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PLANT ACCUMULATIONS ALONG THE ITANHAÉM RIVER BASIN, SOUTHERN COAST OF SÃO PAULO STATE, BRAZIL

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ABSTRACT

Examination of the mechanisms involved in the construction of present-day vegetative deposits along coastal waterways has made it possible to establish depositional patterns that can be compared with those found in similar environments in geologic time. These patterns include not only the composition and transport of the debris but also an estimation of the time involved in its deposition. Six sites with active deposits of plant macrodebris in the coastal basin of the Itanhaém River, São Paulo State, Brazil, were used in the study. In the central portion of the basin, the interior coastal plain is covered with restinga forest (dense, wet tropical forest of low altitudes), while the lower portion consists of mangrove swamps. The coast reflects anthropogenic intervention, and only a few scattered remnants of precolonization dune vegetation remain. The results after three years of study suggest that the accumulation of plant macrodebris in the middle and lower portions of the basin is parautochthonous, since only the leaves of genera typical of the restinga forest and mangrove swamp, respectively, were found. Along the coast the accumulations involved a mixture of parautochthonous and allochthonous elements. On the levee of the Branco River and within the mangrove swamp, deposition was slow, and many of the elements decayed quickly; such accumulations show little potential for preservation and eventual fossilization. A different site, however, reveals the rapid deposition of thick layers of plant debris, presumably associated with storms, and these accumulations are preserved for long periods, constituting good candidates for possible fossilization.

INTRODUCTION

Assemblages of fossil plants, especially in continental areas, constitute one of the main objects of study for paleobotanists. The original accumulation is due to the interaction of various environmental and taphonomic factors, but once unearthed, interpretation will depend largely on understanding the mechanisms active during formation of the taphocoenosis, such as the origin of the plant remains, means of transport, time of deposition, and climate at that time. Biostratinomic studies in present-day environments can thus facilitate the ecological interpretation of the fossil record (Burnham, 1993; Kidwell and Flessa, 1996; Burnham and Johnson, 2004), since they make it possible to observe processes in action and their relationship to the results obtained.

In addition to theoretical biostratinomic studies (e.g., Spicer, 1980; Greenwood, 1991; Martín-Closas and Gomez, 2004; Ferguson, 2005), applied studies have been conducted in various fluvial and lacustrine (Ferguson, 1985; Burnham, 1989; Alexander et al., 1999) or deltaic (Scheihing and Pfefferkorn, 1984; Gastaldo et al., 1987; Gastaldo, 2004) environments. Moreover, modern leaf litter has been examined in various kinds of both temperate and tropical forests (Ferguson, 1985; Burnham, 1990, 1993, 1994; Burk et al., 2005; Burnham et al., 2005; Dorrepaal et al., 2005; Greenwood, 2005; Steart et al., 2005).

A wide variety of environments can develop in any tropical fluvial system, and these may be inhabited by different kinds of vegetation, reflecting the great biodiversity of tropical forest. These plants can be subject to different conditions of deposition, resulting in a wide variety of types of accumulations of plant macroremains (Stout, 1980; Burnham and Spicer, 1986; Burnham, 1993, 1994; Gastaldo, 1994; Gastaldo and Staub, 1999; Burnham et al., 2005). The taphonomic processes encountered in any single tropical fluvial system may be unique, especially since the lack of well-defined seasons can lead to a continuous accumulation of plant remains. Taphonomic studies of plant macrodebris accumulating along rivers in modern forests are important as they help us understand the origins of the elements in fossil accumulations, as well as the physical and chemical processes involved. Such an approach may also be of use in the interpretation of paleofloras which developed along meandering river systems in the past, such as the Paleocene paleofloras of riverside forests in southeastern Brazil in the states of Rio de Janeiro, Minas Gerais, and São Paulo (Duarte, 1974; Duarte and Mello-Filha, 1980; Oliviera-e-Silva, 1982; Ricardi-Branco and Fanton, 2007), although no taphonomic studies have yet been conducted for these areas.

Itanhaém River Basin

In order to observe the accumulation of plant macroremains in a tropical fluvial system, the basin of the Itanhaém River (São Paulo State) was chosen. This basin provides an interesting location for study, since it is drained by three main rivers (Branco, Preto, and Itanhaém) that flow through different environments. The basin of the Itanhaém River is located on the southern coast of the state of São Paulo and is the second largest coastal hydrographic basin in the state, with an area of 930 km^2, mostly located in the municipality of Itanhaém (Camargo et al., 2002). The upper part of the basin is located within the confines of the State Park of the Serra do Mar, which includes well-preserved springs and dense, tropical forest vegetation (Garcia and Pirani, 2003). In the central part of the basin, restinga forest constitutes the predominant vegetation, a humid tropical forest biome (also called the dense ombrophyle forest of low altitudes; see Instituto Brasileiro de Geografia e Estatística, 2004); closer to the coast, this biome is replaced by mangrove swamps and then by dune vegetation. In the central and

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lower parts of the basin, the influence of humans is more pronounced, becoming intense close to the mouth of the river, where the presence of rubbish and sewage, as well as buildings and landfills are found, and many of the historically abundant dunes have been eliminated (Hueck, 1955; Souza and Capellari, 2004). Domesticated crops, such as bananas (*Musa paradisiaca*) and manioc (*Manihot esculenta*) are also cultivated in isolated fields near the river, and various aquatic angiosperms (*Eichhornia azurea*, *Pistia stratiotes*, *Utricularia foliosa*, *Nymphaea rudeana*, *Egeria densa*, and *Cabomba furcata*) and pteridophytes (*Salvinia* sp.) grow along the banks of the rivers (Camargo et al., 2002). All of these have contributed to the debris accumulated along the rivers in the basin, providing a unique laboratory for the study of the dynamics of plant-debris accumulation in and along this tidal river system. The original hypothesis was that there would be a mixture of plant remains from the whole course of the main rivers that drain the basin, with more varied accumulations approaching the coast. The main river draining the basin is the Itanhaém, which is formed by the confluence of the Branco and Preto rivers, as well as the tributaries of the Branco, Mambu, Aguapeú, and Guaraú rivers (Fig. 1).

The area has a humid, subtropical to tropical climate, with relatively little temperature variation, as is the case for all coastal regions of the state of São Paulo (Lamparelli, 1999; Camargo et al., 2002), and an annual average temperature range of 19.6–21.8°C. Annual precipitation varies from 1932.2 mm to 2080 mm, with the largest rainfalls occurring during the summer months of January–March and little rain falling during the winter months of June–August (271.9–283 mm). There is no well-defined dry season, however, and the relative humidity of the air averages ~80%–84% (Lamparelli, 1999; Camargo et al., 2002). The characteristic lack of a seasonal pattern in the tropics suggests that the main variations in water characteristics over time will be a consequence of variation due to the action of the tides and the intensity of rain (Camargo et al., 2002), as well as the characteristics of the underlying aquifers.

Geology

The coastal Quaternary plain of the Itanhaém basin extends some 50 km, with an average width of 15–16 km (Suguio and Martin, 1978; Camargo et al., 2002; Suguio, 2004; Amaral et al., 2006). Its evolution during the Quaternary is related to two events of transgression. During the Holocene (5.100 ka), it was characterized by an estuary-lagoon depositional system. At present, this estuary-lagoon paleosystem is overlain by river sediments from the flood plain of the Itanhaém River and its tributaries. Moreover, the mouth of the Itanhaém River acts as a channel for the tide, so that the river is subject to daily inversions along its course (Giannini and Santos, 1996; Amaral et al., 2006).

METHODOLOGY

Identification of Study Sites

To test the validity of our working hypothesis, we identified locations where plant debris was accumulating, as well as the composition of the plant macrodebris as a function of their transport and the time involved in their deposition. Sites (Table 1) in three distinct environments (central portion, mangrove swamp, and coast beaches) distributed along the main rivers were selected on the basis of the presence of depositional activity, especially that of leaves, since these are relatively easy to identify and quite abundant in the accumulations. The basin was visited monthly for 3 years (2003–2006), with each individual site visited at least once every other month, although certain specific activities required more frequent visitation.

To select the sites in the central portion of the basin, promising levees covered with leaf litter or other plant macrodebris were identified, and the surface of these accumulations was sprayed with a waterproof acrylic spray paint. This technique made it possible to identify the

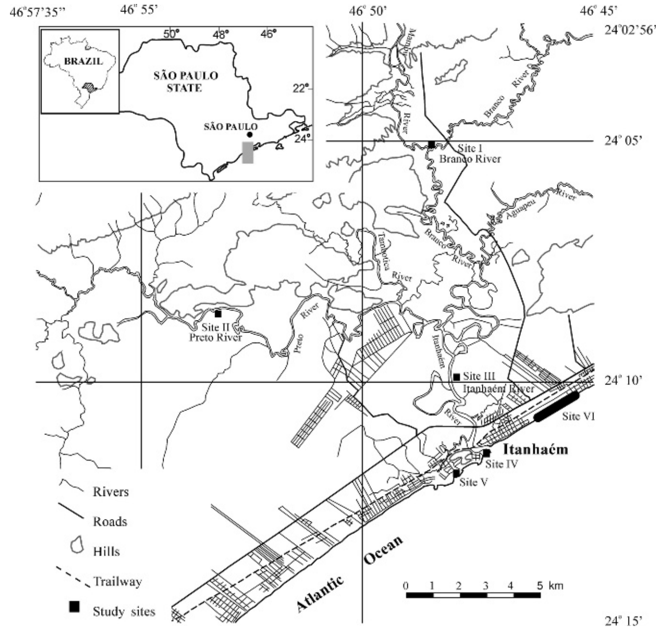

FIGURE 1—Location of area of investigation and study sites. Site I, Branco River; site II, Preto River; site III, Itanhaém River; site IV, Itanhaém River mouth; site V, beach south of mouth; site VI, beach north of mouth.

components of the surface of the initial accumulation, as it could be ascertained whether they were still present at future visits. More recent depositions covering them could be removed, and the older depositions would still be recognizable; the absence of painted leaves would indicate active removal. Using this technique, two main sites were identified, one on the Branco River, where deposition was taking place, and the other on the Preto River, where a relatively thick assemblage of plant macrodebris was found, although it was being eroded. In the lower portion of the basin, a third site in a well-preserved portion of the mangrove swamp was also selected; although such swamps do not extend very far inland along the river, they are quite well developed where they do occur. Moreover, such swamps are known to be locations for the sedimentation of plant remains, even though the daily action of the tides and decomposition tend to prevent accumulation.

Three further sites along the coast near the mouth of the Itanhaém River were also selected for regular observation, one at the mouth of the river itself, and the other two at points just north and just south. The final six locations (Figs. 1, 2; Table 1) were the following:

1. *Site I (Points 1, 2)*.—Located in the central portion of the basin, on the northwest bank of the Branco River ~19 km from where it joins the Itanhaém (Figs. 2A–B). The dominant vegetation is restinga forest, and the site can only be reached by boat during low tide.
2. *Site II (Points 3, 4, 5)*.—Located in the central portion of the basin, on the south bank of the Preto River, ~24 km from where the river joins the Itanhaém (Figs. 2C–D). The dominant vegetation here is also restinga forest, and the site can only be reached by boat during low tide.
3. *Site III (Points 6, 7)*.—Located in the lower portion of the basin, on the east bank of the Itanhaém River, ~3.2 km from the mouth of the river (Figs. 2E–F). The vegetation consists primarily of mangrove trees. This site can only be reached by boat during low tide.
4. *Site IV (Point 8)*.—Located on the south bank of the mouth of the Itanhaém River (Fig. 2G). The dominant vegetation consists mainly of cultivated ornamentals and dune plants. This site can be reached on foot or by boat.
5. *Sites V and VI (Points 9, 10)*.—Located on the coast, with a dominant vegetation of cultivated ornamentals and dune plants (Fig. 2H). These locations are easily accessible on foot.

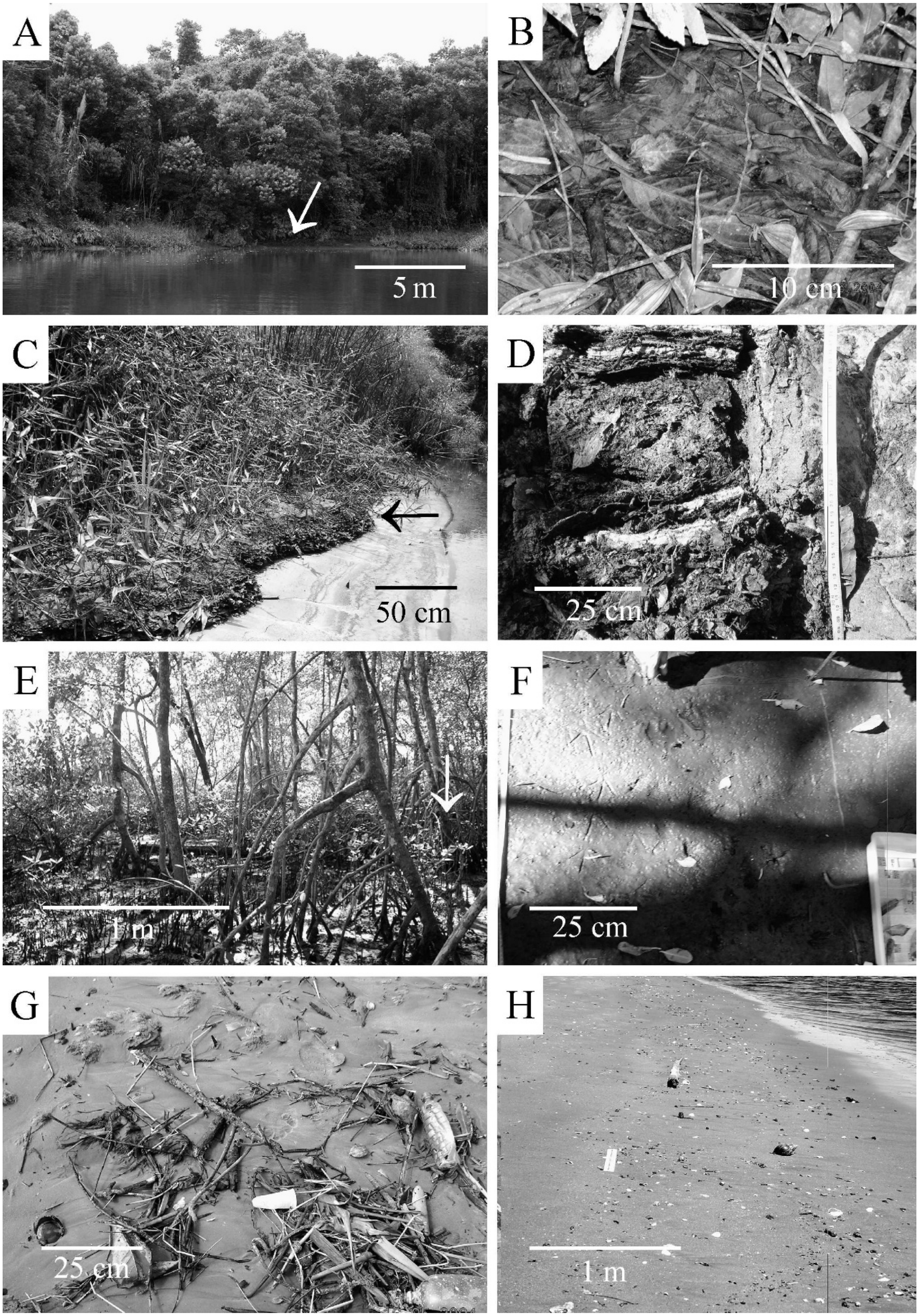

FIGURE 2—Overall view during low tide, showing details of the accumulation of plant macroremains studied. A) View of site I, point 1, with restinga forest in front showing species of trees, especially Fabaceae (*Senna*) and Melastomataceae (*Tibouchina*), as well as clumps of Poaceae; arrow indicates location of study site. B) Detail of accumulation

TABLE 1—Location of deposits of plant debris studied in the basin of the Itanhaém River, including coordinates, type of associated forest, and specific activities at each site.

Sites	Points	Geographic coordinates	Type of forest and habitat	Collection site	Taphonomic experiments and cores
I Branco River	Point 1	24°05′04″S 46°48′34″W	Restinga Forest Levee	X	x
	Point 2	24°05′04.5″ S 46°48′34″W	Restinga Forest Forest soil		x
II Preto River	Point 3	24° 08′ 23.9″S 46° 52′ 54.9″W	Restinga Forest Levee	X	x
	Point 4	24° 08′ 23.5″S 46° 53′ 54.4″W	Restinga Forest Forest soil		x
	Point 5	24° 08′ 23.8″S 46° 53′ 54″W	Restinga Forest aerial		x
III Itanhaém River	Point 6	24° 10′ 30.1″S 46° 48′ 06.3″W	Mangrove swamp Coastal plain	X	
	Point 7	24° 10′ 31.3″S 46° 48′ 07.8″W	Mangrove swamp Coastal plain	X	x
IV Itanhaém River mouth	Point 8	24° 11′ 20.9″S 46° 47′ 28.5″W	Dune and ornamental vegetation Beach	Observed	
V Beach south of mouth	Point 9	24° 12′ 0.4″ S 46° 48′ 41.1″ W	Dune and ornamental vegetation Beach	Observed	
VI Beach north of mouth	Point 10	24° 10′ 0.8″S 46° 45′ 19″W to 24° 10′ 44.9″S 46° 46′ 26.3″W	Dune and ornamental vegetation Beach	Observed	

Sample Collection

Once the sites were identified (Figs. 1–2, Table 1), samples were collected to evaluate the relation of the components of the accumulations to the surrounding vegetation. Two collections were made at each site, a year apart, thus confirming the accumulations found and the diversity observed (Burnham, 1989). At the first site, a thin layer of debris covering a 1 m^2 area of the levee was collected (site I, point 1; see Figs. 2A–B); a single shallow core was also extracted. The second site had a 20 cm layer of accumulated debris, and a 20 × 20 cm block was extracted for the analysis of its composition (site II, point 3; see Figs. 2C–D); a single core was also extracted. The second year, a 30 cm layer of fine sand had been deposited on top of the layer of leaves, and a 20 × 20 × 30 cm block was collected. In the mangrove swamp (site III; see Figs. 2E–F), the thin layer of leaves covering a 1 m^2 patch of the levee (site III, point 6) was collected, and a core extracted (site III, point 7). At the sites located at the mouth of the Itanhaém River (site IV, point 8; see Figs. 2G–H) and along the coastal line (site V, point 9; site VI, point 10), no samples were collected, since the plant macrodebris was widely scattered, although easily identifiable. No significant accumulations of plant debris were found on the beach, since eventual deposits are removed and redeposited twice a day by the action of the tide. The remains were thus observed, but only evaluated qualitatively.

The accumulations collected were immediately pressed in the field to avoid damage, although the 20 × 20 cm blocks were frozen so the original depositional architecture would be preserved. In the laboratory, all plant macrodebris was pressed and dried in an oven at 40°C for several hours. The leaves collected were counted and identified, whenever possible, according to morphotype, using the criteria of Hickey (1979) and the Leaf Architecture Working Group (1999). Criteria of analysis included vein patterns and general leaf shape, as well as characteristics of the base, tip, and margins. Other plant macrodebris, such as fragments of stems, stipules, and petals, were also identified when possible. Samples are housed in the Paleohydrogeologic Laboratory, Department of Geology and Natural Resources, Institute of Geosciences, State University of Campinas, Campinas, São Paulo, Brazil.

A botanical (floristic) study was made of the modern vegetation along the rivers of the Itanhaém basin, with three expeditions for collection of material. Samples of trees, shrubs, herbs, and macroscopic aquatic plants (*Salvinia* sp., *Egeria densa*, and *Nymphaea rudeana*) were collected, with emphasis on sites I–III (Table 1), where leaf accumulations had been collected (See Supplementary Data[1]). Fertile samples were collected, pressed, and dried; they were identified and are housed in the Municipal Herbarium of the city of São Paulo (PMSP). Sample leaves were selected from this material for comparison with the leaves in the plant macrodebris.

Duration of Accumulations

To investigate the time involved in the formation of the accumulations of plant macrodebris studied here, data were collected at each of the sites every 2 months. Plastic nets (1 × 1.5 m with 1 × 1 cm mesh) were staked out for the demarcation of an easily recognizable surface area (Table 1). It was felt that the open mesh of the nets would not interfere with the natural conditions of the environment, yet the plastic would resist degradation for at least a year. Since these nets actually

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from site I, point 1. C) Site II, point 3, showing a layer of plant macrodebris deposited in 1957, which today has a thickness of 20 cm; arrow indicates where block was collected. D) Detail of block of plant macrodebris from Figure 2C. E) Site II, point 7, from interior of mangrove swamp, showing both young and adult *Rhizophora mangle* and *Laguncularia racemosa*; arrow indicates collection site. F) Detail of accumulations collected in mangrove swamp, showing sparse nature of debris. G) Site IV, point 8, showing accumulation of plant debris on the beach, with mixture of leaves, branches, and seeds, as well as rubbish. H) Site V, point 9, showing accumulation of a mixture of elements from the coast and further inland, including tree trunks, shells, and mollusks.

covered an area larger than the 1 × 1 m defined for collection, the number of leaves recovered was corrected by dividing by 1.5. At the first site, two nets were staked out, one on the levee itself (site I, point 1) and the other in a small clearing in the forest ~5 m from the bank of the river (site I, point 2). At the second site, three points were staked out, one on the levee (site II, point 3) and one on the nearby forest floor (site II, point 4); a third net was suspended aerially to catch debris in case the ground cover on the forest floor was washed away by the periodic flooding of the area (site II, point 5). At the third site, a net was staked out on the open floor of the mangrove swamp along the river (site III, point 7). No nets were staked out at the final three sites, owing to the threat of human interference, as the locations are frequented by residents and tourists; moreover, the energy of the waves was likely to remove any nets staked out on the beach. The difficulty of access to the first three sites (accessible only by boat) provided greater security; moreover, the levees are not subject to the extreme action of waves.

All plant debris deposited on the nets was counted after each 30–60 day period, climatic conditions and water level of the rivers permitting. The plant macrodebris, once counted, was returned to the nets. The average bimonthly accumulation of leaves was thus determined for each point throughout the year. Although the total plant macrodebris deposited on the nets during the year was counted, including branches, seeds, small plants and petals, only the information about leaves is considered here.

Although a net was originally installed on the levee at site II, point 3, this was removed three times by unknown agents, presumably the action of the river; the first two times it was located and replaced, but it then disappeared and the data from this specific point were lost.

Cores 7.62 cm in diameter were used to establish the time involved in deposition over a longer period of time. These made it possible to identify the kind of accumulation that would best preserve the external morphology of the leaves, a parameter often utilized in the study of fossil plant assemblages. The composition of the cores was described, and samples were dated in the ^{14}C lab of the Center of Nuclear Energy for Agriculture, University of São Paulo in Piracicaba, Brazil. Only one of the cores (from site II, point 3) had enough material to make dating possible, since well-preserved leaves were found throughout. Figure 3 describes this core and indicates the depths from which the dated samples were taken, as well as the ages obtained. The leaves in the cores removed from site I, point 1, and site III, point 7, were poorly preserved below 10 cm, and the amount of organic material present was insufficient for dating at Center of Nuclear Energy for Agriculture.

RESULTS

Plant Debris Accumulations

A total of 136 species was recorded in the survey of the vegetation growing along the banks of the three rivers; Table 2 indicates the plant species that could be identified in the leaf accumulations collected from all of the locations. For the leaves identified, the parameters used to define the morphotype are included, as well as the number of leaves of each family and genus. In all, some 1296 leaves or leaflets with preserved vein patterns were collected at sites I, II, and III, but only 966 also revealed the preservation of enough other characteristics (shape, tip, base, and margin) to define morphotypes.

Site I, Point 1; Branco River (Figs. 2A–B).—A total of 673 leaves was collected; no seeds were found. Fourteen morphotypes were identified, accounting for a total of 619 leaves; seven of these morphotypes (530 leaves, or 79% of the total) were identified as belonging to plants that grow on the levee under study (Table 2). The other 54 leaves did not reveal enough characteristics to be classified.

Site II, Point 3; Preto River (Figs. 2C–D).—Here a block of leaves was extracted; 585 leaves were recovered from the block, with 312 (53%) well preserved enough to be identified into 15 morphotypes; only 254 (43.4%) could actually be classified (seven morphotypes). All of the classified leaves belong to genera growing along the levee (Table 2). The other eight morphotypes (53 leaves) could not be identified, although this was partly due to the fact that the majority of the leaves in the block were very fragile and became so fragmented during the study that their classification was impossible. No plant debris such as leaves, branches, or flowers was found in the block extracted during the second year; this was probably a result of the flood in January (period of heavy rains in the region). Later that year, erosion of that bank of the river apparently prevented new deposition, so the only assemblage analyzed from the site was the block collected the first year.

Site III, Points 6 and 7; Itanhaém River (Figs. 2E–F).—A total of 40 recognizable leaves was collected, of which 38 (95%) were classified in two morphotypes; branches and some seeds of *Rhizophora mangle* were also identified. The two morphotypes are clearly related to *Laguncularia racemosa* (75%) and *Rhizophora mangle* (20%), both trees native to mangrove swamps (Table 2).

Sites IV, V, and VI; Mouth of Itanhaém River and Coast (Figs. 2G–H).—As described above, three locations at the mouth of the river and along the beach (coastal line) were selected for observation, although no actual collections were made. The accumulations found were composed largely of abundant, yet unrecognizable, branches, as well as seeds, especially those of *Avicennia schaueriana*, *Rhizophora mangle*, *Laguncularia racemosa*, and *Crinum americanum*, along with unidentified members of the Arecaceae (palm) family. Leaves from mangrove trees (*Avicennia schaueriana*, *Rhizophora mangle*, and *Laguncularia racemosa*) and aquatic plants (especially *Egeria densa* and *Salvinia* sp.) were also identified, as well as the remains of marine invertebrates and abundant, anthropogenically deposited rubbish.

Depositional Time of the Accumulations

The year of accumulations on plastic nets yielded results (Fig. 4) varying from 20 to 1013 leaves per net. The total number of leaves accumulated in the interior of the forest (Fig. 4D) was much greater than that found on the levee (Fig. 4C) and on the ground in the mangrove swamp (Fig. 4B). The greatest accumulation of leaves was found on the suspended net, where decomposition was somewhat slower. The cores collected at the three sites were relatively shallow, with the one extracted at site I, point 1, 88 cm deep; the one from site II, point 3, 129 cm; and the core from site III, point 7, 76 cm. Cores from sites I and III were composed mainly of a clay sediment; plant macrodebris was recognizable only for the first 0–10 cm. Below this level, only a few very thin layers (≤1 cm) with recognizable plant remains were present (five layers for site I, point 1, and three for site III, point 7). Most of the plant remains in these cores were partially decomposed, with only the most resistant tissues such as fibers remaining. The core from site II, point 3, however, was different. The predominating sediment was fine sand rather than clay, and it was limited to relatively thin layers between relatively thick accumulations of well-preserved plant macrodebris (Fig. 3). The leaves at the top of the core were deposited ca. 1957, while those at the base date to 1954; this core of 129 cm thus represents ~4 years of sedimentary accumulation of plant macrodebris. In the layers of sand, some poorly preserved fragments of plants were found, but in the thicker accumulations, the leaves deposited >50 years earlier could still be recognized.

DISCUSSION

Relation of Macrodebris to Vegetation

This study has made it possible to begin to understand the formation of plant macrodebris accumulations in the present-day depositional system. The plant remains recovered throughout the study area suggest

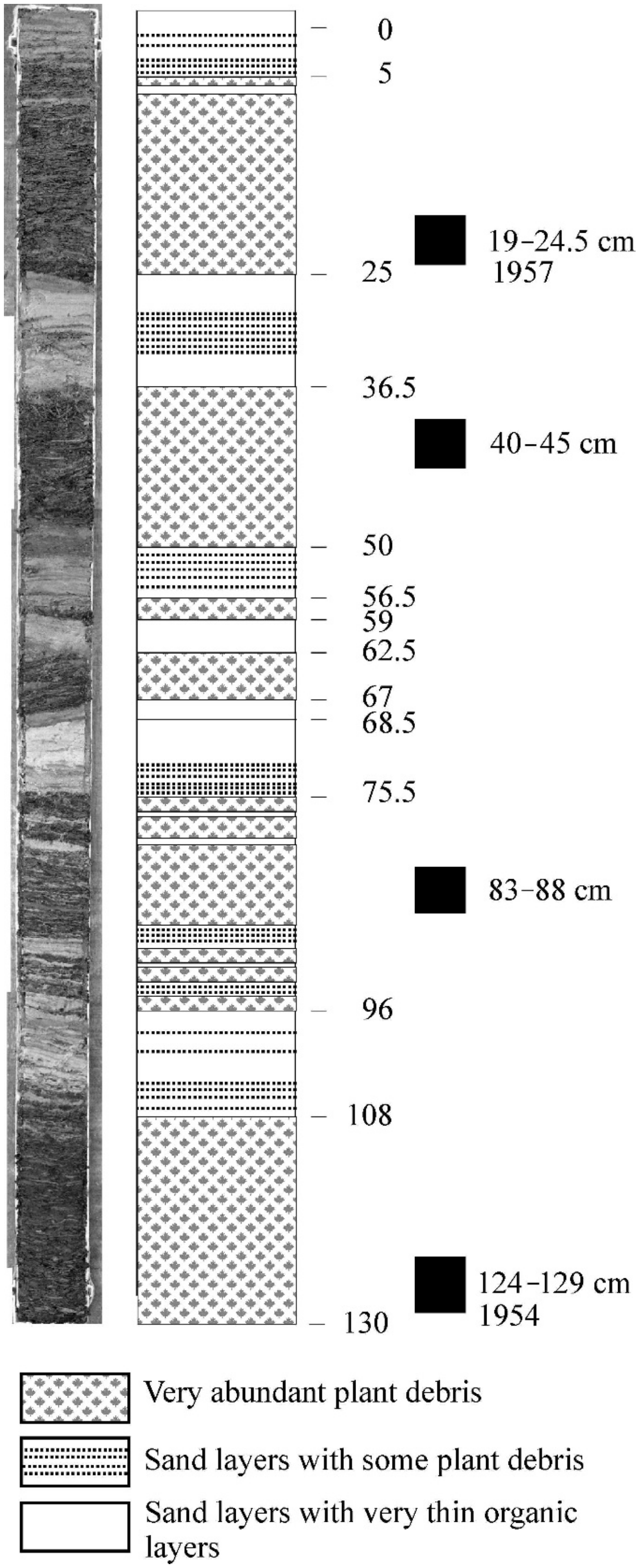


FIGURE 3—Core taken from Site II, point 3, on the Preto River (left), accompanied by a schematic drawing showing details of the thickness and composition of the layers. Note the cyclic nature of thick layers of plant debris interspersed with layers of fine sand containing few plant remains. Black squares show the level of samples collected for ^{14}C dating. Scale in meters.

a relation between composition of plant accumulations and transport (Table 2). At sites I and II, located in the middle portion of the basin (Fig. 1), all of the leaves identified were autochthonous—or, rather, parautochthonous, if the distance traversed from the branch to the ground is considered (Greenwood, 1991; Behrensmeyer and Hook, 1992; Gastaldo, 1994; Kidwell and Flessa, 1996). These leaves were easily correlated with the standing vegetation in the area. All of the morphotypes identified were from plants growing on the levee from which the leaf accumulations were collected. Even those in the 50-year-old block (site II, point 3) were found to correspond to the families of plants found in the forest today.

In the accumulations found at site I, point 1, and site II, point 3, the root systems of Poaceae (grasses) were found *in situ*. The presence of such root systems in the soil indicates truly autochthonous plant remains, even though the leaves of the Poaceae (Gramineae) are rarely preserved. Thus, when evaluating the fossil record, evidence of fibrous root systems may indicate paleosols, as well as the presence of Poaceae in Cenozoic paleofloras.

The parautochthonous accumulations from the mangrove swamp (site III, points 6 and 7), located between sites I and II and the mouth of the Itanhaém River (site IV, point 8), contained only leaves from the mangrove swamp itself, with none from the restinga forest upstream. These results are in agreement with what was found for other tropical ecosystems (Burnham, 1990), with all of the leaves identified at the first three sites coming from the arboreal stratum of the forest (Table 2; see Supplementary Data[1]). Although no collection was made from the sites along the coast and at the mouth of the Itanhaém River (sites IV, V, and VI), careful observation showed that the accumulations included a mixture of parautochthonous and allochthonous elements. Thus, in addition to limited parautochthonous macrodebris of cultivated garden plants from houses near the beach, numerous allochthonous branches and continental mangrove leaves and seeds, as well as aquatic plants (*Salvinia* sp., *Nymphaea rudeana*, and *Egeria densa*) and seeds from the restinga area (Arecaceae) had been carried downstream by the river; moreover, marine mollusk shells, polychaete tubes, and sea urchin spines were also encountered.

These results suggest that in such a meandering tropical river the transport of plant debris is minimal, with only those elements that float easily actually reaching the coast—that is, mainly branches, with a few aquatic plants and seeds, in contrast to what was initially expected. The numerous restinga forest leaves observed floating downstream with the current inside the forest had already been deposited or destroyed before reaching the mangrove swamp. The composition of accumulations at the terminal sites (IV, V, and VI) was quite uniform, and no differences in deposition of plant remains at sites V and VI were observed.

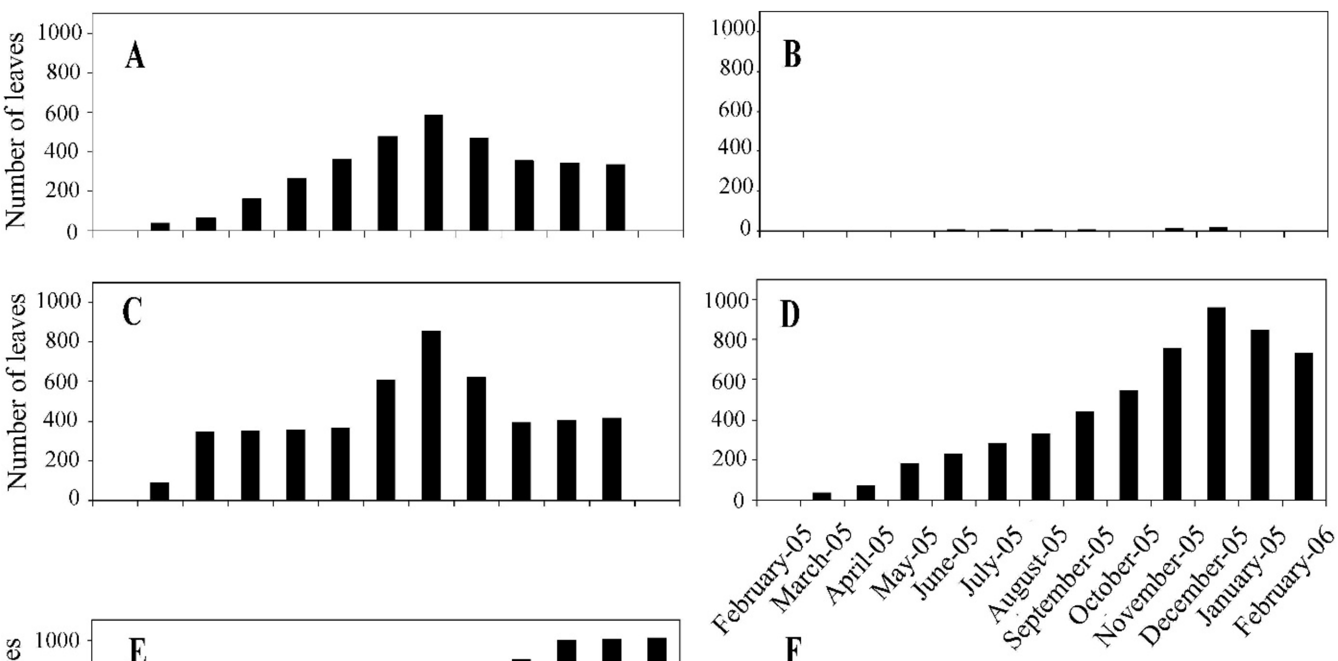
At the sites further inland, deposition varied with the site. At site I, point 1, and site II, point 3, the families Fabaceae (*Inga*), Lauraceae (*Nectandra* and *Ocotea*), and Poaceae were found. A total of 121 and 97 leaves of Lauraceae (*Nectandra*) and Melastomataceae (*Tibouchina* and *Miconia*), respectively, were found at site I, point 1. At site II, point 3, however, leaves of Sapindaceae (*Paullinia*, 73 leaves), Rubiaceae (*Faramea*, 24 leaves), and Clusiaceae (*Calophyllum*, 19 leaves) were more abundant, although these families were not found in the accumulations at site I, point 1. At both of these sites, however, morphotypes B1, B4, P2, and P4, which represent leaflets of Fabaceae (*Inga* and *Senna*; see Table 2), were the most abundant macrodebris, although they were no longer attached to the petiole of the leaves. Both Burnham (1989) and Greenwood (1991) have commented on the predominance and overrepresentation of legumes in tropical forest accumulations, and the transport of these leaflets thus constitutes a taphonomic fact which must be considered when interpreting Cenozoic paleofloras. For the paleoflora of Fonseca Basin, Minas Gerais, Brazil, several authors (e.g., Oliveira-e-Silva, 1982; Ricardi-Branco and Fanton, 2007) mentioned the overwhelming predominance of leaflets of Fabaceae (Leguminosae), especially *Caesalpinia*, *Cassia*, *Mimosa*,

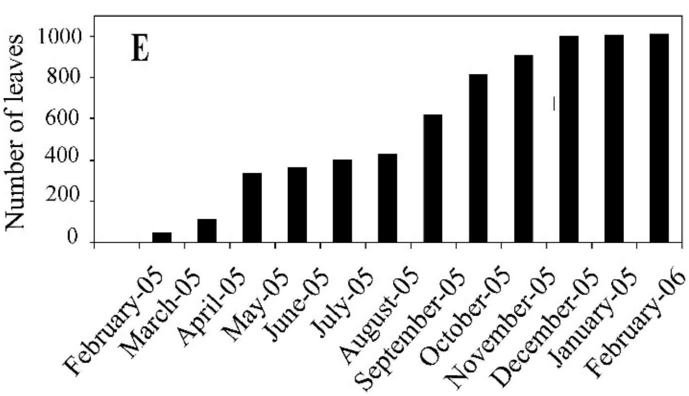
TABLE 2—Morphotypes of leaves identified and the vegetation found at site I (levee of Branco River), site II (levee of Preto River), and site III (mangrove swamp on Itanhaém River). Venation types: Campt = camptodromous; Acro = acrodromous; Parallel = parallelodromous; Craspedo = craspedodromous.

Sites	Morphotype	Venation	Leaf shape	Base form	Tip form	Margin type	Related family	No. of leaves
Site I (Point 1)	B1	Campt	Obovate	Cuneate	Acuminate	Entire	Fabaceae (*Inga*)	160
	B2	Campt	Elliptic	Cuneate	Acuminate	Entire	Lauraceae (*Nectandra*)	121
	B3	Campt	Elliptic	Cuneate	Convex	Entire	Myrtaceae (*Myrcia*)	7
Branco River	B4	Campt	Oblong	Convex	Rounded	Entire	Fabaceae (*Senna*)	140
	B5	Acro	Obovate	Cuneate	Convex	Entire	Melastomataceae (*Miconia*)	25
	B6	Acro	Elliptic	Cuneate	Acute	Entire	Melastomataceae (*Tibouchina*)	72
	B7	Parallel	Ovate	Convex	Acute	Entire	Poaceae	5
Site II (Point 3)	P1	Campt	Elliptic	Complex	Acute	Entire	Lauraceae (*Ocotea*)	4
	P2	Campt	Elliptic	Cuneate	Convex	Entire	Fabaceae (*Inga*)	48
	P3	Campt	Oblong	Cuneate	Convex	Entire	Rubiaceae (*Faramea*)	25
Preto River	P4	Campt	Ovate	Complex	Acuminate	Entire	Fabaceae (*Inga*)	81
	P5	Campt	Elliptic	Convex	Convex	Entire	Clusiaceae (*Calophyllum*)	19
	P6	Craspedo	Elliptic	Cuneate	Acuminate	Crenate	Sapindaceae (*Paullinia*)	73
	P7	Parallel	Elliptic	Cuneate	Acute	Entire	Poaceae (Bambusoidae)	3
Site III (Points 6–7)	M1	Campt	Obovate	Cuneate	Convex	Entire	Rhizophoraceae (*Rhizophora mangle*)	8
Itanhaém River	M2	Campt	Elliptic	Convex	Convex	Entire	Combretaceae (*Laguncularia racemosa*)	30

and *Schizolobium*. These were the most abundant elements and were interpreted as being very abundant in the paleoflora of the Fonseca Basin. A similar conclusion was drawn for the paleoflora of the Oligocene basins of Taubaté (Bernardes-de-Oliveira et al., 2002). The tendency for overrepresentation of the legume family in the present-day taphonomic study, however, suggests that the biodiversity in the paleofloras in these regions should possibly be reinterpreted.

The genera and families identified from the leaves collected during the study of sites I and II were largely Fabaceae, Lauraceae, Clusiaceae, and Myrtaceae, which correspond to dominant elements in the tropical





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Site and years / Venation	Site I, Point 1		Site II Point 3	Site III points 6-7	
	2004	2005	2004	2004	2005
Actinodromous	23	37	81	——	——
Parallelodromous	3	3	4	——	——
Acrodromous	53	54	4	——	——
Camptodromous	183	289	437	——	——
Craspedromous	12	16	78	7	31
Total	274	399	604	7	31

FIGURE 4—Monthly leaf accumulation on nets throughout the year at the study sites (no data available for site II, point 3; see text). A) Site I, point 1, levee in restinga forest along Branco River. B) Site III, point 7, mangrove swamp along Itanhaém River. C) Site I, point 2, restinga forest. D) Site II, point 4, restinga forest along Preto River. E) Site II, point 5, aerial net in restinga forest. F) Total number of leaves collected at each site in 2004 and 2005, arranged by leaf venation type.

forest now (Garcia and Pirani, 2003; Burnham and Johnson, 2004). The presence of Melastomataceae, Sapindaceae, and Poaceae is also typical of a tropical forest, as well as that of Rhizophoraceae, Acanthaceae (*Avicennia*), and Arecaceae, whether in the form of leaves or seeds. These latter elements, also found in abundance at sites III, IV, V, and VI, reflect a tropical forest. The presence of Melastomataceae, Sapindaceae, and Poaceae helps characterize a dense ombrophyle forest of low altitudes or a restinga forest.

Depositional Time and Fossilization

Decomposition is rapid in a tropical forest, although thicker accumulations tend to promote anaerobic conditions and delay decay. Depositional time is thus relevant for the establishment of the conditions favoring fossilization.

Plant macroremains were deposited all year round, but the processes leading to their accumulation seem to have varied from one site to another. The deposits at sites I and III represent the ongoing process of deposition and consequent gradual accumulation of plant macrodebris (Alexander et al., 1999), whereas that found at site II seems to represent isolated depositional events. At sites I and II, the deposition of leaves (Figs. 4A, C–D) followed the same pattern of annual increase until stabilization was achieved. The data (Figs. 4A–C) suggest that it would have taken 3–4 months to accumulate the 350 leaves in the original assemblage collected at site I, point 1. This number of leaves seems to be a critical quantity, as it is quite similar to the 350 leaves found in the net after a year of monitoring, although the number fluctuated throughout the year, reaching a high of 587 during September before returning to the average of 350. The eventual stabilization may have been due to the action of decomposition or erosion, especially since the later observations with diminished leaf counts were made during the summer months, when the temperature was higher and the action of decomposing bacteria tends to increase. The main accumulation of plant macrodebris thus took place during the coldest and least rainy months (between June and August), at a time when the level of the Branco River was the lowest (Lamparelli, 1999; Camargo et al., 2002).

Under these conditions, decomposition and removal (Gastaldo and Staub, 1999) were reduced. These parameters were considered to be the most important, since the trees in the restinga forest and mangrove swamps do not lose their leaves during the winter. The wind was probably responsible for much of the removal of leaves from the trees, as masses of cold, polar air cause strong winds to blow along the Brazilian coast from June through August. The accumulation of debris on the forest floor beside the levee (site I, point 2; see Fig. 4C) also showed a steady increase up to September, although this slowed down and stabilized when the weather became warmer.

The accumulation of leaves in the mangrove swamp at site III (Fig. 4B) was quite limited throughout the year, especially in comparison with the sites I and II inside the restinga forest. Accumulation never surpassed the number of leaves deposited in a single month. This may be directly related to the removal of plant macrodebris by the action of the tide or to rapid decomposition or burial. Similar results were found for mangrove swamps in Belize (Middleton and McKee, 2001).

The deposition of leaves on the levee and floor of the restinga forest was extremely slow (Gastaldo and Staub, 1999). This suggests that the assembly found at site II, point 3 (Figs. 4D–E), must have involved a different process, since, on the basis of the carbon-dating studies, an accumulation of 20 cm of leaves took only a single year. This would be the equivalent of $\sim$1700 leaves$\cdot$m^{-2} per month, which contrasts with the 30–300 per month deposited during the year of the study period at site I. This rapid depositional process may have involved an episodic event (Gastaldo, 1994; Alexander et al., 1999), such as the flooding which took place at the beginning of the second year, although in 2005 the deposit consisted only of sand.

Only a single site preserved the morphological characteristics of the accumulated leaves (shape, vein pattern, apex, etc.) at a depth exceeding 10 cm (Fig. 3). This was site III, point 3, on the Preto River. The conditions found here are presumably those most likely to lead to fossilized preservation—that is, anaerobic conditions, acidic pH, rapid sedimentation and burial, and the acidic water of the river due to the high content of organic matter (Camargo et al., 2002). In contrast, for the accumulations in the mangrove swamp and at site I, point 1, the peat preserves only fragments of the most resistant tissues, such as cuticles, lignin, and palynomorphs (Amaral et al., 2006).

The degree of preservation of the debris is also related to the dynamics of the aquatic environment and the physiochemical characteristics of the superficial and subterranean waters (Gastaldo and Staub, 1999). At site I on the Branco River, for example, the acidic and oxidative nature of the water in the shallow aquifer favors a low degree of preservation of the debris, while site II on the Preto River presents a more reducing environment due to the presence of organic matter in the water and the slower flow of the river. These characteristics would contribute to greater deposition and conservation of the macrodebris, and preservation is indeed greater.

CONCLUSIONS

1. In the basin of the Itanhaém River, São Paulo State, Brazil, accumulations of plant macrodebris were denser on the levees and in the interior of the restinga forest than on the ground of the mangrove swamp. Accumulations at the river mouth and on the coast, when present, were quite limited.

2. The plant macroremains found on the levees reveal a parautochthonous composition, with the morphotype of the leaves in general corresponding to that of genera inhabiting the levee today. Similar results were found for the accumulations in the mangrove swamp, with the morphotype of the leaves in these reflecting that of the plants in the mangrove area. In contrast to expectations, these accumulations show that the debris deposited was largely limited to the area of origin, with leaves removed from the fluvial system before water could transport them downstream. At the river mouth, as well as along the coast, plant debris included a mixture of parautochthonous and allochthonous elements, but the latter consisted basically of seeds, branches, and other more resistant plant structures.

3. The time required for deposition of accumulations of macroplant debris such as those collected oscillates as a function of the location. Thus, for sites I and III, the leaves collected corresponded to 4 months of fallen leaves, although special conditions, such as especially strong currents of flood waters, can lead to the extremely rapid deposition of thick accumulations of leaves, as was found for site III, point 3.

4. In a modern depositional system such as this basin, the layers of leaves with the greatest possibility of being preserved are those found on the levees of rivers, especially rapidly deposited, thick layers that are quickly covered by sediments; moreover, these accumulations preserve the characteristics of the nearby vegetation.

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