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**MANGROVE VEGETATION OF TOBACCO RANGE AND NEARBY
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BY

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1950

PLANT COLLECTOR: [Name]

PLANT NUMBER: [Number]

PLANT NAME: [Name]

PLANT LOCATION: [Location]

PLANT HEIGHT: [Height]

DESCRIPTION

PLANT CHARACTERISTICS: [Description]

PLANT HABITAT: [Habitat]

PLANT USE: [Use]

PLANT COLLECTION DATE: [Date]

PLANT COLLECTOR: [Name]

PLANT NUMBER: [Number]

PLANT NAME: [Name]

PLANT LOCATION: [Location]

MANGROVE VEGETATION OF TOBACCO RANGE AND NEARBY MANGROVE RANGES, CENTRAL BELIZE BARRIER REEF

Colin D. Woodroffe*

The Belize barrier reef runs 200 km south from Ambergris Cay in the north, along the eastern coast of Belize, to the Gulf of Honduras in the south. There are numerous islands on the reef, and these can be divided into three broad types: sand cays, mangrove-sand cays, and mangrove cays (Vermeer, 1959, 1963). These types have been described in detail by Stoddart et al. (1982), who extended them into eleven types: i) Unvegetated sand cay, ii) Vegetated sand cay, iii) Unvegetated shingle cay, iv) Vegetated shingle cay, v) Sand and shingle cay, vi) Mangrove cay, vii) Shelf island (elongate islands of the northern shelf), viii) Mangrove cay with dry sand areas, ix) Mangrove range, x) Moat island (similar to the low wooded islands of the Great Barrier Reef), and xi) Coastal barrier island (barrier beaches associated with the mainland coast).

This paper examines the mangrove vegetation of Tobacco Range and nearby mangrove ranges in the central barrier reef. Mangrove ranges are elliptical mangrove islands or groups of mangrove islands. They are generally found on the broad outer barrier-reef platform, several hundred metres leeward of the reef crest (Fig. 1).

Area of study

The central Belize barrier reef consists of a shallow outer barrier-reef platform, less than 10m deep, separated from the coast by a deeper lagoon. Tidal range is microtidal, mean range at Carrie Bow is 15 cm, and tides are of a mixed semidiurnal type (Kjerfve et al., 1982).

The mangrove ranges which were studied in detail are Tobacco Range, Twin Cays (also known as Water Range), and Blue Ground Range. Tobacco Range is the largest of these. It is located about 2 km leeward of Tobacco Cay and the reef crest (Rützler and Macintyre, 1982; Macintyre et al., 1987). It is approximately 4 km long and 1.7 km wide, and has a central lagoon, generally around 2 m deep. Apart from four small pockets of coconut palms, Tobacco Range is entirely covered by mangrove vegetation. It consists of one large northern island, the interior of which contains shallow interior lagoons and areas of sparse or low mangrove; two long, narrow islands to the south; and a series of smaller islands fringing the central lagoon. The range is underlain by mangrove peat; this was found to be more than 7 m deep in a vibracore on transect IIIb. Not only does peat underlie the island, but it also continues west of the island (I.G. Macintyre, pers. comm.), where the mangrove fringe has undergone recession (i.e. see on transect IIa, Fig. 3). The central lagoon is floored by calcareous mud and sand, but in several places this was found to be underlain by mangrove peat.

Twin Cays lies about 2.3 km leeward of the reef crest, northwest of South Water Cay and Carrie Bow Cay (Rützler and Macintyre, 1982). It is 1.4 km long

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and 1.1 km wide, and comprises two islands separated by a meandering creek. It is similarly underlain by mangrove peat beneath the present mangrove vegetation and the unvegetated areas of the island interior. Halimeda-rich calcareous shelly mud or sand is found in the bed of the major creeks dissecting this range; mangrove peat has not been encountered in the top 60 cm sampled in these channels.

Blue Ground Range is located on the leeward flank of the barrier, 6-7 km west of the reef crest. It is a particularly dissected group of mangrove islands, the entire group being more than 4 km long, and 1 km wide (Fig. 9). These islands, the largest of which is only 0.7 km long, lie amid a series of carbonate shoals composed of Halimeda-rich sand and mud. There is a deep lagoon to the north (> 11 m deep), and the islands are bisected by sinuous creeks, 2-6 m deep. Probing along transect IIa and IIb indicates that the mangrove islands are underlain by mangrove peat, but that this is underlain at 150-200 cm by Halimeda sands, similar to those that make up the adjacent shoals. The shoals to the east of Blue Ground Range (Fig. 9), show evidence that they were previously occupied by mangroves; there were a few remaining stumps in 1987, and the substrate in several places consists of a thin veneer of calcareous sand over mangrove peat.

The climate of this part of the Belize barrier reef is drier than the mainland. On the mainland, more than 2000 mm of precipitation fall annually at Dangriga (Stann Creek), with a wet season from June to October. Carrie Bow Cay appears to receive an annual rainfall of around 1000mm (Rützler and Ferraris, 1982). The prevailing winds are northeast tradewinds, though there are times in the dry season when 'northers' are experienced, low pressure systems with associated fronts bringing winds from the northwest often accompanied by strong swells (Perkins, 1983). The area is subject to hurricanes during the months July to October, and was affected by the passage of a catastrophic storm, Hurricane Hattie in 1961 (Stoddart, 1963, 1974).

Methods

Mangrove vegetation was mapped from ground survey, and by the interpretation of aerial photographs. The mangrove vegetation of Twin Cays was mapped during a field survey in March 1985. Survey was from a boat, and by extensive ground traverses. Vegetation units were mapped on black and white aerial photographs taken in the early 1970s, and using colour oblique photographs taken in 1984. A brief overflight was made to verify the initial vegetation map. Ground survey on Tobacco Range and Blue Ground Range was undertaken in January 1987, and vegetation units were delineated after the ground survey on black and white aerial photography flown in January 1975 by the Royal Air Force at a scale of 1:15,000.

A series of vegetation profile diagrams were constructed at key traverses across each of the ranges. Trees within a 2 m zone, 1 m either side of a tape laid out along the transect, were recorded on the profile diagram. Height was estimated to the nearest 0.5 m, and species were determined. Profile diagrams were drawn in order to illustrate height, density and composition of the vegetation. Dead trees were also noted where stumps could be identified, in order to investigate successional trends. Detailed data on trunk diameters and

density were derived for 40 trees in a sample of each of the major vegetation units from Twin Cays (Fig. 5), using the point-centred quarter method (Cottam and Curtis, 1956). Trunk diameter measurements were taken at breast height where possible, and otherwise were below the first branch, but in the case of Rhizophora above the highest prop root.

The vegetation profile diagrams are intended to give a visual impression of the mangrove vegetation (Figs. 3,4,6,7,8 and 10). It has been necessary to simplify areas of low dense Rhizophora, generalising tree height as less than 2 m, and often reducing tree density schematically by representing only one in five trees on the transect. In several cases, on Tobacco and Blue Ground Ranges, the vegetation on the transects in 1987 does not reflect that which was mapped from the 1975 aerial photography. This is attributed to changes which have occurred in the intervening 12 years, the most widespread of which are, i) the growth of Batis over areas mapped as unvegetated flat, ii) regrowth of Rhizophora over areas mapped as unvegetated flat, and iii) localised dieback of Avicennia.

Vegetation of mangrove ranges

The most widespread mangrove species on the three ranges is red mangrove, Rhizophora mangle L., which forms a fringe around the periphery of many of the islands. In the interior of the ranges there are extensive stands of black mangrove, Avicennia germinans (L.) L., which are exposed on the shore in some locations. There are scattered individuals of white mangrove, Laguncularia racemosa (L.) Gaertn., but it does not form the thickets that it does in other West Indian islands where there has been considerable disturbance to the mangrove vegetation. Buttonwood, Conocarpus erectus L. occurs on transects at the southern end of Blue Ground Range (Fig. 10), but otherwise is restricted in its distribution especially to sandy substrates, occurring on the spit at the southern end of Twin Cays and on the sandy beach at the southern end of Tobacco Range. Batis maritima L. is the most frequent herb found within the mangroves, being especially common over the surface of otherwise unvegetated areas; Sesuvium portulacastrum (L.) L. is found in open areas within the mangroves, and Salicornia perennis Miller and a sterile grass, either Sporobolus virginicus (L.) Kunth or Distichlis spicata (L.) Greene are occasional, as also are tufts of Fimbristylis spadicea (L.) Vahl. Only one specimen of Rhabdadenia biflora (Jacq.) Mull-Arg. was found, that was on Twin Cays; this species appears only to become important on the wetter islands to the south (Stoddart et al., 1982).

While the plants listed above are found within the mangroves, there are several other plants which occur in the small sandy areas at the southern end of these ranges. Table 1 lists all plants sighted or collected on Twin Cays. Plants recorded on the islands of the Belize barrier reef are listed by Fosberg et al., (1982), and those collected previously on Twin Cays, called Water Range in that account, have been documented by Stoddart et al., (1982). Of those listed all but three, Cladium jamaicense, Casuarina equisetifolia and Wollastonia (Wedelia) trilobata, were still there in 1985. Of the 31 plants found on Twin Cays in 1985 and listed in Table 1, 14 were new records for the island.

Five mangrove types have been recognised on the basis of dominant species and vegetation structure, principally height and density. These are:

- i) Rhizophora woodland (greater than 4 m tall).
- ii) Rhizophora thicket (2-4 m tall).
- iii) Rhizophora scrub (less than 2 m tall).
- iv) Avicennia woodland
- v) Avicennia open woodland with Rhizophora

In addition to these five vegetation types, there are unvegetated (or poorly vegetated) flats on both Twin Cays and Tobacco Range. On Twin Cays these are generally bare mudflat surfaces, whereas those on Tobacco Range are often covered by a carpet of Batis. These major units are described below.

Rhizophora woodland

Stands of Rhizophora in which canopy height is generally more than 4 m are most widespread on Twin Cays, but also occur on Tobacco and Blue Ground Ranges. On Twin Cays they occur along much of the windward north and east shores and form the dominant mangrove vegetation on the two small islands at the northern end of the central channel (Fig. 5). Elsewhere this taller Rhizophora is found within the unvegetated flats of the interior, characteristically occurring at the southern end of shallow interior lagoons which characterise many of the unvegetated flats. On Tobacco Range, Rhizophora woodland occurs in a small stand at the northwestern tip of the island (Fig. 2, and transect I, Fig. 3), is found on a series of small islands in the central eastern section of the range, and forms a number of stands in the island interior. On Blue Ground Range, Rhizophora woodland is found around the outside of islands to the north of the range (Fig. 8), and on the northern end of the southernmost islands (i.e. transect VI, Fig. 10).

Rhizophora can grow up to 7-8 m tall in this unit, with trunk diameters of 25-30 cm. There are well developed prop root systems reaching more than 1 m above the ground. Some of the largest trees have formed tortuous recurved trunks which are intricately intertwined. Younger trees are generally straighter where this woodland is actively regenerating. Tree density is variable; older spreading, gnarled trees may be better spaced, but where measured there was around 4500 trees per hectare, with a basal area of 19.9 m² ha⁻¹. On Twin Cays, transects IV, V, VI and VII (Fig. 7 and 8) pass through Rhizophora woodland at their eastern ends. Here individual Laguncularia, up to 6 m tall, are encountered at more than 20 m from the seaward fringe within the Rhizophora woodland. Rhizophora is interspersed with Avicennia along much of the boundary between these two vegetation types; it grades gradually into Rhizophora thicket. Rhizophora woodland more than 10 m tall is found on neighbouring Man of War Cay, which supports a dense colony of frigate birds, whose droppings presumably enrich the substrate.

Rhizophora thicket

Rhizophora thicket is the most widespread mangrove type on Twin Cays, and accounts for a substantial proportion of both Tobacco and Blue Ground Ranges. On Twin Cays it forms the fringe around the islands where there is no Rhizophora woodland, and extends into the interior of the islands. On Tobacco Range it is typical of the fringe around much of the central lagoon, and also fringes much of the outside of the southwestern section of the range (Fig. 2). On

Blue Ground Range it fringes islands where Rhizophora does not reach the stature of Rhizophora woodland, and is the sole vegetation of several of the islands to the south of the range.

The general canopy is 2 to 4 m tall, though there are Rhizophora taller than 4 m and others shorter than 2 m. Prop root systems reach up into the canopy, making this the most impenetrable of mangrove types. Where density was determined this was 4790 trees per hectare, with a basal area of 13.0 m² ha⁻¹; however, density is extremely variable.

Rhizophora scrub

Rhizophora scrub, generally less than 2 m tall, and often less than 1 m tall, is found over extensive areas in the interior of Tobacco Range and Twin Cays, and in one broad, now dissected zone in central Blue Ground Range. Neighbouring plants are usually not entangled, making it much easier to walk through than Rhizophora thicket. Where measured density was 17500 trees per hectare with a basal area of only 7.5 m² ha⁻¹. However, it is evident from transects that the density can vary considerably, reaching as high as 40000 trees per hectare. Rhizophora scrub is found adjacent to the unvegetated flats in the interior of Twin Cays and in a similar setting to interior lagoons on Tobacco Range, but is rarely exposed on the margin of the islands except where the fringe has been eroded. By contrast on Blue Ground Range the main area of Rhizophora scrub is in the centre of the range (transect III, Fig. 10), but it has been bisected by channels, so that Rhizophora scrub is exposed on the banks of the channels through the range (Fig. 9).

In the densest area of this scrub, many of the Rhizophora seem to have been recently established and are little more than saplings, and stands are presumably not of any great age, and may not be able to regenerate themselves over many generations. Where older individuals are established they are recumbent, often with leaves on the ends of branches held below the highest prop root, such that these are clearly not low simply because they are young. Some environmental control appears to be limiting growth, and this is most probably a nutrient limitation (R. Twilley, pers. comm.). The transition from Rhizophora scrub to Rhizophora thicket is fairly distinct.

Avicennia woodland

Woodland in which Avicennia germinans is the major tree, covers much of Tobacco Range, and is an important element of the interior of both Twin Cays and Blue Ground Range. On Tobacco Range, Avicennia woodland is extensive along the northwestern margin, where it is clearly undergoing recession (Fig. 2), with retreat of the fringe indicated by the erosional bench in mangrove peat to seaward of the mangroves. There are also stands of Avicennia left along the eastern margin of the range. Relatively monospecific stands of Avicennia occur just landward of the windward fringing Rhizophora woodland on Twin Cays. Elsewhere low Rhizophora is common with the Avicennia, and this has been mapped as Avicennia open woodland with Rhizophora. A typical stand of Avicennia woodland occurs to the eastern end of transect IV (Fig. 7), and it

seems likely that almost pure Avicennia woodland characterised much of the area that is marked as cleared on Fig. 5. Many tall individual Avicennia are left standing in the clearing. On Blue Ground Range Avicennia woodland is restricted to the interior of islands (i.e. transects IV and V, Fig. 10). Pelicans were nesting in the Avicennia woodland on transect V (Fig. 10) in 1987.

Avicennia reaches up to 6-8 m tall with diameters of 20-30 cm, and where density was measured it was 5760 trees per hectare, with a basal area of 20.9 m² ha⁻¹. The presence of smaller trees indicates that this mangrove type is regenerating. The floor of this mangrove type is covered with pneumatophores 15-20 cm tall, and a spasmodic ground cover of Batis maritima. The older and larger Avicennia have large spreading canopies and appear to shade out seedlings.

Avicennia open woodland with Rhizophora

Similar to but often more widespread than Avicennia woodland are areas of Avicennia open woodland with Rhizophora. In these, Avicennia does not reach such great heights, generally less than 5 m, nor such high densities, but Rhizophora is an important element. On Tobacco Range Avicennia open woodland with Rhizophora generally occurs in the interior, but is exposed on the fringe on the western margin of the central lagoon. On Twin Cays, this is usually a vegetation type found in the interior of the range; Rhizophora is generally low, often less than 2 m tall, forming an understory beneath Avicennia up to 5 m tall. Elsewhere, Avicennia appears to be under stress; there are many stunted, dying and dead Avicennia in the Avicennia open woodland with Rhizophora and in adjacent Rhizophora mangrove types. On Blue Ground Range Avicennia open woodland with Rhizophora forms stands in the interior of islands grading into Avicennia woodland; it is prominent on transect IIa (Fig. 10).

In the typical stand examined, the density of all trees was 6840 trees per hectare, while that of Avicennia of more than 10 cm trunk diameter was only 684 trees per hectare. Average diameter was 4.89 cm and total basal area was 20.9 m² ha⁻¹, similar to that for Avicennia woodland (Table 2). However the basal area for Avicennia alone was only 14.1 m² ha⁻¹. Though very variable the more open nature of Avicennia open woodland with Rhizophora means that Batis is widespread, and Salicornia, Sesuvium and grass occur.

Unvegetated flats

There are many areas in the interior of Tobacco Range and Twin Cays which do not carry dense mangrove vegetation. These either dry at low tide, like the Anderaa flats on Twin Cays, or may remain shallowly flooded (generally less than 50 cm deep) as do the interior lagoons mapped as open water on Tobacco Range. These bare areas often have Rhizophora scrub around them. Seawater floods through these unvegetated flats and the surface water salinity where measured on Twin Cays was 38 parts per thousand, the same as in the main channel. Seawater flows between unvegetated flats by shallow depressions, 10-20 cm below the surface of adjacent mangrove flats, forming an incipient creek

system. Where water remains over the surface there is prolific growth of marine algae.

Surface sediments are fine and largely algal-derived. These can be soft, but a firm substrate composed of mangrove peat is found at up to 50 cm below the surface in all pools traversed during this survey. Creek-floor sediments contain the empty shells of the gastropod Cerithidea.

Many of the areas clearly unvegetated and mapped as unvegetated from the 1975 aerial photography, carried a cover of Batis, or in places regrowth of mangroves, particularly Rhizophora, when surveyed in 1985 or 1987.

Belize mangrove forests in a regional context

Mangrove forests of the New World (and West Africa) are structurally and floristically less complex than those of the Old World (Chapman, 1975). Many of the mangrove forests of the mainland coastline of Central America are in areas receiving a large terrestrial sediment input and are developed over muds (Thom, 1967; West, 1977). Such terrigenous-substrate mangrove forests cover much of the coast of mainland Belize (Wright et al., 1959). On the mangrove ranges of the Belize barrier reef, on the other hand, beyond the influence of terrestrial sediment, the mangrove forests are underlain by mangrove-derived peat. These peats are highly organic (loss on ignition 65-75%).

Mangrove forests developed over an organic, peaty substrate, are found in several carbonate settings in the West Indies. They are extensive in southwestern Florida (Davis, 1940; Gleason et al., 1974; Turmel and Swanson, 1976), Cayman Islands (Woodroffe, 1981) and Jamaica (Digerfeldt and Hendry, 1987). In contrast to their muddy counterparts, a diverse marine biota characterises the prop roots of Rhizophora which hang into deep water in the meandering creeks. Similar mangrove ecosystems have been described from Brazil (Gerlach, 1958), Puerto Rico (Mattox, 1949), and the Bahamas (Howard, 1950; Rützler, 1969).

The structure of mangrove forests in Florida, Puerto Rico, Costa Rica and Mexico has been reviewed by Pool et al. (1977). They classify mangrove types into five classes: i) fringe mangrove, fringing open seawater and frequently flooded by tides; ii) basin mangrove, interior mangrove less frequently flooded; iii) overwash mangrove, completely overwashed by tides; iv) scrub mangrove, dwarfed forms of mangrove; and v) riverine mangrove, mangrove influenced by riverine freshwater input.

In topographic terms much of the mangrove forest on these Belize mangrove ranges would fall into the overwash category of Pool et al. (1977), because the smaller islands are entirely overwashed at the highest tides. However elevational data and observations in March 1985 indicate that Avicennia woodland on Twin Cays is infrequently inundated, and many of the islands may have passed beyond the overwash stage. Where islands are not of the overwash category, Rhizophora woodland of the windward margin of the island may be described as fringe mangrove; much of the interior Avicennia woodland, or Avicennia open woodland with Rhizophora falls into the basin mangrove category of Pool et al. (1977); and Rhizophora scrub is equivalent to the scrub mangrove category.

Table 2 records the structural parameters of the five mangrove types on Twin Cays. These are not directly comparable with the parameters used by Pool et al. (1977), because they only considered trees with diameters greater than 2.5 cm. This was not felt appropriate in this study because so many trees are less than this diameter (mean diameter in Rhizophora scrub was 2.25 cm). Accordingly, individuals that were larger than recently established saplings were included (those trees less than 2.5 cm diameter, however, contribute very little to the total basal area, but their inclusion will make a difference to measures of tree density). Rhizophora scrub of Twin Cays is very similar to scrub Rhizophora described by Pool et al. (1977) from Turkey Point, Florida, with a density of 17400 trees per hectare, and a basal area of 7.5 m² ha⁻¹ in the former, and 25030 trees per hectare and 6.0 m² ha⁻¹ respectively in the latter. These values for density are within the wide range of density evident in this mangrove type from the transects. Scrub Rhizophora has also been reported from basins in the interior of Little Cayman (Stoddart 1980), and around the eastern margin of North Sound, Grand Cayman (Woodroffe, 1981; Brunt, 1984).

The most similar sites to the other mangrove forests on Twin Cays, from all of those recorded by Pool et al. (1977), were a basin mangrove in Rookery Bay, Florida and a fringe mangrove in Ceiba, Puerto Rico. Particularly similar mangrove forests have been described from several parts of Puerto Rico by Cintron et al. (1978) and Zucca (1982).

Stability and change in the vegetation of mangrove ranges

The pattern of mangrove zonation, typical throughout most of the New World mangrove forests, of seaward Rhizophora replaced to landward by Avicennia, is not found throughout the mangrove ranges of the central Belize barrier reef. While this arrangement does characterise the eastern fringe of Twin Cays (i.e. eastern transect IV, Fig. 7) and several of the small islands on Blue Ground Range (i.e. transects IV and V, Fig. 10), there are many areas where Avicennia is exposed on the seaward margin (i.e. transect IIa, Tobacco Range, Fig. 3), or extensive stands of Rhizophora occur throughout the interior of islands.

There is also abundant evidence that the pattern of distribution is changing. This is shown in particular by the extensive unvegetated flats which characterise the interiors of Tobacco Range and Twin Cays, and the dead mangrove stumps which occur throughout each island and have been mapped along the transects. Particularly prominent are the dead stumps of Avicennia, truncated close to the mudflat surface, within either bare or Rhizophora scrub areas of Tobacco Range and Twin Cays.

There are three explanations which can be offered to account for the dieback of Avicennia: hurricane damage, environmental stress, or human clearance. The suggestion that this is the result of hurricane damage, has considerable appeal, because catastrophic storms are known to have had a devastating effect on the topography and vegetation of islands of the Belize barrier reef. Hurricane Hattie which struck the reef in 1961, passing to the north of the study area, is known to have caused extensive mortality of mangroves (Vermeer, 1963; Stoddart, 1963, 1965, 1971, 1974). Defoliation of Rhizophora was widespread; but relatively few observations were made of the storms effect

on Avicennia, or recovery of this species. A large area of devastation at the southern end of Tobacco Range is attributed to Hurricane Hattie by Stoddart et al. (1982) and has changed little since 1972, as shown in their plate 70.

There are several reasons to suppose that environmental factors could pose a limitation on mangrove distribution and be responsible for mortality of one species and its replacement by another. Firstly the fairly clearly defined vegetation units composed of either Rhizophora or Avicennia suggest some underlying environmental factors which control the successful establishment of propagules of either species at a specific site. Surveying across northern Twin Cays, as well as at selected sites on the other ranges, has suggested an elevational range of only around 15 cm over which mangrove forests occur, though with a tendency for Avicennia to occur only in the higher locations.

Salinity is one factor which appears to control mangrove distribution elsewhere, and high salinities in low rainfall areas account for the occurrence of bare mudflats within or landward of mangrove forests (Fosberg, 1961; Giglioli and King, 1966; Spenceley, 1977). Cintron et al. (1978) have described mangrove forests from the arid south coasts of Puerto Rico. They suggest that dieback of mangroves occurs in the interior of small annular islands as a result of high salt concentrations. In their study they recorded a mean salinity of 44 parts per thousand beneath live trees, 72 parts per thousand beneath dead trees, and 87 parts per thousand beneath interior unvegetated flats. They indicated rapid mortality of mangroves where salinities were more than 65 parts per thousand, and intolerance to salinities in excess of 90 parts per thousand.

West (1977) has attributed bare areas in the interior of Ambergris Cay to hypersalinity, and suggested that this might also explain bare areas on other Belizean mangrove cays. On Twin Cays measurements of salinity of water standing over unvegetated flats in the island interior was similar to that of the open water in the central channel (38 parts per thousand). Interstitial salinity, both from water draining into a core hole from Twin Cays, and from water squeezed from soil at depth, did not reach the high salinities reported by Cintron et al. (1978) from Puerto Rico. The highest salinity recorded was 58 parts per thousand which was beneath apparently healthy, regenerating Avicennia woodland. In the unvegetated flat salinities at 25 cm and at 45 cm below the surface were 47 parts per thousand. These measurements were made during low neap tide in March which is usually the driest month of the year. This is the time of the year at which soil salinities have been shown to be at their highest (40-50 parts per thousand) in mangrove substrates in Laguna de Terminos in Mexico (Day et al., 1987), and when they might also be expected to be at a maximum on Twin Cays. The surface of most if not all of each of the mangrove ranges gets flooded by the the highest spring tides, and frequent flooding by seawater is likely to dilute interstitial salinities and prevent hypersalinity building up. There seems little reason to suspect that, even in drought years, salinity in the substrate of these mangrove ranges builds up to levels which would cause mangrove mortality. Another important difference between mangrove dieback on these ranges and that reported from Puerto Rico (Cintron et al., 1978) is that dieback of Avicennia, especially on Twin Cays, appears to have been followed by colonisation by Rhizophora, which is generally less tolerant of high salinity.

It is possible that other environmental factors account for the mangrove dieback. On salt marshes, sulphide levels, ion toxicity or nutrient deficiencies

have each been implicated as causes of dieback (Mendelssohn et al., 1982). On Twin Cays measurements of Eh and sulphide concentrations of the sediment indicates that is partly a function of the vegetation, and the plants themselves may serve to aerate the sediment as well as aeration through the burrowing activity of crabs and other invertebrates (McKee et al., 1988). The higher sulphide levels under unvegetated flats would not appear to inhibit mangrove growth there. While these and other environmental factors may effect the performance of mangrove species, neither the salinities, nor the other factors can be directly linked to mangrove mortality.

The third explanation, deliberate clearing of mangroves, has occurred locally on many of the islands on the Belize barrier reef, especially to enable the construction of buildings on the cays. However, there is no logical explanation for the widescale and disorganised clearing which would be implied, if all unvegetated areas were attributed to human action. There seems little doubt that the majority of those areas mapped as cleared, or unvegetated, on the vegetation maps, are the result of natural and not anthropogenic factors.

Tree stumps, and broad unvegetated areas are most extensive on Tobacco Range and Twin Cays; there are no areas mapped as unvegetated on Blue Ground Range, although the presence of isolated mangrove stumps and mangrove peat on the shoals to the east of the range indicate relatively recent mangrove recession. Hurricane Hattie is known to have caused mortality of mangroves further north along the Belize barrier reef, and it seems most likely that it also had a devastating effect on parts of Tobacco Range and Twin Cays. Avicennia in many of the bare areas, and those areas now recolonised by low Rhizophora scrub may have been truncated as a result of Hurricane Hattie. Rhizophora too may have undergone extensive mortality as a result of the storm, but except for the stumps which do occur as shown on the transects (not all of which resulted from the single storm event), may now be less clear as Rhizophora appears to rot back more rapidly, and many stumps are now truncated below ground level and the only evidence are the sheaths of the roots.

While the tree stumps and bare areas provide evidence of recent mangrove dieback, there is also evidence of a longer term decrease in mangrove area. Mangrove forests appear to have established on the Belizean barrier reef as soon as the previous subaerially-exposed surface was flooded by rising sea level during the Holocene transgression. Mangrove peat has been encountered at the base of numerous cores through Holocene sediments across the barrier reef (Purdy, 1974; Shinn et al., 1982). At Boo Bee Patch reef, just south of the study area, drilling has shown that a Pleistocene patch reef morphology, upon which a Holocene patch reef has been established, is surrounded by basal peat of presumed mangrove origin dated about 8000 years B.P. (Halley et al., 1977). The final stage of the transgression is recorded in mangrove peat deposits on Ambergris Cay, where a basal soil unit is overlain by mangrove peat, in turn overlain by calcareous sediments locally recording regression with lateral extension of the island environments (Ebanks, 1967, 1975).

Purdy (1974) has shown from numerous seismic traverses that many of the present islands on the Belize barrier reef are located over Pleistocene topographic highs. Mangrove ranges may also be located over topographically high points in the underlying Pleistocene limestones, as has been suggested by Stoddart et al. (1982). Results from vibracoring undertaken by I.G. Macintyre and others

indicate that Tobacco Range and Twin Cays were formerly more extensive. The present mangrove ranges appear therefore to represent all that remains of a more extensive early-mid Holocene mangrove forest, preserved because of their relative shelter behind windward reef crests.

There is abundant evidence that all three mangrove ranges are continuing to undergo recession. Erosion of the shoreline is especially pronounced along the northwest of Tobacco Range, where Avicennia woodland is now exposed along a broad fringe of the range, fronted by an eroded peat surface. This area is subject to substantial swell under a northwesterly wind, and will continue to retreat. The entire western limb of the southwestern island of Tobacco Range, has undergone retreat; there are numerous dead Avicennia stumps, perhaps initially killed by Hurricane Hattie, and the surface has continued to erode. Locally Rhizophora seedlings have established on the lagoonward shore of this part of the range, but their establishment is insufficient to reverse the general recession of this part of the shore.

The meandering creeks or bogues which dissect the ranges also appear to be erosional. They are fringed by Rhizophora, beneath the prop roots of which there is a scarp, or overhang in the mangrove peat. Occasionally the undercutting is so extensive that there is collapse of mangroves into the creek. Shallow creeks have incised into the surface, particularly of Twin Cays, connecting interior lagoons to the larger creeks. This appears to be a process by which the ranges are slowly fragmented. The central lagoon of Tobacco Range may similarly be an erosional feature. Shallow cores to the north revealed mangrove peat below the calcareous sediments which comprised the lagoon floor, but probing elsewhere did not reveal a similar sequence in the top metre of sediment. Blue Ground Range has undergone some retreat on its eastern margin, but elsewhere the consistent Rhizophora fringe around most islands suggests little recent change. The Rhizophora scrub belt in the centre of Blue Ground Range is interpreted as having been dissected by the creek system.

Many accounts of the geomorphological role of mangroves have implied that they have the ability to colonise new intertidal habitats, and to 'reclaim land from the sea'. There is now a large body of evidence to demonstrate that this is not always the case (Thom, 1975; Woodroffe, 1983). Fragmentation of mangrove ranges on the Belize barrier reef appears to be yet another instance where mangrove forests are undergoing net decrease, rather than increase, of area.

Discussion

Gradual disintegration of mangrove forests on the Belize shelf occurred during the Holocene transgression as the sea rose from tens of metres below present to reach its present level. This has resulted in a transgressive sedimentary sequence, with mangrove peat recorded above soil, or freshwater peat deposits, from sites around the Gulf of Mexico (Scholl, 1964; Gleason et al., 1974; Ebanks, 1975; Woodroffe, 1981, 1982; Hendry and Digerfeldt, 1989). The seaward margin of the mangrove forests also retreated landwards, especially during those times when sea level was rising most rapidly, and progradation has

only been possible since sea-level rise has decelerated to less than 2 mm yr⁻¹ (Parkinson, 1989).

It needs to be considered whether mangrove dieback observed during mapping of the Belize mangrove ranges might be due to ongoing, or accelerated, sea-level rise. There is presently concern that the sea is rising, and that coastal wetlands may be particularly vulnerable to drowning (Bird, 1993). Such accelerated rise might see mangrove shorelines, such as those in the Everglades, reverting to conditions typical of mid Holocene times when there was a faster rate of relative sea-level rise (Wanless and Parkinson, 1989).

Mangrove forests which do not receive a terrigenous sediment input, and which are consequently underlain by mangrove-derived peat, are likely to be the most susceptible to drowning (Woodroffe, 1988, 1990; Ellison and Stoddart, 1991). Ongoing retreat of the mangrove fringe in Bermuda has been attributed to rapid sea-level rise (Ellison, 1993). The great depth of peat beneath the Belize ranges, and radiocarbon dates from Tobacco Range and other parts of Belize, however, indicate that vertical accretion of peat did keep pace, at least in some places, with rates of mid-Holocene sea-level rise of 4.5 mm yr⁻¹ or more (I.G. Macintyre, pers. comm.).

The recent dieback of mangroves on Tobacco Range and nearby mangrove ranges, superficially resembles the situation which might be expected if sea level were to rise at a rate faster than that at which the substrate could accrete. Shoreline erosion, and death of inland mangrove species and their replacement by more seaward species has been predicted under such circumstances (Woodroffe, 1990). There are, however, a number of reasons for attributing this dieback to storm damage. First, although much of the shoreline of the mangrove ranges is presently being eroded, erosion is generally along those shorelines which are periodically exposed to large waves, and is not universal. In many places there is a pronounced erosional cliff over which Rhizophora roots hang, and there seems no reason why such cliffing should be a feature of gradual sea-level rise. Within the mangrove ranges mortality of mangroves shows no clear spatial pattern in relation to the mangrove types mapped. There is little evidence for death of mangroves in the few years prior to survey, and no signs of ongoing stress; the stumps are preferentially of large trees, which died simultaneously some time ago, and have since been truncated close to ground level. Where profiles were surveyed, as on Twin Cays, there was no indication that death had occurred primarily amongst those trees rooted at the lowest elevations as might be expected if there had been landwards encroachment of Rhizophora into Avicennia which might reflect sea-level rise. Dead Rhizophora and Avicennia are often intermixed.

Further evidence in support of storm damage is the gradient in extent of damage from north to south. The greatest mortality, measured as trees per metre of transect surveyed, occurred on Tobacco Range, and the least was observed on Blue Ground Range. This gradient away from the path of Hurricane Hattie lends further support to the conclusion that the dieback occurred as a result of storm damage. In this case the known history of a devastating storm, reports of widespread storm damage in the area (ie. Stoddart et al., 1982), and the little change which has occurred since the 1972 or 1975 photography, support the contention that mangrove dieback occurred on these ranges primarily as a result

of storm damage. Nevertheless, it may be difficult to differentiate the cause of dieback in other cases, and this example serves to illustrate that dieback of mangroves could be attributed to other factors, such as the effects of sea-level rise, where these may not have had a major impact on mangroves over recent decades.

Conclusion

The mangrove vegetation of Tobacco Range, Twin Cays and Blue Ground Range has been mapped into five mangrove types: Rhizophora woodland (>4 m tall), Rhizophora thicket (2-4 m tall), Rhizophora scrub (<2 m tall), Avicennia woodland, and Avicennia open woodland with Rhizophora. Rhizophora woodland or Rhizophora thicket is characteristic of the margins of most of the ranges. Avicennia woodland typically occurs in the centre of islands, generally on substrate that is less frequently flooded than that beneath Rhizophora; however, to the northwest of the northern ranges it has been exposed on the margin by erosion. Avicennia open woodland with Rhizophora is found in much of the interior transitional between pure Rhizophora and pure Avicennia vegetation types. Rhizophora scrub occurs in the centre of ranges, covering areas that appear to have been stripped of prior vegetation relatively recently. It is restricted to the centre of ranges except where creeks have bisected them. There are also extensive unvegetated flats in the interior of Tobacco Range and Twin Cays.

Mangrove ranges have built up over a substrate of mangrove-derived peat, perhaps over topographic highs in the underlying Pleistocene surface, and many of them appear to have persisted since the development of widespread mangrove forests over the Belize barrier reef during the Holocene transgression. The ranges have been undergoing disintegration; peat, which is encountered beneath adjacent shoals, exposed by shoreline erosion, or found in creeks and lagoons within the range, testifies to the greater extent of mangrove cover relatively recently. Creeks, or bogues, are bisecting the ranges and appear to be an important element in the gradual disintegration of these islands.

Extensive mortality of mangroves has occurred recently, and in places shoreline erosion may be continuing. The extensive unvegetated flats on Tobacco Range and Twin Cays, and the widespread dead tree stumps found throughout these ranges, are probably the result of damage during Hurricane Hattie which devastated much of the barrier reef to the north in 1961. Catastrophic storms are evidently an important factor in accounting for the present vegetation distribution on these mangrove ranges, and contribute significantly to the longer term disintegration of these islands.

Acknowledgements

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TABLE 1: Plants recorded on Twin Cays, March 1985.

Plant species	Collection number (deposited at the Smithsonian Institution)
<u>Eleusine indica</u> (L.) Gaertn.	620
* <u>Eustachys petraea</u> (Sw.) Desv.	616
* <u>Paspalum distichum</u> L.	612
<u>Spartina patens</u> (Ait.) Muhl.	624
* <u>Sporobolus virginicus</u> (L.) Kunth or <u>Distichlis spicata</u> (L.) Greene	601
<u>Cyperus ligularis</u> L.	611
<u>Cyperus peruvianus</u> (Lam.) Williams	618
* <u>Cyperus planifolius</u> L.C.Rich	623
<u>Fimbristylis cymosa</u> R.Br. var. <u>spathacea</u> (Roth) Koyama	619
<u>Fimbristylis spadicea</u> (L.) Vahl	605
* <u>Cocos nucifera</u> L.	sight
* <u>Thrinax radiata</u> Lodd. ex Schultes & Schultes	sight
* <u>Batis maritima</u> L.	633
* <u>Salicornia perennis</u> Miller	628
<u>Philoxerus vermicularis</u> (L.) Beauv.	615
<u>Sesuvium portulacastrum</u> (L.) L.	608
<u>Cakile lanceolata</u> (Willd.) O.E. Schulz	610
* <u>Suriana maritima</u> L.	625
* <u>Euphorbia mesembrianthemifolia</u> Jacq.	614, 632
* <u>Rhizophora mangle</u> L.	634
* <u>Conocarpus erectus</u> L.	607, 627
* <u>Laguncularia racemosa</u> (L.) Gaertn. f.	636
<u>Rhabdadenia biflora</u> (Jacq.) Mull.-Arg.	602
<u>Ipomoea pes-caprae</u> ssp. <u>brasiliensis</u> (L.) V.Ooststr.	609
* <u>Avicennia germinans</u> (L.) L.	635
* <u>Erithalis fruticosa</u> L.	626
* <u>Ageratum littorale</u> A. Gray	617, 622
	631
* <u>Borrchia arborescens</u> (L.) DC.	603
<u>Eclipta alba</u> (L.) Hassk.	606
<u>Eclipta</u> cf. <u>prostrata</u> (L.) L.	621
<u>Vernonia cinerea</u> (L.) Less.	604

* recorded from Twin Cays in 1972 (Stoddart et al. 1982)

Table 2 Structural characteristics of mangrove types on Twin Cays.

Sample Number	Mangrove Type	Canopy Height (m)	Tree Height Mean + S.D. (m)	Density (trees/ha)	Trunk Diameter Mean + S.D. (cm)	Basal Area (m ² /ha)	Component Species	% Density	% Basal Area
1	<u>Rhizophora</u> woodland	5.0-6.0	4.1 +/- 1.1	4500	6.26 +/- 4.19	19.9	<u>Rhizophora</u> <u>Laguncularia</u>	95 5	99 1
2	<u>Rhizophora</u> thicket	3.0-4.0	3.0 +/- 1.0	4790	5.49 +/- 2.12	13.0	<u>Rhizophora</u> <u>Laguncularia</u>	98 2	>98 <2
3	<u>Rhizophora</u> scrub	1.0-1.5	0.8 +/- 0.2	17400	2.24 +/- 0.60	7.5	<u>Rhizophora</u>	100	100
4	<u>Avicennia</u> woodland	4.0-5.0	2.9 +/- 1.3	5760	5.48 +/- 4.06	20.9	<u>Avicennia</u> <u>Rhizophora</u>	92 8	>99 <1
5	<u>Avicennia</u> open woodland with <u>Rhizophora</u>	4.0-5.0	2.7 +/- 1.1	6840	4.89 +/- 3.91	20.9	<u>Avicennia</u> <u>Rhizophora</u> <u>Laguncularia</u>	32 55 13	68 30 2

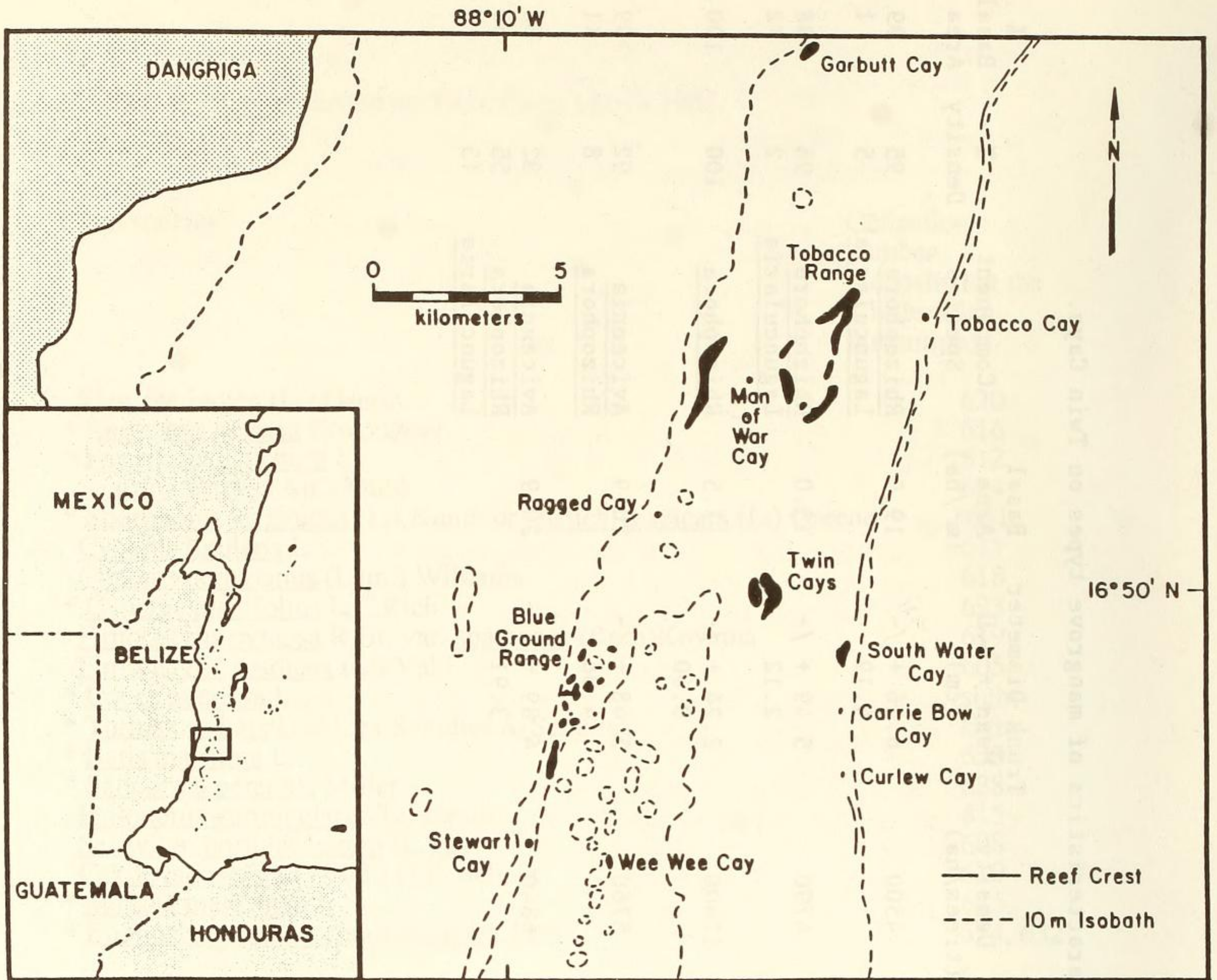

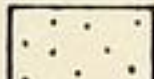
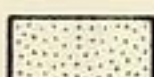


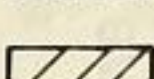
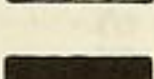
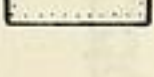


Fig. 1: The central Belize barrier reef showing the location of Tobacco Range, Twin Cays, and Blue Ground Range.

-  Unvegetated Flat
-  Rhizophora Scrub (<2m)
-  Rhizophora Thicket (2-4m)
-  Rhizophora Woodland (>4m)
-  Avicennia Woodland
-  Avicennia Open Woodland with Rhizophora
-  Coconut
-  Open Water
-  Transect

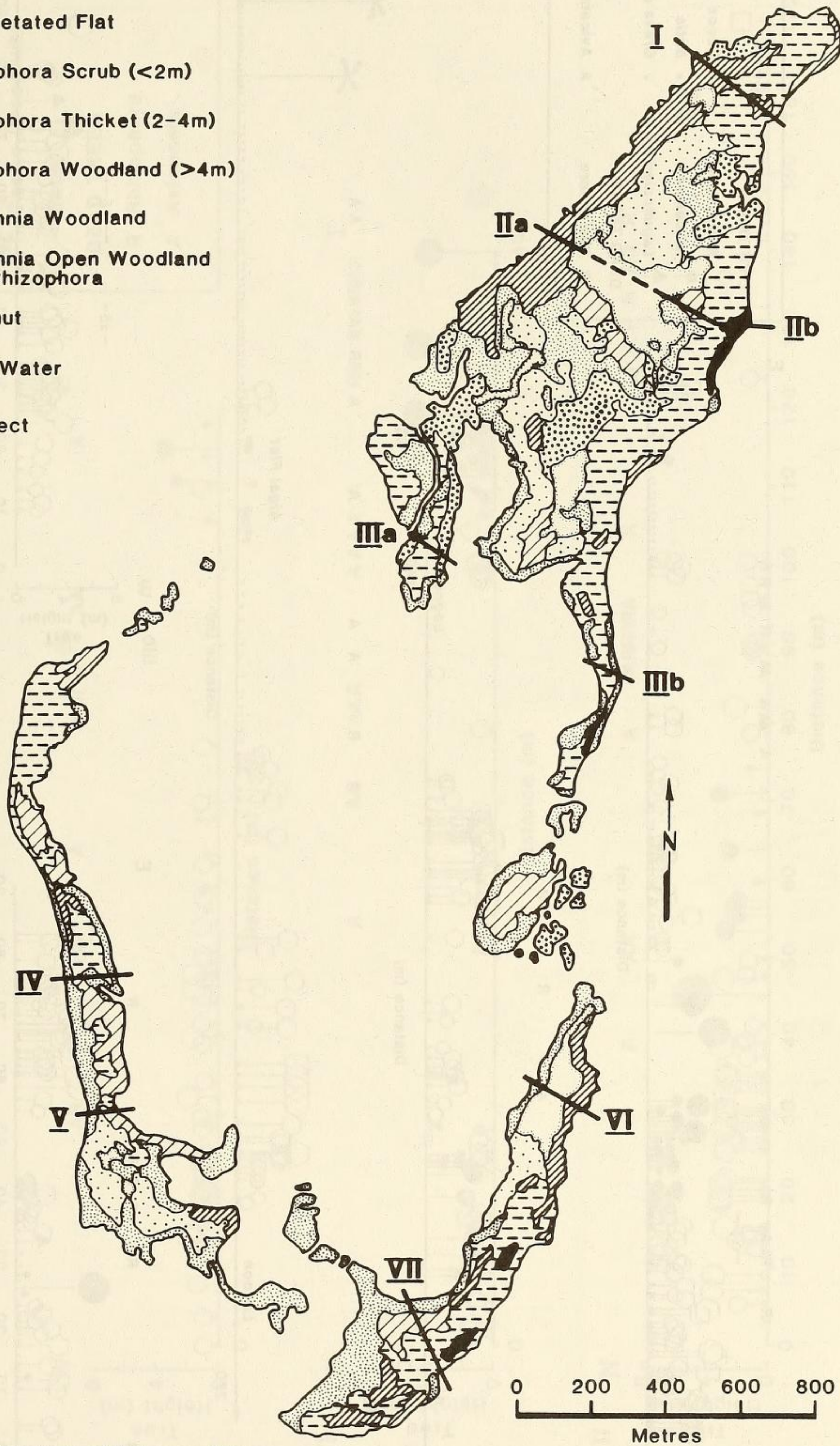


Fig. 2: Vegetation map of Tobacco Range.

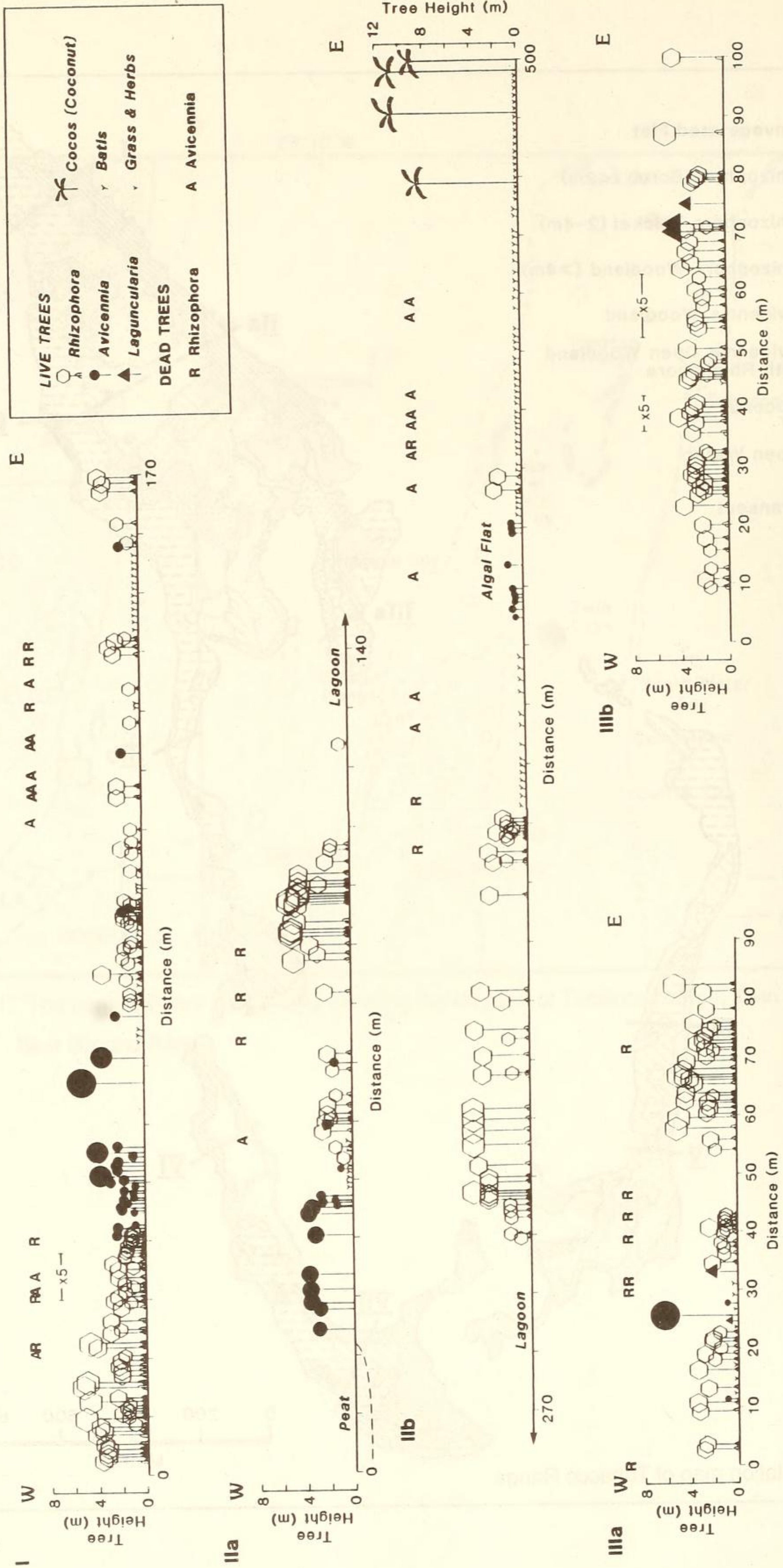


Fig. 3: Transects I-IIIb, Tobacco Range (x5 indicates that the density of *Rhizophora* was five times that shown on the transect).

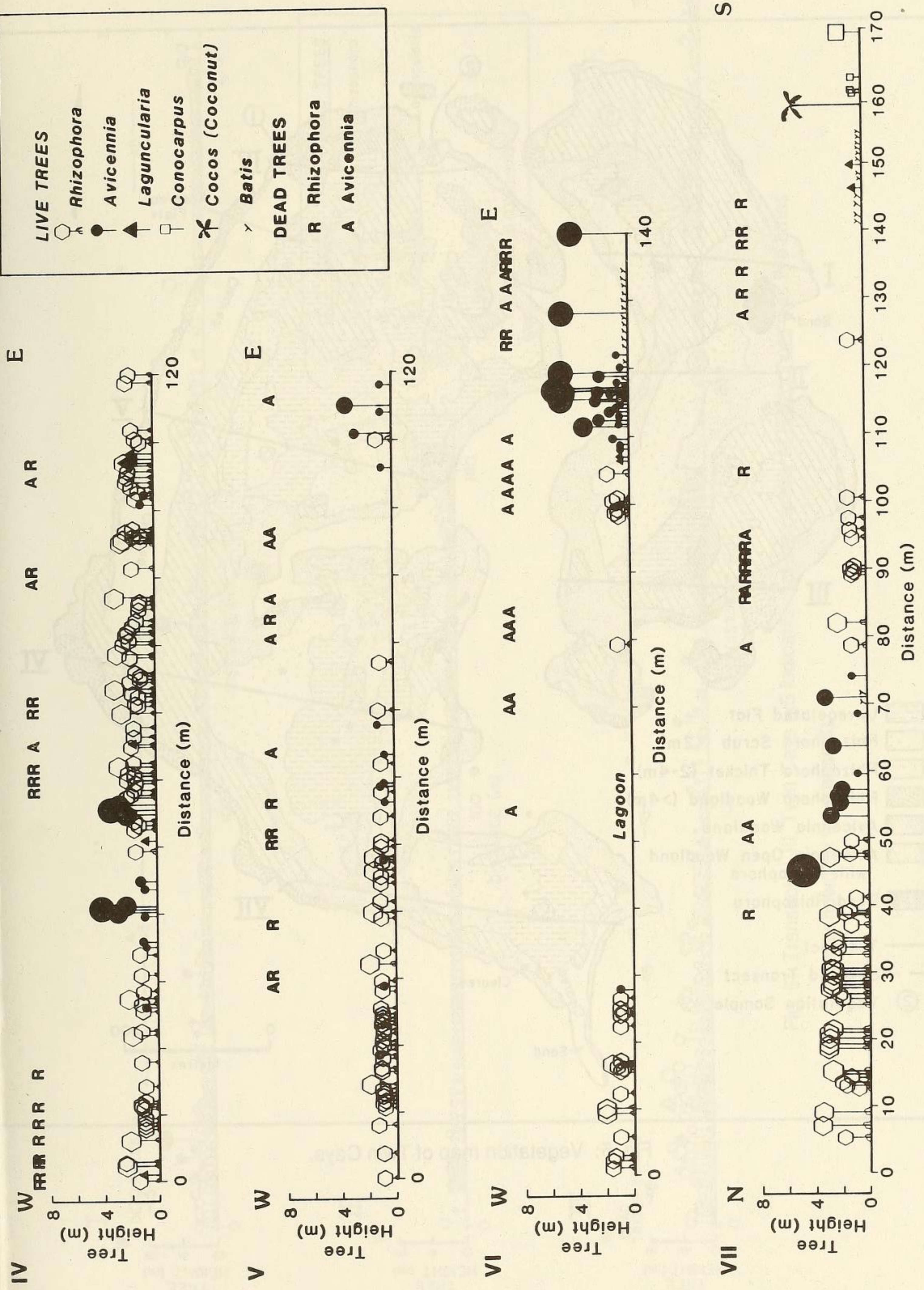


Fig. 4: Transects IV-VII, Tobacco Range (x5 indicates that the density of Rhizophora was five times that shown on the transect).

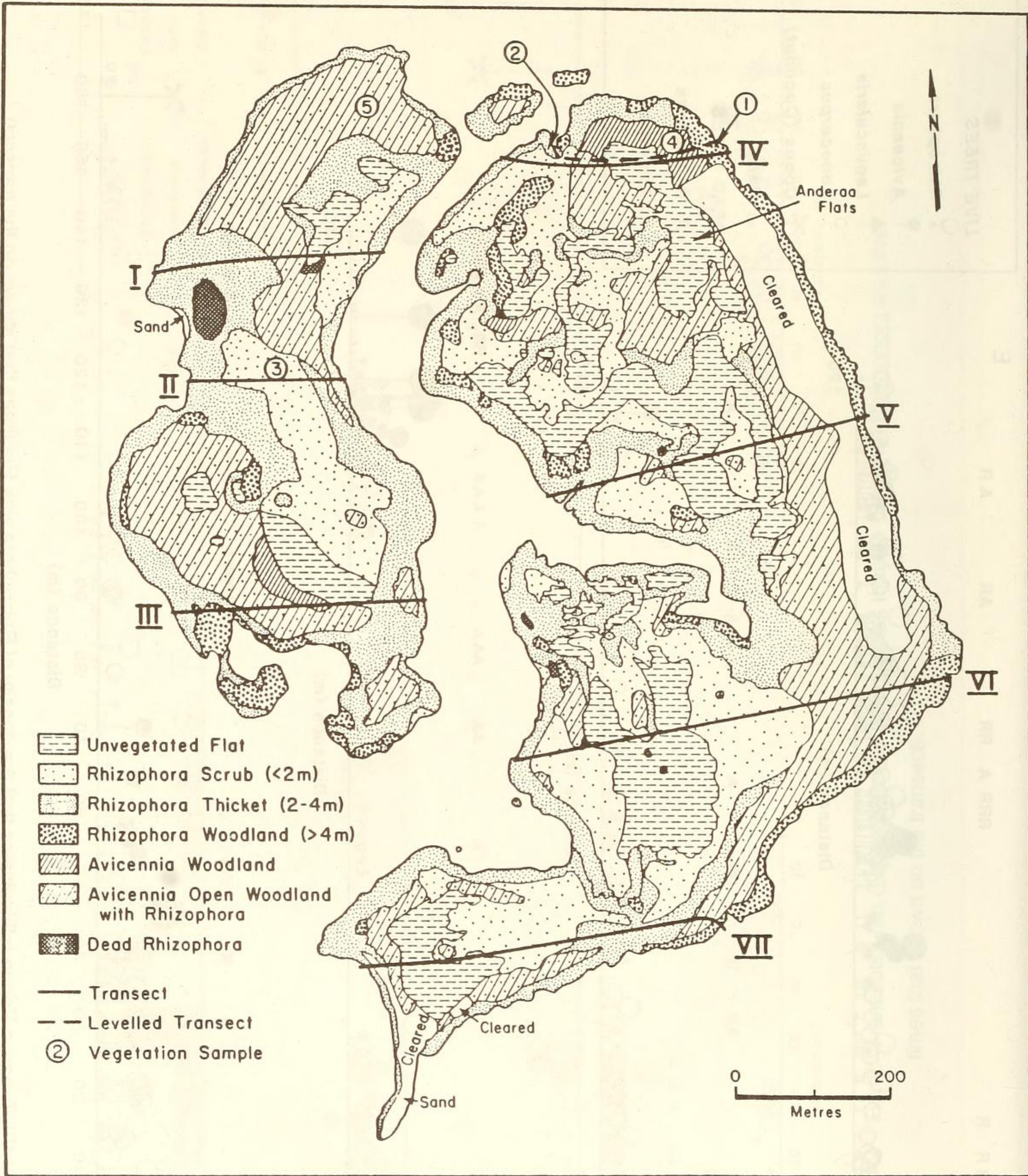
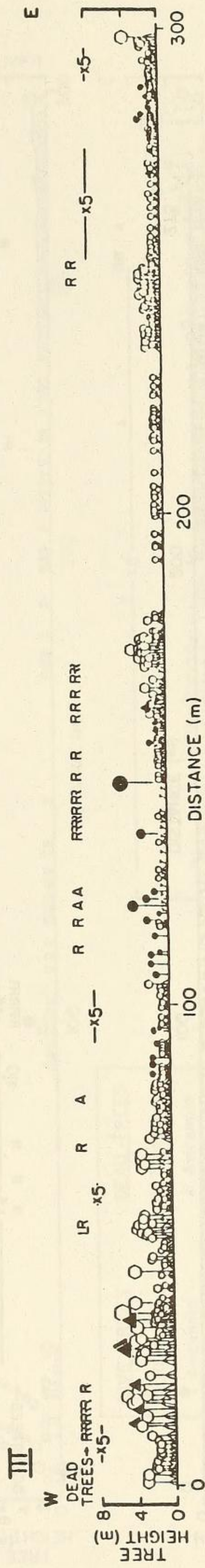
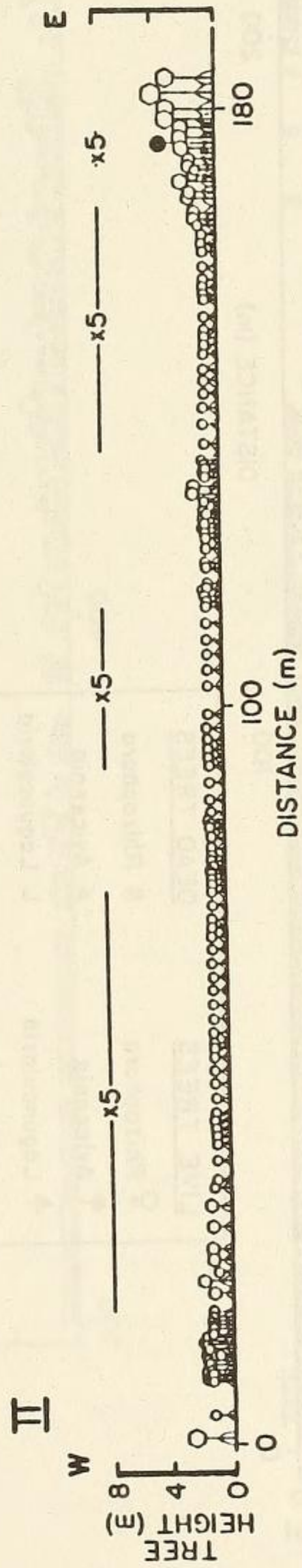
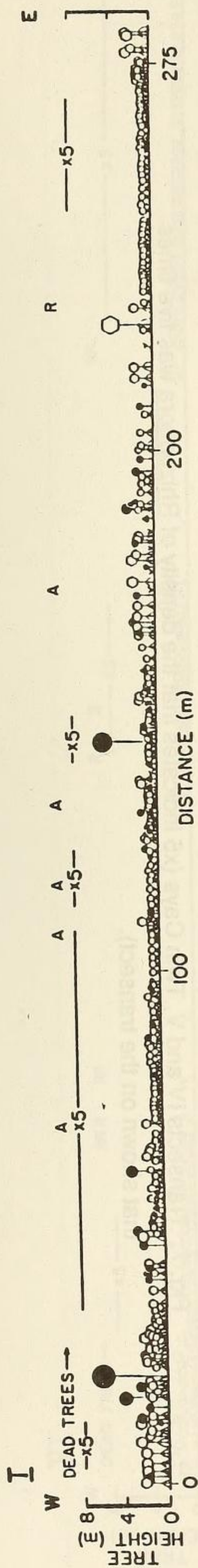


Fig. 5: Vegetation map of Twin Cays.



LIVE TREES		DEAD TREES	
○	Rhizophora	R	Rhizophora
●	Avicennia	A	Avicennia
▲	Laguncularia	L	Laguncularia
∇	Batis		
‡	Salicornia		
v	Sporobolus/Distichlis		

Fig. 6: Transects I-III, Twin Cays (x5 indicates that the density of Rhizophora was five times that shown on the transect).

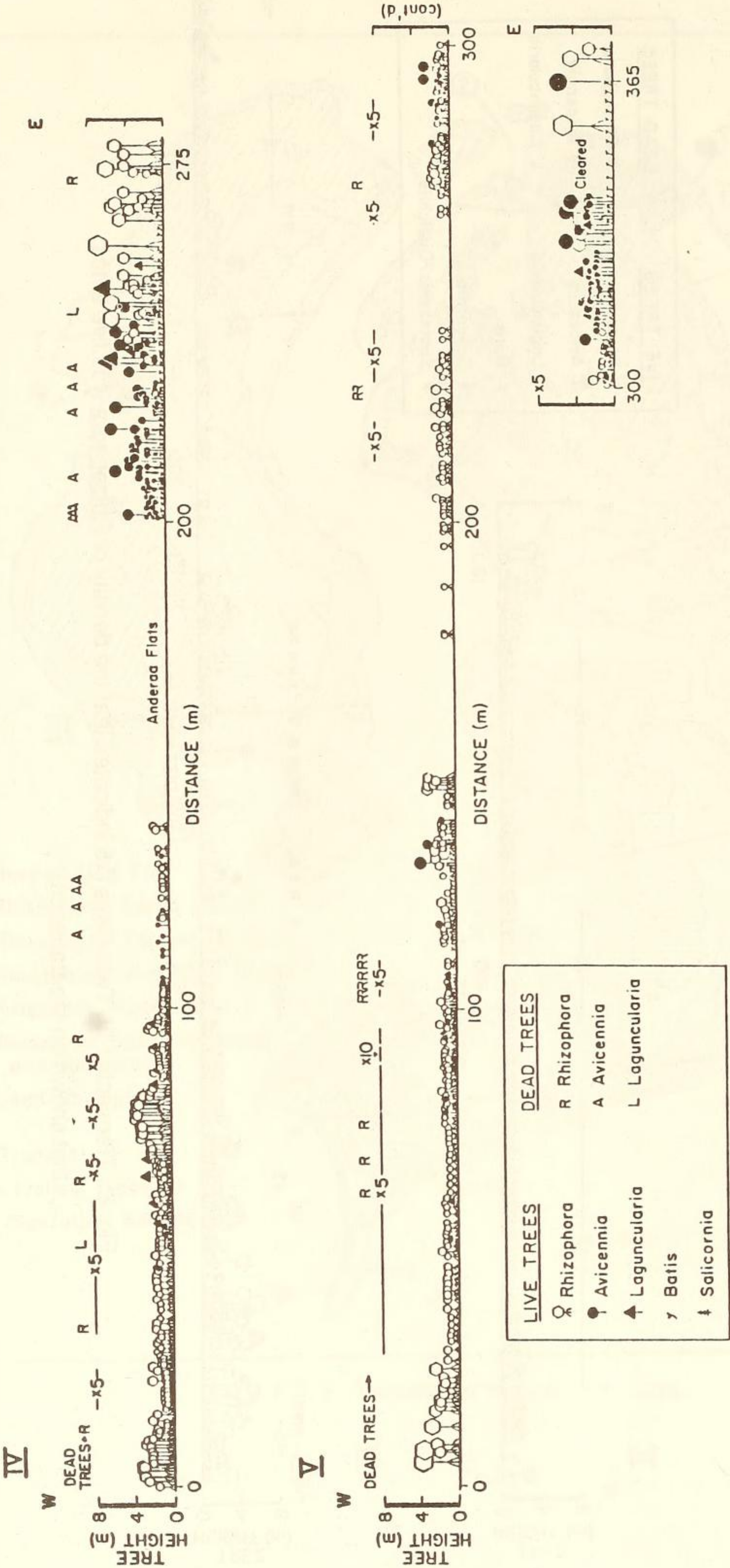


Fig. 7: Transects IV and V, Twin Cays (x5 indicates that the density of *Rhizophora* was five times that shown on the transect).

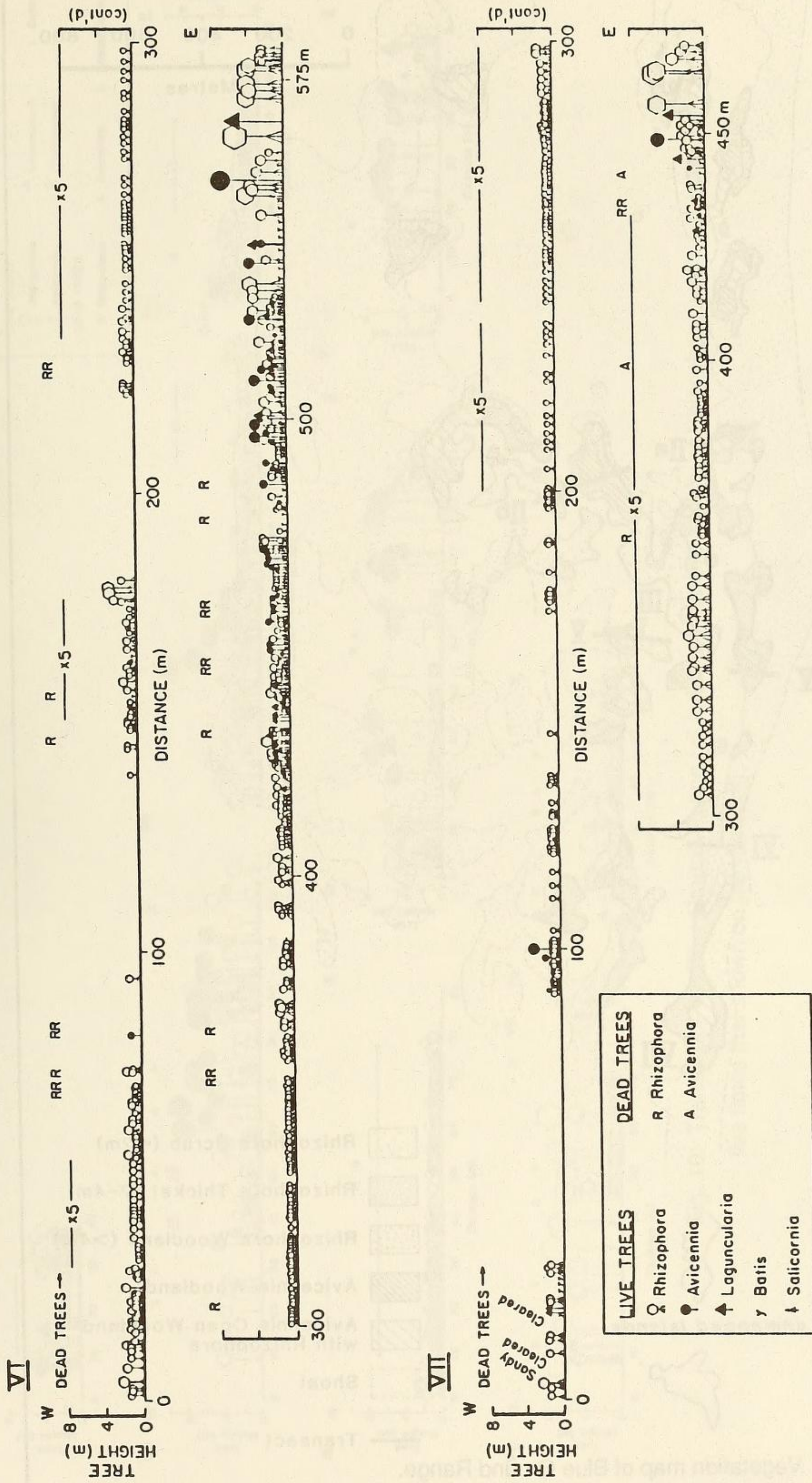


Fig. 8: Transects VI and VII, Twin Cays (x5 indicates that the density of *Rhizophora* was five times that shown on the transect).

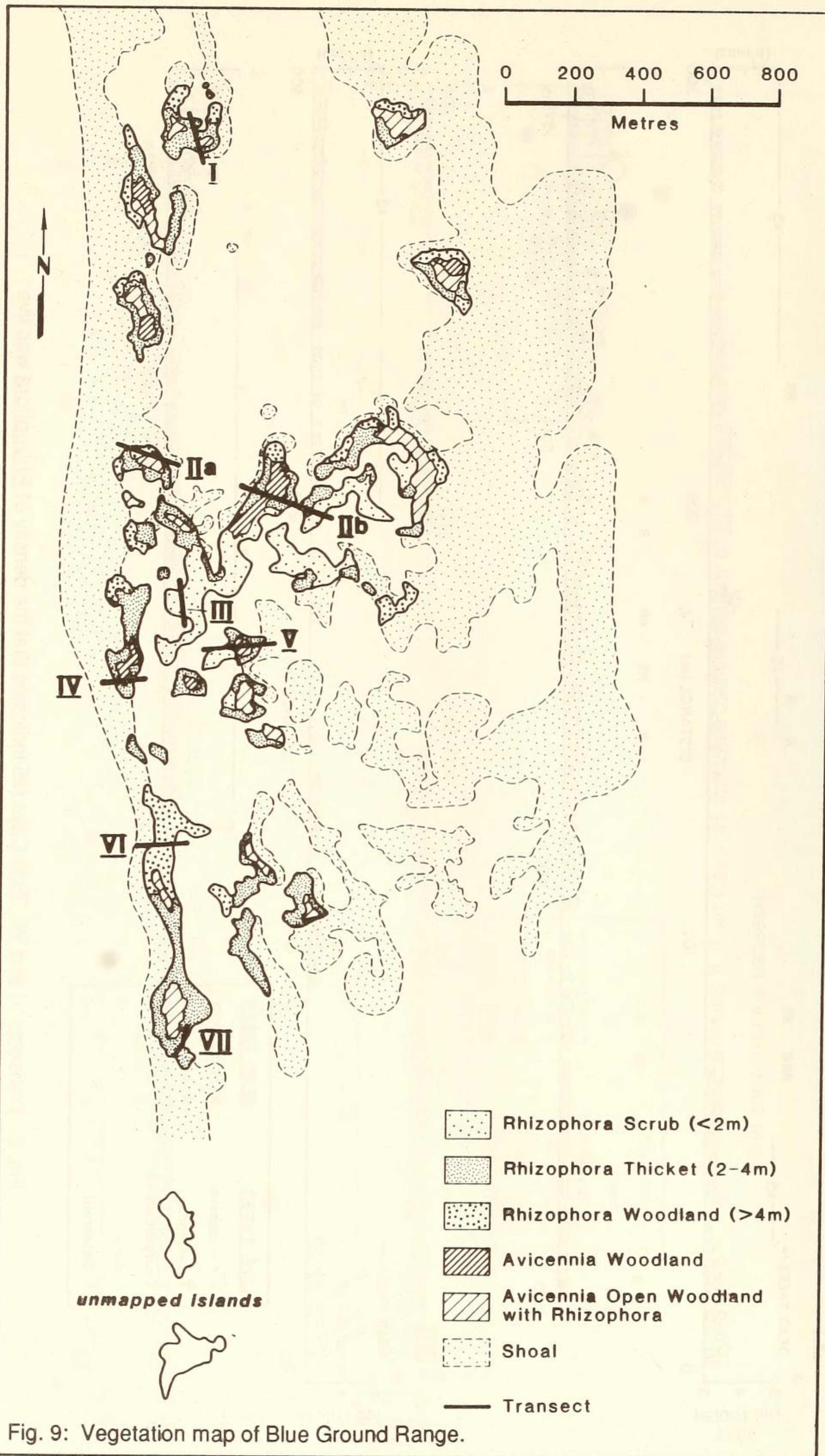


Fig. 9: Vegetation map of Blue Ground Range.

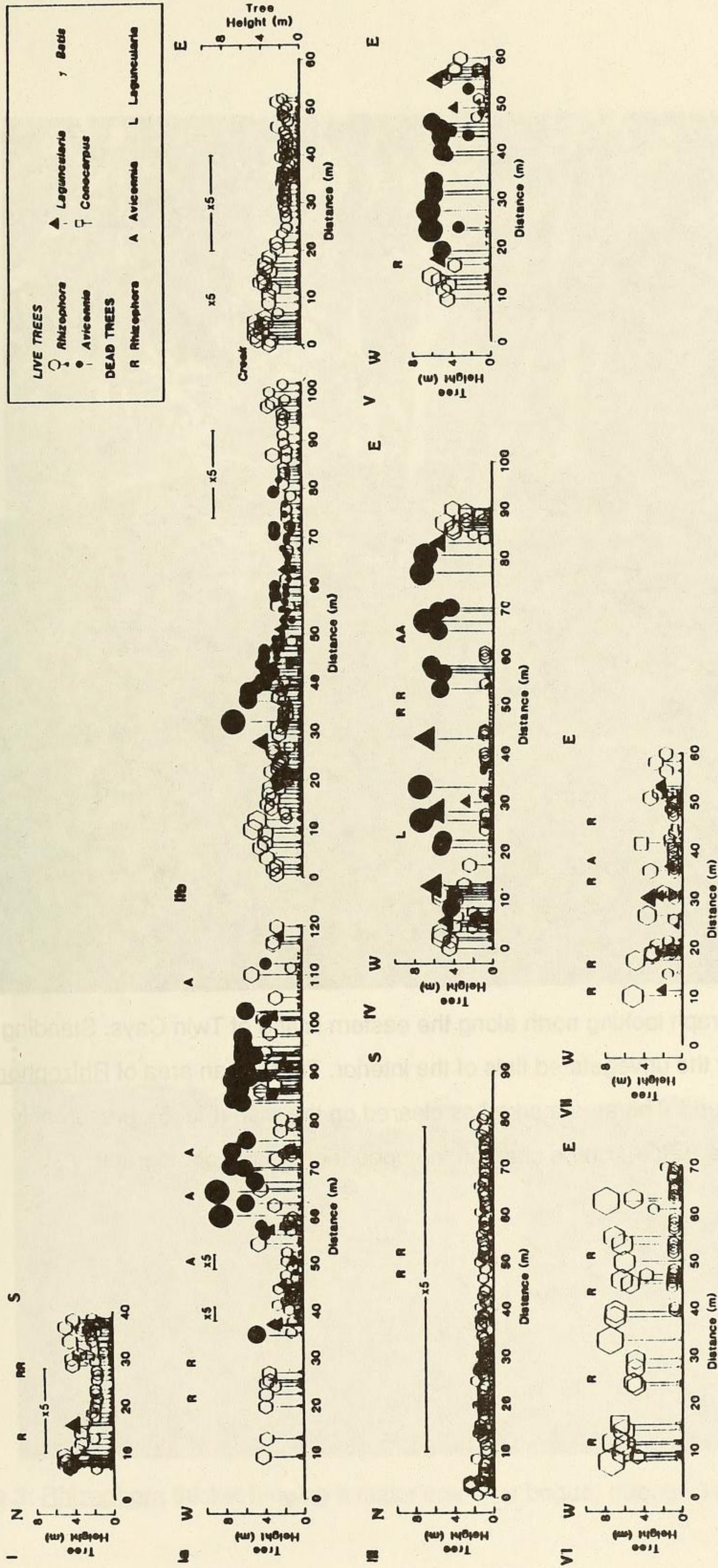


Fig. 10: Transects I-VII, Blue Ground Range (x5 indicates that the density of *Rhizophora* was five times that shown on the transect).



Plate 1: Oblique aerial photograph looking north along the eastern island of Twin Cays. Standing water can be seen over the unvegetated flats of the interior. There is an area of Rhizophora scrub in the left foreground. The area marked as cleared on the map (Fig. 5), presumably devastated by Hurricane Hattie, can be seen on the upper right of the photograph.



Plate 2: Inside Rhizophora woodland, Twin Cays.

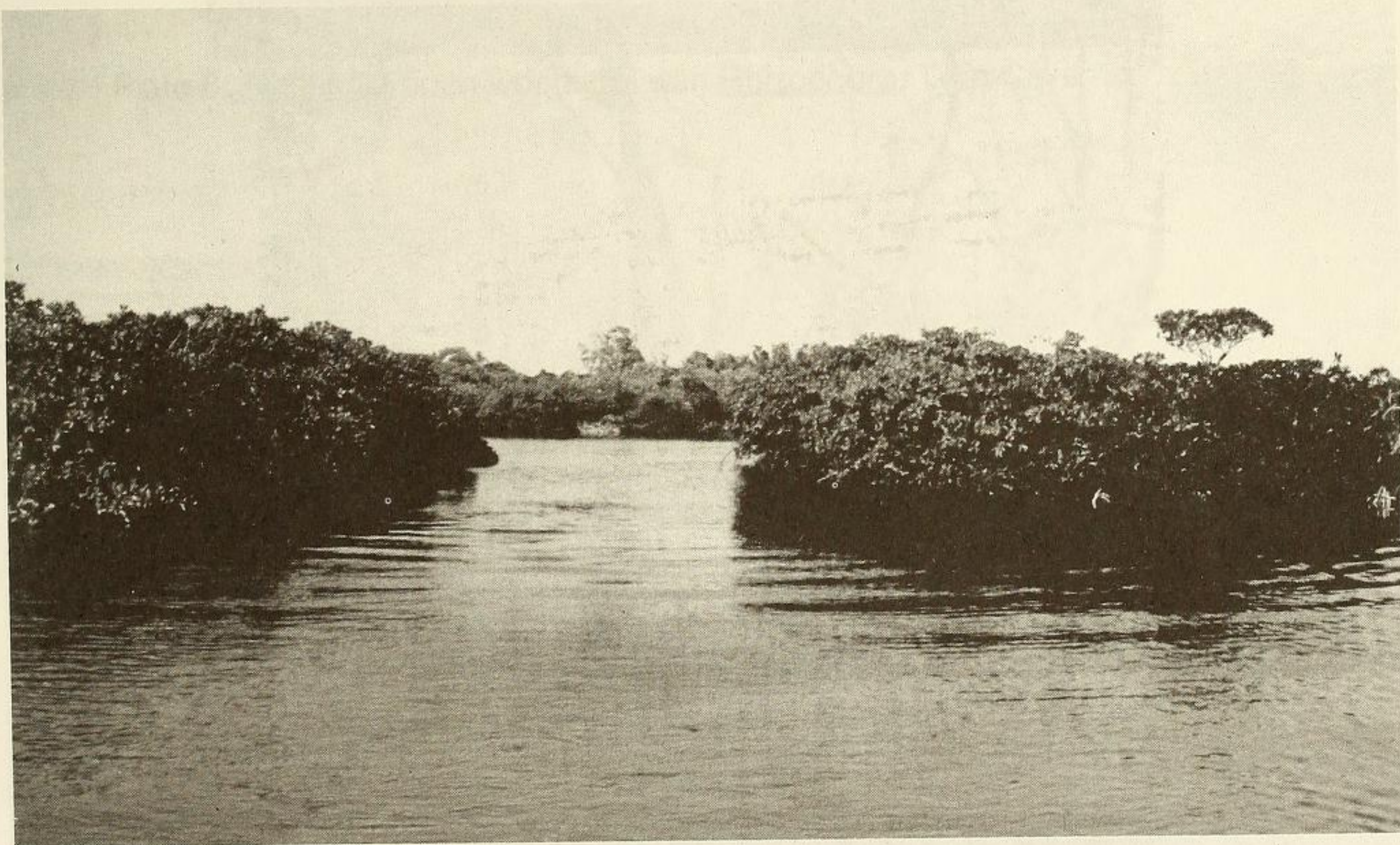


Plate 3: Rhizophora thicket fringing a major creek (or bogue) through Twin Cays.



Plate 4: Rhizophora scrub within the interior of the western island, Twin Cays.



Plate 5: Inside Avicennia woodland, northern Twin Cays.

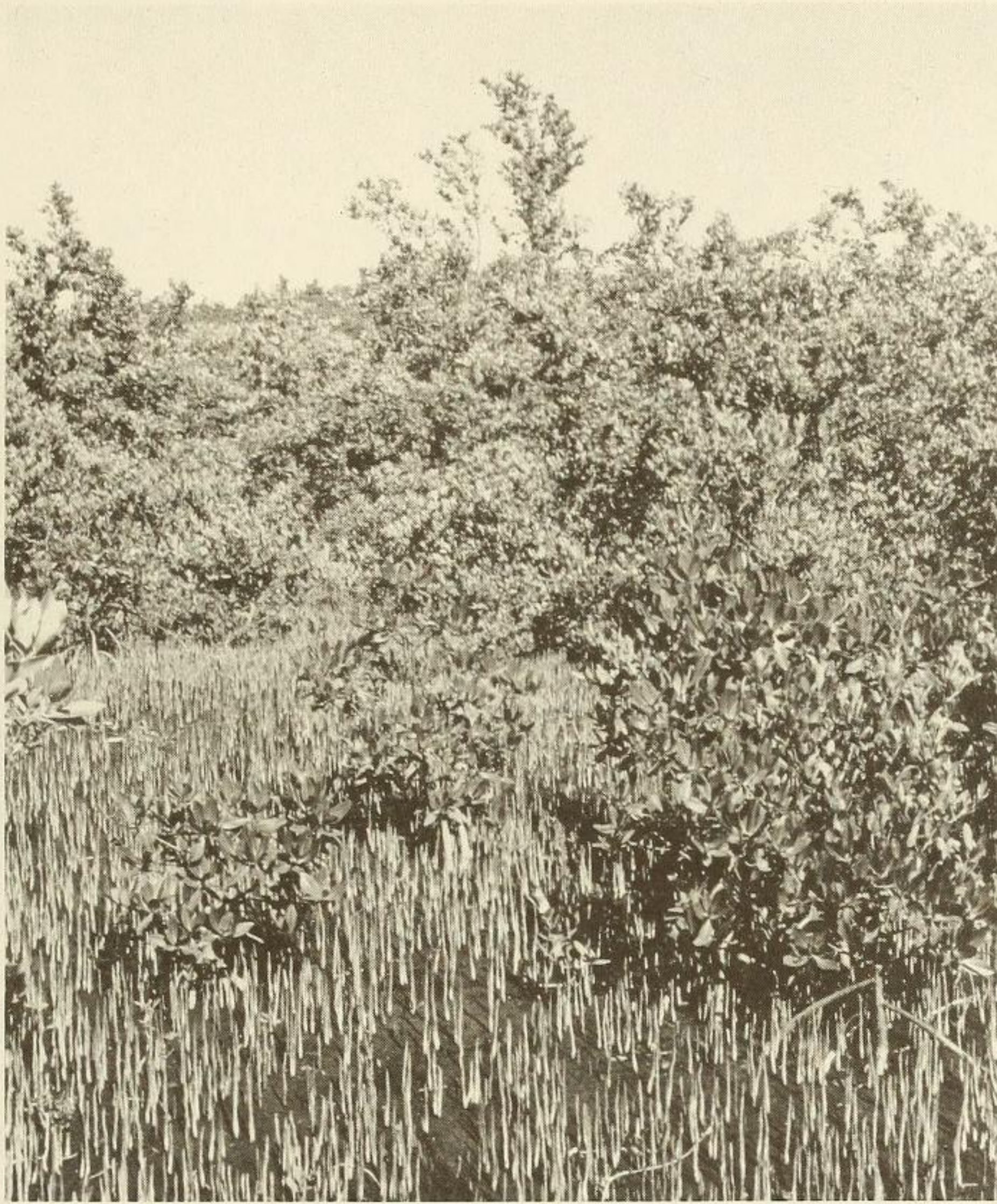


Plate 6: Avicennia open woodland with Rhizophora, Twin Cays.

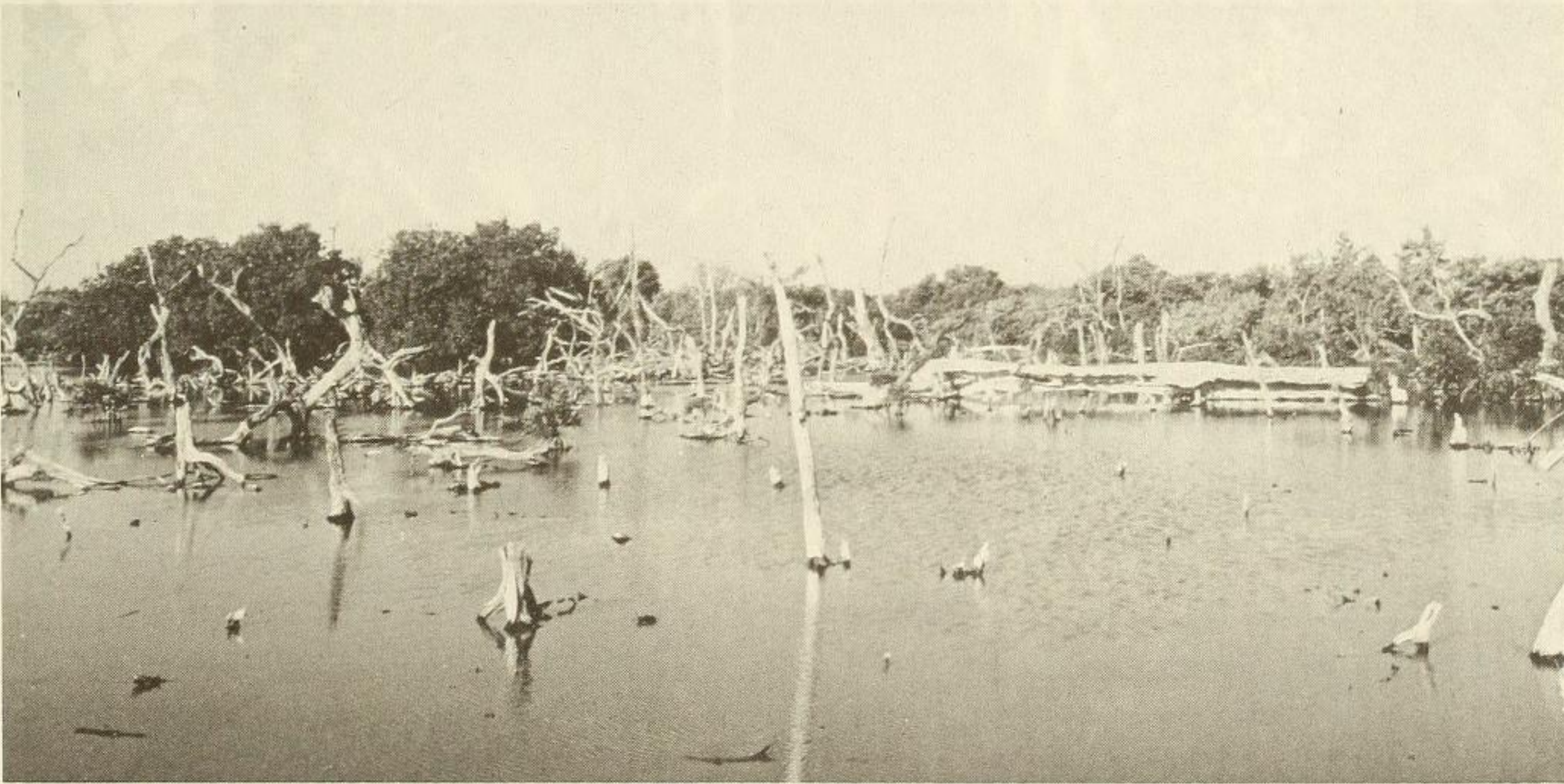


Plate 7: Unvegetated flat on southern end of Tobacco Range, showing extensive dead trees, presumably killed during Hurricane Hattie, 1961.

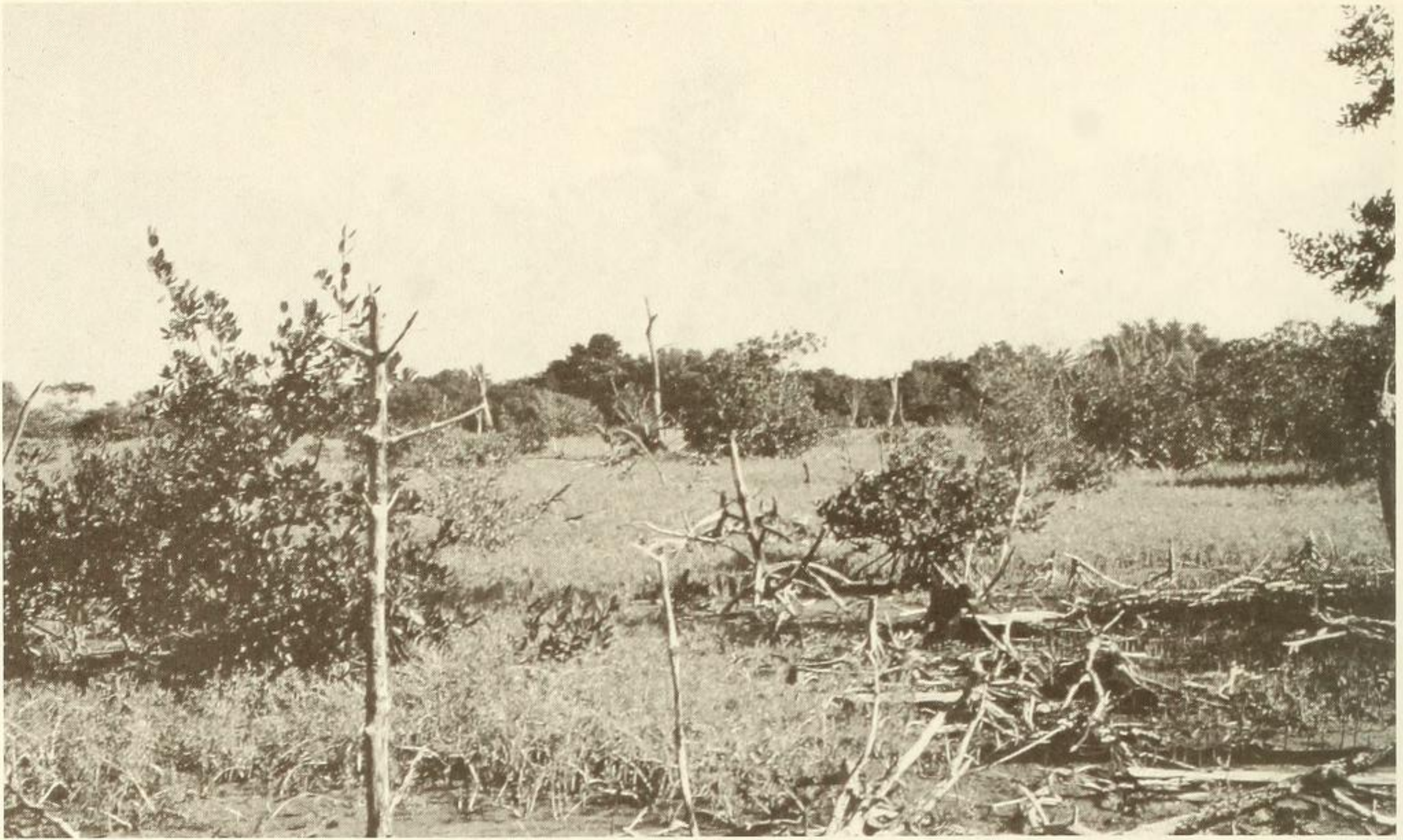


Plate 8: Avicennia open woodland with Rhizophora, with a carpet of Batis, Twin Cays, showing numerous dead Rhizophora trees.



Plate 9: Small meandering creek, fringed by Rhizophora thicket, Twin Cays.

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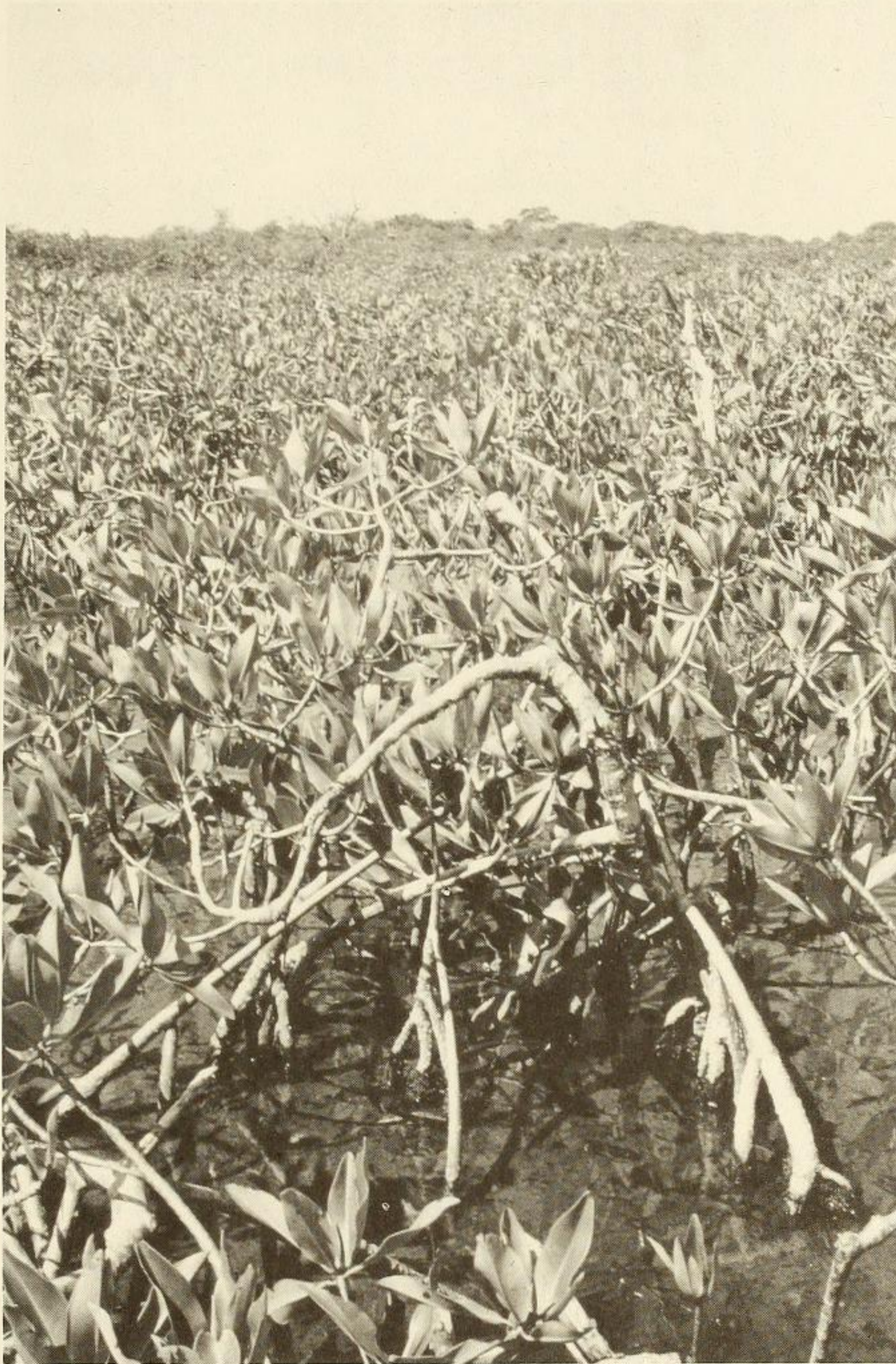


Plate 10: Individual Rhizophora within Rhizophora scrub, Twin Cays, showing that the scrub is composed of mature individuals, and is not always composed of Rhizophora seedlings.

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