
MANGROVES IN PUERTO RICO:
A Structural Inventory

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MANGROVES IN PUERTO RICO: A STRUCTURAL
INVENTORY

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ABSTRACT (continued)

function of this parameter. The complexity of a system is greatest where there is a greater availability of energy subsidies and low intensity of stresses. Stressors affect the systems capacity to renew itself. Low complexity stressed systems are more fragile and susceptible to further stressors. Complex systems may be able to sustain greater manipulation in terms of stressors that do not alter the incoming energy flows. All activities that alter the incoming energy flows lead to rapid deterioration of the ecosystem. The principal rule in managing these wetlands is to protect these energy sources.

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Introduction

Mangroves constitute a major coastal feature within the tropics, where they line an estimated 60 to 70% of shorelines. Important mangrove forests also occur in the subtropics up to 29° to 30° latitude in both hemispheres. Their best development occurs, however, within 23 1/2° north and south of the Equator, where tropical temperatures prevail and along protected shores where wave action does not disrupt the seedlings and mature trees. These sheltered locations are usually rich in soft, fine alluvial sediments containing large amounts of organic matter.

Mangrove forests are open systems that utilize land-derived nutrients; these nutrients are incorporated into plant tissue. In turn, much of the mangrove litter is later exported out of the forest and into coastal areas in the form of very small organic particles. This organic matter, composed of leaves, twigs, flowers and seedlings, is produced at a rate of 8-10 metric tons per hectare per year, a high level of organic production. During the decomposition process, as the litter is broken down into smaller particles it becomes covered by bacteria and fungi that transform the indigestible plant tissues into readily digestible microbial protein.

Detrital particles have a high protein to carbohydrate ratio due to the microbial colonizers, and have relatively more protein than the original litter.

This enriched material sustains a complex food web and most estuarine organisms are dependent on it directly or indirectly.

Mangroves support important fisheries because of these high organic matter exports. This food source is also exploited by many species that visit estuaries only temporarily for breeding or spawning. Some of these fish are reef or coastal dwellers as adults and only utilize mangroves during the juvenile stages of their life cycle.

Mangroves may also be important sustained producers of wood and charcoal. In Puerto Rico Wadsworth (1959) has reported wood volume yields on the order of 2,680 cubic feet per acre after 22 years ($8.5 \text{ m}^3/\text{ha./yr}$). This is only slightly less than the reported 3,106 cu. ft. per acre yield after 25 years ($8.7 \text{ m}^3/\text{ha./yr}$) reported in Thailand for mixed Rhizophora forests (Walsh, 1974).

Mangrove systems also reduce coastal erosion and serve as a naturally renewable protection for low lying coastal areas. In southwest Puerto Rico mangroves are tightly coupled to other marine ecosystems such as reefs and seagrass beds. Reefs provide shelter from wave action; seagrass beds contribute to form substrates which are colonized by mangroves. Mangroves export particulate organic matter which is utilized by many fish and invertebrates. As elsewhere many reef and seagrass fish utilize

the mangrove channels during their juvenile stages. There they find abundant food and shelter during these early and critical stages in their life cycle.

Structural Development

The interaction of various environmental factors such as nutrient availability, fresh water availability, flooding frequency and amplitude of the tides determine the degree of mangrove structural development. The best developed mangroves occur where nutrients are readily available and where tidal flushing contributes to nutrient transport, removes carbon dioxide and promotes root ventilation. Frequent flushing impedes the accumulation of such toxic substances as hydrogen sulfide or salts in the soil.

The degree of development of a mangrove forest is also dependent on the occurrence of natural and human induced stressors acting on the system. Natural stressors in this geographic region include periodic destruction by hurricanes and (along the dry sectors of the coast) salt buildup due to high evaporation rates, especially during episodes of extreme drought. Salt buildup is favored by the restricted flushing due to the small tidal amplitude in this area. Human stressors include channeling, diking and levee and road construction, sedimentation, thermal loading and harvesting.

Mangroves that develop under the influence of a chronic stressor must invest a higher share of their gross production in maintenance. Thus the energy available for growth and construction of structure is limited in proportion to the energy drain imposed by the stressor.

Highly stressed mangroves are scrubby (<2m tall) and slow growing whereas red mangroves (Rhizophora mangle) developing under optimal conditions may attain (in this geographic region) 20-22 meters in canopy height and 45 cm DBH.

Classification of mangrove forests.

Lugo and Snedaker (1974) have classified mangroves into 5 types that can be distinguished on the basis of topography and the pattern of water circulation (flushing). All of these forest types, which are described below, are found in Puerto Rico.

Fringe forests: This type occurs along the seaward edge of forests lining protected shorelines. There is usually a strong horizontal gradient in topography as well as a significant gradient in turbulence and tidal amplitude. Energy derived from the tides and waves decays rapidly inland where tidal flooding is further reduced by the rise in the mangrove floor. The reduced flushing inland results in the establishment of a salinity gradient. Toward the outer edge of the fringe, where greater energy levels prevail, the large, heavy seedlings of the red

mangrove (Rhizophora mangle) become established. Inland this wave and tide energy dissipates and in the higher, less flushed parts of the fringe the black mangrove (Avicennia germinans) becomes the dominant species. The interstitial salinity in black mangrove zones in P.R., Florida and other Caribbean sites averages $59 \pm 4\%$ whereas in the red mangrove belt, the mean of the interstitial salinities was only $39 \pm 1.3 \%$ (Cintron et al. 1978b). This is only about 3-4 ‰ above the salinity of sea water.

Since fringes are exposed they are subjected to periodic destruction by storms waves or scouring by strong currents. During storms, large amounts of debris may be deposited in the outer fringe, reducing circulation to the inner fringe and the basins inland (Cintron et al. 1978 c).

Riverine forests: This forest type develops along the edges of estuaries, often as far as the inland toe of the saline intrusion. It is best developed, however, in the lower course of the estuary. Water flows there are moderate to high and high nutrient inputs prevail. This combination of adequate fresh water and nutrient inputs allows the development of luxuriant stands.

On the periphery of the forest the dominant species is the red mangrove. This is an area where there is greater kinetic energy due to the combination of river flow and tidal motion. The complex root system of the Red Mangrove,

with its extraordinarily developed adventitious ("stilt") roots, allows the establishment of large trees on very unstable, soft soils.

The interstitial salinities in riverine forests are generally lower than those of other forest types, although they may vary significantly during the year. In the dry season, (when rivers run low), higher salinities are the rule, due to the greater influence of the salt intrusions. As river discharges increase during the wet season, the salt wedges are driven seaward and salts are leached from the sediments. In some of our riverine forests the interstitial salinity is in the order of 10-20‰ .

In the inner forest mixed stands of white mangrove (Laguncularia racemosa) and black mangrove occur. Riverine forests are highly productive with litter fall rates in excess of 4 g/m²/day. Canopy heights reach 20 meters in the best developed forests.

Overwash forests: These forests are formed on small islands or projections from land masses (peninsulas). They are characterized by intense flushing by daily tides. The high flushing rates do not allow the formation of strong salinity gradients nor the accumulation and aggradation of the soil or of nutrients, factors which usually lead to a succession of species toward the interior. True overwashed forests are thus monospecific

(dominated by red mangrove).

The amount of flushing and nutrient availability are critical factors that determine the structure and the fate of overwash forests. Thus, overwash islands in coastal, oligotrophic waters may not be as developed as those inside coastal lagoons where higher nutrient accumulation is possible. Excessive flushing leads to erosion and loss of the forest whereas extremely low flushing rates lead to accumulation of debris and vertical aggradation inside the forest with reduced flushing rate toward the core of the island. These islands thus evolve into fringe and basin forests. Cintron et al. (1978 a) have described the formation, aging and decay of these islands in southwest Puerto Rico.

Basin forests: This type of forest develops in inland basins influenced by salt water. Basins are characterized by sheet flows over wide areas of very small topographic relief. Basins generally receive substantial nutrient inputs during the wet season. During the dry season, salinity increases as the salt water intrusions become re-established. Due to the homogeneous sheet flows there may not be strong gradients in salinity within the basin. The dominant species are the white and black mangroves, although where the sheet flows converge into channels, the banks of these become lined with red mangroves. Black mangrove dominates those basin forests where high salinities

prevail (50‰) whereas white mangroves dominate low salinity basins. Mixed forests occur at intermediate salinities (30-40‰).

Depending on the water flow characteristics (hydro-period), basins may or may not be highly developed. Where weak but constant fluxes occur, there is oxygenation, nutrient transport, re-mineralization and there is no accumulation of toxic substances like H_2S and salts. In stagnant basins there is oxygen depletion; mineralization and nutrient re-cycling is slowed down. In these basins salt may accumulate in the sediments. A greater proportion of the gross productivity must be utilized by the system to provide for root ventilation (production of pneumatophores) and to survive at the higher salinity levels. Thus less energy is available for growth.

Some basin forests thus may be subjected to higher natural stresses, and therefore be more sensitive to additional stressors. It is not surprising that white and black mangroves, which are the dominant species inside the basins, have developed coppicing and may re-shoot from the trunk and limbs. This allows the tree to defoliate: totally 'hibernate' through a stressful period and flush again when normal conditions become re-established.

Basin forests may export less particulate matter than fringes or riverine systems due to the weak flows and higher residence times of the water inside the forest. However, a greater proportion of the export is in the

form of soluble organics that are pumped out of the forest by seasonal flooding, by higher tides and/or runoff.

Because of the above considerations basin forests may have variable characteristics. However generally basin forests are well developed with canopy heights which may reach 15-20 meters.

Dwarf forests: Dwarf forests are found in marginal environments where their structural development is limited by edaphic factors, probably the unavailability of nutrients. Mature trees in these forests are usually less than 2 meters tall. Salinity is not the limiting factor. Although the vegetation is limited in height, leaf size is not reduced as usually happens when mangroves are under the influence of a chronic stressor. This type of forest is different than those which may be considered scrub forests and which develop under the influence of a chronic stressor such as high salinity or cold stress. The dominant species in dwarf forests in Florida and Puerto Rico is the red mangrove but white mangrove dominated dwarf forests are found in Southern Brasil (Schaeffer-Novelli et al. 1979).

Classification of Puerto Rico's mangrove habitats

In Puerto Rico Lugo and Cintron (1975) grouped the mangrove formations into two broad categories; the north coast type and south coast type formation. This division is based on the different wave energy and precipitation regimes characterizing each coast. For example, the north coast of the island is within the Subtropical Moist Life Zone (Ewel and Whitmore, 1973), with precipitation greater than the potential evaporation. The south coast is located within the Subtropical Dry Life Zone. Here potential evaporation exceeds precipitation and periods of extended drought occur periodically. This marked inequality in the rainfall regime also results in a greater volume of land drainage toward the sea along the northern slopes. There, the coastal sector has been dissected and beveled into a broad, low-relief plain, crossed by several large streams. The south coast lacks permanent streams of any considerable size, and flows are intermittent.

The north coast is exposed to a high wave energy regime caused by swells generated in the North Atlantic. This high wave energy precludes the establishment of mangroves right at the sea edge. However active long-shore sand movement generated by the incoming wave trains and the large sediment loads brought to the coast by the many rivers have contributed to the formation of a

large dune system that extends along most of this coast. This marginal dune is a natural protection from the pounding of the sea, but it also interferes with the drainage of the coastal lowlands behind it. This leads to the formation of large lagoonal or marsh areas which have been successfully colonized by mangroves. The rivers that cross this broad coastal plain periodically flood these wetlands, bringing nutrients and leaching away salts. These extensive basins are dominated by white and black mangroves while the edges of the lagoons and canals are fringed with red mangroves. In the past, toward the limit of the influence of the salt intrusions fresh water swamps merged with the mangrove forest. Riverine forests occur along the lower portion of the rivers subjected to saline intrusions. Lugo and Cintron (1975) have shown that the end point of the landward saline water intrusion coincides with the landward penetration of mangrove forests on the north coast. Basin and riverine forest types are the predominant types on the north coast. These forests are directly coupled to the terrestrial hydrologic regime and depend on a constant nutrient supply to sustain the high productivity. This is important since mangroves are an open system with little recycling. The litterfall is eventually swept away by tides and sheet flows.

The south coast is less exposed to pounding seas. This is due primarily to the fact that the main land mass

shelters the shelf from the north Atlantic swell. The frequency of calm conditions here is over 85% during winter and summer in the coastal waters. Furthermore, the south coast shelf is generally broad and shallow and contains areas of luxuriant coral growth. This reef development is promoted by the lack of runoff and turbidity. The reefs generally form elongated ribbons parallel to the coast sheltering the inner shelf. This shelter allows mangroves to colonize the coastal areas in direct contact with the sea. Active coral growth by coral species such as finger coral (Porites porites) forms patch reefs within the inner shelf. Welch (1962) has shown how these Porites cays may be overgrown by the calcareous green alga Halimeda and the seagrass Thalassia. These platforms, when at the proper depth, are eventually colonized by mangroves. Because of the high evaporation and lack of runoff, basin forests are not as developed. High salinities develop inland, at only a short distance from the fringe. This results in a chronic stress which severely reduces the structural development within the basin. In fact, in the driest areas basin forests disappear and mangroves only form a narrow fringe backed by hypersaline lagoons and salt flats.

The high interstitial salinities cause a stunting of the vegetation (Cintrón et al, 1978 a) and the inner part of the mangrove fringe, and some basins may be dominated by scrub black mangroves.

South Coast forests are therefore dominated by fringe and overwash types. Basins may be stressed by high interstitial salinities and where developed, may contain scrub mangroves.

These mangroves are not as dependent on terrestrial nutrient and fresh water inputs for their survival and depend on the sea and access to freely circulating sea water for nutrient renewal and salt leaching.

Present Status of Mangroves.

Mangroves originally covered about 24,300 ha (Wadsworth, 1969). This estimate is based on the present coverage of coastal, mangrove derived soils. During the Spanish period mangroves were utilized for wood and charcoal. This extraction must have been intense, and by 1839 the extraction of red and buttonwood mangroves was banned for shipbuilding. (Carrera 1975). In 1866 the Servicio de Montes was established to prepare an inventory and assess the condition of the island's forests (idem) and by 1870 Fernández Ledon was reporting extreme and uncontrollable exploitation of the forest resources by private citizens.

In 1866 the 'Ley de Puertos' was promulgated. This law established a maritime-terrestrial zone of public domain and by definition mangroves fell within this area. However, in spite of this law many mangrove areas were transferred to private owners through 'Concesiones de la Corona'. These 'Concesiones' were given often for the construction of salt works or wood extraction.

A series of destructive hurricanes in 1825, 1837, 1867, 1876 and 1891 must have caused severe attrition of mangrove forests during this period (Carrera 1975).

After the Spanish occupation mangroves were threatened by the expansion of the sugar industry and the reclamation of mangrove areas for agriculture. In 1918, then Governor

Arthur Yager proclaimed a series of mangrove swamps as Insular Forests. This was justified since at the time charcoal was the only fuel being produced on the island. Charcoal was used widely in homes and bakeries and the mangrove forests, suppliers of this commodity, were being filled and destroyed, causing a shortage of fuel and an increase in its price. In order to preserve these forests and avoid the exhaustion of 'an important source of wealth' (Government of Puerto Rico, 1918), 5781 ha of mangroves were incorporated into the Insular Forest System. According to Carrera (1975) there were at this time 7990 ha of mangroves remaining on the island. Thus, 72% of the island's mangroves became Insular Forests.

In 1928 and 1932 two extremely destructive hurricanes crossed the island. The impact of these hurricanes is reflected in the earliest available aerial photography of the island (1937 P.R.R.A.) where many areas which now contain mangroves appeared at that time devoid of vegetation.

By 1938 mangrove coverage was estimated to have been reduced to 6392 ha, a loss of 1598 ha in the intervening 20 years (Carrera 1975). Holdrige (1940) reports that in the San Juan District one would have to cover a large area in order to find a 15 cm DBH tree. The depleted condition of the stands then, is clearly shown by the fact that stem densities were as high as 4200 stems/.7 ha (17,000 stems per acre) of which about 60% were less than 1.3 cm (1/2 inch) DBH and the largest stem was 9.4 cm

3.7 in) DBH (idem). Mangrove wood was utilized mainly for making charcoal and most trees were harvested when less than 8 cm in DBH (Roberts 1942). Mangrove swampland at this time was valued at \$5.00 to \$20.00 an acre, but its price increased tenfold when drained, ditched and banked (idem).

This period was one of intense and conflicting utilization of the mangrove forests. Whereas there was an increasing scarcity of wood for posts, poles, fuelwood and charcoal, there were increasing efforts for reclamation. By 1953 work was under way to reclaim 14,312 ha (35,780 acres) of swamp lands (Koenig 1953). This included 2,240 ha (5,600 acres) in the Tiburones drainage project, where actual work had commenced in February 1949, and 1672 ha (4180 acres) that were to be drained in the Loiza-Rio Grande area. The Loiza-Rio Grande drainage project had as its objectives (1) the protection of lowlands from the overflow of the Loiza, Herrera, Espiritu Santo and Lajas Brooks; (2) diversion of runoff from the higher lands to prevent flooding of the lowlands and (3) drainage of the lowlands by pumping where gravity flow was not possible. Studies for this project started in July 1948 and actual construction was begun in October 1950. The Fajardo Sugar Growers Association had already installed pumps in this area in 1928. (idem). Sugarcane in many of these organic soils gave a high yield of cane but a low yield of sucrose (Roberts 1942).

By 1959 an increase in mangrove areas is noted. This was probably primarily due to the fact that charcoal was no longer the primary fuel used in the island and the fact that Puerto Rico had been free of severe, destructive, hurricanes since 1932. In 1959 there were, according to Wadsworth (1959), 7190 ha of mangrove forests.

The decade of 1960 brought a new cycle of destruction as the island began to industrialize heavily. Large petrochemical complexes were established on the south coast and some mangrove stands were affected. For example, during the construction of the Phillips Petroleum terminal in Las Mareas large quantities of dredged material were deposited in an adjacent mangrove swamp, causing its total destruction (Figs. 1 and 2).

Near San Juan active development in the port area and urban expansion in the periphery of the city especially in the Hato Rey and Isla Verde areas led to the destruction of large mangrove areas. By 1968 mangroves covered 6596 ha, a loss of 594 ha since 1959. This coverage had been reduced to 6405 ha by 1974. Of these about 25 ha are in Culebra and 225 ha in Vieques.

Thus Puerto Rico now retains only slightly more than a fourth of the original mangrove cover estimated by Wadsworth (1969).

Methods

The purpose of the present study was to describe the

basic structural characteristics of Puerto Rican mangroves, the functional differences among the different types and the management implications inherent in the typing scheme.

The structural characteristics of the forest are described in terms of its canopy height, basal area and stem density. The number of species within each plot was also recorded. These parameters were combined by the use of the integrative formula developed by Holdridge (1967).

This index has been widely used in terrestrial vegetation studies by Holdridge (idem) and has been used by Pool et al. (1977) to describe the structure of mangrove forests in Florida, Puerto Rico, Mexico and Costa Rica. This index, known as the Holdridge Complexity Index (C.I.) is computed as follows:

$$c.i. = \frac{(\# \text{ of species}) (\# \text{ of stems}) (\text{basal area}) (\text{max. height})}{1000}$$

Although Holdridge only considers stems equal or greater than 10 cm (4 in) in diameter at breast height (DBH) for the computation of the Complexity Index, in mangrove forests there are generally a large number of smaller diameter trees. To include these in the index we have included in the enumeration all trees equal or greater than 2.5 cm (1 inch) DBH. This follows the practice of Pool et al. (1975 and 1977).

The complexity index is computed for a 0.1 ha plot.

Canopy height was measured with a Ranging^R optical distance measuring instrument. Basal area and density were initially measured in one tenth hectare plots but this approach was found to be extremely time-consuming. To avoid this problem we adopted the use of the wedge prism. This method, originated by Bitterlich (1947), makes it unnecessary to establish a plot. The observer merely employs an angle gauge, in this case a glass prism, and counts all those trees where the image separation is not complete. The prism is rotated from the center of the plot. The number of trees counted, times the prism basal area factor (B.A.F.) gives directly the stand's basal area. Metric prisms were used with calibration factors of 1 and 2.5 m²/ha.

Stem density was computed by measuring the diameter of each counted tree. Each counted individual represents as many stems as the prism basal area factor divided by the individual's basal area expressed in square meters:

$$\text{number of stems} = \frac{\text{B.A.F.}}{\frac{\text{DBH}^2}{4} (3.14) (10^{-4})}$$

In practice a program was prepared to compute stem density from the diameter data.

The Species Importance Value, developed by Curtis and McIntosh (1951) was adapted to integrate the influence

of a given species through its contribution to stand density and basal area. Frequency was not utilized as a contributor to the index since it cannot be readily computed when using the prism.

At each study area, interstitial and superficial salinities were measured using an American Optical hand held refractometer. This instrument is temperature compensated. Interstitial salinities were taken by introducing a PVC pipe into the soil with an end cap and perforated sides. After installation the water inside the pipe was removed with a hand pump and the tube was allowed to fill again by seepage. This water was then used to determine soil water salinity.

Results

Carrera and Lugo (1978) have divided the mangrove areas of Puerto Rico in 8 coastal segments (Fig. 3). We will utilize this scheme to describe the mangrove areas studied during the survey.

The structural data for each forest studied appears in Table 2. This table is ordered by coastal segment as shown in Fig. 3. The structural data contained is mean DBH, number of species, density of stems ≥ 2.5 cm DBH and ≥ 10.0 cm DBH, basal area of the plot based on all stems ≥ 10.0 cm DBH and ≥ 10.0 cm DBH, canopy height and the complexity index computed for stems ≥ 2.5 cm DBH and ≥ 10.0 cm DBH.

In table 4 are shown the Importance Values for live and dead trees (≥ 2.5 cm DBH) at each of the plots studied.

Unless otherwise noted in the text the complexity index given is the modified version, computed on the basis of stems ≥ 2.5 cm DBH.

Region I North - Central Coastline

This region extends from the Río Grande de Arecibo to the Río de Bayamón in Ensenada Boca Vieja. According to Carrera and Lugo (idem) this region has 474 ha of mangroves (7.3% of the mangroves of Puerto Rico) in nine forests.

Mangroves along this coastal segment are found behind sand dunes. The strong north coast swells maintain an

active sediment transport along the shore that clogs the mouths of the rivers that discharge on these sandy shores. Although rivers normally discharge over this bar, or the bar is permeable enough to allow some seepage, peak flows exceed the transmissivity of water causing a surge and lateral flooding. Frequently water accumulates in a low depression behind the coastal dune. Sea water seeps through the dune or is injected over it during times of very heavy seas. Wave swash is a sporadic but important contributor of salt especially to the basins which may be isolated except during periods of exceptional flooding. Along the rivers, salt enters as a discrete wedge along the river bed.

The Cibuco, La Plata - Cocal mangroves

These mangrove areas are typical of the mangrove forest types found in this coastal segment.

The Cibuco River has well developed basin and riverine mangroves. The largest part of this forest is west of the main river channel and mouth. This is an area where several drainage creeks join the main tributary. Surface salinities are 0.89‰ to 3.5‰ but a saline wedge under these brackish surface waters has salinities in the order of 17‰ to 26‰. These wedges penetrate inland along the main channel to 2.5 km and mangroves are found 1.5 km inland.

The riverine forest is dominated by large (> 10 m canopy height) red mangroves whereas the basins are dominated by white mangroves.

Further east, La Plata River provides an interesting example of the configurations attained by some river systems due to the high wave energy regime. The La Plata river has two outlets. This configuration is a result of the meandering of river mouths along the coast until a protected location is found. Rocky headlands provide protection from sand deposition by long-shore currents, when a river encounters the shelter of such a promontory its outlet is stabilized. In the case of the La Plata, meandering by the Cocal has left a series of oxbow lakes that contain mangrove forests (Fig. 4). These oxbow lakes are found just immediately behind the present coastal dune. The most common species there are white and black mangroves. The salinity of the oxbow lakes, recorded during the wet season (December 1979) was 10‰. This is in spite of the isolation of these lakes from the present channel of the La Plata river and the sea. At the time when the salinity was measured no salt stratification was noted.

These oxbow lakes are fringed primarily by white mangroves and scattered red mangroves. Inland from the outer fringe is a basin dominated by black mangroves (87% of the basal area is in Avicennia); numerically the dominance is 98%. Not surprisingly, the interstitial salinity in

this basin is 40‰ (measured during the wet season).

Since these oxbow lakes and their associated basins are isolated it may be expected that during times of drought the interstitial salinities may increase substantially;

hence the dominance by the more salt tolerant black mangroves. Canopy height of these trees is a substantial

13 meters; stem density (≥ 2.5 cm) is 467/.1 ha, the basal area is 2.0 m^2 /.1 ha and the complexity index is 24.30.

A significant percent of the basal area is in stems ≥ 10 cm DBH (70%). The mean DBH at this site was 12.6 cm.

The riverine forest along the main channel of the Río Cocal (Fig. 4) is dominated, in the lower estuary, by large (canopy height 15 m, 14.6 cm DBH) red mangroves. The mouth of this river is blocked for most of the year by a well developed sandbar. The surface of the estuary (to a depth of about 50 cm) was very brackish (0‰ to 2‰); at 75 cm, however, the salinity increased to 13‰ and at 1.5 meters it was 24‰. The salinity by the mangrove roots was 2‰.

The outer red mangrove fringe is often narrow, only one or a few trees wide, and backed by a white mangrove dominated basin (100% of the basal area was in this specie). This basin in the lower estuary is open and parklike, with the large trees (mean DBH = 20.2 cm) well separated from each other. The interstitial salinity was 16‰ only. Canopy height was 7.5 meters, the stem density was a low 37.9/.1 ha, the basal area was 1.15 m^2 /.1 ha and the

complexity index was only 0.33. All of the individuals in the stand that was visited had a DBH greater than 10 cm.

Mangroves extend inland as far as 3.5 km, possibly to the end of the saline intrusion. The thickness of the riverine forest and its development decrease greatly inland. Red mangroves give way to whites as the dominant species lining the channel. Canopy height decreases inland as well as the diameter of the trees. In places dense stands of the fern Achrostichum line the channel.

Salt intrusion in this area is blocked by a series of gates built to protect the sugar cane fields. It is very possible that mangroves here were once far more developed than they are today. Encroachment of terrestrial ecosystems by reclamation probably took place as the lands were utilized for sugar cane and salt control has reduced the degree of salt intrusion, reducing the mangrove habitat and allowing fresh water species to compete successfully against mangroves.

Although the Cocal is a riverine mangrove forest this area behaves during a greater part of the year as a basin forest. This is due to the stagnation of the water and a result of the formation of a bar at the river mouth.

Region II North - East Coastline

This region, which extends from Boca de Cangrejos in Carolina to Punta Mata Redonda in Fajardo, contains

2,021 ha of mangroves. This represents 31.1% of the mangroves of Puerto Rico. The largest mangrove swamp in Puerto Rico, the Piñones-Torrecilla-Vacia Talega complex, is within this segment. This particular swamp covers 1,382 ha.

The Piñones complex extends from the edge of the city of San Juan to the Río Grande de Loíza. In the past, mangroves extended uninterruptedly from that river to San Juan Bay. A series of canals run parallel to the coast, draining the broad mangrove area into the coastal lagoons of Piñones and Torrecillas. Mangroves extend here 2.5 km inland, colonizing the broad shallow basin behind the coastal dune and extending inland to the end of the saline intrusions.

The area is periodically flooded by the Río Grande de Loíza, which contributes nutrients and fresh water and leaches away salt accumulations. Precipitation in this coastal sector is over 1,700 mm, and evaporation 1,836 mm. Although evaporation exceeds precipitation here, as well as at all other coastal locations in Puerto Rico, mangroves here receive large amounts of runoff and flood waters from the moist interior. These inputs reduce the rate of salt buildup and during flooding episodes leach excess salts. Table 1 from Lugo and Cintrón (1975) shows surface and interstitial salinities at this forest. The mean interstitial salinity for the red mangrove dominated zones is in the

order of 35‰ whereas the black mangrove and mixed forests have higher interstitial salinities.

In table 2 we summarize the structural data available for three areas within this forest. The Vistamar plots are within a basin type forest flanking Canal Blasina. Interstitial salinities here were lower than at other locations within this forest. Plot 1 averaged $21‰ \pm 1$ (SE), plot 2 was $25‰ \pm 0$ (SE) and plot 3 was $30‰ \pm 0$ (SE). Plot 1 is dominated by white mangroves and its high complexity index (c.i. ≥ 2.5 cm = 92.2) is due not only to the high basal area ($3.25 \text{ m}^2/.1 \text{ ha}$) but also a high stem density (671 stems/.1 ha). This plot had a high frequency of dead stems (26%); the actual stem density was 905 stems/.1 ha). The total standing basal area is $4.50 \text{ m}^2/.1 \text{ ha}$. The mean DBH was 9.9 cm.

Plot 2, farther inland within the basin, has a lower complexity index (15.8) than plot 1 but a higher complexity index when computed for stems greater than 10 cm DBH (15.8). The dominant species here is also the white mangrove. The total stem density is about 5 times less than at plot 1, the mean DBH was 18.1 cm and the total standing basal area is $3.5 \text{ m}^2/.1 \text{ ha}$ of which $2.9 \text{ m}^2/.1 \text{ ha}$ is living basal area. Dead stems were 31% of all stems counted, but only 17% of the total basal area is in dead trees. These data suggest that this is a mature stand in which most of the dead basal area is in younger, small DBH individuals that have failed to reach the canopy.

The third plot, well within the basin, reflects the increase in soil salinity, the more rigorous conditions, and a change in dominance from white to the more tolerant black mangrove. The complexity index here is the lowest computed (7.02) and there are fewer large diameter trees in the stand. A large number of trees were dead. Of a total standing population of stems of 577/.1 ha only 39% were alive. Of the living basal area of 1 m²/.1 ha, 0.7 m²/.1 ha is contributed by black mangrove and 0.3 by whites. There is a total of 1.2 m²/.1 ha of dead basal area of which 1.1 m²/.1 ha is due to dead white mangroves.

Further east, four plots were studied by Pool et al. (1977), whose data are included in Table 2. The dominant species in terms of importance value in plots I and IV was the white mangrove whereas the dominant in plot II was the red mangrove and in plot III was the white mangrove. The mean complexity index for these plots is 16.7. The mean stem density is 235/.1 ha.

Near the Río Grande de Loíza, in the Vacía Talega sector, some of the best developed red mangrove trees in this forest are found. The complexity index for this stand is 15.4 and the stem density is 189/.1 ha (Pool 1977). The surface salinity here is variable, approaching 0‰ during the rainy season and 30‰ during the dry season. The interstitial salinity, however, is a fairly constant 37-38‰. During the dry season the area may dry completely. The seasonal change in water level is 0.68 m.

The mean canopy height for all of the stands studied in this forest is 13 m.

The Espiritu Santo River

The Espiritu Santo river mangroves occupy 131.4 ha. Mangroves occupy a narrow fringe of about 100 meters width on both sides of the river channel. They extend 3.2 km upstream along the main channel and have also invaded two small tributaries; the Caño San Luis and Quebrada Juan González. The most highly developed forest is the riverine mangrove along the lower portion of the estuary. This observation is supported by data obtained by Mosquera (1979) who found the highest complexity index at a station about 500 meters from the mouth.

In this area two 50 m transects were established perpendicular to the river (Fig. 5). A profile along transect 1 (Profile 1) shows an uniformly low salinity value of 6‰. Red mangroves are the dominant species at the margin. White mangroves increase in importance inland. A relatively high proportion of the red mangrove stems in this area were dead (26.2%) whereas only 2.9% of the dead stems were white mangroves.

The structural development of the vegetation along the margins is impressive. The canopy height reaches 16.5 m; stem densities are variable, 146-323/.1 ha in the plots studied. Basal areas were also high: 3.25-3.70 m²/.1 ha with a large percentage of this basal area (60-100%) in trees \geq 10 cm DBH. The mean DBH's at these plots were 22.97 and 13.43 cm. The complexity indices

for these stands were 17.29 and 34.64.

Inland from the outer margin, there is a decrease in structure. Canopy height decreases to 12-14 m. Basal area also decreases to 1.45-1.75 m²/.1 ha and density is reduced to 68-70 stems/.1 ha.

Profile 2 shows the characteristics of the forest along transect 2. In this area, in the inland plot (no. 2) red mangroves (importance value 81.8%) shared this site with white mangroves (I.V. 11.2%) and Pterocarpus officinalis (I.V. 7.0%) a fresh water species.

Region III Eastern Coastline.

According to Carrera and Lugo's (1978) scheme, this coastal segment extends from Punta Mata Redonda to Punta Patillas. The area contains 1284 ha of mangroves in nine forests. Riverine and basin type forests are the dominant physiographic types. The mangroves in the region occupy two different life zones, the Subtropical Dry and Subtropical Moist (Ewel and Whitmore, 1973).

The northern portion of the east coast is sheltered from the north Atlantic swell by the Cordillera chain. These islands, which form an almost continuous barrier from Fajardo to Culebra, are the emerged tops of eroded, cemented Pleistocene dunes. Further protection from southeasterly swells is afforded by a series of offshore bank barrier reefs and the island of Vieques. This shelter is lost south of Punta Lima and physiographic conditions

are less favorable for mangrove development south of that point.

Medio Mundo

The largest mangrove stand in this coastal segment is Puerto Medio Mundo which comprises 412.5 ha. This mangrove complex (Fig. 6) extends into Medio Mundo Bay and includes extensive stands of dwarf red mangroves, a physiographic type previously not reported for Puerto Rico.

Pool (1977) reports the following characteristics for the fringe forest here: a canopy of intermediate height (8.5 m), high stem density (569/.1 ha), with few stems greater than 10 cm diameter (26/.1 ha), basal area was 1.67 m²/.1 ha of which only 0.34 m²/.1 ha was contributed by stems greater than 10 cm diameter. The complexity index was 16.2 but only 0.2 when computed for stems greater than 10 cm DBH.

Various stands facing Medio Mundo Bay have basal areas of 1.25 m²/.1 ha and canopy heights of up to 9 meters. The fringes facing Medio Mundo Bay and Pasaje Medio Mundo have broad shallow terraces seaward. These are covered by Thalassia which exports large amounts of litter into the mangroves and contributes to build a deep organic peat. Inland, the red mangrove dominated fringe terminates in a distinctive berm. Further inland from this berm, where the salinity is high (50‰) scattered black mangroves

are found. In one transect across a fringe we observed the following structural changes: at the outer margin the interstitial salinity was 42‰ and canopy height was 8.5 m; 18m inland the canopy height was 10 m and the interstitial salinity remained unchanged, at 70 m the canopy height had decreased to 7 m and the salinity had increased to 46‰, from this point on the canopy height decreased to 3.5 m at 120 m where the salinity reached a high 62‰. This entire stand was of red mangroves. A zone of high mortality was observed at 120 m where the interstitial salinity was highest.

The dwarf mangrove forest is located within the Medio Mundo lagoon system (see photographs 1 and 2). This forest is made up of low, twisted-stemmed red mangroves (height about 1.7 m) growing on a deep (1.8 m) peat of mangrove origin overlaying white calcareous sand. The interstitial salinities here are not limiting ($\sim 38‰$) and the stunting must be related to edaphic factors other than excess salts.

Profile 3 illustrates the contrasting physiognomy of the mangroves in this area. This profile was made across one of the channels inside the lagoon system. On both sides the forest is composed of monospecific stands of red mangroves; however the contrast in structure is extremely marked. In plots 1 and 2 the forest is composed of straight boles which attain 16 m. The basal area at plot 1 was $4.7 \text{ m}^2/.1 \text{ ha}$ with a stem density of 2,076 stems/.1 ha.

These high stem densities were associated with a low DBH (6.7 cm). Plot 2, located 20 meters in from the margin, had a lower basal area ($3.7 \text{ m}^2/.1 \text{ ha}$) and density (333 stems/.1 ha) and most of the stems had a DBH greater than 10 cm. Of the basal area cited fully $3.0 \text{ m}^2/.1 \text{ ha}$ were contributed by stems greater than 10 cm in diameter.

In sharp contrast the opposite side is characterized by the dwarf stand. Notice that canopy height decreases sharply from the edge where it is 3.4 m to the basin where it may be only 1.5 m high. The trunks of these trees are twisted and leaf scars are very close together showing that very little growth of the branches takes place.

Ensenada Honda

Further south of the Medio Mundo area is the Ensenada Honda Harbor. The southwest corner of this harbor contains a 81 ha mangrove stand (Fig. 7). A 465 m transect across this forest is shown in Profile 4.

Interstitial salinity rises from 35‰ near the seaward edge of the forest to a peak of 62‰ about 200 m inland. From this point the salinity decreases inland to 33‰ at the inner edge. Four plots were made along this transect. The structural characteristics of these plots are shown in Table 2. The outer fringe is dominated by red mangroves which have a canopy height of 5.7. Stem density was high (749 stems/.1 ha) of which none were ≥ 10 cm

in DBH. The basal area was low ($0.60 \text{ m}^2/.1 \text{ ha}$). The complexity index was 2.56. The mean DBH was only 3.4 cm.

Plot 2, 50 m inland had a higher canopy height (7.2 m), very high stem densities (1,183 stems/.1 ha) and a basal area of $2.05 \text{ m}^2/.1 \text{ ha}$. The complexity index is high due to the high stem density and the presence of 3 species. However the mean DBH was only 5.7 cm.

Plot 3, 435 m inland is within a black mangrove fringe. The canopy height here is 3.51 m, stem densities are high (913 stems/.1 ha) but the basal area is low ($0.80 \text{ m}^2/.1 \text{ ha}$). The complexity index is also low 3.51. The mean DBH is 3.5 cm.

At the innermost plot (Plot 4) the canopy height was 13.6 m and stem density was 168 stems/.1 ha, of these 91 stems/.1 ha were ≥ 10 cm DBH. The basal area was $1.75 \text{ m}^2/.1 \text{ ha}$ of which $1.30 \text{ m}^2/.1 \text{ ha}$ was in stems ≥ 10 cm DBH. The complexity index was 4.00.

The high interstitial salinities 60 to 70 m inland are associated with a stunted vegetation. Further inland the salinity decreases but there is a stand containing dead black mangroves. The high salinities and death of parts of this stand are probably related to the construction of a pier and road that crosses the stand. Patterson-Zucca (1978) has described a similar occurrence in the Daguao area further south.

The Daguao River

Patterson-Zucca (1978) studied a mangrove stand south of the Río Daguao. The landward portion of three transects within a basin had basal areas in the order of 1.39, 0.92 and 1.91 m²/0.1 ha whereas the seaward tree basal areas were 0.98, 0.81 and 1.01 m²/0.1 ha. Landward densities were 243, 234 and 351 stems per 0.1 ha (mean 276.4 stems/0.1 ha). The corresponding seaward values were 212.0, 150.0 and 182 stems/0.1 ha (mean 181.4 stems/0.1 ha). Red mangroves had the highest densities in the seaward portion of the transects whereas black mangroves had the highest densities in the landward portions. The soil salinity for the three transects were 51.9, 54.6 and 62.4‰.

A small berm separates the outer basins and the red mangrove margin from the inner black mangrove dominated basin.

Antón Ruíz River

These mangroves cover an area of approximately 295.3 ha (Fig. 8). This is the largest remaining riverine stand in the island. Whereas north of Punta Lima mangroves can be found fringing the coast, the coastal segments south of that headland are subjected to higher wave energy levels. Mangroves occur as basins or riverine stands. These wetlands receive high inputs of fresh water runoff.

The mangroves of the Antón Ruíz River are among the best developed on the island. Canopy height is from 18 to 22 m, stem densities are 114 to 407 stems/.1 ha of which 29 to 82 stems/.1 ha have diameters greater than 10 cm. The basal area is 1.5 to 2.55 m²/.1ha and 73%, on the average, of this basal area is in stems greater than 10 cm in DBH. The mean DBH for 3 plots was 17.73 ± .87 cm. The complexity index varied from 16.03 to 45.44.

A transect 130 m long was completed perpendicular to the river margin (Profile 5). This transect ran through a mixed stand of red, white mangroves and Pterocarpus. The highest soil salinity value was 15% at plot #1 but salinity decreased rapidly inland to 0% at 60 meters. A small drainage channel at this point was crossed by the transect. These channels bring fresh water and prevent salt buildup in the soils.

In plots 2 and 3 Pterocarpus is the dominant species with an importance value of 59% and 68% respectively whereas plot 1 is dominated by red mangroves (I.V. 56.7%). No mortality was observed in the stand studied except for some fallen trees in the river margins.

The Antón Ruíz mangrove contains the largest remaining stand of Pterocarpus (bloodwood or palo de pollo) in Puerto Rico. Fully 2/3 of this forest is dominated by Pterocarpus. Some of the trees at the western edge of this stand are real giants, reaching heights in excess of 20 meters with thick stems and wide-spread buttress roots reaching more

than 3 m up the trunks. Another uncommon swamp tree, Anonna glabra (Cayure or pond apple) is reportedly found around pond margins in this swamp.

Region IV Southern Coastline

This segment extends from Puerto de Patillas to Bahía de Tallaboa. It contains 939 ha in 15 mangrove areas. One of the largest stands is the mangrove complex between the village of las Mareas and the Central Aguirre in Salinas. This area includes the Mar Negro area and the offshore islands of Cayos de Pájaro and Cayos de Barca. According to the Natural History Society of P.R. (1972) there are 301 ha. of mangroves on the mainland, 39 ha in the inshore islands and 60 ha in the outer keys. Of these 400 ha, 213 ha are of high mangroves 4.5 to 10 m tall and include trees up to 22.5 cm DBH. Stem densities varied from 370 stems/.1 ha to 3,137 stems/.1 ha. These very high stem densities were due to trees less than 2.5 cm in DBH. Basal areas varied from .62 m²/.1 ha to 3.28 m²/.1 ha. The high mangroves are mostly reds.

Behind the tall red mangrove fringe are very shallow hypersaline lagoons that contain black mangroves. These trees are seldom more than 3 m high and many individuals are dying. This report suggests that this mortality may have occurred during the severe droughts which affected the south coast in the late sixties.

Mortality due to hypersalinity is a normal event in this dry region. Mangrove fringes undergo a cyclic growth and deterioration pattern. This is described in detail by Cintrón et al. (1975; 1978a), and will be discussed later in this text.

In general, because of the small tidal amplitude, the high evaporation and lack of rainfall and runoff, there is a tendency for salt to build up in the basins behind the coastal fringe in these south coast sites. Salinities rise very rapidly and reach such high levels that they are not even tolerated by the most tolerant species, the black mangrove. Where this effect is severe only a narrow coastal mangrove fringe dominated by red mangroves is found. Inland from this narrow outer fringe is a hypersaline lagoon frequently containing dead black mangroves. The interstitial salinities in this hypersaline environment usually exceed 90‰.

Cayos Caribe

These islands are part of an arcuate ridge which extends from Punta Pozuelo west toward Cayos de Pájaro (Fig. 9). They are fronted by a broad terrace containing Thalassia. This terrace is a reef flat. Seaward of this flat the slope steepens and there are stands of Acropora palmata (Elkhorn coral). This zone extends about 6 meters off the flat; then it drops at a steeper angle to about 20 meters. The dominant coral in the deeper reef is

Montastrea annularis (Star coral).

There are also seagrass beds landward from the Cays. This area is therefore of particular interest because of the proximity and interactions between three important marine systems: the seagrass beds, the mangroves and the coral reef.

The islands are of a particular physiography too; they (Photograph 3) are tear shaped, separated by scour channels. The outer edge is mostly red mangrove surrounding an inner hypersaline lagoon.

A transect run east to west along one of these cays (Profile 6) clearly shows the salinity rise toward the central basin. The maximum salinity at this time was only 52‰. However, in a similar transect at Punta Pozuelo the interstitial salinity reached 97‰ only 15 m from the fringe. Canopy height decreased sharply toward the inner basin from a maximum of 10 m to less than 2 m inside. The dominant species at the fringe was red mangrove (I.V. 97.3%). The basin contained dead red and white mangroves.

The eastern fringe had a basal area of 3.00 m²/.1 ha and a mean DBH of 14.4 cm. The stem density was 221 stems/.1 ha, 191 stems/.1 ha had DBH ≥ 10 cm. Of the total basal area, 2.8 m²/.1 ha, was in stems ≥ 10 cm DBH. The complexity index was 11.93 and when computed for trees 10 cm in DBH it became 9.63.

A plot near the Western fringe had the following characteristics: canopy height 9.60 m, stem density 255

stems/.1 ha (102 stems/.1 ha \geq 10 cm), basal area was 2.10 m²/.1 ha (1.40 m²/.1 ha \geq 10 cm) and the complexity index was 3.43 (0.91 when computed for stems \geq 10 cm DBH).

Plot 1 had a high seedling density (66/m²) with a mean height of 61.9 cm. Plot 2 contained no seedlings and plot 3 had only 16 seedlings/m² with an average height of 72.5 cm.

Laguna Las Salinas

This mangrove forest is located west of the city of Ponce and comprises an area of 13.6 ha of forest in the northern and southern portions of the lagoon (Fig. 10). A larger area containing approximately 40 ha extends behind the coast to the northeast. This stand consists of patches of stunted vegetation (Photograph 4). The lagoon's inlet has been blocked by sand which impedes tidal flushing.

Four sites, labeled A thru D were established here to measure the interstitial salinities. Site A had an interstitial salinity of 55% , B averaged 58% , C was 68% and D reached 108% . Sites A thru C were characterized by dead black mangrove trees with buried pneumatophores. Near site D were found highly stressed scrubby (1.15m) red mangroves with twisted branches and succulent leaves.

A transect 80 m long (Profile 7) was run along the fringe mangroves at the southern end of the lagoon and near the inlet. The dominant species here was red mangrove with an importance value of 96.9%. The interstitial salinity here was only 35% . Canopy height near this area was 9.0 m, stem density was 386 stems/.1 ha (160 stems/.1 ha \geq 10 cm), basal area was 2.60 m²/.1 ha (1.65 m²/.1 ha \geq 10 cm) and the complexity index was 18.0 (4.75 for stems \geq 10 cm). No mortality was observed in this area.

Region V - South Western Coastline

This coastal region extends from Bahía de Tallaboa to Puerto Real. It contains 998 ha of mangroves, 15.3% of the mangroves of Puerto Rico (Carrera and Lugo 1978).

The shelf area within this coastal segment widens considerably west of Guánica Bay. There it reaches a minimum width at the head of the Guayanilla Submarine Canyon which lies only 2 km offshore (1.1 nm). Off Punta Jorobado the 200 m contour is 4.1 km offshore (2.2 nm). The south coast shelf reaches its maximum width off Punta Tocón where the shelf edge is 9.4 km (5.1 nm) offshore. On the west coast the shelf area widens even more, and off Punta Carenero (Puerto Real) the dropoff is 25 km (13.3 nm) offshore.

This is a very dry coastal segment; in fact it is the driest area in Puerto Rico. Annual rainfall in Ensenada (near Guánica) is 861 mm (U.S. Dept. of Commerce 1970). Unpublished data kindly supplied by Mr. Jorge Rivera López from Magueyes island, yields an even lower annual average (614 mm per year). Evaporation data from the Lajas Experimental station shows that potential evaporation in this region is in the order of 1939 mm.

Under these circumstances it is not surprising that the region lacks permanent streams. The aridity and lack of terrigenous sediment inputs and the wide and shallow shelf area are factors which contribute to promote and support extensive development of coral reefs. The

area, furthermore, is sheltered from severe swell.

Fringing reef development is a prominent feature of this coastal segment. Reefs provide shelter to the inner shelf area and make possible the establishment of mangroves along the coast and on emergent cays where shelter is adequate. The most common mangroves are fringe and overwash types whereas basins are less developed (along the south coast) due to the lack of fresh water availability.

Guánica Bay mangroves

Mangroves in Guánica bay cover an area of 12.8 ha restricted to a narrow fringe at the northeastern side of the bay (Fig. 11). The narrow fringe (about 15 m) is backed by a wide salt flat (Photograph 5).

A 100 meter transect was run along the thickest portion of the fringe and three plots were established at 5, 50 and 100 m (Profile 8). The fringe, where there is the greatest structural development, is dominated by red mangroves (I.V. 75%). White mangroves (I.V. 25%) are also present in the fringe. The canopy height was 10.8 m and the stem density was 251 stems/.1 ha (113 stems/.1 ha \geq 10 cm). The basal area was 2.3 m²/.1 ha of which 1.65 m²/.1 ha is contributed by stems greater than 10 cm DBH. The complexity index was 12.47 (4.03 when computed for stems \geq 10 cm DBH).

Salinity, species composition and structural characteristics changed inland. Interstitial salinities were

45‰ at the outer fringe and increased to 55‰ 100 m inland. Since these measurements were made during a very wet season, it is expected that soil salinities may reach values substantially higher than those here reported.

Plots 2 and 3 are composed of pure stands of black mangroves. The canopy height here was 4.5 m and stem densities were 177 stems/.1 ha (41 stems/.1 ha \geq 10 cm). The basal area was 1.00 m²/.1 ha (0.40 m²/.1 ha \geq 10 cm). This stressed plot, as expected, had a low complexity index of 0.80. A zone of dead black mangroves was found at the edge of the forest toward the salt flat.

The Offshore Islands

As reported earlier, the shelf area of the southwest corner is broader than in most areas of the island. Off Parguera the shelf has a width of 8 to 10 km (Morelock et al 1977). The average depth is 15 to 18 m from shore to shelf edge.

Morelock et al (1977) have conveniently divided the shelf into three sedimentary provinces, namely an outer shelf, a middle shelf and an inner shelf. The outer shelf province is a higher energy environment. Wave energy decreases rapidly toward the inner shelf as it is dissipated against the arcuate, elongated reefs that have their long axis parallel to the coast. The inner shelf province, which lies between Cayo Enrique and the shoreline, is a low wave energy environment. In the innermost

part there is a prevalence of fine grained carbonate silts that tend to accumulate among mangrove roots (idem).

Carbonate sediments, sands and silts produced by coral fragments, mollusks, coralline red and calcareous green algae, echinoderm fragments and the remains of other calcareous organisms are the dominant sediment types.

Reefs have developed on this shelf and now cover about 20% of the area (Morelock et al 1977). The emergent portions of many inshore reefs have been colonized by mangroves (Fig. 12) Cintrón et al. (1978b) have shown that the degree of exposure to the incoming wave regime is a factor limiting the development of mangroves in these offshore islands. Mangrove development is greatest in a zone where intermediate energy levels prevail. The outer cays are extremely exposed and the strong surf does not allow the deposition of the fine sediments needed for the establishment of red mangroves. Occasionally white mangroves will become established on some of the sand keys and develop small but impressive stands. This is not the rule, however. Generally the most exposed keys are devoid of tree cover. On some, mangroves may gain a temporary hold for a time, only to be destroyed during large storms.

Recently a severe storm passed south of Puerto Rico, generating strong swells that hit the southwest coasts with particular force. Photographs 6, 7 were taken on

some of the offshore keys near La Parguera. Large calcareous blocks (see Photographs 8 and 9) were piled into the mangroves growing atop this cay. Waves surging over the reefs and transporting rocks and boulders caused uprooting of the small trees and extreme abrasion of most stems. Most of these trees were girdled by the abrasion and defoliated soon after the storm. The sheltered portion of many stands survived the storm. This damage, impressive as it is, was caused by a storm that did not pass especially near the area; at its closest approach it was still 167 km (90 nm) to the south. Given these circumstances it is understandable why mangrove development at these offshore cays is generally limited to bushy, low mixed stands of red and white mangroves.

Mangrove development is best at intermediate energy levels like these prevailing in the outer part of the inner shelf and the inner part of the middle shelf. Here, although substantial wave energy dissipation has already occurred, there is still enough energy to maintain constant flows of water through the islands. Here we find true overwash islands. Examples of islands of this type are Cayo Enrique and Caballo Blanco.

Cayo Enrique

This island's soil elevation is low (-0.15 m below mlw), and it is flooded by most daily high tides. The interstitial salinity is 36‰ and barely surpasses that of the

surrounding waters (35%). The island is dominated by a single mangrove species, red mangrove. This species has a seed large and heavy enough to allow it to colonize this environment where currents and waves would carry away smaller seedlings.

Canopy height across the island is almost uniform (Profile 9), attaining a maximum value of 9.2 m. Stem densities were 659 stems/.1 ha (64 stems/.1 ha \geq 10 cm) and basal area was a high value of 2.70 m²/.1 ha (0.60 m²/.1 ha \geq 10 cm). The complexity index was 16.37 (c.i. \geq 10 = 0.35). The mean DBH was 8.1 cm. Seedling density was 60 per m² with a mean height of 73.5 cm.

Caballo Blanco

Another overwash island is Caballo Blanco. This island is more sheltered than Cayo Enrique and it is more elevated (+.10 m above mlw). It is composed of a thick bed of organic peat over a coralline foundation. The peat substrate is highly permeable and salinities here are also stable across the length of the island although higher (40 - 45%) than at Enrique.

Canopy height reached 14.8 m. Stem densities varied from 63 to 140 stems/.1 ha (33 to 104 stems/.1 ha \geq 10 cm respectively). Basal area was 1.00 to 1.90 m²/.1 ha (\geq 10 cm stems contributing from 0.80 to 1.75 m²/.1 ha). The complexity index was 0.93 - 3.80 (c.i. = 0.39 - 2.60 for stems \geq 10 cm). A pictorial representation of a

transect across Caballo Blanco is shown in Profile 10.

Inner shelf islands

Further inside the shelf although shelter increases, the energy needed to maintain adequate flushing across the island decreases. The islands within these sheltered portions of the shelf normally have very strong transverse salinity gradients.

Although these islands initiate their development as overwash mangroves established atop Thalassia covered patch reefs, the horizontal expansion of the island and the development of a dense network of roots contribute to dissipate even further the energy of the moving water. Inside the island there is relative stagnation and accumulation of organic remains. These contribute to elevate the soil, reducing even more the frequency of tidal flooding. Salt buildups begin and there may be a replacement of the pioneer red mangrove by the more salt tolerant black mangrove. The island at this stage then develops a core of black mangroves fringed by red mangroves. If the salinity buildup is slow the black mangroves in the core may be of considerable size and diameter. In some other islands the salt buildup is so rapid that only stunted black mangroves develop. Continual accumulation of salt eventually leads to the death of the mangroves at the core. These islands have reached their maturity and have a hypersaline lagoon in their

interior. This scheme is described in Fig. 13 from Cintron et al (1978a). The lines at the left of the illustration indicate that storms may contribute to 'rejuvenate' these islands by leaching salts and enhancing water circulation to the core by partial destruction of the fringe. Extreme storms would result in the initiation of the cycle again.

In Fig 14 from Cintron et al (1978b) a summary is graphically presented of the development of mangroves in this shelf area.

Cayos Turrumote and Laurel

As noted previously, white mangroves can develop fairly complex stands on the offshore cays. This development may have been aided by the fact that Puerto Rico has not suffered a major storm since 1932 except for Hurricane Betsy (Santa Clara) in 1956.

Cayo Turrumote and Cayo Laurel are examples of sand cays with fairly complex stands of white mangroves. A transect across Cayo Laurel is shown in Profile 11. This cay is high and therefore seldom flooded except by storm surges. The substrate is of coarse coralline sand, pebbles and boulders.

Canopy height in this cay reaches 7.3 m. Stem density was 281 stems/.1 ha of which 236 stems/.1 ha had a diameter greater than 10 cm. The total basal area was 3.7 m²/.1 ha of which 3.4 m²/.1 ha was contributed

by the ≥ 10 cm DBH stems. The complexity index is 15.18 (C.I. $\geq 10 = 11.71$). The dominant species is white mangrove with an importance value of 86.13%. Reds are restricted to the sheltered (north) edge of the island facing the lagoon reef.

During the passage of Hurricane David a great deal of the rocky and coarse sand substrate was washed away by the surge over the cays, leaving the root systems exposed. Some partial defoliation occurred at the exposed south side. A wide reef apron contributed to dissipate the energy of the surge and protect the vegetation.

Pitahaya

This mangrove stand extends between Punta Guayacán and Punta Pitahaya and is the largest and best developed stand in the southwest corner of Puerto Rico. The forest here reaches a thickness of one kilometer and stretches for 6.5 km along the coast. It has developed in front of a broad valley which cuts inland toward Barrio Llanos. The valley may concentrate runoff in this area. To seaward the stand receives the shelter of Margarita Reef, a 3.1 km long bank barrier reef located 1.5 km offshore.

The Pitahaya area (Fig. 15) is characterized by well developed fringe forests and poorly developed basin mangroves. In the inner portions of the stand where tidal flushing is reduced, the salinity increases and there

is a reduction in forest structure as well as changes in species composition. Further inland the vegetation gives way to barren salt flats.

Two transects were made at this location. Transect 1 ran 90 meters inland from an inner channel (Profile 12). A steep salinity gradient was observed: Salinity increased from 40‰ near the edge to 70‰, 50 m inland. Red mangrove was the only species in plot 1 (I.V. 100%) whereas at plot 2, about 30m inland, white mangrove stems made up 2.76% of the stem population. Further inland both of these species gave way to black mangrove which formed a pure stand.

The maximum structural development was recorded in the fringe at plot 1. There the canopy height was 12.2 m, stem density was 277 stems/.1 ha (170 stems/.1 ha \geq 10 cm). The mean DBH was 13 cm. Basal area was 2.7 m²/.1 ha (2.3 m²/.1 ha was contributed by stems \geq 10 cm). The complexity index was 9.12 (c.i. \geq 10 = 4.77).

At plot 2 canopy height was 6.0 m, stem density was a high 798 stems/.1 ha (of which only 10 stems/.1 ha were greater than 10 cm). Basal area was 1.85 m²/.1 ha (0.10 m²/.1 ha contributed by stems \geq 10 cm). The complexity index (17.72) is high due to the high stem density but low when computed for stems \geq 10 cm (0.01).

Seedling density at plot 1 was 55 seedlings/m².

Transect 2, at the outer fringe of the mangrove forest (Profile 13) penetrated 80 m inland. Unlike the area of Transect 1 wave energy is relatively high here, as are

turbulence and tidal exchange. This is reflected in the soil salinity along the profile, which remained fairly stable, varying only from 35‰ at the outer fringe to 38‰ at 80 m.

The vegetation is composed of a pure stand of red mangroves. Plot 1 had a canopy height of 13.8 m, stem density was 294 stems/.1 ha (214 stems/.1 ha \geq 10 cm). Basal area was 3.80 m²/.1 ha (3.50 m²/.1 ha in stems \geq 10 cm). The mean DBH was 15.43 cm. The complexity index was 15.42 (c.i. \geq 10 = 10.34). Dead stems were 5.16% of the total stem count.

At plot 2, 75 m inland, canopy height was 8.8 m, stem density was 283 stems/.1 ha (50 stems/.1 ha \geq 10). Basal area was 1.50 m²/.1 ha (0.80 m²/.1 ha in stems \geq 10 cm). The complexity index was 3.74 (c.i. \geq 10 = 0.35). The mean DBH here was 11.18 cm. Dead stems were 5.98% of the total, slightly more than at plot 1.

Seedling density at plot 2 was 92 seedlings/m² with a mean height of 58.4 cm.

Bahía Sucia

Bahía Sucia is an open, lunate embayment at the southwest corner of the island, reaching from Punta Molino to the point of Cabo Rojo. The bay is open towards the southeast, but is partially sheltered from wave trains arriving from this direction by an elongate projecting ridge that extends west from Arrecife Margarita. The depth

along the crest of this ridge is 6.3 to 8.1 m (3 1/2 - 4 1/2 fm).

Since the bay is only partially sheltered, mangroves form a discontinuous fringe. The central portion of the bay, subjected to more intense wave exposure, is free of mangroves. The eastern mangroves comprise about 29 ha (Fig. 16), whereas the western stand contains 15.3 ha (Fig. 17). A large hypersaline lagoon extends behind the low sandy beach behind the central portion of the bay. Surface salinities in this lagoon are high and variable. For example, on August 16, 1979, surface salinity was 100‰ ; on the 6 of September, after the intense rains produced by Hurricane David, salinity had decreased to 18‰ . By the 10th. of November this value had already increased to 61‰ . The lagoon sediments have such high salt levels that the establishment of mangroves is prevented.

In general, fringe mangroves are the dominant physiographic type in the Bahía Sucia area and basins are poorly developed. Poor development of the basins may be due to at least two factors: 1) the lack of runoff to prevent salt accumulation; and 2) wave exposure.

Cintrón et al. (1978c) have shown that wave action in this particular coastal strip is high enough to contribute to the deposition (within the mangrove fringe) of berms of sand and Thalassia debris. These berms may be low (10 - 15 cm), but effectively reduce the exchange of

water in the inner fringe and basin. Salinity behind the berm (interstitial) is much higher and rapidly approaches more than 60‰. The mangroves seaward of the berm have a canopy height of 7 m or more and mean DBH of 17.5 cm, whereas landward of the berm canopy height and DBH decrease to 4.5 m and 6.6 cm respectively.

In most sectors salinity increases so rapidly that only a narrow fringe of red mangrove is found. Behind this fringe the typical profile contains a zone of dead mangroves and a shallow hypersaline lagoon which ends in a wide salitral or salt flat.

Profile 14 shows the vegetation along a fringe in the eastern mangroves of Bahía Sucia. The first 60 m of forest were a pure stand of red mangroves that reached 14.8 m high. Twenty meters inland the canopy height had decreased to 7 m. This decrease in the canopy was coupled with a decrease in diameters from 15.22 cm in the outer fringe to 7.9 cm at plot 2. The berm here was 20 m inland. Salinity behind the berm increased rapidly to a maximum of 63‰ at 130 m. The black mangroves at plots 3 and 4 were scrubby with canopy heights of .5 - 4 m and mean DBH's of 4.2 and 5.3 cm respectively.

Stem densities for plots 1-4 were 193, 520, 333 and 375 stems/.1 ha respectively. Plots 1 and 2 had 150 and 33 stems/.1 ha \geq 10 cm each. Plots 3 and 4 did not have trees \geq 10 cm DBH. Basal areas decreased from 3.00 and 2.15 m²/.1 ha in plots 1 and 2 to 0.65 and 0.40 m²/.1 ha

in plots 3 and 4. In plot 1 $2.8 \text{ m}^2/.1 \text{ ha}$ of the basal area was in stems $\geq 10 \text{ cm}$ whereas at plot 2 this had been reduced to $0.30 \text{ m}^2/.1 \text{ ha}$. The complexity index of the outer fringe (plot 1) was 8.69 (c.i. $\geq 10 = 6.30$).

As expected, the complexity index at the innermost plots (3 and 4) was very low (0.89 and 0.45).

On March 17, 1973, a Greek registry tanker, S.S. Zoe Colocotroni, discharged 5,000 tons of crude petroleum in the vicinity of Arrecife Margarita. Some of this oil was carried into Bahía Sucia, where it stranded and covered 16.5 ha of mangrove sediments. It was estimated that 2.7 ha of mangroves were killed by the oil (Lugo et al. 1978). This estimate did not include those mangroves killed due to the potentially synergistic effects of the combination of oil and high soil salinities.

The bulk of the oil stranded in the western mangroves and the sediments there, still contain substantial amounts of oil, six years after the spill.

During the passage of Hurricane David this coastal sector was exposed to very heavy seas. The seagrass beds were uprooted and large accumulations of Thalassia blades and rhizomes were carried inside the fringe. In places this mound had an elevation of more than 1 meter.

One further characteristic of the mangrove fringes in this area is described by Cintron et al (1978c). Because of the intense wave action, loss of the outer mangroves in a fringe can lead to the formation of a small sandy

beach within the fringe. This beach usually has a steep and high (.4 - .5 m above m_{lw}) berm that cuts the flow of water to the inner mangroves. Behind these coves, are found circular patches of dead mangroves. This process is shown schematically in Fig. 18.

Bahía Salinas

This bay is another wide and shallow embayment in the southwest corner of Puerto Rico. However, whereas Bahía Sucia's axis is pointed in the direction of incoming wave trains, Bahía Salinas is oriented west (225 °) and sheltered from the prevailing seas and swell. Mangroves are found only along the southern portion close to the promontory of Cabo Rojo (Fig. 17). The mangrove fringe here is exposed to a lower energy regime and there is no berm formation to create flushing problems.

Mangroves cover 6.4 ha, mostly reds with some white and black mangroves. The thickness of the fringe is about 75 m and the mangroves are limited landward by a salt flat. In the lower parts of the salt flat black mangroves form a small basin forest.

Soil salinities inside this stand were relatively low (41‰) and leaf litter accumulation very small. This is indicative of the high flux of water with the tides. The first 55 m of the fringe were composed of a pure stand of red mangroves. Landward, reds occur mixed with white mangroves although the contribution of whites is small

(I.V. = 4.7%). The interstitial salinity in this rear area is 54‰. A wide berm 10-15 cm high and 10-17 m wide divides the outer mangrove fringe from the salt flats behind. The outer mangrove fringe rests on a peat bed with a maximum thickness of 60-70 cm. The peat thins inland and ends at the foot of the berm. The sediments at the salitral contain high percentages of gravel and sand and have little organic matter. The interstitial salinity here is 100‰, reaching a peak of 170‰ (Cintron et al. 1978c).

The degree of development in this fringe is moderate. Canopy height varied in our plots from 10.8 to 12.0 m. Stem densities were 184-208 m²/.1 ha; a significant portion were stems \geq 10 cm DBH (175-139 stems/.1 ha). Basal area was 2.10-3.25 m²/.1 ha of which between 1.8-2.90 m²/.1 ha was in stems \geq 10 cm. The complexity index was 6.09-9.43 (c.i. \geq 10 = 5.40-7.18).

Mortality at the plots studied was fairly high (23.3% at plot 1, 9.17% at plot 2). This mortality appears to be natural.

Boquerón Bird Sanctuary

The largest mangrove stand on the west coast of Puerto Rico is a large basin forest behind Laguna Rincón. This stand is within the Boquerón State Forest. Originally this forest contained 202 ha. of mangroves, apparently dominated by black mangroves. During 1965 an area of

177 ha was impounded by dikes built around the forest to utilize this area as a bird refuge. Water level was increased to 1 m within the impoundment. The impact on the mangroves was swift and catastrophic. Massive die-off of the mangroves occurred in the impoundment, mainly due to the fact that during the wet seasons water levels within the impounded area exceeded the height of the pneumatophores, the organs which provide ventilation to the root system. Furthermore, during the dry season the water evaporated and the dikes effectively impeded fresh water surface drainage from the adjacent areas, as well as tidal flushing to leach salts. Loss of the forest canopy exposed the soil to the incoming solar energy and extreme overheating. Massive fish mortalities were recorded almost every year as water levels decreased and large numbers of fish were concentrated in drying ponds that became very hot and oxygen depleted.

Where some fresh water was available, black mangroves were replaced by dense cattail marsh and open areas were covered by water hyacinth. The landmost section of the forest, which is probably representative of what the mangroves within the impoundment were like, has been used as a garbage dump until very recently. This unfortunate chain of events has led to the destruction of most of one of the best developed mangrove stands on the west coast.

To ascertain the characteristics of this forest before the intervention of man in the 1960's a plot was studied behind the dump area west of road PR 301. The dominant species was black mangrove (relative density 94.4%), whereas white mangrove represented 5.6% of the stems. stem density was 400 stems/.1 ha and the total basal area was 6.3 m²/.1 ha. The mean DBH of the black mangrove stems was 14.6 cm whereas the whites mangrove stems averaged only 4.2 cm. The mean canopy height was 7.6 ± .3 m.

The characteristics of the outer mangrove fringe toward Caño Boquerón are: canopy height 4.6 ± 1.2 m stem density 1,380 stems/.1 ha, basal area 2.11 m²/.1 ha. Red mangrove was the dominant species with a relative density of 89.4%. White mangroves had a relative density of 8.3% and blacks 2.2%. The high stem density was due to the small diameter of the vegetation in this stand (2.8 cm for red and 3.0 cm for white mangroves).

Inside the impoundment the dominant species now is white mangrove (relative density 56.7%). The mean DBH of these stems however is only 4.3 cm. These are trees that have colonized the impoundment since the die off. The mean DBH of the black mangrove dead stumps is 10.3 cm.

These white mangrove trees have adjusted to the new prevailing water level. Clumps of seedlings have sprouted from stumps that are almost awash.

Water level is now being actively controlled, even during the dry season, by active pumping of water from Caño Boquerón. This has buffered the wide oscillations in water, salinity and temperature and is definitely a correct step in the active management of the impoundment.

This area however deserves further attention to optimize its management. It may be added that this impoundment was built as a substitute for the natural swamps of El Aregado and Laguna de Guánica (Dept. of Agriculture, 1969) that were drained as part of the Lajas Valley irrigation and development project. Guánica lagoon had an estimated area of 454 ha. (Koenig 1953).

Region VI - Western Coastline

This segment extends from Puerto Real to Barrio Espinar in Aguadilla. It contains 207 ha of mangroves in four forests (Carrera and Lugo, 1978). Although the southern half of the west coast of P.R. is fairly protected and mangroves sometimes develop in contact with the sea, as one progresses north the wave regime becomes more rigorous. This is due to extreme refraction of the north Atlantic swell around the northwest end of Puerto Rico. Active coastal erosion is a severe problem.

Precipitation is also higher and this segment is within the Subtropical Moist Life Zone (Ewel and Whitmore 1973). At Mayaguez (Nuclear Center Meteorological Station) the annual average yearly rainfall is 1,933 mm, 2.2 times

the Ensenada value that we used as typical for the south west coastal segment. River discharge is also considerable and important rivers such as the Guanajibo, Añasco and Culebrinas discharge here.

These conditions are very similar to those that prevail along the north coast. Not surprisingly the dominant mangrove physiographic types are the riverine and basin forests.

Two mangroves areas were studied in detail in this coastal segment: Joyuda Lagoon and Caño Corazones.

Joyuda Lagoon

This water body is a shallow, elongated coastal lagoon separated from the Mona Channel by a narrow sand ridge. It has an open water area of 13.9 ha and a mean depth of 1.28 m (Carvajal-Zamora 1979). Fully 76% of the perimeter is colonized by mangroves. Salinity within the lagoon varies widely. During the wet season salinity may decrease to 8‰ whereas during the dry season it may increase to 19‰ (idem 1979). During periods of extreme drought salinities may reach 44‰ and fish kills may occur (Pagán and Austin 1967). Salinities higher than 10‰ may also occur during periods of heavy seas such as those that occurred in December 1976 (J.G. González cited in Carvajal-Zamora 1979). Salinities at that time reached 25‰ even if this was the wet season.

Mangroves cover 29.6 ha mostly as a narrow fringe

around the lagoon (Photograph 10). These mangroves are extremely well developed and in some parts of the fringe large red mangrove trees attain 22 m. The mean DBH of these stems was 27.5 cm.

In order to assess the structural characteristics of these stands, three transects were established.

(Fig. 19). Transect 1 was located in the fringe at the northwest shore.

Profile 15 shows the characteristics of the mangrove stand at transect location 1. The trees within a 10 meter strip from the edge of the lagoon showed a great deal of structural development. There the canopy reached 22 m. and prop roots were observed emerging from main stems as high as 4 m. Soil salinity was 22‰.

Stem density was 44 stems/.1 ha (all \geq 10 cm) and the basal area was 2.15 m²/.1 ha. These numbers yield a misleading complexity index of 2.08 due to the low stem density and monospecific character of the forest.

In plot 2 there was an increase in soil salinity (43‰) and a decrease in canopy height (13.8 m). Stem density was 178 stems/.1 ha (115 stems/.1 ha \geq 10 cm). Basal area was 1.75 m²/.1 ha (1.55 m²/.1 ha in stems \geq 10 cm). The complexity index was 4.30 (c.i. \geq 10 = 2.46).

Plot 3, located about 50 m inland, is a mixed stand. The dominant species is red mangrove (I.V. = 76.09%) followed by white mangrove (I.V. = 21.21%). All the black mangroves were dead. The interstitial salinity

was 50%. Canopy height was 11.8 m and stem density was 535 stems/.1 ha. Only 21 stems/.1 ha were \geq 10 cm DBH. Basal area was 1.90 m²/.1 ha, with 0.30 m²/.1 ha contributed by stems \geq 10 cm DBH. The complexity index was high, due to the high stem density and number of species (c.i. \geq 2.5 cm = 35.98), but low when computed for trees \geq 10 cm DBH (c.i. \geq 10 cm = 0.22).

Transect 2 was located near the north central portion of the lagoon. Profile 16 shows the characteristics of the vegetation along transect 2. This transect was characterized by a steep salinity gradient behind the outer red mangrove fringe. The inner basin, where salinities reach 68‰, is made up of a pure stand of black mangroves.

Plot 1 at the outer red mangrove fringe had a canopy height of 20.0 m. Stem density was 118 stems/.1 ha (all \geq 10 cm DBH). Basal area was 3.30 m²/.1 ha. The complexity index is 15.58.

Plot 2, 50 m inland, had a canopy height of 11.8 m, stem densities of 153 stems/.1 ha (109 stems/.1 ha \geq 10 cm). Basal area was 2.0 m²/.1 ha (1.85 m²/.1 ha contributed by stems \geq 10 cm DBH). The complexity index was 3.61 (c.i. \geq 10 cm = 2.38).

The inland plot (100 m from the outer edge) had a canopy height of 7.0 m, stem density of 206 stems/.1 ha (none \geq 10 cm DBH) and a low basal area (0.60 m²/.1 ha). The complexity index is low (0.87) as expected. The mean diameter of the trees was only 6.6 cm.

Transect 3 (Profile 17) was located perpendicular to

the inlet leading into the lagoon. Canopy height here was only 8.3 m at the outer red mangrove fringe (plot 1). Stem density was 182 stems/.1 ha of which only 11 were \geq 10 cm DBH. Basal area was 1.0 m²/.1 ha (0.30 m²/.1 ha contributed by stems \geq 10 cm DBH). The complexity index was 1.51 (c.i. \geq 10 cm = .03).

A second plot 50 m inland was within a pure black mangrove stand. Canopy height was 6.3 m and stem density was 85 stems/.1 ha (21 stems/.1 ha \geq 10 cm). Basal area was 0.60 m²/.1 ha of which half was contributed by stems \geq 10 cm DBH. The complexity index was 0.32 (c.i. \geq 10 cm = 0.04). The soil salinity here was 63‰.

Caño Corazones

This inlet is an abandoned mouth of the Guanajibo River whose present mouth is now 1.7 km south, protected by the rocky headland of Cerro Cornelia. A basin and riverine forest 107 ha in extent compose this unit. Urban settlements on the south shore near the mouth have resulted in the loss of some mangroves (Photograph 11). This, however, does not seem to have affected the remaining mangroves beyond the developed areas.

Two transects (Fig. 20) were established here. One transect was made perpendicular to the river channel 500 m inland. The second transect was completed at the end of the 'cul-de-sac'.

Transect one (Profile 18) was characterized by a steep increase in soil salinity from 23‰ in the outer fringe to 68‰ at 80 m. The dominant species was black mangrove except for a narrow outer fringe of red mangroves at the river margin. This was where the greatest structural development is attained.

At plot 1 (outer fringe) canopy height was 14.3 m. Stem density was 227 stems/.1 ha (110 stems/.1 ha \geq 10 cm). Basal area was 2.60 m²/.1 ha (2.00 m²/.1 ha contributed by stems \geq 10 cm DBH). The complexity index was 16.88 (c.i. \geq 10 cm = 3.15).

Canopy height decreased inland and at plot 4 it was 10.6 m. Stem density here was 204 stems/.1 ha (57 stems/.1 ha \geq 10 cm). Basal area had decreased to 1.40 m²/.1 ha (0.65 m²/.1 ha contributed by stems \geq 10 cm DBH). The complexity index was only 3.03 (C.I. \geq 10 cm = 0.39).

The structural characteristics of plots 2 and 3 are presented in Table 2.

At transect 2 (Profile 19) the salinity gradient was more gradual; at 60 m inland the salinity was still 45‰. The red mangrove fringe was also wider, extending to about 70 m, where the soil salinity was 48‰. Beyond this point the stand was a mixed forest of red and black mangroves.

At plot 1 the canopy height was 16.8. Stem density was 152 stems/.1 ha (88 stems/.1 ha \geq 10 cm DBH). Basal area was 2.15 m²/.1 ha of which 1.90 m²/.1 ha were contributed

by stems ≥ 10 cm DBH. The complexity index was 6.16 (c.i. ≥ 10 cm = 3.33). The canopy height at the outer fringe was 20 m.

Because of the shift in the river course this area no longer receives the fresh water inputs it must have received when this was the active mouth. The higher salinities in the basins reflect this reduction in fresh water inputs and the dominance of the influence of salt wedges. The system has adjusted to this new set of conditions and the basins have been colonized by black mangroves that are more tolerant of high salinities.

Caño Boquilla

Just north of Mayaguez and due west of Maní Airport lies Caño Boquilla, possibly an abandoned mouth of the Río Grande de Añasco. This "caño" drains sugar cane land and is lined by a relict fresh and saltwater swamp distinguished by the extremely large size of its red mangrove trees and, farther inland, by a few hectares of Pterocarpus in stands that reportedly reach a canopy height of more than 25 meters (Wadsworth, pers. commun). Red mangroves dominate the fringe forests, intermixed with a few whites and Pterocarpus seedlings. This forest appears fully mature; in some areas death of large trees and subsequent peat decay have led to formation of inner "pools" of considerable size. These pools are used by waterfowl, especially grebes.

Region VII - Northwestern Coastline

This coastal segment extends from Barrio Espinar in Aguadilla to the Río Grande de Arecibo. Most of this coast is characterized by high limestone cliffs (45-60 m) which rise abruptly from a very narrow shelf. High sand dunes may be found seaward from the cliffs.

Some small mangrove stands occur between the sand dune and the cliffs. These swamps tend to be elongate parallel to the coast and are fed sporadically by wave swash overtopping the coastal dune, by seawater percolation through the coarse coastal sands, and by freshwater seepage through the porous limestone.

Fresh water enters these mangroves by direct precipitation, surface runoff and water upwelling from springs.

Because of the limited area available only 48.2 ha of mangroves are found within this coastal segment (Carrera and Lugo, 1978).

Peñon Brusi Mangroves

This well developed mangrove area is found west of the town of Camuy (Fig. 21). The mangroves are separated from the sea by a sand dune with an elevation of 5 meters. A small stream runs along the inland edge of the basin and empties into the ocean thru a gap in the coastal dune. This stream is spring fed.

Behind the coastal dune, on the highest ground around

the basin is found Conocarpus erectus or buttonwood.

Some of these trees reach a DBH of 30 cm. Further inland, in the more elevated but still frequently flooded basin, the white mangrove is the dominant species. White mangroves are dominant in the eastern portion of the basin where the soil salinity eventually reaches 5‰. The fern Achrostichum is common in this part of the swamp.

Closer to the stream mouth the elevation of the soil is lower and the terrain is flooded to deeper levels. The dominant species here was the black mangrove, whereas small open water areas are fringed by red mangroves. The interstitial salinity here reached 40‰ at a depth of 50 cm. At slightly less depth (30 cm) the interstitial salinity was 25‰ whereas at the surface was 14‰ in December 1979.

The canopy height of the forest is 11-14 m. Throughout this forest we found large diameter trees. An outer plot, dominated by black mangroves had a canopy height of 13.8 m and a mean DBH of 19.0 ± 1.6 cm. Stem density was 122/.1 ha of which 60 stems/.1 ha were ≥ 10 cm DBH. The total basal area was 1.8 m^2 /.1 ha of which 1.70 m^2 /.1 ha was contributed by stems ≥ 10 cm DBH. The complexity index was 9.08 (c.i. ≥ 10 cm = 4.19).

The landward portion of this stand was dominated by white mangroves. Canopy height was 11.8 m, stem density was only 59 stems/.1 ha but all were ≥ 10 cm DBH. This plot had a large basal area (3.1 m^2 /.1 ha) all of which

was due to stems \geq 10 cm DBH. The mean DBH was 28.2 ± 1.2 cm. White mangroves contributed $2.6 \text{ m}^2/.1 \text{ ha}$ of the basal area and 49 stems/.1 ha whereas black mangroves contributed the difference ($5.0 \text{ m}^2/.1 \text{ ha}$ and 103 stems/.1 ha). The complexity index was 4.34 (c.i. $\geq 10 = 4.34$).

This mangrove stand is of great interest due to its degree of development which suggests a long disturbance free period and its ease of access. Small trails now cross the edges of the basin providing the stroller a magnificent view of the swamp. This area could be further developed at relatively low cost.

General Structural Characteristics

We have summarized the data presented in Table 3 according to physiographic type to ascertain the structural trends in each type. Since it is obvious that basins are different on the north and south shore of Puerto Rico these data have been separated, and are presented as averages for all basins and averages for north coast and south coast basins. In general, riverine systems have the highest mean basal area ($2.13 \pm 0.18 \text{ m}^2/.1 \text{ ha}$), lowest stem density ($187.36 \pm 26.36 \text{ stems/.1 ha}$) and tallest canopies ($14.37 \pm 1.35 \text{ m}$). Since they have a lower mean species number; (2.71 ± 0.74) they do not have the highest complexity index.

There is also a very dramatic difference between north and south coast basins. North coast basins have

a higher species diversity (3.13 ± 0.13), a higher basal area ($2.08 \pm 0.26 \text{ m}^2/.1 \text{ ha}$) and much taller canopy ($13.05 \pm 0.72 \text{ m}$) than south coast basins. These latter, salt-stressed basins tend to be monospecific (containing only Avicennia) and stunted in height (mean canopy height is $3.72 \pm 0.54 \text{ m}$). Mean basal area on the south coast is only $0.65 \pm 0.13 \text{ m}^2/.1 \text{ ha}$. Mean DBH in the stressed basins is significantly much less than on the north coast ($6.08 \pm 1.03 \text{ cm}$ vs. $13.99 \pm 4.12 \text{ cm}$). Of course the complexity index for north coast basins is much higher (26.00 ± 11.22) than south coast basins (0.71 ± 0.13).

Overwash types, as expected, have the lowest mean number of species (1.60 ± 0.40) excluding the stressed basins. This is to be expected since true overwash types are usually monospecific. North coast basins, on the other hand, have the highest mean number of species probably since the conditions there are least rigorous.

Since an index of the degree of development of a mature forest is given by its canopy height, we have correlated this parameter with the complexity index. The correlation coefficient is high ($r = 0.88$). Complexity is a power function of height. This relation is plotted in Fig. 21. The solid circles correspond to our data whereas the crosses correspond to means for physiographic types obtained from a survey of the current literature.

There seems to be a tendency in the data for physiographic

types to have given ranges of complexity indices. Complexity also, as expected, is lowest in stressed system. In general it seems to increase in the following order: stressed systems → overwash → fringes → basins → riverine forests.

This hierarchical progression seems to be closely associated with nutrient availability. In this particular geographic area most of the overwash and fringe forests are in direct contact with low nutrient coastal waters, whereas basins and riverine systems receive a great deal of land-derived nutrients.

In terms of their structural development, basins are the most fragile systems. They are best developed in those coastal sectors where precipitation exceeds 2,000 mm and rapidly degrade where precipitation is less than 1,000 mm. Basin development in areas of low precipitation may be subsidized by the availability of runoff derived from wetter areas.

Management

Lugo (1976) has developed a series of management guidelines based on the characteristics of each mangrove forest type. These recommendations were also incorporated in Carrera and Lugo (1978).

Overwash mangrove islands

These islands are best managed when left alone. The

rate of growth and regeneration is generally low due to the low nutrients in coastal waters. Selective cutting for the purpose of recreation must be done judiciously and kept to a minimum.

Fringe mangrove wetlands

Mangrove fringes have important roles in terms of organic matter export, shoreline protection, substrates for the attachment of many sessile forms and their associated flora and fauna and they assist in the control of water quality by removing excess nutrients from circulation.

Growth is more rapid and this system may be managed for wood production. Harvesting may be done with the clear cut method if arrangements are made for reseedling. The outer mangrove fringe must be maintained to provide a buffer against disruption of the planted seedlings. Clearcutting should be in narrow strips perpendicular to the shore and there must be maximal removal of debris to assist in the natural regeneration of the area.

Mangroves, according to Odum et al. (1977) are important interface systems (between man's settlements and natural coastal systems). They contribute to regulate nutrient levels since they utilize and actively remove these from coastal waters. However fringes should not be utilized as direct receptors of wastewaters due to their high flushing rates and inadequate retention times.

All construction within fringes should be on pilings to maintain adequate water flows and drainage. All activities should be of low density so that sufficient undisturbed mangrove is left between structures.

Basin Mangrove Wetlands

Basins are also useful as interface systems and have a potential for the application of sewage effluents. Studies by Sell (1977) have indicated that mangroves grew faster when bathed by tidal waters containing higher nutrients due to the addition of sewage effluent. White mangrove basins showed the greatest response in terms of biomass increase. Application of an effluent to a basin must be made so that there is adequate dispersion and that water level does not exceed the height of the pneumatophores.

This forest type is extremely sensitive to changes in the surface sheet flows and water levels. Interference with tidal flooding by diking or alteration of the overland sheet flows can be destructive.

Road construction within mangrove basins should be avoided. Where it is necessary to build access roads these should be on pilings. Elevated, solid fill causeways are most damaging, acting as dikes and obstructing surface flows. Culverts and pipes very often are not large or frequent enough to maintain the proper land drainage. Mangrove stands isolated by dikes quickly die. This impact

is more severe in stressed basins such as those in the south coast.

This forest type can be utilized for timber and wood production. Natural regeneration of the cleared strips is possible but active hand thinning can contribute to increased DBH growth by elimination of slow-growing trees and acceleration of growth in the remaining stems (Wadsworth 1959).

Riverine Mangrove Wetlands

This is one of the most biologically productive physiographic types, and undisturbed estuaries such as the Espiritu Santo have highly diverse fish faunas. According to Lugo (1976) in areas like Puerto Rico these mangroves are valuable assets for the regulation of regional environmental quality. Where land use is intensive, rivers usually carry high sediment loads, become eutrophic and flood more than normal (idem). Riverine mangroves aid in re-establishing the lost environmental quality. Mangrove belts contribute to dampen noise, precipitate dust and have a great deal of overall aesthetic appeal. Their high productivity preadapts this system to sewage uptake. Flood control benefits result since the mangrove forest becomes a storage basin buffering changes in levels and water velocities, especially at times of hurricanes.

It is felt that this function as a buffer ecosystem

is of great importance and Puerto Rico's riverine mangroves must be managed toward these ends.

Riverine mangroves are destroyed by river channelization projects, water diversion, diking and similar activities.

Dwarf Mangrove Wetlands

Dwarf mangrove wetlands are of value due to their uniqueness. Presently we know of only two large areas containing dwarf mangroves. Both areas are in Federally owned lands administered by the U.S. Navy. These areas are presently receiving adequate protection. The largest dwarf stands are within the Roosevelt Roads Naval Station (Photograph 1) and minor stands of dwarf mangroves also occur in Ensenada Honda in Vieques.

These mangroves should not be disturbed since they regenerate very slowly. Studies to ascertain the causes of their stunting should be carried out.

Mangrove's response to stressors

Man's impact on the mangrove ecosystem can result in various types of stresses. Lugo et al (1978) has suggested that the impact of a stressor on an ecosystem is a function of which part of the ecosystem is stressed. Stressors were classified into five types:

Type 1 - Those that alter the nature of the main energy source.

Type 2 - Those that divert a portion of the main energy source before it is incorporated into the system.

Type 3 - Those that remove potential energy before it is stored but after it is transformed by plant photosynthesis.

Type 4 - Those that remove storages.

Type 5 - Those that increase the rate of respiration.

In Fig. 22, from Lugo et al (1979), is shown a simplified model of a mangrove ecosystem. This model shows that those stressors that alter the inflow of the primary energy sources or affect a large portion of the producer compartment are highly detrimental since they affect the system's ability for recovery. Stressors 1, 2 and 3 are of this kind. Stressors of these types that act with increasing severity reduce greatly the possibility of mitigation or recovery. Stressors 1 and 2 are the most severe since in these cases the environment is changed and the productive potential is greatly impaired. There is no possible way to mitigate the operation of these stressors and recovery is not possible. In a mangrove swamp examples of a type 1 stressor are channelization and diking or damming whereas a type 2 stressor is represented by partial changes in hydroperiods.

Stressors 4 and 5 have less serious impact on the ecosystem since they do not directly affect the input energies and the high productivity of the system is not severely impaired. Recovery from these stressors is more

rapid. Harvesting that removes only a small portion of the systems' biomass is considered a type 4 stressor. Hurricanes are also a type 4 stressor since they remove structure from the system. High temperatures are classified as a type 5 stressor.

Since stressors of types 1 and 2 act on and impair the systems productivity these stressors cause exponential or logarithmic responses in the ecosystem. Other stressors that act on the internal components of the system do not cause such dramatic responses and their effects can be described with linear responses (Lugo et al 1978).

The complexity of a system is greatest where there is a great availability of energy subsidies and low intensity of stresses. Since the energy expenditures to survive in this type of environment are low, there is a greater share of the gross production, more net energy, for growth and increase in ecosystem complexity.

This explains why riverine systems, which receive ample subsidies in terms of nutrient inputs, tidal flows and fresh water are so productive and highly complex. As conditions become less ideal there is a reduction in complexity. The presence of various stressors results in loss of complexity. Systems which develop under the presence of a stressor cannot reach high complexity. This is the case of the south coast mangroves where salt is a natural stressor.

Although complexity usually increases with time (and succession) in severely stressed systems this is not the case. Again south coast mangroves are an example where complexity decreases with time due to salinity build ups.

The dominant species in the stressed south coast basins the black mangrove, can loose structure ("die-back") and yet re-sprout after episodes of severe environmental stress.

Lugo and Snedaker (1974) and Lugo et al (1978) have shown that stresses result in a reduction in mangrove leaf size. For example, mangroves in high salinity environments have shorter leaves (Fig. 23). If additional stressors are added, for instance, an oil spill, even smaller leaves are produced in response to the new stressor. In Bahía Sucia there was a decrease of 40% in leaf length from the unpolluted to oil polluted fringes. This represents a 63% decrease in leaf area (Lugo et al 1978). Since this stand also suffered partial defoliation the system lost a significant portion of its photosynthetic surface area.

Stressors also affect the systems' capacity to renew itself. In Fig. 24, we show the weight-length relationship for salinity stressed and non-stressed seedlings of red mangrove. The seedlings from the stressed individuals are smaller and lighter than those from the non-stressed trees. Since the non-stressed seedlings contain more stored food it is expected that they would have a longer

survival time (longer half life) than those originating from the stressed trees.

In general it may be said that low complexity, stressed systems are more fragile and susceptible to all further stressors. On the other hand, complex systems, which are highly productive, are thought to be able to sustain greater manipulation in terms of stressors that do not alter the incoming energy flows.

All activities that can alter the incoming energy flows lead to the rapid deterioration of the ecosystem and elimination of the probabilities of recovery. The principal rule in managing these wetlands is to protect these energy sources. In summary, in the north coastal region the mangrove system is tightly coupled to terrestrial inputs whereas in the south coast arid environment they are less-dependent on the terrestrial environment and more dependent on oceanic inputs. North coast type mangroves are severely threatened by future channelization and drainage projects whereas south coast types are threatened by water borne pollutants such as oil.

Mangroves are systems that take up nutrients actively and as such are not affected by eutrophication. In fact, higher nutrient levels are known to enhance productivity. This is shown by the rapid and vigorous growth of white mangroves along the Martín Peña Canal. Mangroves in these eutrophic environments are acting as natural treatment plants and contribute to enhance the quality of coastal waters.

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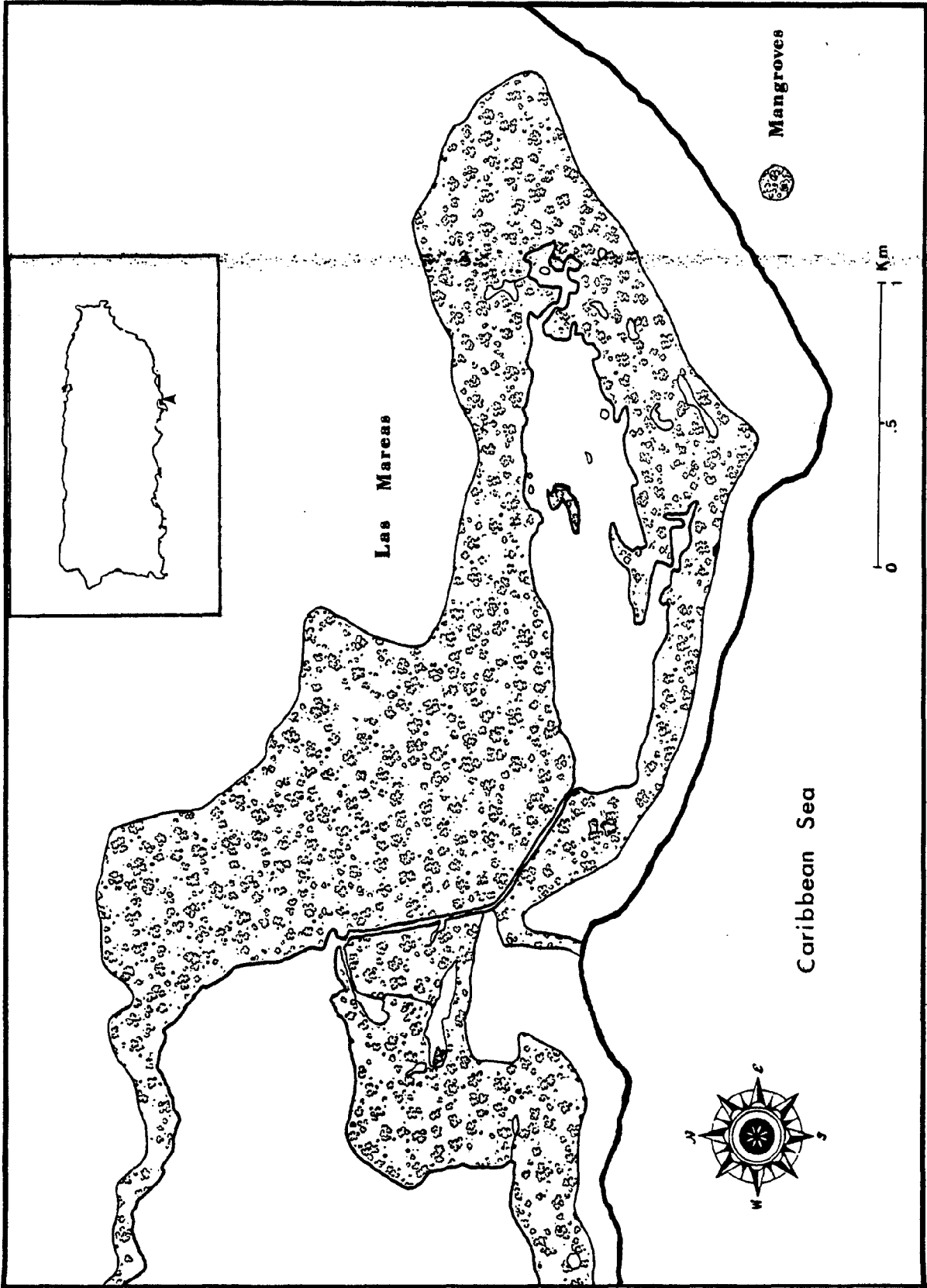


Figure 1.

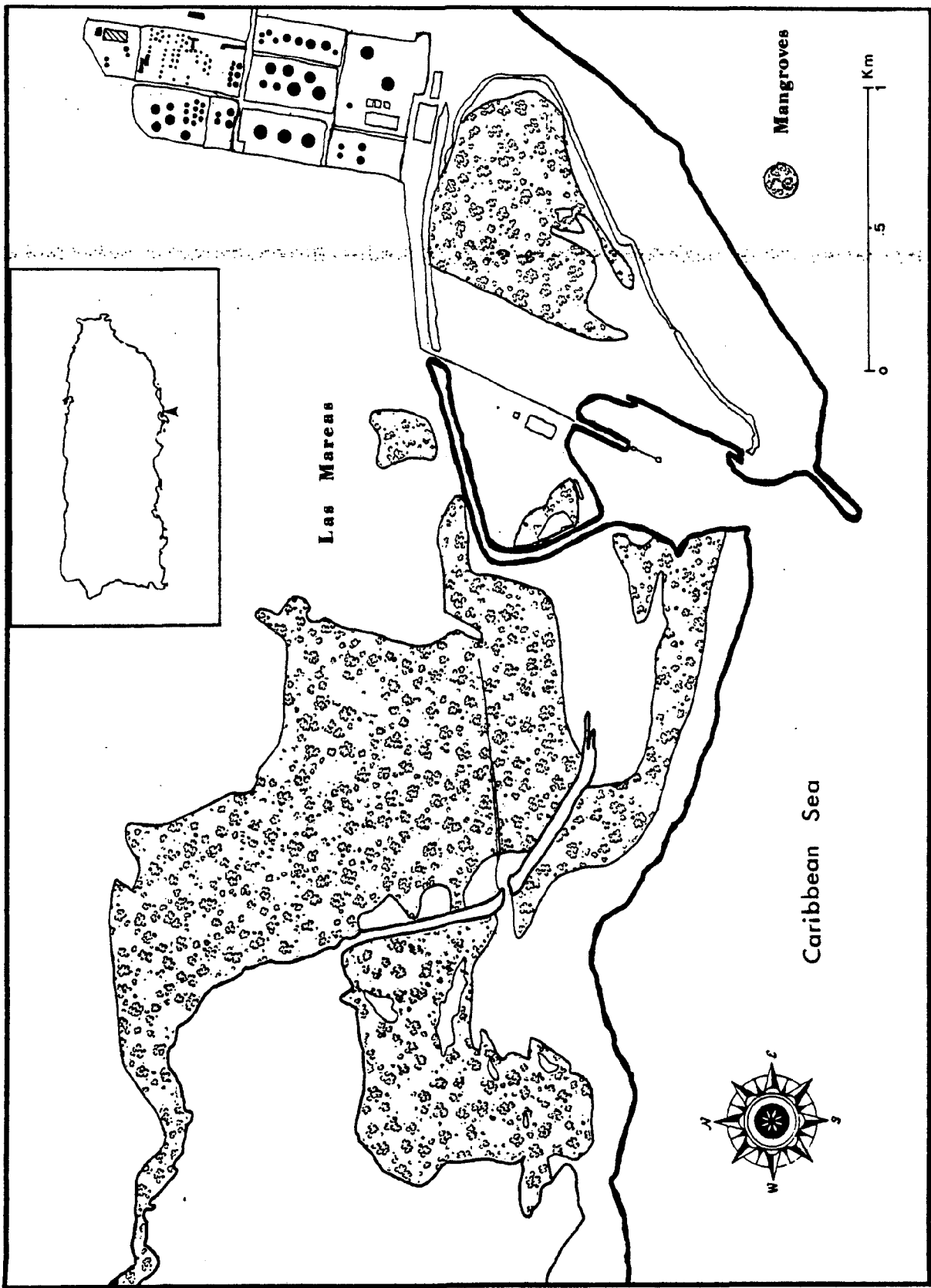


Figure 2.

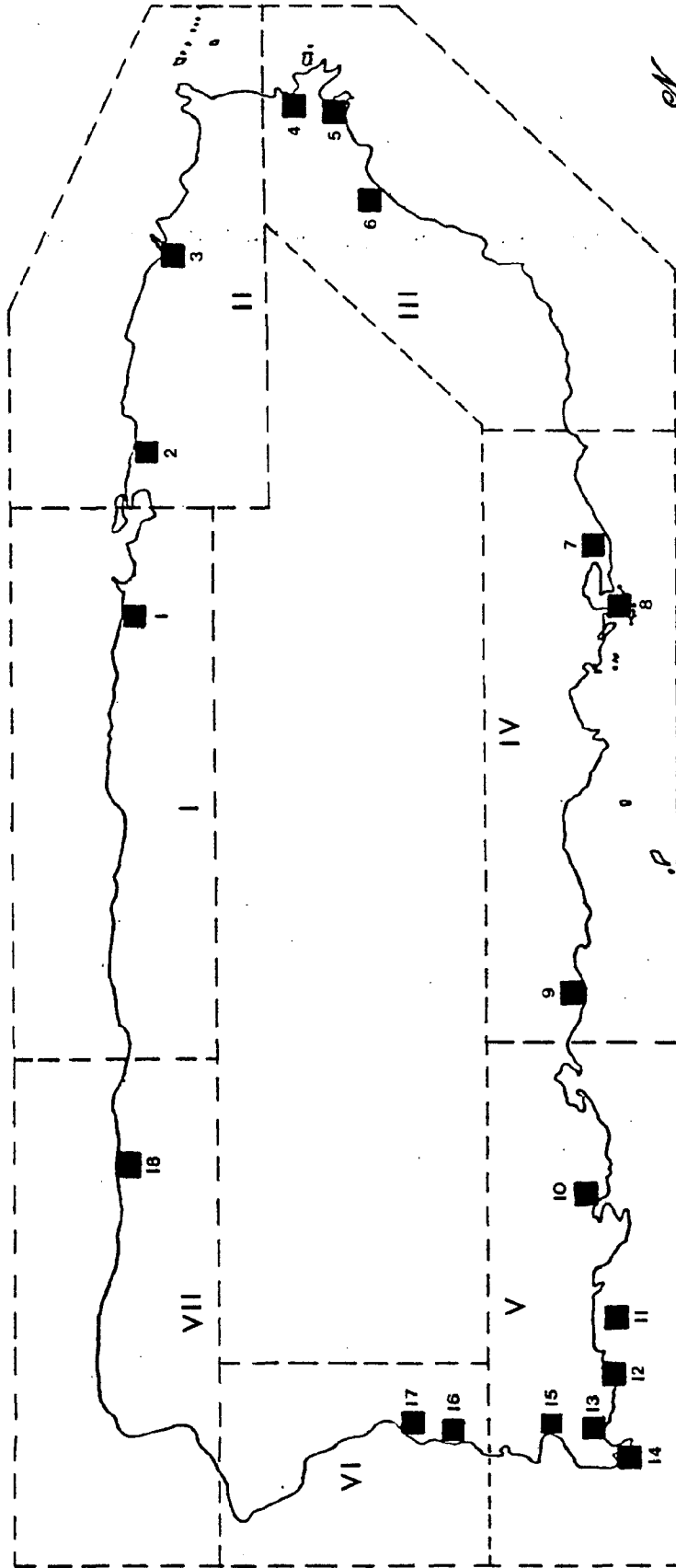


Figure 3. Map showing location of study sites.

- | | |
|---------------------------------------|---------------------------|
| 1. Río Cocal | 10. Bahía de Guánica |
| 2. Piñones, Vacía Talega, Torrecillas | 11. La Parguera |
| 3. Río Espíritu Santo | 12. Punta Pitahaya |
| 4. Bahía Medio Mundo | 13. Bahía Sucia |
| 5. Ensenada Honda | 14. Bahía Salinas |
| 6. Río Antón Ruíz | 15. Refugio Aves Boquerón |
| 7. Las Mareas | 16. Laguna Joyuda |
| 8. Bahía Jobos y Cayos Caribe | 17. Caño Corazones |
| 9. Laguna Las Salinas | 18. Peñón Brusi |

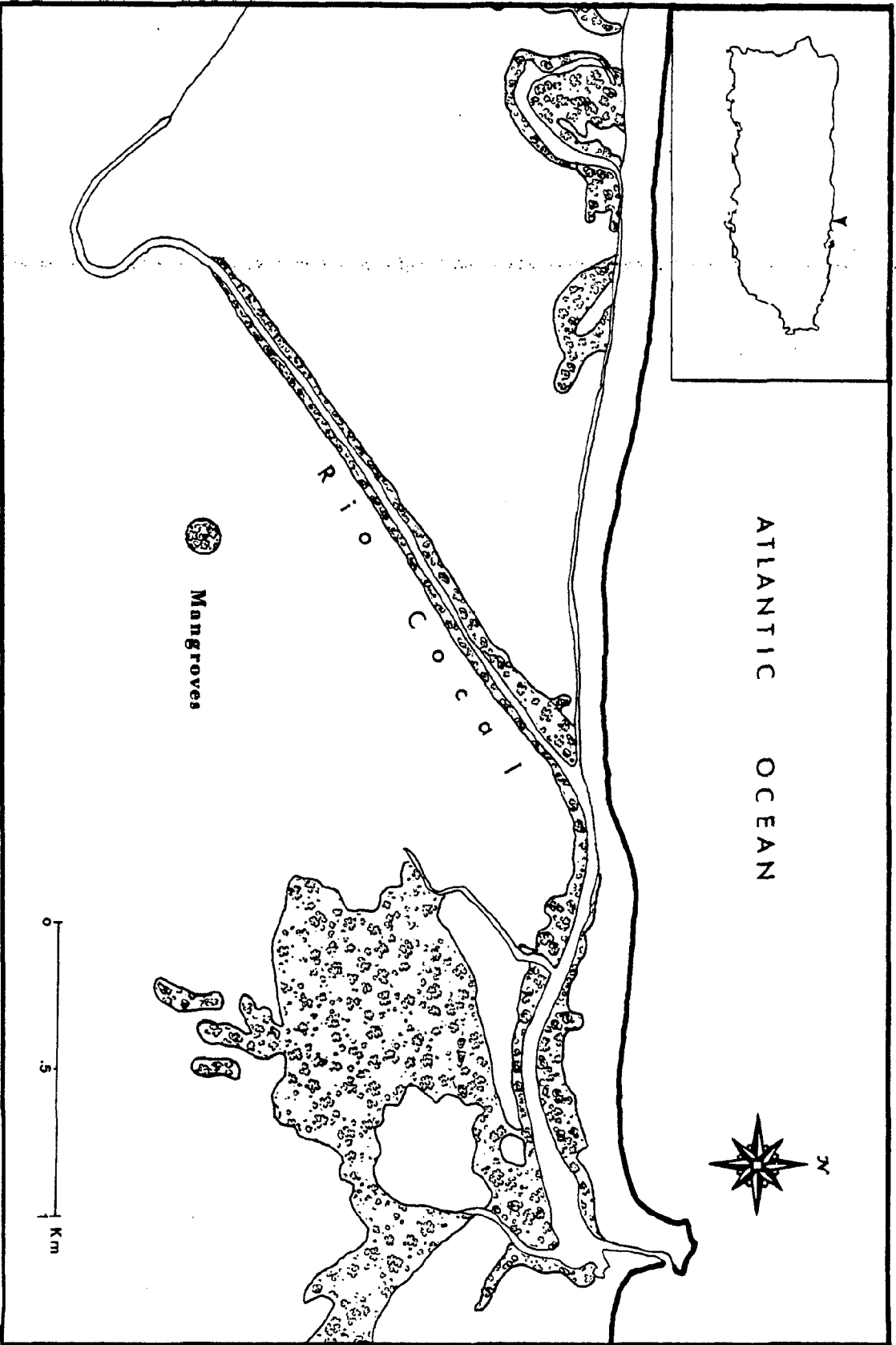


Figure 4.

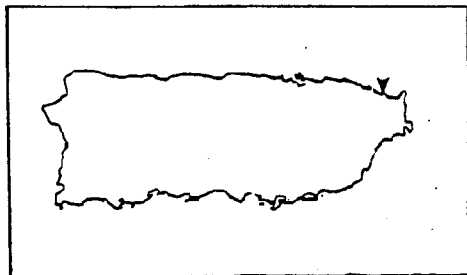
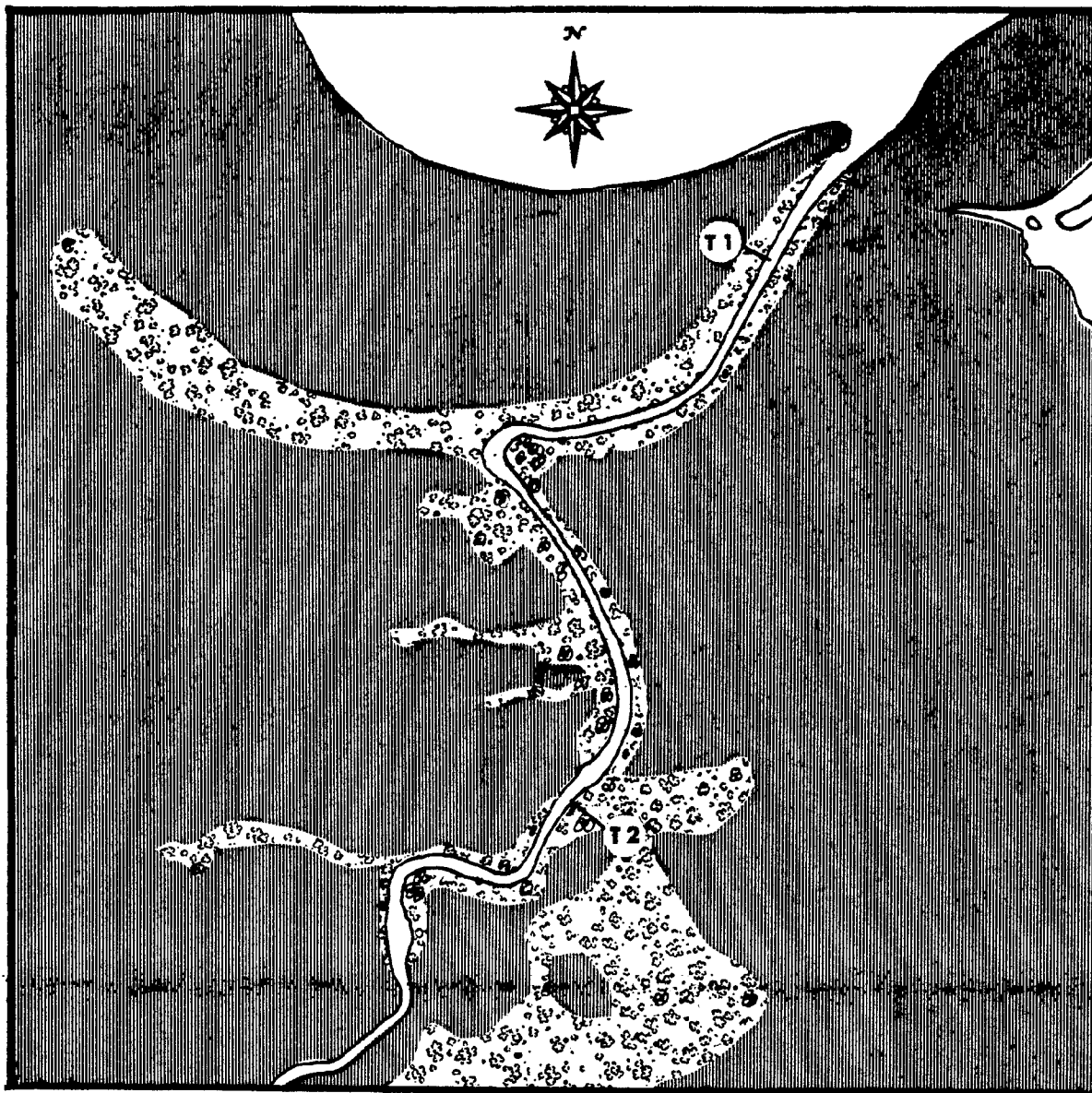
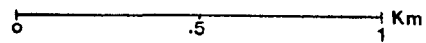


Figure 5.



Espiritu Santo River

-  MANGROVES
-  UPLAND



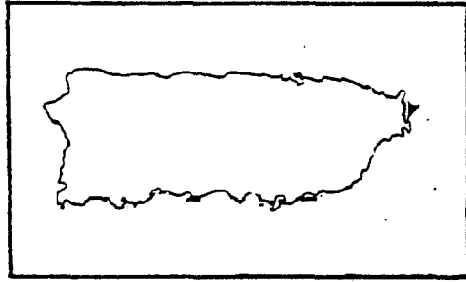
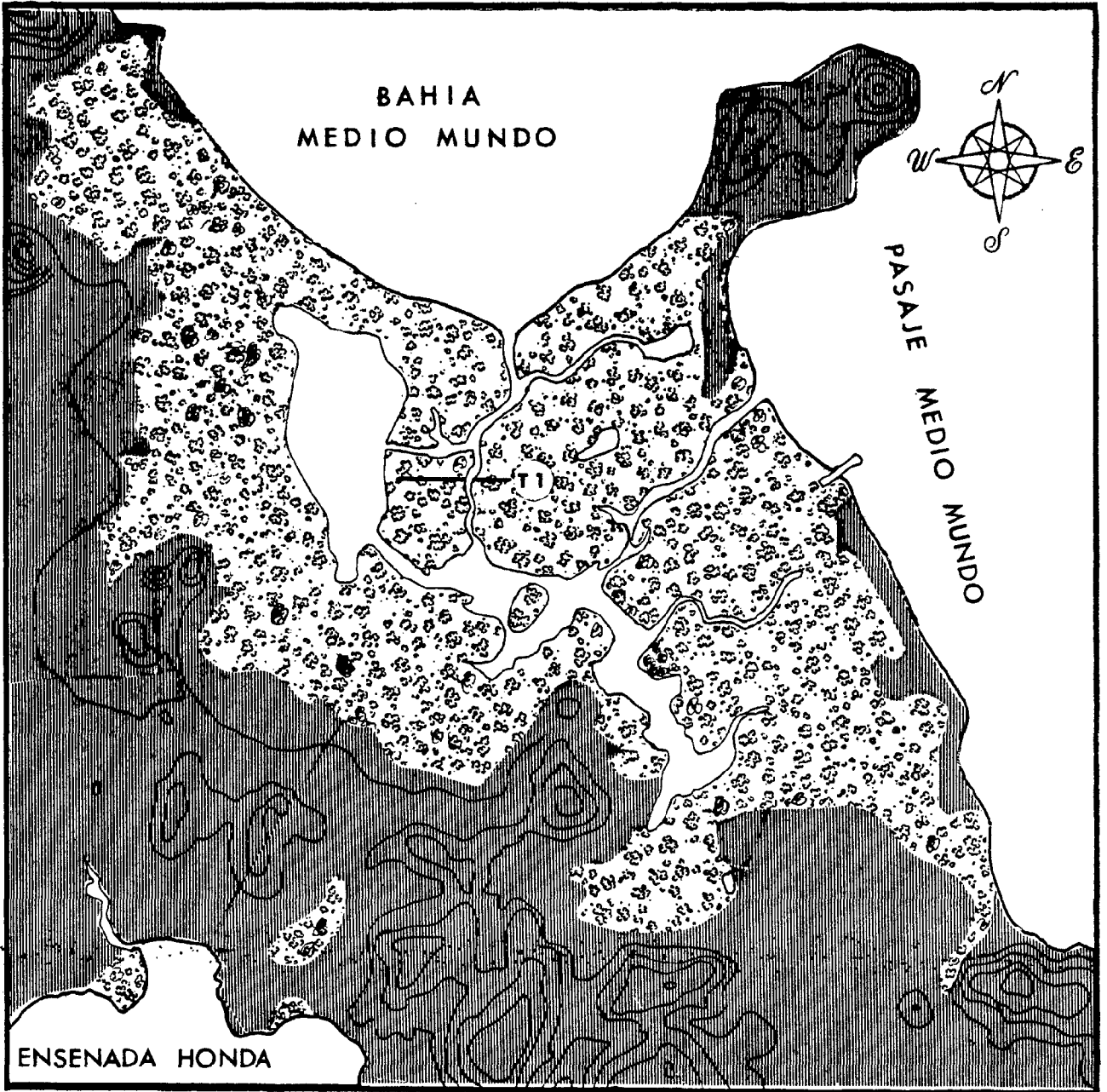


Figure 6.



-  **MANGROVES**
-  **UPLAND**

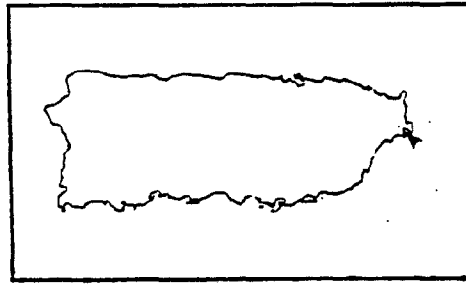
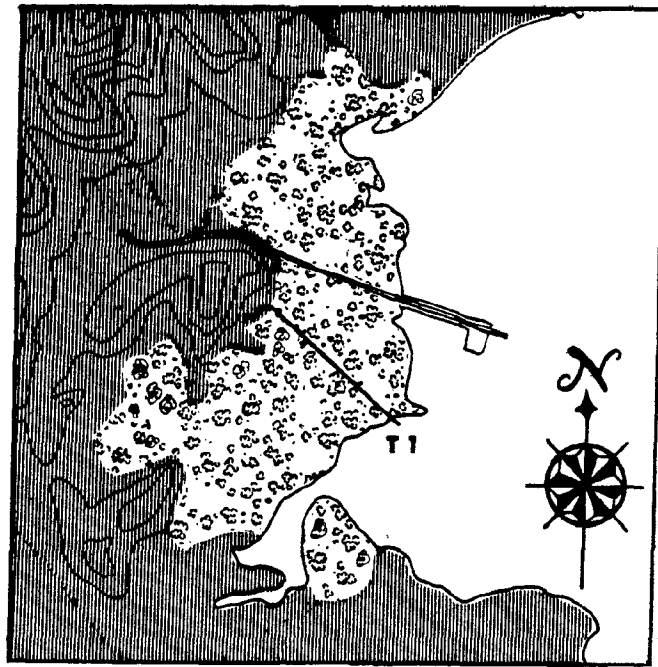



Figure 7.

0 .5 1 Km



ENSENADA HONDA

 - - - - - **MANGROVES**

 - - - - - **UPLAND**

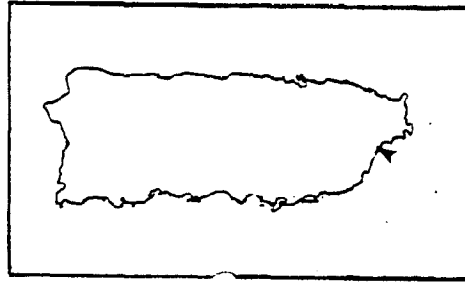
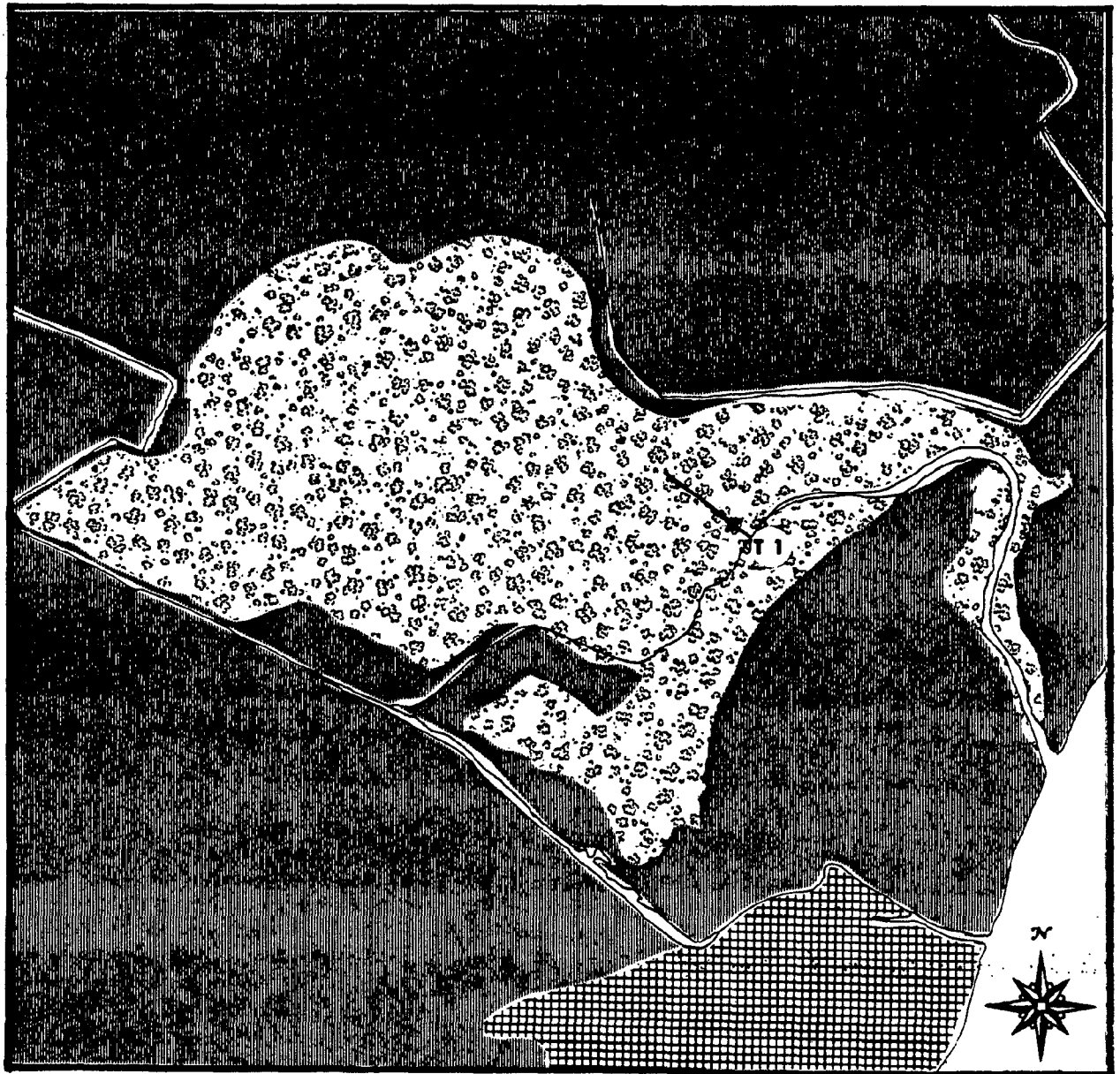


Figure 8.



Anton Ruiz River

0 .5 1 Km

-  **MANGROVE**
-  **UPLAND**
-  **URBAN SETTLEMENT**

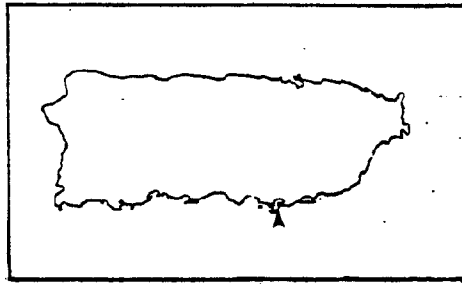
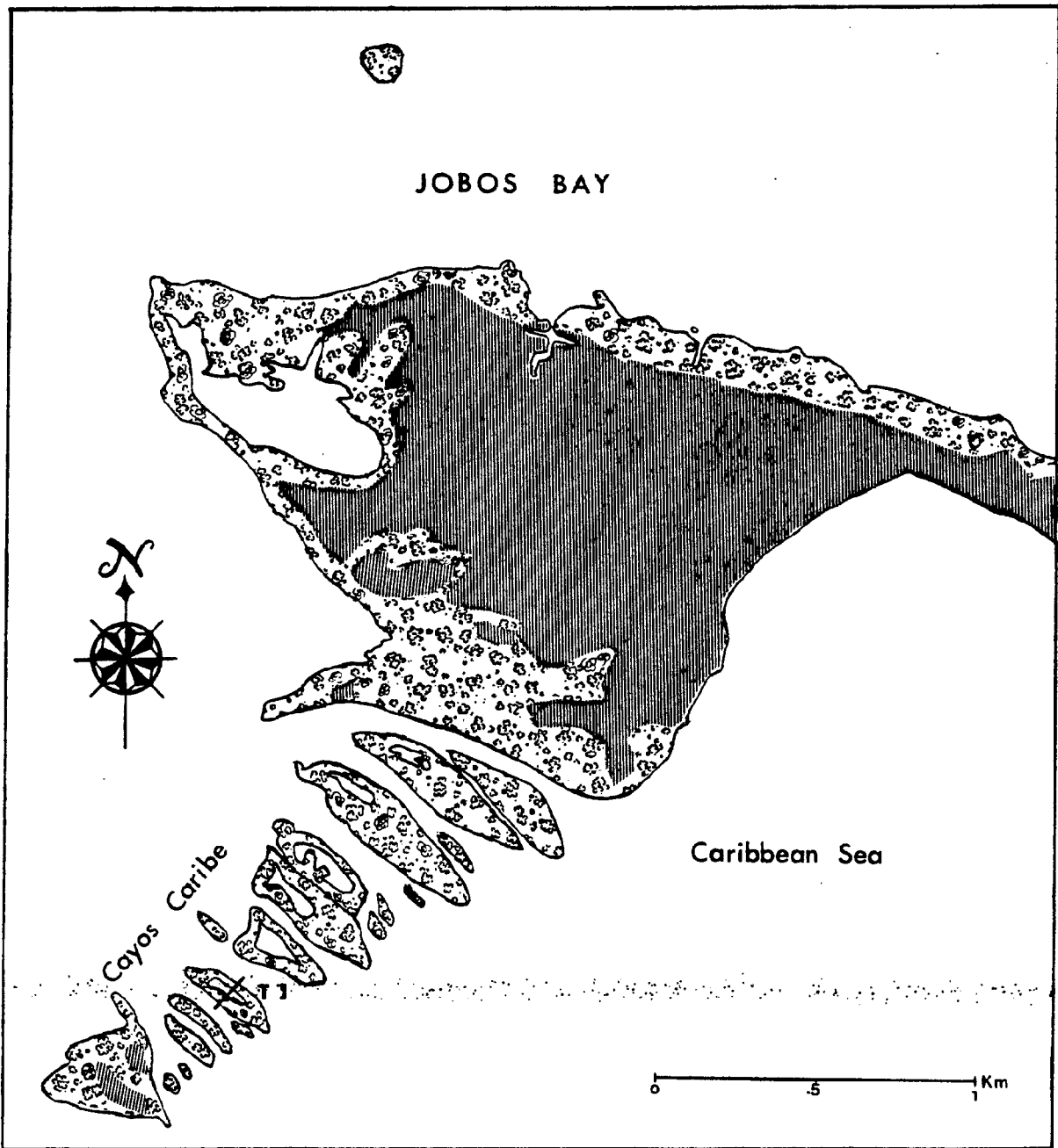



Figure 9.



-  ----- MANGROVES
-  ----- UPLAND

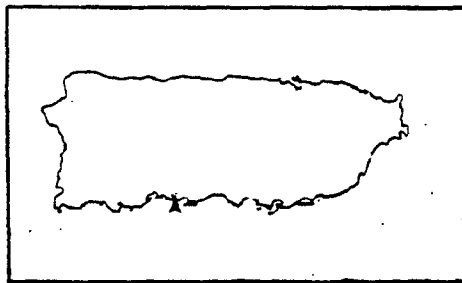
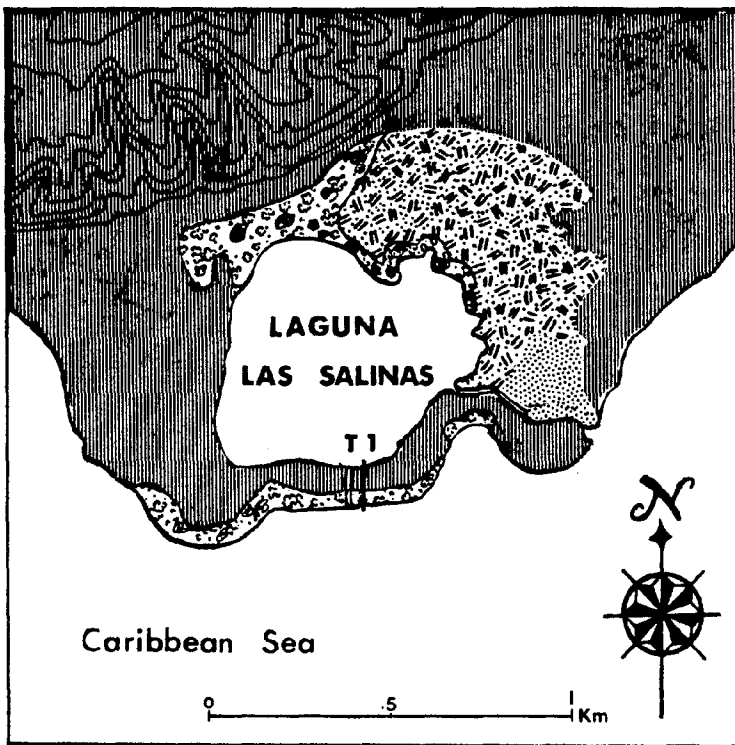






Figure 10.



-  ----- **MANGROVES**
-  ----- **UPLAND**
-  ----- **DEAD MANGROVE**
-  ----- **CLOSURE OF THE INLET BY SAND**

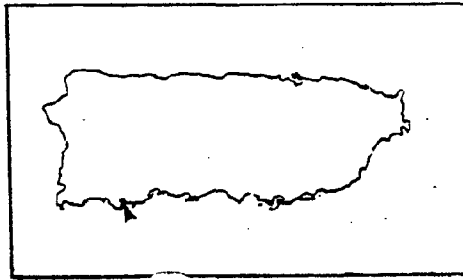
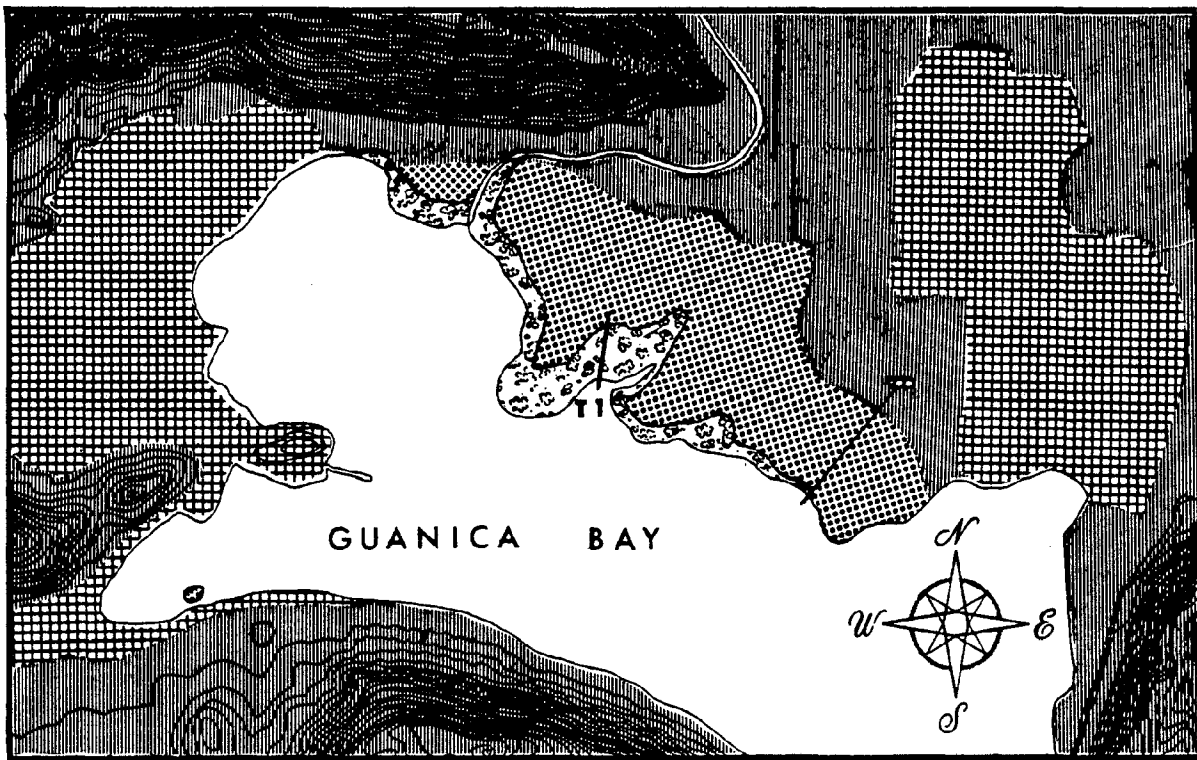




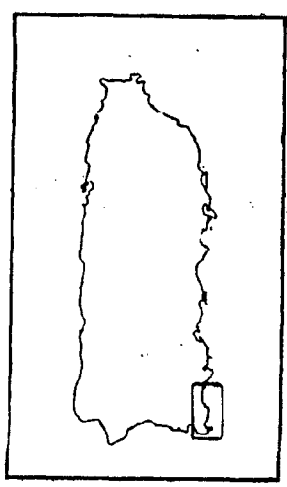


Figure 11.



0 5 Km

-  ----- **MANGROVES**
-  ----- **UPLAND**
-  ----- **SALT FLAT**
-  ----- **URBAN SETTLEMENT**



- | | | | |
|-------------------|--------------------|--|-------------|
| 1 - BAHIA SALINAS | 5 - LAUREL | | MANGROVES |
| 2 - BAHIA SUCIA | 6 - CABALLO BLANCO | | CORAL REEFS |
| 3 - PITAHAYA | 7 - ENRIQUE | | |
| 4 - SAN CRISTOBAL | 8 - TURRUMOTE | | |

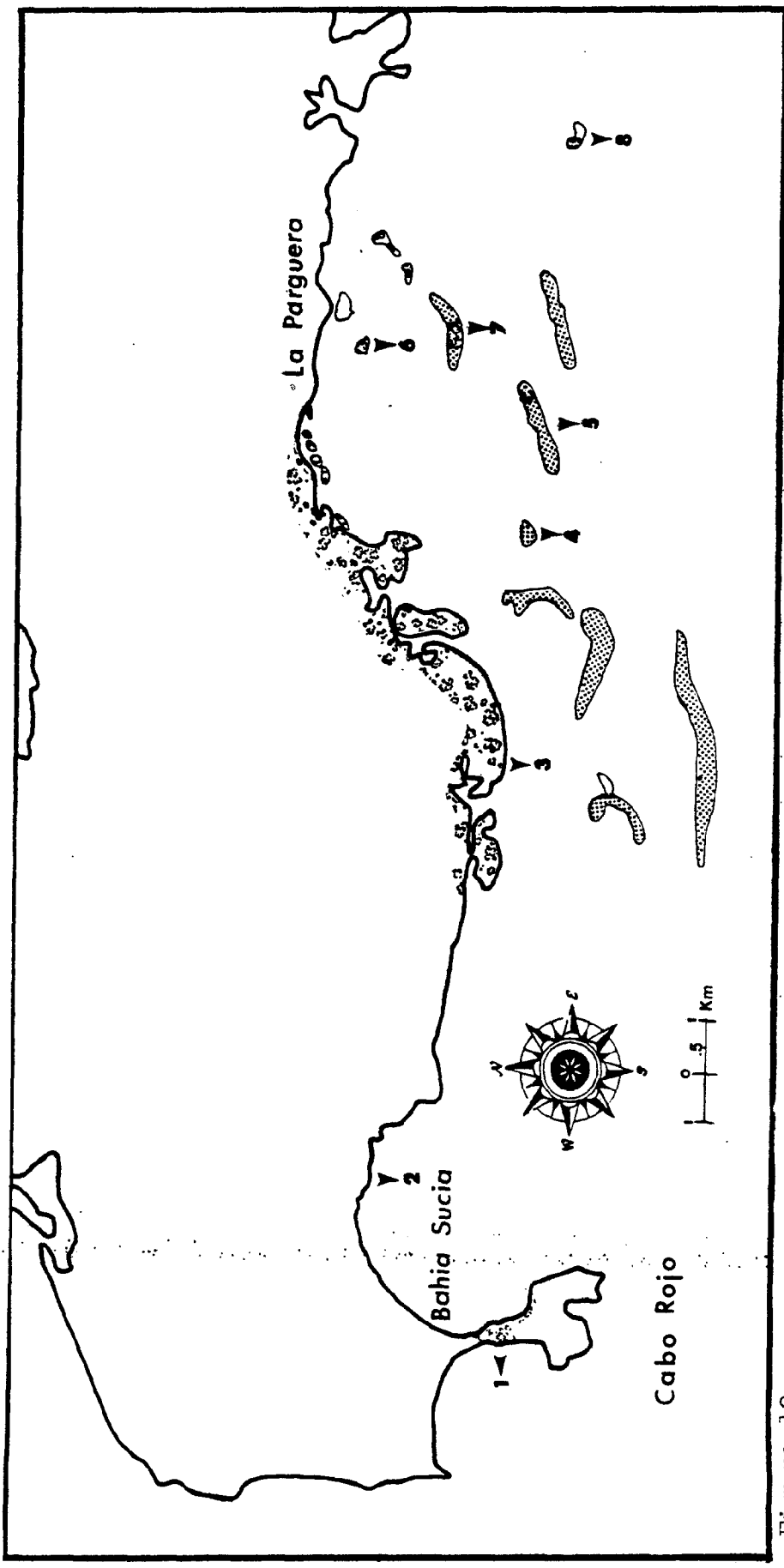


Figure 12.

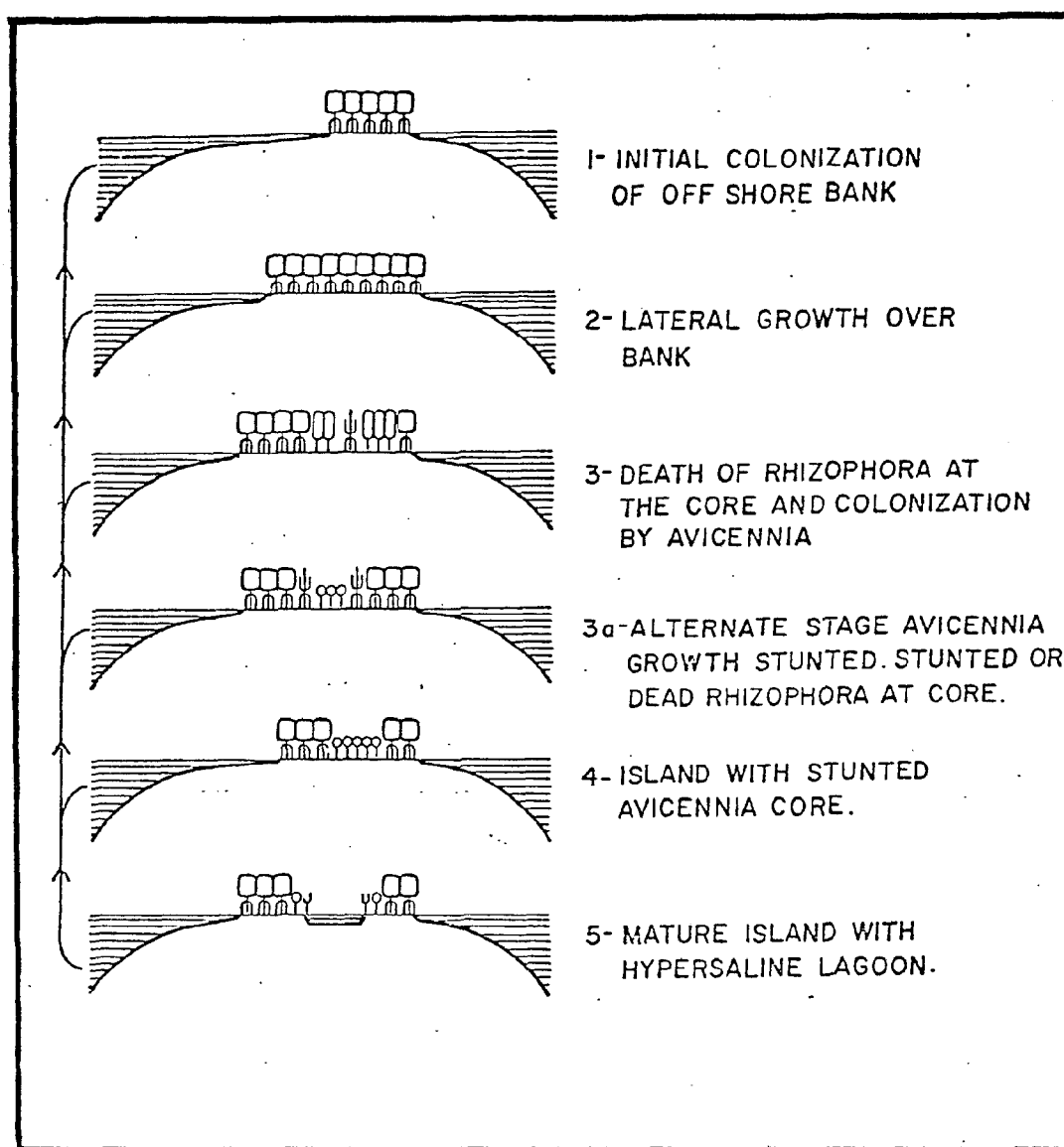


Figure 13.

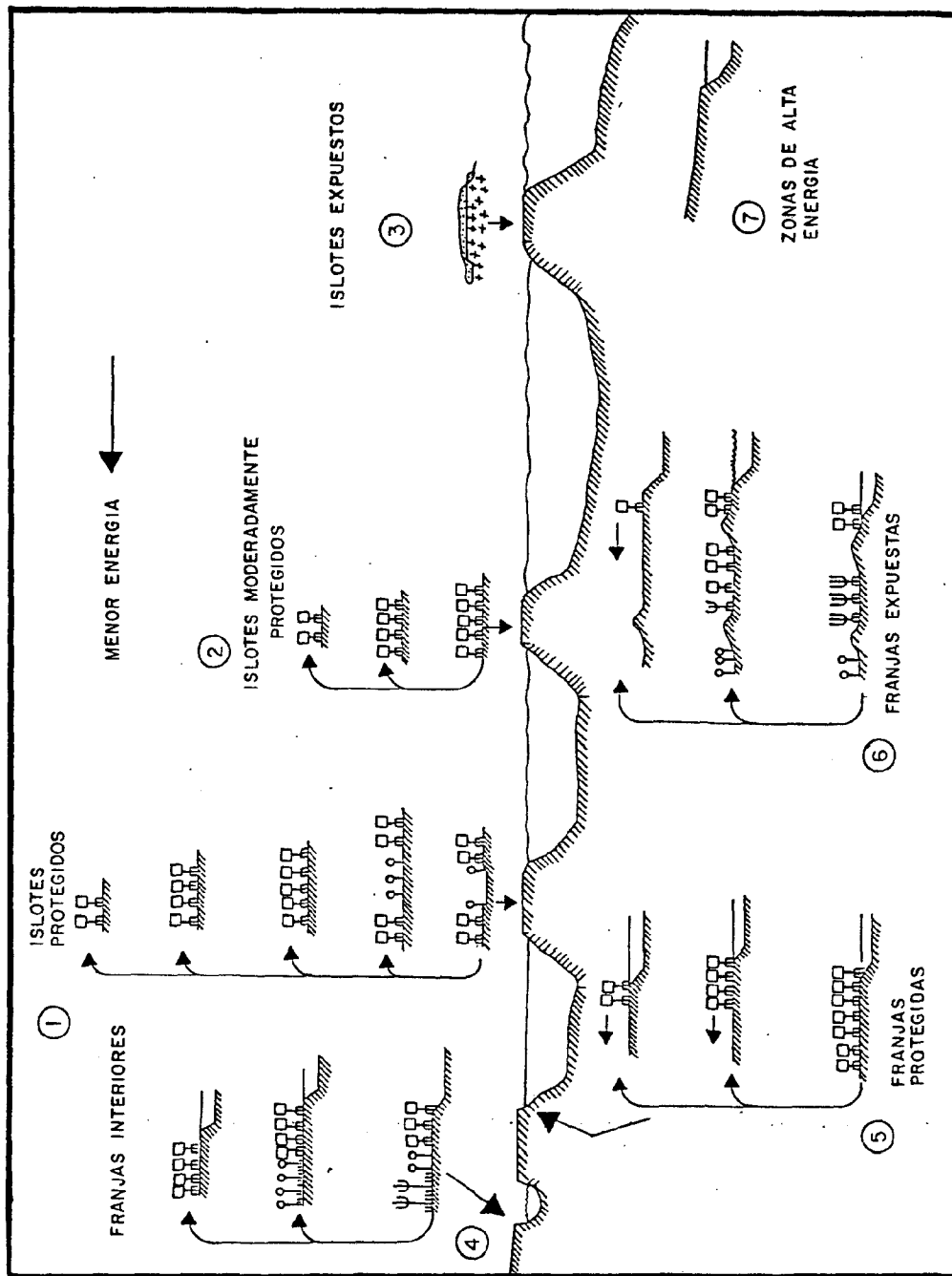


Figure 14.

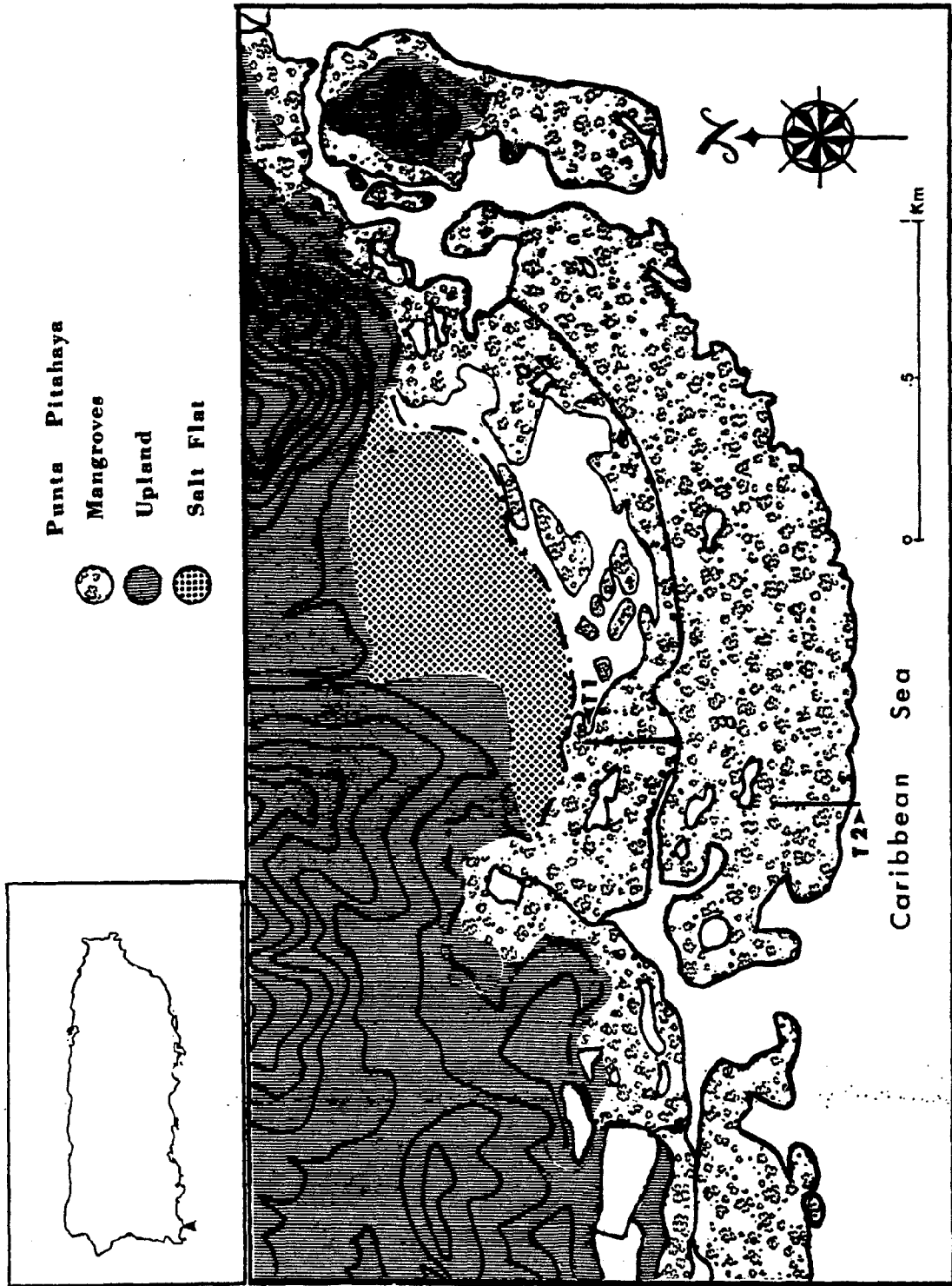


Figure 15.

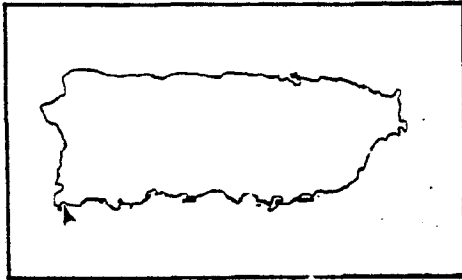
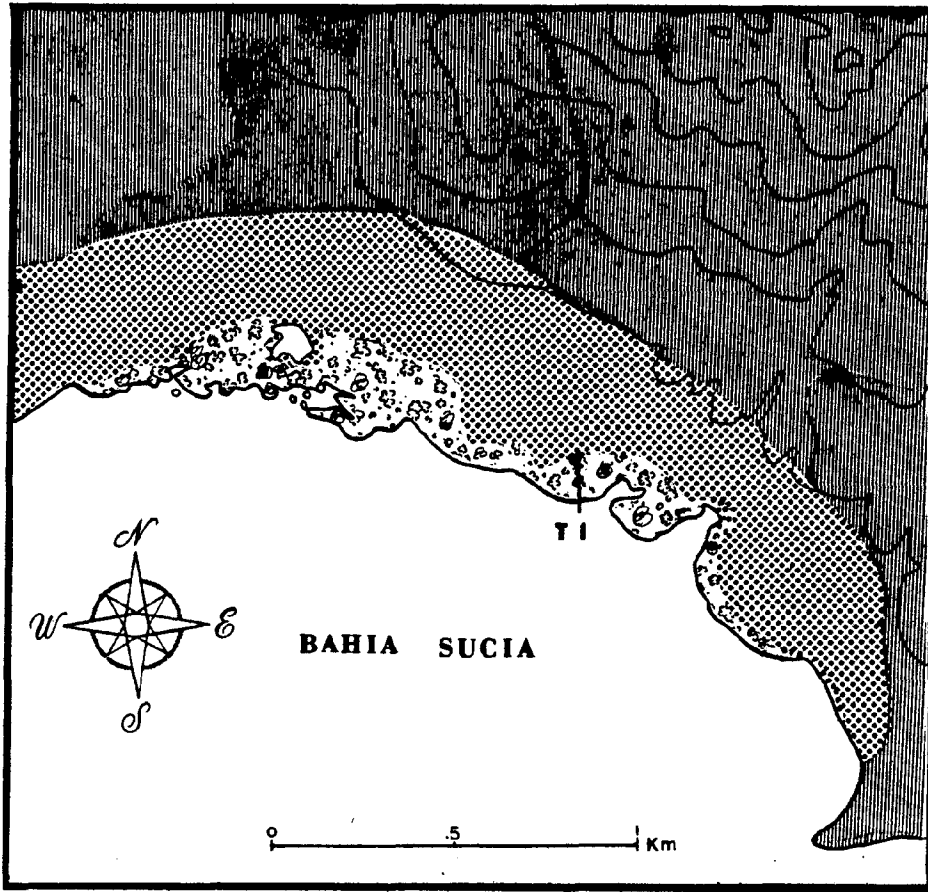




Figure 16.



-  **MANGROVES**
-  **UPLAND**
-  **SALT FLAT**

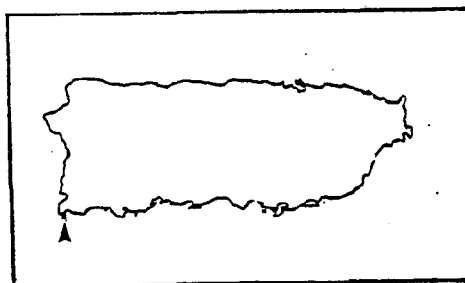
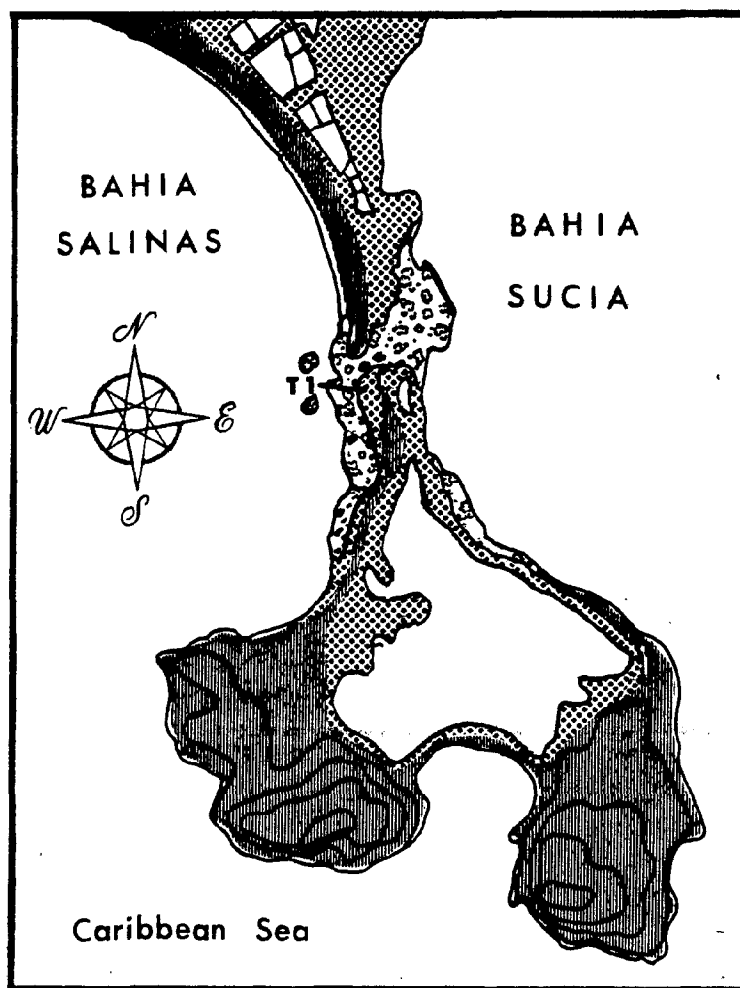


Figure 17.



-  **MANGROVES**
-  **UPLAND**
-  **SALT FLAT**

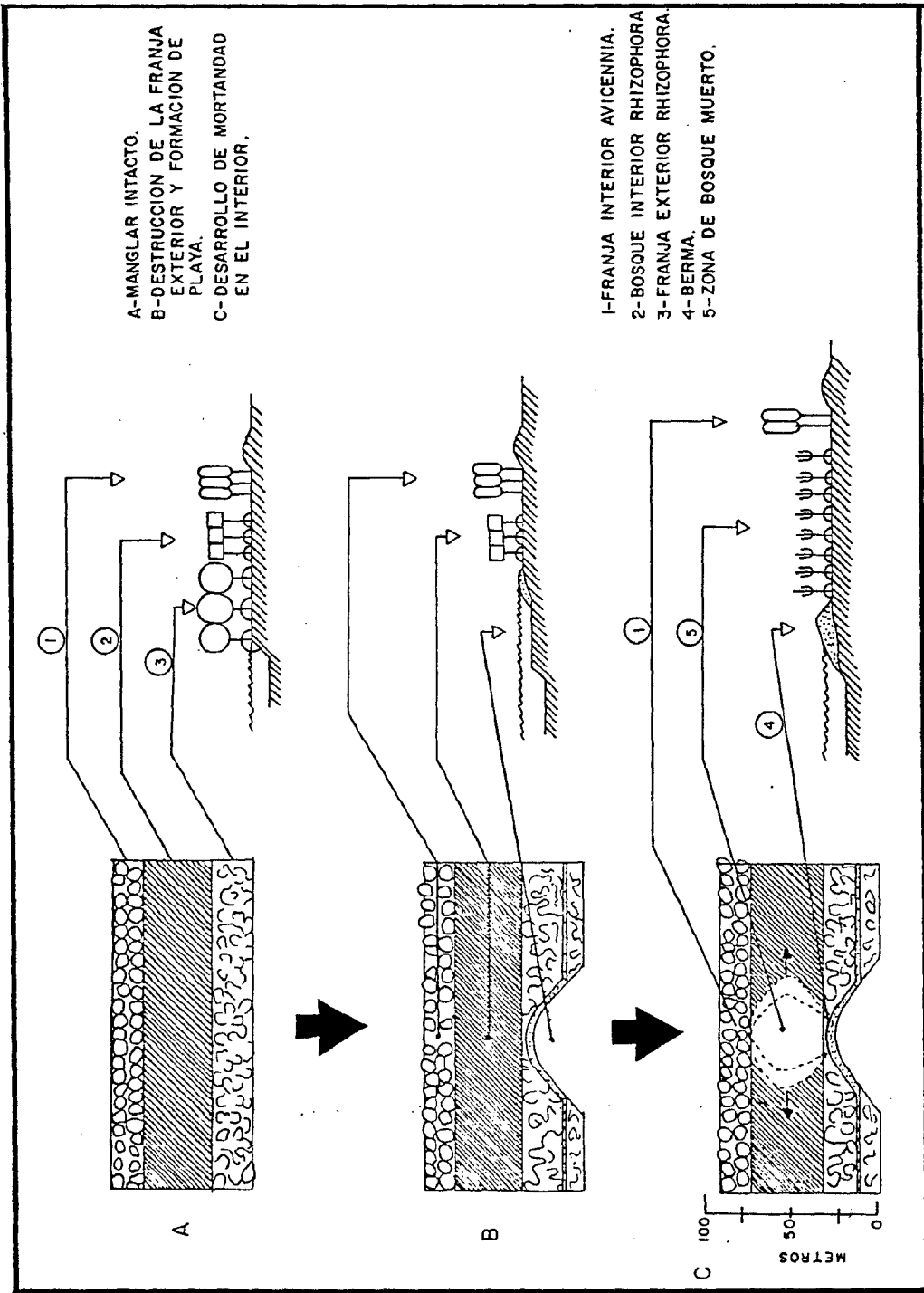


Figure 18.

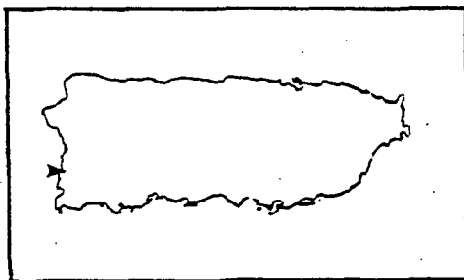
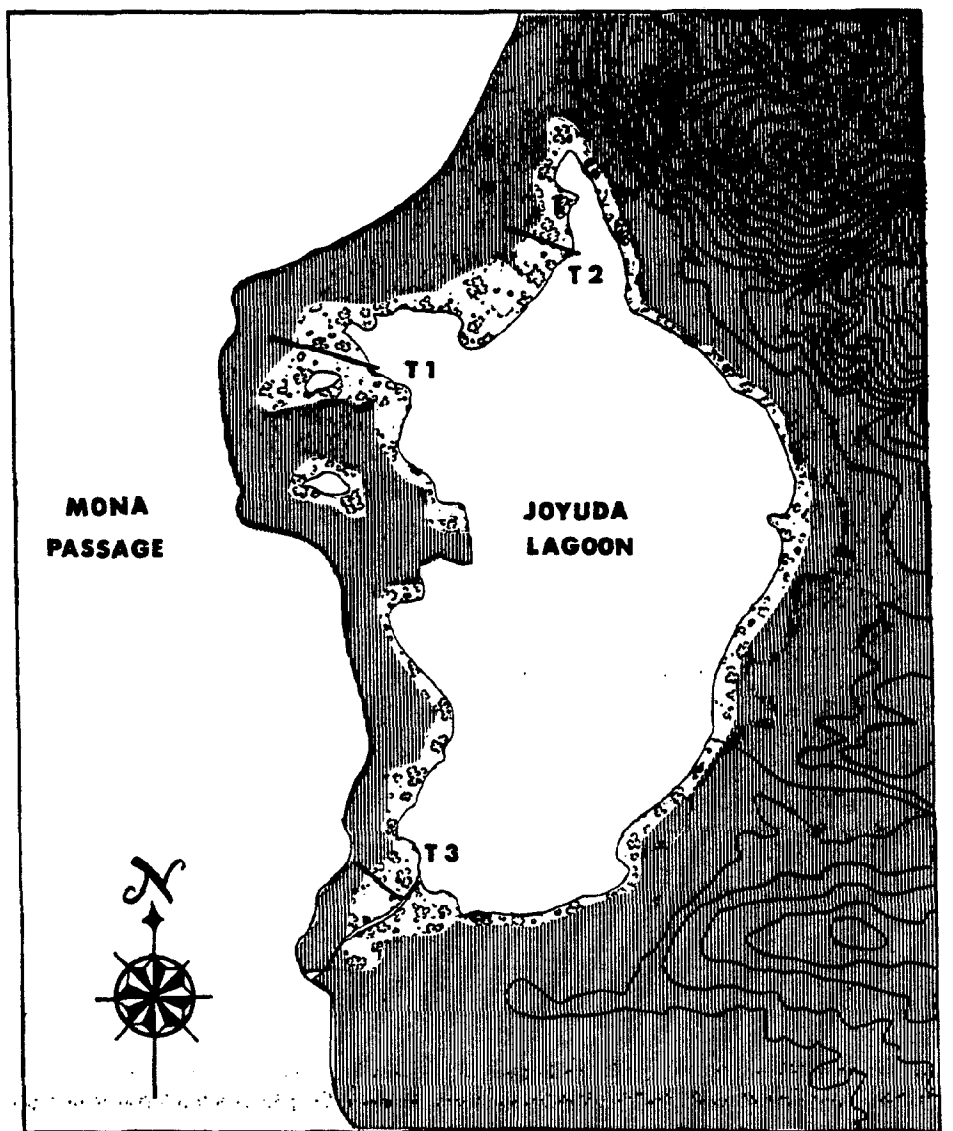




Figure 19.



-  ----- MANGROVES
-  ----- UPLAND

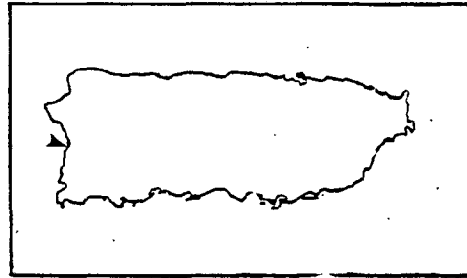
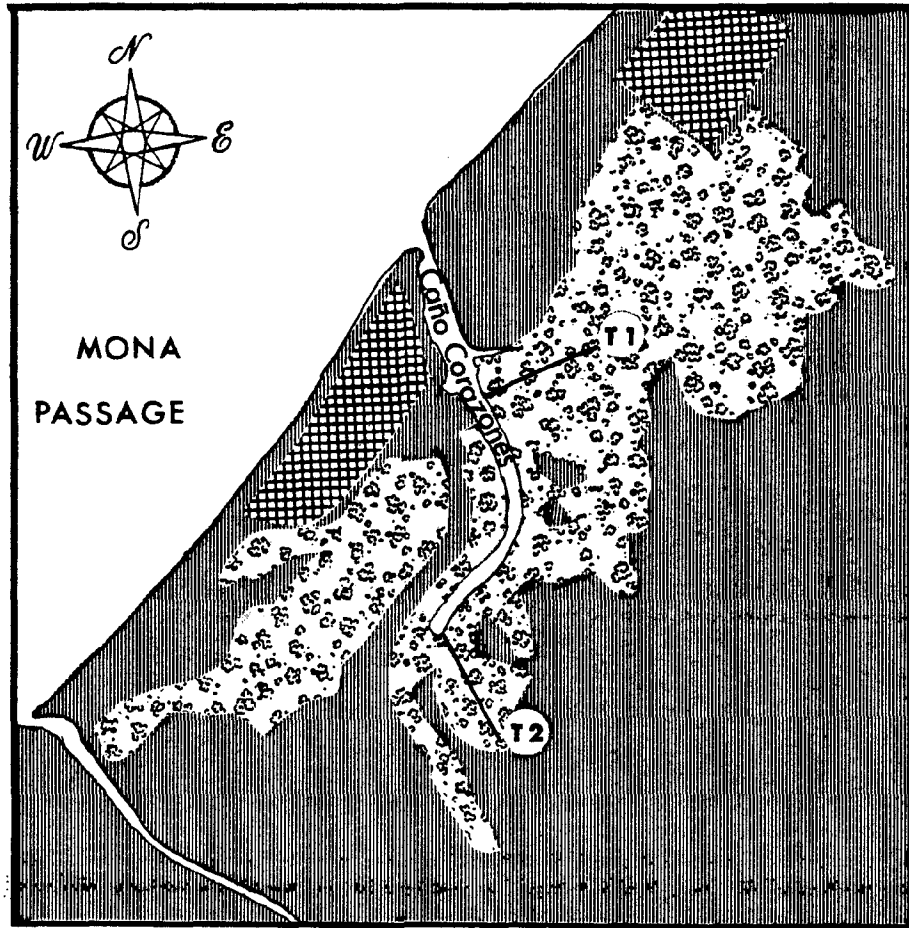


Figure 20.



 MANGROVES

 UPLAND

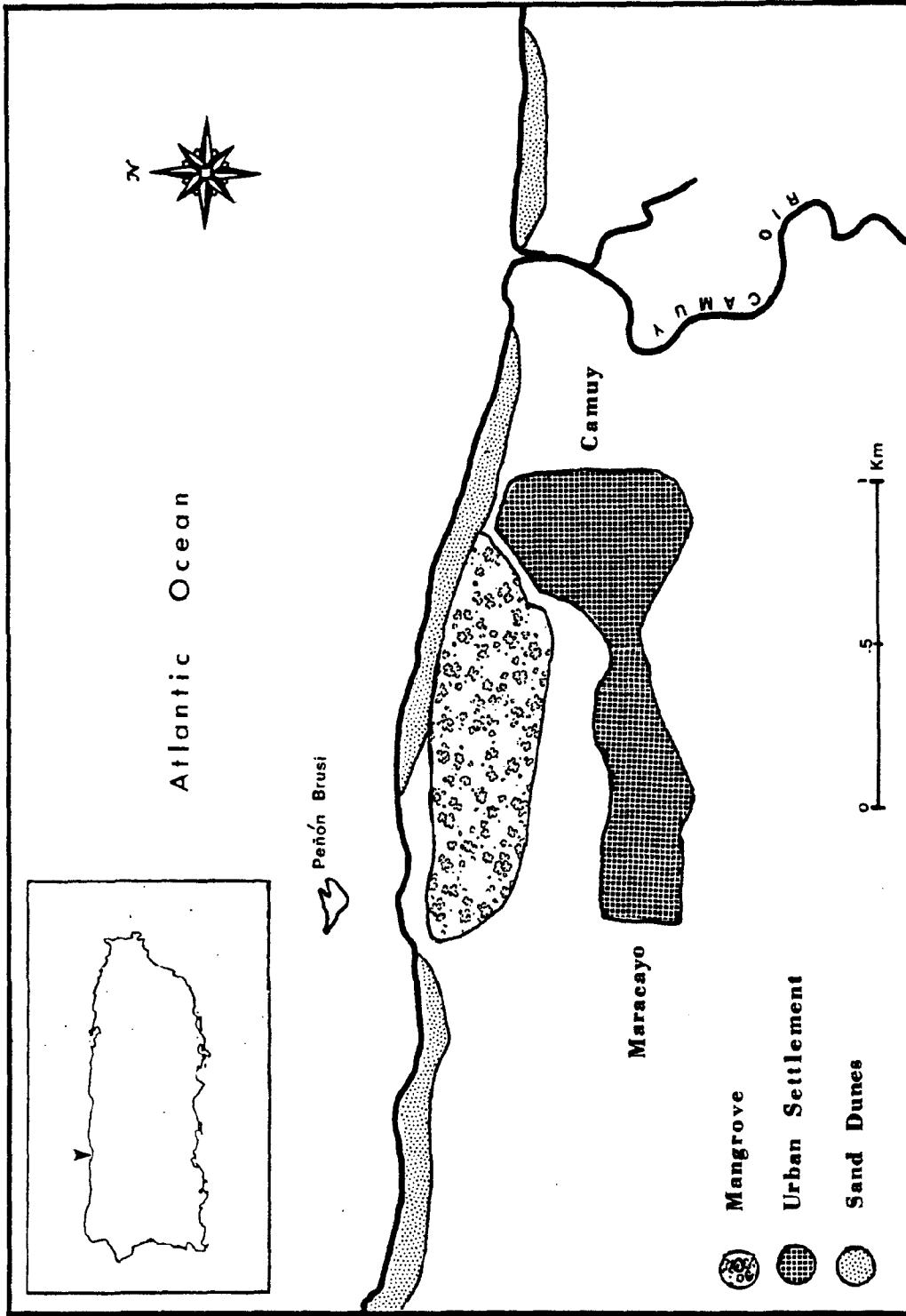


Figure 21.

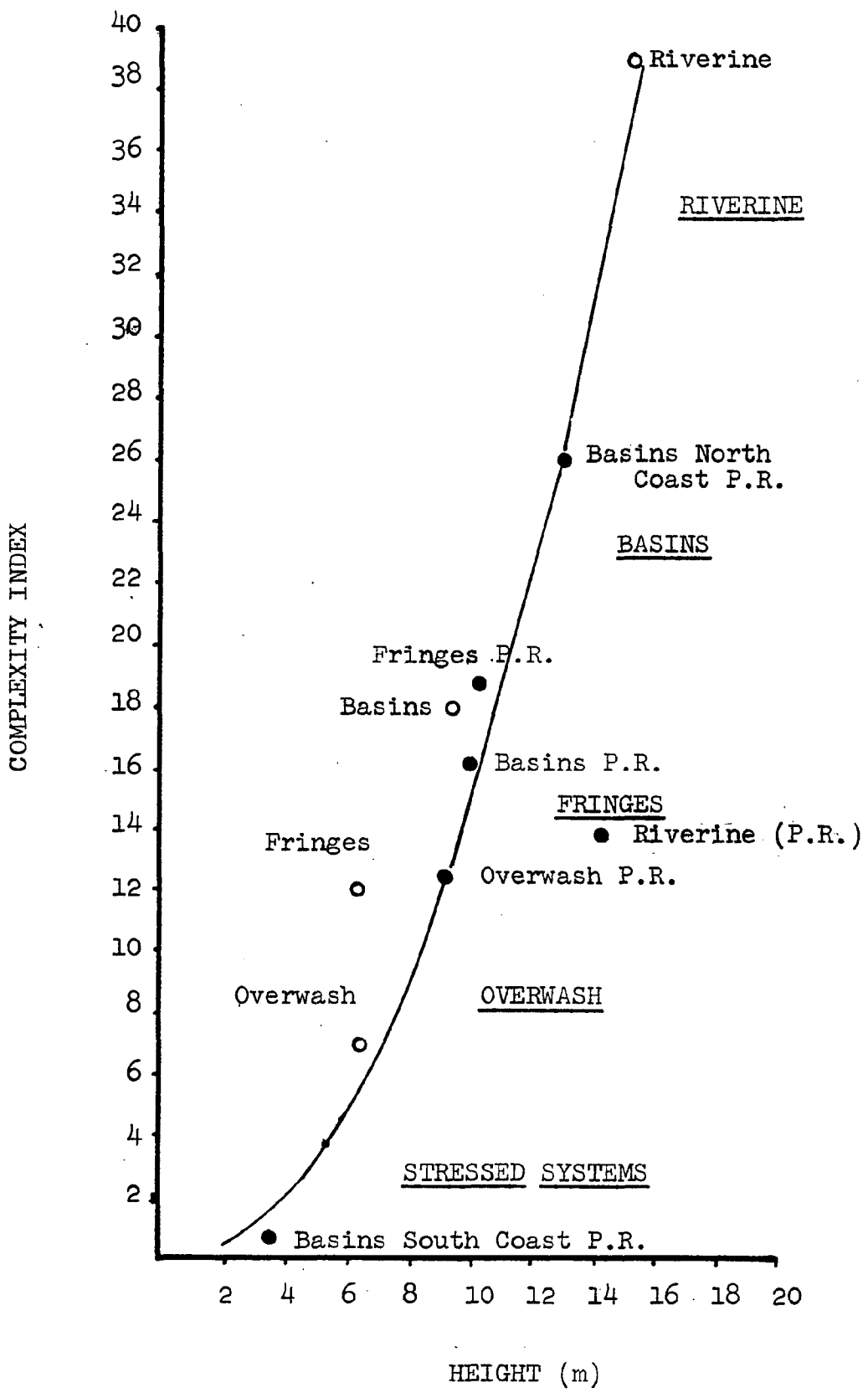


Figure 22

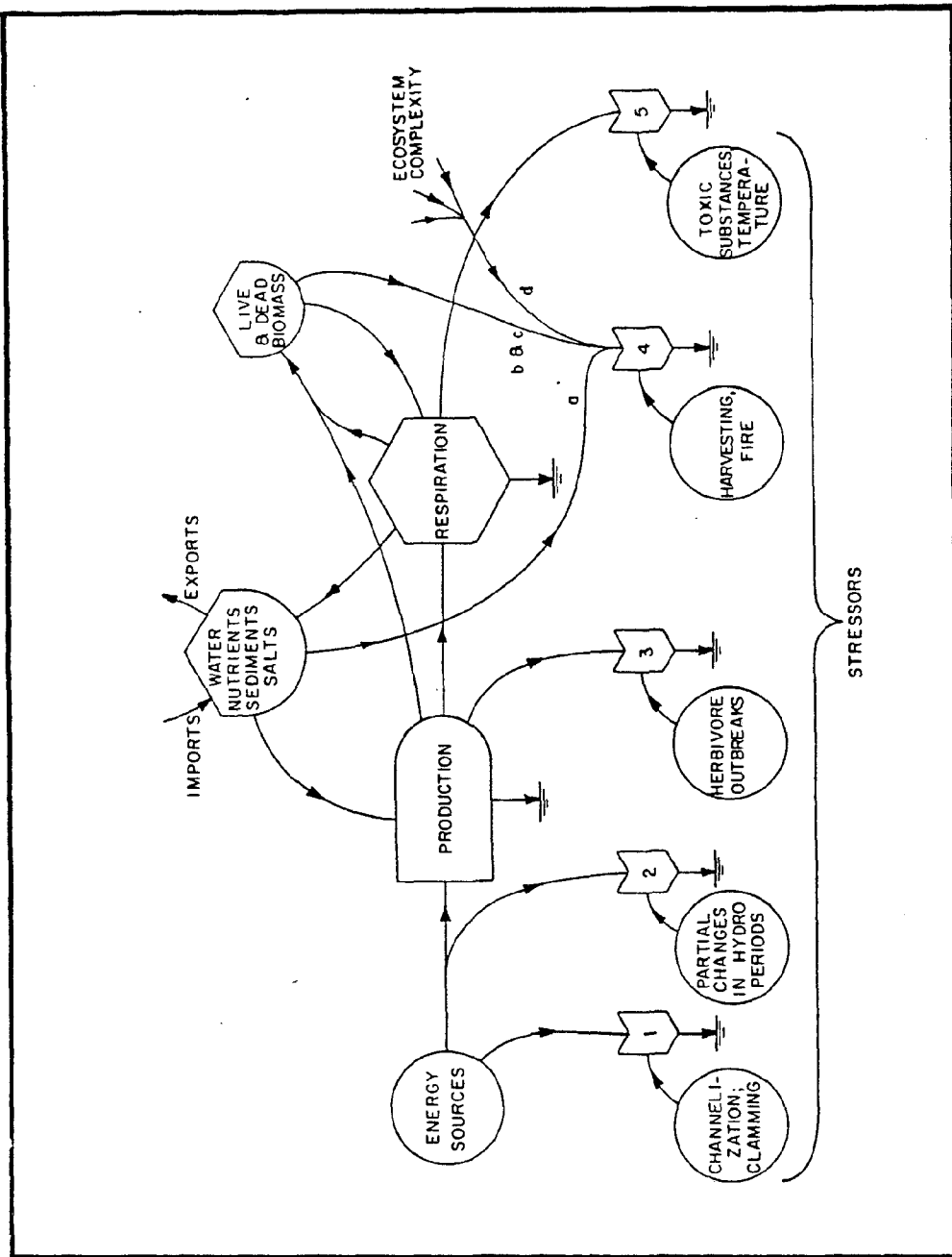


Figure 23

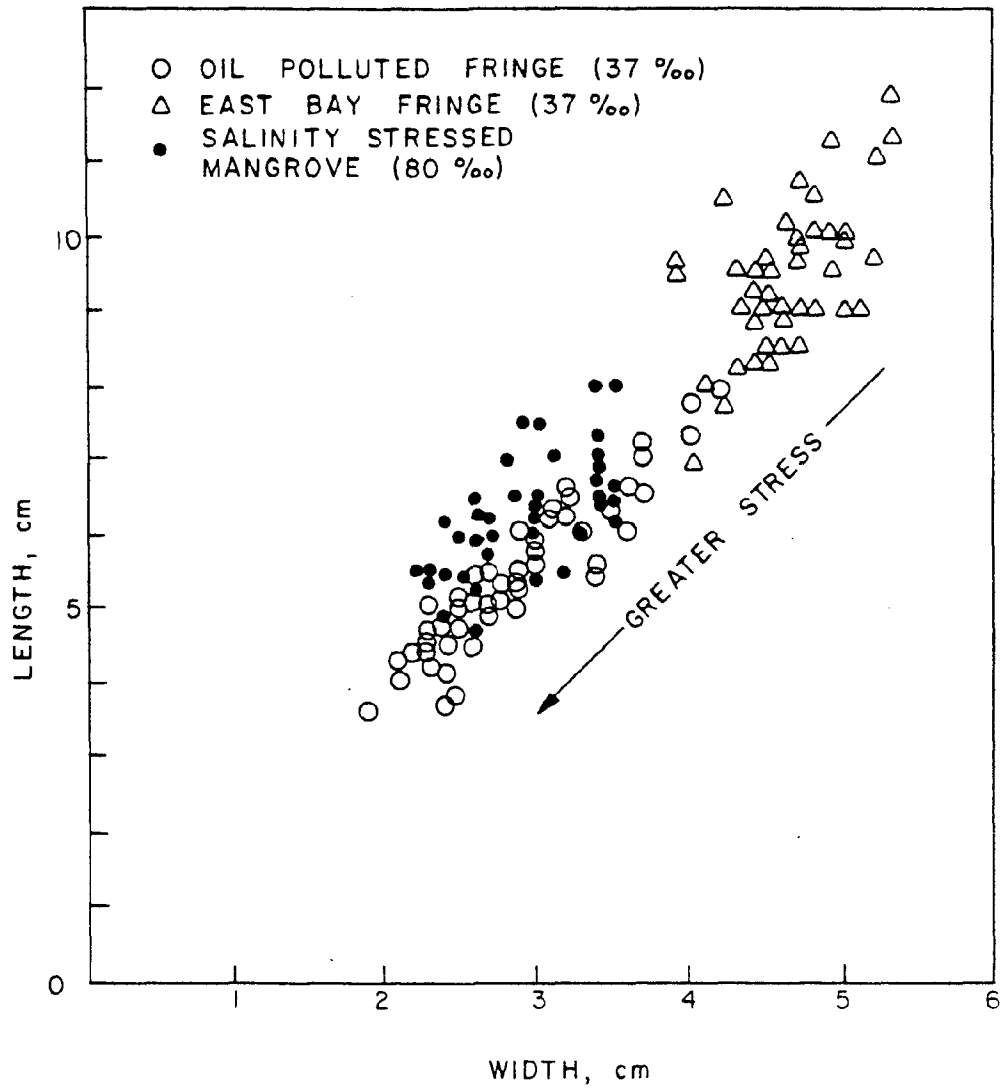


Figure 24.

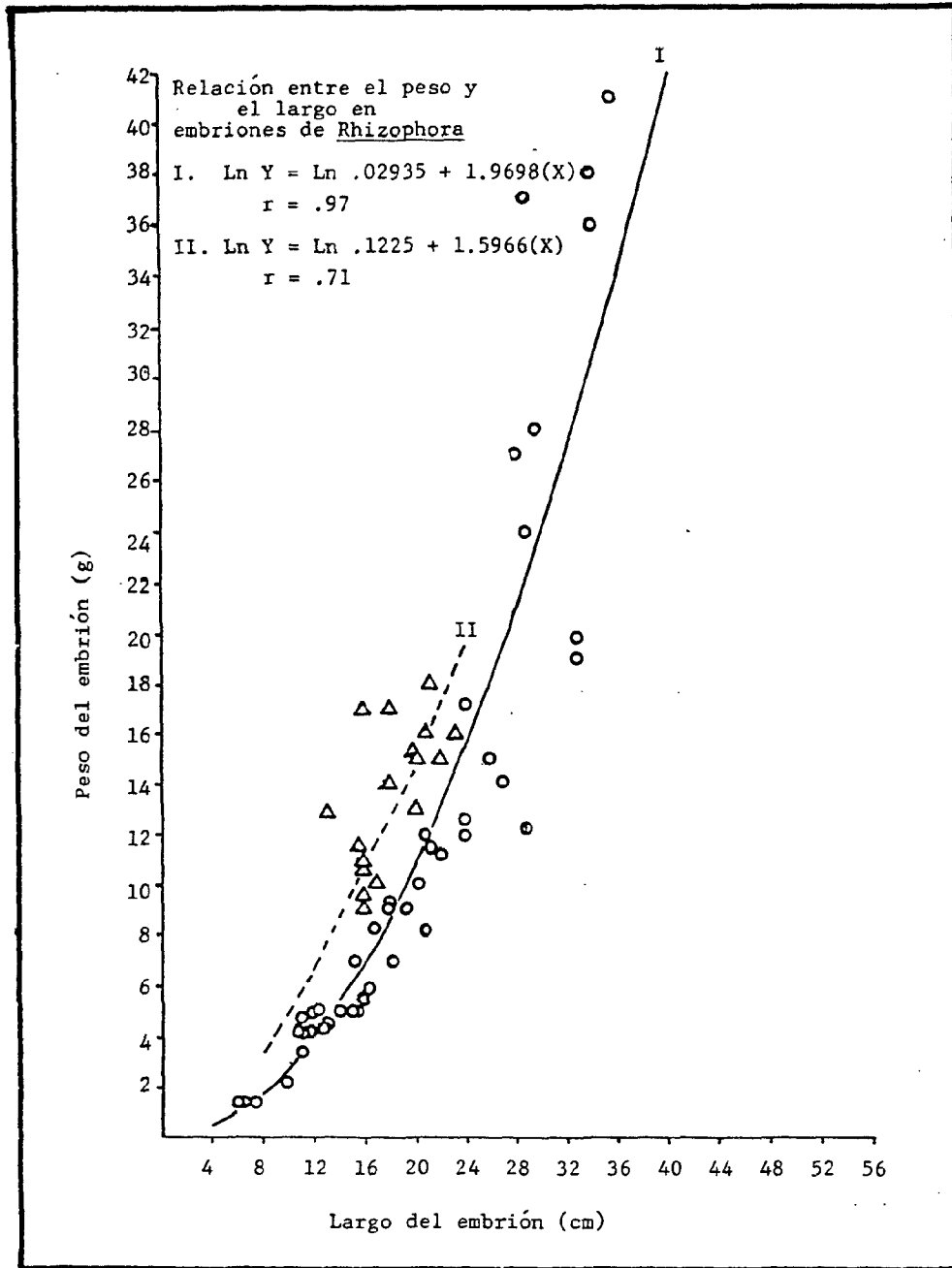
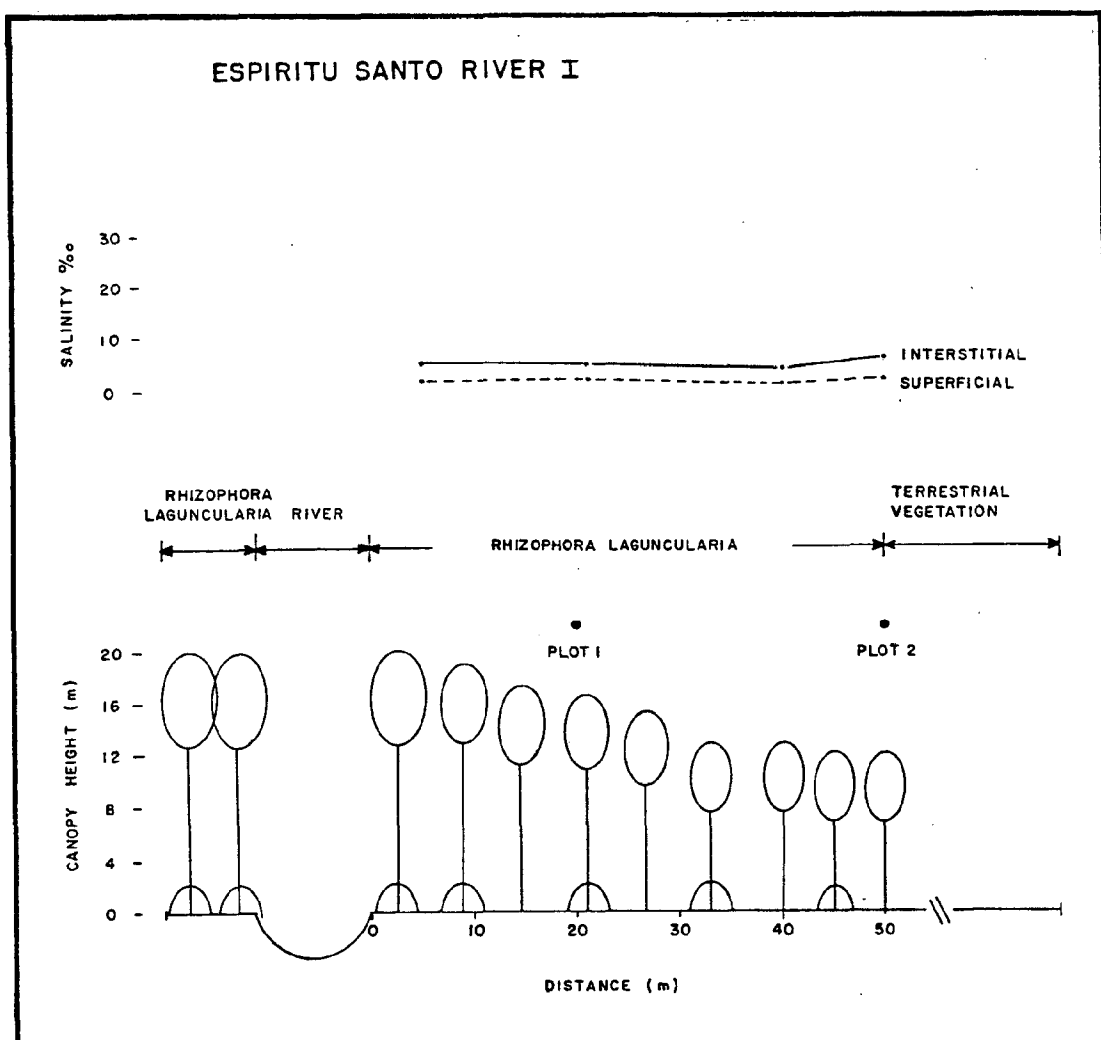


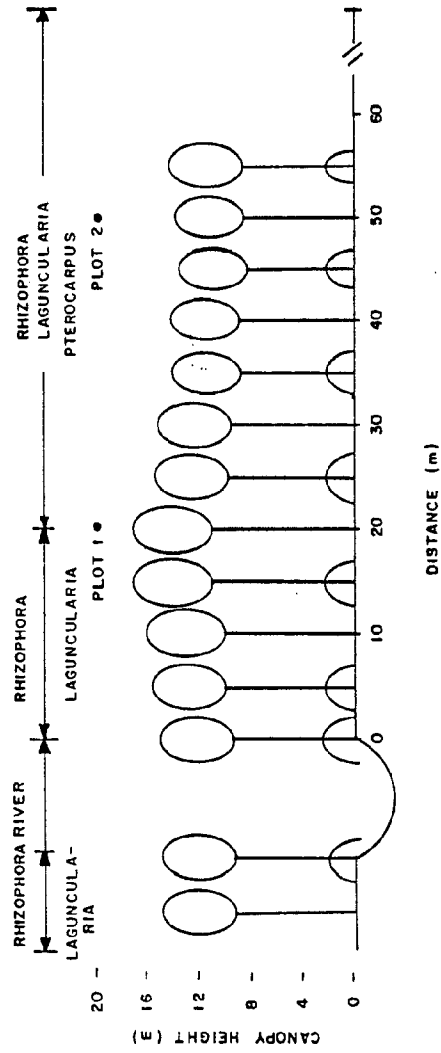
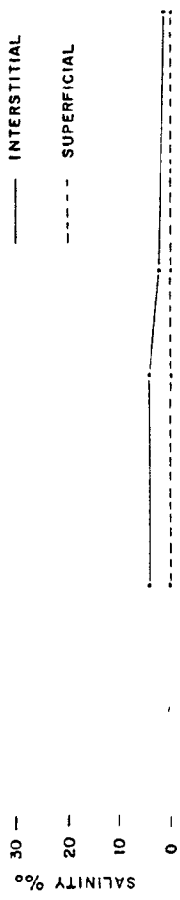
Figure 25

Profile 1

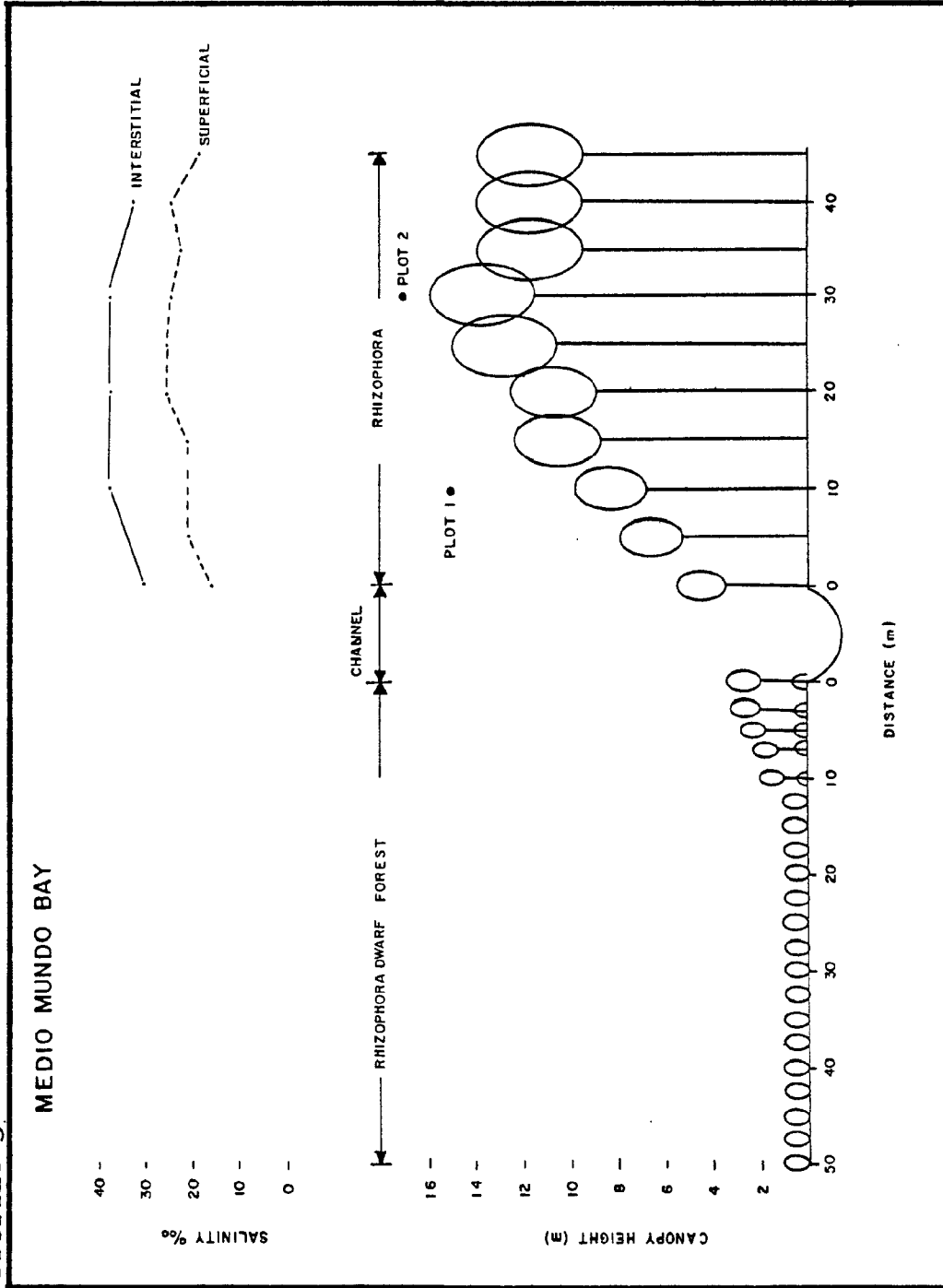


Profile 2

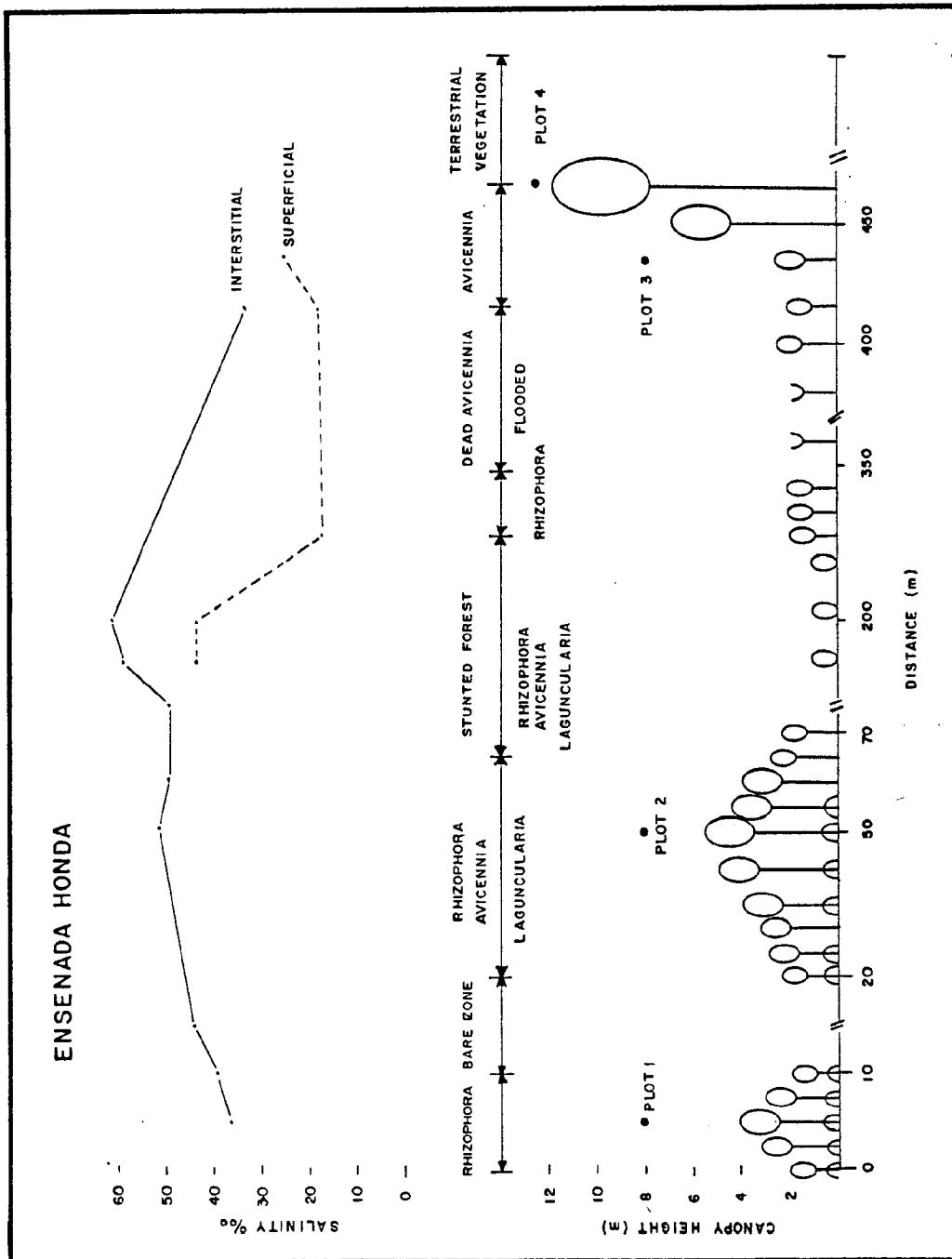
ESPIRITU SANTO RIVER II



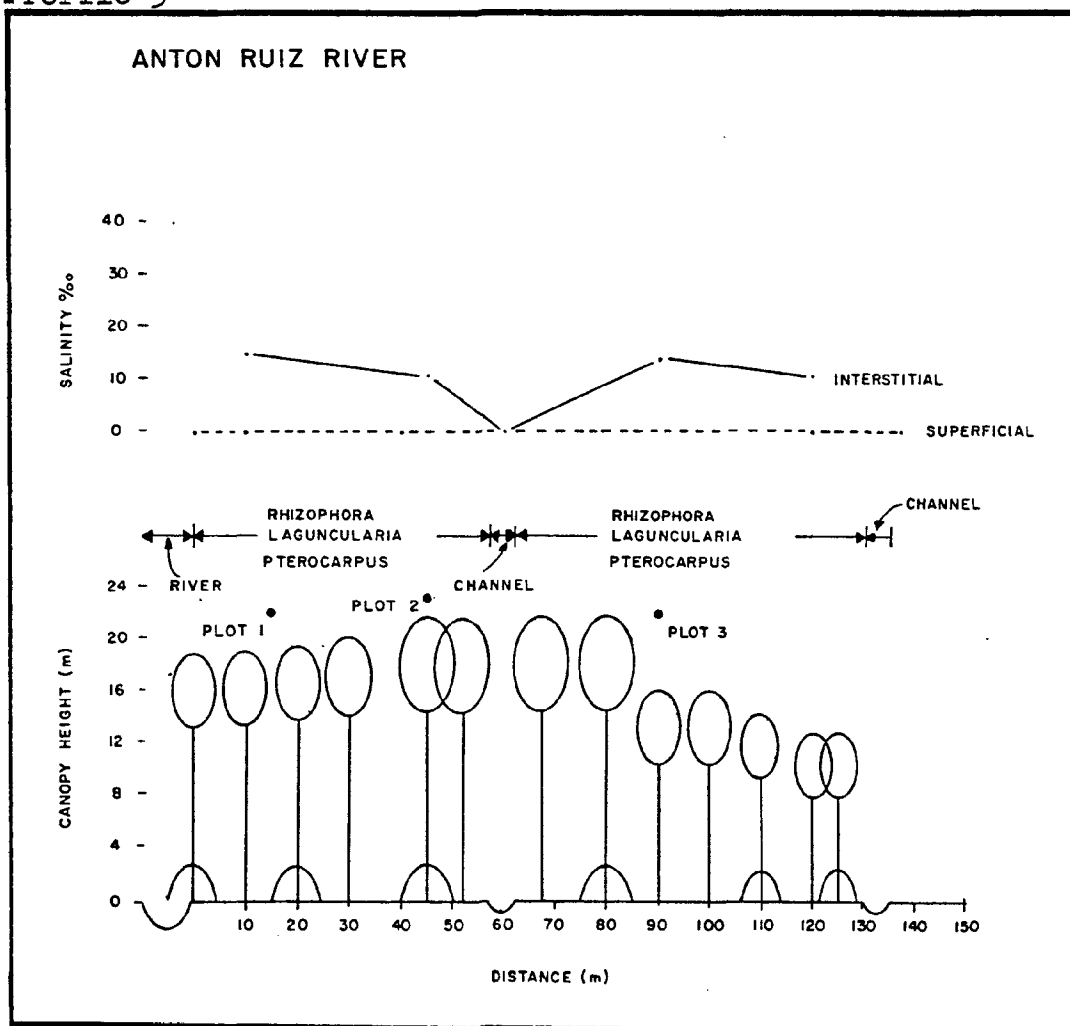
Profile 3



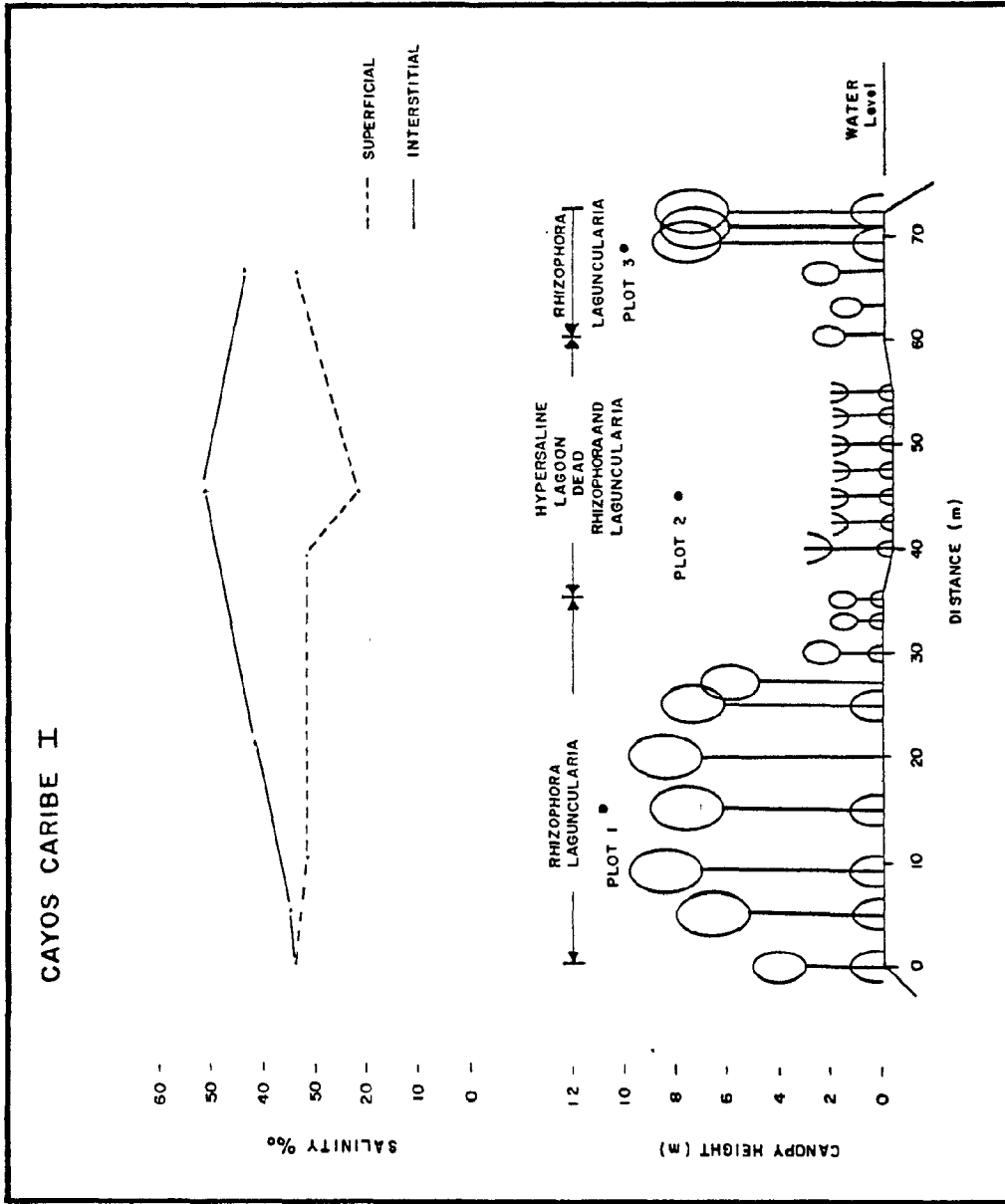
Profile 4



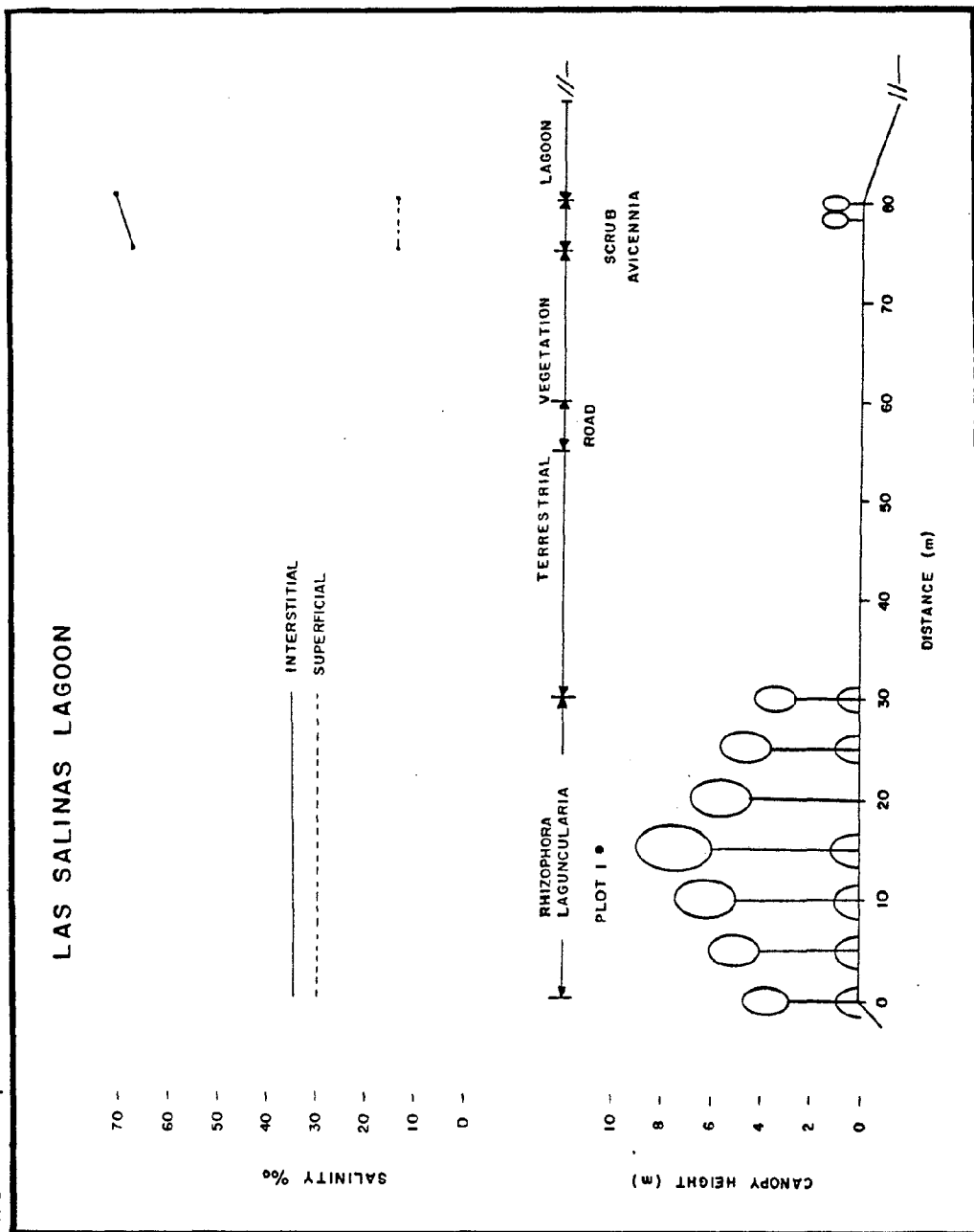
Profile 5



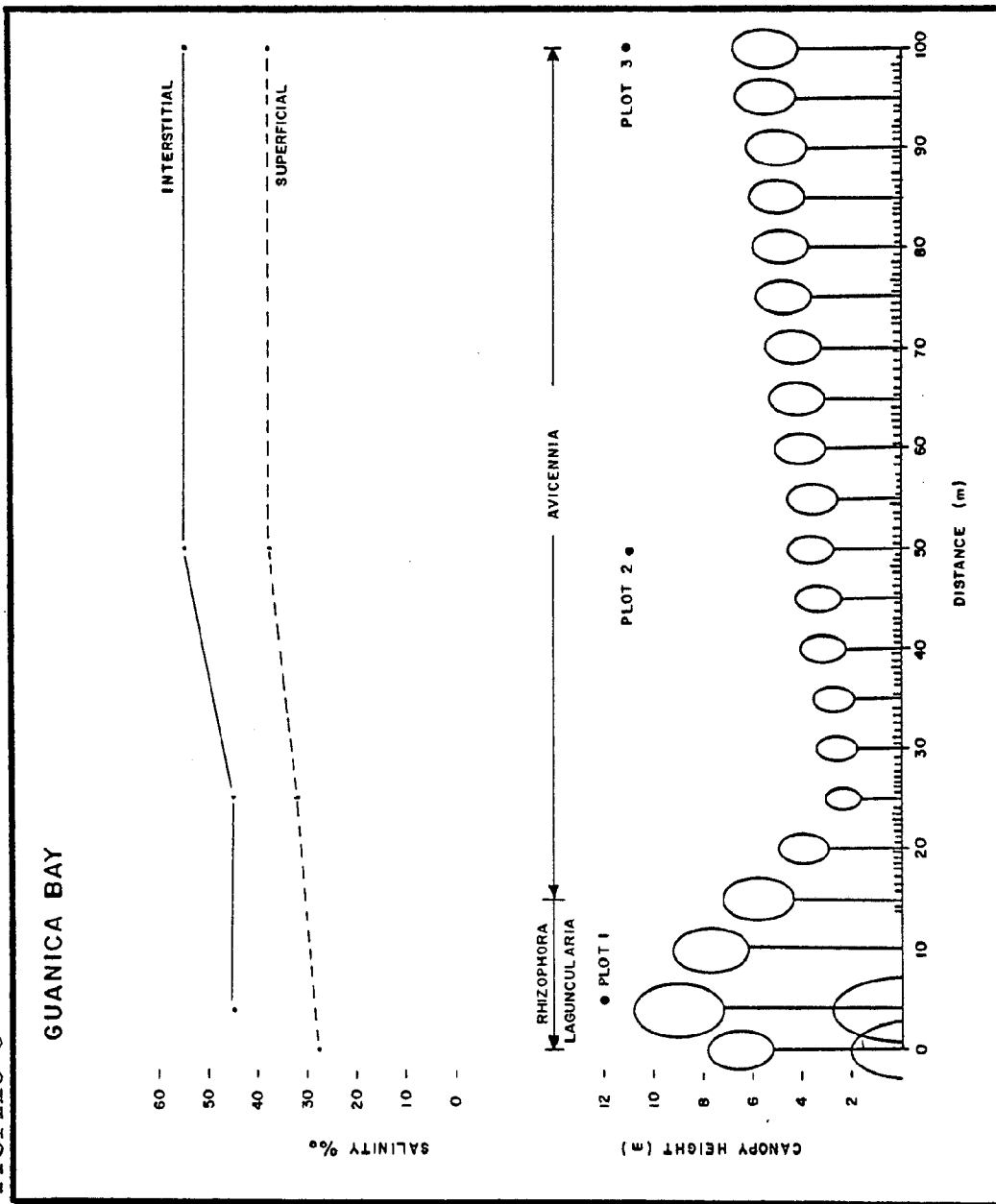
Profile 6



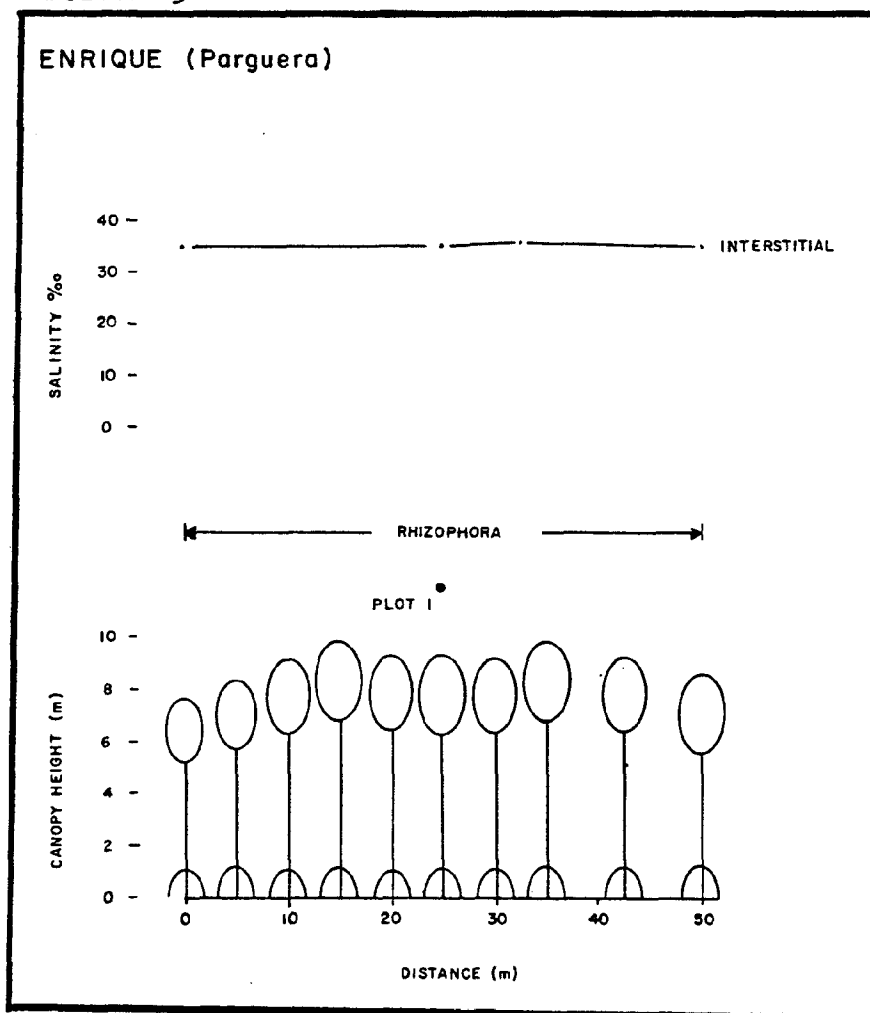
Profile 7



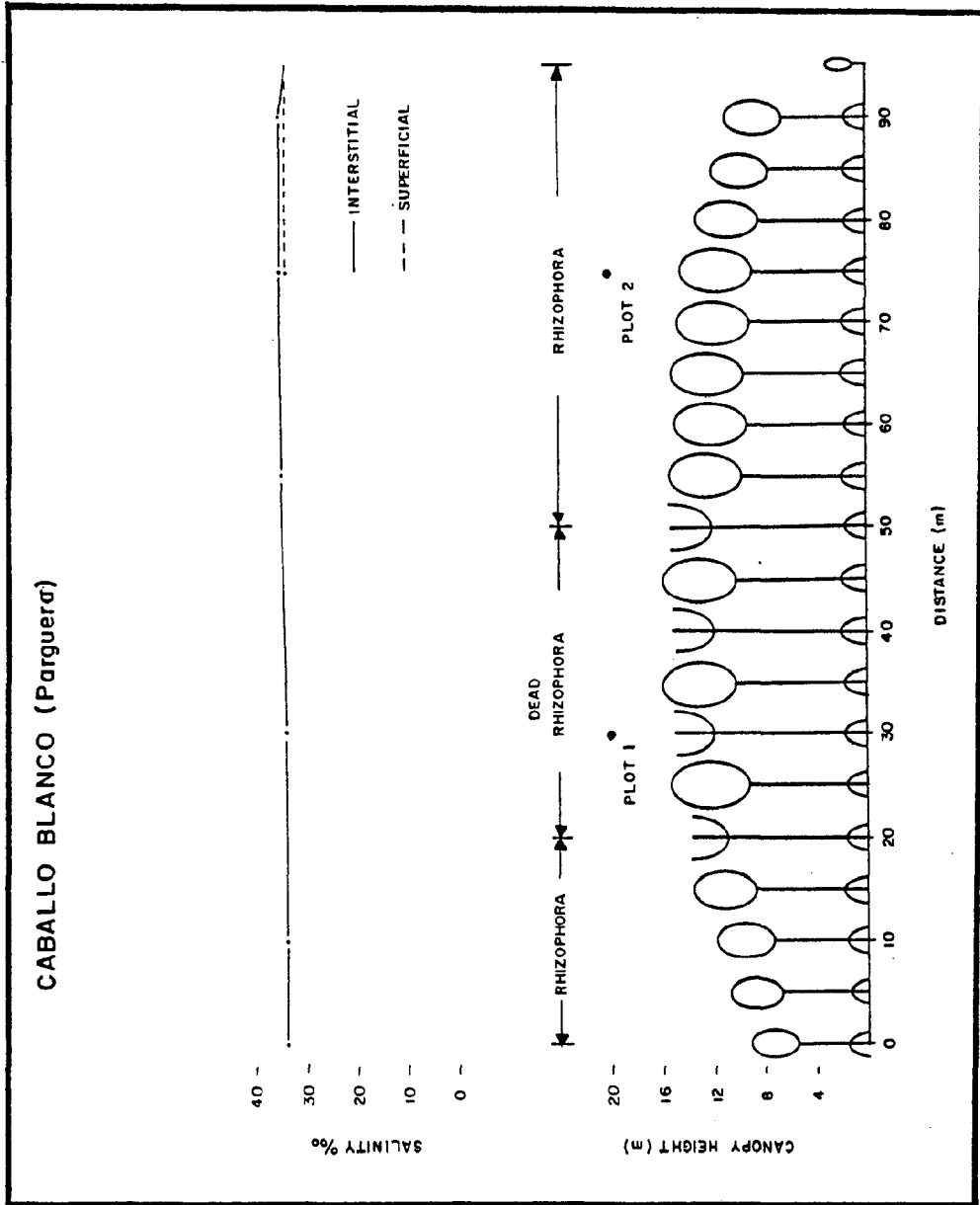
Profile 8



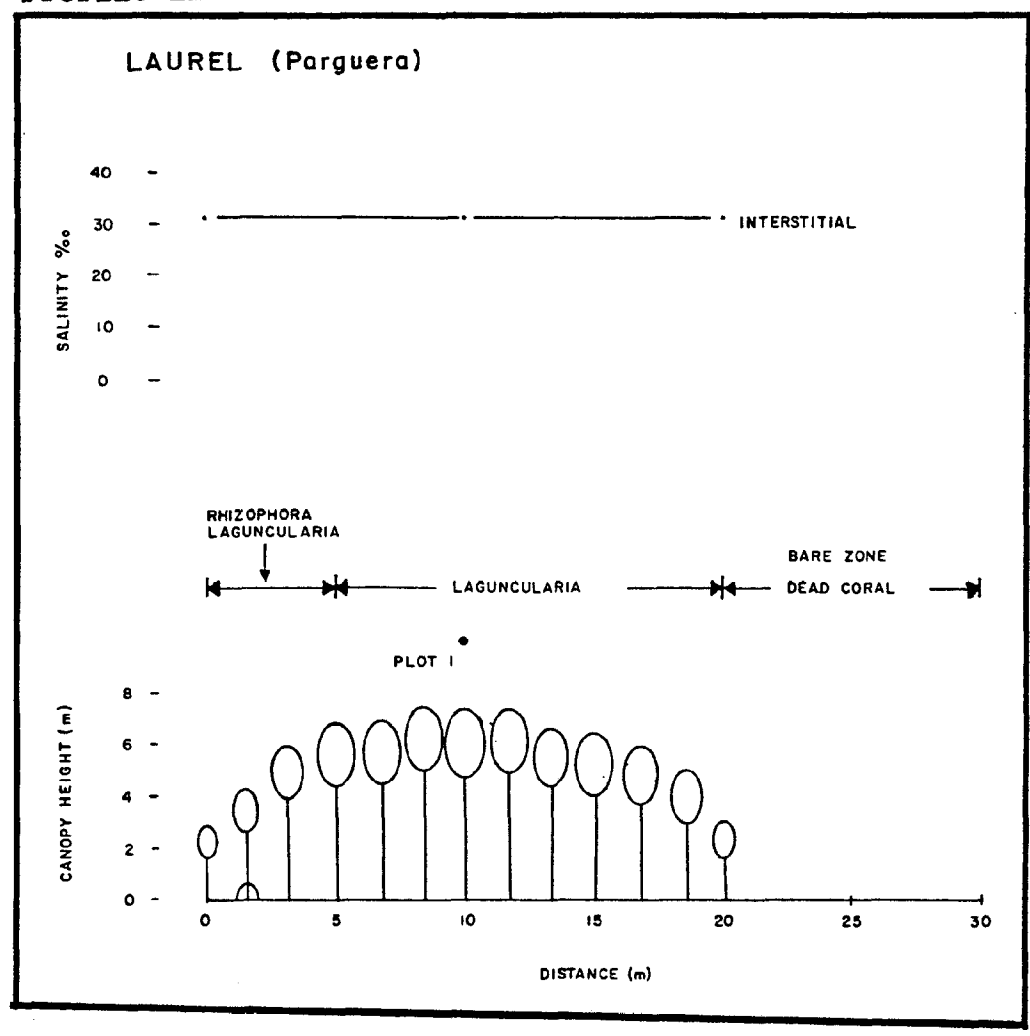
Profile 9



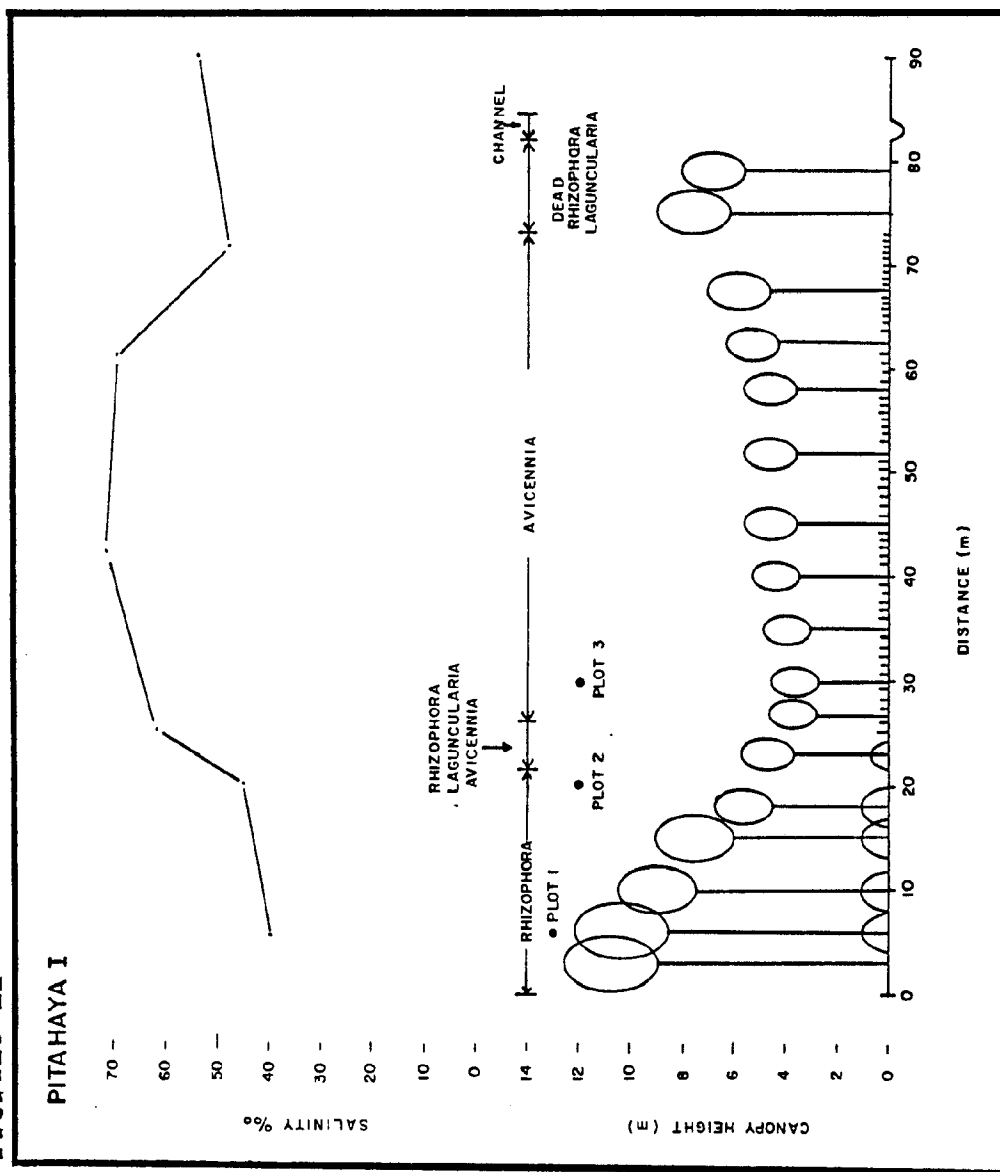
Profile 10



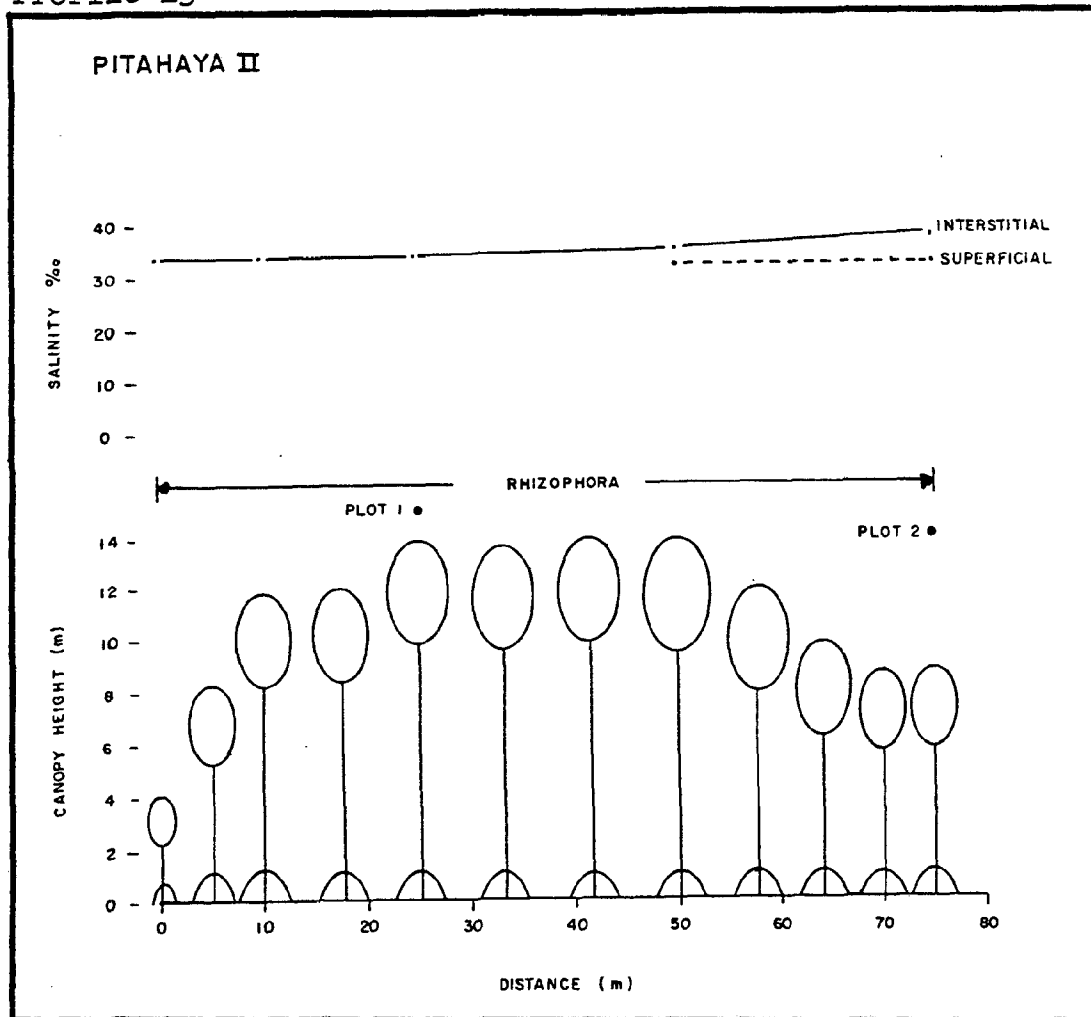
Profile 11



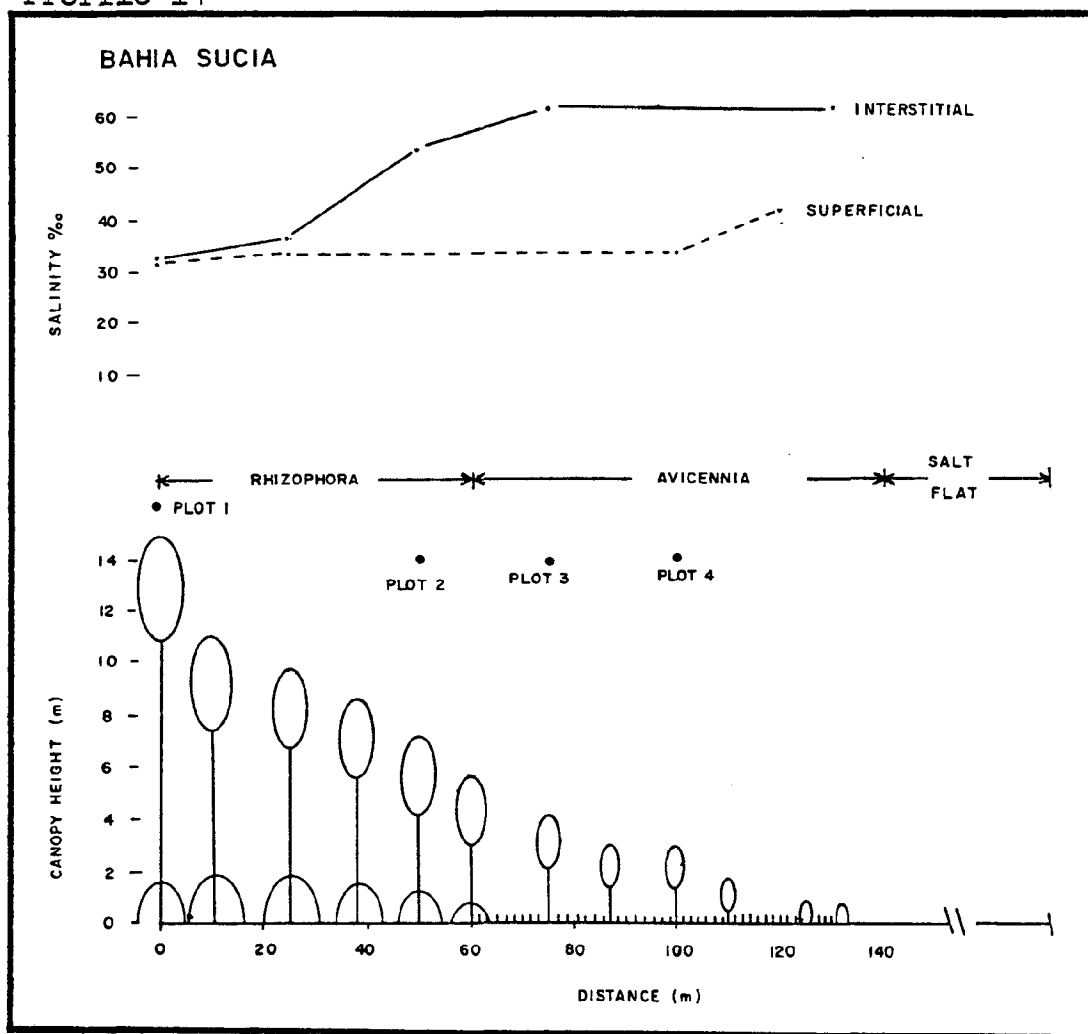
Profile 12



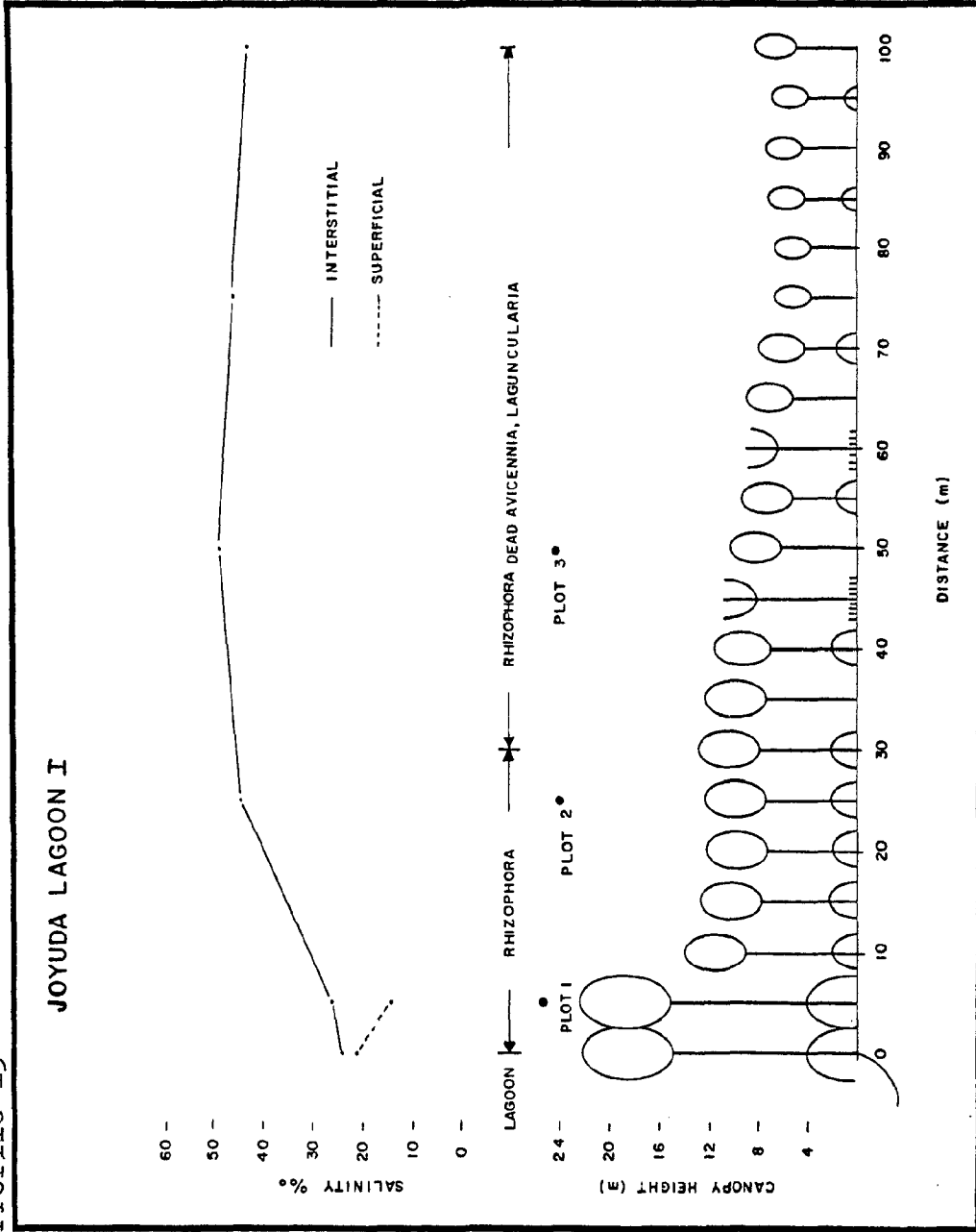
Profile 13



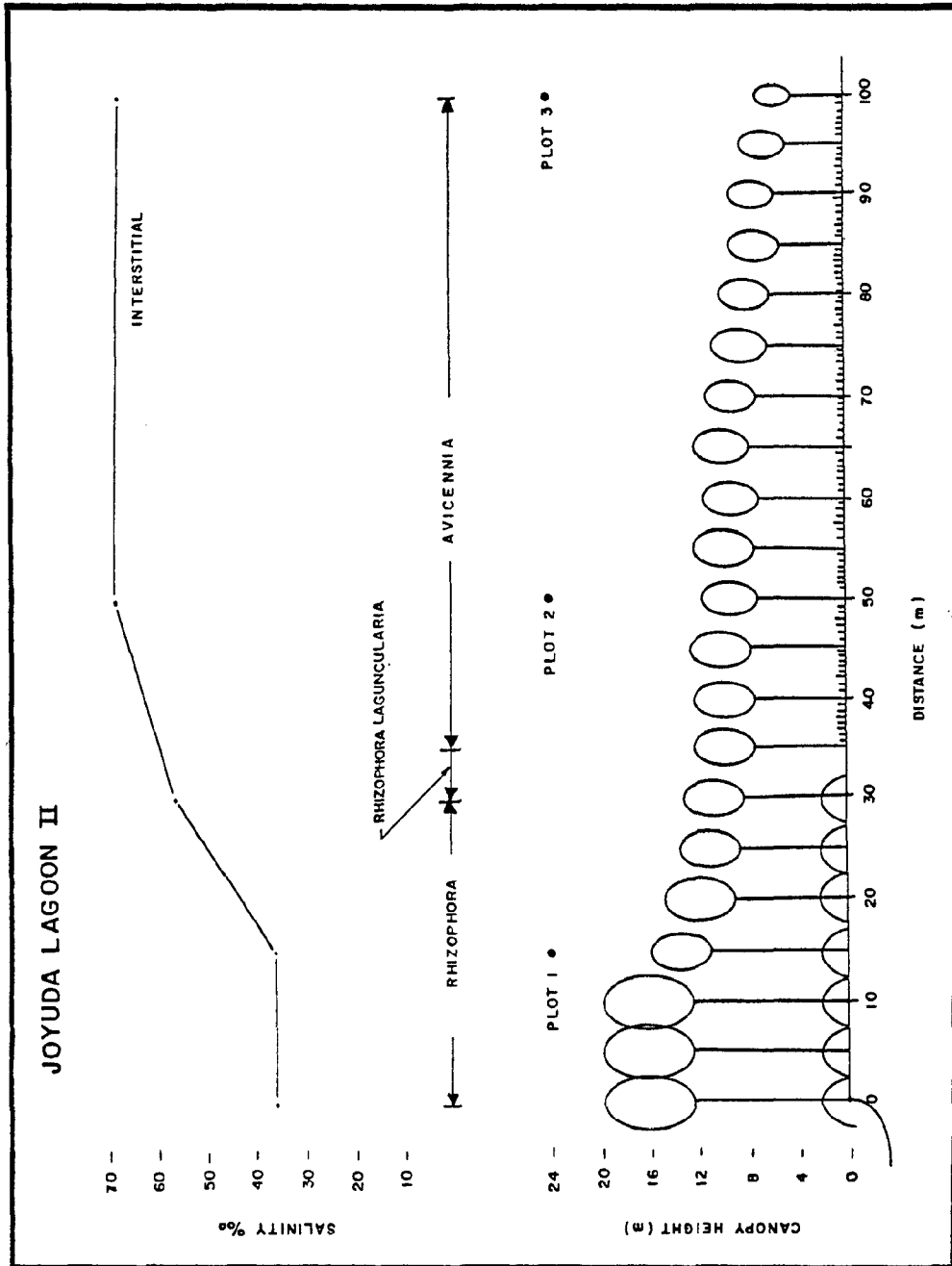
Profile 14

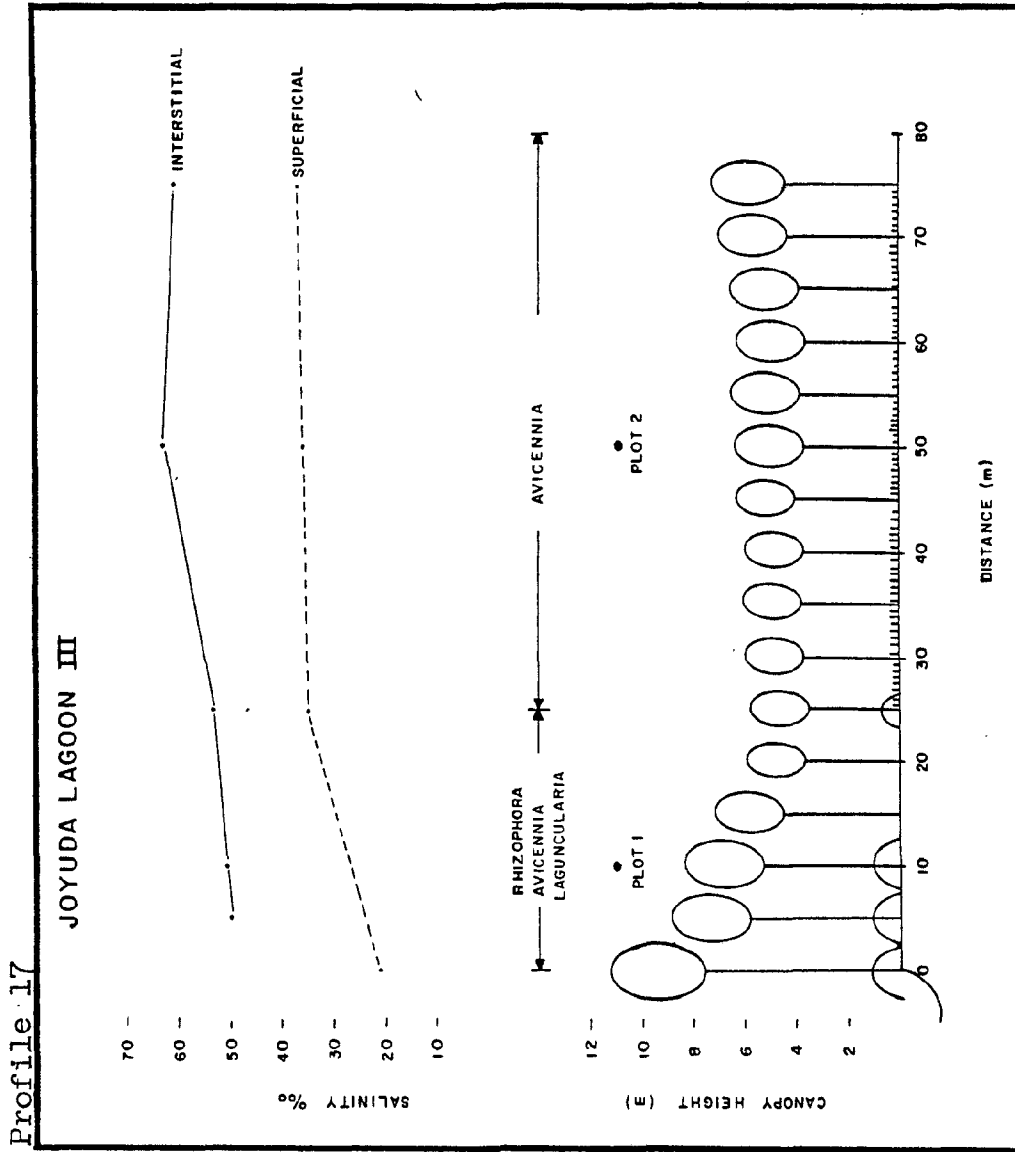


Profile 15

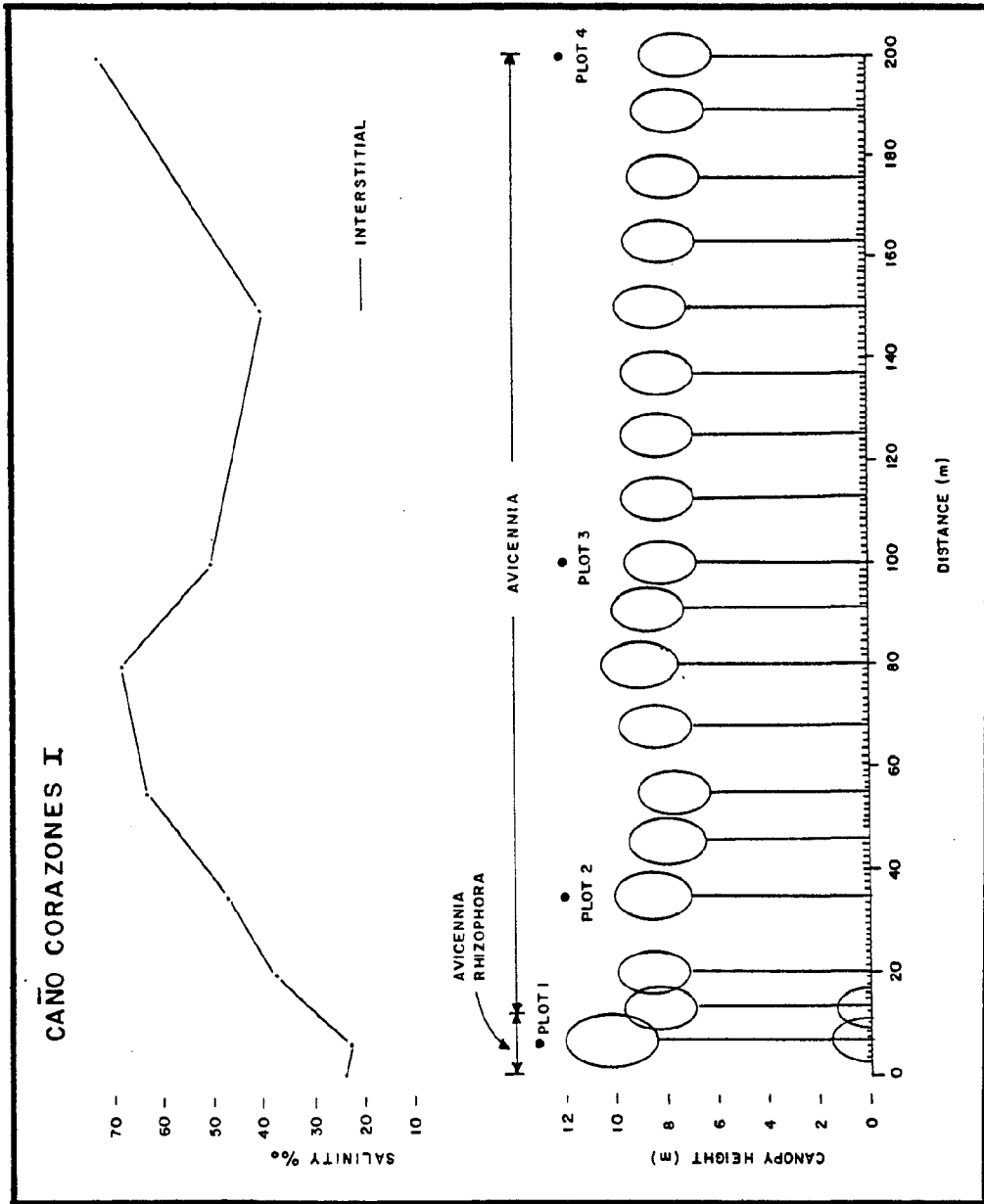


Profile 16





Profile 18



Profile 19

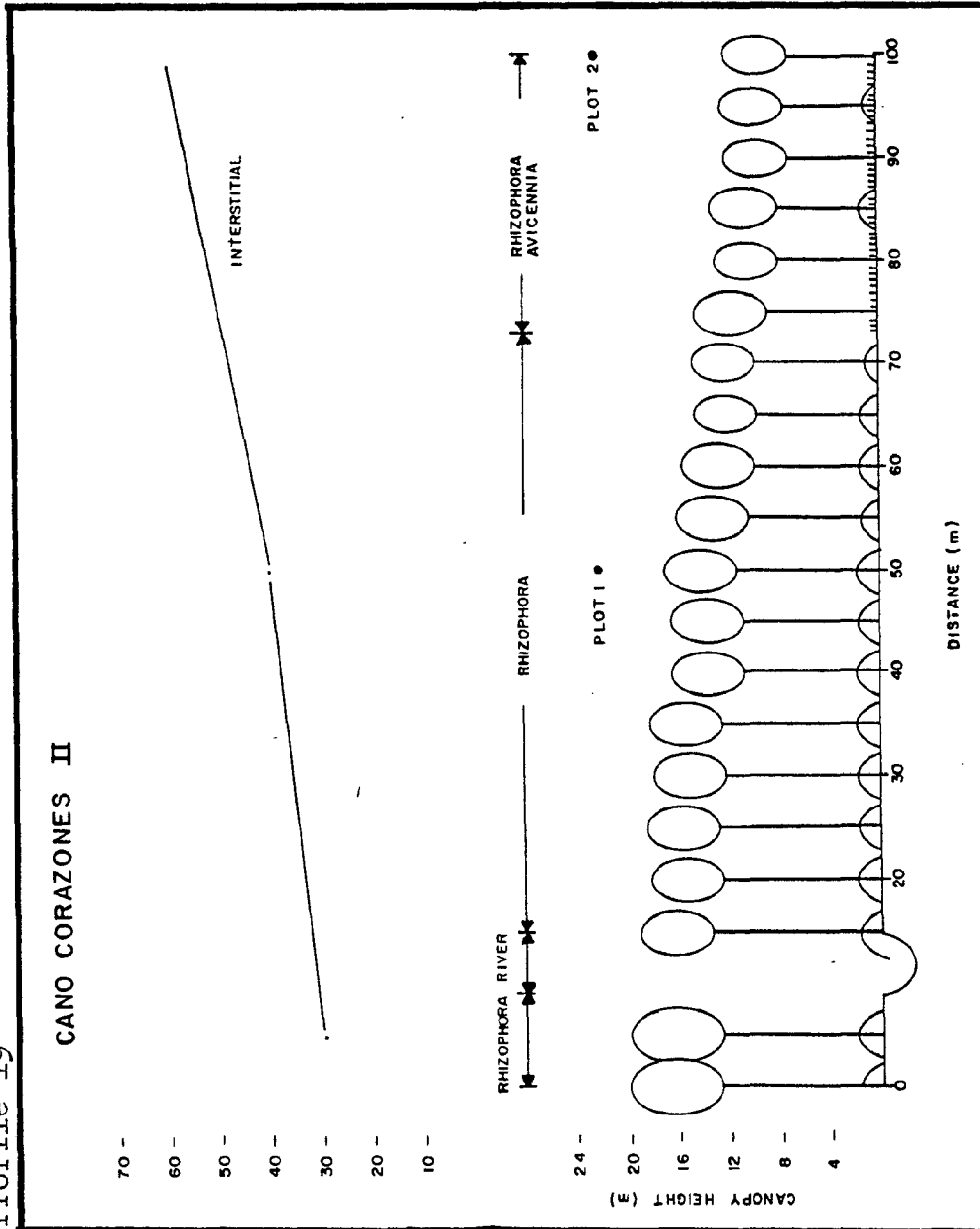


Table 1. Surface and soil interstitial salinities (ppt) for several mangrove forests. Dominant species are shown to illustrate lower soil salinities in red mangrove dominated locations. Table from Lugo and Cintron (1975).

Ecosystem location and dominant species	Date	Surface		Soil interstitial	1/S
		water			
Vacía Talega (<i>R. mangle</i>)	Apr 1974	28.3		32.9	1.16
Vacía Talega (<i>R. mangle</i>)	Apr 1974	30.2		36.2	1.20
Piñones (<i>R. mangle</i>)	Jan 1974	34.6		34.9	1.01
Vacía Talega (<i>A. germinans</i>)	Apr 1974	43.1		66.8	1.55
Piñones (<i>L. racemosa</i> and <i>A. germinans</i>)	Mar 1972	18.3		36.5	1.99
Piñones (<i>L. racemosa</i> and <i>A. germinans</i>)	Dec 1970	18.7		59.8	3.20
Mixed mangrove forest at Isabela, P.R. (3 species)	Sep 1974	10.0		33.3	3.20
<i>R. mangle</i> forest in Haiti	May 1974	50.0		47.5	0.95
Mean (SE)		29.1 (4.7)		43.5 (4.6)	1.80 (0.34)

Table 2. Structural characteristics of mangrove forests of Puerto Rico. All values are from live stems and are expressed in a 0.1 ha basis.

Site	Physio Graphic Type	Mean DBH (cm)	Number of Species	Number of trees $\geq 2.5 \geq 10$	Basal Area (m ²) $\geq 2.5 \geq 10$	Stand Height (m)	Complexity Index $\geq 2.5 \geq 10$
Region 1 North-Central Coastline							
Rio Cocal plot 1	R	-----	1	40	1.15	7.5	0.3
Rio Cocal plot 2	R	-----	2	467	2.00	13.0	24.3
Region 2 Northeast Coastline							
Piñones * I	B	-----	3	197	1.58	14.0	13.1
Piñones * II	B	-----	3	321	1.69	11.5	18.7
Piñones * III	B	-----	3	138	1.69	16.0	11.2
Piñones * IV	B	-----	3	285	2.16	13.0	24.0
Vacia Talega * I	R	-----	3	189	2.09	13.0	15.4
Region 3 Eastern Coastline							
Vista Mar plot 1	B	9.9	3	671	3.25	14.1	92.2
Vista Mar plot 2	B	18.1	3	123	2.90	14.8	15.8
Vista Mar plot 3	B	-----	3	223	1.00	10.5	7.0
Region 3 Eastern Coastline							
Rio Espiritu Santo I plot 1	R	22.9	2	146	3.70	16.0	17.3
Rio Espiritu Santo I plot 2	R	19.8	2	68	1.75	12.3	2.9
Region 3 Eastern Coastline							
Rio Espiritu Santo II plot 1	R	13.4	2	323	3.25	16.5	37.6
Rio Espiritu Santo II plot 2	R	20.0	3	70	1.45	14.3	43.5
Region 3 Eastern Coastline							
Bahia Medio Mundo plot 1	F	6.7	1	1676	4.30	9.8	70.6
							0.3

Table 2. Structural characteristics of mangrove forests of Puerto Rico. All values are from live stems and are expressed in a 0.1 ha basis.

Site	Physio Graphic Type	Mean DBH (cm)	Number of Species	Number of trees ≥2.5 ≥10	Basal Area (m ²) ≥2.5 ≥10	Stand Height (m)	Complexity Index ≥2.5 ≥10			
plot 2	F	13.6	1	280	3.30	2.80	16.0	14.8	8.5	
Ensenada Honda										
plot 1	F	3.4	1	749	0	0	5.7	2.6	0	
plot 2	F	5.7	3	1183	0	0	7.2	52.4	0	
plot 3	B	3.5	1	913	0	0	4.8	3.5	0	
plot 4	B	12.5	1	168	91	1.30	13.6	4.0	1.61	
Ceiba *	F	-----	2	569	26	1.67	0.34	8.5	16.2	0.2
Rio Antón Rufz										
plot 1	R	17.6	3	300	58	2.55	1.75	19.8	45.4	0.3
plot 2	R	19.3	3	114	82	2.15	2.00	21.8	16.0	10.7
plot 3	R	16.3	3	407	29	1.50	0.80	18.0	33.0	1.3
Region 4 Southern Coastline										
Aguirre *	F	-----	3	367	111	2.26	1.39	12.0	29.9	5.6
Bahia de Jobos (a)										
1-6	F	-----	3	1165	26	1.55	0.32	4.8	26.0	0.
7-11	F	-----	3	2059	0	1.44	0	4.4	26.1	0
12-35	F	-----	3	4733	17	1.43	0.17	4.8	97.5	0
Cayos Caribe										
plot 1	F	14.4	2	221	191	3.00	2.80	9.0	11.9	9.6
plot 2	B	2.4	1	0	0	0	0	2.0	0	0
plot 3	F	12.1	2	255	102	2.10	1.40	9.0	9.6	2.6

Table 2. Structural characteristics of mangrove forests of Puerto Rico. All values are from live stems and are expressed in a 0.1 ha basis.

Site	Physio Graphic Type	Mean DBH (cm)	Number of Species	Number of trees $\geq 2.5 \geq 10$	Basal Area (m^2) $\geq 2.5 \geq 10$	Stand Height (m)	Complexity Index $\geq 2.5 \geq 10$
Laguna Las Salinas plot 1	F	10.2	2	386	2.60	9.0	18.0 4.8
Region 5 Southwestern Coastline							
Punta Gorda * I	F	-----	1	178	0.69	7.0	0.9 0
Bahia de Guánica plot 1	F	12.5	2	251	2.30	10.8	12.5 4.0
plot 2	B	9.0	1	177	1.00	4.5	0.8 0.1
Caballo Blanco plot 1	O	16.2	1	63	1.00	14.8	0.9 0.4
plot 2	O	14.1	1	140	1.90	14.3	3.8 2.6
Cayo Enrique plot 1	O	8.1	1	659	2.70	9.2	16.4 0.4
Cayo Laurel plot 1	O	14.1	2	281	3.70	7.3	15.2 11.7
Punta Pitahaya I plot 1	F	13.0	1	277	2.70	12.2	9.1 4.8
plot 2	F	6.0	2	798	1.85	6.0	17.7 0.0
plot 3	B	7.2	3	318	0.55	4.5	23.6 0.0
Punta Pitahaya II plot 1	F	14.6	1	294	3.80	13.8	15.4 10.3
plot 2	F	11.2	1	283	1.50	8.8	3.7 0.4

Table 2. Structural characteristics of mangrove forests of Puerto Rico. All values are from live stems and are expressed in a 0.1 ha basis.

Site	Physio Graphic Type	Mean DBH (cm)	Number of Species	Number of trees ≥2.5 ≥10	Basal Area (m ²) ≥2.5 ≥10	Stand Height (m)	Complexity Index ≥2.5 ≥10
Bahia Sucia							
plot 1	F	15.2	1	193	3.00	15.0	8.7
plot 2	F	7.9	1	520	2.15	7.0	7.8
plot 3	B	5.2	1	333	0.65	4.1	0.9
plot 4	B	4.2	1	375	0.40	3.0	0.5
Bahia Salinas							
plot 1	F	15.0	1	175	2.90	12.0	6.1
plot 2	F	12.9	2	208	2.10	10.8	9.4
Region 6 Western Coastline							
Laguna Joyuda I							
plot 1	F	27.5	1	0	0	22.0	0
plot 2	F	12.4	1	178	1.75	13.8	4.3
plot 3	B	7.8	3	535	1.90	11.8	35.9
Laguna Joyuda II							
plot 1	F	20.5	2	118	3.30	20.0	15.6
plot 2	B	14.7	1	153	2.00	11.8	3.6
plot 3	B	6.6	1	206	0.60	7.0	0.9
Laguna Joyuda III							
plot 1	F	9.8	1	182	1.00	8.3	1.5
plot 2	B	12.1	1	85	0.60	6.3	0.3
Caño Corazones I							
plot 1	R	13.7	2	227	2.60	14.3	16.9
plot 2	R	15.6	1	166	1.60	11.8	3.1
plot 3	R	11.7	1	156	1.95	11.3	3.4
plot 4	R	10.7	1	204	1.40	10.6	3.0

Table 2. Structural characteristics of mangrove forests of Puerto Rico. All values are from live stems and are expressed in a 0.1 ha basis.

Site	Physio Graphic Type	Mean DBH (cm)	Number of Species	Number of trees $\geq 2.5 \geq 10$	Basal Area (m^2) $\geq 2.5 \geq 10$	Stand Height (m)	Complexity Index $\geq 2.5 \geq 10$
Caño Corazones plot 1	II R	16.2	1	152	2.15	20.0	6.5
	R	14.9	2	101	1.70	12.8	4.4
Peñón Brusi plot 1	B	19.0	3	122	1.80	13.8	9.08
	B	28.2	2	59	3.10	11.8	4.34
							4.31

* data from Pool 1977

(a) data from the Natural History Society of Puerto Rico
as cited by Pool 1977.

F Fringe

B Basin

R Riverine

O Overwash

Table 3. Structural characteristics and complexity index (expressed in 0.1 ha.) for each physiographic type. This table is based on the data in table 2 for each physiographic type.

Physiographic Type	\bar{X} S \bar{X}	No. Species	Basal Area		Density		Mean DBH		Height	Complexity Index	
			≥ 2.5	≥ 10	≥ 2.5	≥ 10	≥ 2.5	≥ 10		≥ 2.5	≥ 10
Fringe	\bar{X} S \bar{X}	2.20 .63	2.20 .93	1.60 .24	696.30 210.78	101.27 14.38	10.92 .85	15.15 .94	10.28 .93	18.84 5.18	4.42 .96
Basin (North)	\bar{X} S \bar{X}	3.13 .13	2.08 .26	2.08 .26	279.71 70.63	74.14 11.97	13.99 4.12	.00 .00	13.05 .72	26.00 11.22	4.71 2.05
Basin (South)	\bar{X} S \bar{X}	1.00 .00	.65 .13	.48 .08	300.75 42.98	41.00 -----	6.08 1.03	11.60 .35	3.72 .54	.71 .13	.07 ---
Basin (Total)	\bar{X} S \bar{X}	1.95 .23	1.60 .22	1.11 .25	306.33 49.80	71.29 12.49	8.68 1.19	12.13 .99	9.67 1.02	16.08 5.22	3.11 1.31
Riverine	\bar{X} S \bar{X}	2.71 .74	2.13 .18	1.81 .22	187.36 26.36	85.00 8.68	16.27 .99	18.61 .86	14.37 1.35	13.75 4.20	6.48 2.16
Overwash	\bar{X} S \bar{X}	1.60 .40	2.17 .47	1.37 .56	461.60 203.55	92.60 38.41	13.14 1.75	14.20 1.29	9.18 2.64	12.46 4.55	3.76 2.70

Table 4. Importance values for live and dead trees (≥ 2.5 cm DBH) at each plot studied.

Site	Taxon	% Basal Area		% Density		Importance Value	
		+	-	+	-	+	-
Region 1 Northcentral Coastline							
Río Cocal							
plot 1	Laguncularia	85.19	14.81	71.11	28.89	78.15	21.85
plot 2	Rhizophora	10.42		1.80		6.10	
	Laguncularia		8.33		8.25		8.29
	Avicennia	72.92	8.33	82.05	7.90	77.49	8.12
Region 2 Northeast Coastline							
Río Espiritu Santo I							
plot 1	Rhizophora	83.72	11.63	69.42	26.21	76.57	18.92
	Laguncularia	2.33	2.33	1.46	2.91	1.90	2.62
plot 2	Rhizophora	40.0		44.12		42.06	
	Laguncularia	60.0		55.88		57.94	
Río Espiritu Santo II							
plot 1	Rhizophora	96.92		99.07		98.00	
	Laguncularia	3.08		0.93		2.00	
plot 2	Rhizophora	79.31		84.29		81.80	
	Laguncularia	13.79		8.57		11.18	
	Pterocarpus	6.90		7.14		7.02	
Region 3 Eastern Coastline							
Bahía Medio Mundo							
plot 1	Rhizophora	91.50	8.50	80.73	19.27	86.12	13.89
plot 2	Rhizophora	91.70	8.30	84.04	15.92	87.89	12.11
Ensenada Honda							
plot 1	Rhizophora	100.0		100.0		100.0	
plot 2	Rhizophora	55.81		78.67		67.24	
	Avicennia	16.28	4.65	6.42	1.42	11.35	3.04
	Laguncularia	23.26		13.50		18.38	
plot 3	Rhizophora	100.0		100.0		100.0	
plot 4	Avicennia	89.74	10.26	89.84	10.16	89.79	10.21
Río Anton Ruíz							
plot 1	Rhizophora	50.98		12.67		31.83	
	Laguncularia	15.69		2.67		9.18	
	Pterocarpus	33.33		84.67		59.00	
plot 2	Rhizophora	65.12		48.25		56.69	
	Laguncularia	13.95		4.39		9.17	
	Pterocarpus	20.93		47.37		34.15	

Site	Taxon	% Basal Area		% Density		Importance Value	
		+	-	+	-	+	-
plot 3	Rhizophora	27.78		5.08		16.43	
	Laguncularia	11.11	16.67	0.97	1.45	6.04	18.12
	Pterocarpus	44.44		92.49		68.47	
Region 4 Southern Coastline							
Cayos Caribe I							
plot 1	Rhizophora	96.67	3.33	98.64	1.36	97.67	2.33
plot 2	Laguncularia		100.0		100.0		100.0
plot 3	Rhizophora	61.36		51.23		56.30	
	Laguncularia	34.09	4.55	38.25	10.88	36.17	7.72
Laguna Las Salinas							
plot 1	Rhizophora	96.15		97.67		96.91	
	Laguncularia	3.85		2.33		3.09	
Region 5 Southwestern Coastline							
Bahía Guánica							
plot 1	Rhizophora	70.83		69.12		69.98	
	Laguncularia	25.00	4.17	23.16	7.12	24.08	5.95
plot 2	Avicennia	100.0		100.0		100.0	
plot 3	Avicennia	100.0		100.0		100.0	
Caballo Blanco							
plot 1	Rhizophora	48.78	51.22	49.61	50.39	49.20	50.81
plot 2	Rhizophora	95.00	5.00	93.96	6.04	94.48	5.52
Cayo Enrique							
plot 1	Rhizophora	96.43	3.59	97.05	2.95	99.51	3.26
Cayo Laurel							
plot 1	Rhizophora	13.51		14.23		13.87	
	Laguncularia	86.49		85.77		86.13	
Punta Pitahaya I							
plot 1	Rhizophora	100.0		100.0		100.0	
plot 2	Rhizophora	94.59		97.24		95.90	
	Laguncularia	5.41		2.76		4.10	
plot 3	Avicennia	100.0		100.0		100.0	
Punta Pitahaya II							
plot 1	Rhizophora	97.44	2.56	94.84	5.16	96.14	3.86
plot 2	Rhizophora	93.75	6.25	94.02	5.98	93.89	6.12
Bahía Sucia							
plot 1	Rhizophora	90.91	9.09	84.65	15.35	87.78	12.22

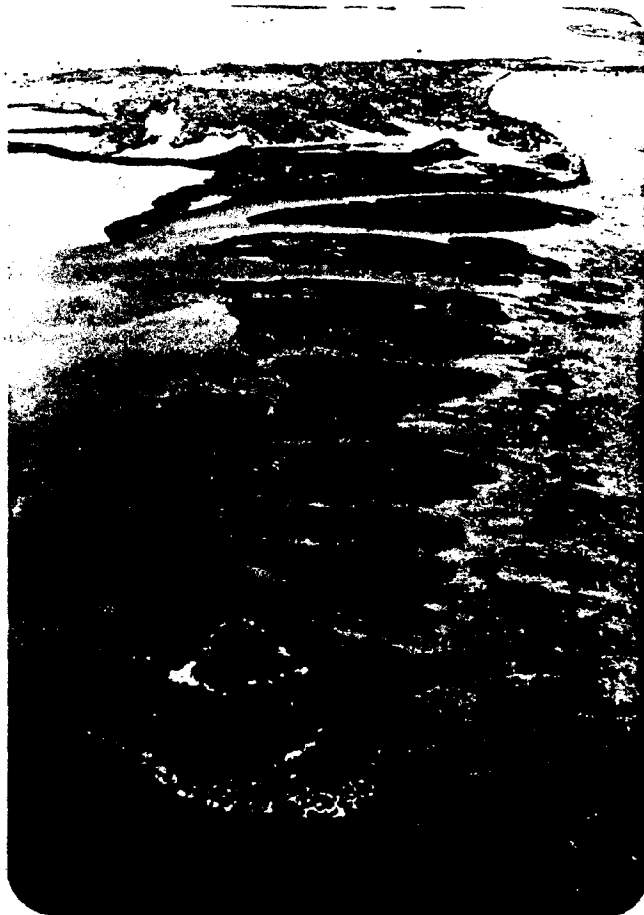
Site	Taxon	% Basal Area		% Density		Importance Value	
		+	-	+	-	+	-
plot 2	Rhizophora	100.0		100.0		100.0	
plot 3	Avicennia	100.0		100.0		100.0	
plot 4	Avicennia	100.0		100.0		100.0	
Bahía Salinas							
plot 1	Rhizophora	81.69	18.31	76.75	23.25	79.22	20.78
plot 2	Rhizophora	83.33	12.50	85.59	9.17	84.46	10.84
	Laguncularia	4.17		5.24		4.71	
Region 6 Western Coastline							
Laguna de Joyuda I							
plot 1	Rhizophora	95.56	4.44	84.62	15.38	90.09	9.91
plot 2	Rhizophora	89.74	10.26	82.41	17.59	86.08	13.93
plot 3	Rhizophora	63.64	9.09	58.88	20.56	61.26	14.83
	Laguncularia	22.73		19.68		21.21	
	Avicennia		4.55		0.88		2.70
Laguna de Joyuda II							
plot 1	Rhizophora	91.18	2.94	94.26	3.28	92.72	3.11
	Laguncularia	5.88		2.46		4.17	
plot 2	Avicennia	100.0		100.0		100.0	
plot 3	Avicennia	100.0		100.0		100.0	
Laguna de Joyuda III							
plot 1	Rhizophora	83.33	16.67	76.15	23.85	79.74	20.26
plot 2	Rhizophora	100.0		100.0		100.0	
Caño Corazones I							
plot 1	Rhizophora	75.86	10.34	72.47	20.91	74.17	15.63
	Avicennia	13.79		6.62		10.21	
plot 2	Avicennia	86.49	13.51	76.15	23.85	81.32	18.68
plot 3	Avicennia	73.58	26.42	45.22	54.78	59.40	40.60
plot 4	Avicennia	65.12	34.88	52.99	47.01	50.06	40.94
Caño Corazones II							
plot 1	Rhizophora	95.56	4.44	93.25	6.75	94.40	5.60
plot 2	Rhizophora	15.79		16.67		16.23	
	Avicennia	73.68	10.53	63.49	19.84	68.59	15.19



Photograph 1. Aerial view of part of the Los Machos lagoon system, Ceiba, Puerto Rico.



Photograph 2. Dwarf red mangroves at Los Machos lagoon system, Ceiba Puerto Rico.



Photograph 3. Aerial view of the Cayos Caribe. The mangrove islands have developed in the sheltered lagoon behind the reef flat.

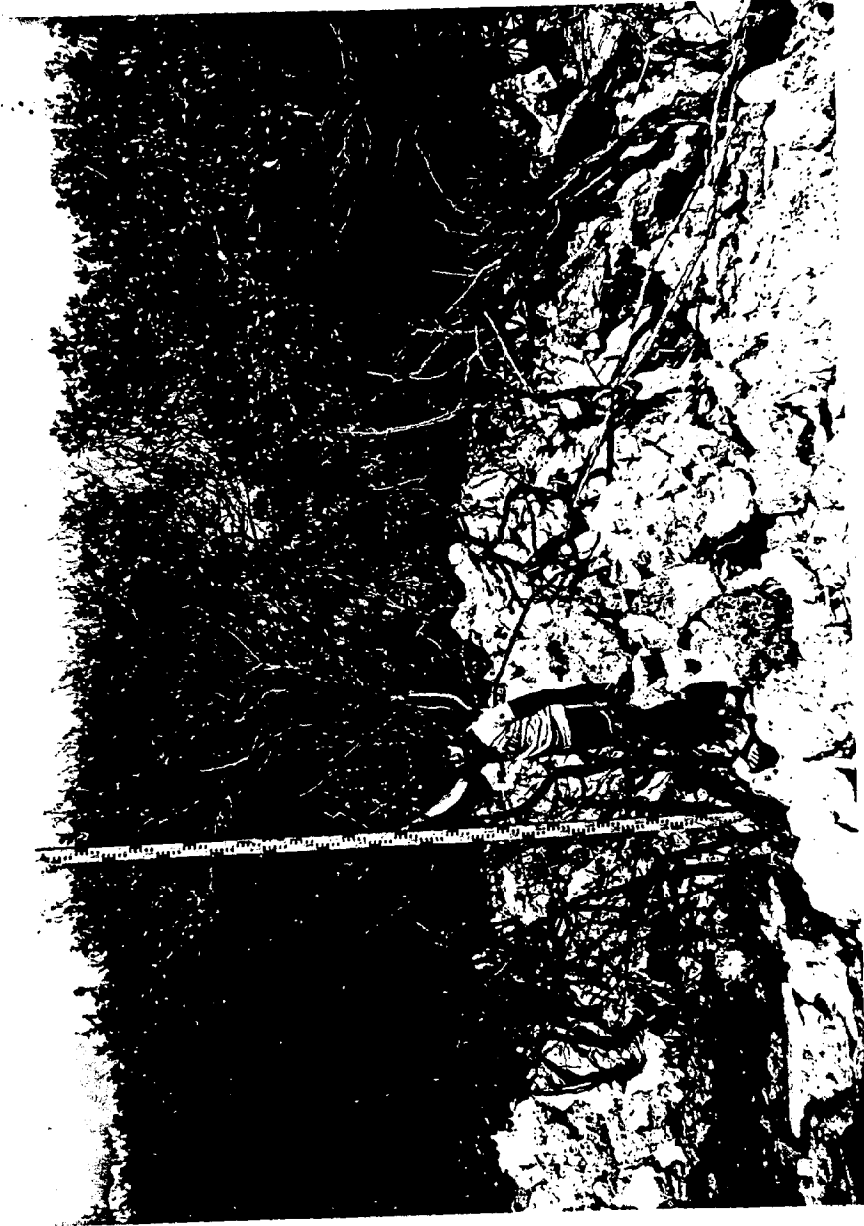


Photograph 4. Aerial view of Laguna de Las Salinas and stunted mangroves. Also shown are stations A to D at the inlet.



Photograph 5. Aerial views of the narrow mangrove fringe of the northern portion of Guanica bay. Notice the extensive salt flats behind this fringe.





Photograph 6. Calcareous boulders carried by strong swell into a mangrove covered sand cay, southwest, Puerto Rico.



Photograph 7. View of reef debris piled into a sand cay. Waves were generated by recent hurricane David, Southwest of Puerto Rico.



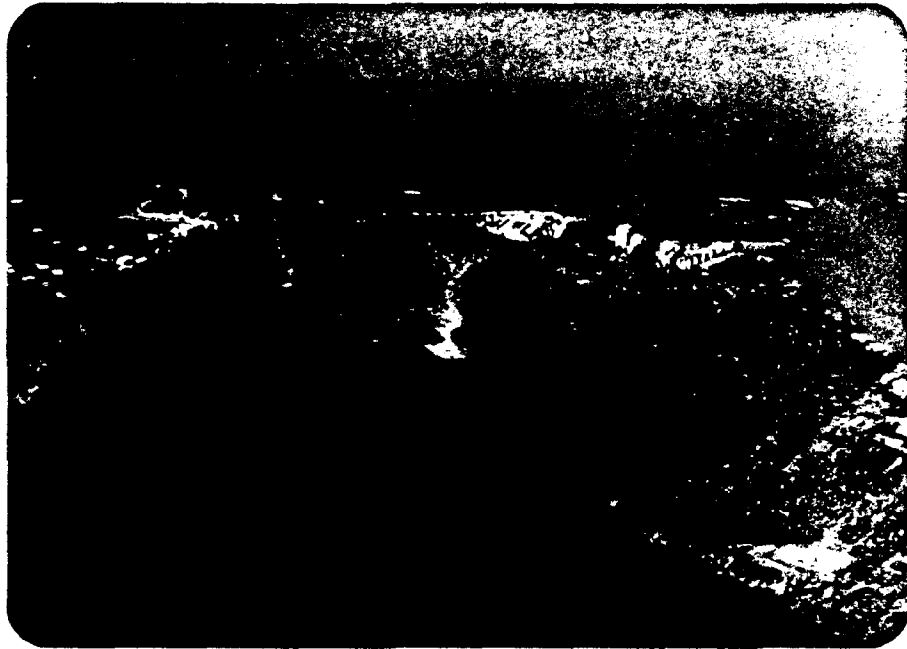
Photograph 8. Coral blocks carried by storm waves into a small mangrove stand in an offshore sand cay, southwest, Puerto Rico.



Photograph 9. Close up of a large blade of Acropora palmata. This particular blade is almost 1 meter across and was pushed by the hurricane generated waves inside the sand cay mangroves.



Photograph 10. Aerial view of the mangroves
fringing Joyuda Lagoon, western Puerto Rico.





Photograph 11. Aerial views of Caño Corazones mangroves. The left view shows the urbanized area near the inlet. Also shown is a sand bar which partially blocks the channel. The right view shows the mangrove forest which extends to the north.

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