
Modern and Quaternary Palynological Studies in the Caribbean and Atlantic coasts of Northern South America: A Paleoecologically-Oriented Review

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ABSTRACT

The present paper reviews the palynological studies developed on modern and Quaternary sediments from northern South America, in order to plan future paleoecological work. The present coastal flora and vegetation as related to sedimentary environments and human disturbance are also reviewed, because they are needed to interpret the spatial and temporal patterns of palynological assemblages.

Most of the modern analog studies developed so far, are oriented to find a general relationship between palynomorphs in sediments, potential vegetation sources and coastal environments. Detailed studies are scarce, and quantitative calibrations of proxies are lacking. Concerning Quaternary studies, most records embrace the last glacial cycle, and the emphasis is placed on the last glaciation and the climate of the Amazonia lowlands during the Last Glacial Maximum. In the coasts, a characteristic, symmetric and recurrent vegetation succession has been recorded during the glacial regressive and transgressive phases. Holocene pollen records are interpreted mainly in terms of sea level rise after the last glaciation. However, detailed studies on the last two millennia, useful for prediction purposes in a Global Change perspective, are lacking.

Future work suggested include: 1) detailed modern-analog local studies, preferably near the coring sites, 2) calibration of proxies, especially for parameters such as temperature, salinity and distance to the coast and 3) high-resolution studies on shallow cores, accurate dating and isotopic analysis to provide temperature, sea-level and human-disturbance record during the last centuries.

Key words: South America, Palynology, Paleoecology, Modern analogs, Quaternary, Global Change

RESUMEN

Este artículo es una revisión de los estudios palinológicos efectuados hasta ahora en el norte de Sudamérica, en sedimentos actuales y cuaternarios, con el objetivo de planificar investigaciones futuras.

La mayoría de los estudios de análogos modernos se han orientado a establecer relaciones generales entre los palinomorfos en los sedimentos, las fuentes potenciales de los mismos y los ambientes de sedimentación costeros. Los estudios más detallados son escasos y no existe ninguna calibración de indicadores ecológicos o ambientales indirectos (proxies). Con respecto al Cuaternario, la última glaciación y el clima de las tierras bajas de Amazonia durante el último máximo glacial han sido los temas preferentes. En las regiones costeras, se ha registrado una sucesión simétrica y repetitiva, de la vegetación ligada a los cambios del nivel del mar durante las glaciaciones. Los estudios palinológicos del Holoceno se refieren principalmente al ascenso del nivel del mar después de la última glaciación, pero no existen estudios detallados de los dos últimos milenios, que pudieran contribuir a predecir el futuro, en el marco del Cambio Global.

Las principales líneas de investigación futuras que se proponen son: 1) estudios detallados de análogos modernos, 2) calibración de proxies, sobre todo en lo referente a temperatura, salinidad y distancia a la costa y 3) estudios de alta resolución de perforaciones someras, junto con dataciones detalladas y estudios isotópicos, para obtener registros de la temperatura, el nivel del mar y la influencia humana, durante los últimos siglos.

Palabras clave: Sudamérica, Palinología, Paleoecología; Análogos modernos, Cuaternario, Cambio Global

Introduction

Neotropical coastal palynology, although not as developed as for example mountain palynology, has shown a great potential for paleoecological purposes, mainly related to record past climates, sea level changes and human disturbance (for example, Thanikaimoni 1987). In addition, many studies on pre-Quaternary palynostratigraphy and paleoecology deal with coastal sediments (Germeraad *et al.* 1968; Frederiksen 1985), and has permitted to develop evolutionary and biogeographical hypotheses on coastal vegetation, especially mangroves (Graham 1995; Rull 1998b, c).

In northern South America (Fig. 1), despite the success of palynology in recording vegetational, climatic and sea-level changes during the Late Pleistocene and Holocene (Van der Hammen 1963; Tissot *et al.* 1988), very few of these works have been carried out. The present palynoflora and the patterns of modern pollen sedimentation are not well known, except for the classical works of Muller (1959) and Van der Hammen (1963). Recently, a paleoecological project within the frame of the Global Change has started on the Venezuelan coasts (Rull, & Vegas-Vilarrúbia, in press; Rull *et al.*, 1999) in order to 1) record the natural component of past changes in climate, sea level and

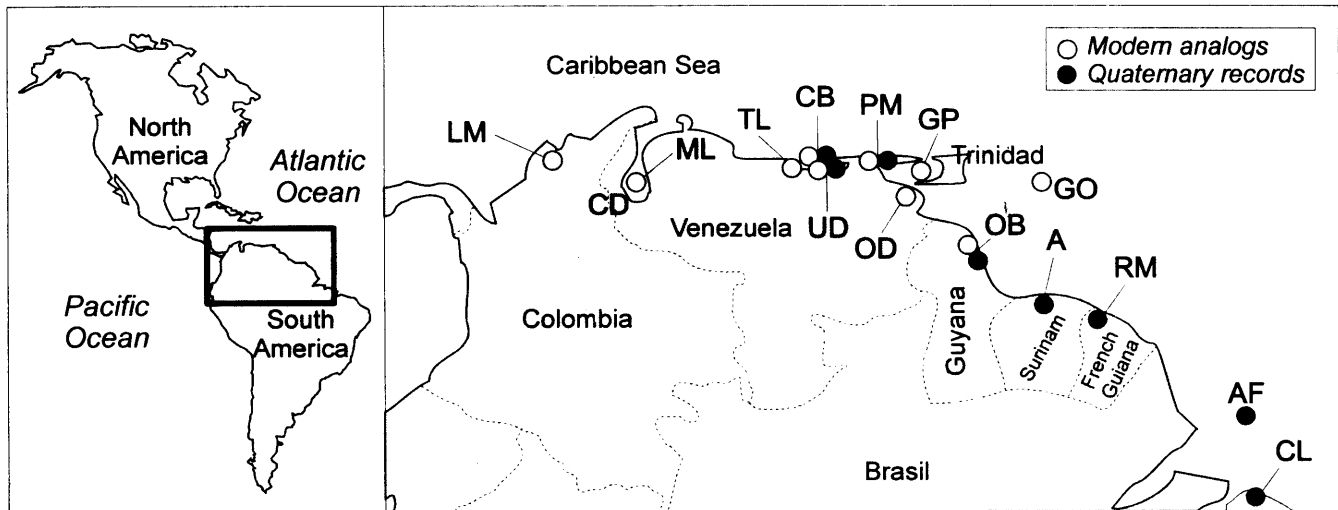


Figure 1

Location of sites referred in the text. LM = Lower Magdalena, CD = Catatumbo delta, ML = Maracaibo Lake, TL = Tacarigua lagoon, CB = Cariaco basin, UD = Unare delta, PM = Playa medina, OD = Orinoco delta, GP = Gulf of Paria, GO = Guianas Offshore, OB = Ogle Bridge, A = Alliance, RM = River Mana, AF = Amazon fan, CL = Curuça lagoon.

vegetation (especially during the last millennia), to be considered in the prediction of future situations and 2) study the relationships between pollen assemblages and sedimentary environments, to facilitate paleoenvironmental studies. However, a great amount of taxonomic and sedimentological work is still needed to reach fully satisfactory results. The present paper is a first step that reviews the main results obtained so far in the study of present palynomorph sedimentation and the Quaternary studies, in the northern South American coasts, in order to plan the future work. The review is subdivided into four main parts: 1) an overview of the coastal sedimentary environments, 2) a summary of the more relevant plant communities related to them, 3) a view of present palynomorph sedimentary patterns as modern analogs and 4) the most significant paleoecological results obtained so far. Finally, some proposals for future studies are erected.

Coastal Sedimentary Environments

The classification of coastal clastic environments used so far for palynological purposes roughly coincides with current sedimentological knowledge, but a comparison of environmental classifications is beyond the scope of the present paper. It was proposed initially by Hopping (1967), and further refined by Lorente

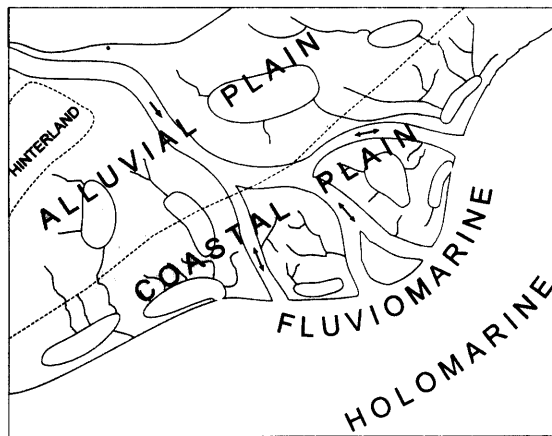


Figure 2

Sketch of the coastal sedimentary environments, according to Hopping (1967) and Lorente (1986). Arrows indicate the main directions of water currents.

(1986). There are four main provinces, as related to topography and seawater influence (Fig. 2): the 'hinterland', the alluvial plain, the coastal plain and the

marine domains. The 'hinterland' is constituted by the more interior and elevated sites, its major transport agent being rivers, and the main sinks, freshwater lakes. The alluvial plain is situated between the 'hinterland' and the coastal plain and is not under the influence of tides, therefore, waters are also fresh. Characteristic subenvironments of this environment are seasonal or permanent floodplains and lakes, depending on the precipitation regime of their catchment area. In seasonally-flooded alluvial plains, sediments suffer aerial exposure, with the consequent oxidation of sedimentary organic matter, which is preserved only locally in lakes, ponds, abandoned channels (oxbow lakes) and swamps. The coastal plain is the outermost continental belt, and can be further subdivided into upper and lower coastal plain. Both are under the influence of tides, but the upper coastal plain is only affected by the higher, less frequent tides; whereas the lower coastal plain, also called the tidal belt or the mangrove belt, is directly under the influence of normal tides, and is permanently flooded by brackish to saline waters. It is worth to mention that brackish waters can penetrate upstream through the main river channels, extending locally lower coastal plain conditions (mainly related to waters and biota) into the upper coastal plain.

In a deltaic complex, Muller (1959) distinguished three main landscape regions. In the upper delta, seasonal fluctuations in water level predominate and well developed levees are present, thus coinciding with the alluvial plain. The central delta shows less pronounced levee building and tidal fluctuations are restricted to the *caños* (river channels), a situation typical of the transition between the alluvial plain and the upper coastal plain. Finally, in the outer delta, the influence of tidal fluctuations is strongly felt and an adequate supply of mineral sediment is present, therefore coinciding with the lower coastal plain. The central delta and the outer delta together are called the lower delta by Lorente (1986), using the criterion of tidal influence. Flooding is one of the most conspicuous characteristics of coastal systems, and terms such as 'marsh' or 'swamp' are frequent in the literature, and sometimes used indistinctly. However, according to Van der Hammen (1963) the term 'swamp' implies permanent inundation, whereas 'marsh' refers to an environment with marked seasonal fluctuations in the water-content of soil, ranging from flooded to very dry. No special mention to the water salinity is done in this terminology.

Marine environments close to the coast line, from the mangrove belt to approximately 50 km offshore (depending on the delta size, marine currents and the type of shelf), still show some continental influence, through the river discharges, and are called fluvio-marine. Holomarine or normal marine environments start where the fluvial influence ceases.

Present Vegetation

The following description of the coastal vegetation belts is based on the published literature, and focused on a general taxonomic characterization. However, some additional environmental features that could be of importance for paleoecological interpretation will also be mentioned. The purpose is not to give a complete account of all the botanical work developed in the Northern South American coasts, but to exemplify typical sea-land transects of paleoecological interest in which most palynological studies have been developed. Unfortunately, most studies are in the so-called 'gray' literature (Conde & Alarcón 1993), like for example unpublished undergraduate thesis, reports of restricted

circulation, local journals and books, etc. There are also some scattered individual observations in local or regional floras, but studies on coastal vegetational gradients as related to their determining factors are lacking, except for few comprehensive works like the classical study of Surinam by Lindeman (1953). For this reason, descriptions are based on the work carried out mainly in the Orinoco delta and the Guianas, Trinidad (Bacon 1993), and the northern coasts of Brasil (Kjerfve & Lacerda 1993). Central America, although geographically close to northern South America, is biogeographically different, because of the long history of isolation due to the very recent closure of the Panama isthmus (Duque-Caro 1990; Graham 1992).

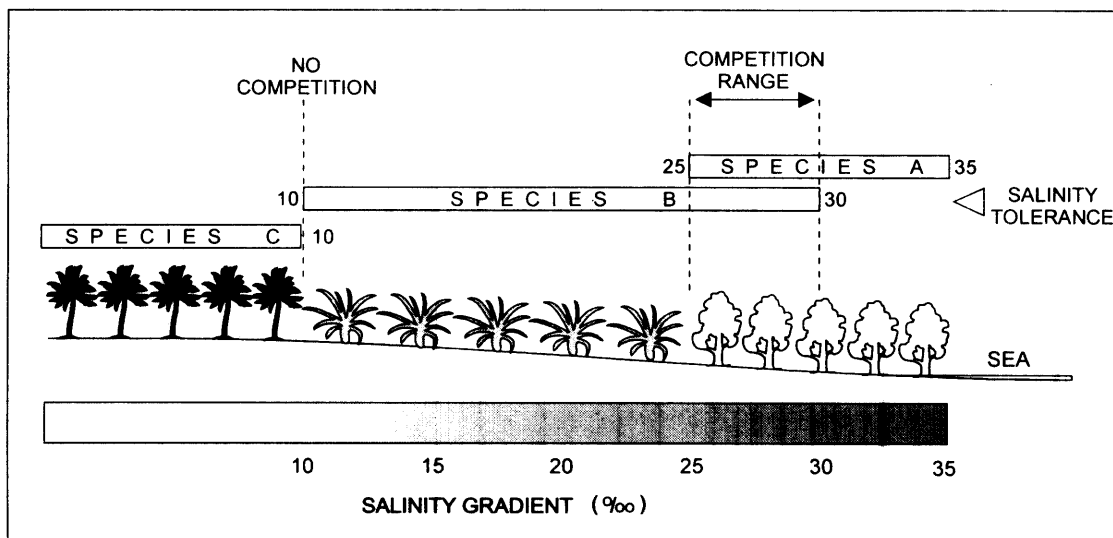


Figure 3
Hypothetical example of vegetation zonation in coastal environments, related to the salinity gradient and the competition among species.

TYPES	FRESH		BRACKISH			SALT
	Oligotrophic	Eutrophic	Oligohaline	Mesohaline	Polyhaline	Euryhaline
	< 100 (mg Cl/l)		(100-1,000)	(1,000-10,000)	(10,000-17,000)	Hyperhaline (>17,000)
1						
2						
3						
4						
5						
6						
7						
8						
9						
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12						
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29						

Figure 4

Salinity tolerance for the principal coastal plants of Surinam living on swamps and marshes (Lindeman 1953). 1 - *Iresine, batis*; 2 - *Sporobolus, Sesuvium, Fimbristylis*; 3 - *Avicennia, Eleocharis mutata*, 4 - *Laguncularia*; 5 - *Rhizophora*; 6 - *Cyperus articulatus*; 7 - *Mariscus*; 8 - *Cyperus polystachyos*; 9 - *Acnida cuspidata*; 10 - *Acrostichum*; 11 - *Fimbristylis ferruginosa, F. spadicea*; 12 - *Ruppia, Paspalum, Brachypteris, Rhabdadenia*; 13 - *Rosenbergiodendron*; 14 - *Hibiscus, Paspalidium, Phragmites*; 15 - *Machaerium, Torulinium, Scirpus*; 16 - *Typha, Jussieua leptocarpa, Mikania, Cissus parkeri*; 17 - *Leersia*; 18 - *Neptunia*; 19 - *Cydista, Eclipta, Ipomoea tiliacea, Canna*; 20 - *Montrichardia*; 21 - *Panicum, Solanum, Entada, Ceiba, Coccoloba, Crataeva*; 22 - *Sacciolepis, Phaseolus*; 23 - *Hura, Annona; Cyperus giganteus, Thalia, Aeschynomene, Jussieua affinis, J. decurrens, J. erecta, J. suffruticosa, Luziola, Cissus sicyoides, Paullinia, Ipomoea park., I. subrevoluta, Azolla, Salvinia, Pistia, Nymphaea, Hydrocotile, Nymphoides*; 25 - *Andira, Triplaris, Erythrina, Cordia, Bactris, Inga, Diospyros, Cecropia, Spondias, Couroupita, Tabebuia*; 26 - *Blechnum, Helyconia, Ghrysobalanus*; 27 - *Dryopteris, Nephrolepis, Pityrogramma, Cyperus haspan*; 28 - *Fuirena, Rhyncospora cyperoides, Eleocharis interstincta, Jussieua nervosa*; 29 - *Lagenocarpus guianensis, Eleocharis plicarhachis, Rhyncospora triflora*.

One of the most conspicuous characteristics of the coastal vegetation is the zonal arrangement of communities, which more or less parallels the sedimentary environments and is governed by both physical and biological factors. The interplay among seasonal flooding, tide activity and mesotopography produce a salinity gradient from the sea to the continent, that is an important controlling factor. It is responsible, for example, of the occurrence of mangroves in the saline lower coastal plain, and swamp forests in the alluvial floodplains. However, despite the progressive and continuous character of the salinity decrease, plant communities are arranged in few, distinct belts with sharp boundaries and short ecotones, if any, due to species replacement (Emlen 1977). Indeed, each vegetation belt has its typical components, and they only rarely occur in more than one of these plant communities. This is caused to two main ecological factors, namely salinity tolerance and interspecific competition (Holland *et al.* 1990; Shugart 1990). The simplest case is that of hypothetical species B and C from Fig. 3, which boundary is sharp due only to the salinity tolerance of each plant. However, salinity tolerance itself cannot explain the zonal pattern. For example, Figure 4 shows the tolerance to salinity of the most important species of the Surinam coasts. Two main observations are pertinent. The degree of overlapping is notorious, and the whole picture suggests a continuum with no definite boundaries. To exemplify the effect of interspecific competition in overlapping ranges, the hypothetical example of Fig. 4 can be used. Hypothetical species A is stenohaline, able

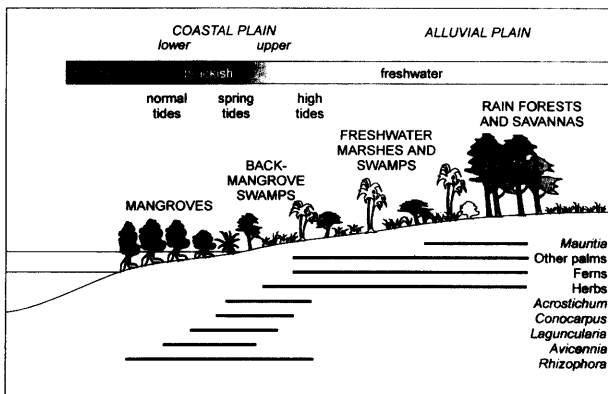


Figure 5

Idealized transect showing the main vegetation coastal belts in northern South America, as related to sedimentary environments and salinity. Discussion and references in the text.

to live in a narrow range of high salinities; whereas B is euryhaline, and can develop in a wider but lower salinity

range. The potential ranges of both species overlap in the region of 25-30 ‰, but their effective ranges have a sharp contact at 25 ‰, due to the competitive superiority of A at these salinities. Usually, stenohaline species are more efficient in their narrower salinity ranges, while euryhaline taxa, although they can tolerate wider ranges are less efficient in a particular interval, especially toward the extremes (Margalef 1977). Although the described seem to be among the main driving factors of the zonal pattern of coastal vegetation, others such as edaphic oxygen, light penetration, temperature, precipitation, evapotranspiration, wave energy, sedimentation, nutrients, etc. have been proposed as to be of importance (review in Pannier & Pannier 1989). A general idealized scheme of the vegetation zonation in the northern South America coasts can be seen in Fig. 5. In it, four main zones can be distinguished, from the coast to inland terrains: mangrove forest, back-mangrove swamps, freshwater marshes and swamps, and inland forests and savannas. Although dune and beach ridge vegetation is present in some areas, it is of little palynological importance (Muller 1959). The outermost vegetation belt is the mangrove (also called mangrove forest or mangrove swamp), a uniform vegetation type, permanently inundated by saline to brackish waters, dominated by mangrove-forming trees with regional differences in occurrence and composition: *Rhizophora* (Rhizophoraceae), *Avicennia* (Avicenniaceae), *Laguncularia racemosa*, *Conocarpus erectus* (Combretaceae) and *Pelliciera rhizophorae* (Pellicieraceae). The latest is restricted to a small region of central America and the pacific coast of Colombia and Ecuador (Tomlinson 1986), but the others are widespread in the region considered. An internal zonal pattern can also be seen within the mangrove fringe. A typical sea-land arrangement is *Rhizophora-Avicennia-Laguncularia-Conocarpus* (Chapman 1976), but local variations can occur. In the Orinoco delta and the Guianas, mangroves are formed mainly by the association of *Rhizophora-Avicennia*, while *Laguncularia* occurs only locally or in lower numbers (Muller 1959; Van der Hammen 1963). *Conocarpus* is almost restricted to upper, more stable substrates, and is not considered an important mangrove-forming tree by some authors (Tomlinson 1986). The dominance of either *Rhizophora* or *Avicennia* in the mangroves is dependent on salinity and sedimentological characteristics. The first one is always dominant in the most seaward belt, on the flooded mud-flats, while the second needs a more silty and settled soil, and is more common in the inner mangrove belt. Both can penetrate inland along the estuaries and 'caños', but *Avicennia* disappears first upstream, and *Rhizophora* latter, attaining the boundary with freshwaters (Van der Hammen 1963). Only scattered freshwater occurrences of *Rhizophora* have been recorded (Lindeman 1953), and it can be considered

an indicator of the boundary brackish conditions. Among the associated mangrove taxa, *Acrostichum aureum* (mangrove fern, Acrostichaceae), *Hibiscus tiliaceus* (Malvaceae), *Sesuvium portulacastrum* (Aizoaceae), *Iresine* (Amaranthaceae) and other herbs may occur, especially at the margins (landward), where the forest is a little more open, and in elevated sites (Van der Hammen 1963; Tissot *et al.* 1988; Kjerfve & Lacerda 1993). *Epiphytes* of the families *Orchidaceae* and *Bromeliaceae* are common in coasts where mangroves are close to montane forests. Among the main secondary invaders of mangroves under disturbance, *Dalbergia* (Papilionaceae) and *Rhabdadenia* (Apocynaceae) deserve mention (Kjerfve & Lacerda 1993; Rull & Vegas-Vilarrubia, in press).

There are many environmental features associated to the existence of mangroves, but from a sedimentological point of view, protection from wave action and an adequate supply of silt and clay are essential, in order to provide a suitable substrate for the mangrove trees to grow. This implies the existence of sand or coral barriers and wet climates in the catchment area, with enough precipitation to guarantee a minimum amount of erosion and fluvial transport and, consequently, sediment supply. For this reason, the arid coasts often do not possess the abundance of suitable physiographic features to enable mangrove to develop (Chapman 1976).

Behind the mangrove belt grow the so-called back-mangrove swamps, which are in the lower/upper coastal plain transition, where the influence of tides is more restricted and waters are fresh to slightly brackish, but flooding is permanent. This swamps can support forested (swamp forests or lower delta plain forests) or open vegetation (herbaceous swamps or lower delta plain peat swamps). The more characteristic components of the swamp forests are *Symphonia globulifera* (Guttiferae), *Vismia cayennensis* (Hypericaceae), *Pterocarpus officinalis*, *Mora excelsa* (Papilionaceae), *Bombax aquaticum* (Bombacaceae), *Virola surinamensis* (Myristicaceae), *Ilex* (Aquifoliaceae), *Tabebuia* (Bignoniaceae), *Carapa guianensis* (Meliaceae), and the palms *Jessenia*, *Euterpe*, *Manicaria sacchifera*, *Maximiliana regia* and *Bactris* (Muller 1959; Van der Hammen 1963 1988; Sheihing & Pfefferkorn 1984; Bacon 1993). The 'forêt marécageuse' (tidal forest) of Tissot *et al.* (1988) is similar in both composition and physiography. The 'morange' palm *Mauritia flexuosa* can occur where the forest is not too high and waters are fresh or almost fresh. Concerning the herbaceous swamps, they are dominated by *Cyperus giganteus* (Cyperaceae), *Typha angustifolia* (Typhaceae), *Acnida* (Amaranthaceae), *Sagittaria* (Alismataceae) and others. Other components are *Isoetes* (Isoetaceae), *Utricularia* (Lentibulariaceae), *Eichhornia* (Pontederiaceae), *Nymphaea* (Nymphaeaceae), *Polygonum* (Polygonaceae),

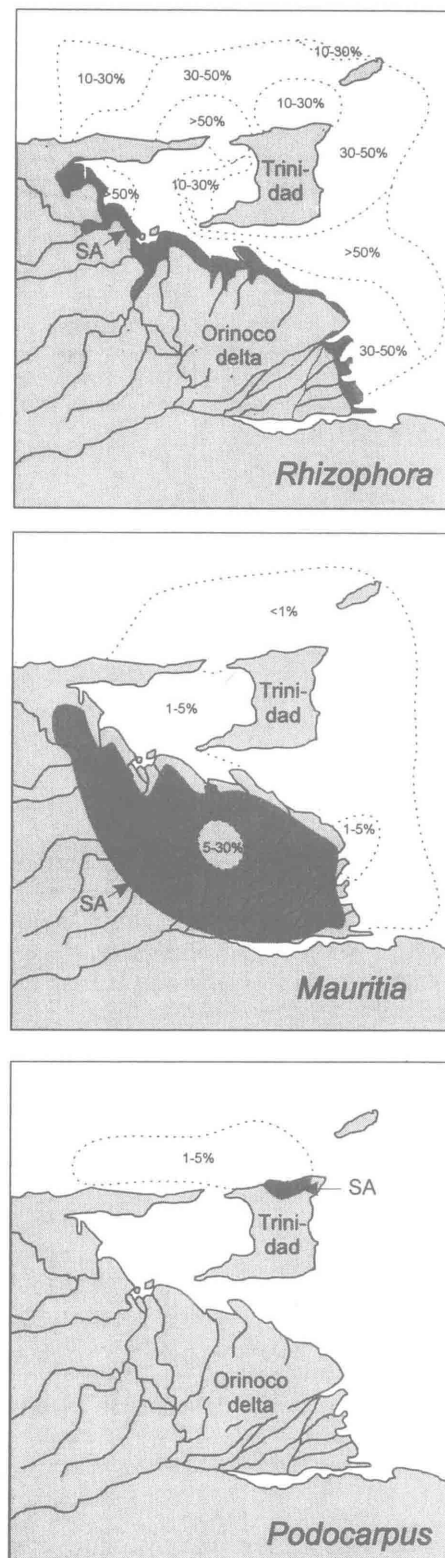


Figure 6
Relative abundance patterns of selected pollen in the Orinoco delta, as representative of different transport mechanisms. Redrawn from Muller (1959).

Cuphea (Lythraceae), *Jussiaea* (Oenotheraceae) and grasses (Van der Hammen 1963). Similar communities have been described as 'savannes marécageuses' (tidal savannas) by Tissot *et al.* (1988). In the Orinoco delta, *Blechnum* (Blechnaceae) and *Sphagnum* can be locally important on extensive peatlands up to 10 m depth. (Sheihing & Pfefferkorn 1984).

In the upper coastal plain/alluvial plain transition (central delta), where seasonal variations in water level predominate, several types of freshwater marshes and swamps can be found, in which trees, palms or herbs may predominate, but all of them are always present. For example, in Guyana, Van der Hammen (1963) distinguishes between the palm marsh forest and the palm marsh woodland, both dominated by palms (mainly *Euterpe*, *Manicaria* and *Maximiliana*), but the first one with trees as accompanying taxa (*Symphonia*, *Tabebuia*, *Pterocarpus*, *Cassipourea* [Rhizophoraceae], *Eschweilera* [Lecythidaceae], *Manikara* [Sapotaceae]) and the second with shrubs and bushes (*Clusia* [Guttiferae], *Tabebuia*, *Ilex*). In the Orinoco delta, this zone is also called the back-swamp by Muller (1959), who distinguishes the *Erythrina* swamp forest, the palm swamp, and the herbaceous swamp. In the first one, *Erythrina glauca* (Papilionaceae) is dominant but some palms like *Manicaria* and *Euterpe* may also occur. The palm swamp is an open, bush-like vegetation with emerging clusters of palms (*Mauritia*, *Manicaria*, *Euterpe*). A special case occurs when the soil is permanently waterlogged and forms a freshwater swamp in which almost pure stands of *Mauritia flexuosa* or 'morichales' cover extensive. Finally, the herbaceous swamps are of several types, depending on the dominance of ferns, sedges, low shrubs or floating grasses. These herbaceous communities form extensive peatlands in the center of the delta, being their main constituents *Montrichardia arborescens* (Araceae), *Leersia hexandra*, *Echinochloa colonum*, *Paspalum* (Poaceae), *Eichhornia crassipes*, *Heliconia* (Musaceae), *Eleocharis* (Cyperaceae), *Blechnum*, etc. (Sheihing & Pfefferkorn 1984). According to Muller (1959), these three communities (*Erythrina* forest, palm swamp and herbaceous swamps) can be intermingled in a mosaic pattern according to the sediment supply and the water regime, and probably constitute different seral stages of a single ecological succession.

The rain forests of the alluvial plain (upper delta) are flooded only seasonally by freshwaters. In the Orinoco delta, they are situated on the higher levees, and are submitted to intense human disturbance for agricultural purposes (Muller 1959). According to Sheihing & Pfefferkorn (1984), the upper delta plain forests form three layers: an upper story over 30 m high, an intermediate story of 20-25 m, and an open shrub layer. The upper story is dominated by *Ceiba pentandra* (Bombacaceae) and *Ficus prinoidea* (Moraceae). In the

intermediate story, *Inga* (Mimosaceae), *Erythrina*, *Swartzia leptopetala*, *Peltogyne* (Caesalpiniaceae), *Ficus*, *Cordia* (Boraginaceae), *Cecropia* (Moraceae), *Guazuma ulmifolia* (Sterculiaceae) and *Ouratea caracasana* (Ochnaceae) are present. The main components of the open scrub are *Faramea* (Rubiaceae) and *Gynesium sagittatum* (Poaceae). The inland savannas occur where a pronounced alternation exists of moisture and drought. During the rainy season large areas may be inundated, whereas the rest of the year the soil dries out completely. The vegetation is dominated by grasses and sedges, with intermingled shrubs and low trees, generally of *Curatella americana* (Dilleniaceae) and *Byrsonima crassifolia* (Malpighiaceae). Gallery forests and 'morichales' along the river courses are also frequent (Van der Hammen 1963, 1988).

Similar vegetation zones have been recognized in other tropical areas, but with different floral components. The most similar are those from the Central American Caribbean and Atlantic coasts, where the main mangrove trees are the same (except for the occurrence of *Pelliciera* in some areas), but the components of the other vegetation zones vary, since it is a different biogeographical region (Jacobs 1982; Rodgers & Horn 1996; Phillips *et al.* 1997). In south India, Caratini *et al.* (1973) recognized at least three zones from the coast to inland: mangrove (with *Rhizophora* seawards and *Avicennia* landward), back-mangrove, and slightly or non-saline soils. Although most taxa are different, the same physiognomy could be recognized in these coastal ecosystems. Similarly, in tropical Africa (Gulf of Guinea), Poumot (1989) summarized the coastal vegetation in the following four-stepped zonal pattern: mangrove-open forest-rain forest-savanna. In general, the same or very similar coastal belts have been reported from elsewhere, although they are in different biogeographical regions (Walter 1977; Chapman 1976; Flenley 1979; Tomlinson 1986).

Modern Analogs

Paleoecological and paleoenvironmental interpretations based on palynology are commonly derived after the definition of characteristic palynomorph assemblages that are associated to a given range of environmental/ecological conditions. There are two approaches in the definition of associations. The first one attempts to group the palynomorphs *a priori* considering the individual ecological requirements of each component or using objective (statistical) classification criteria. The second, also called the 'modern analog' approach, relates the assemblages found in recent sediments to the present ecological conditions, and extrapolates this relationship to the past (Birks & Birks 1980). A constraint of the first approach is that some important pre- and post-depositional processes such as

differential pollen production and dispersal, reworking, etc. are neglected. Both approaches are fully successful for Quaternary paleoecology, but its reliability diminishes progressively in former times, because the differences among present and past floras increase with the age of sediments. However, almost all the present plant families, and most genera were already present at the beginning of the Neogene (Muller 1980). This is also true for the tropics in general (Germeraad *et al.* 1968), and for Northern South America, in particular (Lorente 1986; Muller *et al.* 1987). Furthermore, recent studies on the southern Caribbean margin show that more than a half of the pollen and spore types found in modern sediments show clear botanical affinities with Tertiary fossils (Rull & Vegas-Vilarrúbia, in press). As a consequence, the application of modern palynological analogs to Neogene paleoecology in Northern South America can provide useful results.

The following summary is based on the few studies available from Guyana, French Guayana, Venezuela and Colombia. It is not an exhaustive account, but a summary focused on the common features that can lead to generalizations.

General

Pollen and spores are found in modern sediments from the flooded alluvial plains (upper delta) to the near-shore shelf, where a sudden dropping to 500 grains/g of sediment or less is observed and maintained until the shelf edge. In the inland non-flooded terrains, no pollen is preserved (Muller 1959; Van der Hammen 1963; Rull & Vegas-Vilarrúbia, in press). An important general result is that the present palynomorph associations are arranged in sea-land gradients, in correspondence with the sedimentary environments and the vegetation and, therefore, the different sectors of the sea-land transect can be characterized palynologically. This is crucial for paleoecology, because the stratigraphic variations in pollen assemblages can be interpreted in term of lateral displacements of the vegetation belts, related to sea-level and climatic changes (Poumot 1989). However, not all the palynomorphs are found in the same environment or vegetation type in which are originated, due to transport. The main transport agents are rivers and marine currents, whereas dispersion by wind is minority and restricted to certain taxa. Three examples of these transport mechanisms are given by Muller (1959), in the Orinoco delta. The pollen of *Rhizophora* is produced in the mangrove belt, but is found offshore (more than 50 miles) in percentages around 50% (Fig. 6). In concentration numbers (grains/g of sediment), however, it shows a progressive decrease with the distance to the coast. Muller (1959) interpreted this fact as a size-sorting effect. This pollen is small (<20 μ m) and has a high buoyancy, that allows transportation to more distant areas

than the others, thus increasing in percentage seaward. On the other hand, the medium heavy pollen of *Mauritia* is of local deposition and is found almost exclusively in the central delta (Fig. 6), where these palms grow, its proportions being closely related to the abundance of the plant. This is also true for the 'morichales' of inland savannas (Rull 1992b; 1998a). Finally, an example of wind dispersion is that of *Podocarpus* (Podocarpaceae) (Fig. 6), which only possible source around the Orinoco delta are the mountain forests of northern Trinidad, and its pollen is transported in small quantities to the west (consistently with the direction of the predominant winds), thanks to its aerial sacci.

Mangrove pollen and spores

The better represented mangrove trees in the modern pollen assemblages are *Rhizophora* and *Avicennia*, whereas *Laguncularia* and *Conocarpus* are commonly scarce or absent). It is striking, for example, the absence of *Conocarpus* pollen in the Orinoco delta samples (Muller 1959), and in the sediments collected within an almost pure stand of these tree, in Playa Medina, both in Venezuela (Rull & Vegas-Vilarrúbia, in press).

The pollen of *Rhizophora* is by far the more abundant, reaching values of 80% in the source area (the mangrove belt), and is commonly over-represented in relation to the abundance of the mother plant. However, this is not true under special circumstances. For example, Phillips *et al.* (1997) reported a site in the adjacent Panama Isthmus, where this pollen is under-represented, probably due to the narrowness of the mangrove fringe. Similarly, Rull & Vegas-Vilarrúbia (in press), found the same situation in a disturbed mangrove community. The *Rhizophora* pollen diminishes landward, but is still present in low percentages in the central delta, beyond the upstream limit of the *Rhizophora* vegetation. Apparently, some wind transport is involved (Muller 1959). The pattern of this pollen offshore has already been discussed. The three species of *Rhizophora* that occur in the region (*R. mangle*, *R. racemosa* and *R. harrisonii*) have different ecological requirements (for example, *R. mangle* is the most salinity-tolerant), and a morphological differentiation of their pollen would be useful in paleoecology. Unfortunately, this differentiation is very difficult, especially with light microscope, the standard in these tasks (Van de Hammen 1963; Muller & Caratini 1977). A contrasting case is that of the *Avicennia* pollen, which is under-represented, considering the abundance of the mother plant. For example, Van der Hammen (1963) found abundance's of 25-40% of this pollen in a pure *Avicennia* forest, and lower ones in mixed *Rhizophora-Avicennia* forests from Guyana. The *Avicennia* pollen is scarce or absent in the

central Orinoco delta, and settles comparatively soon offshore, indicating low transport capacity (Muller 1959).

The spores of *Acrostichum* are more abundant behind the mangrove fringe, close to their mother plants, although they are present, but in low numbers, in other areas. Its transport by rivers and currents was shown by Tschudy (1969) in the Maracaibo lake. The largest percentages of *Acrostichum* spores in sediments are in the mouths of the main tributaries, and in the northwest, where they are transported by the dominant counterclock lake currents. The source of these spores seem to be the freshwater swamps of the Catatumbo delta. Indeed, although it is called the 'mangrove fern', *Acrostichum* has a wide range of tolerance to the water salinity and can grow successfully in freshwaters (Tomlinson 1986). Rull & Vegas-Vilarrúbia (in press), suggest that *Acrostichum* spores can be indicators of disturbance without further land use, since their maximum abundance was found in clearings from a human-disturbed *Rhizophora* community.

The pollen of *Sesuvium* is mentioned by Tissot *et al.* (1988) as a mangrove type, but no information about their modern pattern of sedimentation is available.

The pollen of *Iresine* has not been properly identified, but a pantoporate Chenopodiaceae-Amaranthaceae type occurs associated to *Rhizophora* (Van der Hammen 1963; Rull & Vegas-Vilarrúbia, in press).

Pollen and spores from marshes and swamps

Palmae pollen and fern spores are among the most frequent and abundant palynomorphs in the coasts, from the back-mangrove to the alluvial plain, with a variable amount of transport to the shelf. Van der Hammen (1963) differentiated four morphological categories of palm pollen: monocolpate, trichotomocolpate, *Astrocaryum acaule* type and *Mauritia*, the most frequent being the monocolpates and *Mauritia*. The first category includes pollen from important components of the swamp and marsh vegetation like *Euterpe* and *Maximiliana*, and is widespread. The pollen of *Mauritia* is of local deposition and has been discussed in the general section. A special case is that of *Cocos nucifera*, a cultivated palm which, in spite of their dense and monospecific crops, is under-represented in the surface pollen assemblages (Rull &

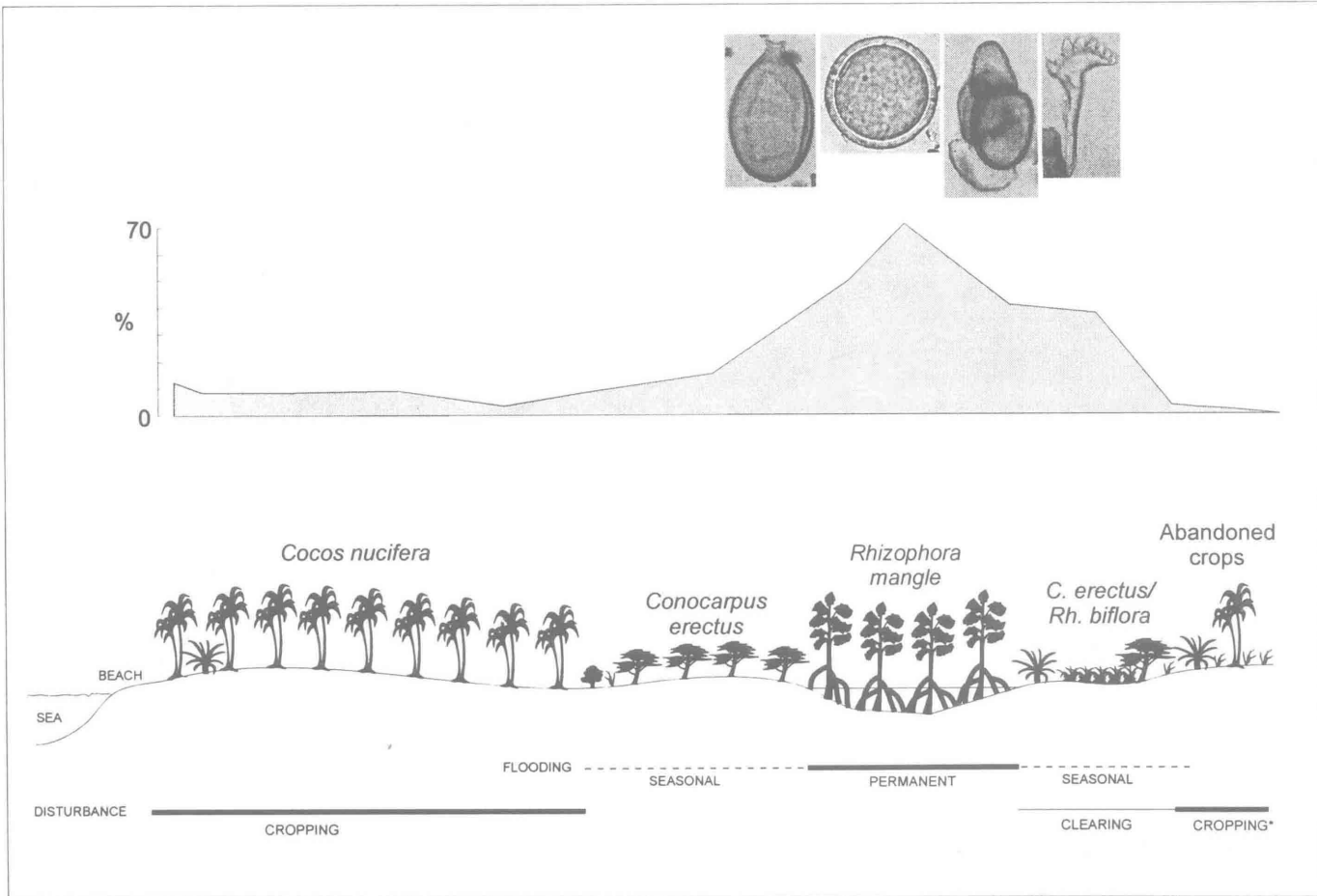


Figure 7
Relative abundance of several unknown palynomorphs in the recent sediments of Playa Medina, showing their association to aquatic environments. Redrawn from Rull & Vegas-Vilarrúbia (in press).

Vegas-Vilarrúbia, in press). Ferns are mainly represented by spores of *Acrostichum* (treated with the mangrove types), and of the *Polypodium* type, which includes all monoletes spores either psilate or verrucate. The spatial arrangement of the *Polypodium* type was considered valid for other sporomorphs like *Acrostichum*, *Amaranthaceae*, *Cyperaceae*, *Ilex*, *Virola*, and psilate palmae by Muller (1959), who found their maximum abundances in the transition between the *Rhizophora* belt and the 'morichal'. In the coastal belt the percentages are lower. Heavy types like for example the verrucate monoletes settle earlier and are scarce in the shelf, but other, more buoyant types show a wide and diffuse distribution due to the existence of multiple source areas and mass production. Among the representatives of marsh and swamp trees, it is worth to mention that the heavy pollen of *Symphonia* occurs almost exclusively where the mother plant grows; while the pollen of *Erythrina* and *Pterocarpus*, in spite of the abundance of their mother plants, are very scarce and with a limited distribution, because of the small amount of pollen produced by the flowers of both genera (Muller 1959). Other pollen and spore types with few and scattered occurrences are *Bombax aquaticum*, *Caesalpinia*

(*Caesalpinaceae*), *Caryocar* (*Caryocaraceae*), *Ceiba*, *Ceratopteris*, *Croton* (*Euphorbiaceae*), *Melastomataceae*, *Malpighiaceae*, *Malvaceae*, *Meliaceae*, *Mimosaceae*, *Myrtaceae*, *Annonaceae*, *Proteaceae*, *Moraceae*, *Anacardiaceae*, *Lecythidaceae*, *Umbelliferae*, *Nymphaeaceae*, *Polygonum*, *Typha*, *Pistia*, *Jussiaea*, *Sagittaria*, *Lycopodium* (*Lycopodiaceae*), *Isoetes* (*Isoetaceae*), *Hymenophyllum*-type (*Hymenophyllaceae*), and *Sapotaceae*.

Inland forests and savanna pollen and spores

The more characteristic pollen of this group belongs to Gramineae, Compositae, and some trees, as well as *Mauritia*, in the savanna 'morichales'. Gramineae pollen is widely distributed, but scarce in coastal areas (Muller 1959; Van der Hammen 1963). It is more abundant in the alluvial plain levees than in the swamp areas, and it is assumed that both wind and water currents play some role in its transport from inner savannas and cultivated areas. A similar situation is found for the Compositae, which predominant source seems to be the

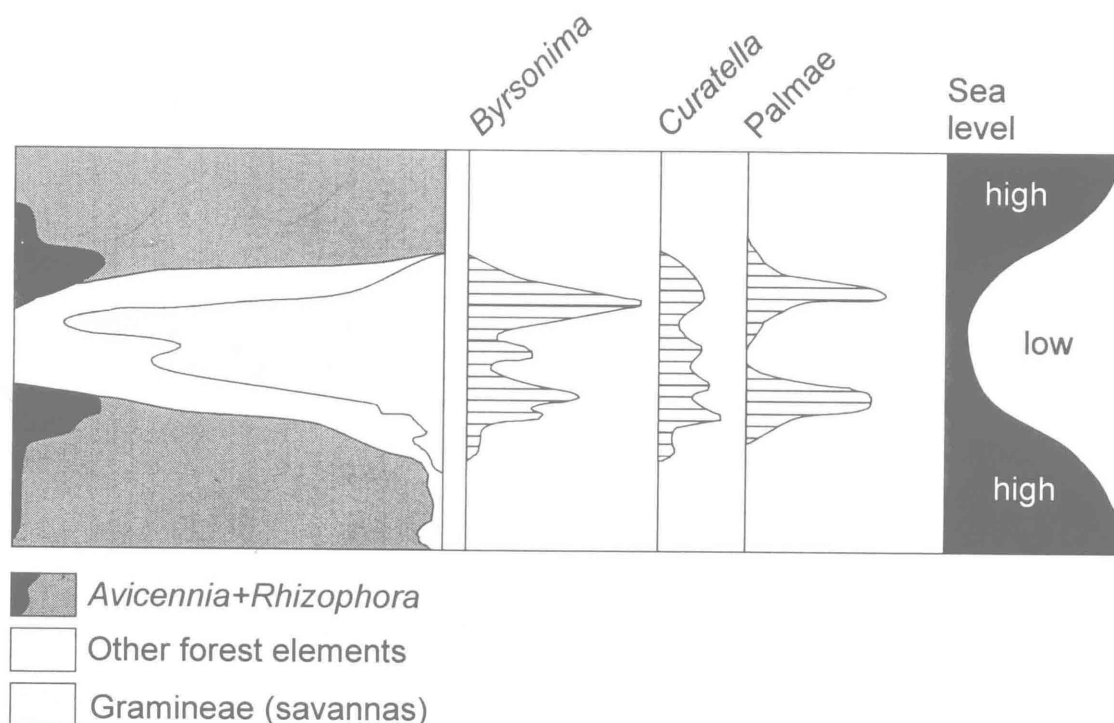


Figure 8

Typical pollen succession in a sea-level lowering during a glacial oscillation. Redrawn from Van der Hammen (1974; 1988).

cultivated areas.

Among tree pollen, some genera from inland forests, like for example many Bombacaceae, Sapotaceae, *Terminalia*-type (Combretaceae), *Cecropia* and *Anacardium*-type (Anacardiaceae), are present due to the combination of multiple source area and wind transport. In a small disturbed mangrove community, where the supply of *Rhizophora* pollen is small, the pollen of trees from adjacent inland forests (*Poulsenia*-type [Moraceae], Sapotaceae, Proteaceae, *Alchornea* [Euphorbiaceae]) can be of some quantitative importance (Rull & Vegas-Vilarrúbia, in press). The pollen and spores of some mountain forest components reach the coastal and shelf environments through long-distance transport by wind. The example of *Podocarpus* (see general section) is illustrative, and is also valid for the arboreal ferns *Pteris* and *Hemitelia*. An extreme case of long-distance dispersal that has become famous is that of *Alnus* (Betulaceae), transported by rivers from the northern Andes to the Orinoco delta, separated by more than 800 km (Muller 1959).

Fungi spores and particulate organic matter

According to Muller (1959), fungi live mainly in soils of the back-swamp vegetation, where contribute to the decomposition of the organic matter. In this way, they are less affected by initial wind transport than other palynomorphs, and are transported mainly by water currents. They are more abundant in the swamps of the upper coastal plain and central delta than in the mangrove belt, and they settle near the coast, being negligible in the shelf (Muller 1959; Van der Hammen 1963). In disturbed mangrove sites they can be largely dominant and, furthermore, the identification of these spores helps to characterize the different subenvironments and vegetation types, thus having a great potential for paleoecology (Rull & Vegas-Vilarrúbia, in press).

Among the particulate organic matter components, the cuticles show a general distribution similar to the fungi (Muller 1959), but in considering the whole organic assemblages, the patterns appear more complex. Lorente (1990) sampled several subenvironments of the upper Orinoco delta plain and was able to differentiate among oxbow lakes, *Montrichardia* back-swamps, crevasse spays and levees, on the basis of textural characteristics and particle identification. In the lower Magdalena river (Colombia), the same author characterized in the same manner four subenvironments: swamps, shallow lakes, alluvial flood plains and lagoons (Lorente 1992). The main parameters that allow differentiation of these subenvironments are the particle size and shape distribution, as well as the relative proportions of cuticles, humic gels, woody remains, epidermis fragments, algal remains, amorphous particles, insect remains, fungal remains, charcoal, resins,

etc. (Lorente 1986). Using the same methods on the Tacarigua hypersaline to freshwater lagoonal complex from the central Venezuelan coasts, Rull (1995) found a very heterogeneous distribution and pointed out that in certain systems, besides the sedimentary subenvironments, other characteristics such as for example the sources of the different particles and the post-depositional processes, should be considered to explain the composition of the organic matter assemblages. Offshore, a strong correlation exists between kerogen density and distance to the coast (Nwachukwu & Barker 1985).

Aquatic palynomorphs

The aquatic palynomorphs more commonly found in sediments are freshwater algae remains, and remains from the marine microplankton, like dinoflagellate cysts and linings of foraminifers. Among the first ones, the more significant from a palynological point of view are *Botryococcus* and *Pediastrum*. They are extremely rare or absent (*Botryococcus*) in the general modern deposition studies discussed here, probably because they are restricted to the sediments of water bodies where they live. The finding of *Botryococcus* colonies in the sediments of a coastal lagoon of northern Colombia (Lorente 1992) supports in part this statement, but their absence in modern sediments is contrasting with their frequent occurrence in ancient coastal sediments. On the contrary, dinoflagellate cysts are very abundant in the marine side. They were considered indicators of marine environments by Muller (1959), who called them *Hystrix*, because of their absence from the delta and the littoral zone. They are widespread and abundant throughout the shelf, but more abundant in certain zones, probably because salinity, temperature and nutrient differences. Inshore-offshore gradients in dinoflagellate assemblages have been recognized in many areas of the World (Wall *et al.*, 1977; Mudie & Harland, 1996). Several species can live in brackish environments, like estuaries and coastal lagoons, and might be important to characterize coastal environments. Others are typically neritic, and could be important to record transgressive phases. The components of these assemblages, however, vary with latitude, due to several oceanographic factors. In northern South America, studies of dinoflagellates on modern sediments have been carried out offshore in the Atlantic Ocean, in front of the Guianas, and in the Gulf of Paria shelf, between the Orinoco delta and Trinidad (Fig. 1). Offshore sediments have less than 100 cysts/g and are composed mainly by two biofacies (I and III). Biofacies I is dominated by an unidentified form (Organism A), and correlates well with a belt of low salinity of the southern part of the North Atlantic Ocean, related with the Equatorial Counter Current (Williams, 1968). Biofacies III is dominated by another unknown

taxon (Organism B), and is closely associated with a high-salinity and low-nutrient water mass in the center of the North Atlantic current gyral (Sargasso Sea), related with the North Equatorial Current. Other important component in these oceanic samples is *Leptodinium aculeatum*, which is widespread in the north Atlantic, and reaches its maximum abundance in the north-west coast of Africa (Williams, 1968). The Gulf of Paria is a large, coastal embayment of low salinity (average 27 ‰) due to the influence of the Orinoco delta. Seven bottom samples taken under 10 to 28 m of water, show cyst assemblages of the type VI (Tropical/Subtropical-Estuarine) (Wall *et al.* 1977). The dominant cysts is *Operculodinium centrocarpum*, followed by *Spiniferites bulloideus*, *S. ramosus*, *S. mirabilis*, *Nematosphaeropsis balcombiana*, *Lingulodinium machaerophorum* and the *Peridium* group, all of them with broad environmental and thermal tolerance (Mudie & Harland, 1996). All the *Leptodinium* species found (*L. aculeatum*, *L. paradoxum*, *L. sphaericum*, *L. patulum* and *L. striolatum*), as well as *Hemicystodinium zoharyi*, are restricted to the more oceanic side, near Trinidad; whereas *Peridinium conicum* and *P. subinermis*, are present only in the samples closer to the Orinoco delta. The five *Leptodinium* species tend to occur together in a world-wide context, and represent primarily oceanic and transitional coastal-oceanic systems, being commonly absent in estuarine and shelf environments. On the contrary, *Peridinium* species have a more estuarine and coastal character (Wall *et al.*, 1977).

Concerning the foraminiferal linings, patterns are similar to those of dinoflagellates, but they occur also in several river mouths of the Orinoco delta. They are also present in coastal lakes and lagoons of northern Venezuela, under brackish conditions (Tschudy 1969; Rull & Vegas-Vilarrúbia, in press), but in lower quantities. Not all the foraminifers possess these linings, that are chitinous inner tests of the juvenile stages of certain taxa. In the shelf adjacent to the Orinoco delta, the linings are similar to those of *Cibicides* and *Planulina* (Muller 1959), but a definite identification is not yet available. Many of the unknown remains found by Rull & Vegas-Vilarrúbia (in press) in the sediments of a mangrove community from Venezuela appear to be parts of aquatic organisms, since they are restricted to pond sediments (Fig. 7).

Quaternary Studies

Glacio-eustatic cycles

The sea level oscillation corresponding to the last glaciation was first recognized by Van der Hammen (1963) in the Ogle Bridge borehole (Guyana) through a combination of radiocarbon dates and pollen analysis. The pollen signal is very clear, and consists of a strong increase of Gramineae pollen, deposited in poor and open

savannas, far behind the shoreline, in a stratigraphic interval between two radiocarbon dates of >45 and ~8.6 ¹⁴C ka BP. This was interpreted as a regressive situation, since the site is now at the outermost coastal belt, and supported a previous observation of Muller (1959), who found a pollen assemblage typical from deltaic or very near-shore conditions (27% of *Rhizophora* and dinoflagellates absent) in a sample dated as ~17.8 ¹⁴C ka BP from a 40 m water depth marine core taken in front of the eastern coasts of Trinidad. The extent of the sea-level decrease was estimated by Van der Hammen (1963) in more than 70 m. At present, the most widely accepted value for the worldwide sea-level shift during the Last Glacial Maximum (~18 ¹⁴C ka) is of ~120 m, initially proposed by Fairbanks (1989), working on buried coral reefs from Barbados. The interval older than 45 ka BP was considered by Van der Hammen (1963) as the Riss/Würm interglacial, and interpreted as a phase of a sea level higher than at present. After the Würm glaciation, a transgression started at about the Pleistocene-Holocene boundary, as reflected in the returning of pollen assemblages characteristic of mangroves and delta front. The same regressive-transgressive pollen sequence was found in Alliance (Surinam) but it was recorded several times in a recurrent pattern (Wijmstra 1969 1971). Using the first occurrences of *Symphonia* and *Alnus*, the section was dated as Plio-Pleistocene and, therefore, the palynological record was assumed to represent the eustatic cycles connected to the glacial-interglacial alternation (Van der Hammen 1974, 1988). It is very interesting that all cycles show the same characteristic palynological and, consequently, vegetational succession. Indeed, the regressive sequence is: *Rhizophora* mangrove, *Avicennia* mangrove, palm swamp forest, *Byrsonima* savanna woodland, grass savanna and *Curatella*, whereas the transgressive sequence is symmetrical (Fig. 8). Similar eustatically-forced 'palynocycles' were reported in the Asian and African tropics in undated recent sediments, and applied to the Neogene (Poumot 1989). However, these are asymmetrical, and consist of five main phases. During the lowest sea level fern spores dominate, followed by a peak of back-swamp open forest taxa (palm and *Pandanus* [Pandanaeae]) pollen in the transgression and ending with a mangrove maximum in the highest sea level. The regressive sequence is different, because it coincides with a drier climate and therefore, the mangrove fringe is reduced. The regressive assemblages are dominated by back-mangrove open forests of Euphorbiaceae and Rubiaceae and then by savanna herbs, before to return to the spore peak. The glacial/interglacial alternation was also characterized by Hoorn (1997) and Haberle (1997) in the submarine Amazon fan, using the Holes 930, 931, 932, 936, 938, 940A, 944A 946 and 946A of the Ocean Drilling Program Leg 155. Due to the

high transport capacity of the Amazon system, a mixture of Andean, tropical lowland and reworked Cretaceous and Tertiary palynomorphs were present in these sediments. According to Hoorn (1997), glacial intervals were characterized by an increase of fern and allied spores, reworked and corroded taxa and fungal spores, suggesting a higher amount of erosion due to the lowering of the base level of rivers, and supporting the existence of the fern spores phase of Poumot (1989), during the low sea-level stage. Interglacial sediments have a low content of fossils from the continent, and are dominated by marine representatives. An additional information is that glacial deposits show low amounts of palynomorphs from lowland savannas, thus not supporting the refuge hypothesis, according to which tropical lowland forest ecosystems survived to the dry glacial conditions in localized refugia among extensive savanna areas (Haffer 1982). Haberle (1997) provided additional evidence in the same sense, through the finding of only moderate changes in the pollen of savanna elements during the glacial-interglacial alternation. Instead, this author found an increase in pollen of cold-adapted trees (mainly *Podocarpus*, *Alnus* and *Hedyosmum*) during glacial times (21 to 17 ka BP). This was interpreted as an expanded distribution of these taxa in the Amazon basin due to cold climates, and is more consistent with a model that proposes a moderate savanna expansion in the last glacial, based on a uniform reduction of precipitation of 20-25% (Haberle 1997). Noteworthy is that pollen diagrams from the Amazon delta fan contrast with the high dominance of grass pollen found in the glacial intervals from Guyana and Surinam. It is expected that differences between the sedimentological characteristics of a fan that receives the

deposits of the huge Amazon catchment area and the organic sediments locally deposited in coastal plain environments are involved.

The glacial increase in the frequency of montane forest taxa was also recorded by phytolith analysis of sites 932 and 933 (Piperno 1997), and interpreted as the response to a widespread climatic cooling of ca. 5-7 °C, as proposed by Colinvaux *et al.* (1996) after localized lowland pollen records. According to Piperno (1997), however, this is not incompatible with a pronounced drying and the consequent forest reduction and open land expansion, a situation deduced from both phytolith and charcoal analysis for last glacial sediments (22-11 ka BP). Carbon isotope analysis of sedimentary lignin of site 932 also argues against the development of extensive savannas during the last glacial (Goñi 1997).

The Late Glacial and the Holocene

The Late Glacial has been studied in detail in marine cores from the Cariaco Basin, near the Venezuelan coasts, using non-palynological methods. The characteristic postglacial stadials and interstadials, including the more intense of these cold oscillations, the Younger Dryas (11 to 10 ¹⁴C ka BP), have been found (Overpeck *et al.* 1989; Peterson *et al.* 1989; Lin *et al.* 1997). Palynological analysis are in progress (Rinaldi 1996a and b), but it seems that the Younger Dryas coincides with a significant increase of grass pollen, both in percentage and concentration, and a concomitant decrease of arboreal pollen, interpreted as a cold and dry phase. A postglacial core of about 4 m (A-240/18) had been taken earlier (1957) in the Cariaco basin during the R/V Atlantis cruise (Wall 1967). However, no clear paleoecological conclusions were derived due to the lack of time control and the small number of samples analyzed for dinoflagellates.

In northern Brasil, postglacial cooling was expressed in the presence of *Podocarpus* pollen, in the sediments (Behling 1996). This tree is now almost restricted to the mountain forests and very rare at low elevations, its pollen being absent from Holocene diagrams, and rare in modern samples. However, in the pollen profile of the Curuça lagoon, at 35 m a.s.l., it reaches 2% of the pollen sum, which is interpreted by Behling (1996) as the evidence of *Podocarpus* populations living within lowland forests, due to the existence of cooler climates, supporting the observations of Colinvaux *et al.* (1996).

The Holocene pollen records have been characterized by the dominance of *Rhizophora*, until the last five millennia, when another spectacular increase of herbs has been recorded, and continued until today. Mangrove elements were reduced to 20% or less of the pollen assemblages. A similar situation has been observed in Guyana, French Guiana, Surinam and Brasil

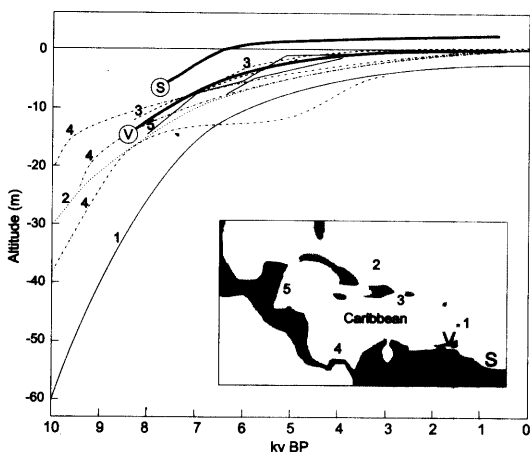


Figure 9

Comparison of two Holocene sea-level curves from northern South America (V - Venezuela, S - Surinam) recorded palynologically with other Caribbean curves. Details in Rull *et al.* (1999).

(Van der Hammen 1963; Wijmstra 1969 1971; Tissot *et al.* 1988; Tissot & Marius 1992; Behling & Lima da Costa 1994), but it has been interpreted in different ways. According to Van der Hammen (1963), the transgression initiated in the Pleistocene-Holocene boundary culminated about 6.5 ka BP with a sea level 2-2.5 m higher than the present one, and a regression started around 6 ka BP, followed by the so-called Atlantic transgression, and the Subboreal regression around 5 ka BP. Finally, a relative rise of sea level started again, and continued until the present day. Therefore, the increase of open vegetation representatives is anomalous, because it occurred in a transgressive situation, and was interpreted by Van der Hammen (1963) as caused by human activity (fires and cultivation). In contrast, Tissot *et al.* (1988), working on the Mana estuary (French Guiana) considered that the Holocene transgression culminated around 5 ka BP, and then the sea level has been stable until today. This stability would have favored the progradation of the coast line towards the sea with the consequent displacement of the ecological belts in the same direction and, therefore, the replacement of mangroves by herbaceous back-swamps ('savannes marecageuses') in the sampling sites. However, these authors considered the possibility that human activities accentuated the vegetation change initiated around 5 ka BP (Tissot *et al.* 1988; Tissot & Marius 1992). There is still a controversy about the occurrence or not of a phase of higher level than today during the early Holocene. One of the most reliable sea-level indicators is the palynological record of dated mangrove sediments (Kidson 1982; Ellison 1989; Pirazzoli 1991). This approach has been followed in several localities of the study area, with different results. In Guyana (Van der Hammen 1963) and Brasil (Behling & Lima da Costa 1994), the inland occurrence of 6.5 to 7.5 ka old mangrove pollen assemblages points towards a sea level above the present one by the early Holocene. However, this has not been recorded in Surinam (Roeleveld & Van Loon 1979) and Venezuela (Rull *et al.*, 1999), where a rapid early Holocene increase was followed by a stabilization, after reaching the present sea-level high around the mid-Holocene or earlier (Fig. 9). According to by Ellison & Stoddart (1991), this has been the rule for most part of the Caribbean; however, their raw observations are contrasting with those of northern South America, because mangroves were absent from most of their study sites during the early Holocene and did not established and expanded until the stabilization of the sea level, at 6.5 ka BP. These authors proposed that mangrove development has been impeded by the rapid sea-level rise, because of their inability of maintaining themselves within tidal limits, with sedimentation rates above 12 cm/100 years. A similar value is given by Parkinson *et al.* (1994). Therefore, in the early Holocene, mangroves would have been persisted '...in refuge mode,

as disorganized scattered individuals or narrow coastal fringes...' (Ellison & Stoddart 1991). However, the occurrence of extensive mangrove communities during the early Holocene in the northern South American coasts is out of question, since the palynological evidence is not compatible with the occurrence of only individuals or small populations. On the other hand, average sedimentation rates for the sections that recorded these mangroves are of 24 cm/100 y in Guyana (Van der Hammen 1963), 25 cm/100 y in French Guiana (Tissot *et al.* 1988) and 13 cm/100 y in Venezuela (Rull *et al.*, 1999). Early Holocene mangroves were also recorded palynologically in the western African coasts (Thanikaimoni 1987). Thus, paleoecological data does not support the hypothesis of Ellison & Stoddart (1991), which is also questioned by modern data from Florida (Snedaker *et al.* 1994).

For the sake of completeness, two unpublished Holocene palynological works developed in the Unare delta (Venezuela) should be mentioned. However, no clear conclusions in terms of sea-level or climatic variations were derived (Gómez 1993; Monsalve & Roa, in prep.).

Human disturbance

Concerning human disturbance of coastal ecosystems, it has been mentioned the interpretation of Van der Hammen (1963) in relation with the late-Holocene increase of open vegetation, as a result of human practices. This influence seems to have been negligible in areas of low accessibility, as for example many swamps of the Orinoco delta, where the human disturbance (documented in the field but not recorded palynologically) seems restricted to the alluvial plain forests and savannas (Muller 1959). In more accessible areas, however, mangroves and other coastal communities of the Caribbean area have been submitted to human practices as for example wood extraction, pollution, felling or burning and subsequent cultivation, touristic activities, etc. (Ellison & Farnsworth 1996). In northern Venezuela, an early-mid Holocene mangrove community was recorded palynologically in a site which is today cultivated (Rull *et al.*, 1999). The ancient pollen assemblage reflect a mangrove in which *Avicennia* was probably co-dominant with *Rhizophora*, and montane forests in the surrounding step slopes, no herbaceous ecosystems occurred at the vicinity. In contrast, modern pollen assemblages are dominated by herbs (Gramineae, Cyperaceae, Cenopodiaceae-Amaranthaceae) and *Acrostichum*. The pollen of *Avicennia* is absent, because the plant is no longer present at the site, and *Rhizophora* (<3%) is more rare than the cultivated *Cocos nucifera* (~5%). In the cultivated areas (now or in the last decades), soils are not flooded, and the palynomorphs are commonly degraded, whereas in the cleared but not

cultivated flooded areas, the spores of the mangrove fern *Acrostichum* are common. The mangroves of these coasts have been probably submitted to human action since about 5 to 6 ka BP (Sanoja 1992), but the activity increased with the arrival of Europeans, in the 16th century (Conde 1993). Similar dates, based on archaeological evidence were found in northern Brasil, but Behling (1996) opened the possibility of an earlier arrival of the first paleoindians, due to the occurrence of moderate amounts of charcoal since around 10.8 ka BP.

In other tropical areas, as for example the Asian low latitudes, a recent floral impoverishment has been observed in the pollen assemblages, due to the degradation of mangroves, due in part to natural causes, but mainly to the human activities (Caratini *et al.* 1977; Thanikaimoni 1987).

General conclusions and proposals

According to the evidence presented, modern analog studies in northern South America have been oriented mainly to the relationship between sedimented palynomorphs, potential vegetation sources and coastal sedimentary environments. In this sense, after classical studies as for example that from the Orinoco delta, the general patterns of palynomorph distribution are known, but studies like those of Playa Medina or the lower Magdalena showed that local variations within subenvironments can be important. Therefore, more detailed local studies are needed, preferably in the regions near coring or outcrop sampling sites, for a better paleoenvironmental interpretation of past pollen records. On the other hand, a common procedure in modern analog studies is the calibration of proxies, that is, the establishment of quantitative relationships between fossil abundances and measured environmental parameters, such as temperature, water chemistry, sea levels, etc. In this way, provided a good statistical association, past values for these environmental parameters can be estimated from the abundance of key fossils (proxies). These studies are lacking in the region studied here. It would be interesting to develop them, especially with parameters that have proved to be useful in paleoenvironmental studies, such as salinity. Rull (1992a, 1997a, 1998b) used a salinity index derived from the quantitative relationship between marine and freshwater algae remains. However, its usefulness is still relative, and interpretations are of the type: 'fully marine', 'brackish', 'freshwater environments' etc. A calibration of the salinity index with modern analogs would increase the potential of this tool as paleoenvironmental indicator. Concerning sea levels, past lateral displacements of coastal vegetation belts connected to them would be accurately measured after calibration of pollen assemblages in transects, considering the parameter 'distance to the coast'.

Most Quaternary palynological records embrace the last glacial cycle, and the related sea level change. Emphasis is done on the environmental and biotic conditions of the lowlands during the Last Glacial Maximum which, based on the evidence available so far, seem to have been under cold climates, whereas the refuge hypothesis, based on the existence of supposedly arid climates is progressively losing credibility. A characteristic vegetation succession has been recorded during regressive and transgressive phases. It seems to be symmetrical and recurrent, as shown in the longest pollen record embracing several glacial oscillations (Alliance well). Holocene pollen records are interpreted mainly in terms of sea level rise after the last glaciation, acting as the main control by determining the coastal sedimentary rates. A discussion exists about the existence or not of an upper limit in these rates, beyond which mangrove development would be impeded. One of the most used sea level indicators is the dating of mangrove peats, palynologically characterized as such. In order to predict future climates and sea levels, two time domains have to be considered, within the current Global Change perspective: the last glacial/interglacial cycle and the last two millennia (Eddy 1992). In the northern South American coasts, the second aspect is poorly developed and needs to be considered urgently. Typical studies must include high-resolution sampling of shallow cores or most recent outcrops and accurate radiocarbon dating of as much levels as possible. In them, palynological evidence for *in situ* mangrove sediments (as sea level indicators) is essential, and oxygen isotopic analysis of fossil shells would be decisive to provide temperature trends. Results from the Cariaco and Amazon fan cores will hopefully provide the first data in this respect. From a palynological point of view, and according to the experience accumulated so far, coring in coastal lagoons can probably provide the best records and are encouraged. These records could also provide information on human activities like for example burning, agriculture, etc. whose records are very scarce in the region.

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