such as Skeletonema costatum and Thallassiosira nordenskioldii (Prakash et al., 1973). Thus, there is evidence that the waters leaching from mangrove areas appear to be rich in biologically active substances which can stimulate or regulate phytoplankton production in adjacent waters.

10. FISHERIES

Given the continuous availability of large amounts of nutritious organic matter in mangrove lined areas, it is not surprising that large numbers of organisms aggregate and utilize it. The sheltered nature of these areas also contribute to make them important as nurseries. Mangrove areas thus export protein to coastal areas in the form of aquatic organisms that use the mangrove areas for their early development and then migrate offshore. Well known are the massive migrations of mullets and shrimp from these areas. This is high quality protein that links mangroves directly to other coastal systems like coral reefs, seagrass beds, and ultimately to man.

A preliminary analysis of published lists of the fish fauna of mangrove areas in Florida (USA), the Caribbean and Brazil shows that there are more than 275 species of fish belonging to 66 families that are in some way associated with mangrove areas in these regions. Turner (1977) found a positive correlation between commercial yields of penaeid shrimp, the area of intertidal vegetation and latitude. The predicted annual yields per area of intertidal vegetation for the latitudinal range of 0-20° range from 39-159 kg/ha.

11. CLIMATIC CONSTRAINTS ON DEVELOPMENT

Mangroves do not necessarily need rain water, since they extract fresh water from the sea, but the amount of rainfall influences the extent of mangrove development in two ways. First, rainfall determines the rates of soil weathering, erosion and transport, and thus the rate of formation of deltas and other shallow coastal sedimentary features. Since these areas are the optimal substrate for mangrove growth, their rate of formation can indirectly determine the extent of coastal mangroves. Second, high temperatures, causing overall high evapotran spiration rates in the tropics, would quickly lead to a salt build-up in the inner parts of mangroves, if it were not for the flushing and leaching of salts by rainwater. According to Macnae (1966, 1968), mangroves develop best in Australia in areas receiving more than 2,500 mm/yr. Below 1,500 mm/yr, salt flats begin to form.

Precipitation and evapotranspiration

Rainfall in the Greater Caribbean is very low. Open sea areas receive only 800-1000 mm/yr. However, because of the large amount of solar radiation received at the surface there is a great deal of evaporation and moisture in the air. When the moisture laden air masses are lifted against the slopes of an island there is condensation and rainfall develops. The windward slopes of high islands are moist for this reason. Convection due to heating of the island mass is another important rain-producing mechanism. Since the land masses gain more heat than the surrounding seas, convection cells and rainstorms develop over the hot interior of islands often in the hot summer afternoons.

These rainfall producing mechanisms contribute more rain to the interior of the larger islands than to the coast. Furthermore, the "leading edge" of some islands can be drier than the "trailing edge" and the high islands may have a "rain shadow" zone because of the adiabatic heating of the subsiding air. Low and small islands get very little rain at all. On low islands, and in the "rain shadow" side of the larger islands there are commonly severe water deficits. During the year precipitation is much less than potential evapotranspiration. Under these circumstances, although there may be low areas influenced by salt water, mangroves may be unable to colonize there, due to excessive salt accumulations. The intense radiation turns these low flat areas into natural evaporation ponds. Salt crusts form at the surface and interstitial salinities are much beyond those tolerated by mangroves ($>$ 90‰).

Under these circumstances mangroves develop as a fringe, quite often narrow, in which salinity levels are suitable. Because of the steep salinity gradient inland the landward trees quickly become scrubby and poorly developed. Between the swamp and higher ground one finds a hypersaline lagoon (often containing dead or dying trees) and salt flats.

Therefore, both rainfall and topography influence the development of basin and fringe forest types. Where precipitation is greater than evapotranspiration basin forests are well developed. The interstitial salinity in these basins is low and they may be dominated by the white mangrove. Where precipitation levels are less than evapotranspiration (< 1500 mm) basins begin to degrade until they disappear, giving way to the formation of broad salt flats and shallow hypersaline lagoons. In areas where precipitation is less than potential evapotranspiration soil salinity becomes a dominant factor controlling the structural characteristics of the forests. Because of the limited amplitude of the tide in most of the Caribbean, high salt levels may be reached relatively short distances from the edge of the fringe.

12. VULNERABILITY TO STRESSORS

A stressor may be defined as a condition that causes an energy drain and a loss of potential energy that could be used to do useful work in a system (Odum 1967). The sustained operation of a stressor (a chronic stressor) constitutes a constant energy drain and prevents the system from attaining high levels of development. A stressor may also occur periodically, causing transient episodes during which maintenance costs are increased. The resiliency of the system is its ability to respond to and recover from a stressor.

Mangrove areas are subjected to natural and man induced stressors both of which can impinge on the system in a chronic or acute mode. For instance, hypersalinity can be a chronic natural stressor in many areas of the Caribbean. Storms and droughts are examples of acute events. Some pollutants can be chronic stressors in polluted areas, or behave as acute stressors during a spill followed by effective cleanup. In general, it is obvious that in a rigorous environment the structural development of the forest will be arrested. In more optimum environments development will proceed further until the structure is limited by site characteristics such as nutrient availability, water turnover rate and climatic limiting factors such as hurricane recurrence rates.

In the following section some natural and man induced stressors are described and their impact on mangrove forests is discussed. The reader is referred to Odum and Johannes' (1975) excellent review for additional information.

12.1. Natural Stressors

12.1.1. Tropical cyclones

Cyclonic disturbances develop in the north Atlantic, Caribbean, and Gulf of Mexico during the months of June thru November, although they form outside of this "season" in rare instances. These cyclones have high sustained winds, which near their center reach speeds that range from 65 km/hr (40 mph) in a tropical depression to more than 119 km/hr (74 mph) in a hurricane. Mangroves are vulnerable to these disturbances due to their coastal location, their shallow root system (most of which is in the upper 30 cm of the soil), the poor cohesiveness or load bearing ability of most mangrove soils and their exposure to waves, surge and erosion by strong water flows.

Wind speeds greater than 93 km/hr can cause defoliation and winds in excess of 130-160 km/hr will bring down trees. Wadsworth and Englerth (1959) reported that during hurricane Betsy in a black mangrove forest in southern Puerto Rico, 59% of a sample of 62 trees had been overthrown. The maximum reported wind speed in San Juan, 21 km (13 miles) from the storm's center was 185 km/hr (115 mph). These trees were 26 years old and had diameters (DBH) between 10 cm and 30 cm (4 to 12 in). Black mangroves have very shallow root systems and lack prop roots. The canopy structure also appears to influence this type of forest's sensitivity to wind damage. Canopies of even height without emergents and gaps are more resistant. Mature low density black mangrove "orchard" forests appear to be very susceptible to windthrow.

Red mangrove forests, especially in exposed locations, develop an extraordinarily complex and dense root supporting system. This anchorage provides excellent protection from windthrow. Upright (straight bole) trees are only found inland in sheltered locations. At the fringes, however, wave scour may be a more severe problem than wind.

High wind speeds also cause extreme flexing of the stems and separation of the bark from the woody tissue. Violent rubbing between adjacent branches can cause girdling. Even if the tree is not defoliated these branches will die and the trees will appear "burned" after the storm. In an exposed location this type of damage will be more severe in the windward part of the forest.

Stoddard (1969) recorded the damages to mangrove areas during hurricane Hattie in British Honduras (Belize). Hurricane Hattie had winds gusting to 322 km/hr (200 mph). In this area there was absolute devastation within 1.6 - 3.2 km (1 - 2 miles) of the storm's track. The zone of almost complete destruction extended to 32 km (20 miles). In that zone, only small mangrove patches in the leeward portion of the largest islands survived.

During storms large amounts of sand and other materials may be dumped into the mangroves. The accumulation of these materials impairs gaseous exchange thru lenticels and pneumatophores and may cause widespread mortalities. Usually defoliation ensues within 3-4 weeks. Børgesen (1909) described an instance where large amounts of sand and gravel were washed into Krausse's lagoon (St. Croix, U.S.V.I.) by the hurricane of 1899. Before the hurricane, the lagoon contained many mangrove islands with open water channels and bare flats. Dense R. mangle forest occurred in the western landward side. After the storm, the vegetation died and the wood was used as fuel for a nearby sugar-mill. Craighead and Gilbert (1962) and Craighead (1964) have similarly described post-hurricane mortalities due to marl deposition over roots in the Ten Thousand Island area in Florida.

Storm waves in Puerto Rico during hurricane David (1979) uprooted large tracts of seagrass beds in various areas. This material was deposited in large quantities ashore. In southwestern Puerto Rico, seagrass accumulations reached 2 m or more high in places, forming a dike in front of the mangrove fringe. Large amounts were carried inside the mangroves. These inordinate accumulations have caused dieoffs in the mangrove because of smoothering and restrictions in tidal exchange, leading to hypersaline conditions. Tabb and Jones (1962) report similar occurrences in North Florida Bay as a result of Hurricane Donna.

When fringe trees die but remain standing they eventually lose their aerial roots and the associated root community (Tabb et al. 1962). In exposed locations whole cays and fringes may be scoured away by waves. Large boulders and limestone blocks were deposited by waves in some mangrove covered coral islands in southwestern Puerto Rico by Hurricane David. In Cayo Turrumote a boulder rampart 0.5-1 m in height was deposited against the mangrove forest. Recovery is determined by the after storm configuration of the coasts. In places sediment deposition may raise the level of the soil so much that the area cannot be successfully recolonized by mangroves. In other areas shoals and other structures may have been formed and become available for establishment. Recolonization is slow but ultimately the newly formed banks and shores become stabilized by seagrasses and mangroves, starting the forest development cycle anew. Forest development during the first years is slow and is a function of seed availability. The edges of channels and shorelines quickly develop thickets. The inner parts of the swamps usually develop more slowly since the entry of seedlings is impaired by debris and standing dead trees.

Alexander (1967) reported that extensive flooding by salt water (salinity 30‰) during Hurricane Betsy caused severe plant kills (scorching) of non-salt tolerant species in the southeastern Everglades. The damage was increased by impounding caused by man made dikes. The surface waters freshened slowly after the storm, taking about two months to revert to normal values.

12.1.2. Tidal waves

Tidal waves are not frequent in the Caribbean but these destructive waves are known to have caused widespread damage in the past to low lying coastal areas. In 1946, a tidal wave destroyed a large mangrove forest situated at the head of Bahía de Samaná in the Dominican Republic (Sachtler 1973). It is estimated that 4500 ha of a total of 6500 ha were destroyed. The surviving stands were those of black mangroves found in the innermost portions of the swamp.

The area recovered from this event rapidly. Presently basal area and density (for stems $>$ 2.5 DBH) in the R. mangle stands are between 17.5-21.5 m^2/ha and 463-714 stems/ha, respectively. Mean diameter of the stand for this even aged forest (now 36 years old) is between 19.6 and 21.9 cm (Cintrón and Alvarez, unpublished).

12.1.3. Eustatic sea level rise and coastal erosion

Sea level is presently rising at the rate of 30 cm/100 years. This marine transgression has favored the expansion of mangroves over areas previously occupied by terrestrial plants. There is little doubt that this has induced a regressive movement in the seaward margin of mangroves in many areas. Hoffmeister (1974) reports the erosion of a rock pavement of fossilized roots of black mangroves in Florida. Zieman (1972) has found circular beds of Thalassia testudinium growing over red mangrove peats. These peats were deposited in hammocks which were submerged by the sea level rise. Extensive areas within Card Sound (Florida) show severe fringe erosion. The shallow banks in front of the mangrove fringes are sand - or seagrass - veneered red mangrove peat deposits. In Puerto Rico, peat areas are found on the bottom of shallow embayments overlain by sand. In Bahía de Samaná (D.R.) there is serious erosion of the fringe in considerable segments of the mangrove-lined bayhead shoreline.

12.1.4. Hypersalinity

As discussed earlier, hypersalinity is a chronic stressor in most coastal areas of the Caribbean and is one of the dominant factors controlling the structural characteristics of these forests. Carter et al. (1973), Burns (1976), Hicks and Burns (1975), and Lugo et al. (1975) have demonstrated that there are increases in respiration and decreases in net productivity with increases in soil salinity. The higher maintenance costs are also associated with stunting. As interstitial salinities increase the canopy height decreases (Cintrón et al. 1978, Fig. 1). The diameter of the trees also decreases as well as basal area, wood volume and complexity index (Martínez et al. 1981).

The control that salinity exerts over the physiographic characteristics of a stand in an arid environment is exemplified by some mangrove islands on the south coast of Puerto Rico (Cintrón et al. 1975, 1978). The development of a mangrove island over time is shown schematically in figure 2. Initially mangroves colonize shallow banks, expanding laterally over them. The growth of the trees at the outer margins is more vigorous and these trees may attain greater heights. Circulation to the inner parts of the island may be reduced by active growth at the margins. Red mangroves in the core are replaced in time by black mangroves as salinities increase. If soil salinities remain high but stable an island will develop an outer ring of red mangroves and an inner core of well developed black mangroves. Where salinities are too high the core will consist of dwarfed blacks. If circulation is further restricted there will be a dieoff at the core leaving an annular island with a hypersaline lagoon as in step 5 of figure 2.

Wave flushing at the windward edge of the island allows the red mangrove fringe to be thicker than on the protected side of the island (Fig. 3). In fact, where there is unimpaired circulation the island may remain in stage 1 or 2 indefinitely. The maturation process takes place in the islands in more sheltered localities.

Fringes may also suffer from a similar aging process. In time extensive areas of the inner swamp die and shallow lagoons and salt flats are formed. These diebacks occur following periods of drought.

In dry regions, mangrove areas may be unstable with coverage fluctuating between periods of expansion (usually following storms or a succession of very wet years) and contraction (usually triggered by a succession of dry years). In very dry areas, basins may disappear altogether leaving only a thin red mangrove fringe backed by shallow bare hypersaline lagoons and salt flats.

These areas of dead mangroves are a common feature in dry coastlines. Bacon (1970) described the "Red Swamp," situated between the Blue and Caroni Rivers in Trinidad. Examination of aerial photographs taken between 1942 and 1966 showed a gradual expansion of the dead areas. Reclamation work in the region may have been responsible for accelerating this dieoff by interfering with water movements.

Servant et al. (1978) report the characteristics of one of these hypersaline areas on the islet of Fajou in Guadeloupe. This area is separated by a porous bar from the sea. Seawater penetrates the basin and evaporates, concentrating salts within. Salinities are reduced transiently during episodes of heavy seas when water washes into the basin or when heavy rains leach some of the salts away. This stressful cycle is a common feature of many shallow hypersaline lagoons in the Caribbean area. In most of these arid areas the system is delicately poised and man's intervention by reducing water flows or impounding areas by structures such as causeways and roads often exarcebates these naturally occurring stressful conditions causing mortalities too.

12.2. Man Induced Stressors

12.2.1. Channelization, diversion of fresh water

Channelization and fresh water diversion schemes are extremely damaging. Mangroves are open systems and require continuous nutrient inputs to maintain their high rates of productivity and other ecosystem processes. Furthermore, in arid areas reduction of fresh water input quickly results in the onset of hypersaline conditions and mangrove dieoff.

12.2.2. Impoundment

Impoundment is another stressor that leads to rapid deterioration and death of mangrove areas. Diking cuts off mangroves from nutrient flows' it may raise water levels or lengthen the hydroperiod, causing the lenticels and pneumatophores to become covered with water. This impairs or stops gas exchange. In other instances lowering water levels or reducing flows causes salinity to increase rapidly as salt water evaporates.

In 1965, the Department of Agriculture of Puerto Rico built a dike impounding a 177 ha mangrove stand and flooding it to a 1 m depth. The purpose was to artificially create a habitat for wading birds. A massive dieoff followed immediately. The area had contained an extensive and well developed black mangrove forest (DBH ~ 10 cm). Only those trees on higher ground survived and then did so by producing extremely long pneumatophores (36.1 cm ± 0.5 as against 10-15 cm in normally flooded areas). There has been very limited natural restoration of the area. The dikes restrict tidal flushing so that during the dry season the impounded area dries up. The loss of the canopy exposes the impounded water and soil to the sun and extreme overheating during the dry season. Dissolved oxygen in the heated surface water (temperature > 30° C) drops below 0.5 mg/L.

White mangroves have recolonized some areas by becoming established over the stumps of fallen trees. The water depth reached during the wet season appears to limit the areas that can be colonized by mangroves.

Impoundment can also occur when roads are built through mangrove basins if care is not taken to preserve water flows. Patterson-Zucca (1978) has described the impact of road building on a mangrove swamp. In St. Thomas, construction of a road near Compass Point isolated and killed a small mangrove area. Hypersalinity may have been the cause of that dieoff.

12.2.3. Sedimentation

Mangroves are adapted to high sedimentation environments, but sudden deposition of large quantities of sediments can cause mortality. Under natural conditions, excessive sedimentation occurs as a result of catastrophic penomena like storm generated waves or floods. Man, however, is often the cause of severe sedimentation problems in some mangrove areas. Cintrón and Pool (1976) reported that sand extraction from a coastal dune for airport construction reduced the dune height from 12 m to only 3 m. During 1967, storm waves overwashed the residual dune, carrying large amounts of sand into a mangrove forest. Sand deposition varied from more than one meter to a thin sand veneer more than 260 m inland. All the mangroves were killed where sand deposits were higher than 30 cm, and some trees died where the sediment depth was between 20 and 30 cm. The area covered by the sand wedge has been colonized by Australian pine (Casuarina equisetifolia).

Kolehmainen (cited by Odum and Johannes, 1975) noted an area in Puerto Rico where fibrous waste from a sugar mill escaped from settling ponds and killed most of the trees in a black mangrove (A. germinans) stand.

Deposition of dredge spoils into mangrove areas will also cause large scale mangrove mortalities. During the late 1960's, dredged material was discharged into the Punta Picúa penninsula on the north coast of Puerto Rico, causing the total destruction of a large mangrove tract. This area too has been extensively colonized by Australian pine.

Deforestation and loss of soil can increase the rate of sedimentation in low lying swamps, causing shallow lagoons to become salt flats and killing inner swamp trees.

12.2.4. Thermal pollution

In shallow stagnant areas water temperatures may reach more than 43° C (110° F). These areas are not reseeded since temperatures may be limiting (Craighead 1964). McMillan (1971) reported that temperatures of 39-40° C for 48 hours caused death of rooted but stemless *A. germinans* seedlings.

The cooling water plumes from electric generating plants often approach this temperature. In Puerto Rico, Banus and Kolehmainen (1976) have suggested that temperatures above 38° C (100° F) define the beginning of deterioration of mangrove trees. These stressed trees have small leaves (Lugo and Cintrón, 1975), are partially defoliated (only terminal leaves remain), chlorotic and produce dwarfed seedlings. The mangrove root community is much more sensitive to high temperatures than the mangrove trees (Kolehmainen et al. 1974). The species composition and biomass of mangrove root communities was unaffected by temperatures below 34° C (93° F). Between 34° and 35° C (93 and 95° F) the number of species decreased abruptly, and above 35° C (95° F) the number of species was inversely related to the water temperature. At higher temperatures, 37.5-39.7° C (99.5-103.5° F), blue green algae became common, forming floating mats in the water surface.

12.2.5. Oil

Mangroves are extremely sensitive to oil pollution because of fouling of the gas exchange surfaces. Heavy coating of the intertidal root region or pneumatophores invariably causes death of the trees. In addition to acting as a mechanical barrier oil contains soluble toxic fractions. These compounds can be toxic to the roots and to the microbial populations in the soil.

The initial response of mangroves exposed to severe oil fouling appears to be defoliation. Defoliation may be partial or total, depending on the amount of oil remaining in the roots and substrate. Following the Peck Slip oil spill in eastern Puerto Rico, the heavily impacted areas lost 50% of the canopy in 43 days and 90% after 85 days (Cintrón et al. 1981). Total loss of the canopy was irreversible in the oil stressed red mangroves. In the marginal areas where the trees were exposed to sublethal amounts of oil defoliation was followed by production of smaller, often deformed, new leaves.

Lugo et al. (1981) have suggested that different forest types exhibit different susceptibility to oil pollution. For instance, riverine forests appear to be least vulnerable to oil pollution since the surface freshwater flows move the oil slicks away. Oil spilled in the ocean has little chance of entering the river mouth since salt water enters as a bottom flow. The greatest vulnerability for this forest type would occur during the dry season when surface flows are reduced or if the spill occurs up river or inside the estuary. In exposed locations, sand bars formed in front of river mouths can hinder oil penetration.

Basin mangroves are most susceptible to stressors that originate inland and therefore are less vulnerable to seaborne oil. Often (but not always) basins are isolated from fringes by berm. Basins are most vulnerable during periods of spring tides. They can be severely impacted by spills that originate from inland facilities and pipelines. Since oil would be retained for a long time in a basin its effects would be devastating.

Fringe and overwash forests are the most vulnerable to seaborne oil. Oil enters the fringe and accumulates inside. In the outer edge of the fringe water motion assists in cleansing the root surfaces. For this reason, there may not be any defoliation of the trees in the outer edge and complete canopy loss inside. In very sheltered locations, however, defoliation may be total.

Presently, there are no practical means to remove oil from mangrove areas. For this reason, it is imperative to prevent the entry of oil by using booms and sorbent barriers. Oil tends to penetrate into the porous mangrove sediments and persist for very long time periods. Residual amounts of oil are still found in Bahía Sucia in southwestern Puerto Rico after a spill that occurred in 1973. In areas in which there are high rates of water exchange oil is leached out and seedlings are brought in so that recuperation from an acute event occurs quickly. Where large residual amounts of oil persist recovery may be considerably delayed. In fact, residual amounts of oil may impede the reestablishment of a well developed stand.

The "successful" establishment of red mangrove seedlings in an area impacted by oil does not mean that the site is on its way to recuperation. Red mangrove seedlings are very tolerant to stressors but this tolerance decreases as the plant develops and requires more from the external environment rather than from its ample storages. This independence is prolonged by the slow growth rate of the seedlings (0.4-0.5 cm/mo during the first months). This, and the continual replacement of dead seedlings by new arrivals gives the false impression that natural regeneration is occurring. It seems, however, that when significants amounts of oil remain in the sediment, seedlings dieoff as their initial high tolerance decreases. The development of saplings into mature trees may be dependent upon the rage at which oil is leached or degraded.

12.2.6. Mining

There are no known mining activities currently occurring in mangrove areas of the Caribbean. The energy crisis has pressed consideration of the use of peats as energy sources and mining of these peats has been contemplated in the Negril's Great Morass in Jamaica.

In Puerto Rico, sand was mined from mangrove lined coastal lagoons during the 1960's. This activity created pits 18 m deep in places in lagoons whose original depth was only 1-2 m. These pits trap saline water and are depositional basins for organic sediments with high oxygen demands. As a result, the pits are persistently anoxic below 2 m, the BOD_5 in the bottom waters often exceeds 200 mg/L and NH_4 as (N) may be in excess of 15 mg/L (Ellis 1976).

13. RECOVERY

Natural ecosystems have growth strategies and adaptations that allow them to recover from periodic natural perturbations. Because of this inherent resiliency, ecosystems will restore themselves spontaneously once the disturbance has subsided. Assuming that there are no residual effects left by the stressor(s) an ecosystem will normally revert to a state very similar to its pre-stressed condition. Under the influence of residual stressors and/or an increased recurrence rate of acute events, the system will only achieve a simpler level of organization (Odum 1981).

In general, then, human intervention in the restoration process could be limited to removing the stressor that is causing the degradation and allowing the system to restore itself. It is wasteful and useless to attempt to restore areas artificially if the stressor has not been removed or residual amounts are left.

In the case of mangroves, the rate of recovery in a benign environment is a function of the size and proximity to seed sources. The conservation of ample seed stocks insures quick and natural regeneration with minimal human intervention.

In some areas, it may be desirable to accelerate the recovery of a stand by preparing the terrain and insuring an even distribution of seedlings by planting. Pulver (1976) gives some preliminary guidelines for the transplant of saplings (0.5-1.5 m in height). Planting saplings, however, is more difficult and costly than planting seedlings and the saplings must be removed from natural stands. The following points should be considered before artificial restoration is attempted:

- Select candidate sites carefully. If the area has contained mangroves before, determine the cause of loss and make sure the stressor has been removed. Naturally, "blank" areas may be hypersaline or too elevated for successful establishment.

- Because of the ease of handling and planting, red mangroves are one of the most suitable species for restoration projects, but they may not always be appropriate. The selection of the species to plant should be made on the basis of the dominant species at nearby locations having similar elevation, hydroperiods and exposure.

- Soil elevation should be low enough that the area is frequently flooded by tidal water, and there is adequate circulation. Stagnant areas tend to overheat.

- Measure interstitial (soil) salinities. Areas with interstitial salinities above 55‰ are not suitable for restoration by red mangroves.

- Areas must be sheltered from wave action and current scour.

- Remove dead standing wood and clean-up the area. Floating or falling debris will uproot and damage planted seedlings.

- Control the spacing of seedlings. Dense plantings result in stagnation (slow growth) due to excessive competition. For Rhizophora sp. the recommended spacing for seedlings is 0.6-1.2 m (Watson 1928).

- Recently, fallen seeds may be collected from nearby mangrove areas or they may be collected from trees. Use only ripe seeds. For red mangrove, use those seeds in which the abscission layer has developed (these are easily detached from the parent tree). Select healthy seeds and discard malformed or damaged propagules. Maintain the collected material wet and avoid exposing it to overheating during transportation and before planting. Seeds can be carried in an inexpensive foam icebox or a wet burlap sack.

- Red mangrove seedlings should not be inserted too deeply in the substrate. The seed should be planted deep enough so that it will not fall over (Watson 1928). For a 20-30 cm seedlings the planting depth should be 4-7 cm.

Since initial growth rates and mortality of red mangrove seedlings are very low it is impossible to judge the success of a restoration project on the basis of a few month's observations. The restored area should be checked annually to replace dead saplings and/or remove unwanted new arrivals.

14. CONCLUSION: CONSERVATION NEEDS

Island coastal marine ecosystems are in jeopardy in many areas of the Caribbean, due to high populations, mounting pressures to develop, a limited land base, and inadequate impact assessment procedures. In the smaller islands inland and coastal ecosystems are intimately linked. Inland activities like deforestation, agriculture on steep slopes, raising of domestic animals, road building and many others can increase sediment levels in estuarine and coastal waters, contributing to the degradation of coastal ecosystems. Protection of the marine resources depends on developing land use practices that will not impair the productivity of mangroves, seagrass beds and coral reefs.

Society derives direct benefits from the conservation of these coastal ecosystems. They are part of the resource base upon which islands depend. There are very practical reasons for their conservation, including the products they yield (fisheries) and their role in protecting the coasts from storm damage, as well as their more intangible values. Tourism, an important source of income, can be developed to take advantage of their uniqueness and great beauty. Natural reserves or parks can be established to protect especially important areas; these attract local as well as international tourism and also stimulate scientific research, all of which benefit the local economy. They are valuable educational assets.

On a more modest scale, small projects can be developed to take advantage of areas of particular scenic beauty. This kind of project, when designed for mangroves, needs to take into account the fact that mangrove areas are naturally prone to flooding; structures built in these areas are susceptible to recurrent damage by flood waters and storms unless they are constructed with flooding in mind. Because of the danger of storms, no permanent population centers should be encouraged to develop in mangroves, since the occupants would always be at risk.

In summary, mangroves are among the most productive coastal ecosystems known to science. In addition to their aesthetic and recreational values, they form an important part of the economic resource base of Caribbean islands because of their intimate ties to coastal fisheries, seagrass beds and coral reefs. In many areas they still evoke negative reactions, because of a lack of understanding of their importance. Though highly resilient in the face of natural stressors, mangrove forests are extremely vulnerable to many stressors caused by human activity, including sedimentation, channelization, diking, draining, and many kinds of pollution. An understanding of their role in coastal protection and the nurture of fish and wildlife should lead to more enlightened mangrove management practices throughout the Caribbean.

15. BIBLIOGRAPHY

Alexander, T. R. 1967. Effects of Hurricane Betsy on the southeastern Everglades. Quart. J. Fla. Acad. Sci. 30(1):10-24.

Bacon, P. R. 1970. The Ecology of Caroni Swamp, Trinidad. Central Statistical Office, Trinidad. 68 pp.

Banus, M., and S. W. Kolehmainen. 1976. Rooting and growth of red mangrove seedlings from thermally stressed tress. Pp. 46-53. In: G. W. Esch and R. W. McFarland (Eds) Thermal Ecology II. CONF 750425 Technical Information Center ERDA, Springfield, Va.

Bird, E. C. F. 1976. Coasts. An introduction to systematic geomorphology, volume 4, Australian National University Press, Canberra, 282 p.

Børgesen, F. 1909. Notes on the shore vegetation of the Danish West Indian Islands. Bot. Tidsskr. 29:201-59.

Burkholder, P. R., L. M. Burkholder, and L. R. Almodóvar. 1967. Carbon assimilation of marine flagellate blooms in neritic waters of southern Puerto Rico. Bull. Marine Sci. 17(1):1-15.

Burns, L. A. 1976. A model of mangrove ecosystems, rationale, data analysis, and model formulation. pp. 53-84. In: H. T. Odum (Ed) Guidelines for management of mangroves in south Florida. Contract No. 14-1610004-426. Final Report to U.S. Dept. of the Interior. Center for Wetlands, Univ. of Fla. Gainesville, Fla.

Carter, M. R., L. A. Burns, T. R. Cavinder, K. R. Dugger, P. L. Fore, D. B. Hicks, H. L. Revells, and T. W. Schmidt. 1973. Ecosystems analysis of Big Cypress Swamp and estuaries. EPA 904/9-74-002, U. S. Environmental Protection Agency, Region IV, Atlanta. 478 pp.

Cintrón, G., A. E. Lugo, D. J. Pool, and G. Morris. 1975. Los manglares de las costas áridas de Puerto Rico e islas adyacentes. Memorias del Segundo Simposio Latinoamericano sobre Oceanografía Biológica. Universidad de Oriente, Cumaná, Venezuela. 2:137-150.

Cintrón, G. and D. J. Pool. 1976. Efectos de la deposición de arena e inundación en un manglar en Puerto Rico. Tercer Simposio Latinoamericano de Oceanografía Biológica. San Salvador, El Salvador.

Cintrón, G., A. E. Lugo, D. J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. Biotrópica 10(2):110-121.

Cintrón, G., A. E. Lugo, and R. Martínez. 1980. Structural and functional properties of mangrove forests. A Symposium Signaling the Completion of the "Flora of Panama," University of Panama. To be published in: Monographs in Systematic Botany, Missouri Botanical Garden.

Cintrón, G., C. Goenaga, and A. E. Lugo. 1980a. Observaciones sobre la ecología de las franjas de manglar en zonas áridas. Memorias del seminario sobre el estudio científico e impacto humano en el ecosistema de manglares. UNESCO, Montevideo. 405 p.

Cintrón, G., A. E. Lugo, R. Martínez, B. B. Cintrón, and L. Encarnación. 1981. Impact of oil in the tropical marine environment. Technical Publication, Division of Marine Resources, Dept. of Natural Resources of Puerto Rico.

Cintrón, G. and Y. Schaeffer-Novelli. 1981. Introducción a la ecología del manglar. Seminario sobre ordenación y desarrollo integral de las zonas costeras, Guayaquil, Ecuador, 18-27 May 1981. 20 p. EC/80/006.

Craighead, F. C. 1964. Land, mangroves, and hurricanes. Fairchild Trop. Garden Bull. 19:5-32.

Craighead, F. C. and V. C. Gilbert. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quart. J. Fla. Acad. Sci. 25:1-28.

Cundel, A. M., M. S. Brown, R. Stanford, and R. Mitchell. 1979. Microbial degradation of <u>Rhizophora</u> <u>mangle</u> leaves immersed in the sea. Estuarine and Coastal Marine Science, 9:281-286.

Davis, J. H. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Inst. Washington Pub. 517:303-412.

Ellis, S. R. 1976. History of dredging and filling of lagoons in the San Juan Area, Puerto Rico. U. S. Geological Survey, Water Resources Investigations 38-76. U. S.G.S. Ft. Buchanan, P. R. 25 p.

Etkins, R. and E. S. Epstein. 1982. The rise of global mean sea level as an indication of climatic change. Science 215(4530):287-289.

Febvay, G. and A. Kermarrec. 1978. Formation de la litiere en foret littorale et en foret de montagne humide. Bulletin de Liaison du Groupe de Travail, Mangroves et Zones Cotiere, Guadeloupe, 4:79-80.

Gill, A. M. and P. B. Tomlinson. 1977. Studies on the growth of the red mangrove (Rhizophora mangle L.). 4. The adult root system. Biotrópica, 9(3):145-155.

Hicks, D. B. and L. A. Burns. 1975. Mangrove metabolic response to alterations of natural freshwater drainage to southwestern Florida estuaries. Pp. 238-255. In: G. E. Walsh, S. C. Snedaker, and H. J. Teas (Eds). Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Hoffmeister, J. E. 1974. Land from the sea. University of Miami Press, Coral Gables, Fla. 143 p.

Kolehmainen, S. E., T. O. Morgan, and R. Castro. 1974. Mangrove root communities in a thermally altered area in Guayanilla Bay, Puerto Rico. Pp. 371-390. In: J. W. Gibbons and R. R. Scharitz (Eds) Thermal Ecology. CONF. 730505. U. S. AEC. Augusta, Ga.

Lugo, A. E. and S. C. Snedaker. 1974. The ecology of mangroves. Ann. Rev. Ecology & Systematics 5:39-64.

Lugo, A. E. and G. Cintrón. 1975. The mangrove forests of Puerto Rico and their management. Pp. 825-846. In: G. E. Walsh, S. C. Snedaker, and H. J. Teas (Eds). Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Lugo, A. E., G. Evink, M. M. Brinson, A. Broce, and S. S. Snedaker. 1975. Diurnal rates of photosynthesis, respiration, and transpiration in mangrove forests of Florida. Pp. 335-350. In: F. B. Golley and E. Medina (Eds). Tropical Ecological Systems, Springer-Verlag, N. Y.

Lugo, A. E., G. Cintrón, and C. Goenaga. 1981. Mangrove ecosystems under stress. Pp. 129-153. In: G. W. Barrett and R. Rosemberg (Eds). Stress Effects on Natural Ecosystems. John Wiley & Sons Ltd.

Macnae, W. 1966. Mangroves in eastern and southern Australia. Austral. J. Bot. 14:67-104.

Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. Advances Marine Biol. 6:73-270.

Martínez, R., L. Encarnación, G. Cintrón, L. Cruz, and M. Aponte. 1981. Características estructurales de los manglares de Puerto Rico. Proceedings VII Simposio Latinoamericano sobre Oceanografía Biológica. 15-19 Nov. 1981, Acapulco, Mexico.

McMillan, C. 1971. Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. Ecology 52:927-30.

Negrón, L. N. 1980. La producción de hojarasca en el manglar ribereño del Espíritu Santo. M.S. thesis, Univ. of Puerto Rico, Rio Piedras, P. R. 73 pp.

Negrón, L. and G. Cintrón. 1981. Estructura y función del manglar de Laguna Joyuda, Mayaguez, Puerto Rico. Proceedings VII Simposio Latinoamericano sobre Oceanografía Biológica, 15-19 Nov. 1981, Acapulco, Mexico.

Odum, E. P. 1981. The effects of stress on the trajectory of ecological succession. Pp. 43-47. In: G. W. Barrett and R. Rosemberg (eds), Stress Effects on Natural Ecosystems. John Wiley & Sons Ltd.

Odum, H. T. 1967. Work circuits and systems stress. Pp. 81-138. In: Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems (H.E. Young Ed.). Univ. of Maine Press. Orono, Maine.

Odum, W. E., and R. E. Johannes. 1975. The response of mangroves to man induced environmental stress. Pp. 52-62. In: E. J. Ferguson Wood and R. E. Johannes (Eds), Tropical Marine Pollution. Elsevier Oceanography Series, Amsterdam, Netherlands.

Patterson-Zucca, C. 1978. The effects of road construction on a mangrove ecosystem. M.S. thesis, Univ. of Puerto Rico, Río Piedras, P. R. 77 pp.

Pool, D. J., A. E. Lugo, and S. C. Snedaker. 1975. Litter production in mangrove forests of southern Florida and Puerto Rico. Pp. 213-237. In: G. E. Walsh, S. C. Snedaker, and H. J. Teas (Eds), Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Prakash, A. 1971. Terrigenous organic matter and coastal phytoplankton fertility. In: J. D. Costlow (Ed), Fertility of the Sea. Proc. Int. Symp. Fertility Sea, Sao Paulo, Brasil. Gordon and Breach Science Publishers, London and New York.

Prakash, A., M. S. Rashik, A. Jensen, and D. V. Subba Rao. 1973. Influence of humic substances on the growth of marine phytoplankton: Diatoms. Limnol. Oceanogr. 18:516-524.

Pulver, T. R. 1976. Transplant techniques for sapling mangrove trees, Rhizophora mangle, Laguncularia racemosa, and Avicennia germinans, in Florida. Florida Marine Research Publications No. 22. Florida D.N.R. Marine Research Laboratory, St. Petersburg, Florida. 14 pp.

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science, 166:72-76.

Sachtler, M. 1973. Inventario y fomento de los recursos forestales: República Dominicana, Inventario Forestal. PNUD/FAO FO:SF/DOM 8 Informe Técnico 3. Roma.

Servant, J., N. Jean-Bart, and O. Sobesky. 1978. Le phenomene "Etang Bois-Sec": Une zone d'hypersalure en mangrove. Bulletin de Liaison du Groupe de Travail, Mangroves et Zones Cotiere, Guadeloupe, r:64-65.

Snedaker, S. C. and D. J. Pool. 1973. Mangrove forest types and biomass. Pp. C-1, C-13. In: The role of mangrove ecosystems in the maintenance of environmental quality and a high productivity of desirable fisheries. Final report to Bureau of Sport Fisheries and Wildlife. Contract No. 14-16-008-606, Center for Aquatic Sciences.

Stoddart, D. R. 1969. Post-hurricane changes on the British Honduras Reefs and Cays: Re-Survey of 1965. Atoll Res. Bull. 131:1-25.

Tabb, D. C., D. L. Dubron, and R. B. Manning. 1962. The ecology of northern Florida Bay and adjacent estuaries. Florida State Board Conserv. Tech. Ser. Pub. No. 39. 81 pp.

Tabb, D. C., and A. C. Jones. 1962. Effects of Hurricane Donna on the aquatic fauna of North Florida Bay. Transactions of the American Fisheries Society. 91(4):375-378.

Turner, E. R. 1977. Intertidal vegetation and commercial yields of Penaeid shrimp. Transactions of the American Fisheries Society. 106(5):411-416.

Wadsworth, F. H. and G. H. Englerth. 1959. Effects of the 1956 hurricane on forests of Puerto Rico. Caribb. Forester 20:38-57.

Watson, J. G. 1928. Mangrove forests of the Malay Peninsula. Malayan Forest. Rec. 6:1-275.

Zieman, J. C. 1972. Origin of circular beds of Thalassia (Spermatophyta: Hydrocharitaceae) in south Biscayne Bay, Florida, and their relationship to mangrove hammocks. Bull. Marine Sci. Gulf Caribb. 22(3):559-574.

Forest Type	g organic matter/m^2·day Gross Primary Productivity	Total 24 hr Respiration	Net Primary Productivity
Riverine	24.0	11.4	12.6
Basins	18.0	12.4	5.6
Fringes	13.2	11.3	8.8
Hammocks	3.8	1.2	2.6
Dwarf	2.8	4.0	--

Table 1. Summary of primary productivity and respiration data for different mangrove forest types. Based on Lugo and Snedaker (1974) review.

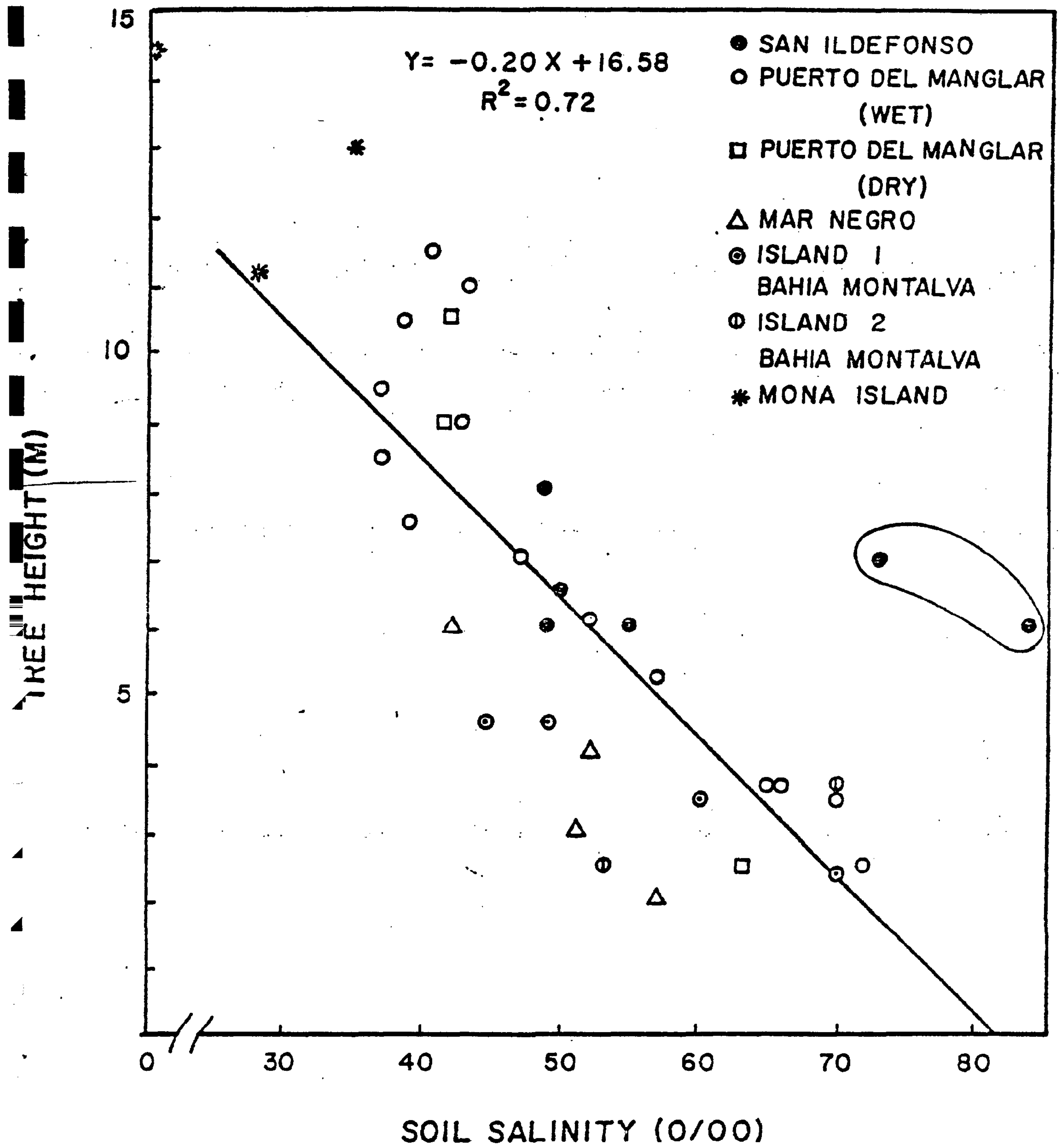

Fig. 1. Relationship between tree height and soil salinity in mangroves of arid coastlines of Puerto-Rico and adjacent islands (Cintrón et al., 1978).

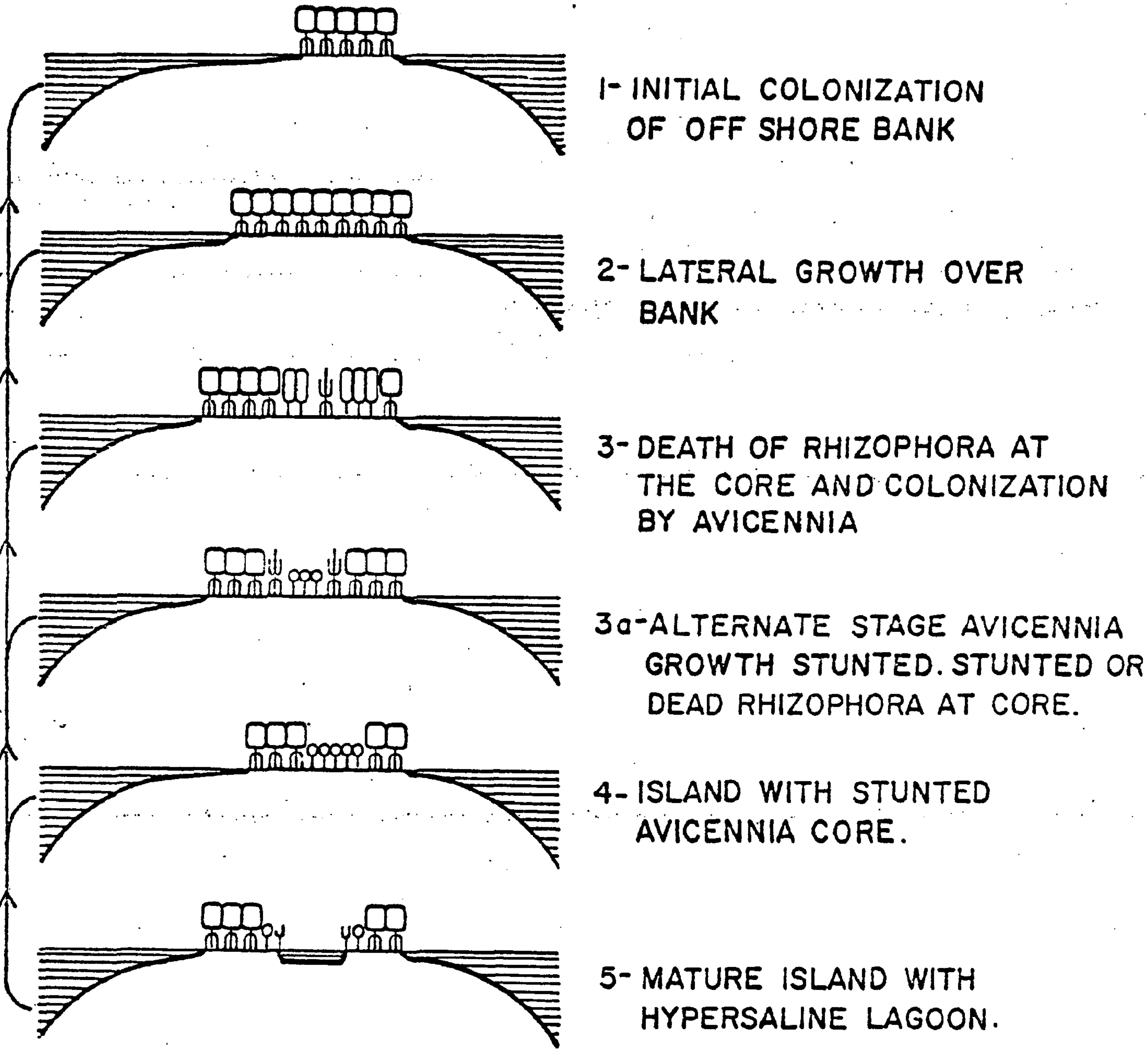

Fig. 2. Conceptual scheme of mangrove succession for mangrove islands in arid coastlines (Cintrón et al., 1978).

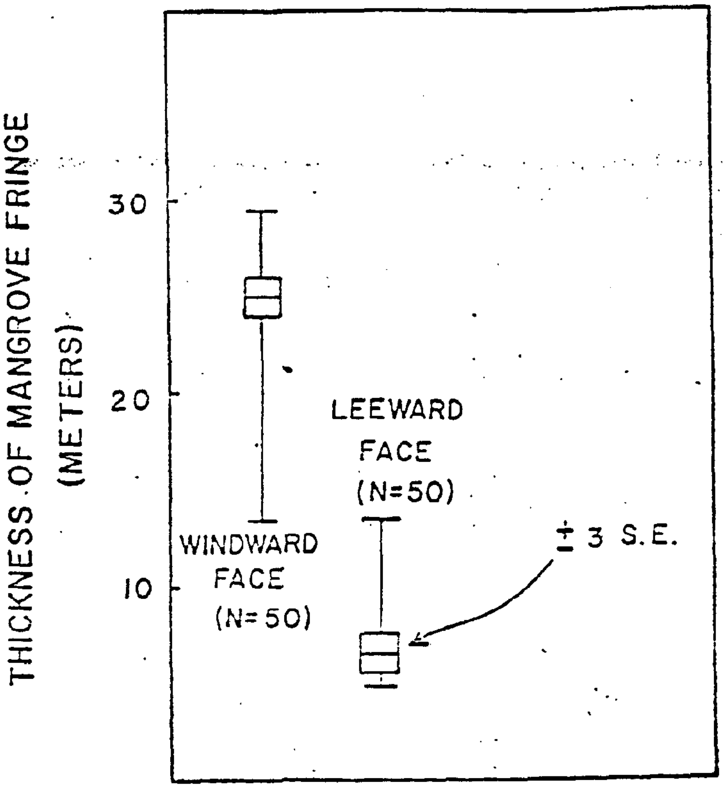

Fig. 3. Thickness of the red mangrove fringe in the mangrove islands of La Parguera (Cintrón et al., 1978).