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VEGETATION AND SOILS OF TIDAL FLOODPLAINS OF THE AMAZON ESTUARY: A COMPARISON OF VÁRZEA AND TERRA FIRME FORESTS IN PARÁ, BRAZIL

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MONTAGNINI, F. & MUÑIZ-MIRET, N. 1999. **Vegetation and soils of tidal floodplains of the Amazon estuary: a comparison of várzea and terra firme forests in Pará, Brazil.** The floodplains of sediment-rich rivers comprise 200 000 km^2 of the Amazon basin. Varying flood regimes within this region contribute to different forest formations along the basin. This study compared tree species composition, forest-floor litter biomass, and soil chemistry of three sequentially-aged secondary forest stands of tidal "várzea" (5, 15, and 35 years old) and one "terra firme" (non-inundated) stand of mature forest in the southern Amazon estuary. Tree species diversity was much lower in the várzeas than in the terra firme. Total tree basal area was highest in the terra firme, followed by the 35-, 15-, and 5-year várzeas respectively. In each várzea site, the Leguminosae and Palmae families comprised more than 50% of total basal area. Forest-floor litter was significantly higher in the terra firme than in the várzea sites. Water drainage was an important influence on vegetation and soil chemistry among the várzea sites. Concentrations of basic cations (Ca, Mg and K) and extractable P were higher in the soils of the three várzeas than of the terra firme. The pH of the top soil in the terra firme was significantly lower than in all other sites except the oldest várzea. Total C concentration in the soil was highest in the 5- and 35-year várzeas. Total soil N also was higher in the tidal várzeas than in the terra firme site. Interpretation of these findings was limited due to lack of proper site replication, and because age and inundation regimes both varied among sites. However, the results tend to confirm the expectation that soils of tidal várzeas are more fertile than those of terra firme sites, and that tidal várzeas present a more limited species composition than terra firme forests.

Key words: Amazon estuary - soil chemistry - vegetation composition - tidal flood plain - várzea - terra firme

MONTAGNINI, F. & MUÑIZ-MIRET, N. 1999. **Pertumbuhan dan tanah di dataran banjir pasang-surut di muara sungai Amazon: perbandingan antara hutan várzea dengan hutan terra firme di Pará, Brazil.** Dataran mendap sungai yang kaya dengan bahan mendapan meliputi kawasan seluas 200 000 km^2 daripada lembah Amazon. Perubahan regim banjir di kawasan ini menyebabkan perbezaan pembentukan hutan di sepanjang lembah tersebut. Kajian ini membandingkan kandungan spesies pokok, biojisim sarap di lantai hutan, dan kimia tanah bagi tiga dirian hutan sekunder

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dengan umur berturutan bagi pasang-surut várzea (5, 15 dan 35 tahun) dan satu dirian terra firme (tidak dibanjiri) hutan matang di utara muara sungai Amazon. Kepelbagaian spesies pokok lebih rendah di várzea berbanding dengan spesies pokok di terra firme. Jumlah luas pangkal kawasan didapati tertinggi di hutan terra firme, diikuti dengan hutan várzea yang masing-masing berumur 35, 15 dan 5 tahun. Dalam setiap tapak hutan várzea, kaum Leguminosae dan Palmae mengandungi lebih 50 % daripada jumlah luas pangkal. Sarap di lantai hutan adalah lebih tinggi di tapak terra firme berbanding dengan tapak várzea. Saliran air merupakan pengaruh penting dalam pertumbuhan dan kimia tanah di tapak várzea. Kepekatan kation asas (Ca, Mg dan k) dan P boleh ekstrak adalah lebih tinggi dalam tanah di tiga várzea berbanding dengan tanah di terra firme. Kandungan pH lapisan atas tanah di tapak terra firme adalah lebih rendah dengan bererti berbanding dengan semua tapak lain kecuali tapak várzea yang tertua. Jumlah kepekatan C dalam tanah didapati tertinggi di tapak várzea yang berumur 5 dan 35 tahun. Jumlah N tanah juga lebih tinggi di várzea yang mengalami pasang surut berbanding dengan tapak terra firme. Ulasan bagi penemuan ini terhad kerana kekurangan pengulangan tapak yang sesuai, dan juga kerana kedua-dua regim umur dan regim penimbunan berubah- ubah di tapak. Bagaimanapun, keputusan mengesahkan andaian bahawa tanah di kawasan pasang surut várzea lebih subur berbanding dengan tanah di tapak terra firme. Tanah pasang surut várzea juga menunjukkan kandungan spesies yang lebih terhad berbanding dengan hutan terra firme.

Introduction

The floodplains of sediment-rich rivers comprise 3% (about 200 000 km^2) of the Amazon basin (Ayres 1993). The floodplains, termed "várzea da maré" (tidal várzeas) specifically refer to the lands located within the tidal region of the delta (Ayres 1993, Hiraoka 1995). The ocean tides influence the flow regime of the várzeas up to the locality of Obidos, as far as 850 km from the mouth of the Amazon river in the Atlantic (Barrow 1985). Therefore, although accurate estimates of the extent of tidal várzeas are not available, they comprise a relatively large portion of the Amazon basin. Tides hold up river discharge, rather than allow the penetration inland of salt water; therefore tidal várzeas are flooded regularly with fresh water (Barrow 1985). Várzea soils are periodically enriched by sediment deposition during seasonal or tidal floods (Junk 1984), resulting in relatively higher soil fertility than non-flooded, or "terra firme", lands (Junk 1984, Barrow 1985, Martinelli *et al.* 1993, Barrios *et al.* 1994, Konhauser *et al.* 1994). Compared to terra firme forests, the vegetation of várzea forests is restricted to species adapted to flood regimes and oxygen-deficient soils and is limited in diversity (Peters 1992).

Species composition in várzeas varies with frequency and duration of flooding, sedimentation rates and soil texture (Junk 1984, Puhakka & Kalliola 1993). Different forest formations can be identified in várzeas at different points along the Amazon basin where flood regimes differ (Pires & Prance 1985). For example, várzeas of the Amazon estuary undergo less pronounced but frequent tidal floods while várzeas of the upper Amazon may be flooded continuously for several months during annual river fluctuations (Anderson & Ioris 1992). Detailed information on tree species composition is currently lacking for the lower Amazon (Ayres 1993).

As part of a larger research project on land use alternatives for the Amazon basin, this study examined the tree species composition and soil chemistry of three regenerating várzea stands and compared them with adjacent non-flooded lands. Study sites were located in the southern portion of the Amazon estuary in Abaetetuba (Pará, Brazil) and comprised three tidal várzea sites of sequentially-aged secondary forests (5, 15, and 35 y old) and one terra-firme (non-inundated) stand of mature forest surrounded by floodplains. The results are expected to contribute to a better understanding of the vegetation and soils of the tidal várzeas of the Amazon estuary in comparison to those in seasonal floodplains of the upper Amazon. It was expected that tidal várzeas would present a more limited species composition and higher soil nutrients than the terra firme site.

Methods

Site description

The study site was located in a 50-ha private experimental field station on the Amazon estuary in Abaetetuba, 80 km southwest of Belém, Pará, Brazil (1° 40'S, 48° 55'W) (Figure 1). The station is located on one of many islands in the Rio do Pará, a tributary of the Amazon estuary, and is surrounded by approximately 300 ha of mature and late secondary forests. Like much of eastern Amazonia, Abaetetuba has a tropical monsoon climate. Rainfall in the adjacent city of Belém averages 2732 mm per year, with peaks (more than 200 mm/month) in January-May and lows (less than 100 mm/month) in October and November. The average annual temperature is 25 °C (Hiraoka 1995).

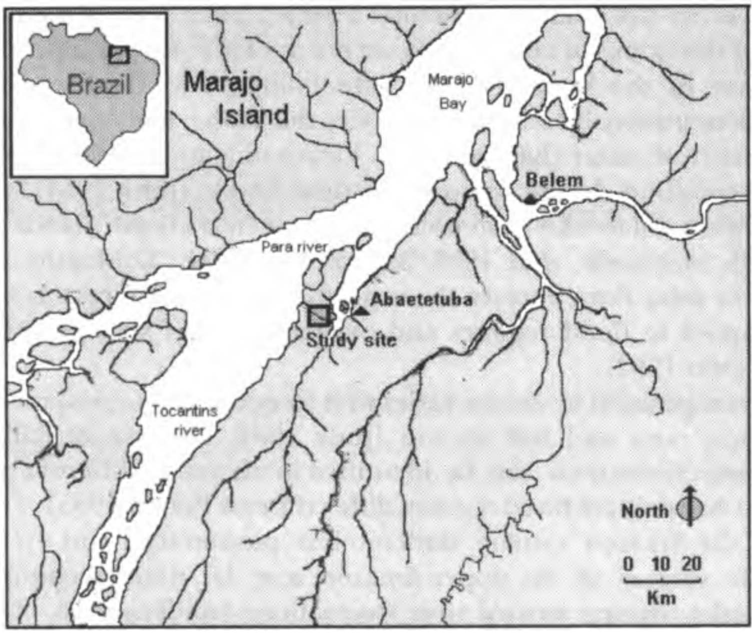

Figure 1. Map of the southeast portion of the Amazon estuary, showing the location of the study site

Islands in the várzeas of the estuarine region consist of flat, low-lying terrain, developed over quaternary sediments. High ground within the islands does not exceed 5 m above the highest tidal levels. Except for a few flood-free sites, locally called "icas", tidal várzeas are periodically flooded. Frequency of flooding depends on the tidal regimes and the land's elevation and position relative to tidal water sources (Hiraoka 1995). Many tidal várzeas are flooded twice daily whereas relatively higher grounds may only be flooded during the full and new moon phases (Hiraoka 1995). Tidal várzeas are flooded for 2 or 3 h at a time. This contrasts with floodings in the upper Amazon that can last several months.

The white-water Tocantins River is the main source of water to this area (Hiraoka 1995). The river carries and deposits sediments from the weathered soils of the Brazilian highlands, which have created the deep and recent alluvial soils in the estuary. Soils of the study area have been described by Winkler Prins (1993) and by Hiraoka (1995). Soils are Entisols, composed of a thin surface layer of organic matter (generally <1 cm thick), a thin to moderate (1-3 cm thick) (A) horizon which overlies a mottled (C) horizon, and a gleyed (Cg) horizon. The mottled zone reflects small daily and larger seasonal fluctuations of the water- table. The gleyed horizon, continually saturated, oxidises very rapidly when exposed to air. Below the Cg horizon lies buried peat (Winkler Prins 1993, Hiraoka 1995). Kaolinite, illite, and mica are the dominant clay forming minerals, reflecting the source area of sediments. Soil nutrient status varies spatially, reflecting factors such as tidal regimes, high water table, differences in local relief, past management, and distance from stream channels. Overall, soils have low cation exchange capacity (20–40 cmol kg^{1}), and low pH (4.0–6.0). The texture (clay to silty clay loam) is indicative of the composition of suspended materials. The combination of high clay content, high and fluctuating water-table, and presence of extensive swampy areas are responsible for the anaerobic conditions of most tidal várzea soils (Hiraoka 1995).

This study was conducted from July to August 1993 on four sites (three tidal várzeas and one terra firme) considered representative of the region. The three tidal várzea sites supported differently-aged regenerating forests: a 5–8-y-old stand (which we call 5-year várzea), a 15–18-y-old stand (15-y várzea), and a 35–40-y- old stand (35-y várzea). These tidal várzeas were originally cleared for cultivation of sugar cane, which was subsequently abandoned after the decline in sugar cane prices around 1975. A non-flooded ica site (which we call terra firme) was studied to contrast with the three tidal várzea sites. According to local informants, this terra firme forest had never been clear cut. The soil in the terra firme site was sandier than the tidal várzea sites, particularly on the surface layers, while the lower layers consisted of yellow silt loam.

Characterisation of the vegetation

Each tidal várzea stand was approximately 1.5 ha, and the terra firme stand was about 6 ha in size. A single one-hectare plot was established at random in each of the four study sites to survey trees and arborescent palms that were greater than or equal to 10 cm in diameter at breast height (dbh). All trees and arborescent palms were measured for top height (or stem height in the case of palms) and dbh. Height measurements were obtained for all açaí (*Euterpe oleracea*) palms with stems greater than 1.3 m tall, even if they had a diameter < 10 cm. Stem height of açaí was measured to the base of the leaves. Tree and palm species were identified using the herbarium specimens of the Goeldi Museum in Belém.

Means and standard errors were calculated to compare dbh and height measurements of all trees and arborescent palms (dbh >10 cm) among sites. (Calculated means used individual trees as repetitions.) In the same manner, means and standard errors were calculated for the dbh and crown heights of trees only (palms excluded). The trees and palms in each site were sorted and counted in the following diameter classes (cm): 10–15, 16–20, 21–30, 31–40, 41–80 and >80. Basal area ($m^2 ha^{-1}$) for all trees and palms (dbh >10 cm) was calculated. In order to compare vegetation composition among the four study sites, importance values were calculated as the average of relative density and relative basal area for the most abundant species at each site.

Forest-floor litter

Forest-floor litter was collected in all sites within ten randomly chosen 1 × 1 m plots. Litter was air-dried for 1–2 weeks until constant weight using a precision scale. Samples were sorted into the following fractions: wood, including bark and twigs (<2.5 cm in diameter); palm leaves; non-palm leaves; and other plant parts. Analysis of variance and test for means for each fraction of forest-floor litter was calculated using Fisher's LSD (n=10, $p < 0.05$) to compare the amounts of litter between sites.

Soil chemistry

Composite soil samples (three subsamples) were taken at five random locations in each of the four sites. Samples were taken with a 2.5 cm diameter slotted soil recovery probe at 0–5, 5–15, 15–30, 30–45 and 45–60 cm of depth. Chemical analyses were performed following procedures described by Anderson and Ingram (1993). The pH was measured in a 1:2.5 mixture of soil to deionised water using a combination electrode and a Fisher Accumet 915 digital pH meter. Total nitrogen and carbon were measured by dry combustion using a Leco CHN-600 carbon Nitrogen Determinator (Leco Corp., St. Joseph, Michigan). Ca, Mg, K, Al and microelements (Fe, Mn, and Cu) were extracted with a diluted H_2SO_4-HCl (Melich's) solution using a 1:5 proportion of soil:solution. Cations were measured using a Jarrel Ash Inductively Coupled Atom Scan Spectrometer (Thermo Jarrell Ash, Franklin, Massachusetts). Extractable-P was measured colorimetrically at 880 nm wavelength using a Perstorp Analytical Flow Solution Analyzer (Perstorp Analytical, Wilsonville, Oregon) after extraction in Melich's solution and reaction with ascorbic acid and a molybdate reagent. Analysis of variance and LSD tests for means were used to compare soil variables by site and depth (n=5, $p< 0.05$).

Results

Tree species composition

Species and families found in the tidal várzea and terra firme sites are presented in Appendices 1 and 2. Fifty-two species of trees and arborescent palms, representing 24 families and 43 genera, were identified in the terra firme. Thirty-eight tree species were identified in the three tidal várzea sites combined, including 18 families and 36 genera. Twenty-six tree species were found in the 35- y-old várzea forest while 21 species each were found in the younger tidal várzea stands.

Total tree basal area ($m^2 ha^{-1}$) of selected species was highest in the terra firme (40.2), followed by the 35-year várzea, (28.8), the 15-y várzea, (15.1) and the 5-y várzea (12.9) (Tables 2 and 3). Together, the Leguminosae and Palmae families comprised 64 , 63 and 83% of the total basal area in the 5-, 15- and 35-y tidal várzeas respectively. In the terra firme, the families with the largest basal area were the Leguminosae (19%) and the Lecythidaceae (10%). Conversely, although Leguminosae and Lecythidaceae had the largest basal area, no four families comprised more than 46% of basal area in the terra firme (Table 1).

Table 1. Basal area of plant families in the three várzea and one terra firme sites

Site	Family	Basal area	
		$m^2 ha^{-1}$	(%)
5-y várzea	Leguminosae	5.02	39.0
	Palmae	3.24	25.2
	Euphorbiaceae	2.67	20.8
	Anacardiaceae	0.75	5.8
	Myristicaceae	0.53	4.1
15-y várzea	Leguminosae	6.73	44.5
	Euphorbiaceae	3.01	19.9
	Palmae	2.82	18.6
	Myristicaceae	1.27	8.4
	Rubiaceae	0.43	2.9
35-y várzea	Leguminosae	13.30	46.1
	Palmae	10.60	36.8
	Verbenaceae	1.62	5.7
	Euphorbiaceae	1.17	4.1
	Myristicaceae	1.00	3.5
Terra firme	Leguminosae	4.39	19.4
	Lecythidaceae	4.11	10.2
	Unknown 8	3.54	8.8
	Anonaceae	3.00	7.5
	Meliaceae	2.89	7.2
	Bignoniaceae	2.74	6.8

In all the three várzea stands studied, *Pterocarpus amazonicus* (Leguminosae, Papilionoidae) had the highest importance value. The rubber tree (*Hevea brasiliensis*, Euphorbiaceae) was second in importance in the 15-y várzea and third in the 5-y várzea. Other species with high importance values were *Avicennia nitida* (Verbenaceae) in the 35-y várzea, *Virola surinamensis* (Myristicaceae) in the 15- and 35-y várzeas, and *Swartzia accuminata* (Leguminosae, Caesalpiniodeae) in the 5-y várzea. A total of twelve species occupied 2 % or more of the basal area in at least one tidal várzea site (Table 2).

In the terra firme site, 18 different species occupied at least 2 % of the basal area (Table 3). The four most dominant species or genera were *Tabebuia* sp. 1, unknown species 8 (common name, "angara"), *Eschweilera matamata*, and *Pentaclethra macroloba*, in that order. Six species were found in both the three tidal várzea and one terra firme sites: *Carapa guianensis, Cassipourea guianensis, Hevea brasiliensis, Ormosia coutinho, Virola surinamensis* and *P. macroloba*. Additionally, two genera were found in all four sites: *Cecropia* spp. and *Tabebuia* sp. 1 (Appendices 1 and 2).

As expected, the diameters of all trees and arborescent palms were significantly larger in the terra firme than in the várzea sites ($p < 0.05$). The density per hectare of trees and arborescent palms for all diameter classes was greatest in the terra firme (Figure 2). Among the tidal várzea sites, the largest number of individuals in the smallest diameter class (10-15 cm) was found in the 35-y várzea (244), followed by the 5-y várzea (241) and 15-y várzea (197).

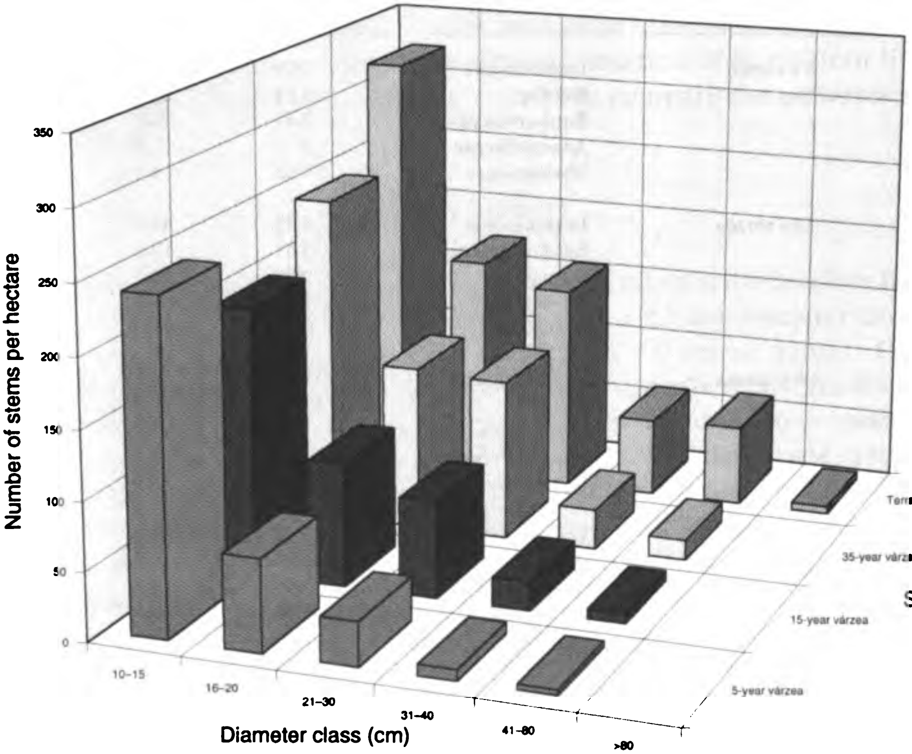

Figure 2. Frequency distribution of tree diameters in the three várzea and one terra firme sites

Table 2. Density, basal area, and importance values of selected várzea species. Species selected had a basal area >2% in at least one site. Importance values (I.V.) were calculated as the average of relative density and relative basal area. All values are on a per hectare basis.

Spesies	Family	5-y -várzea					15-y -várzea					35-y-várzea				
		Density		Basal area		I.V.	Density		Basal area		I.V.	Density		Basal area		I.V.
		Stems	(%)	m^2	(%)		Stems	(%)	m^2	(%)		Stems	(%)	m^2	(%)	
Avicennia nitida	Verbenaceae	4	1.06	0.05	0.42	0.74	2	0.49	0.06	0.39	0.44	23	3.53	1.62	5.65	4.59
Bombax spp.	Bombacaceae	7	1.86	0.10	0.75	1.31	4	0.99	0.12	0.81	0.90	25	3.84	0.66	2.31	3.08
Euterpe oleracea	Palmae (Arecaceae)	5	1.33	0.01	0.07	0.70	0	-	-	-		9	1.39	0.10	0.35	0.87
Genipa americana	Rubiaceae	6	1.60	0.13	1.00	1.30	9	2.22	0.43	2.85	2.54	1	0.15	0.03	0.10	0.13
Hevea brasiliensis	Euphorbiaceae	53	14.10	2.03	15.80	15.00	55	13.60	2.11	14.00	13.80	16	2.46	1.05	3.66	3.06
Mauritia flexuosa	Palmae	19	5.05	3.24	25.10	15.10	17	4.20	2.82	18.60	11.40	110	16.90	10.50	36.40	26.70
Phyllantus spp.	Euphorbiaceae	33	8.78	0.64	5.00	6.89	50	12.30	0.90	5.91	9.11	7	1.08	0.11	0.40	0.74
Platymiscium spp.	Leguminosae (Mimosoideae)	-	-	-	-	-	4	0.99	0.50	0.81	0.90	2	0.31	0.02	0.07	0.19
Pterocarpus amazonicus	Leguminosae (Papilionoideae)	171	45.20	3.32	25.80	35.50	211	52.10	6.13	40.50	46.30	371	57.00	11.20	38.90	48.00
Spondias lutea	Anacardiaceae	6	1.60	0.75	5.79	3.70	-	-	-	-	-	-	-	-	-	-
Swartzia acuminata	Leguminosae (Caesalpiniodeae)	22	5.85	1.34	10.40	8.13	-	-	-	-	-	16	2.46	1.15	3.99	3.23
Virola surinamensis	Myristicaceae	21	5.59	0.53	4.12	4.86	24	5.93	1.27	8.40	7.17	29	4.45	1.00	3.49	3.97
Other species		29	7.98	0.73	5.75	6.86	29	7.18	0.80	7.73	7.46	42	6.43	1.32	4.68	5.56
Total		376	100	12.87	100	100	405	100	15.14	100	100	651	100	28.76	100	100

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Crown heights for all trees and arborescent palms (including açaí) were significantly higher in the terra firme (11.9 m) and the 35-y várzea (11.4 m) than in the other two sites under study (Table 4).

Table 3. Density, basal area, and importance values of selected terra firme species. Species selected had a basal area >2% in at least one site. Importance values (I.V.) were calculated as the average of relative density and relative basal area. All values are on a per hectare basis

Species	Family	Density		Basal area		I.V.
		Stems	(%)	m^2	(%)	
Carapa guianensis	Meliaceae	27	1.61	1.98	4.93	3.27
Dipteryx odorata	Leguminosae (Papilionoideae)	36	4.61	2.02	5.03	4.82
Eschweilera matamata	Lecythidaceae	50	6.45	3.62	9.02	7.74
Goupia glabra	Celastraceae	16	2.07	2.59	6.43	4.25
Guatteria spp.	Annonaceae	7	0.92	1.97	4.90	2.91
Hevea brasiliensis	Euphorbiaceae	16	2.07	1.11	2.77	2.42
Jacaranda copaia	Bignoniaceae	5	0.69	0.92	2.29	1.49
Maximiliana spp.	Palmae	41	5.30	1.24	3.08	4.19
Parinari spp.	Chrysobalanaceae	4	0.46	1.87	4.65	2.56
Pentaclethra macroloba	Leguminosae (Mimosoideae)	66	8.53	2.46	6.11	7.32
Swartzia spp.	Leguminosae (Caesalpiniodeae)	48	6.22	2.05	5.10	5.66
Tabebuia sp. (1)	Bignoniaceae	101	13.10	1.74	4.33	8.72
Tapirira cf. *guianensis*	Anacardiaceae	36	4.61	1.16	2.90	3.76
Xylopia spp.	Annonaceae	36	4.61	1.03	2.56	3.59
Unknown 2 (Tereu)		20	2.53	0.90	2.24	2.39
Unknown 6 (Fava)	Leguminosae	7	0.92	0.88	2.19	1.56
Unknown 8 (Angara)		57	7.37	3.54	8.80	8.09
Unknown 10 (Cinzeira)		7	0.92	2.47	6.14	3.53
Other species		193	27.00	6.63	16.53	21.80
Total		773	100	40.20	100	100

Table 4. Trees and arborescent palms (dbh >10 cm): basal area, dbh, and height (means and standard errors) in the three várzea and one terra firme sites (means and standard errors)

Site	Basal area	Dbh	Height	
	$(m^2 ha^{-1})$	Trees & palms	Trees & palms	Açai
5-y varzea	11.2	16.8 (0.45)	7.60 (0.29)	2.00 (0.06)
15-y varzea	13.9	18.7 (0.44)	5.19 (0.13)	1.84 (0.02)
35-y varzea	28.3	21.1 (0.39)	11.39 (1.47)	3.10 (0.12)
Terra firme	39.2	20.9 (0.62)	11.94 (0.19)	* *

* There were no açai palms in terra firme stands.

Forest-floor litter

For non-palm leaves, the amount of forest-floor litter was significantly higher in the terra firme (452 g m^{-2}) than in the tidal várzea sites which ranged from 54.8 to 166 g m^{-2} (Figure 3). Biomass of woody debris in the terra firme (238 g m^{-2}) was also significantly higher than that of the 15- and 35-y várzeas (Figure 3). Palm leaf accumulation was significantly higher in the 35-y várzea than in the terra firme (Figure 3).

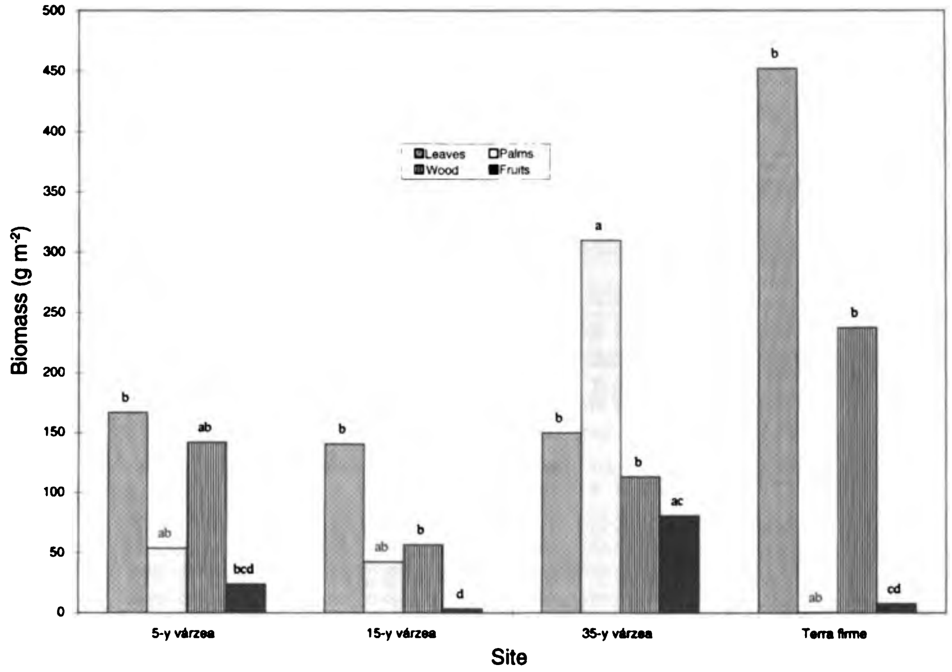

Figure 3. Forest-floor litter biomass in the three várzea and one terra firme sites. For each forest-floor category, differences among sites are statistically significant when bars are indicated by different letters. Note: In the terra firme, the amount of palm leaf litter was very small and it appears as zero in the figure due to the scale used.

Soil chemistry

Total C concentration in the soil was higher in the 5- and 35-y várzeas than in all other sites at all five depths examined (Table 5). Soil total C concentrations in these two sites were in the range of 4.21–11.04 % and were similar in both sites at any given depth. The 15-year várzea and terra firme had soil C levels in the range 0.38–3.96 %. The three tidal várzea sites showed higher soil C at the lowest depth, particularly in the youngest stand. This trend was not seen in the terra firme, where there was a steady decrease of C concentration with increasing depth.

Total N concentration in the soil showed a similar trend to that found for soil C. Higher N concentrations were found in the 5- and 35-y várzeas (0.28–0.46 %). Soils in the 5-y várzea had significantly higher total N than the 15-y várzea and terra firme at all depths except 0–5 cm (Table 5).

Table 5. Total soil C, N, pH, exchangeable Ca, Mg, K, and extractable P in the three várzea and one terra firme sites (means and standard errors). For each variable and depth, differences among sites are statistically significant ($p< 0.05$) when standard errors are followed by different letters.

Site	Depth (cm)	C (%)	N (%)	pH	Ca	Mg	K	P (mg kg^{-1})
						(cmol kg^{-1})		
5-y várzea	0- 5	5.22 (0.60) ab	0.40 (0.03) a	5.1 a	5.07 (0.83) a	2.78 (0.30) a	0.18 (0.01) a	1.4 (0.30) b
	5-15	6.40 (1.17) a	0.46 (0.06) a	5.1 ab	4.98 (0.55) a	2.64 (0.26) ab	0.10 (0.01) a	0.56 (0.15) bc
	15-30	5.59 (1.51) a	0.35 (0.07) a	4.8 b	4.95 (0.48) ab	2.45 (0.32) b	0.12 (0.01) ab	0.24 (0.15) a
	30-45	6.77 (1.48) a	0.36 (0.06) a	4.6 bc	4.07 (0.39) a	2.19 (0.24) b	0.09 (0.01) ab	0.41 (0.21) a
	45-60	11.04 (2.45) a	0.41 (0.06) a	4.2 b	4.98 (0.55) a	2.64 (0.26) b	0.10 (0.01) a	0.19 (0.08) a
15-y várzea	0–5	3.96 (0.55) bc	0.40 (0.04) a	5.5 a	6.02 (0.37) a	3.31 (0.15) a	0.19 (0.02) a	1.47 (0.38) b
	5–15	2.36 (0.54) bc	0.26 (0.04) bc	5.5 a	2.43 (0.27) b	2.20 (0.23) b	0.13 (0.03) a	0.68 (0.26) b
	15–30	1.51 (0.29) bc	0.18 (0.02) bc	5.3 a	3.89 (0.49) b	3.11 (0.15) ab	0.13 (0.01) a	0.52 (0.39) a
	30–45	1.99 (0.45) bc	0.21 (0.02) bc	5.0 a	3.22 (0.31) a	2.60 (0.06) ab	0.17 (0.07) a	0.38 (0.31) a
	45–60	3.00 (0.82) bc	0.23 (0.05) bc	4.7 a	2.43 (0.27) b	2.20 (0.23) b	0.13 (0.03) a	0.27 (0.12) a
35-y várzea	0– 5	5.91 (1.13) a	0.45 (0.06) a	5.0 ab	6.68 (0.64) a	2.84 (0.36) a	0.17 (0.01) a	2.63 (0.47) a
	5–15	4.21 (1.33) ab	0.35 (0.08) ab	4.7 c	3.84 (0.62) a	2.53 (0.29) ab	0.13 (0.02) a	1.4 (0.27) a
	15–30	4.33 (1.62) ab	0.30 (0.08) ab	4.5 c	5.15 (0.32) a	2.89 (0.36) ab	0.14 (0.02) a	0.42 (0.16) a
	30–45	4.53 (1.50) ab	0.28 (0.07) ab	4.5 c	4.14 (0.55) a	2.42 (0.24) ab	0.14 (0.02) a	0.40 (0.20) a
	45–60	5.83 (1.57) b	0.32 (0.06) ab	4.3 ab	3.83 (0.62) a	2.53 (0.29) ab	0.13 (0.02) a	0.07 (0.03) a
Terra firme	0– 5	2.93 (0.25) c	0.23 (0.02) b	4.6 b	0.33 (0.17) b	0.43 (0.13) b	0.07 (0.00) b	0.78 (0.19) b
	5–15	1.38 (0.13) c	0.14 (0.01) c	4.8 ab	0.03 (0.15) c	0.17 (0.05) c	0.01 (0.00) b	0.23 (0.10) bc
	15–30	0.77 (0.17) c	0.11 (0.01) c	4.8 ab	0.09 (0.05) c	0.20 (0.05) c	0.03 (0.00) c	0.12 (0.12) a
	30–45	0.57 (0.12) c	0.09 (0.01) c	4.8 ab	0.06 (0.05) b	0.17 (0.04) c	0.02 (0.00) b	0.31 (0.11)a
	45–60	0.38 (0.08) c	0.06 (0.01) d	4.8 a	0.03 (0.02) c	0.17 (0.05) c	0.01 (0.00) b	0.76 (0.58)a

Overall, soils were moderately acidic (pH 5–6) to strongly acidic (pH 4–5) (Brady 1990) at all depths. At 0–5 cm, the soil pH in the terra firme was significantly lower than in all other sites except the oldest várzea. There was a marked tendency in tidal várzea sites for pH to decline with increasing depth (Table 5). Soil pH in the terra firme remained relatively constant with increasing depth.

Exchangeable Ca and Mg concentrations were significantly higher in the tidal várzea soils than in the terra firme at all depths (Table 5). The soil exchangeable K concentrations were significantly higher in the tidal várzea sites than in the terra firme at all depths except 30–45 cm (Table 5). Soil extractable P was significantly higher in the 35-year várzea than in all other sites at 0–5 cm and 5–15 cm (Table 5).

The terra firme soils showed significantly higher concentrations of exchangeable Al at 0–5 cm and 15–30 cm (Table 6). Soil exchangeable Fe concentrations were higher in the tidal várzea sites than in the terra firme, and they tended to increase with depth while the opposite was true of terra firme (Table 6). Soil exchangeable Mn was significantly higher in all the tidal várzea sites than in the terra firme at all depths (Table 6). Soil exchangeable Cu concentrations were significantly higher in the tidal várzea than in the terra firme sites at 30–45 cm and 45–60 cm.

Table 6. Exchangeable soil Al, Fe, Mn, and Cu in three várzea and one terra firme sites (means and standard errors). For each variable and depth, differences among sites are statistically significant ($p < 0.05$) when standard errors are followed by different letters.

Site	Depth (cm)	Al (cmol kg^{1})	Fe	Mn	Cu
				(mg kg^{1})	
5-y várzea	0–5	2.38 (0.45) b	315 (105) ab	108 (15.5) a	2.15 (0.23) b
	5–15	3.04 (0.50) a	496 (247) ab	93.7 (15.3) b	3.62 (1.31) a
	15–30	2.34 (0.35) b	748 (253) b	99.5 (14.8) a	3.25 (0.58) ab
	30–45	2.73 (0.41) b	883 (277) ab	101 (3.56) ab	3.07 (0.51) a
	45–60	3.04 (0.50) a	804 (184) ab	104 (15.8) a	2.67 (0.33) a
15-y várzea	0–5	3.04 (0.29) b	234 (48.3) b	97.8 (13.2) a	15.2 (7.98) a
	5–15	3.17 (0.29) a	230 (46.4) bc	68.5 (10.6) bc	14.5 (12.7) a
	15–30	2.76 (0.19) b	313 (74.7) c	60.6 (12.4) b	3.5 (1.56) a
	30–45	3.01 (0.21) a	619 (92.1) bc	102 (30.8) ab	3.84 (0.76) a
	45–60	3.17 (0.29) a	893 (196) a	77.8 (19.2) ab	3.36 (0.89) a
35-y várzea	0–5	2.62 (0.18) b	544 (174) a	121 (31.9) a	2.74 (0.74) b
	5–15	2.99 (0.15) a	822 (160) a	146 (9.98) a	2.40 (0.51) a
	15–30	3.03 (0.16) b	132 (85.5) a	122 (8.62) a	2.55 (0.56) abc
	30–45	3.30 (0.21) a	1235 (68.1) a	120 (12.3) a	2.52 (0.44) a
	45–60	2.99 (0.15) a	1172 (54.1) a	89.5 (16.5) a	2.61 (0.34) a
Terra firme	0–5	6.06 (1.19) a	109 (23.7) b	1.34 (0.62) b	0.89 (0.30) b
	5–15	2.43 (0.31) ab	56.2 (14.7) c	0.25 (0.11) d	0.33 (0.09) a
	15–30	5.99 (1.31) a	30.4 (8.32) c	0.50 (0.44) c	0.35 (0.20) c
	30–45	3.27 (0.73) a	32.6 (8.61) d	0.15 (0.14) c	0.14 (0.03) b
	45–60	2.43 (0.31) b	24.5 (5.68) c	0.04 (0.03) c	0.28 (0.12) b

Discussion

Vegetation characteristics as influenced by drainage

Soil water drainage influences species distribution in floodplain forests (de las Salas 1987), and this was evident in the tidal várzea sites. Within each site the vegetation composition was a mosaic that corresponded to a water drainage pattern. For example, *Montrichardia arborescens*, Araceae (aninga), an arborescent monocot, was the predominant species in permanently ponded areas along streams, while various other trees and palms were abundant on islands of higher ground. This phenomenon, which also occurs on a much larger scale in the Peruvian Amazon, was described by Puhakka and Kalliola (1993). In the present study, another example of the influence of water drainage was the distribution of *Tabebuia* spp. which were found only on the drier 15-year várzea. *Tabebuia* spp. were also found in the terra firme, where they were among the most abundant trees. Similarly, two tree species, *Ormosia coutinho* and *Maxhonia* spp., were found only on the wetter várzea sites (the 5- and 35-y várzea stands). *Omorsia coutinho* (buiussú) was described by Le Cointe (1947) as a tree found in the Amazon estuary up to the lower Xingú River that grows in lower lands along streams and swamps.

In the tidal várzea sites of the present study, the Leguminosae was the dominant family due to the overwhelming numbers of *Pterocarpus amazonicus.* The Leguminosae and Palmae families comprised over half of the individuals in the tidal várzea sites. The importance of palms in Amazonian floodplains is well documented (e.g. Kahn 1991). As in this study, Ayres (1993) found that *P. amazonicus* was the most abundant species in a mature forest of a seasonal várzea of the white-water Solimoes River; however, in contrast to this study, Ayres found that in a várzea forest on the Solimoes River, five families (as opposed to two) comprised about half of the individuals represented: Euphorbiaceae (18.8%), Leguminosae (16.0%), Lecythidaceae (7.0%), Annonaceae (5.5%), and Myrtaceae (5.8%) (Ayres 1993).

As expected from its better drainage and older age, the terra firme showed higher tree species diversity than the tidal várzea sites: approximately 20 % more genera were found in the terra firme site than in all the three tidal várzeas together. The highest numbers of identified individuals were represented in the following families: Leguminosae (23%), Bignoniaceae (14%), and Lecythidaceae· (7%). Other families of importance included the Meliaceae, Palmae, and Annonaceae, each with 6% of the total number of individuals.

The basal area of the terra firme site was 51% greater than that of the 35-y várzea. This finding is consistent with other studies reporting that várzeas have less density and lower basal area than terra firme (Ayres 1993). The basal area of the 35-year várzea (28.7 m^2 ha^{-1}) was comparable to that of mature forest in seasonal várzeas in the Solimoes River (33–47 m^2 ha^{-1}) (Ayres 1993).

Forest-floor litter

In the present study, the accumulation of non-palm leaves and wood was higher in the terra firme than in the tidal várzea sites. Similarly, Klinge (1977) reported higher woody debris in the terra firme than in the várzeas of the Solimoes River. Since in the present research the total biomass of litter was not significantly different between the várzeas and terra firme, the biomass of palm leaves might compensate for the lower woody biomass in the várzea sites: palm leaves had a higher biomass in várzea sites and were significantly higher in the 35-year várzea than in the terra firme. In the 35-y várzea the high accumulation of palm leaves and fruits was associated with the large numbers of the palm *Mauritia flexuosa.*

The lower accumulation of non-palm leaves in the tidal várzea sites could be due to their removal by floodings (Herrera 1985, Pires & Prance 1985, Nortcliff & Thornes 1988). Removal of litter by flooding was evident from studies in a Puerto Rican palm floodplain forest where the biomass of the total forest-floor litter ranged from 800 g m^{-2} to 156 g m^{-2}, with the lowest biomass occurring after a large flood (Frangi & Lugo 1985). While Frangi and Lugo (1985) reported that floods rearranged the floor litter including trunks and palm leaves, we saw that overland flooding was less likely to transport large palm leaves at our sites. In fact, the leaves of the *M. flexuosa* palms tend to accumulate around the stems forming small islands of debris.

These findings may imply that in periodically flooded forests, the influence of litter on soil nutrient cycling may not be directly related to the specific location of a tree in a site, since in most cases the litter does not decompose *in situ.* Instead, most litter is probably transported by water and left to decompose elsewhere downstream. In a periodically flooded system, trees may provide key services, including nitrogen fixation in water saturated soils where N is mostly bound to organic compounds and is generally inaccessible to plants. Additionally, those trees that do tend to accumulate debris near their stem base may enhance the development of higher grounds by increasing the deposition of sediments and anchoring the soil with their litter or roots.

Soil drainage and its influence on soil chemistry

Variations in soil nutrient content and pH between tidal várzea sites may be attributed to differences in soil water saturation. For example, higher levels of soil total N and C and lower pH in the 5- and 35-y várzeas may have resulted from a greater accumulation of organic matter due to slow decomposition in water-saturated soils. The slow oxidation of high quantities of organic substrates occurring under these anaerobic conditions yields hydrogen cations, and therefore results in lower pH (Mitsch & Gosselink 1993). This may explain the decreases in pH with increasing depth observed in the three tidal várzea sites. In addition, the low pH and high C and N levels found at the lowest depth of all várzea sites probably can be attributed to buried peat found at these depths (Winkler Prins 1993).

Microelements, including Mn, Fe and Cu, are somewhat more available to plants in soils under restricted drainage and in acid conditions than in well-aerated soils (Brady 1990). This was the case for exchangeable Mn and Fe in this study, since higher exchangeable levels of these elements were found in the sites with lowest pH (the 5- and 35-y várzeas) at most depths. Likewise, at the lowest (more water-saturated) depths, the tidal várzea sites had significantly higher Cu levels than the terra firme.

As expected, the tidal várzea soils had higher levels of basic cations (Ca, K, and Mg) and higher extractable P than the terra firme. Furch and Klinge (1989) also reported higher levels of soil exchangeable Ca and Mg in the seasonal várzeas of the white-water Solimoes River in Central Amazonia compared to terra firme lands. As in other studies (e.g. Barrios & Herrera 1994), soil total N at our site was higher in the tidal várzeas than in the terra firme. Total N levels in the tidal várzea sites of the present study were 30–50% higher than those reported for seasonally flooded alluvial soils along the Orinoco River (Barrios *et al.* 1994). However, in contrast to the present study, Furch and Klinge (1989) found lower levels of total N in the várzea soils of the Solimoes River compared to those in the terra firme. Our findings confirm the expectation for generally higher fertility in várzeas than in non-inundated forests, due to periodic enrichment by sediment deposition in the flooded sites (Junk 1984, Barrow 1985, Martinelli *et al.* 1993, Barrios *et al.* 1994, Konhausen *et al.* 1994).

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Appendix 1. Várzea tree species (dbh > 10 cm)

Species	Common name	Family
Alibertia edulis A. Rich.	Purui-pequeno	Rubiaceae
Avicennia nitida Jacq.	Ciriuba	Verbenaceae
Bombax spp.	Mamorana	Bombacaceae
Bowdichia spp.	Sucupira	Leguminosae (Papilionoideae)
Calophyllum brasiliense Camb.	Jacareuba	Guttiferae
Campsiandra spp.	Acapurana	Leguminosae (Caesalpiniodeae)
Carapa guianensis Aubl.	Andiroba	Meliaceae
Caryocar microcarpum Ducke	Piquiarana	Caryocaraceae
Cassipourea guianensis Aubl.	Laranja-do-mato	Rhizophoraceae
Cecropia spp.	Imbauba	Moraceae
Clitoria racemosa Benth.	Palheteira	Leguminosae (Papilionoideae)
Euterpe oleracea Mart.	Acai	Palmae (Arecaceae)
Ficus sp. (1)	Caxinguba	Moraceae
Ficus sp. (2)	Cibolera	Moraceae
Genipa americana L.	Jenipapo	Rubiaceae
Guarea guidonia (L.) Sleumer	-	Meliaceae
Guarea spp.	Jatauba	Meliaceae
Hevea brasiliensis Muell. Arg.	Seringueira	Euphorbiaceae
Hura crepitans L.	Assacu	Euphorbiaceae
Licania guianensis Kuntze	Jutauba	Rosaceae
Licaria cf *aritu* Ducke	Louro aritu	Lauraceae
Macrolobium bifolium (Aubl.) Pers.	Ipeuba	Leguminosae (Caesalpiniodeae)
Mauritia flexuosa L. *f.*	Miriti	Palmae
Maxhaumia spp.	Limorana branca	Leguminosae (Caesalpiniodeae)
Ormosia coutinhoi Ducke	Buiussu	Leguminosae (Papilionoideae)
Pentaclethra macroloba (Willd.) Kuntze	Paracaxi	Leguminosae (Mimosoideae)
Phyllanthus nobilis	Andorinha	Euphorbiaceae
Pithecellobium sp. (1)	Farinha seca	Leguminosae (Mimosoideae)
Pithecellobium sp. (2)		Leguminosae (Mimosoideae)
Pithecellobium sp. (3)	Jarandeo	Leguminosae (Mimosoideae)
Platymiscium spp.	Mutuchirana	Leguminosae (Papilionoidae)
Pterocarpus amazonicus Huber	Mututi da varzea	Leguminosae (Papilionoideae)
Rhizophora mangle L.	Mangue vermelho	Rhizophoraceae
Spondias lutea L.	Taperiba	Anacardiaceae
Sterculia pruriens (Aubl.) Schum.	Tacacazeiro	Sterculiaceae
Swartzia acuminata Willd. *ex* Vog.	Pitaica	Leguminosae (Caesalpiniodeae)
Symphonia globulifera L. *f.*	Anani	Guttiferae
Tabebuia sp. (1)	Culhao de bode	Bignoniaceae
Virola surinamensis (Rol.) Warb.	Ucuuba branca	Myristicaceae
Unknown 1	Fava	Leguminosae(Papilionoideae)
Unknown 2	Louro	Lauraceae
Unknown 3	Pes-de-pato	
Unknown 4	Galagala	

Appendix 2. Terra firme tree species (dbh > 10 cm)

Species	Common name	Family
Ambelania acida Aubl.	Pepino	Apocynaceae
Aspidosperma spp.	Carapanauba	Apocynaceae
Astrocaryum tucuma Mart.	Tucuma	Palmae
Bowdichia nitida Spruce *ex* Benth.	Sucupira	Leguminosae (Papilionoideae)
Carapa guianensis Aubl.	Andiroba	Meliaceae
Cassipourea guianensis Aubl.	Laranja preta	Rhizophoraceae
Cecropia spp.	Imbauba	Moraceae
Chrysophyllum spp.	Guajara	Sapotaceae
Cordia alliodora (Ruiz & Pav.) Oken	Laurel	Boraginaceae
Didymopanax morototoni Decne. & Planch.	Morototo	Araliaceae
Diospyros duckei Sandwith	-	Ebenaceae
Dipteryx odorata (Aubl.) Willd.	Cumaru	Leguminosae (Papilionoideae)
Eschweilera matamata Hub.	Matamata	Lecythidaceae
Goupia glabra Aubl.	Cupiuba	Celastraceae
Guarea spp.	-	Meliaceae
Guatteria spp.	Envira	Annonaceae
Hevea brasiliensis Muell. Arg.	Seringueira	Euphorbiaceae
Hirtella spp.	Marirana	Chrysobalanaceae
Inga spp.	Inga	Leguminosae (Mimosoideae)
Iriartea exorrhiza Mart.	Paxiuba	Palmae
Jacaranda copaia (Aubl.) D. Don	Parapara	Bignoniaceae
Lecythis spp.	Sapucaia	Lecythidaceae
Maximiliana spp.	Inaja	Palmae
Ocotea spp.	-	Lauraceae
Oenocarpus distichus Mart.	Bacaba	Palmae
Ormosia coutinhoi Ducke	Buiussu	Leguminosae(Papilionoideae)
Parinari spp.	Parinari	Chrysobalanaceae
Paypayrola cf. *grandiflora* Tul.	-	Violaceae
Pentaclethra macroloba (Willd.) Kuntze	Paracaxi	Leguminosae (Mimosoideae)
Pithecellobium latifolium (L.) Benth.	Ingarana	Leguminosae (Mimosoideae)
Pouteria lasiocarpa Planch. & Triana	-	Sapotaceae
Rheedia macrophlylla (Mart.) Planch. & Triana	Bacuripari	Guttiferae
Swartzia spp.	Pacapeua	Leguminosae (Caesalpiniodeae)
Tabelnuia sp. (1)	Culhao de bode	Bignoniaceae
Tabelnuia sp. (2)	Ipe vermelho	Bignoniaceae
Tapirira cf. *guianensis* Aubl.	Tatapiririca	Anacardiaceae
Tetragastris pilosa Cuatrec.	Breu	Burseraceae
Tovomita secunda Poepp. *ex* Planch. & Triana	Mangueirana	Guttiferae
Trichilia LeCointei Ducke	Paracuuba	Meliaceae
Triplaris spp.	Tachi	Polygonaceae
Virola surinamensis (Rol.) Warb.	Ucuuba	Myristicaceae
Vismia guianensis (Aubl.) Choicy	Lacre	Guttiferae
Vochysia eximia Ducke	Quaruba	Vochysiaceae
Vouacapoua americana Aubl.	Acapu	Leguminosae (Caesalpiniodeae)
Xylopia spp.	Envira preta	Annonaceae
Unknown 5	Louro	Lauraceae
Unknown 6	Fava	Leguminosae
Unknown 7	Amisca	
Unknown 8	Angara	
Unknown 9	Aquariquara	
Unknown 10	Cinzeira	
Unknown 11	Marario	
Unknown 12	Tereu	