Mangrove Ecosystems of Latin America and the Caribbean: a Summary

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1. Mangroves and Man in Pre-Columbian and Colonial America

In various countries of the American continent, there is strong archeological evidence of mangrove utilization by Pre-Columbian and even Pre-historical human groups. Pre-Columbian inhabitants traditionally used mangroves for many purposes, including wood and energy production. The use of mangroves varied from site to site, depending on the particular characteristics of the population who started mangrove utilization during the transition period from nomad to fixed habits, between 9,000 to 3,000 years BP; however, several common features are evident (Alvarez-León, 1993).

In tropical coastal areas, the expansion of mangrove forests probably triggered, 6,000 years ago, important social changes among itinerant human groups, especially inducing an initial settling process of gatherer, fisher, and hunter communities. In Venezuela 6,000 or 5,000 years ago, human populations possibly coming from the inner lands of Venezuela, occupied the mouths of the rivers that descend from the Paria Sierra, and other coastal areas, many of them covered by mangroves (Sanoja, 1992), in a process similar to the one hypothesized by Widmer (1988) for the South coast of Florida, USA. Mangroves, as a resource, including wood, resins, fibers and dyes, and also proteins of animal origin, provided a spectrum of resources for diverse types of extraction and encouraged some incipient forms of cultivation of native edible plants. Extraction of mangrove oysters by the indigenous populations of the coastal areas could have induced a kind of seminomad exploitation, which can be compared to the use of soil by slash-and-burn farmers (Veloz Maggiolo & Pantel, 1976, cited in Sanoja, 1992).

The nomadic human groups frequently formed semi-permanent settlements along the coast, close to lagoons and bays, where an abundant and easy to collect protein-rich diet was provided by molluscs (Reichel-Dolmatoff, 1965). In these areas, they left large amounts of shells and organic and "cultural" debris, called "conchales" or "concheros" in Spanish speaking countries and "sambaquis" in Brazil. These remains provide important information on the characteristics of these populations including food habits and utilization of natural resources (Perdomo-Rojas, 1978; Prahl et al., 1990).

Castaño-Uribe (1989) suggests that in Colombia the process of colonization by the human population was a continuous chronological sequence, with great implications for the cultural development of the entire continent. An example of this was the finding in mangroves and adjacent areas along the Atlantic coast of Colombia, of the most ancient ceramics of the American continent (c.a. 2,400 years BP) a discovery of pivotal cultural importance (Reichel-Dolmatoff, 1985). Along the extensive mangrove fringes of the Pacific and the Caribbean coasts of northern South America, the development of human groups resulted in distinct patterns of cultural adaptation which can still be recognized today. Their technology was continuously being changed and optimized for the exploitation of these resource-rich, non-seasonal wetlands, to provide the necessary infrastructure for the establishment of large human groups, whose economy was based on the collection of molluscs and on fisheries. The experience

diversified and expanded through the continent (Castaño-Uribe, 1989).

In Panamá there is evidence of human settlements in mangrove areas about 5,000 years BP; these people made tools out of mangrove wood (D'Croz, 1993). The importance of fishing of euryhaline species from mangrove-bordered estuaries and channels for pre-Columbian human settlements located in the central coast of Panamá at that time has also been noted (Cook & Ranere, 1992). Utilizing fences, harpoons, fishhooks and other primitive tools, many of them made of mangrove wood, people from these settlements caught estuarine and coastal species belonging to the Carangidae, Batrachoididae, Ariidae, and Clupeidae.

In Brazil the pre-Columbian record extends from 3,500 to 2,000 years BP, when deposits of shells and fish bones from mangrove species were accumulated in mounds by nomad populations of fisherman and collectors (Beltrão, 1976).

In Peru, the Tumpis Culture, which settled in the Tumbes region, had an important role in Pre-Columbian America. They formed a large coastal population dedicated to agriculture, fishing and commerce, and are considered the best navigators of the Peruvian coast. They developed to a high degree the art of carving several mangrove bivalves, including *Spondius* sp., *Ostraea* sp., and *Anadara grandis*. To the *Spondius* shell, known to the Andean people as "Mullu", they attributed magical powers and after carving zoomorph or phytomorph figures they were offered during certain religious rituals (Echevarría & Sarabia, 1993).

The migration of human populations to the coastal areas is also testified, in Venezuela, by the presence of archaeological preceramic places of shellfish pickers and fishers in the Tucacas area, Falcón State, where nowadays there is a large extension of mangroves (Cruxent and Rouse, 1958). In the southern Pacific coast of Costa Rica huge "concheros", testify to the early settlements of indigenous communities. The indians of Puerto Rico (probably the Arawaks) occasionally ingested the red mangrove seedlings; this is a custom actually observed among the fishermen, who sustain that it helps them to quench their thirst during their prolonged fishing journeys (Carrera, 1975). In the Los Roques Archipelago, 100 km north of the Venezuelan coast, indians used mangroves intensively. As a consequence of this exploitation, some of these mangroves

disappeared almost totally on some of the islands of the archipelago (Antczak & Antczak, 1987). Almost five centuries later, mangrove products still occupy a very important rank in the Venezuelan indian economy. In the Delta Amacuro State, indian populations use mangrove wood in the construction of poles and pilings for houses and jetties (Flores, 1977).

Archeological evidences suggest that mangroves were used intensively by the Arawak indians in Puerto Rico (Carrera, 1975). Many of the "concheros" are found in the coastal zone of this island (Carrera, 1975). Among the molluscs consumed by the indians are two mangrove species commonly found on the red mangrove: *Crassostrea rhizophorae* and *Isognomon alatus* (Carrera, 1975).

In Latin America, mangroves were the subject of curiosity since the discovery. Spanish colonizers were much attracted by mangroves, as can be inferred from the words of the historian Gonzalo Fernandez de Oviedo y Valdés, who wrote that the mangrove is " ... a tree of the best that in these places exists, and it is common in these islands ... rare and admirable trees to sight, because of its forms it is not known another being similar". This author is allegedly the first to mention, at the beginning of the XVI century, American mangroves (Rodríguez, 1984; Schaeffer-Novelli & Cintrón, 1990.). He added an inventory of mangrove uses. In 1595, Sir Walter Raleigh, in relation to some trees surrounding the channels at the mouth of the Orinoco Delta, mentions that these trees are capable of living in salty water. Tejera (1977) has catalogued other historical references on mangroves in the Americanist literature.

During the colonization, the indian opposition lead to the virtual extinction of native populations along the coasts of the entire continent. By the time of the European conquest, mangroves represented such a nuisance to troops and horses that Cristobal de Molina, for example, described the mangroves in 1552 in Peru as the "most difficult land of these kingdoms". However, this did not hamper the discovery of the quality of mangrove timber for construction, and the exploitation was immediately started, mostly for poles and boat construction, and later for tannin. From the 16th century on mangrove timber was exported from Colombia to Peru and reached an amount of 6,000 poles a year in the 17th century. In 1677 for instance, thousands of mangrove poles were exported to Cuba from the Pacific coast Colombia (Prahl *et al.*, *1990*) Commerce of bark was also very

intense. Ecuador for example exported to neighboring countries nearly 600 tons of bark per year from 1879 to 1906 (Bodero, 1993).

During the colonial period the commerce of mangrove products was so important that the colonial authorities produced specific legislation to protect and manage the use of this resource. In 1760, the King of Portugal and Brazil, D. José issued one of the first, if not the very first, law to protect and adequately manage mangrove resources in Brazil. The law included specific penalties to be applied to people who cut the trees that had not been previously debarked. This is an example of environmentally sound lobbing by leather merchants who wanted to guarantee abundant high quality material for their tanneries, an important product of which was parchment for manuscripts, books and diplomas. In fact, as early as the XVII century, the Portuguese made methodical studies of the properties of the tannin from the bark of different species of *Rhizophora, Avicennia, Sonneratia* and *Xylocarpus* from many places in South India, Molucca, and Sri Lanka. These studies enabled them to select the best sources of raw materials for their tanneries, usually located in Portugal. The interest in the Brazilian mangroves grows only after the Portuguese supremacy in Asia was on a downward trend; the bark of the tree species of the mangroves bordering the Atlantic Ocean had been recognized as producing tannin of a lesser quality.

The Edict of the King of Portugal also indicates concern with sustainability of production, hence the banning of the practice of "ringing" the trunks to extract the bark. The Edict also reflects the accurate observation concerning the growth and regeneration pattern of mangroves South of Cabo de São Roque, since the species of that coastal area grow slowly and do not reach the height and importance of the species of the Northern Atlantic coast of South America or of the Indian Ocean and Southeast Asia. Other examples of sound management legislation occurred in other parts of the Colonial Americas.

The exploitation of mangroves in Puerto Rico was so intense, that in 1839 a Royal Edict set up a "Junta" with the duty to protect, among others, *Rhizophora mangle* and *Conocarpus erectus*; their wood could not be used in the naval industry (Carrera 1975).

During the second half of the XIX Century, the Curazao's people exploited the mangroves especially *Rhizophora mangle* of the Roques Archipelago, off the

coast of Venezuela, using it as firewood for the furnaces of steamships; as a residual product, tannins were extracted from the crust (Amend, 1992).

Resources derived from mangroves have been utilized from pre-colombian times to the present. Presently, some forest products from mangroves are widely utilized in rural constructions, also as sticks in horticultural crops and they are still used for the extraction of tannin. However, only recently they have been considered as an ecosystem. This change in attitude in evaluating mangroves has been in many cases due to the negative experiences in attempting to manage single resources in isolatiton.

2. Extent and Distribution of Mangrove forests in Latin America and the Caribbean

In Latin America and the Caribbean, mangroves occur in all maritime countries except the three Southernmost nations Chile, Argentina and Uruguay. Only recently, however, efforts have been developed to survey the mangrove cover in these countries. Table 1 shows the most recent, and probably reliable, available estimates of mangrove area in Latin American and the Caribbean.

The major comprehensive estimate of mangrove areas in this region was published by Saenger *et al.* (1983), based on available information given by forest and environmental authorities and from scientific reports from the countries. This estimate shows that the total mangrove area is approximately 6.7 million ha, with 70% (4.8 million ha) occurring along the Atlantic Ocean and the Caribbean and only 30% (1.9 million ha) distributed along the Pacific coast. The largest forests are located in Brazil, Mexico, Cuba and Colombia.

Although this estimate has been widely accepted as representative, recent surveys suggest that it is an overestimate. The data presented in Table 1, include figures from Saenger *et al.* (1983), for countries where no other information is available. According to recent estimates, mangrove cover in Latin America and the Caribbean is approximately 4.1 million ha, which is only about 60% of the total given in Saenger *et al.* (1983). For example, in Brazil, during the late 80's, a complete survey by satellite imagery and aerial photography of all coastal states, showed that mangrove cover is approximately 1.01 million ha with nearly 85% of the total forests in the northern

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coast of the country (Hertz, 1991). Considering that this is possibly underestimated by 20% to 30% (Kjerfve and Lacerda, 1993), the final figure is less than half of the 2.5 million ha proposed by Saenger *et al.* (1983).

In Venezuela mangroves occur along nearly 35% of the coastline. Saenger *et al.* (1983) estimated that mangrove cover reaches 673,600 ha, while the most recent figure is only 250,000 ha (MARNR, 1986), which is only 37% of the previous estimate. For several countries however, the estimates by Saenger *et al.* (1983) are in accordance with the most recent ones and in some cases even lower.

In Ecuador, a detailed study by remote sensing techniques covering the evolution of mangrove areas during the last two decades (CLIRSEN, 1984; MAG, 1991), showed the mangrove cover to be 161,770 ha, with nearly 70% of total mangrove area (110.000 ha) located in Guayas Province. This number is approximately the same of that proposed by Saenger *et al.* (1983) of 160,100 ha. For other countries like Cuba, where mangrove forests cover approximately 4.8% of the country's surface, a recent estimate from the Ministry of Agriculture gives a total mangrove area of 529,700, which is nearly 25% larger than the estimate proposed by Saenger *et al.* (1983).

The relative importance of mangroves for each country is illustrated by comparing the ratio between total mangrove area and total surface area of each country and the ratio between mangrove surface and coastline length (Table 1). Among the continental countries the percentage of the total surface covered by mangroves ranges from 0.01% in Peru to 3.1% in Belize. Mangrove area/coastline length ratios ranges from 2 in Peru to 326 in Guyana. For insular countries the percentage of total mangrove area can be as high as 27.6% in the Cayman Islands and 10.2% in the Bahamas, to less than 0.01% in Bermuda, while mangrove/coastline ratios range from less than 1 for Bermuda to 142 in Cuba. This rough representation shows that mangroves are the most important forest formation in certain countries and they should have a priority place in management and conservation.

Notwithstanding differences, recent data confirm Saenger's *et al.* (1983) relative distribution of mangroves of Pacific and Atlantic coasts of Latin America and Caribbean. The Pacific coast with approximately 1.16 million ha, has 28.5% of the total mangrove cover, while the Atlantic coast has approximately 2.14 million ha (52.8% of the total) and

the Caribbean insular countries approximately 0.76 million ha or 18.7% of the total (Table 2).

Recent estimates of world mangrove cover vary and range from 15 to 30 million ha, with an average of 21.8 million ha (Saenger *et al.*, 1983; Lugo *et al.*, 1990; Twilley *et al.*, 1992) . Latin American and Caribbean mangroves represent approximately 18% of this total. However, considering the figures on Table 2 we conclude that they represent approximately 28.6% of the World total mangrove cover; African mangroves cover about the same area whereas mangrove cover in the Indo-Pacific region, represents nearly half of the world's mangroves.

Nearly all countries of the region are now mapping their mangroves to estimate area and density distribution. There is growing concern with the importance of these forests and with their health and survival in the coastal region. In several countries, mangroves are being cut and replaced by other biological or engineered structures, such as large scale mariculture in Ecuador, tourism in southeastern Brazil and harbor and industrial complexes almost everywhere. On the other hand, replanting and recuperation programs are being carried out in degraded mangrove areas such as those presently occurring in Cuba and Brazil. Therefore, although thé data given Table 1 are, to our knowledge, the most recent, they are not final, and will certainly be changing in the near future.

3. Biogeographical Considerations

The New World mangrove flora is believed to have evolved later than the more diversified mangrove flora of the Indo-Pacific. The genera *Rhizophora* and *Avicennia* are believed to have evolved earlier and therefore they were able to spread through the Tethys Sea into what is presently the Mediterranean and thence to the East coast of the Americas and the West coast of Africa. They may have reached the Caribbean by the early Eocene (some 55-50 million years BP), when the distance from the Tethys Sea was considerably smaller.

Mangrove pollen of *Rhizophora*, *Avicennia* and *Pelliciera* has been reported from the Gatuncillo Formation, Panamá, of the middle to late Eocene (c.a. 40Ma BP) (Graham, 1989). Around the same time extensive *Rhizophora* and *Avicennia* forests covered the North of the South America coast. However they disappeared from the palynological record of

Table 1. Recent estimates of mangrove cover and the respective percentage of total countries' area and length of the coastline in the Latin American Continent.

	Area (ha)	% country surface	mangrove area/coastline	Author
Continental countries				
USA	190,000	0.02	10	Odum *et al.* (1982)
Mexico	524,600	0.27	56	Yàñez-Arancibia *et al.* (1993)
Belize	73,000	3.10	189	Saenger *et al.* (1983)
Guatemala	16,040	0.15	40	Jimenez (1992)
Nicaragua	60,000	0.50	66	Saenger *et al.* (1983)
Honduras	121,340	1.08	148	Jimenez (1992)
Costa Rica	41,330	0.08	32	Jimenez (1992)
El Salvador	35,235	1.65	45	Jimenez (1992)
Panamá	171,000	2.22	69	D'Croz (1993)
Colombia	358,000	0.31	148	Alvarez-León (1993)
Ecuador	161,770	0.60	72	MAG (1991)
Peru	4,791	0.01	2	Echevarria & Sarabia (1993)
Venezuela	250,000	0.27	76	MARNR (1986)
Guiana Françesa	5,500	0.06	15	Saenger *et al.* (1983)
Guyana	150,000	0.70	326	Saenger *et al.* (1983)
Suriname	115,000	0.70	298	Saenger *et al.* (1983)
Brazil	1,012,376	0.12	134	Hertz (1991)
Insular countries				
Trinidad & Tobago	7,150	1.40	20	Bacon (1993)
Jamaica	10,624	1.02	7	Bacon (1993)
Cuba	529,700	4.80	142	Padron (1992)
Haiti	18,000	0.65	10	Saenger *et al.* (1983)
Republica Dominicana	9,000	0.20	7	Saenger *et al.* (1983)
Puerto Rico	6,500	0.71	-	Saenger *et al.* (1983)
Bahamas	141,957	10.18	40	Bacon (1993)
Bermuda	20	<0.01	<1	Ellison (1993)
Guadelope	8,000	4.49	20	Saenger *et al.* (1983)
Martinique	1,900	1.73	7	Saenger *et al.* (1983)
Cayman Islands	7,268	27.60	45	Bacon (1993)
Antilles*	24,571	----	-	Bacon (1993)

* Includes only the islands from where reliable mangrove surveys have been reported (Anguilla, Antigua, Aruba, Barbados, Barbuda, Bonaire, Curaçao, Dominica, Grenada & Grenadines, Montserrat, Nevis, St. Kitts, St. Lucia, St. Vincent, Turks & Caicos).

Table 2. Mangrove forest cover in the Atlantic and Pacific coasts of Latin America, including the Caribbean Islands, compared to World mangrove forest areas.

	Mangrove area (ha)	(% of the total)	Author
Atlantic Coast	2.143.356	(52.8)	This study
Pacific Coast	1.154.289	(28.5)	This study
Caribbean Islands	764.690	(18.7)	This study
Total	4.062.335	(100)(28.6)	This study
Africa	3.257.700	(22.9)	Diop (1993)
Southeast Asia	6.877.600	(48.5)	Saenger et al. (1983)
World total	14.197.635	(100)	This study

this area by the Paleocene (Wijmstra, 1969). Later palynological registers along the Americas show abundant mangroves (Graham, 1989; 1992), that confirm the early Eocene as the probable date of mangrove arrival to the New World.

By the time of the arrival of the first mangrove genera to the American continent, the Panamá isthmus was still open, allowing for the colonization of the western coast of the Americas. The closure of the Tethys Sea route and the lowering of the temperature of the South African coast by the Benguela Current would have prevented the migration of more recent mangrove genera. This hypothesis was supported by Chapman (1974) and others, and has been well accepted by most mangrove scientists.

Mepham (1983) argued against the hypothesis of the origin of mangrove flora in southeast Asia and their distribution by radiative dispersal from a single hypothetical source in this area. He proposed a broader Tethyan region as the place where angiosperms first acquired the mangrove habit, and where most contemporary mangrove genera originated. However, he also agrees that migration through Tethyan distribution routes by the early-middle Tertiary was probably the major route of colonization of North and South America, the Caribbean and the West coast of Africa by the early mangrove genera Rhizophora and Avicennia. This route is believed to be confirmed by the widespread pollen of Nypa in late Eocene deposits (ca. 40 million years BP) along the present Mediterranean coast, England, North America, West Africa and Northeastern Brazil (Dolianiti, 1955; Muller, 1961; Macnae, 1968). It is interesting to note that the distribution of fossils, which is widely used as an argument in favor of a single centre of dispersion, may also be interpreted as indicating that

mangroves arrived in this region from a Tethyan origin as proposed by Mepham (1983), rather than originating there. But the fossil evidence for Pleistocene mangroves is so scarce, that reconstructions of mangrove distributions are merely speculative (Woodroffe & Grindrod, 1991).

A contrasting view on the origins of New World mangroves is provided by Hou (1960); van Steenis (1962) and Muller and Caratini (1977). These authors proposed that at least for the Rhizophoraceae, the family originated in the Eocene in Southeast Asia together with inland relatives (e.g. Carallia and Anisophylla). This agrees with the most accepted views of mangrove origin. From southeast Asia, the Rhizophoraceae would have extended their distribution eastward, and not westward, through trans-Pacific land bridges to tropical South America, reaching the Caribbean before the rise of the Panamá Isthmus and therefore being able to cross to the Atlantic and colonize North and South America and West Africa. However several Pacific islands do not have mangroves, an unexpected situation if the migratory route to the New World had crossed this ocean. Woodroffe & Grindrod (1991) suggested that idiosyncrasies of mangrove distribution, nonetheless, could be understood in the light of sea-level and other environmental fluctuations during the Quaternary.

Fig. 1 shows different views on the origin of mangroves and the proposed routes to the New World, it gives major fossil sites and possible origin. The configuration of the continents is as far as possible that believed to have occurred at the end of the Cretaceous (100 to 70 million years BP) after Mepham (1983) and Degens (1990).
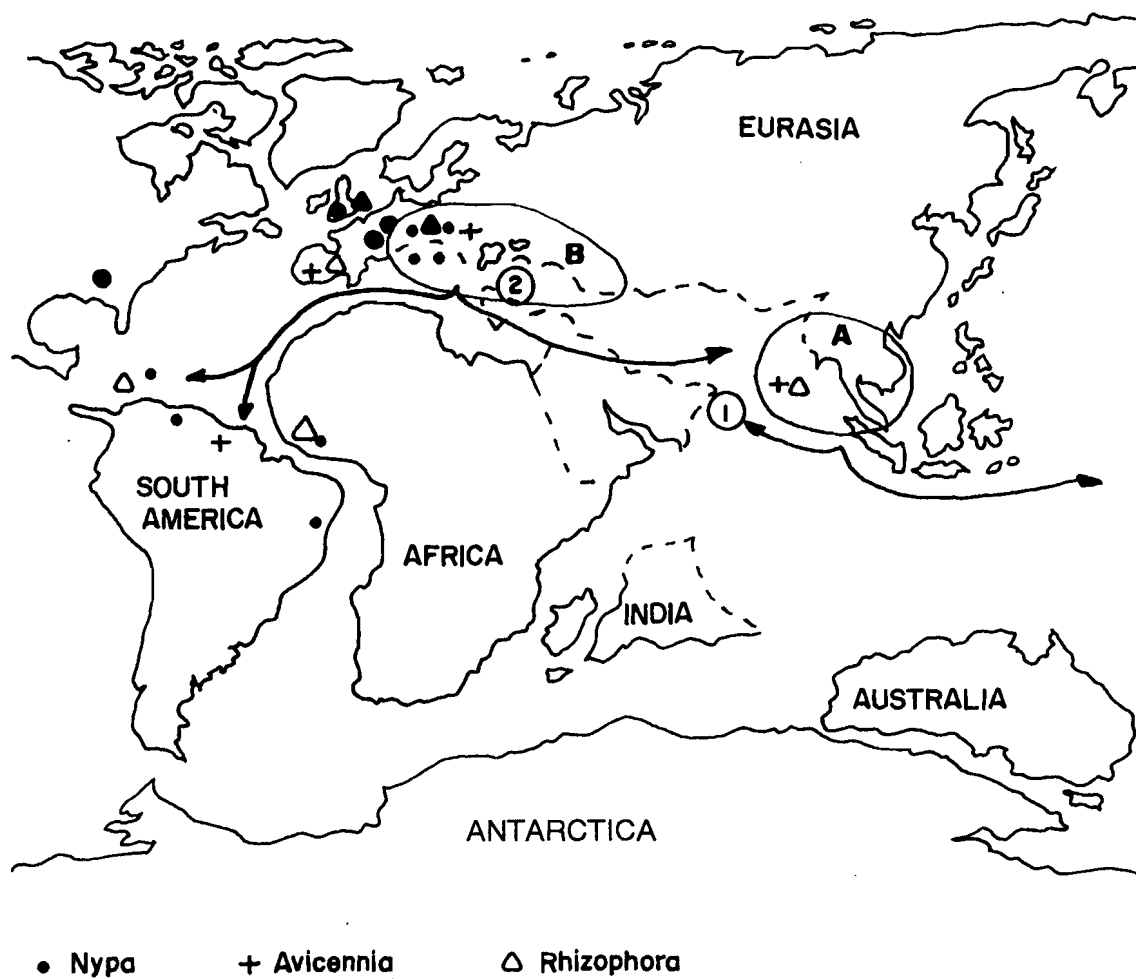
Fig. 1. Palynological record and proposed origin centers and migration routes of New World mangroves. A- Southeast Asia origin center. B- Thethian Sea origin center. 1- Migration through the Thethys Sea to the Atlantic and trans-Pacific migration. 2- Migration from the Thethys Sea to SE Asia and the Atlantic and through the Panamá Isthmus.

It seems quite clear that the view of Chapman (1975), on a migration route through the Tethyan Sea and then to the New World, is supported by the fossil record and is more readily acceptable than a trans-Pacific migration. However, different centres of dispersion and speciation along the Tethys Sea proposed by Mepham (1983), must be considered.

The distribution of mangroves along the American continent prior to the full development of glaciations in the Pleistocene, seems to reflect the climatic conditions of that time (Wijmstra, 1969). During the Eocene period, the mangrove flora extended to higher latitudes. *Nypa* for example was very common along the Caribbean basin from Northeastern Brazil to Southeastern USA (Muller, 1961; Dolianiti, 1955;

Thanikaimoni, 1987), as well as *Pelliciera rhizophorae*; the distribution of both species was drastically reduced later, probably as a result of more pronounced seasonal rainfall, longer dry periods probably higher salinities (Germeraad et al., 1968; Muller, 1980; Jimenez, 1984), and sea-level and coastline geomorphological changes (Woodroffe & Grindrod, 1991). *Nypa* disappeared from the Americas and the West coast of Africa while *P. rhizophora* presents a scattered and very restricted distribution, from the Pleistocene to present. Along the coast of what is today Suriname, mangrove forests spread over large areas of the continental shelf following regressions of the sea, and colonized large plains landward during transgressive periods (Wijmstra, 1969).

Presently, mangrove forests are unevenly distributed along the American continent's coastline, with the Atlantic and Caribbean coasts harboring nearly 70% of the total mangrove area. While along the Atlantic coast they form a nearly continuous belt from South United States to South Brazil, along the Pacific coast they have a more restricted distribution due to climatic constraints generated by the oceanographic conditions along the Peruvian and California coasts, where the upwelling of cold waters of the Humboldt Current waters suppresses convective activity and results in extremely arid climates, high soil salinity and almost totally absent freshwater input, restricting the extension of mangrove forests (Lacerda & Schaeffer-Novelli, 1992). Along the Pacific coast of South America mangroves extend only to lat. 5°32'S, at the Piúra River estuary, in northern Peru. Their Northern Pacific limit however, reaches lat. 30°15', in Puerto de Lobos, Mexico. On the Atlantic coast mangroves extend northward to Bermuda (lat. 32°20'N) and St Augustine, Florida (28°50'N); and southward to Laguna, Santa Catarina, in South Brazil (lat. 28°30'S). With the exception of the South Pacific coast, the latitudinal limits of mangroves are determined by the frequency, duration, and intensity of cold winter temperatures, rainfall and/or frost. The western limit of mangroves in the American continent are the Galápagos Islands, off the coast of Ecuador (long. 91°W, lat. 0°) from where A. germinans, L. racemosa, C. erectus and R. mangle have been reported (Chapman, 1975; West, 1977). The eastern limit are Fernando de Noronha Islands, off the coast of Pernambuco, Brazil (long. 32°24'W; lat. 3°50'S), where a small forest of L. racemosa covers approximately 0.15 ha at the estuary of Maceio River, Sueste Bay, which drains the most important watershed of these islands (Hertz, 1991).

4. Flora Composition and Distribution

4.1 Mangrove trees

Contrary to southeast Asia, which has nearly one hundred taxa of mangrove plant species (Mepham & Mepham, 1985; Rao, 1987) Latin America and Caribbean mangroves have a reduced number of tree species. Further taxonomic research is needed, because of the high population variability among species of each genus and because of the length of the Latin American and Caribbean coasts. Basic biological surveys have yet to be done for areas of northern South America and some Caribbean Islands.

Latin American and Caribbean mangroves include only 11 tree species and one variety. The Rhizophora (Rhizophoraceae) and Avicennia (Avicenniaceae) are dominant with 4 species each. Other genera are Laguncularia and Conocarpus (Combretaceae) and Pelliciera (Pellicieriaceae), all with only one species each. Conocarpus seems to have an endemic variety (Bacon, 1993) in the Northern Caribbean islands (Table 3).

The genus Rhizophora (Fig. 2) is represented by R. mangle L.; R. harrisonii Leechman, R. racemosa G.F.W. Meyer and R. samoensis (Hochr.) Salvosa. R. mangle is the most widespread, it occurs along all the tropical and sub-tropical Atlantic Coast from Bermuda to Santa Catarina, South Brazil, and although restricted by extreme climatic conditions, it is present from Baja California, Mexico to North Peru, at the Tumbes River estuary (Breteler, 1969; Savage, 1972; Cintrón & Schaeffer-Novelli, 1992). R. racemosa and R. harrisonii have more restricted distribution. Along the Atlantic coast, both species occur from Central America, Guyanas and Trinidad to northern Brazil (Bacon, 1970). The southern limit of these two species had been established by Prance et al. (1975) at the equator, and extended to Maranhão (2°40'S) by Santos (1986). In this area, large (up to 20m tall) fringes of both species occur generally landward of R. mangle belts. Along the Pacific coast these two species occur from South Mexico to Ecuador (Flores-Verdugo et al. 1992; Jimenez, 1992). The fourth species of Rhizophora is R. samoensis, which was first reported for the Pacific coast of Colombia, c.a. 5°N (West, 1956; Hueck, 1972). Later Horna et al. (1980) and Twilley (1990) recorded R. samoensis for the coast of Ecuador (lat. 1°N to 3°20'S). A recent survey of the mangroves of Ecuador (MAG, 1991) however, does not include this species. R. samoensis may be a variety of R. mangle (Hou, 1960). However, Mepham (1983) does consider it as a true species. The occurrence of R. samoensis along the Pacific coast of South America is far from established and still requires more systematic work.

The geographical distribution of the genus Avicennia (Fig. 3) is similar to that of Rhizophora. One species, A. germinans L., has a pan-continental distribution, from Bermuda, lat. 32°20'N to Atafona, lat. 21°37'S, in southeastern Brazil on the Atlantic and from Puerto de Lobos, Mexico, lat. 30°15'N to Piúra River estuary, Peru, lat. 5°32'S on the Pacific (West, 1977; Cintrón & Schaeffer-Novelli, 1992; Echevarria & Sarabia, 1993; Ellison, 1993; Lacerda & Rezende, 1993). Avicennia schaueriana Stapf. & Leech. is also widely distributed, endemic in the Atlantic coast,

R. mangle ——— ; R. harrisonii — — — — ; R. racemosa —●— ; R. samoensis +

Fig. 2. New World distribution of the genus *Rhizophora*

and spreads from the Caribbean Island of St. Kitts, lat. 17°30'N to Laguna, Brazil, lat. 28°30'S (Bacon, 1993; Cintrón & Schaeffer-Novelli, 1992). The other two species *A. bicolor* Standl. and *A. tonduzii* Moldenke, have been recorded only on the Pacific coast of Central America from Costa Rica to Panamá (Cintrón & Schaeffer-Novelli, 1983; D'Croz, 1993; Jimenez, 1992).

The family Combretaceae (Fig. 4) has two widely distributed species: *Laguncularia racemosa* Gaertn. and *Conocarpus erectus* L. The first has a distribution similar to that of *A. germinans*, although it does not extend as far north as Bermuda, its northern limit along on the Atlantic coast is Florida, USA, lat. 30°N)

(Savage, 1972). *C. erectus* has a smaller range of distribution, in the Atlantic coast where it extends from Florida, lat. 28°5'N, to the coast of Rio de Janeiro, Brazil, lat. 22°55' (Araújo & Maciel, 1979). A variety of this species *C. e. sericeus* has been recorded in the northern Caribbean Islands (Bacon, 1993).

The family Pelliceriaceae (Fig. 5), is represented by *Pelliciera rhizophorae* Pl. & Tr., which was widely distributed in the Caribbean, Central America and northern South America during the Miocene (Graham, 1977). Today it is restricted to sites of the coasts of Central America and the Pacific coast of South America (Winograd, 1983; Roth & Grijalva, 1991; Roth, 1992). Significant stands of the species

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are found only in the very wet Pacific coast of Costa Rica, where annual rainfall may be as high as 6,000mm (Jimenez, 1984). These forests are probably relicts of a wide distribution of *P. rhizophorae*, and could be due to low tolerance of high water salinity caused by dry climatic conditions (Jimenez, 1984).

4.2 Associated flora

Many plant species occur associated with mangrove forests in Latin America and the Caribbean. The diversity could be due to climatic conditions and proximity of other pristine ecosystems. A complete list of such flora however, is a mere curiosity, since it varies from region to region and even from forest to forest in a given region. Some of these species appear to be associated with mangrove forests throughout their distribution range in Latin America and the Caribbean. Among them the fern *Acrostichum aureum* L. and the Malvaceae *Hibiscus tiliaceus* L. are the most widespread, they occur in most mangroves of the World. These species frequently form dense belts along the landward edge of mangroves, on more elevated sites and around dry and saline areas inside mangroves. *A. aureum* biology has been studied by Lamberti (1969) in Brazil and by Medina *et al.* (1990) in Puerto Rico. Notwithstanding this, the biology and ecology of these two species are insufficiently known.

In the very humid Pacific coast of Central America, many tropical forest species "invade" mangrove forests, such as the Leguminosae vine *Dalbergia brownei* (Jacq) Urban, and the Apocynaceae liana *Rhabdadenia biflora* (Jacq) Hull (Jimenez, 1992). In Venezuela, mangroves are frequently invaded by the Lorantaceae *Phthirusa marina*. This liana has also been reported as a typical component of mangrove forests in French Guyana (Lescure, 1977). From the Amazon estuarine region to the coast of Maranhão State, North Brazil, where mangroves are seldom exposed to high or even moderate salinity, various typically freshwater macrophytes occur among true mangrove species, such as the Araceae *Montrichardia arborescens* Schott and the Leguminosae *Mora oleifera* (Triana) Duke (Mochel, 1993; Pantoja, 1993). Many palm species e.g. *Euterpe oleraceae* Mart., are common in these mangrove forests.

The glicophytes that occur in association with mangroves of Venezuela are evergreen communities of *Symphonia globulifera* L. (Clusiaceae); *Virola surinamense* (Myristicaceae); *Pterocarpus officinalis* Jacq. (Papilionaceae); *Mora excelsa* (Caesalpiniaceae) and *Pachira aquatica* (SW) Aubl. (Bombacaceae) and the

endemic *Tabebuia aquatilis*. Among the palms, *Mauritia flexuosa* L.; *E. oleracea* and *Phenankospermum guyanense* are frequent (Huber & Alarcon, 1988).

From Rio de Janeiro to Santa Catarina State, SE Brazil, mangroves occur adjacent to mountain rain forests, and are host to a great diversity of epiphytes of the families Bromeliaceae and Orchidaceae in particular *Tillandsia usneoides* L., *T. stricta* Solander and *Vrizia* spp. (Lacerda, 1984). High diversity of epiphytes is also common in *R. harrisonii* forests of southern Ecuador (MAG, 1991). In the Pacific coast of Mexico and in the coast of Venezuela, *Pachira aquatica* typically occurs as a member of the mangrove community (Flores-Verdugo *et al.*, 1992).

Typical salt marsh species also occur in New World mangroves, though they are in general restricted to pioneer formations at the seaward fringe of the mangrove forest, to natural gaps under the canopy and occasionally as fringes of tidal creeks and channels. They occupy large areas of landward margins of mangroves in drier Caribbean islands such as British Virgin Islands and Turks & Caicos (Bacon, 1993). This marginal distribution is due to light attenuation by the mangrove canopy (Reitz, 1961; West, 1977; Santos, 1989; Costa & Davy, 1992; Bacon, 1993).

The most common grass along the mangroves of the Atlantic coast of Latin America and the mainland Caribbean coast is *Spartina alterniflora* Loisel, a world wide distributed salt marsh species. It has been recorded from almost all mangroves of the continent typically at the seaward fringe along the forests. This species may play an important role in the dynamics and environmental conditions of mangroves (Lacerda & Abrão, 1984; Costa & Davy, 1992), it promotes sediment fixation and trapping of chemical elements in the mangrove environment. In Insular Caribbean *Sporobolus virginicus* substitutes *S. alterniflora* in these habitats (Bacon, 1993). In the Pacific, saltmarsh-mangrove association has not been reported (D'Croz, 1993).

Other salt marsh species specialize in colonizing areas disturbed by hurricanes or anthropogenic activities. *Sesuvium portulacastrum* L. (Aizoaceae) and *Blutaparon vermiculare* L. Mears (Amaranthaceae), have been reported as typical of such areas forming very dense communities that may permanently occupy disturbed mangrove areas (Lacerda & Hay, 1982). In many saline areas of the Venezuelan coast these species occur generally associated with *C.*

A. germinans ——— ; A. schaueriana – – – ; A. bicolor —●— ; A. tonduzzi – + –

Fig. 3. New World distribution of the genus *Avicennia*

erectus and other halophytes such as *Atriplex pentandra*, *Salicornia fruticora* and *Batis maritima* (Huber & Alarcon, 1988).

Common salt marsh species associated with mangroves include the Batidaceae, *Batis maritima* L., widely distributed throughout the Americas and the Caribbean; the Chenopodiaceae *Salicornia ambigua* Michx., along with *B. vermiculare*, *Portulaca pilosa* L., *Cakile lanceolata*, *Ipomea pes-caprae* and *S. portulacastrum* occupy high salinity areas inside mangroves; and the Gramineae *Sporobolus virginicus* L. Kunth and *Paspalum vaginatum* Swartz, frequently occur in more sandy areas (Pannier & Pannier, 1985; Huber & Alarcon, 1988).

Other typical mangrove associates are submersed macrophytes, seagrasses and macroalgae and fungi. Among the seagrasses, *Holodule wrightii* Aschers, *Halophila baillonis*, Potamogetonaceae, *Thalassia testudinum* Konig, Hydrocharitaceae and *Ruppia maritima* L., Zannicheliaceae, are recorded throughout the Atlantic and Caribbean mangroves (Acosta-Fabelo, 1974; Phillips, 1992;). Seagrass bed are not common in the Pacific coast (D'Croz, 1993).

Macroalgae and fungi have recently been studied by mangrove scientists throughout the Americas. Cordeiro-Marino *et al.* (1992) listed over 150 taxa from the mangroves of Latin America and the Caribbean. The highest diversity occurs among the

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L. racemosa ——— ● ——— ; C. erectus —————; C. erectus sericeus ———

Fig. 4. New World distribution of the genera *Laguncularia* and *Conocarpus*.

Rhodophyta with 78 species and the lowest among the Phaeophyta, less than 15 species. In the Caribbean due to high water transparency and association with coral reefs, algae diversity is maximum, with 109 species and a high degree of endemism, nearly 70% among the Rhodophyta.

Low water transparency and salinity variation typical of most continental mangroves, is probably the cause of the small number of species compared to the Caribbean (Oliveira Filho, 1984). The North Pacific region, including Central America, presents the lowest algal diversity with only 10 species, however, this region is the poorest studied of all coasts of the American continent. Therefore, this low diversity

may just represent a lack of taxonomic work in the region.

Mangrove macroalgae are mostly found on the roots of mangrove trees (over 50% of the species). Other hard substrates like rocks, stones and large shell fragments, account for nearly 30% of the species, while soft mud and sandy substrates account for the other 20% of the species (Cordeiro-Marino *et al.*, 1992).

In most mangroves, the macroalgal community of trunks and aerial roots, is dominated by the Bostrichietum association, which includes the genera *Bostrichia*, *Caloglossa* and *Catenella*. These include 12

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Fig. 5. New World distribution of the genus *Pelliciera*

typical species with year round reproduction (Braga *et al.*, 1990). Another typical association is in the sediment, the so called Rhizoclonietum association, formed mostly by over 10 species of green algae of the genera *Rhizoclonium*, *Enteromorpha* and *Cladophora* (Pedrini, 1980). Typical tropical species of *Caulerpa*, *Acetabularia*, *Halimeda*, *Sargassum* and *Penicillus* are frequent in the clear-water mangroves of the Caribbean (Pannier & Pannier, 1989)

Marine fungi of mangroves belong to all groups of higher fungi of warm waters. They infest submersed roots, stems and twigs, as well as sessile animals and algae. Over 30 species of marine fungi occur in New World mangroves. However, only a few seem to be host-specific (Kohlmeyer & Kohlmeyer, 1979).

The distribution and species composition of the mycoflora is determined by the duration of submergence of the parts of the tree infested by the fungus and of its physiology. Submersed parts have a different mycoflora from the non-submersed parts. However, at high tide level, marine and terrestrial fungi overlap. Host-specific species generally have a restricted distribution while more omnivorous species tend to have a wider one (Kohlmeyer, 1969).

Among the New World mangrove marine fungi, typical host-specific species reported are the Ascomycetes; *Didymosphaeria rhizophorae* J. & E. Kohlm.;

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Table 3. Updated list of species of "true mangrove" trees in Latin America and the Caribbean and their distribution limits.

	Atlantic Ocean		Pacific Ocean	
	North	South	North	South
Family Rhizophoraceae				
Rhizophora mangle L.	Bermuda, 32°20'	Praia do Sonho, Brazil, 27°53'	Puerto de Lobos, Mexico, 30°15'	Tumbes River, Peru, 3°34'
R. harrisonii Leechman	Estero Real, Nicaragua, 13°	Rio Preguiças, Brazil, 2°40'	Chantuto, Mexico, 15°15'	Guayas R., Ecuador, 2°20'
R. racemosa G.F.W. Meyer	Estero Real, Nicaragua, 13°	Rio Preguiças, Brazil, 2°40'	Chiquirí River, Panamá, 10°	Guayas R., Ecuador,2°20'
R. samoensis (Hochr.) Salvosa	No ocurrence		Restricted to the Pacific Coast from Ecuador (3°S) to Panamá (10°N)	
Family Avicenniaceae				
Avicennia germinans L.	Bermuda, 32°20'	Atafona, Brazil, 21°37'	Puerto de Lobos, Mexico, 30°15'	Piúra R., Peru, 5°32'
A. schaueriana Stapf. & Leech	St. Kitts Is., Carib., 17°30'	Laguna, Brazil, 28°30'	No occurrence	
A. bicolor Standl.	No occurrence		Restricted to the Pacific coast of Central America	
A. tonduzii Moldenke	No occurrence		Restricted to the Pacific coast of Central America	
Family Combretaceae				
Laguncularia racemosa Gaertn.	Florida, USA 28°50'	Laguna, Brazil, 28°30'	Estero Sargento, Mexico, 29°17'	Piúra R., Peru, 5°32'
Conocarpus erectus L.	Florida, USA 28°50'	Lagoa de Araruama, Brazil, 22°55'	Estero Sargento, Mexico, 29°17'	Tumbes R., Peru, 3°34'
Conocarpus e. sericeus	Endemic to Northern Caribbean Islands 20°N to 25°N		No occurrence	
Family Pellicieriaceae				
Pelliciera rhizophorae	Prinzapolca R., Nicaragua,13°	Cartagena Bay, Colombia, 9°	Gulf of Nicoya, Costa Rica, 9°30'	Esmeralda R. Pl. & Tr. Ecuador, 1°

Sources: Araújo & Maciel (1979); Bacon (1970, 1993); Breteler, (1969); Calderon (1983); Chapman (1975); Cintrón & Schaeffer-Novelli (1983; 1992); Flores-Verdugo *et al.* (1992); Horna *et al.* (1980); Hueck (1972); Jimenez (1984, 1992); Prance *et al.* (1975); Rincón & Mendoza, 1984); Roth (1992); Roth & Grijalva (1991); Santos (1986); Savage (1972); Stoffers (1956); West (1956, 1977); Winograd (1983).

Keissleriella blepharospora J. & E. Kohlm.; and the Deuteromycetes, *Cytospora* sp., on *R. mangle*. On *A. germinans*, host-specific species of marine fungi are *Leptosphaeria avicenniae* J. & E. Kohlm. and *Mycosphaerella pneumatophorae* Kohlm. (Kohlmeyer, 1968; 1969).

Most terrestrial fungi described from New World mangroves occur as parasites of living leaves, only a few were described as wood-inhabiting. Most frequent host-specific terrestrial fungi on *R. mangle* are the Ascomycetes *Anthostomella rhizophorae* Visioli, *A. rhizomorphae* Berl ex Voge; *Physalospora rhizophorae* Bat. & Maia and *P. rhizophoricola* Bat. & Maia (Batista *et al.*, 1955; Stevens, 1920; Vizioli, 1923). Among the Deuteromycetes, the genus *Pestalotia* (Guba, 1961) and *Cercospora* (Craeger, 1962), show the highest species diversity. Host-specific terrestrial fungi were also reported for *L. racemosa* and included the Ascomycetes *Irene laguncularie* (Earle) Toro, *Micropeltis laguncularie* Wint and *Physalospora laguncularie* Rehm (Kohlmeyer, 1969). Among the Deuteromycetes, *Helminthosporium glabroides* F.L. Stevens has been reported (Seymour, 1929).

Marine fungi play a key role in litter decomposition processes and nutrient cycling. Important species such as *Pestalotia*, *Nigrospora* and *Gliocidium*, which show marked succession during the different phases of the decomposition process (Fell & Master, 1973). Studies in the Laguna de Tacarigua (Venezuela) showed that Deuteromycetes and Phycomycetes, in particular *Aspergillus* and *Penicillum* were the dominant fungi involved in the litter decomposition process of mangrove organic matter (Barreto, 1988)

5. Mangrove Fauna

The fauna of mangrove forests includes elements from marine and terrestrial habitats. Few animal species, however, are exclusive inhabitants of mangroves, hence the difficulty of characterizing a "true" mangrove fauna. In most species their presence depends on season, tides, life cycle stage and other factors. Of the 358 macroinvertebrates and vertebrates found in a 4,000 ha mangrove swamps in Trinidad, only the Cirripede *Chthamalus rhizophorae* was strictly confined to this habitat; although many of the other species were most commonly found associated with mangroves, and it is only in this sense that they can be called mangrove fauna. Most of the animals to be found in mangroves also occur elsewhere in

other coastal habitats, and even in areas hundreds of km apart from the coastal strip, as in the case of the scarlet ibis, *Eudocimus ruber* (Conde & Alarcón, 1993).

Whether transient or permanent, the mangrove fauna is large and diversified. Over 140 species of birds and 220 species of fish and hundreds of species of terrestrial and marine invertebrates, create high diversity assemblages along otherwise low biodiversity mudflats.

Due to the accelerated destruction of inland forests, in some Latin American and Caribbean countries, many mangrove areas have become important sanctuaries and stepping stones in the migratory routes of various species, which otherwise would be threatened with extinction. For example, the monkey *Chipodes satanas* finds refugee in the extensive mangrove forests of Maranhão, northern Brazil, as well as the manatee *Trichechus manatus* and the scarlet ibis *Eudocimus ruber*. A small population of the American crocodile, *Crocodilus acutus*, inhabits the mangroves of Tumbes River, Peru. In Venezuela and many Caribbean islands, small populations of the endangered *C. acutus* inhabit mangrove lagoons, which have become their main remaining shelters. In Ecuador, at the Churute Mangrove Ecological Reserve, the only population west of the Andes of the "Canclón", *Anhima cornuta*, finds shelter.

In some localities, where waters are extremely transparent, the red mangrove (*Rhizophora*) roots provide settling space for the attachment of many invertebrate species, which in some areas, in particular in the Caribbean, can be highly diversified. This colorful community, where many species and taxa are represented - where sponges, bivalves, and algae predominate - can grow into a huge biomass on some roots.

Among the more common species of this community is the mangrove oyster *Crassostrea rhizophorae*, which can be a very important staple in the economies of the mangrove forests villagers. In Jamaica, 17 species of sponges and 17 of tunicates are commonly found in this habitat that can support also dense masses of the commercially important mangrove oyster *Crassostrea rhizophorae*, *Isognomon bicolor* and the mussels *Brachidontes exustus* and *B. citrinus*. In Venezuela, 33 species of sponges and 12 of tunicates have been cited from mangrove roots (Sutherland, 1980; Díaz *et al.*, 1985; Orihuela *et al.*, 1991). Among the sponges of the sessile community

the more common are: *Tedania ignis, Haliclona viridis, Spongia zimocca, Halichondria magniconulosa, Desmacellia jania,* and *Lissodendoryx isodictyalis.* The algae include *Acanthophora spicifera, Bryopsis plumosa, Caulerpa verticillata, C. racemosa, Cladophora fascicularis, Dyctyota bartayresii, Spermothamnion investiens* and *Ulva lactuca.* The tunicates are: *Botrylloides nigrum, Botryllus niger, Didemnum* sp., *Diplosoma listerianus, Ecteinascidia conklini., E. turbinata, Microcosmus exasperatus, Phallusia nigra, Polyclinum constellatum, Pyura momus, Styela canopus* and *Symplegma viridae.* Other organisms present are the octocoral *Telesto riisei;* the bivalves *Brachydontes* sp., Crassostrea *rhizophorae* and *Isognomon alatus;* the cirriped *Balanus eburneus;* the annelid *Spirorbis* sp; the bryozoans *Schizoporella* sp., and *Bugula* sp.; the polychaete *Sabellastarte magnifica;* and the actinid *Aiptasia pallida* (Sutherland, 1980; Díaz *et al.,* 1985; Orihuela *et al.,* 1991). Species lists are also provided for Florida, USA, (Bingham, 1992); Quintana Roo, Mexico (Inclón-Rivadeneyra, 1989); Puerto Rico (Rodríguez & Stoner, 1990); and Belize (Ellison & Farnsworth, 1992).

In some localities (for example, Cocinetas Lagoon, Venezuela), the mangrove oyster present is *Crassostrea virginica,* a larger species than *C. rhizophorae* and apparently more tolerant of salinity extremes (MARNR, 1991c). At some place in Venezuela, as Boca de Caño Lagoon and Tacarigua Lagoon, where great amounts of sediments are in suspension, the sessile community on the mangrove roots is very poor, represented by a few specimens of *Crassostrea rhizophorae* and other bivalves, algae with scant cover, and isolated and poorly developed sponges. Prop root communities are typically zoned in relation to tidal levels and tolerance to desiccation during tidal emersion. Sessile community distribution in Trinidad showed an upper *Chthamalus* zone, a mid-tidal *Balanus* zone and a lower tunicate/sponge zone (Bacon, 1970). The sessile community of the mangrove roots has been considered very stable (Sutherland, 1980); however, it can be removed almost entirely by resuspension and salinity changes produced by hurricanes or unusual torrential rains. Recuperation of biodiversity in such community was slow; after twenty months it had not reached the original structure and only 45% of species originally attached to the red mangrove roots had recolonized the habitat (Orihuela *et al.,* 1991). Variability of water temperature, wave exposure, root type, proximity of roots to the barrier reef affect epibiont distribution and richness in Belizean mangroves (Ellison & Farnsworth, 1992). Biological factors also play a role in the structuring of this community; the spatial

heterogeneity probably results from differential larval recruitment (Sutherland, 1980; Bingham, 1992). The biomass of epibionts can be so large that it can affect root growth and production (Perry 1988; Ellison & Farnsworth, 1990).

The complex habitat that results from the imbrication of numerous red mangrove prop roots, provides refuge and nursery ground for many species of fishes. The number of species, density and biomass of fishes found in that environment can be up to several orders of magnitude larger than nearby ecosystems, such as beds of *Thalassia* and other species of seagrasses (Thayer *et al.,* 1987). In a fringe mangrove in south Florida, 36 species were collected exclusively in the mangrove prop root system, while 24 species were sampled solely in the adjacent ecosystems (Thayer *et al.,* 1987). Furthermore, juveniles of commercially important fishes, as the gray snapper *Lutjanus griseus,* feed exclusively in the prop root habitat (Thayer *et al.,* 1987).

Benthic epifauna and infauna in mangroves frequently show patterns of zonation related to sediment type, depth of tidal flooding, and mangrove forest type. In Port Royal, Jamaica, the crabs *Panopeus herbstii, Uca thayeri, Pachygrapsus gracilis,* and *Goniopsis cruentata* showed reduction in numbers . along transects from the sea landwards in relation to the mangrove vegetation zones (Warner, 1969).

The fauna associated with mangroves along the Pacific coast of Latin America is composed of numerous species living in the mangrove trees, the ground and the brackish waters of the tidal channels. Crustaceans are among the most noteworthy taxa related to the mangrove swamps; this group has been very well described by Abele (1972). The most common arboreal crab is *Aratus pisonii,* although other species such as *Goniopsis pulchra* can be observed occasionally in mangrove trees. The soil of the mangroves is the habitat for other crabs, such as *Cardisoma crassum, Ucides occidentalis,* and several species of *Uca.* The tidal channels hold large populations of hermit crabs of the genus *Clibanarius,* the portunids *Callinectes arcuatus* and *C. toxotes,* and xanthidae *Panopeus purpureus,* among others. Some of these decapods feed on detrital material from the mangrove's litterfall, as reported for *Uca, Sesarma, Cardisoma* and *Ucides* (Abele, 1972). Other species are filter feeders (*Petrolisthes*), predators and scavengers (*Callinectes*) and some include mangrove leaves in their diet.

Many of the aforementioned genera are also found in the Caribbean and the Atlantic coast of Latin America. Likewise, *Aratus pisonii* is one of the most common crustacean in the New World mangroves, and perhaps the only true marine arboreal crab in that region. This species is found in mangroves that grow in marine, estuarine, hypersaline and freshwater habitats (Conde & Díaz, 1989a,b; Conde *et al.*, 1989; Conde & Díaz, 1992ab; Díaz & Conde, 1989), where it shows size and life history traits gradation closely related to mangrove productivity (Conde & Díaz, 1992a; Conde & Díaz, 1989b; Conde *et al.*, 1989,1993). Population dynamics of *Aratus pisonii* are related to rainfall and tide regime (Conde & Díaz, 1989a; Conde, 1990; Díaz & Conde, 1989). *Goniopsis cruentata*, apparently a predator of *A. pisonii* (Warner, 1967), can be observed occasionally on mangrove trees; although most of the time, it can be sighted on the mangrove ground. In the same habitat and in the sand flats close to mangrove forest, many species of *Uca* are present; among them, *U. mordax* and *U. rapax* are very common (Conde & Díaz, 1985). *Ucides cordatus* is very abundant in some mangrove forests. Several species of the blue crab *Callinectes* are caught the fishermen in mangrove lagoons. Another species usually associated to the most terrestrial zone of mangrove forests of the Caribbean is *Cardisoma guanhumi*, a commercial species which has been severely depleted in some localiities and a very important staple in the economies of some mangrove forest villagers.

The importance of coastal lagoons including those fringed by mangroves to penaeid fisheries has been repeatedly highlighted (Edwards, 1978). Several species of penaeid shrimps are related to the Pacific coast mangroves, most important *Penaeus occidentalis*, *P. vannamei*, *P. stylirostris* and *P. californiensis.*; although, as much as nine species have been reported to use the mangrove swamps as nursery area (D'Croz and Kwiecinski, 1980). Some of these shrimps enter the mangrove swamps as small post-larvae seeking the protection and food available in this brackish habitat; later, they move offshore as juveniles. These penaeids are the major component of the coastal shrimp fishery in the Pacific coast of Latin America. A similar pattern is found in the Caribbean. Mangrove lagoons are instrumental in the life cycle of the four species of *Penaeus*: *P. brasiliensis*, *P. notialis*, *P. schmitti* and *P. subtilis* found in the Caribbean. They enter the lagoons as juveniles, where they find a highly productive and almost predator-free environment (Stoner, 1988). In Laguna Joyuda, Puerto Rico, as much as 955 kg wet weight of shrimp can

be produced yearly per hectare (Stoner, 1985). Recruitment of juvenile shrimps to the lagoon is discontinuous through the year, but highly correlated to the rainfall pattern (Stoner, 1988).

Molluscs are found attached to the mangrove trees, example are some scavenger snails such as *Littorina*, *Nerita*, and filter feeders such as the oysters *Ostrea cortezensis* and *O. columbiensis*. The muddy bottoms of the mangrove swamps are inhabited by bivalves: *Chione subrugosa*, *Tellina ecuatoriana*, *Tagelus spp.*, *Anadara spp.*, and *Mytella guyanensis*. In the Caribbean coast, the mangrove oyster *Crassostrea rhizophorae* is ubiquitous. Another species of bivalve is *Isognomon alatus*.

Besides providing nursery grounds and refuge for many species of shrimps, mangrove lagoons play the same role for many species of fishes. In their waters large predators are not common, hence, the predation pressure over juveniles, including those of species whose adults live in deeper waters, is reduced. Although many species can be found in these lagoons, a small number of species-up to six or seven-represent most of the total catch. In the western Atlantic mangroves, three groups of fishes have been identified by Stoner (1986): resident small flatfish; several species of transient juveniles; and small planktivores. In some localities, a fourth group-marine catfishes-appears (Phillips, 1981; Yáñez-Arancibia *et al.*, 1980). A high percentage of juveniles belongs to species that are not resident in the lagoons and that live offshore as adults; up to 55% (Stoner, 1986) or 46% (Yáñez-Arancibia *et al.*, 1980). Among the most common fishes in mangrove swamps of the Pacific coast are: the mullet *Mugil curema*, the "mojarra" *Eucinostomus californiensis*, and several snooks: *Centropomus armatus*, *C. robalito*, *C. nigrescens* and *C. unionensis*. All of these fishes are found as juveniles in the mangrove channels.

In coastal lagoons of the Caribbean coast of Venezuela the most common species are the catfish *Arius herzbergii* and *Cathorops spixii*; the snooks *Centropomus undecimalis*, *C. ensiferus*, *C. pectinatus*, and *C. parallelus*; the mullets *Mugil liza*, *M. brasiliensis*, and *M. curema*; the mojarras *Eugerres plumieri*, *Diapterus rhombeus* and *Gerres cinereus* (Ginés *et al.*, 1972; Pagavino, 1983; Cervigón & Gómez, 1986). Less abundant, but present are the Atlantic tarpon (*Tarpon atlanticus*), juveniles of the horse jack *Caranx hippos*, the ladyfish *Elops saurus*, and the hogchoker *Trinectes maculatus brownii* (Pagavino, 1983). In the Caribbean, a great diversity of typical coral reef fishes are frequently found in mangroves (Alvarez-León, 1993).

Species lists and analysis of community structure are provided by Austin (1971), Phillips (1981), Stoner (1986) and Yáñez-Arancibia *et al.* (1980).

In addition to the aquatic fauna, some birds, reptiles and mammals inhabit mangrove forests. Many of them are resident or, in one or other stage of their life cycles, visit mangrove forests, as part of any of their daily activities or during their migrations. More than 150 species of birds have been listed for mangroves in Venezuela. Among the birds that have been reported as typical of Venezuelan mangroves are the yellow warbler (*Dendroica petechia*), the bicolored conebill (*Conirostrum bicolor*), the clapper rail (*Rallus longirostris*), the great-tailed grackle (*Cassidix mexicanus*), the spotted tody-flycatcher (*Todirostrum maculatum*), and the rufous crab-hawk (*Buteogallus aequinoctialis*). Common to all the seven places where inventories have been carried out are the common egret (*Casmerodius albus*), the black vulture (*Coragyps atratus*), the scarlet ibis (*Eudocimus ruber*), and the brown pelican (*Pelecanus occidentalis*) (MARNR, 1986). *E. ruber*, an endangered species in many places of the world, is very common in Venezuelan mangroves. This seems to be the only country where there are still considerable reproductive colonies of this bird (Gremone *et al.*, undated). Other common species are *Pelecanus occidentalis*, the magnificent frigatebird (*Fregata magnificens*), the great-tailed grackle (*Cassidix mexicanus*), the tricolored or Louisiana heron (*Hidranassa tricolor*), the great or common egret (*Casmerodius albus*), the white ibis (*Eudocimus albus*), *Ardea cocoi*, *Bubulcus ibis*, *Egretta tricolor*, *E. caerulea*, *Egretta alba*, the anhinga (*Anhinga anhinga*), the american wood ibis (*Mycteria americana*), the glossy ibis (*Plegadis falcinellus*), the limpkin (*Aramus guarauna*), the wattled jacanã (*Jacana jacana*), the collared plover (*Charadrius collaris*) and the common stilt (*Himantópus himantopus*) (Figueroa & Seijas, 1986). Non-reproductive visitors are: *Egretta rufescens*, the great blue heron (*Ardea herodias*), the flamingo (*Phoenicopterus ruber*), the blue winged teal (*Anas discors*), numerous species of Nearctic Limicolae, the laughing gull (*Larus atricilla*), the gull billed tern (*Gelochelidon nilotica*) and the Caspian tern (*Hydroprogne caspia*) (Figueroa & Seijas, 1986).

Among the species that hibernate in the Venezuelan mangroves are *Calidris mauri* and *Micropalama himantopus*; the osprey (*Pandion haliaetus*) has also been pointed as a winter visitor (Figueroa & Seijas, 1986). The Neartic migratory species include *Egretta rufescens*, *Butorides virescens virescens*, *Anas discors*, *Pluvialis squatarola*, *Numenius phaeopus*, *Tringa*

melanoleuca, *T. flavipes*, *Actitis macularia*, *Catoptrophorus semipalmatus*, *Arenaria interpres*, *Limnodromus griseus*, *Calidris canutus*, *C. alba*, *C. mauri*, *C. minutilla*, *Larus atricilla*, and several species of *Gelochelidon*, *Hydroprogne* and *Sterna*, among them *Hydroprogne caspia* and *Sterna maxima* (Figueroa & Seijas, 1986). Non aquatic common species are the orange-winged parrot (*Amazona amazonica*), which forms great groups, the yellow-headed parrot (*Amazona ochrocephala*), the pale-vented pigeon (*Columba cayennensis*), and dense populations of the macaws *Ara chloroptera* and *A. severa* (Figueroa & Seijas, 1986). Venezuelan mangroves and flats are very important as feeding grounds for thousands of flamingos (*Phoenicopterus ruber*) that reproduce in the islands close to the Venezuelan coast. Besides, flamingos nest in a mangrove complex in western Venezuela, being this only one the four locations in the Caribbean where this species reproduces. In the Pacific coast, many of these genera, and in some cases the same species, are present, such as the pelicans *Pelecanus erythrorhinchus* and *P. occidentalis*, the spoonbill *Ajaia ajaja*, the kingfisher *Chloroceryle americana*, and the egret *Bubulcus ibis*.

Among the reptiles are: *Iguana iguana*, the spectacled caiman *Caiman crocodylus fuscus*, the American crocodile *Crocodylus acutus*, the arboreal snake *Corallus hortulanus* (Figueroa & Seijas, 1986). Marine turtles, among them *Chelonia mydas* are very common in the Caribbean, mainly in those places where *Thalassia* beds are associated with mangroves. Other turtles sighted in the waterways of the huge riverine mangroves of eastern Venezuela are *Podocnemis unifilis* and *Phrynus gibbus*.

Mammals are represented by the opossum *Didelphis marsupialis*, the crab-eating raccoons *Procyon lotor* on the Pacific coast and *P. cancrivorus* on the Atlantic; the otters *Lutra annectens* on the Pacific coast and *L. longicaudis* on the Atlantic, and the weasel *Mustela frenata* (Aveline, 1980; Figueroa & Seijas, 1986; MARNR, 1986; Alvarez-León, 1993), the reeds *Odocoileus virginicus* and *Mazama mazama* and many monkey species. Other mammals reported for Venezuelan mangrove forests are the crab-eating fox (*Cerdocyon thous*), the cottontail rabbit (*Sylvilagus floridanus)*; the jaguar, *Panthera onca*, and the South American tapir, *Tapirus terrestris*, the ocelot (*Felis pardalis*), the giant anteater (*Myrmecophaga tridactyla*), the howler monkey (*Alouatta seniculus*), the capuchin or ring-tail monkey (*Cebus* sp.), the paca (*Agouti paca*), the kinkajou (*Potos flavus*), agoutis (*Dasyprocta guamara*) and several species of bats; many of those species are intermittent or regular visitors

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(Salvatierra, 1983; Figueroa & Seijas, 1986; MARNR, 1986; Bisbal, 1989). Among the aquatic mammals that have been observed in the pristine mangroves of the Orinoco Delta are several endangered species, including the manatee *Trichechus manatus*, the river dolphin, *Sotalia guianensis*, and the Amazon dolphin, *Ina geoffrensis*.

6. Mangrove Forest Structure and Development

6.1 Physiognomy of mangrove forests

Mangrove forests are best developed in a tropical climate, where the coldest winter temperature is above 20°C and temperatures are fairly constant throughout the year (< 5°C of variation). Highly developed forests are also associated with low wave energy, protected shorelines, abundant freshwater supply, allowing for the deposition and accumulation of fine, organic muds, and water salinity range between 5 and 30 ppt. Under such conditions, a large tidal amplitude will also allow the extension of mangrove forests farther inland, forming large forest belts which can extend over 60 km landward from the sea (Lugo & Snedaker, 1974; Walsh, 1974).

Under these optimal environmental conditions in the dynamic and humid regions, mangrove forests attain their maximum growth. Red mangrove (*Rhizophora*) forests 40 to 50m in height and more than 1.0m in diameter have been reported in Ecuador and Colombia (West, 1956; Hueck, 1972; Lacerda & Schaeffer-Novelli, 1992). At the Southern coast of Costa Rica and several areas of the Panamanian coast, where seasonality is less pronounced and annual rainfall ranges from 2,100 to 6,400mm, mangrove trees exceed 35m in height and a biomass of 280 tons.ha^{-1} (Jimenez, 1992). Well developed black mangrove forests, with trees up to 30m in height and 0.7 m in diameter, occur on the coasts of Suriname, French Guyana and Northern Brazil, frequently with biomass over 200 ton.ha^{-1} (Lacerda & Schaeffer-Novelli, 1992).

The structure of mangrove forests along the American continent has been categorized by Lugo & Snedaker (1974). These authors recognized 6 different forest types: Fringe, Riverine, Basin, Overwash, Dwarf and Hammock forests. The last three types are supposed to be specific cases of the first three types (Cintrón et al., 1985). Briefly the major characteristics of these forest types are:

Basin forests occur inland in drainage depressions channelling terrestrial runoff toward the coast. Water flow velocities are slow and extensive areas with a low profile are flooded. They are particularly sensitive to inundation, and export of mangrove litterfall to coastal areas is minimal. They export Carbon mostly in dissolved form (Twilley, 1985).

Fringe forests occur along the borders of protected shorelines and islands and are periodically flooded by tides. Due to their greater exposure to waves and tides and their great developed root system, they are particularly sensitive to erosion and marine contamination. Nutrient cycling and litterfall dynamics are highly dependent on episodical climatic events rather than the ecophysiology of the forest itself. Variable and important amounts of nutrients and Carbon from marine origin participate in nutrient cycling processes of these forests (Lacerda et al., 1988a; Ovalle et al., 1990; Rezende et al., 1990; Silva et al., 1991).

Riverine forests occur along rivers and creeks and are flooded daily by tides. They generally consist of tall straight-bole trees and the low surface waterflow velocity precludes redistribution of ground litter. Fluvial nutrients and constant freshwater frequently support high productivity rates in these forests. However, when freshwater flow dominates over the tidal prism, such as in the Amazon and Orinoco river estuaries, riverine mangrove forests may decrease or even disappear in the strong competition with freshwater macrophytes.

The classification described above, however, in not valid for certain mangrove areas and may change very rapid following changes in coastal geomorphology. For example, in deltaic areas in Tabasco, Mexico, where distributionary diversion is quite common, the sequence of mangrove developments may be drastically altered following a shift in the center of active sedimentation and freshwater discharge (Thom, 1967). Along the Pacific coast of Colombia, high sediment loads brought by rivers, create depositional environments that are rapidly colonized by mangroves and change completly the pattern of forest distribution of previously established mangroves (Alvarez-León, 1993).

Zonation and succession patterns of American mangroves have been described by several authors. However, their omnipresence and suitability of the concept has been questioned (Rodriguez, 1987) and it is our view that these two parameters, although

important in certain areas are extremely site specific and no expected pattern can be forecasted safely.

Another important aspect of mangrove forest structure is the variability of major structural parameters according to a latitudinal gradient. Table 4 shows the variability of major structural parameters along the spectra of latitudes throughout the American continent where mangrove forests occur.

Apart from latitude, the major factors controlling mangrove forest structure are wave action, rainfall and freshwater runoff which controls important environmental variables such as erosion/sedimentation rates, aridity, salinity, nutrient inputs, and soil quality (Kjerfve et al., 1993).

Although mangroves preferentially occupy tidal fringes along marine coasts, inland mangroves are typical in some arid areas of the Caribbean. These forests occur as far inland as 15 km in Barbuda (Stoddart et al. (1973), and 50 km in Inagua Island in the Bahamas (Lugo, 1981). Similar formations were also reported associated to freshwater plants in Lake Izabal in Guatemala (Brinson et al., 1974) and the South coast of Cuba (Lacerda, 1992, pers. obs.). In Paraguaná Peninsula, Venezuela, stands of C. erectus occur 10 km from the coast.

These formations attracted greater attention, since they seem to have no connection with the ocean. However, in general, they have high water and soil salinity, apparently due to some connection to the sea. In Lake Izabal, a long seawater wedge reaches the lake during the extreme of the dry season (Brinson et al., 1974). At Inagua and Barbuda, kartz formations possibly allow for the instrusion of tidal water very far inland. At Cuba it seems that a salt water lens, underneath the freshwater marshes extends far inland. There is also the possibility that these mangroves are relict forests from the Pleistocene, when connection with the sea would could have been permanent (Stoddart et al., 1973).

The colonization of these inland mangroves, at least where they are definitively relict forests, is still a puzzle. Since mangrove seedlings cannot float underground, the colonization of inland areas depends on episodic flooding events of abnormal sea level rise during hurricanes and strong storms when waves and swells usually reach far inland. This seems to be the case in Cuba and has been hypothesized by Lugo (1981) for other Caribbean man-

groves. However, this colonization process has not been described in detail.

6.2 Primary production, biomass distribution and allocation

Net above ground primary productivity of mangroves is the sum of wood growth and total litterfall. While litterfall has been studied by many authors throughout the American continent, wood growth has seldon been monitored. Therefore, estimates of net primary productivity of mangroves are few.

Wood growth seems to be influenced by the availability of freshwater and nutrients. Fringe and riverine mangrove stands in Laguna de Terminos, Mexico, under humid conditions (1,680 mm of rainfall) showed very different values (Day et al., 1988); fringe forest wood growth was significantly smaller (772 g.m^{-2}.yr^{-1}) than riverine forest ($1,206$ g.m^{-2}.yr^{-1}). Under more arid conditions found in Puerto Rico (810mm rainfall), Golley et al., (1962), estimated a smaller wood growth rate of 307 g.m^{-2}.yr^{-1}.

Based on these values and litterfall rates, net primary productivity for these forests was estimated as 2,457, 1,606 and 781 g.m^{-2}.yr^{-1}, for the Mexican riverine, fringe and Puerto Rican forests respectively. Other estimates for mangrove primary productivity were provided through gas exchange experiments in various mature south Florida mangroves (Miller, 1972; Carter et al., 1973; Lugo et al., 1975;). These studies found much higher values ranging from 2,044 to 5,475 g.m^{-2}.yr^{-1} probably due to the method used. To our knowledge no study has focused on the belowground production and even belowground biomass data are scarce.

Table 5 lists various mangrove litterfall data from different sites on the American continent. Leaf litter is the major component of total litterfall of mangrove forests, regardless of forest type, latitude or climate. In general, it sums up to over 70% of the total litterfall. From the available data no clear relationship is found between rainfall and litterfall. The data suggest that a relationship between latitude and annual litterfall is not clear and that local, site specific differences seems to be overwhelming determining litterfall rates, and sites very close together show different litterfall values (Lugo & Cintrón, (1975); e.g. in Puerto Rico Island Musa (1986), Table 5.

Biomass distribution in mangrove forests was one of the most studied aspects of New World mangroves. However most authors had studied aerial

biomass and few data exists on underground biomass, also most studies are on *R. mangle*; *A. germinans* and *A. schaueriana*, and *L. racemosa*; nearly no study has dealt with less widely distributed mangrove tree species such as *R. harrisonii*, *R. samoensis* or *R. racemosa*, or *A. bicolor*.

Table 6 lists biomass distribution data for various mangrove forests throughout the American continent. Highest aboveground biomass are found roughly between 10° North and 10° South. No assumption can be made regarding belowground biomass, however it is very important in relation to aboveground parts ranging from 20% to 64% of the total forest biomass. The few data available suggest that stressed mangrove communities such as those in arid climates tend to show higher percentages of belowground biomass, but definitive conclusions are hampered by the existence of little information.

7. Physical Environment

7.1 Mangrove soils

Dominant soils in continental mangroves are mostly entisols, but sometimes istosols. Riverine mangroves generally grow on immature clay soils (clay hydraquents). On tidal flats mangrove grow on mineral (sulfaquents) and organic (sulfahemists) soils. Seaward fringe mangroves grow on acid sulfate soils whereas in many Caribbean islands mangroves grow on bioclastic, coralline sands (Alvarez-León, 1993).

A detailed study of mangrove soils was done on the Guianas coast (Brinkman & Pons, 1968; Augustinus, 1978), where extensive mangroves have grown on the young coastal plains. Marine clays of the Comowine phase (later than 1,000 BP) are found in a band along most of the Guianas with their surface at about high tide level. The sediments are saline with brown or reddish-brown mottles when leached at the surface. Original pyrite content is low to medium, but thin layers of pyrite clay occur in places. These clays on which pioneer *Avicennia* forest develops alternate with ridges of coarse or shelly sand. Soils of river and estuary levees in areas dominated by *Rhizophora* show less variation in soil depth and degree of soil formation than marine clays.

In Venezuela, other detailed classification of mangrove forest soils was carried out by MARNR (1986). Mangroves are found mainly in istosols and entisols. In arid zones, however, mangroves grow in

aridisols. In the alluvial plains of the Atlantic coast, soils saturated during long periods (hydraquents) prevail, they are associated with superficial tropohemists in the plain basins. In the rest of the landscape, tropofibrists and sulfaquents occur. In the Caribbean coast of Venezuela, mangroves are associated with coastal lagoons, growing in acid soils of sandy texture (tropofibrists) with high concentrations of organic matter (sulfaquents). In the arid zones soils have predominantly a loamy-sand texture to loamy-clay with torripsaments to sulphic hydraquents.

Rapid accretion of mud and sand characterizes the coast of the Guianas, the dominant mud type being a reduced olive gray pelite. In Guadeloupe, mangrove soils were found similarly under reducing conditions, with redox potential of -300 mV indicating strong anaerobiosis (Febvay & Kermarrec, 1978).

Recent studies by Thibodeau & Nickerson (1986); Nickerson & Thibodeau (1985) and Lacerda *et al.* (1993) showed that, at least close to the rizosphere of mangrove plants, mangrove soils are highly influenced by the physiological activity of the roots which is different depending on plant species. For example, consistently lower redox potential have been reported for *Rhizophora* soils when compared to *Avicennia* soils. Also the organic content and composition of mangrove soils are directly related to the above vegetation. Carbon isotopic studies showed that over 95% of the Carbon present in mangrove soils originate in the mangrove litter (Lacerda *et al.*, 1986).

7.2 Hydrology

The hydroperiod of the fringe-overwash mangroves lasts only hours and occurs daily as a result of high tide wash, which is the only water input to this type of wetland. Riverine mangroves present hydroperiods which may last from hours to days. The frequency of the hydroperiods may be daily or seasonal, with deep waters. Water-level fluctuations within riverine mangroves are large and follow stream discharge patterns. Stream flow and tides represent the major water fluxes of this type of mangrove forest. Basin mangroves have hydroperiods of perennial duration, continuous frequency, and shallow waters. Fresh ground-water discharge, overland runoff, and surficial and underground saltwater intrusion are the water inputs to this type of mangroves (Zack, & Roman-Mas, 1988).

In general major transport of water occurs during short periods (1 to 2 hours) of the tidal cycle

Table 4. Structural parameters of New World mangrove forests.

Location	Type	Latitude	rainfall (mm)	height (m)	DBH (cm)	Basal Area (m^2.ha^{-1})	Density (t.ha^{-1})	Author
Estero Pargo (ME)	F	18°30'N	1,680	6.0	5.6	23.3	7,510	Day et al. (1988)
La Lechuguila (ME)	F	25°30'N	459	4.5	11.4	-	4,341	Flores-Verdugo (1986)
Marismas (ME)	F	21°45'N	1,200	5.2	16.9	-	1,461	Flores-Verdugo (1986)
Agua Brava (ME)	F	22°45'N	1,200	7.5	14.0	-	3,203	Flores-Verdugo (1986)
Isla Venado (NI)	F	11°55'N		25.0	14.0	14.9	440	Roth (1992)
Ilha Comprida (BR)	F	25°00'S		8.6	9.3	21.2	-	Adaime (987)
Sepetiba Bay (BR)	F	23°00'S	1,500	6.1	7.8	21.6	4,510	Silva et al. (1991)
Majana (CU)	F	21°30'N	1,200	10.0	-	20.6	3,527	Padron et al. (1993)
Sipacate (ES)	F	13°00'N		9.0	-	9.2	3,400	Oxloj (1987)
Darién (PA)	F	8°00'N	2,200	22.0	>10	35.0	320	Mayo (1965)
Tacarigua (VN)	F	10°50'N	990	9.5	60	2.7	-	MARNR (1986)
Morrocoy (VN)	F	10°40'N	1,065	11.0	-	10.2	440	MARNR (1986)
Cocinetas (VN)	F	11°50'N	277	7.0	-	30.0	4,000	MARNR (1986)
Barra Navidad (ME)	R	19°11'N	750	4.9	-	14.0	2,090	Zamorano (1990)
Mona Island (PR)	R	18°00'N	810	13.0	-	27.3	-	Cintrón et al. (1988)
Boca Chica (ME)	B	18°30'N	1,680	20.0	8.6	34.2	3,360	Day et al. (1988)
El Verde (ME)	B	25°30'N	627	7.0	-	11.9	1,430	Flores-Verdugo (1987)
Ilha do Cardoso (BR)	B	25°00'S	2,269	8.7	9.5	25.9	3,735	Peria et al. (1990)
Tacarigua (VN)	B	10°50'N	990	15.3	10.4	30.1	790	Rodríguez & Alarcón (1982) *
Morrocoy (VN)	B	10°40'N	1,065	25.0	-	66.8	1,320	MARNR (1986)
Cocinetas (VN)	B	11°50'N	277	7.5	20.0	16.8	1,280	MARNR (1986)
Orinoco Delta (VN)	R	9°00'N	2,290	28.0	-	65.1	1,000	MARNR (1986)
San Juan (VN)	R	10°10'N	2,055	28.0	-	27.5	350	MARNR (1986)
Paria Gulf (VN)	R	10°25'N	960	28.0	-	13.8	380	MARNR (1986)

Forest types are: F=Fringe; B=Basin; R=Riverine.

immediately after the changing of flow direction (Kjerfve et al., 1993). Major hydrochemical changes also occur during these short periods (Lacerda et al., 1988b; Ovalle et al., 1990; Rezende et al., 1990).

Mangroves grow most prolifically on deltaic plains that are subject to regular flooding during high tides and have ample supply of freshwater via regular or episodic river flooding or rainfall. The hydro-period of inundation of fringe-overwash mangroves usually only lasts a few hours but occurs daily during high tides. This is the only water input to this type of wetland. Riverine mangroves, on the other hand, usually exhibit longer hydro-periods, which may last from hours to days and depend not only on tidal flooding but also on river regime.

Water-level fluctuations within riverine mangroves vary greatly and increase with increasing river and stream discharges. Basin mangroves often have hydro-periods of perennial duration, and are often covered in shallow water on a continuous basis. Ground-water seepage and overland flow, as well as some saltwater intrusion, are the main water sources for this type of mangrove system (Zack & Roman-Mas, 1988).

In general major rates of water transport in mangrove systems occur during short periods (1-2 hours) of the tidal cycle, immediately before and after high water standstill, when the flow direction also changes. Although stream velocities can be substantial, the flow within the mangrove vegetation is slow

and sluggish and seldom exceeds 5 cm s⁻¹. Major hydrochemical water and soil changes can occur during these short periods (Lacerda *et al.*, 1988; Ovalle *et al.*, 1990; Rezende *et al.*, 1990; Kjerfve *et al.*, 1993).

A critical factor for the well-being of mangrove ecosystems is the availability of freshwater, usually indicated by the ratio of rainfall to evapotranspiration, R/E. Although mangroves are found in both humid (R/E > 1) and arid climates (R/E < 1) in Latin America and the Caribbean, mangrove structural development and growth rates are by far greater in humid equatorial areas with plentiful rainfall, preferably distributed relatively evenly during the year (Blasco 1984; Snedaker, 1984; Kjerfve, 1990). Most of the Latin American mangrove wetlands, as well as the mangrove wetlands on the larger islands in the Caribbean, are distributed along coasts where R/E > 1. Notable exceptions are the northern coast of Peru, portions of the Caribbean coasts of Colombia and Venezuela, the coast of Ceará in Brazil, and most of the smaller islands in the Caribbean, where R/E < 1. The most extensive and best developed mangrove systems in Latin America and the Caribbean exist in regions with ample freshwater supply and R/E > 1, including the Pacific coast of Colombia, the Caribbean coasts of Panamá and Nicaragua, and the north Brazil coasts of Pará and Maranhão. Whereas mangroves flourish in the Orinoco River delta, this is not the case in the Amazon River where the discharge is so tremendous (average 175,000 m³ s⁻¹) that the constantly fresh conditions in the mouth region of this world's largest river cause invasion of freshwater glycophytes which successfully out-compete mangroves.

Rainfall by itself apparently does not limit the growth of mangrove wetlands, as these exist in arid as well as wet climates (Galloway, 1982). However, rainfall does serve an important role as a primary control in leaching residual salts from mangrove soils, and thus acts to reduce soil salinity. Salts are deposited by tidal flooding in mangrove wetlands. In arid areas or regions with a strongly seasonal rainfall pattern, a barren salt flat often develops as a rim landward of the mangroves, where soil salinities often exceed 70 ppt and restrict mangrove development (Kjerfve, 1990).

Other factors being equal, coasts with a great tidal range can be expected to have more extensive mangrove wetlands because of a greater potential for tidal flooding. Such conditions are encountered along the humid Pacific coast of Colombia with spring tides reaching 3.9 m at Buenaventura, and

also along the humid coasts of Pará and Maranhão in northern Brazil where at places semidiurnal spring tides exceed 7 m. On the other hand, in the inner part of Baja California, México, where the climate is arid, mangroves are poorly developed in spite of daily tides with a range greater than 7 m. In contrast, all of the Gulf of México and the Caribbean Sea is microtidal, sometimes diurnal and sometimes mixed, with a range less than 0.5 m (Kjerfve, 1981; Seim *et al.*, 1987). Here, the tide is of little consequence in terms of affecting mangrove distribution.

The difference in distribution of mangroves along the east and west coasts of South America is easily explained by the distribution of ocean currents. Temperature is the primary control of mangrove distribution (Kjerfve, 1990), and the surface water temperatures, even in relatively nearshore coastal waters, along the west coast of South America can be as low as 12C. The reason is the northward flowing cold-water Humboldt (or Peru) current and the presence of one of the most intensive wind-driven cold-water upwelling systems on earth along the coasts of Peru and Ecuador. As a result, mangroves only begin to appear at latitude 5°32'S in the estuary of Piúra in northern Peru and further north. Along the east coast of South America, the situation is completely different, and water temperatures are usually well above 20° except for the coast along the Cabo Frio upwelling system in the state of Rio de Janeiro. The warm-water Brazil current flows southward along the Brazilian coast, and mangroves are flourishing as far south as 32°20'S at Praia do Sonho, Santa Catarina.

8. Natural and Anthropogenic Impacts

8.1 Herbivory

The role of mangrove leaves in marine coastal food chains has been emphasized repeatedly (Odum & Heald, 1972,1975; Lugo & Snedaker, 1974). In New Guinea up to 20 percent of the leaves are consumed by herbivores (Johnstone, 1981). Insect herbivores remove up to 35% leaf area of Australian mangrove plants; but in general the leaf area losses are smaller than those reported for several terrestrial communities (Robertson & Duke, 1987); although occasionally massive defoliations may occur (Whitten & Damanik, 1986; Lee, 1991). Similar percentages have been indicated for American mangroves (Lacerda *et al.*, 1983; Farnsworth & Ellison, 1991). However, several authors have reported small proportions of damage to mangrove leaves, typically less than 8% of the

Table 5. Litterfall, rainfall and location of New World mangrove forests (g.m-2.yr-1.).

Location	Type	Latitude	Rainfall	Leaf litter (%)	Total litter	Author
Agua Brava, (ME)	F	22°45'N	1,200	821 (81%)	1,015	Flores-Verdugo (1986)
Estero Pargo, (ME)	F	18°30'N	1,680	594 (71%)	834	Day et al. (1988)
Itacuruçá, (BR)	F	23°00'S	1,500	697 (73%)	960	Silva (1988)
Bertioga, (BR)	F	23°53'S	2,200	376 (90%)	416	Ponte et al. (1984)
Agua Brava, (ME)	R	22°45'N	1,200	749 (59%)	1,263	Flores-Verdugo (1986)
El Verde, (ME)	R	23°25'N	627	980 (89%)	1,100	Flores-Verdugo et al. (1987)
Laguna Mancha, (ME)	R	21°30'N	1,250	749 (59%)	1,236	Rico-Gray & Lot (1983)
Boca Chica, (ME)	R	18°30'N	1,680	881 (70%)	1,252	Day et al. (1988)
Vacia Talga (PR)	R	18°00'N	890	931 (70%)	1,322	Lugo & Cintrón (1975)
Chame (PA)	R	8°40'N	1,500	- -	900	D'Croz, 1993
Chiriqui River (PA)	R	8°30'N	2,500	- -	2,000	D'Croz, 1993
Barra de Santiago (S)	R	13°40'N	-	- -	993	Ramirez & Nuñez (1988)
Barra Navidad, (ME)	B	19°11'N	750	1,029 (80%)	1,287	Zamorano (1990)
Laguna Joyuda (PR)	B	18°00'N	900	714 (77%)	919	Musa (1986)
Laguna Joyuda (PR)	B	18°00'N	900	415 (81%)	511	Musa (1986)
Majana (CU)	B	21°30'N	1,200	- -	1,060	Cuba (1993)
Florida (USA)	B	25°-27°N	-	404 (75%)	538	Day et al. (1988)
Florida (USA)	D	26°00'N	-	88 (72%)	122	Day et al. (1988)
Tacaragua (VN)	B	10°50'N	990	1,000 (71%)	1,400	Barreto et al. (1989

Forest types are: F=fringe; R=riverine; B=basin; D=dwart

total leaf area (Heald, 1971; 86; Onuf et al., 1971; Beever et al., 1979; Lacerda et al., 1986), but higher defoliation rates (Farnswoth & Ellison, 1991), including mass defoliation, do not seem to be uncommon. In a Belizean mangrove forest, Farnsworth & Ellison (1991) found that herbivores damaged 4.3 to 25.3% of Rhizophora mangle leaf area and 7.7 to 36.1% of Avicennia germinans leaf area. R. mangle was more frequently damaged than A. germinans (Farnsworth & Ellison, 1991), even though the second species has a higher content of nitrogen (Ernesto Medina, personal communication). In mangroves of the Sepetiba Bay (Brazil) Avicennia schaueriana had less leaf area eaten than Rhizophora mangle and Laguncularia racemosa (Lacerda et al., 1986).

Herbivory rates vary widely from site to site and are related to several factors, including species, leaf age, branch height, orientation of branches, seedling height and distance to nearest neighbor, presence of a canopy, and chemical composition of leaves, including ash, crude fiber, water content, soluble carbohydrates and phenols (Lacerda et al., 1986; Farnswoth & Ellison, 1991). Herbivores in Belize

include the common mangrove tree crab, Aratus pisonii; the gastropod Littorina angulifera; Lepidoptera larvae, including Megalopyge opercularis, Automeris sp., Phocides pygmalion, and other unidentified species; Coleoptera larvae (mainly Chrysomelidae and Lampyridae); Homoptera (Aphididae, Blattidae, Cicadellidae, Cercopidae and Diaspididae); unidentified leaf miners; and larvae of unknown identity.

Leaf area damaged has shown a great variability (Lacerda et al., 1986). In the Caribbean the rate of direct grazing by crabs and insects on live mangrove leaves is small (Heald, 1971; Onuf et al., 1977; Beever et al., 1979).

The isopod Sphaeroma terebrans was cited as the agent that damaged many of the mangroves of southwestern Florida (Rehm & Humm, 1973). This species bores into the tips of aerial roots of the red mangrove tree Rhizophora mangle, destroying root apices and, possibly, initiating lateral budding and the proliferation of lateral roots (Gill & Tomlinson, 1977; Simberloff et al., 1978). Sphaeroma terebrans can affect up to 83% of the tips in some localities and

Table 6. Biomass allocation, forest type and rainfall in New World mangrove forests (ton.ha⁻¹).

Location	Latitude	Type	Rainfall	Aboveground	Belowgroung	Total	Author
Itacuruçá, (BR)	23°00'S	F	1,500	65	16 (20)	81	Silva et al. (1991)
Darien, (PA)	8°00'N	R	2,200	279	190 (41)	469	Golley et al. (1975)
Florida (USA)	25°00'N	D	-	8	8 (50)	16	Lugo & Snedaker (1974)
Florida (USA)	25°30'N	Island	-	8	14 (64)	22	Lugo & Snedaker (1974)
Puerto Rico (PR)	18°00'N	F	890	63	50 (44)	113	Golley et al. (1962)

Forest types are: F=fringe; R=riverine; B=basin; D=dwarf.

frequently prevents roots from reaching the substrate (Rehm, 1976). This process would stimulate a beneficial action of branching (Simberloff et al., 1978), although Ribi (1981) has not found any evidences to support this effect.

On mangrove cays off the coast of Belize, the isopod *Phycolimnoria clarkae* attacks the submerged roots of the red mangrove *Rhizophora mangle*, reducing root relative growth rate by 55% (Ellison & Farnsworth, 1990). These isopods do not stimulate lateral branching, as was postulated by Simberloff et al. (1978) for the isopod *Sphaeroma terebrans* in Florida. The epibionts that grow on submerged roots inhibit isopod colonization and thus facilitate root growth (Ellison & Farnsworth, 1990).

Another species, *Sphaeroma peruvianum*, can cause a 50% decrease in the growth rate of the prop roots of the red mangrove (*Rhizophora mangle*) in the Pacific coast of Costa Rica and a decrease of 52 to 62% in net root production (Perry, 1988). In Cuba, a new species of Pyralidae (Lepidoptera) larvae is a root borer of red mangrove roots (Padron et al., 1993).

The mangrove tree crab *Aratus pisonii*, although omnivorous (Díaz & Conde, 1988), in some localities can have up to 42% of its diet based on mangrove leaves (Lacerda et al., 1991). In Pine Island (Florida, USA), Beever et al. (1979) found that *Aratus pisonii* can damage up to 80.6% (mean=46.8%) of the leaves of the red mangrove and up to 7.1% (mean=3.3) of the leaves area; these numbers translate in a mean consumption of 35.3 cm³ of leaf area per month. *A. pisonii* is an important biomass exporter; Warner (1967) estimated that the average output of *Aratus* is 207 eggs per day per m². Most of this effort is consumed by aquatic organisms, given that the survival rate from egg to adult is only 0.041% (Warner, 1967). Another contribution of *Aratus* as a biomass exporter

is through frass. Beever et al. (1979) estimated that an adult *Aratus* would introduce 8.8 cm³ of frass per month into the aquatic system.

In Australian mangroves, Smith (1987ab) found that crabs belonging to the family Grapsidae can shape mangrove species distribution and abundance, through selective predation of propagules. In some Neotropical mangrove forests the results do not support the dominance-predation model (Smith et al., 1989). In Florida, no *Rhizophora mangle* propagules were eaten (Smith et al., 1989). However, in Panamá, more propagules were consumed in the low intertidal, *Rhizophora*-dominated forest than the high intertidal, *Avicennia*-dominated forest, but there seems to be less predation on *Rhizophora* in Florida and Panamá than in Malaysia and Australia (Smith et al., 1989). The predators responsible for consumption of propagules appear to be the grapsids *Aratus pisonii* and *Sesarma curacoense*; unidentified burrowing crabs; unidentified water-borne organisms (probably fishes); and the snails *Melampus coeffus* and *Cerithidea scalariformis* (Smith et al., 1989). The grapsid *Goniopsis cruentata* has also been observed to frolic with *Rhizophora* propagules in Venezuela (J. E. Conde, *personal observation*). Other important herbivores are the Scolitidae (Coleoptera) which attack the seedling of the red mangrove (Padron et al., 1993).

8.2 Hurricanes and tropical storms

The consequences of hurricanes Hugo, Gilbert, and Joan, that struck the Caribbean in 1988-1989, were studied in many terrestrial plant communities and populations (Walker et al., 1991). Nevertheless, mangrove forests were not specifically evaluated in that issue.

Tides and waves, which may cause excessive siltation or erosion, produced by hurricanes and storms are considered natural stressors of mangroves (Lugo, 1980). In the model of Cintrón et al. (1978), hurricane

cycles are one of the most important external factors in mangrove function. Hurricanes may act as catalysts of succession or may retard or stop it in any of its cyclic stages (Lugo, 1980). Also, they could prevent mangrove forest from reaching structural complexity, as could be the case in Florida (Lugo, 1980). Periodic exposure of Caribbean mangroves to hurricanes and storms has been suggested as one of the mechanisms responsible for the low structural complexity and lack of climax elements in those forests (Roth, 1992).

Although there is an extensive literature where accounts of mangrove damage by hurricanes is included, most of them are descriptions of the immediate consequences, and do not consider the long-term effects and the responses of mangroves to these climatic disruptions (Roth, 1992). The damages can include defoliation, shearing of branches and trunks, and uprooting of trees (Roth, 1992). The process of recuperation is slow (Lugo & Snedaker, 1974), and depends on species and topographic characteristics, sedimentation and drainage patterns, and proximity to the hurricane pathway (review in Roth, 1992). The regeneration of the mangrove forests usually starts immediately thanks to the surviving seedlings and saplings (Alexander, 1967; Wunderle et al., 1992).

Roth (1992) carried out a detailed study of the impact of hurricane Joan and the regeneration of a mangrove forest in Nicaragua. Thirty-six percent of the trees died, representing 68% of the basal area of the pre-hurricane stand. The supression was not random, larger trees were the most affected. As a consequence, the complexity index was lowered. Abundant regeneration by all the original mangrove species appears to have been favored by the hurricane. Seventeen months after Hurricane Joan struck the mangrove stands, seedlings of Rhizophora mangle, Avicennia germinans and Laguncularia racemosa were growing in great numbers throughout the stand, except on those places where the fern Acrostichum was present. The responses of Rhizophora mangle, Avicennia germinans and Laguncularia racemosa to the damages produced by the hurricane were dissimilar (Roth, 1992). Sprouting capacity and initial seedling density were the lowest in R. mangle. This species, however, showed the highest seedling survival rate and an intermediate seedling growth rate. L. racemosa showed the highest sprouting capacity, although its seedling survival rate was the lowest. Initial seedling density was highest in A. germinans, but seedlings grew slowly.

Roth (1992) points out that post-hurricane mangrove stands development is relevant to its management. It would appear that periodic, small-scale harvests, could offer a combination of protection and profitable use in those places where hurricanes are frequent.

8.3 Oil contamination

Contamination of mangrove swamps by oil is common place in much of the tropics, and has received much attention from scientists, in particular those working in threatened areas such as the Caribbean and Gulf of Mexico coasts. Mangroves, due to their particular geographic and hydrographic settings, are particularly vulnerable to oil contamination (Gundlach, 1987).

Major causes of oil contamination in mangroves are spills of various sizes following tanker accidents and other shipping incidents, damaged pipelines and blow-outs. Other, generally small-scale contamination events occur during loading and unloading operations in ports and terminals, such as overloading of tanks, tank cleaning, malfunction of valves and carelessness while connecting and disconnecting hoses. Such "small" spills however, can involve up to 5 tons of oil (Baker, 1982). Without doubt accidents involving large tankers cause the most impressive impacts on mangroves, since they involve large quantities of oil up to a hundred thousand barrels, and may affect pristine mangrove forests along extensive coastlines with devastating and long lasting consequences.

New World mangrove forests have witnessed many such accidents, in particular during the 1960-1970's, when regulation and safety procedures were not commonly in use. Between January 1974 and June 1990, 31 oil spills occurred near coastlines in the Caribbean, Florida, the Bahamas and the east coast of Mexico (Burns et al., 1993). Other spills occurred in the open Caribbean and Atlantic, in the Amazon and Orinoco Rivers and unspecified localities in the Caribbean. One of the first accidents to receive attention from mangrove scientists was the spill of nearly 70,000 barrels of crude oil from the "Argea Prima", in Puerto Rico in 1962. Oil accumulated preferentially on mangrove roots and large mortality of invertebrates, fish and turtles were reported (Díaz-Pferrer, 1962). Along the Panamá coast, Rützler & Sterrer (1970), reported reduction of many invertebrate species after the soaking of mangrove sediments with diesel oil from a 15,000 barrel carelessness while connecting and disconnecting spill

from the "Witwatter", in 1968. Jernelöv *et al.* (1976) described short-term and long-term effects of a spill of crude oil from the "St Peters", along the Ecuador/Colombian coast. Short-term effects followed a thick oil covering of roots and trunks, resulting in partial defoliation, large mortality of sessile animals and reduction in crab density. After removal of oil by wave action, defoliated parts recuperated as well as invertebrate populations through migration from non-affected areas. Chan (1976; 1977) studying the effects of a small (1,500 to 3,000 barrels) spill of crude oil in Florida Keys, showed that *R. mangle* seedlings were killed when over 50% of their surface was oiled and *A. germinans* trees were also killed when 50% of the pneumatophores were oiled.

More recent accidents involving oil spills and mangroves received better attention and detailed studies. For example, the effects of the 37,000 barrels of crude oil spill from the "Zoe Colocotroni", in a Puerto Rican mangrove were monitored for over 10 years after it occurred, by many authors. A summary of their major findings showed that three years after the spill, *R. mangle* and *A. germinans* trees which were defoliated following the spill had died, and associated fouling communities were reduced to a great extent (Nadeau & Bergvist, 1977). After four years, the oil present in sediments had been highly weathered, even in the most affected areas. Recolonization by seedlings from unaffected adjacent mangrove forests was observed for the first time (Page *et al.* 1979). However, two years later, the remaining oil in the sediments was still affecting the infauna, although colonization processes were already in progress (Gilfillan *et al.*, 1981).

In Venezuela, Bastardo (1991,1993) studied the dynamics of mangrove leaf decomposition under the influence of hydrocarbons in the Tacarigua coastal lagoon. The results suggested that decomposition rates were accelerated by the presence of hydrocarbons. However, after 14 days of exposure there was no traces of hydrocarbons left.

Finally the best studied case of oil spill in American mangroves followed the spill of nearly 8 million liters of medium weight crude oil on April 27th, 1986, from a ruptured storage tank in the Caribbean coast of Panamá (Jackson *et al.*, 1989). After 20 days, the oil spilled over the coral reefs fringe and reached the mangroves.

Upon reaching the mangroves, the oil accumulated on proproots and pneumatophores, immediately killing the fouling communities. When defoliation started, just one month after the spill, branches lacking the weight of leaves flexed upward lifting the roots and thus killing also the subtidal epibiota that had escaped from direct oiling.

A band of defoliated trees was apparent within two months of the spill and it widened thereafter. After 10 months a band of dead mangrove trees (18 to 100 m wide) had been formed and after 19 months dead mangroves occurred along 27km of coastline. After 15 months over 60% of roots were dead, broken or rotting. *Rhizophora mangle* seedlings planted in the area failed to produce leaves, therefore the mangrove fringe habitat was largely destroyed and will not recover until new trees will be able to grow there.

The results of these studies allowed the proposition of a pattern of events occurring in mangroves affected by oil spills. Getter *et al.* (1981), compared the effects of 5 oil spills on mangrove areas of Gulf of Mexico and the Caribbean Sea. Despite the different circumstances of these spills, there were a number of common effect which included a series of stress symptoms and damages. In general at all sites, defoliation immediately follows the spill, resulting in deaths of the three, depending on the proportion of crown defoliated. Leaf deformation was also a common symptom at all al sites. Mortality of seedlings generally occurred later due to availability of internal reserves.

Stress symptoms observed following an oil spill, are leaf necrosis, root malformation and alterations in leaf morphology; these major symptoms correlate well with most others, and always correlate with the degree of stress imposed on the plant. Mangrove leaves become significantly and proportionally shorter and narrower just after the onset of the stress (Getter *et al.*, 1985).

Tree mortality due to oil contamination has been frequently related to the obvious blocking of gas-exchange surfaces by the oil coating. However, the waxy nature of mangrove surfaces, both leaves or seedlings, could minimize the effect of the coating (Getter *et al.*, 1985). Mortality seems to be more likely a result of the toxicity of the oil derivates and/or dispersants which results in the degradation of plant metabolism. Toxic effects on roots decrease transpiration in mangrove plants. Physical damage of stomata is common due to coating affecting gas exchange and photosynthesis, an unbalance of the

transpiration/osmotic regulation system will immediately lead to permanent damage to the plant's metabolism (Getter et al., 1985; Getter & Ballou, 1985).

Significant differences in response to oil by different mangrove species have also been reported and have been attributed to the differences in the physiology of the various mangrove species. For example, R. mangle seedlings resist better and recuperate faster than A. germinans, from chronically exposed sites. This seems to be related to the "filtering" capacity of R. mangle roots to cope with the saline environment. This mechanism which has been shown to be effective for salt exclusion and trace metals exclusion (Lacerda et al., 1986), is also probably efficient in avoiding the uptake of toxic substances derived from oil. On the other hand, A. germinans that lacks this filtering mechanism and regulates osmotic balance through excretion of salt through glands in the leaves, would more readily absorb toxic oil derivatives (Getter et al., 1985).

Site conditions and type of oil, are the key determinants of mangrove recovery after a spill (Jacobi & Schaeffer-Novelli, 1990). Removal of oil is dependent on the export of sediment particles and litter deposited in the sea. These fluxes are dependent on tidal amplitude and the consequent extension of flooded area during high tide (Ovalle et al., 1990). Removal time will be different along a given forest, resulting in a uneven distribution of the effects. For example Burns et al. (1993) demonstrated that up to 20 years are necessary for deep mud coastal habitats to recover from the toxic effects of catastrophic oil spills. Defoliation and mortality are more intense in the inner parts of forests, where oil stays longer and weathering forces such as waves and currents are less effective. The outer fringe generally shows less serious effects, such as partial defoliation, root loss and loss of fouling communities. This difference however, will be smaller at very protected sites, where there is lack of intense waves or currents, the seaward fringe can also be strongly affected. Also, the use of dispersants greatly reduces the retention of petroleum hydrocarbons in mangrove sediments, reducing their availability for plant uptake and accelerating weathering processes, and therefore the forest recuperation.

9. Mangrove Uses

Mangroves play an important role in tropical coastal economies providing many goods and services for the human population. These include: coastline protection and stabilization, nursery for a variety of economically important shellfish and finfish, and source of important products for the coastal human populations in the form of timber, firewood and charcoal, chemicals, medicine and waterways for transport, enrichment of marine coastal waters by nutrients, and an environment for aquaculture, although some of these benefits are at present poorly understood or unrecognized in Latin America countries. Examples of the importance of such direct and indirect benefits provided by mangrove are significant for the rational management of the Latin America coastal belt.

Waterways protection using mangroves are common in Ecuador and Colombia. In Brazil, mangroves have recently been included in the management plans of marinas and coastal condominiums. In Panamá, up to 60% of total shrimp fisheries is based on 5 species which depend on mangroves for completing their development. Along the Maranhão coast, North Brazil, the huge shrimp production includes two species of shrimps which develop in the local mangrove waters. Apart from these indirect benefits, mangrove products themselves are particularly important for many coastal populations. Firewood and charcoal seems to be the major uses of mangroves in Latin America. In countries like Nicaragua, where nearly 80% of households uses wood for cooking, mangroves provide a significant percentage of firewood. In Brazil annual firewood extraction reaches up to 9,000 m³. In Honduras the use of firewood may range from 80,000 m³ to 120,000 m³, while in El Salvador, with only 350 km² of mangroves, up to 30,000m³ of firewood are extracted annually. In Brazil, mangroves are a regular source of firewood for bakeries and potteries, even along the most developed areas of the Southeastern coast (Araújo & Maciel, 1979).

Charcoal production is another major use of mangrove wood, although only a fraction of the total yield is collected due to inefficient extraction techniques. In Costa Rica up to 1,300 m³ of mangrove charcoal is produced annually in the Terraba-Sierpe forests, while in Panamá this may reach up to 7,400m³. Mangrove bark is still a source of tannin in most Latin America countries. Bark yields range from 1,840 to 4,490 kg.ha⁻¹ in Costa Rica, and bark

production in Panamá may reach over 400 tons.yr^{-1}. At the Parnaíba River Estuary, Piauí, Brazil, mangroves support over 10,000 people who depend on artisanal crab fishing.

Despite their importance for most coastal tropical countries in Latin America, mangrove ecosystems have been witnessing an accelerated rush for their resources, most of the time without the necessary care to maintain their integrity and threatening their sustainable utilization. Estimates of deforestation in mangrove areas of Latin America are few. Central America has annual cover losses estimated for Nicaragua (385 ha); for Guatemala (560 ha) and for Costa Rica (45 ha), mostly for conversion into rice fields, salt ponds and mariculture. In Ecuador nearly half of the mangrove area (ca. 80,000 ha) has been deforested for various purposes, in particular for shrimp ponds, during the last two decades. In the Ilha Grande Bay, southeastern Brazil, which harbored nearly 600 ha of mangrove forests in the early 80's, nearly 80% of it have been reclaimed to build condominiums and marinas.

Apart from deforestation itself, degradation of large mangrove areas is taking place in many Latin America countries due to misuse of coastal resources. Diversion of freshwater for irrigation and land reclamation purposes has been one of the major actions leading to mangrove degradation (Conde & Alarcón, 1993). The mangroves of Guanabara Bay, Rio de Janeiro, which reached nearly 50km^2 in the beginning of the century, is presently nearly totally degraded with less than 15 km^2 of pristine forests, mostly due to clearcutting of creek and river banks, oil spills, solid wastes dumping and decreased freshwater inputs. In French Guyana over 20,000 ha of mangroves have been cut for rice culture and large amounts of fungicides, pesticides and fertilizers are being used (K. Wood. pers. comm.). In the insular Caribbean and the Caribbean coast of Venezuela, tourism development in coastal regions has been the major destroyer of mangrove areas (Aristiguieta, 1980; Hudson, 1983; Bacon, 1987). One of the few mangrove silviculture experiments in Latin America was carried out in Venezuela from 1969 until the mid 80's. In 1969 a vast area was granted to TAMAVENCA (Taninos y Maderas de Venezuela), in concession for 30 years to exploit timber in the Guarapiche Forest Reserve, San Juan River. This mangrove use has been considered a well planned forestry enterprize (Canales, 1983). However the results were not satisfactory. In 1983 only 20% of the proposed area were actually exploited and with a low yield of 150 m^3.ha^{-1}

of timber compared to over 500 m^3.ha^{-1} expected. Recovery from this damage is still incomplete (Medina, E. pers. com.).

Pressures and menaces on mangrove forests vary from country to country, and even within a country, nearby localities can suffer different consequences. In some places the damage is inflicted slowly, and the degradation rate escapes the eye. In other instances, degradation occurs instantly and can reach dramatic proportions. These deleterious actions have not gone uncontested. A rich legislation has been developed in many countries. Since D. José's Edict, in the XVIII century, in Brazil, up to the 70's, when Carlos Andrés Pèrez, promulgated a presidential decree to specifically protect the Venezuelan mangroves, efforts have been made to face mangrove degradation within a legal frame. The results have varied and were not always successful. Another avenue for mangrove preservation has been that of non-governmental organizations which develop programs in mangrove conservation awareness. The success of this approach however remains to be evaluated and is a long term task. Finally, rational sustainable use and development of mangroves in Latin America and the Caribbean is a task in which scientists play an important, but theirs is not the only role. Politicians, planners, decision makers, engineers, entrepreneurs, villagers should also be involved in the conservation of a resource whose ecological, scenic, medicinal, aquacultural and silvicultural values, among others, are unique and a heritage to be preserved.

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