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Variability of Mangrove Ecosystems Along the Brazilian Coast

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ABSTRACT: Brazilian mangroves extend from 4°30′N to 28°30′S, varying greatly in growth form, species distribution patterns, and stand structure, in spite of a limited floristic diversity. We divided the Brazilian coastline into eight units, within which physiographic and climatic conditions are relatively uniform, and described mangrove occurrence, species distribution and structural attributes characteristic of each segment. In general, greatest mangrove coverage and greatest forest stature are found in areas with a large surplus of rainfall over potential evapotranspiration and macrotidal regimes. An exception was the segment containing the mouth of the Amazon river, where freshwater systems dominate over brackish or marine associations. We believe that the variability in species associations and the dominance of each in a given environment is predominantly determined by the characteristics of the landforms that can be colonized by each species in a given region. The type, size, and frequency of occurrence of available landforms is a function of the particular mix of fluvial, tidal, and wave energies found in a region. Different species colonize these sites depending on their adaptations and edaphic preferences. Climate affects mangrove colonization and growth. We suggest that Brazilian mangroves play a minor role in modifying the geomorphic setting; the spatial arrangement of the various forest types is a response to the underlying topography and edaphic conditions, and to the constraints imposed by climatic and hydrologic factors. The spatial arrangement of species does not necessarily show successional processes, but may be the result of direct and differential colonization on appropriate substrates.

Introduction

According to Saenger et al. (1983) there are about 25,000 km² of mangrove forests in Brazil. Mangroves are found from 04°30′N to 28°30′S, under a wide range of environmental conditions. This great diversity in growing conditions is reflected in variable tree form, spatial arrangements of species, and stand structural attributes. Some potential floristic variability is limited by the fact that western hemisphere mangrove forests are species poor (8 species in only 5 genera in the New World; 7 species in 4 genera in Brazil). Mangrove species have wide environmental tolerances, adapting to growth in different environments. It is therefore natural to find forests with different structural characteristics in different geographic zones. This paper reviews information available on geographic variations in structural and floristic characteristics of mangrove forests. The task is complex; Brazil has 7,400 km of coastline, not all of it easily accessible. Structure and floristics of its mangrove forests have been poorly studied. Often the only information available is in early descriptive ac-

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counts such as those of Luederwaldt (1919). In general, Brazilian mangroves remain poorly described.

The Concept of Energy Signature and the Development of a Coastal Mapping System for Brazil

Mangrove stands grow under the influence of many environmental factors that vary in intensity and periodicity. In general, mangroves develop best where suitable topography is subjected to large tidal ranges and ample inputs of river water, rainfall, nutrients, and sediments. Where all these factors are present, mangroves can reach their maximum development. In optimal environments the red mangrove *Rhizophora* reaches heights of over 40 m. Mangroves also develop in environments where some factors may be limiting. In these more rigorous environments forest structure is reduced, although the same species may be present. For instance, at its southern latitudinal limit in Brazil, red mangrove (*R. mangle*) grows as a shrub barely reaching 1.5 m high.

The factors that control solar energy utilization are modeled in Fig. 1. Photosynthetic energy capture and its conversion into forest structure is regulated by the availability of subsidiary energies from tides, freshwater, sediment input, and rainfall, and by such biotic factors as the pool of available species. Stressors, also shown, drain energy that otherwise could be allocated to greater structure. Stressors like periodic drought, hurricanes, and hypersalinity commonly occur in mangrove stands, removing structure or slowing development. The amount of structure at maturity represents the maximum possible utilization of the energies at the site. Sites with similar "energy quality signatures" (as defined by H. T. Odum 1968) supporting the same species pool should develop similar structural complexity. This is why the Lugo and Snedaker (1974) system of physiographic mangrove classification works so well. Each category represents a set of similar energy signatures, so that within each category mangrove stands reach similar levels of development.

To assist our interpretation of mangrove forests in Brazil, we divided the coastline into eight mapping units (Fig. 2) in which broad environmental conditions and physiography are similar. From the literature reviewed, we prepared standard vegetation profiles based on the authors' descriptions and figures. Climatological information is taken from published weather station data (Ministério de Agricultura 1972). Potential evapotranspiration (PET) was estimated from monthly rainfall and temperature data according to the method of Thornthwaite and Mather (1957). Tidal data are from National Oceanic and Atmospheric Administration (1986).

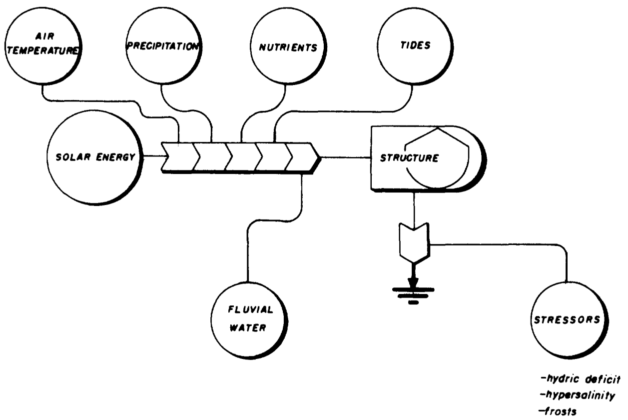


Fig. 1. Diagram illustrating the major forcing functions acting upon mangrove systems. Symbols used are those of the energy language of H. T. Odum (1968).

Variation in the Principal Forcing-Functions Along the Brazilian Coast

Tides

Tidal amplitudes (mean ranges and spring tidal range) decrease southward along the Brazilian coast (Fig. 3). The coastal area north of São Luis (segments I, II, and III) is strongly macrotidal with amplitudes > 4 m. South of São Luis tidal subsidies decrease; much of the coast, except the area between Vitoria and Santos, is in the low mesotidal range (about 2 m).

Rainfall and Potential Evapotranspiration

Mean annual rainfall is over 2,000 mm north of São Luis (Fig. 4). According to Macnae (1966), mangroves develop better where precipitation is above 1,500 mm yr^{-1} and reach maximum development in areas receiving more than 2,500 mm yr^{-1}. Areas north of São Luis generally meet requirements for maximum development. Potential evapotranspiration is high (> 1,500 mm yr^{-1}) but lower than rainfall. The water surplus results in large runoff and riverine inputs into these segments of the coast.

Between Fortaleza and Rio de Janeiro (segments IV, V, VI, and VII) rainfall and potential evapotranspiration are similar on a yearly basis, but the climate is strongly seasonal. Most of the region suffers droughts of varying length, and hypersalinity becomes a greater stressor. Salt flats (barren areas with high soil salt concentrations) become important in this region, and salt is harvested from evaporation ponds in some places. South of Rio de

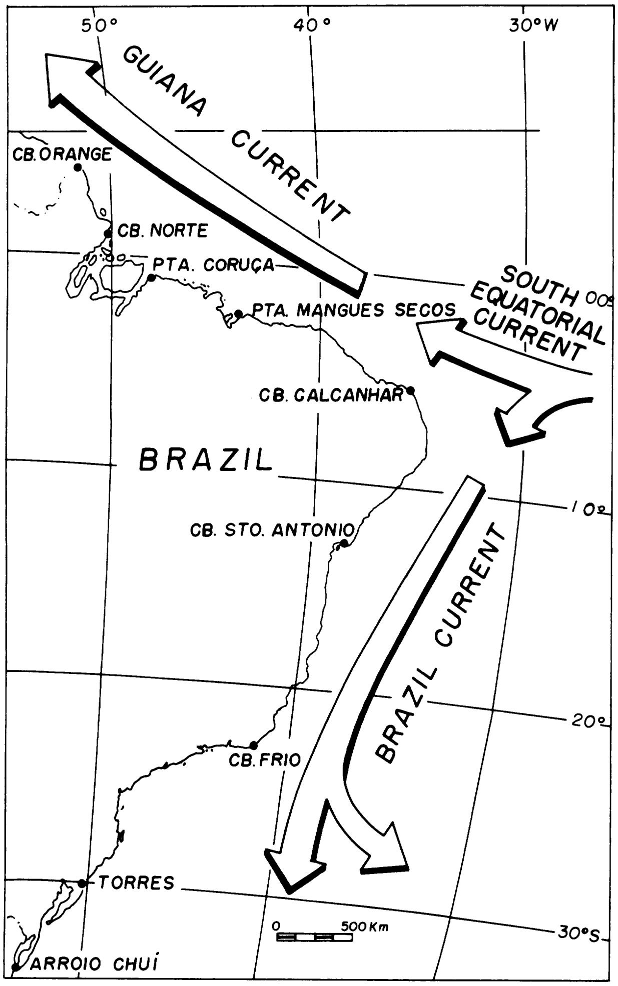


Fig. 2. Map of Brazil showing the eight physiographic/climatic segments. Coastal currents are also shown.

Janeiro the proximity of the Serra do Mar contributes to substantially increased rainfall, so that coastal segments VII and VIII also have high rainfall subsidies.

Temperature

The southern limit of mangrove forests occurs at Laguna (28°30′S) where the mean annual temperature is 19.6°C, the mean temperature for the coldest month is 15.7°C, and the annual mean temperature range is 8.0°C (Fig. 5). Within the tropical zone, mean annual temperatures are above 23°C, but just beyond the Tropic of Capricorn, mean temperatures drop sharply and the annual mean temperature range increases. Cananéia, at 25°S, experiences sporadic frosts.

Low temperatures become limiting in segment VIII. Temperatures are not suitable for mangroves beyond Laguna.

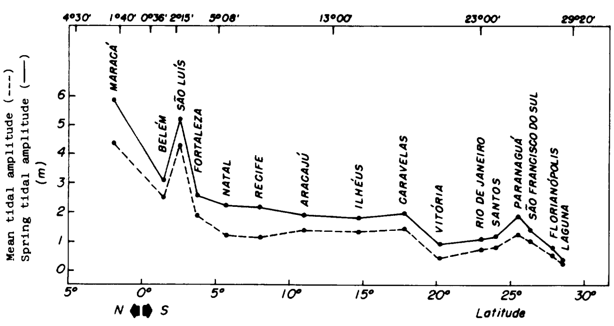


Fig. 3. Tidal amplitude along the Brazilian coast (National Oceanic and Atmospheric Administration 1986).

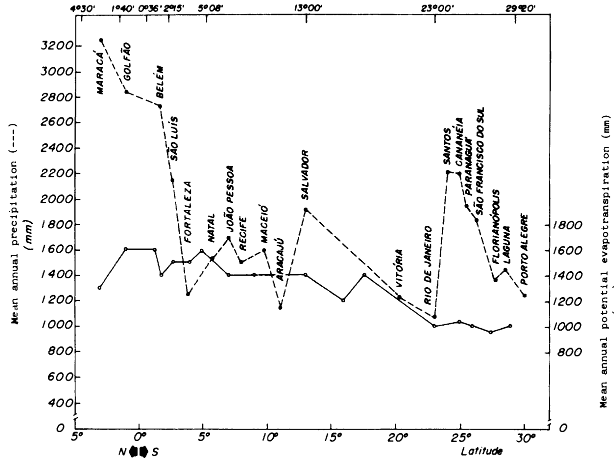


Fig. 4. Precipitation and potential evapotranspiration values along the Brazilian coast (Thornthwaite and Mather 1957; Ministério de Agricultura 1972).

Description of Mapping Units

Segment I: Cabo Orange (04°30′N) to Cabo Norte (01°40′N)

This segment extends from the right bank of the Oiapoque River in northern Brazil south to Cabo Norte, the northern limit of the Amazon delta.

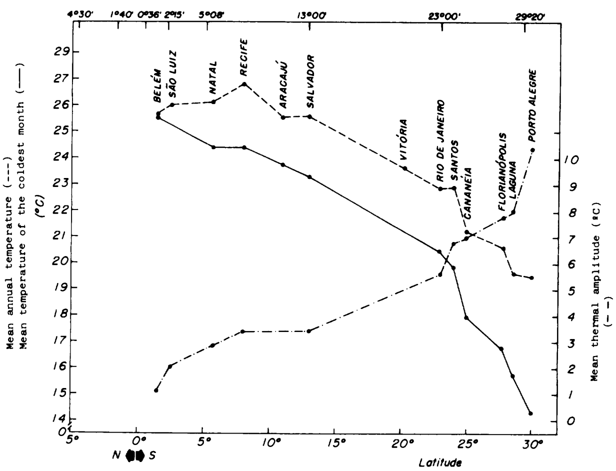


Fig. 5. Mean air temperatures along the Brazilian coast (Ministério de Agricultura 1972).

The coast is alluvial, nearly flat, and floods during the wet season. Shallow waters extend offshore for great distances. The area is influenced by the Amazon plume, which carries sediments northwest along the coast (Fig. 2). It is also dissected by various rivers that drain a humid hinterland. The climate is wet with an annual rainfall mean of 3,250 mm. Mean tidal range is 4.4 m and spring tides reach 5.8 m. Large tides and the discharge of the many rivers in the region presumably compensate for the summer (July to December) dry period. Potential evapotranspiration is about 1,300 mm yr^{-1}.

This segment is characterized by homogeneous forests dominated by black mangrove (*Avicennia*) called *siriubais.* The trees are tall (15–20 m) and well-formed, growing in open stands (Magnanini 1952; Hueck 1972). Forests form an extensive and continuous coastal belt from Cabo Orange to the Araguari River in segment II. Mangroves colonize coastal rivers, extending upstream for considerable distances (ca. 20 km, Hueck 1972). As salinity diminishes, *Pterocarpus* is sometimes found within the siriubal. *Rhizophora* stands are more conspicuous in the estuarine portions of rivers under a more direct marine influence. Figure 6 shows two profiles from this segment. The upper profile (Ponta dos Indios, Rio Oiapoque) is located near the mouth of the river. Here *Rhizophora* is fronted in places by *Montrichardia,* a giant herb that tolerates deep flooding by fresh water, and by *Laguncularia.* The lower profile (Rio Amapazinho) is at an upstream site that supports a black mangrove stand typical of the riverine forests in the region.

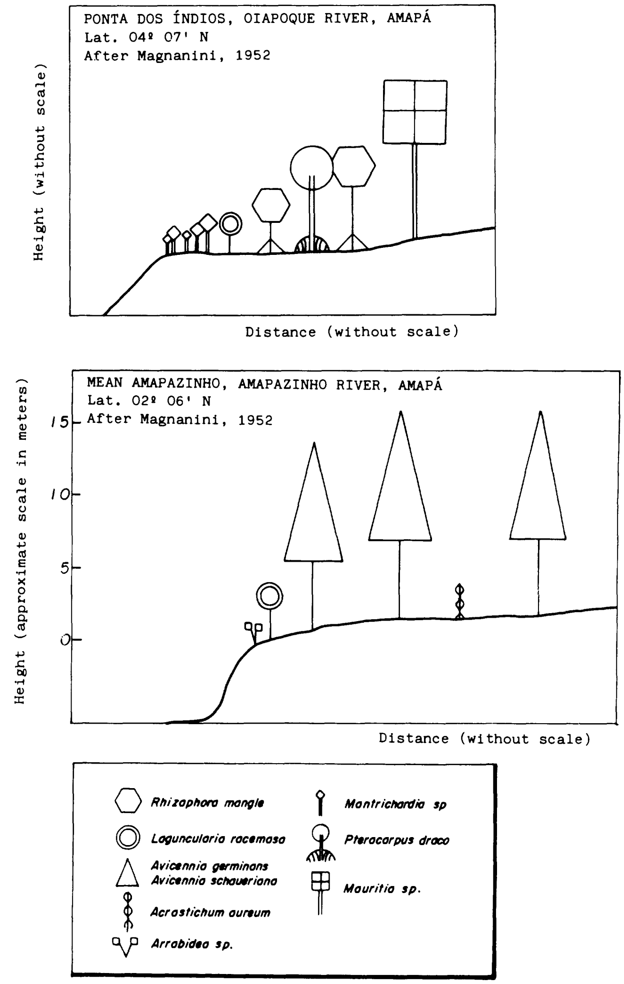


Fig. 6. Vegetation profiles, segment I. *Montrichardia* and *Rhizophora* edge a várzea dominated by *Mauritia* (burití) at the Oiápoque. At the Amapazinho, black mangrove stands (*siriubais*) may be fronted by a narrow fringe of *Laguncularia* and a grass (from Magnanini 1952).

Segment II: Cabo Norte (01°40′N) to Ponta Curuçá (00°36′S)

This segment is physiographically part of the Amazon delta and is mostly made up of islands of uniformly low relief. Maximum elevations are about 15 to 20 m above sea level; only these higher features remain above flood waters during the wet season. The climate is humid (2,900 mm yr^{-1} rainfall). The dry season is about four months long. Mean tidal amplitude is 2.5 m and reaches 3.1 m during spring tides. Potential evapotranspiration is estimated at 1,600 mm.

Mangrove development and coverage is poor in this segment because of the overwhelming influence of the freshwater Amazon discharge. Mangroves are mixed with freshwater swamp formations. On the north side of the Amazon delta, north of Macapá, mangroves again begin to dominate. Elsewhere in this segment, they are limited to the offshore islands of the delta. *Avicennia* forms *siriubais* in slightly higher elevations and lower salinity environments, while *Rhizophora* occurs where the salt water influence is stronger, or flooding is deeper.

Segment III: Ponta Curuçá (00°36′S) to Ponta Mangues Secos (02°15′S)

This coastal plain is deeply dissected by many wide-mouthed estuaries that penetrate inland for several km. The climate is humid (2,000–2,500 mm yr^{-1} rainfall). The dry season lasts 1 to 6 months. Potential evapotranspiration is 1,400 to 1,500 mm yr^{-1}. Mean tidal amplitude is 4.3 m, reaching 5.2 m during spring tides.

Rhizophora dominates the fringe forests, reaching 20 m in height, backed by *Avicennia* or *Laguncularia* stands at higher elevations (Fig. 7). Low energy depositional environments may be colonized by *Spartina. Conocarpus* is found at the tran-

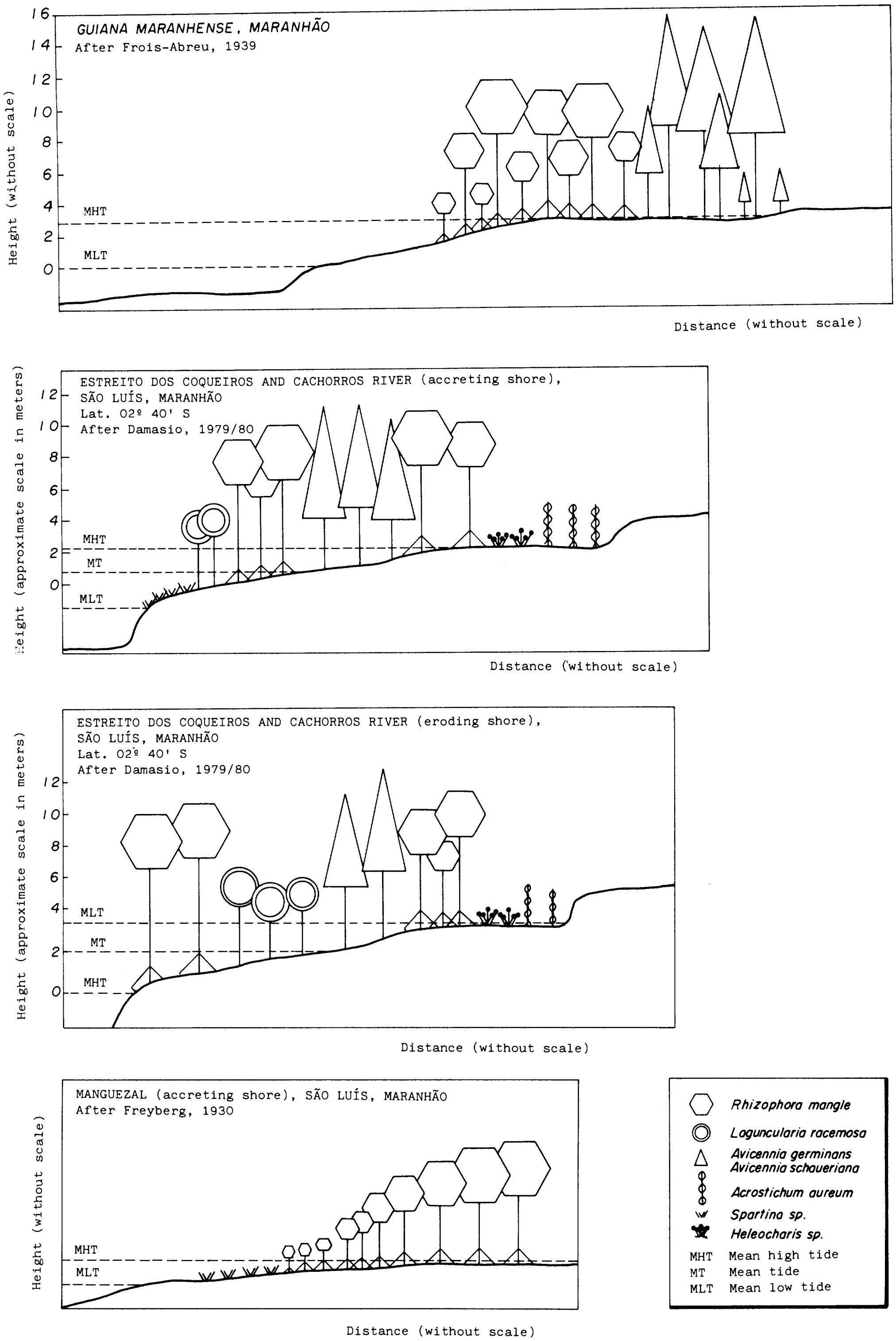


Fig. 7. Vegetation profiles, segment III. The mangrove littoral belt contains stands of *Rhizophora* backed by *Avicennia*; muddy depositional shores are colonized by *Spartina* and/or *Laguncularia* (from Frois-Abreu 1939, Damasio 1980a, 1980b, and Freyberg 1930).

sition between mangrove and higher, nontidal lands (Damasio 1980a, 1980b).

Segment IV: Ponta Mangues Secos (02°15′S) to Cabo Calcanhar (05°08′S)

This coastal segment is almost rectilinear and subject to high wave energy. Sandy beaches, sand dunes, and sandstone bluffs are characteristic features. Alluvial deposits are restricted to the margins of the few rivers. The climate is dry, with a long, pronounced dry season. Annual rainfall (1,250 mm) is lower than potential evapotranspiration (1,500–1,600 mm). The dry climate allows solar salt production. Mean tidal amplitude is 2 m, reaching 2.6 m at spring tides. Mangroves are poorly developed along this coast due to the lack of freshwater runoff and prolonged droughts. High salt concentrations limit mangroves to the immediate mouths of rivers.

Segment V: Cabo Calcanhar (05°08′S) to Reconcavo Baiano (13°00′S)

This segment is characterized by straight, narrow, sandy beaches backed by the higher Barreiras formation. Offshore, drowned relicts of this formation form "reefs" running parallel to the modern coastline. The coast is exposed to high wave energy. A branch of the South Equatorial Current (the Brazil Current) flows southward, bringing low nutrient tropical waters (Fig. 2). The climate is dry and strongly seasonal; annual rainfall (1,100–1,500 mm) is equal to or less than annual potential evapotranspiration (1,400 mm). The dry season lasts for 3 to 6 months. Mean tidal amplitude decreases from 1.7 to 1.3 m southward along this segment; spring tidal amplitudes vary from 2.2 to 1.8 m.

Because of the high wave energy on the coast, mangroves develop in protected areas in association with many estuaries and some coastal lagoons (Figs. 8 and 9). Either *Rhizophora* or *Laguncularia* may appear as pioneering species, *Spartina* may occur in some accreting zones. Basin forests may contain either *Avicennia* or *Laguncularia*, or mixed stands of both species. Stands may reach more than 10 m in height and a few are taller than 20 m.

Segment VI: Reconcavo Baiano (13°00′S) to Cabo Frio (23°00′S)

Sandy beaches are the dominant feature along this coast. Near the central portion of the segment (Vitoria), a mountain range approaches the coast, restricting the width of the coastal plain. At the southern terminus, large, shallow coastal lagoons are found behind narrow sand spits (restingas).

Precipitation (1,200 mm yr^{-1}) and potential evapotranspiration (1,180 mm yr^{-1}) are similar, and there is no marked dry season. Rainfall is greater during the Southern Hemisphere summer, decreasing southward. Localized upwelling of cool, deeper waters caused by strong onshore winds may contribute to the drier climate near Cabo Frio. Here large, barren sand dunes and shallow, high salinity coastal lagoons dominate the landscape. Tidal ranges vary from 1.3 to 0.7 m. The spring tidal range is 1.8 to 1.0 m.

Large mangrove forests are commonly found behind the barrier beaches (Fig. 10). In some sheltered areas like Acupe (Baía de Todos os Santos), *Spartina* pioneers on rapidly accreting sites (Dias-Brito and Zaninetti 1979). *Laguncularia* is reported to be dominant in Baía, established on reduced sandy clay soils. *Rhizophora* is found only at the margins, forming a narrow fringe. Elsewhere *Rhizophora* is more dominant, forming almost monospecific fringes and dominating in basin-type, more deeply flooded environments. *Avicennia* and *Laguncularia* may also occur. Well-developed forests may be 15 m tall.

Segment VII: Cabo Frio (23°00′S) to Torres (29°20′S)

The Serra do Mar is very close to the ocean in this segment, especially to the north. The narrow coastal plain is interrupted by seaward extensions of the mountains, leaving lunate stretches of sandy beach between rocky headlands. Near the segment's southern end the influence of the mountains diminishes; the wider coastal plain is fronted by straight sandy beaches. Wave energy is high and shelf sediment transport is very active. Elongated coastal lagoons are formed behind long sandy barriers.

Rainfall increases southward, from 1,090 mm yr^{-1} at Rio de Janeiro to 1,400 mm yr^{-1} at Torres. Where the Serra do Mar is very close to the coast, higher rainfall may occur. Potential evapotranspiration is about 1,000 mm yr^{-1}. There is a water surplus throughout the segment. Tidal ranges are < 1 m and as low as 0.24 m at Laguna (28°30′S). Spring tides vary from a maximum of 1.8 m to a low of 0.37 m.

One of the most studied mangrove segments of Brazil is illustrated in Figs. 11 through Fig. 14 (Figs. 11–14). In Baía de Guanabara (Fig. 11), fringes are dominated by *Rhizophora*, or in sheltered sites by *Spartina* and *Laguncularia*. Dias-Brito et al. (1982) described the mangrove associations of Guaratiba. Here, behind a sandy barrier island, *Spartina* colonized recently deposited sediments, forming marshes that are almost totally flooded at high tide. *Rhizophora* generally colonized organic mucks and fine silts, whereas *Avicennia* was found on higher ground and formed the most extensive

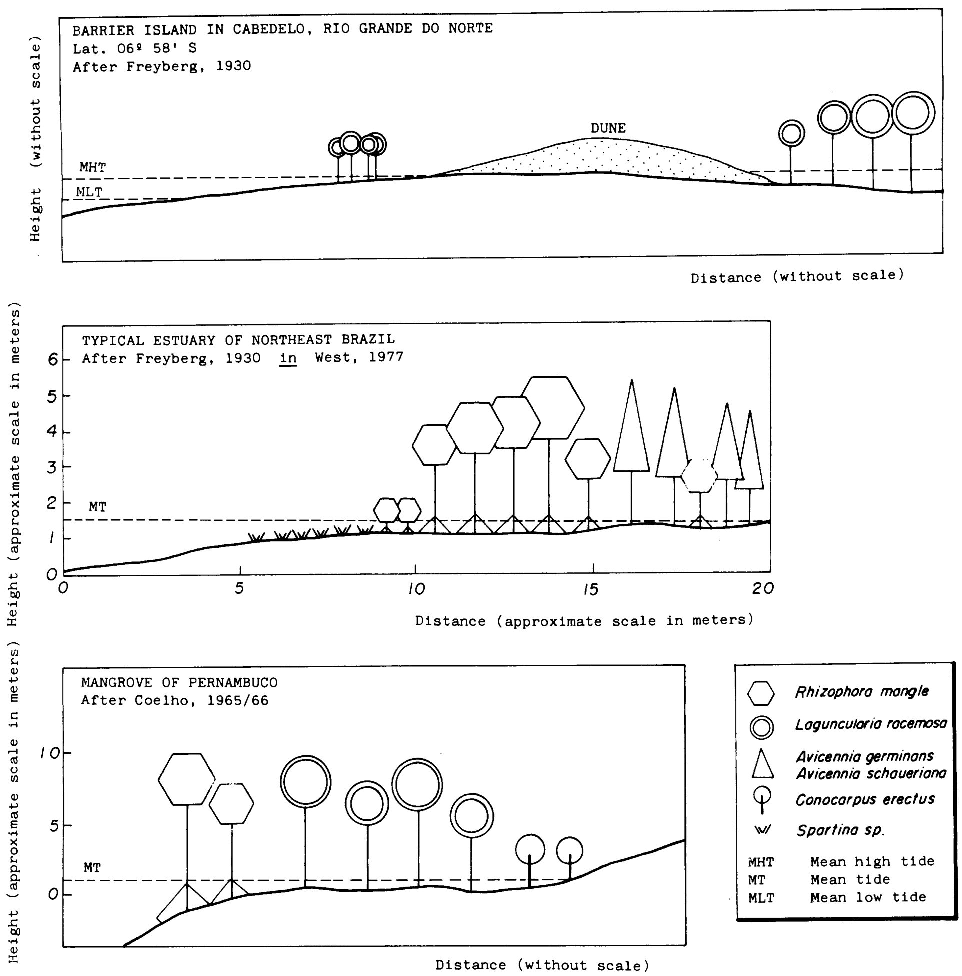


Fig. 8. Vegetation profiles, segment V. *Laguncularia* is commonly found in sandy barrier island environments. In the estuaries a mature *Rhizophora* fringe is backed by *Laguncularia* stands. Mud banks with flat slopes may be colonized by *Spartina* (from Freyberg 1930, West 1977, Coelho 1965/66).

forests. Erosion of the *Rhizophora* fringe may leave *Avicennia* stands bordering tidal channels. Further inland, these stands thin out and the canopy height decreases to less than 4 m (*Avicennia* may reach 15 to 20 m heights in this region). Here *Salicornia* occurs, among the scattered *Avicennia* trees. Beyond is a barren area, reached only by the highest tides, where salt crusts may be observed on the dry sediment surface.

The next large mangrove area occurs to the south near Santos (Fig. 12). Mangrove forests line the banks of Canal da Bertioga and extend inland several hundred meters. The fringe is either *Rhizophora* or *Avicennia*; *Avicennia* apparently appears at the edge only when the *Rhizophora* fringe is lost to erosion. The inner parts of the fringe contain *Avicennia* and *Laguncularia* as well as *Rhizophora*. Further inland, this mixed forest grades into a more deeply flooded area dominated by well-developed *Rhizophora*. Stand height ranges up to 12 m. At Itanhaém, further south, mangroves are found along the lower part of the river. The outer fringe is dominated by *Rhizophora*, followed by *Avicennia* and then *Laguncularia*. The transition to higher ground is characterized by *Hibiscus*, *Crinum*, and *Acrostichum* (Lamberti 1969).

In the Iguape-Cananéia region, accreting areas usually contain *Spartina* and *Laguncularia*, whereas *Rhizophora* occurs in the more mature sites. Basins are characterized by mixed forests of *Avicennia* and *Laguncularia*. At Cananéia, red mangrove fringes are backed by basins dominated by *Laguncularia* (Fig. 13). Fringes reach 10 m height, but a strong structural gradient is reflected in basin stands barely 2.5 m tall. This gradient may not appear in frequently overwashed sites, such as Ilha de Pai Matos. Paranaguá (25°30'S) can be considered part of the Cananéia system (Fig. 14). From this point south a decline in the structural development of red mangroves occurs. At Joinville (26°17'S), *Avicennia* dom-

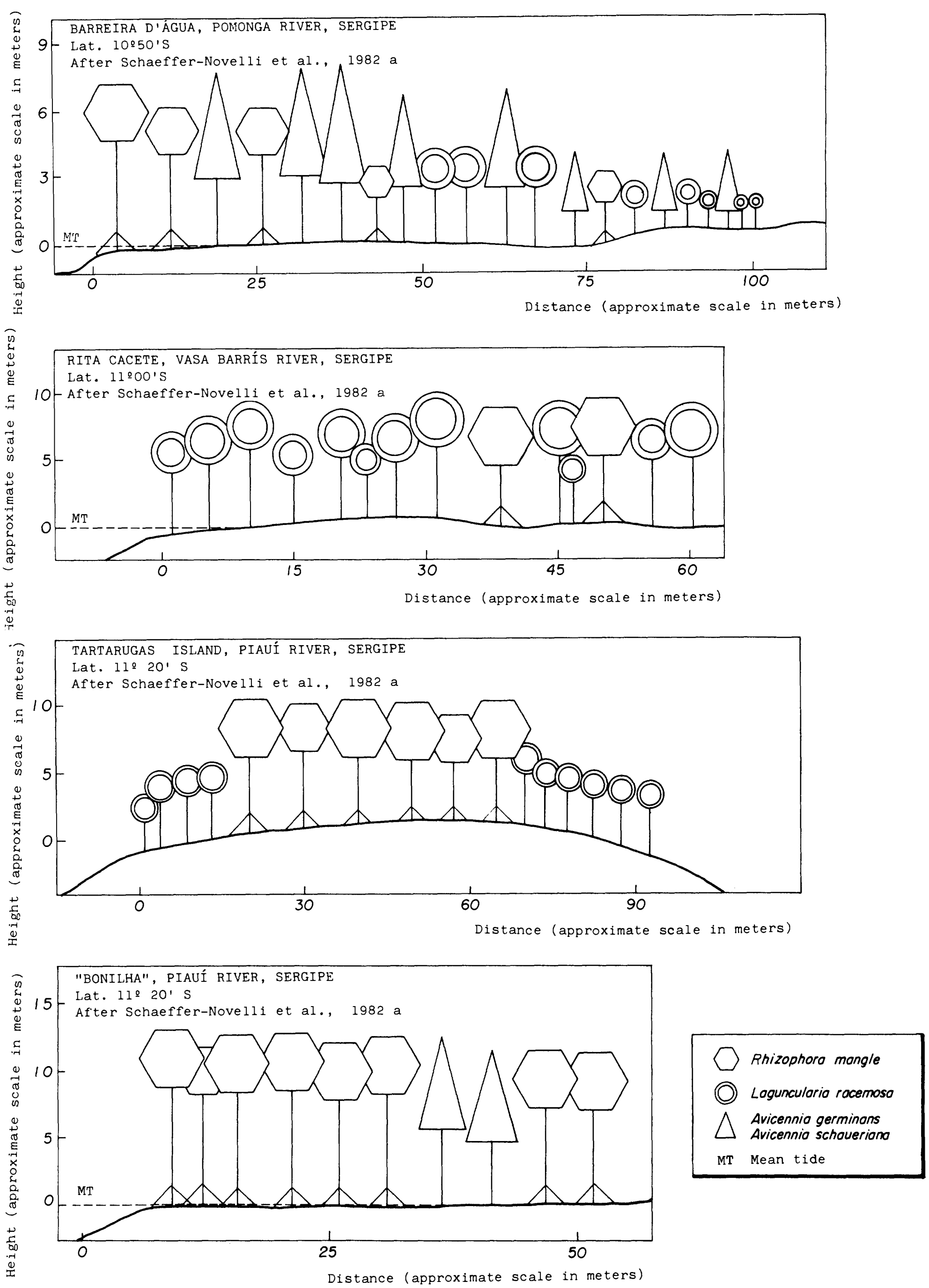


Fig. 9. Vegetation profiles, segment V. The top profile is from a site in the lower estuary with a sandy and firm substrate. Mixed stands are fronted by *Rhizophora*. In the Vasa Barris River, well-developed stands of *Laguncularia* are found in less saline environments near the head of the estuary. Riverine islands (Piaui River) may be surrounded by young *Laguncularia*, growing over soft mud banks. In this river, *Rhizophora* stands are found upriver as well (from Schaeffer-Novelli 1982a).

inates the fringes and *Laguncularia* the basins. Basins are shorter than fringes. At Rio Ratones (27°30′S), *Avicennia* trees are tallest (5–12 m). *Rhizophora* reaches its southern latitudinal limit not far from this site at Praia do Sonho (27°53′S). It grows there as a stunted bush 1.5 m tall or less.

The south latitudinal limit for *Avicennia* and *Laguncularia* is at Rio Ponta Grossa, 28°30′S. *Laguncularia* generally occurs as a low shrub less than 2 m tall, whereas *Avicennia* still reaches 9 m tall and 33 cm diameter at breast height, forming open stands within the low scrub of *Laguncularia*, *Hibis-*

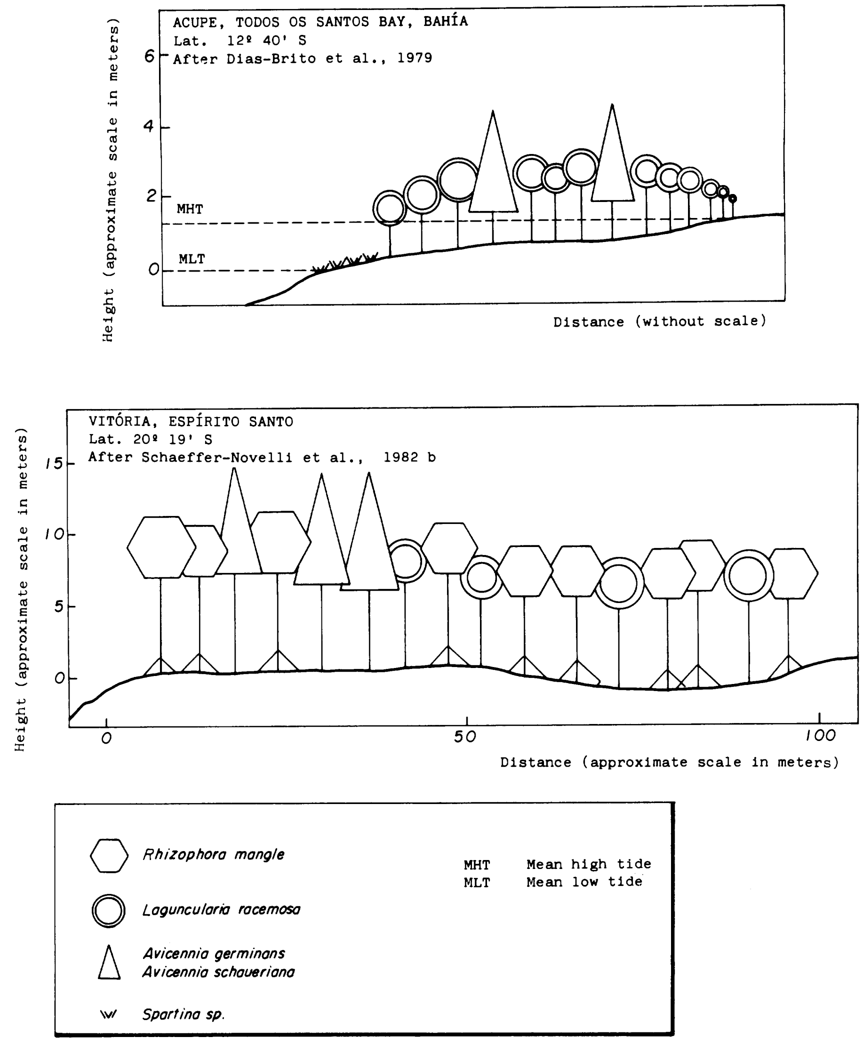


Fig. 10. Vegetation profiles, segment VI. At Todos os Santos Bay accreting margins are colonized by *Spartina*. *Laguncularia* is the most abundant species on soft, reduced substrates; *Avicennia* is more common on firmer, sandier substrates. In Vitoria and Faninetti, deeply flooded margins are colonized by *Rhizophora*. Broad salt flats may be found behind the mangrove fringe (from Dias-Brito and Zaninetti 1979, Schaeffer-Novelli 1982b).

cus, and *Acrostichum*. Fringe areas on the rivers and lagoons are colonized by an association of *Paspalum* and *Spartina*, *Scirpus maritimus*, and *Juncus*.

Segment VIII: Torres (29°20′S) to Chui (33°35′S)

This coastal segment is composed exclusively of exposed, straight beaches and low dune systems fronting a wide, sandy quaternary coastal plain. A series of long, shallow coastal lagoons are found behind these beaches. Lagoa dos Patos, the most notable, covers an area of 11,000 km^2.

A significant climate change occurs in this segment. The mean annual temperature is < 20°C; mean annual temperature amplitude is > 10°C. These conditions are unfavorable for mangrove development in spite of extensive landforms suitable for their establishment. Salt tolerant grasses and sedges are the dominant wetland vegetation. Rainfall (1,500 mm yr^{-1}) is greater than evapotranspiration (1,000 mm yr^{-1}). The mean tidal amplitude is 0.22 m; spring tidal amplitude is 0.24 m.

Discussion and Conclusion

The variation in mangrove forest types and the dominance of each type in a given environment are related primarily to characteristics of the landforms colonized by the trees. This concept is shown graphically in Fig. 15. The particular mix of fluvial, tidal, and wave energies acting in a region creates a landscape whose geomorphology is a function of the energy signature of that region. The size, type, and frequency of occurrence of these different geomorphic structures will vary from site to site. These

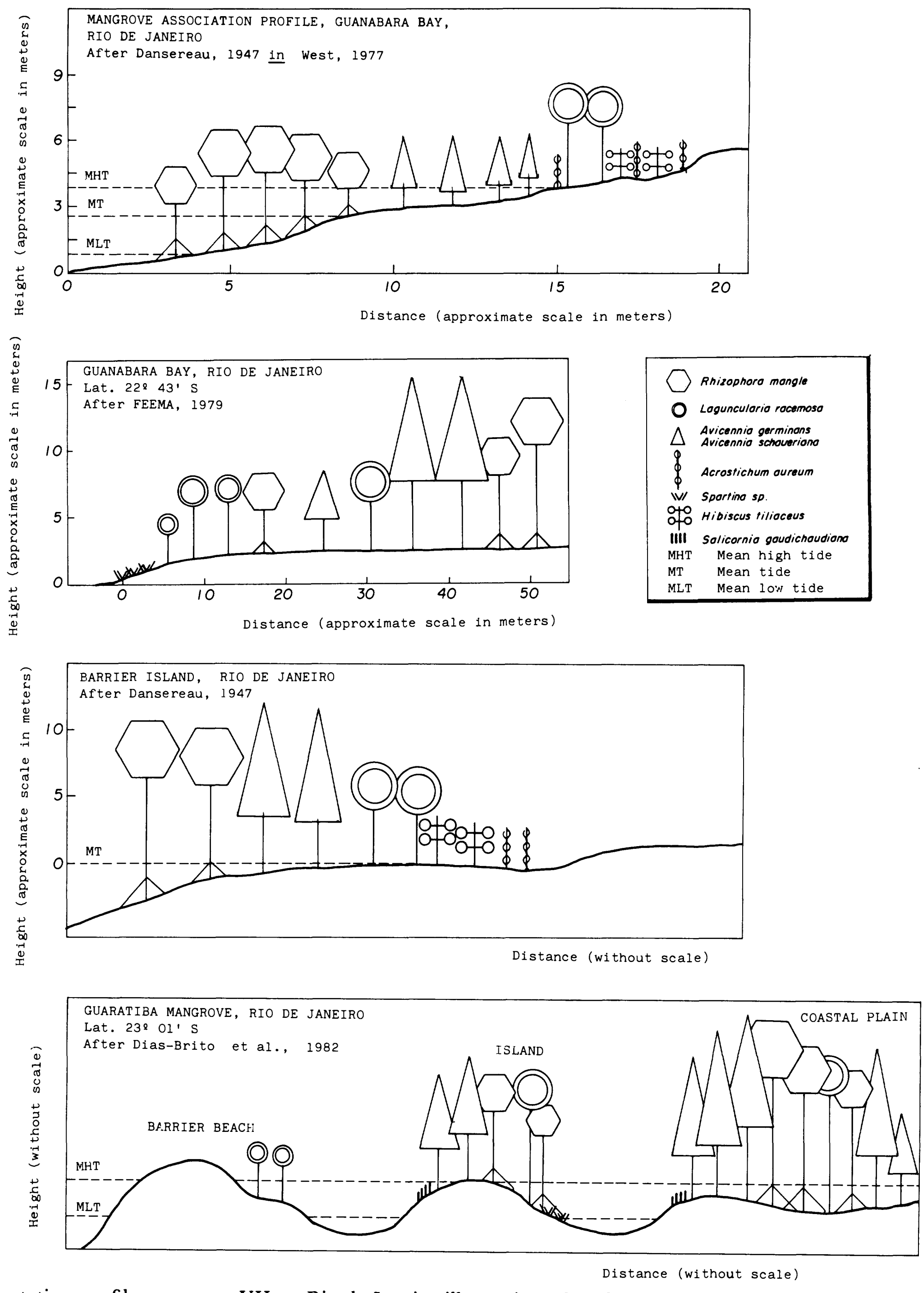


Fig. 11. Vegetation profiles, segment VII, at Rio de Janeiro illustrating *Rhizophora* as the dominant species in the fringes along with *Spartina* and *Laguncularia* in sheltered sites. The bottom profile shows mangrove stands with *Avicennia* forming fringes along tidal channels (from Dansereau 1947, West 1977, FEEMA 1979, Dias-Brito et al. 1982).

structures are the sites on which mangrove stands develop. They are colonized by different species in a pattern that depends on each individual species' adaptation to growth at different tidal or flood water elevations, and to edaphic differences such as particle size, redox potential, etc. Throughout the American tropics, slight topographic differences can cause major floristic and structural differences in mangrove forests (Thom 1967, 1975).

Climate can modify the area colonized by mangroves. In dry environments, less well flushed areas (back-basins and back-fringes) accumulate salt

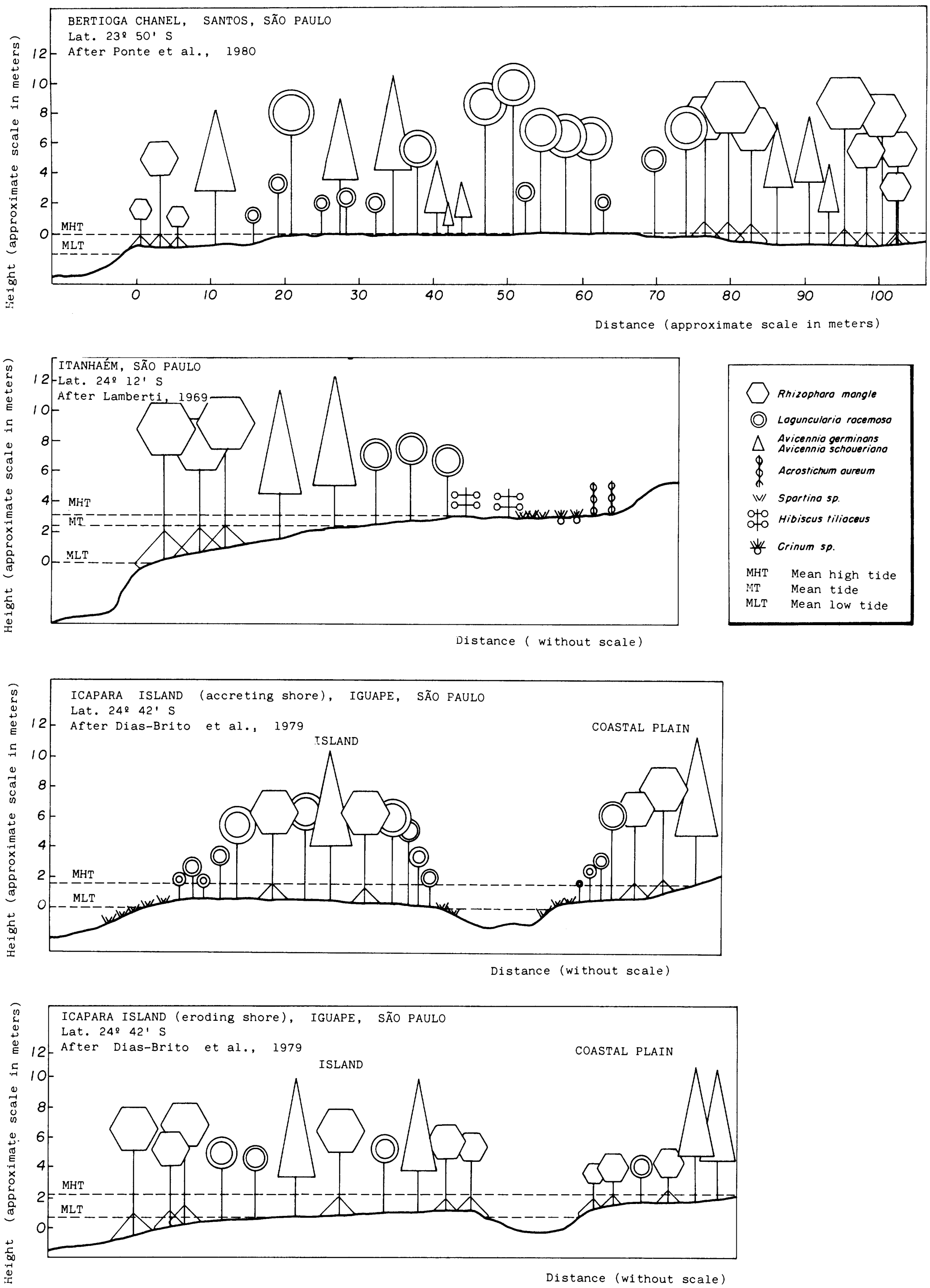


Fig. 12. Vegetation profiles, segment VII, showing forest lining the banks along channels and rivers. The inner parts are mixed stands with *Avicennia, Laguncularia,* and *Rhizophora* trees (from Ponte et al. 1980 unpublished report, Lamberti 1969, Dias-Brito and Zaninetti 1979).

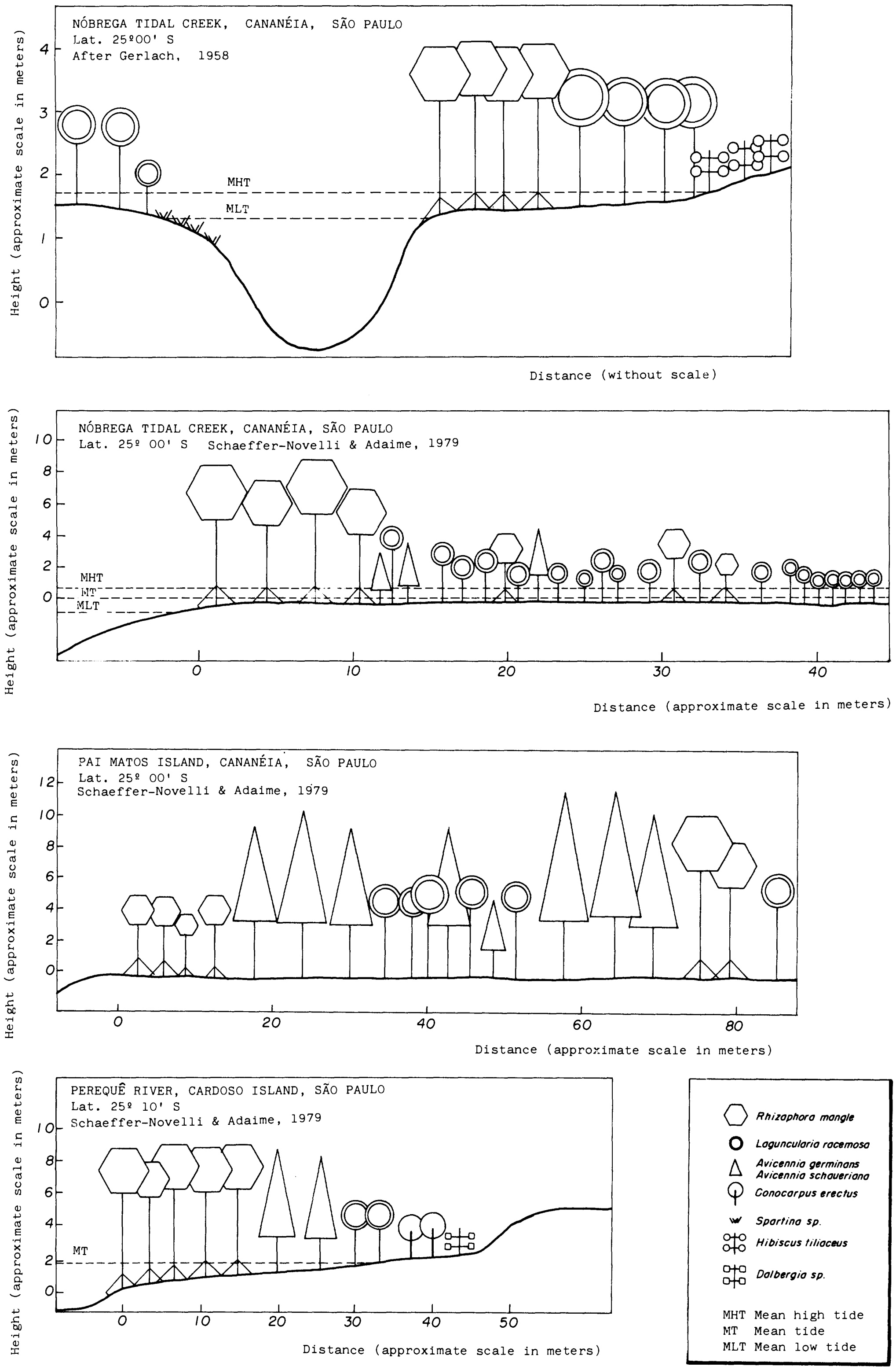
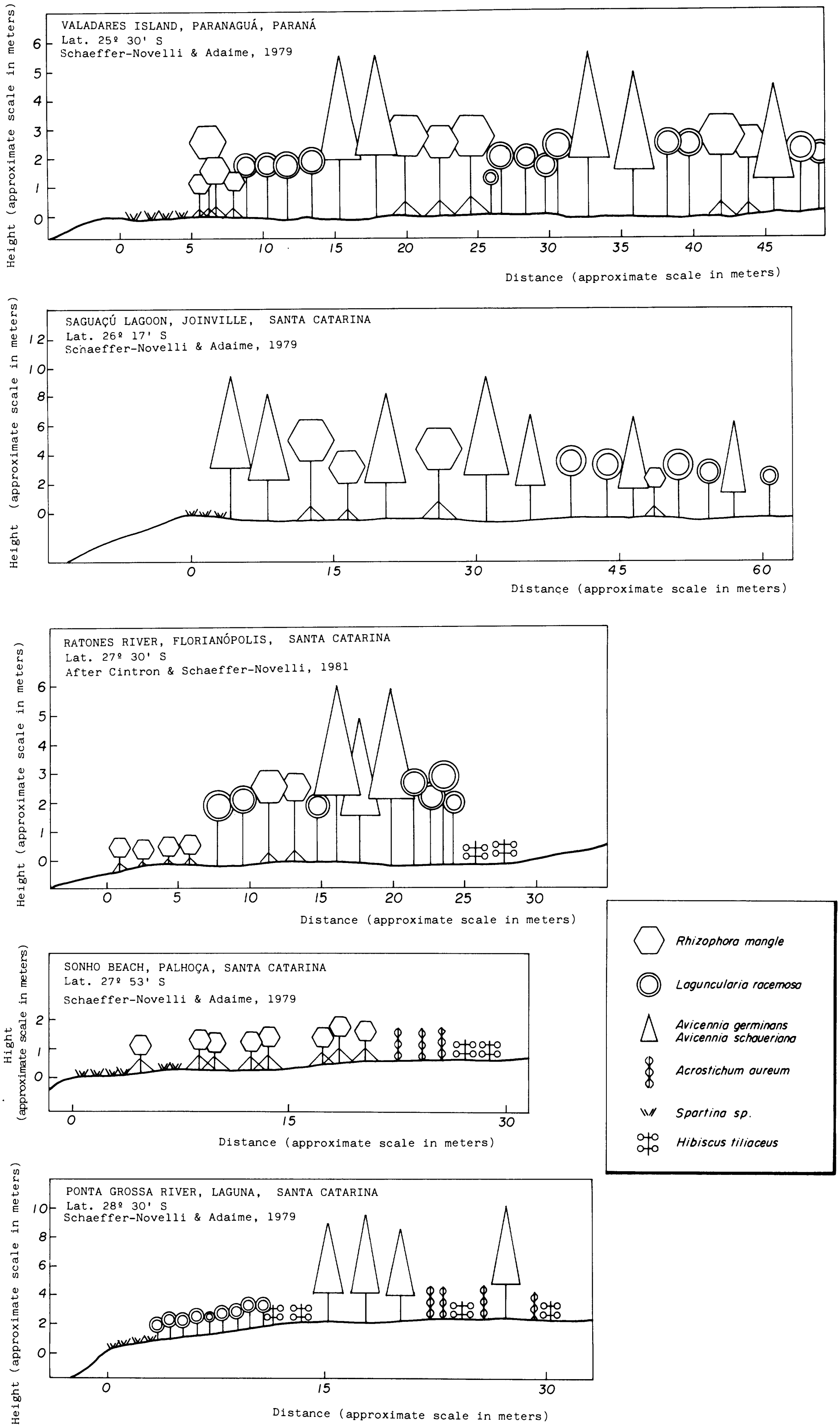


Fig. 13. Vegetation profiles, segment VII, illustrating red mangrove fringes backed by basins dominated by *Laguncularia*, with strong structural gradients in the vegetation. The low, frost-prone basins of *Laguncularia* are fronted by a taller *Rhizophora* fringe. Basins are better developed in overwash environments covered mostly by trees as at Pai Matos Island (from Gerlach 1958, Schaeffer-Novelli and Adaime 1979).


VALADARES ISLAND, PARANAGUÁ, PARANÁ
Lat. 25º 30' S
Schaeffer-Novelli & Adaime, 1979
Height (approximate scale in meters)
0
1
2
3
4
5
6
0
5
10
15
20
25
30
35
40
45
Distance (approximate scale in meters)
SAGUAÇÚ LAGOON, JOINVILLE, SANTA CATARINA
Lat. 26º 17' S
Schaeffer-Novelli & Adaime, 1979
Height (approximate scale in meters)
0
2
4
6
8
10
12
0
15
30
45
60
Distance (approximate scale in meters)
RATONES RIVER, FLORIANÓPOLIS, SANTA CATARINA
Lat. 27º 30' S
After Cintron & Schaeffer-Novelli, 1981
Height (approximate scale in meters)
0
1
2
3
4
5
6
0
5
10
15
20
25
30
Distance (approximate scale in meters)
SONHO BEACH, PALHOÇA, SANTA CATARINA
Lat. 27º 53' S
Schaeffer-Novelli & Adaime, 1979
Hight (approximate scale in meters)
0
1
2
0
15
30
Distance (approximate scale in meters)
PONTA GROSSA RIVER, LAGUNA, SANTA CATARINA
Lat. 28º 30' S
Schaeffer-Novelli & Adaime, 1979
Height (approximate scale in meters)
0
2
4
6
8
10
0
15
30
Distance (approximate scale in meters)
Rhizophora mangle
Laguncularia racemosa
Avicennia germinans
Avicennia schaueriana
Acrostichum aureum
Spartina sp.
Hibiscus tiliaceus

through evaporation beyond mangrove tolerance, and bare mud flats are a significant element of the landscape. In areas with sporadic frost, growth in regions farthest away from large water bodies may be limited by the much lower temperatures and more frequent frost. Thus, in very dry or cold environments, basins do not develop extensively and may contain only stunted trees. The dominant processes in each of these environments are different. Mangrove forests adapt to the type, intensity, and periodicity of natural processes.

Chapman (1976) and West (1977) reported the southern latitudinal limit for Western Hemisphere mangroves at Araranguá, Brazil (29°S), probably using Bigarella (1946) as a source. We believe that these "mangroves" may have been thickets of *Hibiscus* and/or *Acrostichum,* both of which grow considerably farther south than red, black, or white mangrove.

On the northern side of the neotropics (29°18'N), *Avicennia* grows as a scattered scrub tree (<1 m) in *Spartina* marshes at its most northerly occurrence near Galveston Island, Texas (Sherrod and McMillan 1981). This location has a mean annual temperature of 21°C; the mean for the coldest month is 12°C and the mean temperature range is 16.3°C (National Oceanic and Atmospheric Administration 1983). South of Galveston, near Harbor Island (~ 27°50'N), *Avicennia* forms thickets 1 to 2 m tall. Here, the lowest monthly mean temperature is 14°C (Markley et al. 1982). Although in Brazil *Avicennia* apparently does not reach latitudinal limits as extreme as in Texas, much larger trees are found at its southern limit. At both northern and southern extremes the stands or thickets occur close to the edge of water bodies. In the case of *Laguncularia* in Brazil and of *Avicennia* in Galveston, the species reach their latitudinal limits as isolated or scattered shrubs in the *Spartina* marsh.

The degree of structural development of mangrove stands depends on site factors that determine the growth rate of individual trees. At maturity, stands of similar floristic composition may differ in height and/or tree density depending on how fast they have been able to grow. Since many events of landscape change occur in pulses (deposition or erosion of islands or banks, for example), most mangrove stands tend to be even-aged. In optimal environments, stands of tall, large diameter trees with wide spacing can develop. In more stressed environments, or where maturity cannot be reached due to episodic destructions, the stands are characterized by small diameter trees, with small space requirements and high densities.

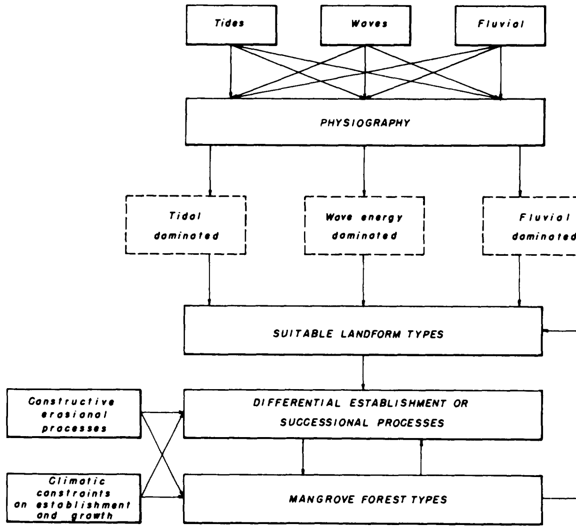


Fig. 15. Conceptual model of the variability in mangrove forest types. Plants establish over a template of landforms typical of the energies acting on the landscape. The configuration of the landforms largely determines species and spatial patterns. Climate limits the ultimate degree of structural development at maturity.

We suggest that most Brazilian mangroves play only a minor role in modifying the geomorphic setting, and that the spatial arrangement of the various forest types is a response to features of the underlying topographic and edaphic conditions and the constraints imposed by climatic and hydrologic factors. The spatial arrangement of species thus is not necessarily a result of successional processes (Davis 1940) but reflects direct and differential colonization of appropriate substrates.

An understanding of the variability of the Brazilian forest types awaits a more complete study of geomorphic processes and of how these create suitable substrates. We also need to study mangrove species' edaphic preferences and ecophysiology, fields cited by Snedaker (1982) as most likely to lead to further breakthroughs in mangrove distribution studies.

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Fig. 14. Vegetation profiles, segment VII, illustrating a decline in the structural development of red mangroves and a dominance of *Avicennia* at the fringes at some sites. At Sonho Beach, *Rhizophora* reaches its latitudinal limit as low, scrubby and scattered trees. However, *Avicennia* develops into 8-m tall trees at its limit (from Schaeffer-Novelli and Adaime unpublished, Cintron and Schaeffer-Novelli 1981).

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