FOREST STRUCTURE, FLORISTIC COMPOSITION AND SOILS OF AN AMAZONIAN MONODOMINANT FOREST ON MARACÁ ISLAND, RORAIMA, BRAZIL

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Maracá is a riverine island located in the Rio Uraricoera in Roraima State (Brazil) and has an area of about 100,000ha. A forest type dominated by *Peltogyne gracilipes* Ducke (Caesalpiniaceae) occurs on Maracá Island on a range of soil types. This study compares the structure, floristic composition and soils of the *Peltogyne* forest with the most widespread lowland forest type on Maracá. Three 0.25ha plots were set up in each of three forest types: *Peltogyne*-rich forest (PRF), *Peltogyne*-poor forest (PPF) and forest without *Peltogyne* (FWP). Within each plot all trees (≥10cm dbh) were recorded. Seedlings and saplings were sampled in subplots of 2m × 1m (seedlings) and 4m × 4m (saplings). In the PPF and FWP, Sapotaceae were the most important family with the highest relative dominance and relative density values. Caesalpiniaceae showed high values in the PRF and PPF. *Licania kunthiana*, *Pradosia surinamensis* and *Simarouba amara* occurred in the canopy layer in all the forest types. *Peltogyne* dominated the canopy in the PRF and comprised 20% of stems and 53% of the total basal area of all trees ≥10cm dbh, and 91% of the stems and 97% of the total basal area of individuals ≥50cm dbh. In PPF, *Lecythis corrugata* and *Tetragastris panamensis* were the most abundant species, followed by *Peltogyne*. In the FWP the most abundant trees (≥10cm dbh) were *Licania kunthiana* and *Pradosia surinamensis*. In all forest types, the soils were sandy and acid with low concentrations of extractable phosphorus and exchangeable cations, but the soils under PRF were notably richer in magnesium.

Keywords. Amazonia, Caesalpiniaceae, disturbance, magnesium, monodominant.

INTRODUCTION

The structure and floristic composition of the Amazonian lowland rainforest has been studied in several areas in Brazil (Black et al., 1950; Takeuchi, 1961; Prance et al., 1976; Campbell et al., 1986; Prance, 1990; Rankin-de-Merona et al., 1992; Thompson et al., 1992a; Almeida et al., 1994), Bolivia (Boom, 1986), Ecuador (Balslev et al., 1987; Korning & Balslev, 1994; Valencia et al., 1994), Peru (Gentry, 1988) and Venezuela (Uhl & Murphy, 1981; Buschbacher, 1984). These authors have shown that the number of species of trees ≥10cm diameter at breast height (dbh) per hectare in the lowland evergreen rainforests varies from about 80 for forests which are seasonally dry to about 300 for forests without a dry season. The latter are perhaps the most species-rich forests occurring in the world (Gentry, 1988).

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Monodominant stands of the deciduous *Peltogyne gracilipes* Ducke within the evergreen forest on Maracá Island were first described by Milliken & Ratter (1989). They occur in large strips varying from a few to several hundred hectares and are conspicuously leafless in the late dry season (late December to early April). This forest type is dominated by *P. gracilipes* (henceforth usually referred to by its generic name only) of the Caesalpiniaceae, in which *Peltogyne* accounts for up to 75% of the basal area (Milliken & Ratter, 1989). Therefore, the forest can be designated as monodominant, since by definition monodominant forests have one species with 50% to 100% dominance. As measures of dominance, the number of trees, basal area, biomass or canopy cover can be used (Connell & Lowman, 1989). *Peltogyne* forests had already been mentioned by the explorer A. Hamilton-Rice (1928) reporting his expedition of 1924–1925 to Rio Branco, Uraricoera and Parima. He described a forest dominated by *pau roxo* (purple tree), the local name for *Peltogyne* – referring to its spectacular purple heartwood, occurring especially near the banks of the Rio Uraricoera. He expressed his surprise at the dominance of *pau roxo* and emphasized that monodominant stands are not common in Amazonia. Silva (1976), in her taxonomic review, mentioned that the geographical distribution of *P. gracilipes* is restricted to Roraima State, with this species occurring mainly on slopes and along the river Amajaí. Therefore, *Peltogyne* forests do not occur only on Maracá, but also on the mainland. A forest dominated by a *Peltogyne* species (probably not *P. gracilipes* in view of Silva 1976) was reported by Myers (1936) on sandy floodplains in British Guiana.

Although Milliken & Ratter (1989) and Robison & Nortcliff (1991, 1994) provided some data for vegetation and soils respectively of *Peltogyne* forests on Maracá, no detailed or comparative studies have been made of their ecology. Connell & Lowman (1989) pointed out that although monodominant tropical rainforests have been recorded in several parts of the world (Africa (Eggeling, 1947; Gérard, 1960; Swaine & Hall, 1981), America (Davis & Richards, 1934; Marshall, 1934; Beard, 1946; Richards, 1952; Buschbacher, 1984; Milliken & Ratter, 1989; Martijena & Bullock, 1994), Asia (Whitmore, 1984; Rai & Proctor, 1986; Edwards et al., 1993; Swamy & Proctor, 1995), Australia (Connell & Lowman, 1989)), they have seldom been studied by ecologists. The *Peltogyne* forest is the first monodominant forest to be described for Amazonia.

This paper describes the structure and species composition of a *Peltogyne* forest and its environment and compares its features with other forest types on Maracá and in Amazonia.

MARACA ISLAND

Maracá Island is located between 3°15′ and 3°35′N, 61°22′ and 61°58′W in Boa Vista district, Roraima State, northern Brazil (Fig. 1) and is formed by the division and reunion of the Rio Uraricoera which runs as two arms around it, the northern Furo Santa Rosa and the southern Furo Maracá. The island is about 60km long and

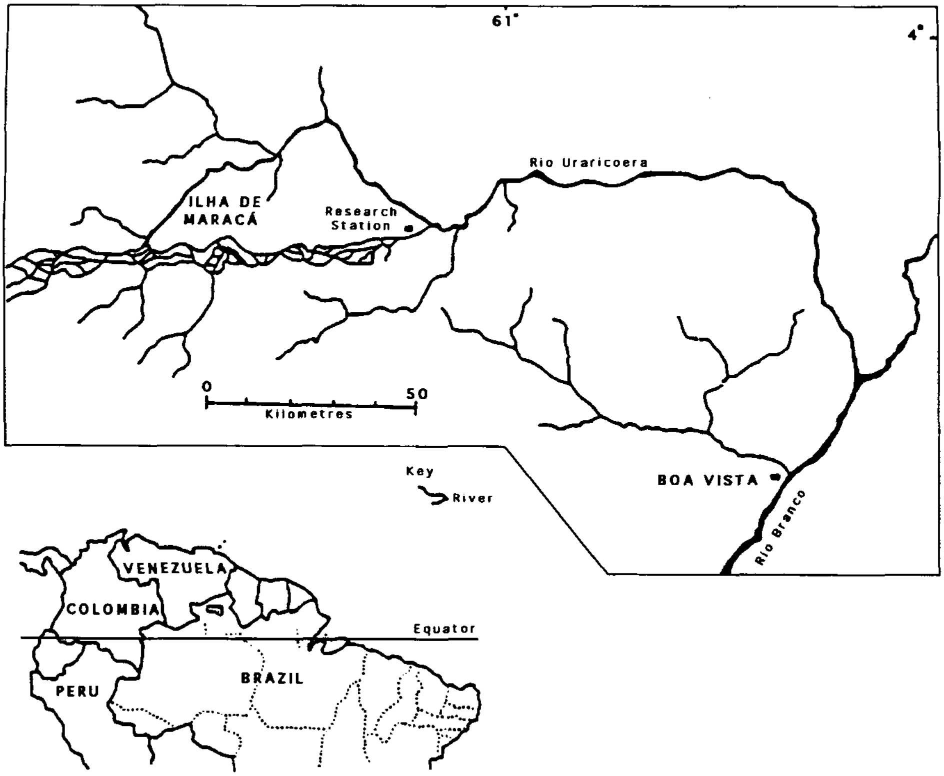


FIG. 1. Location of Maracá Island.

15–25km wide with an area of about 100,000ha. Although a fluvial island, it has not been formed by riverine deposition, but is a part of the Northern Amazonian Dissected Plateau (RadamBrasil, 1975). The island has been protected by law from human interference since 1978 when it was established as the first ecological reserve of the Secretaria Especial do Meio Ambiente (SEMA). In 1989 SEMA was abolished and the reserve (Estação Ecológica de Maracá) was transferred to the Instituto Brasileiro do Meio Ambiente (IBAMA – The Brazilian National Environmental Institute).

According to Nimer's (1991) classification for the northern region of Brazil, Maracá Island falls into the band with 1750–2000mm annual rainfall. From 1989 to 1993 the mean annual rainfall was 1783mm (source: IBAMA-Roraima). In general, the wettest month is July and the driest is February (Fig. 2). The dry season is more windy, with a predominance of the *Alísios* wind from the NE (Nimer, 1991). Temperature data collected daily in a Stevenson screen in the field station clearing from 1 January 1991 to 31 December 1992 (Fig. 2) showed mean monthly maxima ranging from 35.3°C (June–July) to 40.7°C (October–November) and mean monthly minima ranging from 22°C (July) to 24.4°C (May). The forests at the eastern part

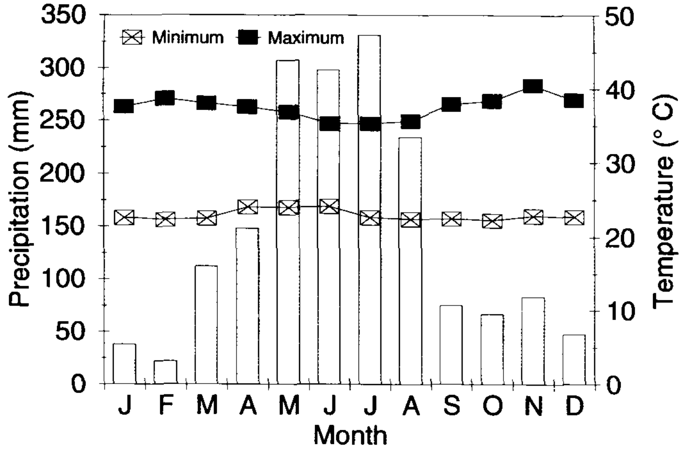


FIG. 2. Mean monthly precipitation (from 1989 to 1993) and mean monthly maximum and minimum temperatures in a Stevenson screen in the field station clearing in 1991 on Maracá Island, Brazil.

of the island are located at the climatic transition between the savanna subtype (Aw) and monsoon subtype (Am) of the tropical rain climate (A) (Eidt, 1968). Data on soils, topography, geology and geomorphology of Maracá Island are given in Thompson et al. (1992a) and Nascimento (1994).

METHODS

Study sites and plots

Three forest types were chosen according to the occurrence of *Peltogyne* trees. Forests with a dominance of *Peltogyne* trees were designated as *Peltogyne*-rich forest (PRF), while forests with sparse occurrence of this species were designated as *Peltogyne*-poor forest (PPF), and those where it was absent, as forest without *Peltogyne* (FWP).

Maracá Island has about 84% forest cover, of which 40% (34,136ha) is semi-deciduous closed canopy forest (Furley et al., 1994), which corresponds to the tropical semi-evergreen rainforest of Whitmore (1984). According to the field data provided by Milliken & Ratter (1989), Robison & Nortcliff (1991, 1994) and this study, most of the semi-deciduous forest on Maracá can be considered as PRF or PPF, which cover about 30% of the island, most frequently in the central area.

Plot selection

In July 1991, three replicate plots of 50m x 50m were sited in each of the three forest types (Fig. 3). Plots 1–3 were in PRF, plots 7–9 in PPF and plots 10–12 in FWP. All these plots were within an area of 4km^2 (near trail no. 1 of the Maracá system; Milliken & Ratter, 1989) and the PRF in this area is called PRFa and the FWP,

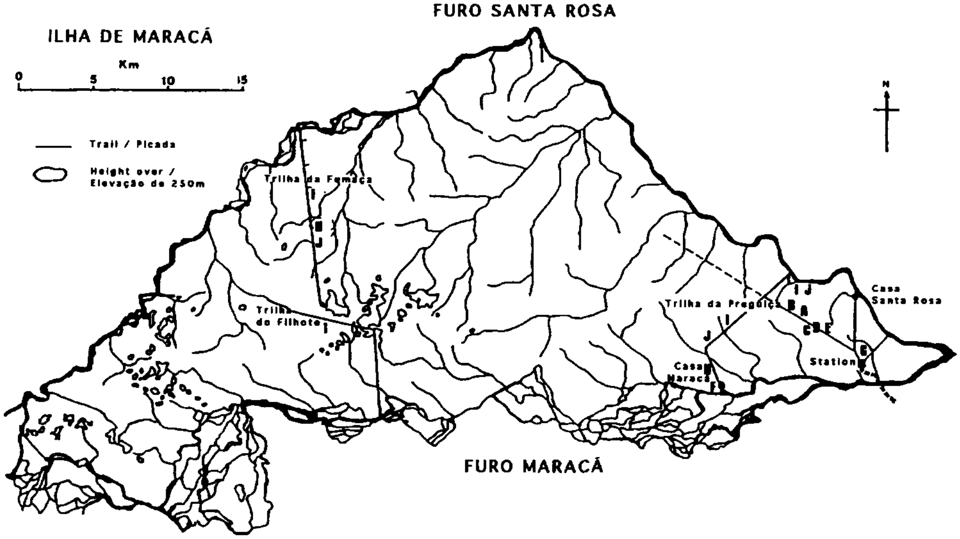


FIG. 3. The location of the study forests (A, PRFa; B, PPF7; C, PPF8; D, PPF9; E, FWPa; F, PRFb; and G, FWPb) and other areas of PRF (H (2 localities), Milliken & Ratter 1989 and I (4 localities), Robison & Nortcliff 1991) and PPF (J (3 localities), Robison & Nortcliff 1991) on Maracá Island, Brazil.

FWPa. The PRFa and FWPa plots were randomly located; the PPF plots had to be subjectively located because this forest type is very local. In November 1991, another three plots (plots 4–6) were set up in chosen locations in another area of PRF (called PRFb) about 6km south of the first one. Plots PRFb 4 and PRFb 5 were located on each side of the river bank in the Furo Maracá very close to Casa Maracá. Plot PRFb 6 was located on a small island (2ha in area) in the river. The plots were not seasonally flooded despite their proximity to the river, but they are almost certainly temporarily waterlogged in some years following exceptionally high rainfall. Three plots of a FWP (called here FWPb) already analysed by Thompson et al. (1992a) (and designated by them as their plot numbers 3, 5 and 6) were given the numbers 13–15 and included in our phytosociological analyses (Fig. 3).

Human disturbance of the plots

According to Proctor & Miller (pers. comm.) most forests in the eastern part of Maracá are secondary, possibly dating from the nineteenth century. In the FWPb plots 13–15, charcoal was found on the surface and at 10cm, 20cm and 50–100cm depths in soil pits. Thompson et al. (1992a) also found charred logs on the soil surface and other vestiges of fire within two of their plots. However, the causes of the fires remain unknown. Archaeological remains such as pottery and stone axeheads were found near these plots (Proctor & Miller, pers. comm.).

No signs of charcoal or charred logs were found on the soil surface of plots 1–12 of the present study but they often occurred at 25cm depth or more in the soil pits. Charcoal occurrence at a range of depths is common in Amazonia and can be related to climatic changes or human activities, or both (Sanford et al., 1985). Archaeological remains were never found near or in any of plots 1–12. Most of these plots are located far from the river (except plots PRFb 4–6, which are 20–100m from it) and the savanna border (except plots FWPb 13–15, which are about 1km from it). It is well known that disturbance of the forest by shifting cultivators occurs mainly in areas bordering rivers (Sanford et al., 1985) or savanna vegetation, but is generally small in scale. The PRFa, PRFb and PPF are possibly primary. However, the floristic similarity between the FWPa plots and the putatively secondary-forest FWPb plots suggests that the former too have been much disturbed.

Soil sampling and analysis

A soil pit (about 150cm deep) was sited in the middle of plots 1–3 (PRFa), 7–9 (PPF) and 10–12 (FWPa). Soil samples were collected from each horizon in March 1992. Each soil sample was air-dried and sieved through a 2mm mesh, and 150g subsamples were stored for up to six months in air-tight polythene bags until shipment to the University of Stirling for analysis.

Soil surface (0–10cm) samples were collected from the middle of each of 10 randomly selected 10m × 10m subplots within plots PRFa 1–3, PPF 7–9 and FWPa 10–12 in June 1992 and PRFb 4–6 in July 1992. For these soil samples, extractable nitrogen and phosphorus rather than total nitrogen and phosphorus were analysed. For the plots FWPb 13–15, the data of Thompson et al. (1992a) for soil samples collected in June 1987 were used.

Chemical analysis of soil samples largely followed Thompson et al. (1992a) and is described in Appendix 1.

The water-table was measured in one soil pit (about 150cm deep) in each of the three plots in each forest group. The measurements were made at 14–18-day intervals from 9 April to 6 August 1992.

Vegetation inventory

Within each plot the diameters of all trees and lianas ≥10cm dbh were recorded between September and November 1991 and they were marked with permanent aluminium tags. For trees with large buttresses or prop roots reaching more than 1.3m high the diameters were measured at 30cm above these protrusions. In each plot of PRFa, PPF and FWPa, all trees were examined for the presence of lianas, but only trees that directly supported one or more, as opposed to those with lianas merely crossing from the crowns of adjacent trees, were considered as liana supporters. Only lianas ≥10cm dbh were identified. Standing dead trees and fallen trunks (dbh ≥10cm) were also recorded. For trees with multiple stems, each stem was measured separately and the tree basal area was considered as the sum of the basal area of each stem ≥ 10cm dbh. During the enumeration, each tree was identified as far as possible and the determination confirmed from collected specimens. Voucher specimens are lodged in the Herbarium of Instituto Nacional de Pesquisas da Amazônia (INPA) (Manaus, Brazil) and the Herbarium of the Royal Botanic Garden Edinburgh (E) (Scotland). Most of the infertile specimens are also in the Herbarium of Museu de Ciências de Roraima (Boa Vista, RR, Brazil).

A profile diagram of trees over 6m tall was made for one plot in PRFa 2, PPF 7 and FWPa 10 along a 60m × 7.5m strip (of which 50m was within one of the sample plots). The height of each tree was estimated by comparison with an 8m pole and, in addition, independent estimates were made for each tree by two persons and the average used. Heights of trees >20m tall were later checked with a clinometer (Haga gauge).

Seedlings (≤ 0.5m in height) and saplings (>0.5m height, <10cm dbh) were sampled in five subplots of 2m × 1m (seedlings) and 4m × 4m (saplings). These subplots were located in a stratified random way within each of the forest plots. The density of herbs and small palms in the 4m × 4m subplots was also recorded.

Data analysis

Soil data. Comparisons of the surface soil data among forest types were made by two-way nested ANOVA, where factor A (forest type) was considered fixed and factor B (plots) random. If significant differences among levels of a factor occurred they were checked using a Tukey test (Zar, 1984).

Vegetation data. The data were analysed using the FITOPAC package designed for PC computers by George Shepherd (Department of Botany, University of Campinas, São Paulo, Brazil). Relative density (RD) and relative dominance (RDo) of each family and species were calculated according to the formulae of Cottam & Curtis (1956): $RD = 100\ n_i/N$, $RDo = 100\ (BA_i/BA)$; where n_i = the number of individuals of the family i or species i, N = total number of individuals, BA_i = basal area of the family i or species i, BA = total basal area. The cover value index (CVI) of Förster (cited in Oliveira-Filho et al., 1989) for each species and family was calculated by summing the relative values of density and dominance. This index was considered most suitable to rank the families and species as equal weighting is given to density and basal area.

Species similarity between each plot was calculated using Morisita's index (Brower & Zar, 1977):

$$Im = 2\ \Sigma\ X_i.Y_i/(A+B)N_x.N_y,$$
$$\text{where } A = X_i(X_i-1)/N_x(N_x-1) \text{ and } B = Y_i(Y_i-1)/N_y(N_y-1);$$

where X_i is the number of individuals of species i in community X, Y_i is the number of individuals of species i in community Y, N_x is the total number of individuals in community X, and N_y is the total number of individuals in community Y. This index is based on Simpson's index of dominance and according to Brower & Zar (1977) refers to the probability that individuals randomly drawn from each of the two communities will belong to the same species, relative to the probability of randomly selecting a pair of specimens of the same species from one of the communities. Morisita's index varies between 0 and 1, and values higher than 0.5 mean high similarity between communities.

Species diversity was measured using two indices: the Shannon index ($H' = -\Sigma p_i \ln p_i$, where $p_i = n_i/N$ and n_i is the number of individuals of species i and N is the total number of individuals), and Simpson's index ($Ds = 1 - \Sigma(n_i(n_i-1)/N(N-1))$ (Brower & Zar, 1977)). According to Taylor (1978), they are usually normally distributed when a number of replicates have been taken and therefore it is possible to apply parametric statistics to compare them. The Simpson index is, as the Shannon index, based on the proportional abundances of species. The former index is more affected by rare species while the latter is sensitive to a shift in the dominance of the species (Peet, 1974).

Since one of the main aims of this study was to investigate the effect of the dominant *Peltogyne* on the other canopy species, the diversity indices for the PRF plots were also calculated excluding data for *Peltogyne*. In this case if the forest types had initially the same total tree density, the number of canopy trees in PRF would be less than in PPF and FWP.

A one-way ANOVA was used to compare the mean diversity values among forest types and a Tukey test was used for the multiple comparison (Zar, 1984). Rank-abundance diagrams (Begon et al., 1990) for the first 10 most abundant species were plotted for each forest type. Species-area curves were drawn for each plot of each forest type. All the analyses, except the rank-abundance diagrams and species-area curves, were carried out separately for trees with dbh ≥10cm, ≥30cm, and ≥50cm.

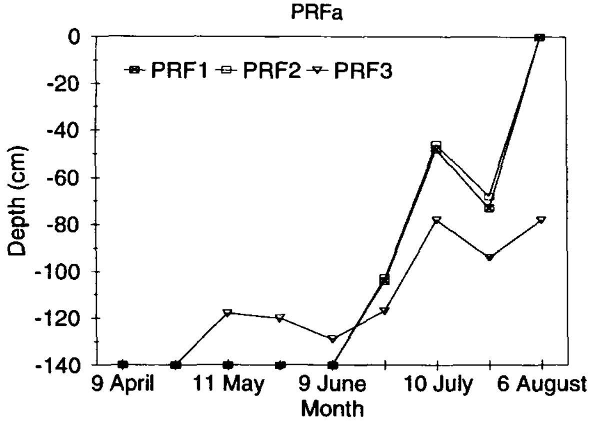
RESULTS

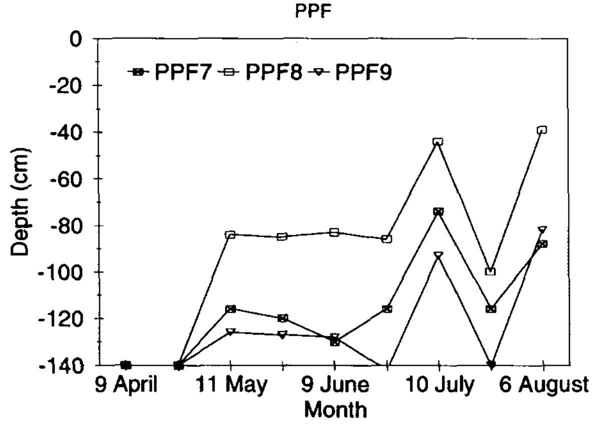
Soil pits

Profile descriptions for the plots, including chemical and textural data, are given in full in Nascimento (1994) (PRFa, PPF and FWPa), Thompson et al. (1992a) (FWPb) and Robison & Nortcliff (1991) (PRFb). Data for one representative pit in PRFa, PPF and FWPa are given in Table 1. The soils had neither a surface organic horizon nor a root mat. They were in most cases very sandy and well drained. All soils were poor in nutrients but not podzolized. PRFa soils were always richer in magnesium than FWP and had high values of the Mg/Ca quotient, especially in the deepest horizons. The soil water-table from June to August (wet season) was higher in PRFa than in FWPa (Fig. 4) and reached the soil surface in two PRFa plots on 6 August.

TABLE 1. Soil chemical properties and particle size composition from each soil horizon from pits in three different forest types on Maracá Island, Brazil.

Horizon depth (cm)	pH	Loss on ign. (%)	Ntotal mg g^{-1}	Ptotal µg g^{-1}	K^+	Na^+	Ca^{2+}	Mg^{2+}	Total acidity	Al^{3+}	H^+	CEC	Mg/Ca	Base sat. (%)	Clay (%)	Silt (%)	Sand (%)
					mequiv.kg^{-1}												
PRFa 1																	
0–13	4.7	2.26	0.76	86	1.54	0.11	2.96	2.77	8.7	3.1	5.6	16.1	0.9	45.8	13	15	72
13–39	4.8	0.83	0.29	77	0.57	0.05	0.28	1.11	11.0	4.6	6.4	13.0	4.0	15.4	14	15	71
39–86	5.1	0.32	0.09	52	0.53	0.07	0.27	0.95	7.2	3.3	3.9	9.1	3.5	20.1	14	15	71
86–134	4.9	0.51	0.18	75	0.31	0.11	0.11	1.54	12.5	6.1	6.4	14.6	14.0	14.2	15	13	72
PPF 7																	
0–15	4.6	1.80	0.43	36	0.86	0.05	0.85	0.93	5.2	3.9	1.3	7.9	1.1	33.9	16	10	74
15–28	4.5	1.35	0.45	43	0.91	0.05	0.40	0.85	6.5	5.3	1.2	8.7	2.1	25.4	27	13	60
28–51	4.8	3.02	0.35	36	1.48	0.06	0.33	1.52	8.2	6.3	1.9	11.6	4.2	29.2	56	10	34
51–141	5.0	4.95	0.27	25	1.44	0.09	0.38	1.39	10.2	8.1	2.1	13.5	3.7	24.4	55	10	35
FWPa 10																	
0–15	4.6	0.71	0.25	25	0.37	0.08	0.33	0.27	3.5	2.2	1.3	4.6	0.8	23.2	11	11	78
15–33	4.8	0.93	0.22	33	0.21	0.06	0.03	0.11	4.5	3.8	0.7	4.9	3.7	8.4	14	13	73
33–72	4.7	0.51	0.15	27	0.25	0.04	0.04	0.11	5.5	5.0	0.5	5.9	2.7	7.4	16	11	76
72–148	4.6	1.40	0.13	26	0.25	0.05	0.02	0.07	6.2	5.6	0.6	6.6	3.5	5.6	23	8	69





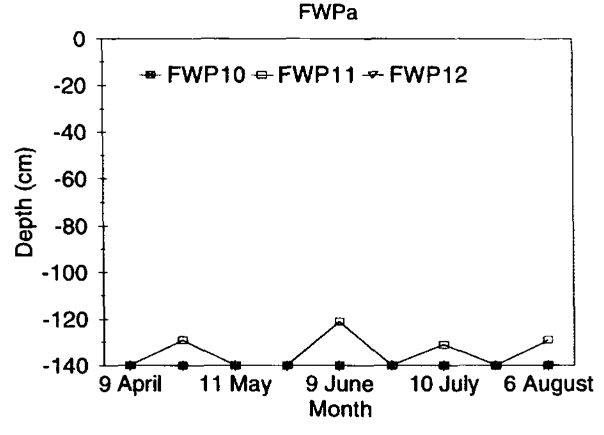


FIG. 4. Soil water-table in each plot of PRFa, PPF and FWPa on Maracá Island, Brazil.

TABLE 2. Soil chemical properties ($n = 11$ samples per plot) and particle size composition ($n = 3$ per plot) from surface soil (0–10cm deep) from three plots in five forest groups on Maracá Island. n.a. = data not available. Values within a row followed by different letters are significantly different, others non-significant (two-way nested ANOVA, $P \leq 0.05$, multiple comparisons by Tukey test).

	PRFa	PRFb	PPF	FWPa	FWPb
Loss on ignition (%)	2.34^{a}	4.25^{b}	1.85^{a}	0.83^{a}	1.02^{a}
pH_{H_2O}	4.6^{a}	4.3^{a}	4.4^{a}	4.4^{a}	4.9^{a}
N_{ext} (μg g^{-1})	2.01^{a}	n.a.	2.09^{a}	1.13^{a}	n.a.
P_{ext} (μg g^{-1})	2.15^{a}	n.a.	2.00^{a}	0.80^{b}	5.09^{c}
Exchangeable cations (mequiv.kg^{-1})					
K^+	1.09^{a}	1.06^{a}	1.00^{a}	0.45^{b}	0.66^{a}
Na^+	0.05^{a}	0.15^{b}	0.04^{a}	0.03^{a}	0.05^{a}
Ca^{2+}	1.35^{a,d}	1.85^{a,d}	0.95^{a,b}	0.46^{b}	2.33^{c,d}
Mg^{2+}	3.43^{a,b}	4.72^{a}	1.88^{b}	0.56^{c}	1.77^{b}
H^+	2.00^{a}	3.80^{a}	2.70^{a}	1.30^{a}	3.59^{a}
Al^{3+}	4.30^{a}	14.4^{b}	3.10^{a}	2.00^{a}	7.00^{a,b}
CEC	12.2^{a,b}	26.0^{c}	9.72^{a,b}	4.84^{a}	16.3^{b}
Base saturation (%)	50.0^{a}	31.1^{a}	40.2^{a}	31.2^{a}	31.3^{a}
Mg^{2+}/Ca^{2+}	2.58^{a}	2.53^{a}	1.98^{a,b}	1.24^{c}	0.80^{c}
Mg^{2+}/total base	0.58^{a}	0.59^{a}	0.48^{a,b}	0.38^{c}	0.37^{c}
Clay (%)	16^{a}	35^{b}	16^{a}	12^{a}	12^{a}
Silt (%)	6^{a}	21^{b}	6^{a}	3^{c}	4^{c}
Sand (%)	78^{a}	45^{b}	78^{a}	86^{c}	86^{c}

Surface soils

Soil chemical and particle size composition from surface soils is given in Table 2. The surface soils had similar characteristics in all the plots. They were sandy and acid with low concentrations of extractable nitrogen and phosphorus and exchangeable cations. However, PRFa, PRFb and PPF soils had in general the highest concentrations of exchangeable cations, especially for magnesium, with the highest Mg/Ca quotients and Mg/total base quotients occurring in PRFa and PRFb. The PRF soils had less sand and more silt than FWP (Table 2), and varied from loamy sand (78% sand) to silt clay (45% sand). The values of loss-on-ignition were higher in PRF, although the difference was only statistically significant between the PRFb plots and the other forest types. A medium base saturation (31% to 55%) was found for all soils.

Forest structure

Canopy height. Profile diagrams are shown in Figures 5–7. The PRFa had the highest canopy (25–35m), while the lowest was found for PPF (20–26m). All forest types had emergent trees reaching over 40m tall, with PRFa having the most emergents and the tallest trees. It also had a better developed understorey (10–20m tall). The

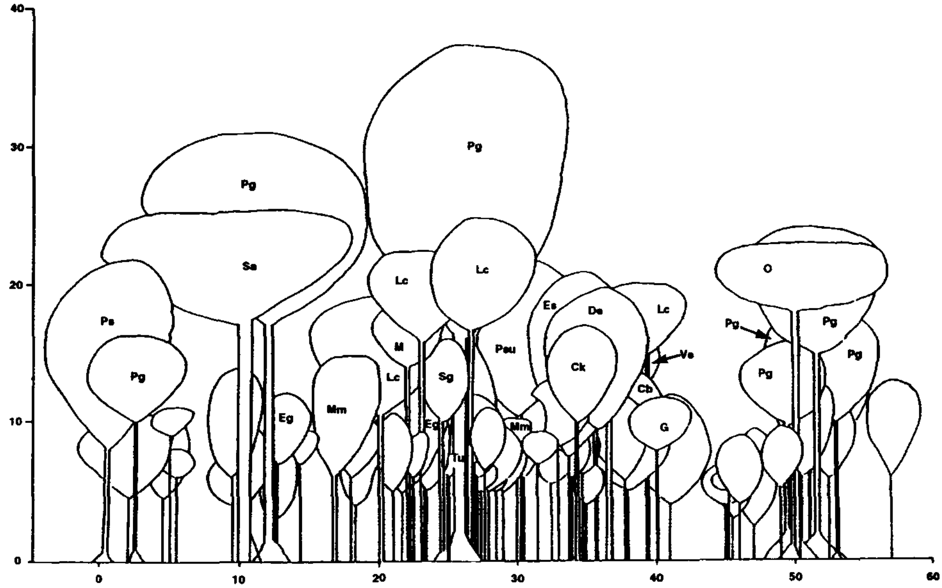


FIG. 5. Profile diagram (60m × 7.5m) of forest at plot PRF2 on Maracá Island, Brazil. Trees less than 6m tall excluded. Symbols for trees ≥10cm dbh: Cb, *Chomelia barbellata*; Ck, *Chaunochiton kappleri*; De, *Duroia eriopila*; Eg, *Ecclinusa guianensis*; Es, *Enterolobium schomburgkii*; G, *Guapira* sp.; Lc, *Lecythis corrugata*; M, *Machaerium* sp.; Mm, *Maximiliana maripa*; O, *Ormosia smithii*; Pg, *Peltogyne gracilipes*; Ps, *Pradosia surinamensis*; Psu, *Pouteria surumuensis*; Sa, *Simarouba amara*; Sg, *Swartzia grandifolia*; Tu, *Tabebuia uleana*; Vs, *Vitex schomburgkiana*.

PPF had a less well-developed understorey while the FWPa had an open canopy and a poorly developed understorey.

Basal area and density. The mean basal areas in three different dbh classes for each forest group are given in Table 3. PRF and PPF always had higher basal area values than FWP. However, in the majority of cases the differences were not statistically significant.

The diameter distribution patterns of plants were similar among forests and each plot showed a reversed-J shape curve. All plots had a high density of stems 10–30cm in dbh and a paucity of trees more than 50cm dbh, with the largest trees occurring most often in PRF. No significant differences among forests were found for the number of individuals, but PRF tended to have more small trees (10–30cm dbh) than the other forests (Table 4). Seedling and sapling abundance was also higher in PRF (Table 4). In both PRFa and PRFb, *Peltogyne* accounted for about 60% of all seedlings, while its saplings accounted for 40% of all saplings. The lowest densities of small palms and large-leaved herbs were found in PRF (Table 5). The number of standing and fallen dead trees ≥10cm dbh was similar among forest types, with

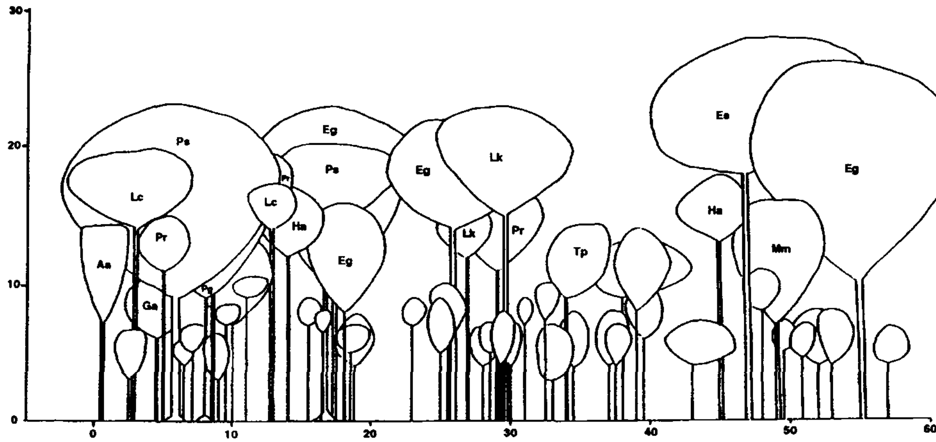


FIG. 6. Profile diagram (60m × 7.5m) of forest at plot PPF9 on Maracá Island, Brazil. Trees less than 6m tall excluded. Symbols for trees ≥10cm dbh: Aa, *Astrocaryum aculeatum*; Eg, *Ecclinusa guianensis*; Es, *Enterolobium schomburgkii*; Ga, *Gustavia augusta*; Ha, *Himatanthus articulatus*; Lc, *Lecythis corrugata*; Lk, *Licania kunthiana*; Mm, *Maximiliana maripa*; Pg, *Peltogyne gracilipes*; Pr, *Pouteria reticulata*; Ps, *Pradosia surinamensis*; Tp, *Tetragastris panamensis*.

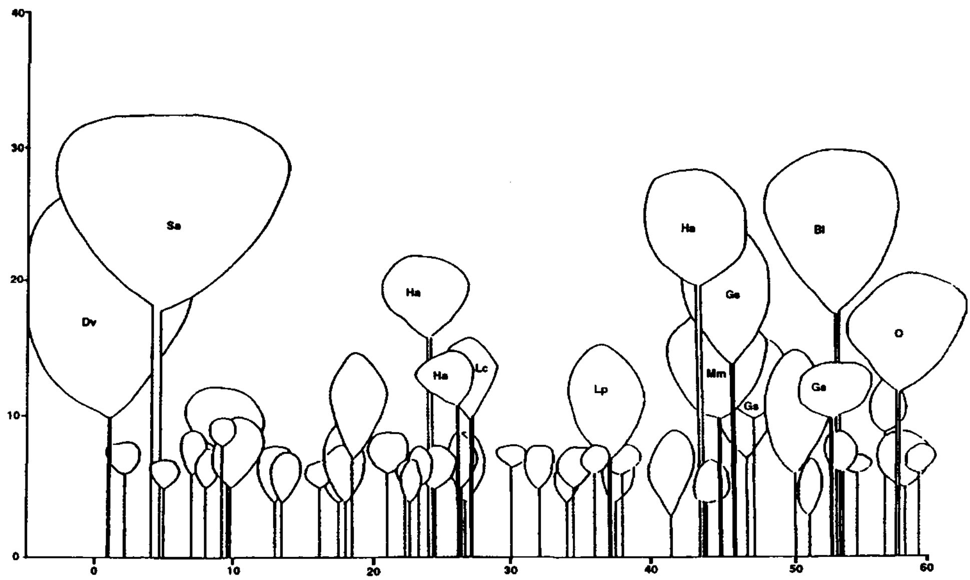


FIG. 7. Profile diagram (60m × 7.5m) of forest at plot FWP10 on Maracá Island, Brazil. Trees less than 6m tall excluded. Symbols for trees ≥10cm dbh: Bl, *Brosimum lactescens*, Dv, *Drypetes variabilis*; Gs, *Guatteria schomburgkiana*; Ha, *Himatanthus articulatus*; Lc, *Lecythis corrugata*; Lp, *Lindackeria paludosa*; Mm, *Maximiliana maripa*; O, *Ormosia smithii*; Sa, *Simarouba amara*.

TABLE 3. Mean (and ranges) of basal areas ha^{-1} of trees in three size classes in three replicate 50m × 50m plots in five forest groups on Maracá Island. Values within a row followed by different letters are significantly different, others non-significant (one-way ANOVA, $P \leq 0.05$, multiple comparisons by Tukey test).

	Forest types				
Dbh class	PRFa	PRFb	PPF	FWPa	FWPb
≥10cm	32.8[a]	39.1[b]	33.1[a]	27.1[a]	24.0[a]
	(25.2–38.3)	(36.7–43.1)	(30.4–34.9)	(25.6–28.1)	(22.0–26.9)
≥30cm	22.8[a]	28.3[a]	24.9[a]	19.3[a]	15.2[a]
	(15.3–28.9)	(23.2–37.0)	(22.6–27.4)	(16.4–21.4)	(13.4–17.4)
≥50cm	13.1[a]	19.1[a]	13.3[a]	7.8[a]	8.4[a]
	(6.3–21.8)	(8.9–29.2)	(11.2–16.4)	(5.8–10.9)	(3.3–12.1)

TABLE 4. Mean stem density in three replicate 50m × 50m plots in five forest groups on Maracá Island. Seedlings, ≤50cm tall; saplings >50cm tall and <10cm dbh; small trees ≥10cm dbh; trees, ≥30cm dbh and large trees, ≥50cm dbh.

			Mean stem density				
Size class	Plot size (m^2)	No. of subplots	PRFa	PRFb	PPF	FWPa	FWPb
Seedlings (m^{-2})	2	5	23.23	8.13	10.73	8.33	6.22
Saplings (m^{-2})	16	5	3.31	2.91	2.34	1.58	2.92
Small trees (ha^{-1})	100	25	401	463	321	295	379
Trees (ha^{-1})	100	25	83	75	101	89	59
Large trees (ha^{-1})	100	25	31	43	33	28	23

TABLE 5. Means (and ranges) of density (m^{-2}) of small palms and large-leaved herbs (Marantaceae and Bromeliaceae) on the floor of three replicate 50m × 50m plots in five forest groups on Maracá Island. Values within a row followed by different letters are significantly different, others non-significant (two-way nested ANOVA, $P \leq 0.05$, multiple comparisons by Tukey test).

	Number of individuals (m^{-2})				
	PRFa	PRFb	PPF	FWPa	FWPb
Marantaceae	0.56[a]	0[b]	2.56[c]	4.21[c]	2.18[c]
and Bromeliaceae	(0–1.19)		(0.19–6.69)	(2.81–5.87)	(0.1–4.1)
Small palms	0.87[a]	0[b]	0.96[a]	1.98[c]	0.43[a]
	(0.44–1.25)		(0.81–1.06)	(1.44–2.81)	(0.3–0.6)

Marantaceae: *Calathea elliptica, Monotagma* spp.
Bromeliaceae: *Aechmea rubiginosa, Bromelia goeldiana.*
Palms: *Maximiliana maripa, Astrocaryum aculeatum.*

TABLE 6. Mean number (range in parentheses) of dead trees, standing and fallen, per size class in three replicated 50m × 50m plots in four forest groups on Maracá Island. Data not available for FWPb.

Forest	Size class (dbh) ≥10cm	≥30cm	≥50cm
PRFa	7.3 (4–12)	3.7 (2–5)	2.7 (2–3)
PRFb	7.0 (4–11)	1.7 (0–3)	1.3 (0–3)
PPF	9.7 (9–10)	3.7 (2–6)	1.0 (1–1)
FWPa	6.7 (5–8)	1.3 (0–2)	0.3 (0–1)

TABLE 7. Average percentage of trees supporting one or more lianas in three replicate plots in three forest groups on Maracá Island. A, all species except *Peltogyne*; B, individuals of *Peltogyne* only.

	PRFa		PPF		FWPa
Plot	A	B	A	B	A
1	59	67	44	29	19
2	35	36	42	17	22
3	26	38	17	0	26
Mean	40	47	34	15	22

a tendency for more dead trees in PPF, but when only large dead trees (≥50cm dbh) were considered PRF had higher values than FWP (Table 6).

Lianas and forest type. PRFa had more trees supporting one or more lianas than the other forest types (Table 7) and about 50% of the *Peltogyne* trees supported lianas in PRFa, while in PPF only 15% of them had lianas.

Floristics

Level of identification. About 90% of the individuals ($n = 1666$) have been identified to species, with 110 trees identified to genus and 35 trees determined only to family or not at all. However, the trees of the last group (determined to family only or completely indetermined) have been assigned to 16 taxa, representing 1.8% of total trees recorded. A species list with authorities, families and type of forest is given in Appendix 2. Where species have only been determined to family level or merely assigned to indeterminate taxa, collection numbers are cited.

Family composition. The list of families of trees ≥ 10cm and their numbers of species, relative density and relative dominance for each forest type is shown in Table 8. The

TABLE 8. The 10 most important families of trees ≥10cm dbh occurring in three replicate 50m × 50m plots in five forest groups on Maracá Island, with number of species (*n*), relative density (RD) and relative dominance (RDo). Within columns the highest values (excluding 'others') are in bold. The selected families occurred in the leading 15 families in at least three of the forest groups.

	PRFa			PRFb			PPF			FWPa			FWPb		
Family	*n*	RD (%)	RDo (%)	*n*	RD (%)	RDo (%)	*n*	RD (%)	RDo (%)	*n*	RD (%)	RDo (%)	*n*	RD (%)	RDo (%)
Burseraceae	—	—	—	—	—	—	2	11.4	6.1	2	6.5	6.5	3	8.2	10.0
Caesalpiniaceae	2	21.9	**53.3**	**5**	**29.4**	**63.3**	1	4.7	20.0	1	0.3	0.04	1	0.3	0.4
Chrysobalanaceae	3	2.1	1.9	1	0.7	0.1	4	7.9	9.5	2	12.0	20.4	1	6.40	18.6
Lecythidaceae	1	8.1	4.3	—	—	—	4	12.6	9.6	2	7.1	7.0	1	4.4	4.2
Mimosaceae	1	1.0	1.8	2	14.7	10.7	2	0.9	0.9	2	1.0	0.2	1	0.6	0.2
Moraceae	1	0.3	0.05	1	0.2	0.6	1	3.2	3.0	1	2.3	2.7	4	8.2	**20.3**
Palmae	2	7.5	6.6	—	—	—	3	8.8	6.7	3	9.1	7.4	2	7.6	5.3
Rubiaceae	5	8.3	2.2	**5**	6.7	2.1	4	5.0	1.6	4	5.2	1.0	**8**	8.2	5.1
Sapotaceae	**6**	**24.7**	15.5	3	14.7	9.2	**8**	**26.6**	**30.7**	**6**	**26.2**	**36.7**	**8**	**15.2**	15.6
Simaroubaceae	2	6.2	4.6	1	0.9	0.2	2	4.4	6.3	1	1.6	4.6	1	1.2	1.2
Others (24 PRFa; 23 PRFb; 26 PPF and FWPa and 31 FWPb)	24	19.9	9.7	24	32.7	13.8	23	14.5	5.6	27	28.7	3.5	40	39.7	19.1

Sapotaceae had the highest relative density in all the forest types except the PRFb plots where the Caesalpiniaceae occupied this position. The Caesalpiniaceae had the highest dominance in the PRFa and PRFb, contributing up to 63.3% of the basal area, while the Sapotaceae had the highest relative dominance in the FWPa and FWPb (up to 36.7% of the basal area). In PPF, the Caesalpiniaceae were also important (20% of the basal area) but less so than the Sapotaceae (30.7%). It should be mentioned that the importance of the Caesalpiniaceae is based almost entirely on a single species: *Peltogyne gracilipes*.

Lists of the 15 most important species of trees ≥10cm, ≥ 30cm and ≥50cm dbh and their contributions to density and basal area are given in Tables 9–13.

Peltogyne gracilipes had the highest density in all diameter classes in PRFa and PRFb (Tables 9, 11, 13) contributing from 20.1% (PRFa) and 26.0% (PRFb) (trees ≥10cm dbh), through 54.1% and 62.5% (≥30cm dbh) to 91.3% and 81.3% (≥50cm dbh). In PPF this species occupied seventh place with 5% of trees (≥10cm dbh) (Table 9), while *Tetragastris panamensis* and *Lecythis corrugata* were the most abundant trees, together contributing 11% of the total number. In FWP, *Licania kunthiana* (FWPa) and *Duguetia lucida* (FWPb) were the most common trees (≥10cm dbh) with 11% and 8% of the total respectively (Table 10). When minimum dbh was increased to 30cm or 50cm, *Licania kunthiana* had the highest values of density in FWP (Tables 11–13). *Ecclinusa guianensis*, *Lecythis corrugata* and *Pradosia surinamensis* were among the most abundant species in all forest types.

For all three diameter classes, *Peltogyne* had the highest percentage basal area in PRF with values varying from 52.8% (PRFa) and 62.2% (PRFb) (≥10cm dbh) to 91.3% and 81.3% (≥ 50cm dbh). By contrast, in the FWP the most dominant species, *Licania kunthiana*, accounted for on average 20.2% (FWPa) and 18.6% (FWPb) (≥10cm dbh), and 25.7% and 36.0% (≥50cm dbh). In PPF, *Peltogyne* was less abundant with 5% of stems ≥10cm dbh, but it had some large trees (>50cm dbh) and with 20% of the total basal area was the most dominant species in this forest type also, followed by *Pradosia surinamensis* (14%) and *Ecclinusa guianensis* (10%) (Table 10). For trees ≥50cm, *Peltogyne* had also the highest percentage basal area (42.4%) with *Pradosia surinamensis* in second place with 22.6% (Table 13).

Species-area curves. The species-area curves showed a tendency to reach a plateau (Fig. 8, p. 26) in all PRF and PPF plots. However, in FWP this tendency was less clear. The mean number of tree species (≥10cm dbh) was: PRF, 23; PPF, 32 and FWP, 36.

Community similarity. Plots within each forest type showed high similarity in species composition, with values of Morisita's index always higher than 0.36. A dendrogram was produced by applying the group average clustering method (Greig-Smith, 1983; Pielou, 1984; Kershaw & Looney, 1985) (Fig. 9, p. 27). The dendrogram showed that plots were split into two main groups. The first group had plots from PRF, except PRFa 3, and the second group had plots from FWP, PPF and also PRFa 3.

TABLE 9. The 15 most important series of trees ≥10cm dbh occurring in three replicate 50m × 50m plots in PRFa, PRFb and PPF on Maracá Island, with number of individuals (*n*), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa					
Peltogyne gracilipes	77	12.97	20.05	52.76	72.81
Ecclinusa guianensis	46	1.76	11.98	7.17	19.15
Pradosia surinamensis	36	1.78	9.38	7.23	16.60
Maximiliana maripa	28	1.60	7.29	6.52	13.81
Lecythis corrugata	31	1.06	8.07	4.30	12.38
Tabebuia uleana	28	0.92	7.29	3.73	11.02
Simarouba amara	13	0.99	3.39	4.01	7.39
Alseis longifolia	18	0.22	4.69	0.88	5.57
Picramnia spruceana	11	0.14	2.86	0.56	3.43
Chomelia barbellata	9	0.23	2.34	0.93	3.27
Enterolobium schomburgkii	4	0.44	1.04	1.80	2.84
Himatanthus articulatus	7	0.16	1.82	0.66	2.48
Peltogyne paniculata	7	0.13	1.82	0.53	2.36
Chaunochiton kappleri	4	0.30	1.04	1.21	2.25
Pouteria reticulata	7	0.09	1.82	0.38	2.20
Others (32 spp.)	58	1.79	15.12	7.33	22.45
PRFb					
Peltogyne gracilipes	113	18.24	25.98	62.15	88.12
Zygia sp. 2	53	1.94	12.18	6.61	18.80
Pradosia surinamensis	47	2.07	10.80	7.06	17.86
Eugenia cupulata	44	0.70	10.11	2.37	12.49
Cordia sellowiana	24	0.82	5.52	2.79	8.31
Zygia sp. 1	11	1.19	2.53	4.05	6.58
Casearia ulmifolia	19	0.22	4.37	0.74	5.11
Alseis longifolia	16	0.27	3.68	0.94	4.61
Pouteria surumuensis	9	0.32	2.07	1.10	3.17
Apeiba schomburgkii	7	0.45	1.61	1.52	3.13
Chomelia barbellata	9	0.26	2.07	0.90	2.97
Ecclinusa guianensis	8	0.30	1.84	1.01	2.85
Hymenaea courbaril	9	0.23	2.07	0.78	2.85
MTN 17	9	0.20	2.07	0.70	2.77
Rinorea brevipes	9	0.16	2.07	0.54	2.61
Others (27 spp.)	48	2.25	11.03	6.74	17.77
PPF					
Peltogyne gracilipes	16	4.98	4.68	20.05	24.73
Pradosia surinamensis	25	3.46	7.31	13.91	21.22
Ecclinusa guianensis	34	2.51	9.94	10.08	20.03
Tetragastris panamensis	37	1.50	10.82	6.05	16.87
Lecythis corrugata	37	1.37	10.82	5.50	16.32
Licania kunthiana	23	2.28	6.73	9.16	15.88
Maximiliana maripa	24	1.47	7.02	5.93	12.94

TABLE 9. (*continued*).

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Simarouba amara	14	1.58	4.09	6.03	10.12
Pouteria reticulata	16	0.63	4.68	2.53	7.21
Brosimum lactescens	11	0.74	3.22	2.97	6.19
Couratari multiflora	3	0.94	0.88	3.78	4.66
Pouteria hispida	6	0.65	1.75	2.61	4.37
Himatanthus articulatus	7	0.31	2.05	1.25	3.29
Alseis longifolia	7	0.13	2.05	0.52	2.57
Drypetes variabilis	5	0.19	1.46	0.78	2.25
Others (40 spp.)	77	2.01	22.50	8.85	31.35

Diversity and evenness. A total of 135 tree species was sampled in 3.75ha (fifteen 50m × 50m plots) (see Appendix 2). The mean species richness, diversity indices and evenness for the trees of the three replicated plots in each forest type are given in Table 14. These values were always lower in PRF. With an increase of minimum dbh for sampling to 30cm, the values of the diversity indices and number of species decreased in all forest types. However, the evenness values decreased only in PRF, reflecting the increase in dominance of *Peltogyne* (Tables 9, 11 and 13). This pattern was even stronger when only trees ≥50cm dbh were considered (Table 14).

The values of the diversity indices for trees (≥10cm dbh) of the PRF plots, calculated excluding *Peltogyne*, showed the same patterns as above, with values always lower than those of the other forest types (Table 14). However, for trees ≥ 30cm dbh, again with *Peltogyne* excluded from the calculations of the Simpson index for PRF plots, some values increased, showing that *Peltogyne* interfered more with the species diversity owing to its greater dominance in this size class.

DISCUSSION

Physical environment

The surface soils of the plots are, in general, sandy, with a low percentage of clay, total phosphorus and exchangeable calcium and potassium. They can be considered among the poorest soils recorded in Amazonian lowland evergreen rainforests (Thompson et al., 1992a) (Table 1). However, in most plots the values of available phosphorus are moderate (Table 2), and percentage base saturation is relatively high. Statistically significant differences were found mainly between PRF soils and soils from FWP. Soils from PRF had a tendency to have more silt and be richer in nutrients than soils from FWP, with most obviously higher magnesium, Mg/Ca quotients and Mg/total base quotients. The high magnesium seems to be a feature of the soil parent material and does not reflect merely surface-enrichment by the vegetation (Table 1). Robison & Nortcliff (1994) pointed out that many of the soils

TABLE 10. The 15 most important species of trees ≥10cm dbh occurring in three replicate 50m × 50m plots in FWPa and FWPb on Maracá Island, with number of individuals (*n*), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
FWPa					
Licania kunthiana	35	4.13	11.33	20.23	31.55
Ecclinusa guianensis	34	2.90	11.00	14.24	25.24
Pradosia surinamensis	25	3.28	8.09	16.08	24.17
Maximiliana maripa	18	1.19	5.83	5.82	11.65
Lecythis corrugata	21	0.86	6.80	4.20	10.99
Tetragastris panamensis	12	1.22	3.88	5.97	9.86
Himatanthus articulatus	19	0.68	6.15	3.34	9.49
Pouteria hispida	12	1.10	3.88	5.38	9.26
Simarouba amara	5	0.95	1.62	4.64	6.26
Guatteria schomburgkiana	11	0.31	3.56	1.54	5.10
Brosimum lactescens	7	0.55	2.27	2.69	4.96
Duguetia lucida	11	0.15	3.56	0.73	4.29
Ocotea fasciculata	7	0.37	2.27	1.82	4.09
Drypetes variabilis	7	0.24	2.27	1.19	3.46
Couratari multiflora	1	0.58	0.32	2.85	3.18
Others (36 spp.)	84	18.51	27.17	9.28	36.45
FWPb					
Licania kunthiana	22	3.35	6.45	18.63	25.08
Brosimum lactescens	23	2.07	6.74	11.51	18.26
Pouteria hispida	24	1.63	7.04	9.06	16.10
Tetragastris panamensis	12	1.61	3.52	8.97	12.49
Astrocaryum aculeatum	25	0.88	7.33	4.92	12.25
Duguetia lucida	27	0.44	7.92	2.47	10.39
Lecythis corrugata	15	0.76	4.40	4.21	8.60
Crepidospermum goudotianum	15	0.16	4.40	0.92	5.32
Ficus sp. 1	1	0.88	0.29	4.88	5.18
Himatanthus articulatus	12	0.25	3.52	1.39	4.91
Clarisia racemosa	3	0.65	0.88	3.64	4.52
Pouteria surumuensis	6	0.45	1.76	2.49	4.25
Duroia eriopila	10	0.23	2.93	1.25	4.19
Lindackeria paludosa	11	0.12	3.23	0.65	3.88
Pinzona coriacea	8	0.23	2.35	1.30	3.65
Others (55 spp.)	127	4.27	37.24	23.71	60.95

underlying the PRF have the highest concentrations of exchangeable magnesium recorded on Maracá Island.

PRF is frequently related to the lower undulating regions, with lower slopes and broad valley bottoms having poorer drainage (Robison & Nortcliff, 1994). PRF seems to follow old drainage systems (Nascimento, 1994) from NE to SW. However,

TABLE 11. Species of trees ≥30cm dbh occurring in three replicate 50m × 50m plots in PRFa, PRFb and PPF on Maracá Island, with number of individuals (*n*), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa					
Peltogyne gracilipes	46	12.35	54.12	72.06	126.17
Pradosia surinamensis	10	1.24	11.76	7.21	18.97
Ecclinusa guianensis	6	0.62	7.06	3.62	10.68
Simarouba amara	3	0.86	3.53	4.99	8.52
Lecythis corrugata	4	0.36	4.71	2.08	6.79
Maximiliana maripa	4	0.30	4.71	1.78	6.49
Enterolobium schomburgkii	3	0.37	3.53	2.18	5.71
Chaunochiton kappleri	2	0.27	2.35	1.58	3.93
Licania apetala	1	0.26	1.18	1.52	2.70
Vitex schomburgkiana	1	0.12	1.18	0.69	1.87
Tabebuia uleana	1	0.10	1.18	0.57	1.75
Chomelia barbellata	1	0.08	1.18	0.45	1.63
Licania kunthiana	1	0.07	1.18	0.42	1.60
Ormosia smithii	1	0.07	1.18	0.42	1.60
Himatanthus articulatus	1	0.07	1.18	0.41	1.50
PRFb					
Peltogyne gracilipes	55	16.48	62.50	77.69	140.19
Zygia sp. 2	9	0.87	10.23	4.10	14.32
Pradosia surinamensis	6	0.91	6.82	4.31	11.13
Zygia sp. 1	5	1.00	5.68	4.71	10.40
Tabebuia uleana	2	0.29	2.27	1.36	3.63
Apeiba schomburgkii	2	0.20	2.27	0.97	3.24
Zollernia grandifolia	1	0.33	1.14	1.58	2.71
Alexa canaracunensis	1	0.19	1.14	0.88	2.01
Ficus sp. 1	1	0.18	1.14	0.86	2.00
MTN 342	1	0.17	1.14	0.81	1.94
Cordia sellowiana	1	0.17	1.14	0.80	1.93
Chomelia barbellata	1	0.11	1.14	0.53	1.67
Himatanthus articulatus	1	0.11	1.14	0.53	1.66
Ecclinusa guianensis	1	0.10	1.14	0.48	1.62
Pouteria surumuensis	1	0.08	1.14	0.40	1.54
PPF					
Peltogyne gracilipes	11	4.85	10.89	25.93	36.82
Pradosia surinamensis	14	3.15	13.86	16.81	30.67
Ecclinusa guianensis	16	1.94	15.84	10.36	26.21
Licania kunthiana	12	1.92	11.88	10.29	22.17
Simarouba amara	10	1.46	9.90	7.79	17.69
Lecythis corrugata	6	0.59	5.94	3.15	9.09
Tetragastris panamensis	5	0.75	4.95	4.02	8.97
Maximiliana maripa	6	0.47	5.94	2.50	8.44
Couratari multiflora	2	0.90	1.98	4.81	6.79

TABLE 11. (*continued*).

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Brosimum lactescens	3	0.60	2.97	3.21	6.18
Pouteria hispida	3	0.53	2.97	2.86	5.83
Pouteria reticulata	3	0.36	2.97	1.94	4.91
Aspidosperma nitidum	2	0.28	1.98	1.48	3.46
Himatanthus articulatus	2	0.20	1.98	1.07	3.05
Drypetes variabilis	2	0.17	1.98	0.89	2.87
Enterolobium schomburgkii	1	0.17	0.99	0.91	1.90
Chomelia barbellata	1	0.16	0.99	0.86	1.85
Pouteria cladantha	1	0.11	0.99	0.59	1.58
Pouteria venosa	1	0.10	0.99	0.54	1.53

it is important to note that although PRF can occur in poorly drained areas (Milliken & Ratter, 1989; Furley & Ratter, 1990) it is not restricted to these sites. On the contrary, most of the PRF transects on Maracá reported by Milliken & Ratter (1989) were on well-drained soils, with the highest value (60%) of relative dominance of *Peltogyne* on a sandy and well-drained soil on the Fumaça trail (Fig. 3). This forest type was never found on seasonally flooded areas on Maracá Island. However, the water-table in two PRFa plots reached the soil surface at the end of the wet season, but this was probably for only a very short period. Thompson et al. (1992b) showed such rapid water-table level falls at the end of the wet season in other Maracá forests. Therefore, PRFa cannot be considered a waterlogged forest, since water-logging generally implies long-term presence of the water-table within 60cm of the soil surface or occurrence of annual flooding (Cochrane et al., 1985).

Available phosphorus has been reported to be negatively related to the abundance of the Caesalpiniaceae in the Korup forest in Cameroon (Gartlan et al., 1986), but this was not so on Maracá. The higher concentrations of total nitrogen found in PRF may not be related to the presence of *Peltogyne*, since inspection of several roots showed this species is not nodulated. It is known that its family (Caesalpiniaceae) is mainly non-nodulated (Alexander, 1989).

Forest structure

The forest formation. The Maracá forests range from a type (found on the western tip of Maracá) similar to that of Central Amazonia to a floristically and structurally different type at the eastern end of the island (Milliken & Ratter, 1989). According to RadamBrasil (1975) the forests of Maracá should be classified as 'Floresta Estacional Semidecidual' (semi-deciduous seasonal forest) at the eastern tip and 'Floresta Densa' (dense [evergreen] forest) at the western end. However, the FWP of the eastern part of Maracá should be considered as a tropical lowland evergreen

TABLE 12. Species of trees ≥30cm dbh occurring in three replicate 50m × 50m plots in FWPa and FWPb on Maracá Island, with number of individuals (*n*), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
FWPa					
Licania kunthiana	19	3.42	21.59	23.57	45.17
Ecclinusa guianensis	19	2.35	21.59	16.20	37.79
Pradosia surinamensis	14	2.92	15.91	20.13	36.04
Tetragastris panamensis	8	1.17	9.09	8.08	17.17
Pouteria hispida	5	0.88	5.68	6.06	11.75
Simarouba amara	4	0.93	4.55	6.44	10.98
Maximiliana maripa	6	0.47	6.82	3.27	10.09
Brosimum lactescens	3	0.45	3.41	3.12	6.53
Lecythis corrugata	3	0.44	3.41	3.05	6.46
Couratari multiflora	1	0.58	1.14	4.01	5.15
Ocotea fasciculata	2	0.29	2.27	2.02	4.29
Aspidosperma eteanum	1	0.19	1.14	1.32	2.46
Guatteria sp.	1	0.17	1.14	1.17	2.31
Himatanthus articulatus	1	0.11	1.14	0.78	1.92
Aniba hostmanniana	1	0.11	1.14	0.77	1.90
FWPb					
Licania kunthiana	12	3.03	19.05	26.60	45.65
Brosimum lactescens	11	1.58	17.46	13.85	31.31
Tetragastris panamensis	9	1.53	14.29	13.41	27.69
Pouteria hispida	9	1.16	14.29	10.19	24.48
Lecythis corrugata	4	0.39	6.35	3.46	9.81
Ficus sp. 1	1	0.88	1.59	7.70	9.29
Clarisia racemosa	2	0.62	3.17	5.45	8.63
Pouteria surumuensis	3	0.35	4.76	3.10	7.86
Alseis longifolia	1	0.42	1.59	3.65	5.24
DS 628	1	0.33	1.59	2.91	4.50
Pouteria ? torta	1	0.17	1.59	1.45	3.04
Swartzia dipetala	1	0.16	1.59	1.39	2.98
Ecclinusa guianensis	1	0.13	1.59	1.13	2.72
Cordia sellowiana	1	0.11	1.59	1.01	2.60
Simarouba amara	1	0.11	1.59	0.94	2.53
Pinzona coriacea	1	0.10	1.59	0.86	2.45
Ormosia coarctata	1	0.09	1.59	0.78	2.37
Ocotea fasciculata	1	0.08	1.59	0.72	2.31
Didymopanax morototoni	1	0.08	1.59	0.71	2.30
Dialium guianense	1	0.07	1.59	0.66	2.25

rainforest (*sensu* Whitmore, 1984) rather than a semi-deciduous seasonal forest, since less than 6% of the trees are deciduous (Thompson et al., 1992a). On the other hand, semi-deciduous forests do occur in the eastern part of Maracá. Thompson et al.

TABLE 13. Species of trees ≥50cm dbh occurring in three replicate 50m × 50m plots in five forest groups on Maracá Island, with number of individuals (*n*), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

	n	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa					
Peltogyne gracilipes	21	8.94	91.30	90.87	182.18
Simarouba amara	1	0.64	4.35	6.47	10.82
Licania apetala	1	0.26	4.35	2.65	7.00
PRFb					
Peltogyne gracilipes	26	12.73	81.25	89.07	170.32
Zygia sp. 1	2	0.56	6.25	3.91	10.16
Pradosia surinamensis	2	0.47	6.25	3.29	9.54
Zollernia grandifolia	1	0.33	3.13	2.34	5.46
Tabebuia uleana	1	0.20	3.13	1.40	4.52
PPF					
Peltogyne gracilipes	7	4.23	28.00	42.41	70.41
Pradosia surinamensis	6	2.25	24.00	22.55	46.55
Couratari multiflora	2	0.90	8.00	9.04	17.04
Licania kunthiana	2	0.54	8.00	5.42	13.42
Tetragastris panamensis	2	0.45	8.00	4.52	12.52
Ecclinusa guianensis	2	0.44	8.00	4.41	12.41
Simarouba amara	2	0.43	8.00	4.36	12.36
Brosimum lactescens	1	0.40	4.00	4.07	8.07
Pouteria hispida	1	0.32	4.00	3.23	7.23
FWPa					
Pradosia surinamensis	6	1.75	28.57	29.93	58.50
Licania kunthiana	6	1.51	28.57	25.70	54.27
Simarouba amara	3	0.81	14.29	13.75	28.03
Pouteria hispida	2	0.52	9.52	8.84	18.36
Couratari multiflora	1	0.58	4.76	9.93	14.69
Brosimum lactescens	1	0.24	4.76	4.17	8.93
Lecythis corrugata	1	0.23	4.76	3.94	8.70
Tetragastris panamensis	1	0.22	4.76	3.75	8.51
FWPb					
Licania kunthiana	6	2.27	35.29	36.00	71.29
Tetragastris panamensis	4	1.04	23.53	16.51	40.04
Brosimum lactescens	2	0.71	11.76	11.30	23.06
Ficus sp. 1	1	0.88	5.88	13.95	19.83
Clarisia racemosa	1	0.45	5.88	7.20	13.08
Alseis longifolia	1	0.42	5.88	6.62	12.50
DS 628	1	0.33	5.88	5.27	11.15
Pouteria hispida	1	0.20	5.88	3.15	9.03

TABLE 14. Mean species diversity (Simpson's and Shannon's indices) for trees ≥10cm dbh, ≥30cm dbh and ≥50cm dbh of three replicated 50m × 50m plots in five forest groups on Maracá Island. (Standard deviation in parentheses.)

Forest	Simpson's index (1/Ds)	Shannon's index (H′)	No. of spp.	Evenness*
Trees ≥10cm dbh				
PRFa	9.11(1.91)	2.58(0.18)	26(2.52)	0.79(0.04)
PRFb	7.16(2.78)	2.27(0.43)	21(4.93)	0.74(0.09)
PPF	13.28(3.40)	2.86(0.27)	32(8.02)	0.84(0.02)
FWPa	17.64(1.58)	3.02(0.08)	31(2.89)	0.88(0.01)
FWPb	26.62(7.42)	3.37(0.14)	42(2.31)	0.90(0.02)
Trees ≥30cm dbh				
PRFa	3.19(0.17)	1.49(0.12)	8(1.53)	0.72(0.02)
PRFb	2.57(0.98)	1.19(0.49)	7(3.79)	0.65(0.07)
PPF	10.08(4.10)	2.23(0.25)	13(2.08)	0.88(0.04)
FWPa	7.31(1.25)	1.95(0.20)	9(2.08)	0.88(0.02)
FWPb	9.15(4.94)	1.98(0.48)	10(4.16)	0.91(0.02)
Trees ≥50cm dbh				
PRFa	0.85(0.74)	0.23(0.20)	2(0.58)	0.33(0.29)
PRFb	1.20(1.06)	0.47(0.45)	2(1.53)	0.47(0.41)
PPF	9.96(7.75)	1.45(0.50)	5(2.00)	0.92(0.09)
FWPa	5.33(1.63)	1.26(0.24)	4(1.00)	0.92(0.01)
FWPb	8.7(10.66)	1.21(0.49)	4(1.73)	0.90(0.15)

* H′/ln(number of species).

(1994) found 45% of the trees to be deciduous in an area about 3km north of the FWPb plots and this area was considered by them to be a small patch of semi-evergreen forest. It is important to note that *Peltogyne* did not occur there, but PRF can also be classified (*sensu* Beard, 1944) as semi-deciduous forest, since at least 35% of the trees ≥10cm dbh are deciduous, with *Peltogyne* accounting for about two-thirds of the deciduous individuals. If only trees ≥30cm dbh are taken into account the PRF should be considered deciduous rather than semi-deciduous, since *Peltogyne* accounts for more than 54% of the trees in this dbh class and other deciduous trees such as *Cordia sellowiana*, *Chaunochiton kappleri*, *Enterolobium schomburgkii*, *Simarouba amara* and *Tabebuia uleana* occur frequently as a canopy component. Milliken & Ratter (1989) also suggested that some areas of *Peltogyne* forest should be classified as deciduous seasonal forest, since the proportion of deciduous trees exceeds two-thirds. The pattern of deciduousness in *Peltogyne* is interesting. Smaller individuals (up to 20cm dbh) appear to be evergreen and seem to be immature. Above that size, the trees are partly or wholly leafless from the beginning of December to late March which coincides with the dry season on Maracá.

Thus the PRF is a deciduous or semi-deciduous forest, and occurs in soils with more nutrients than the evergreen FWP. This reinforces the observations of Furley

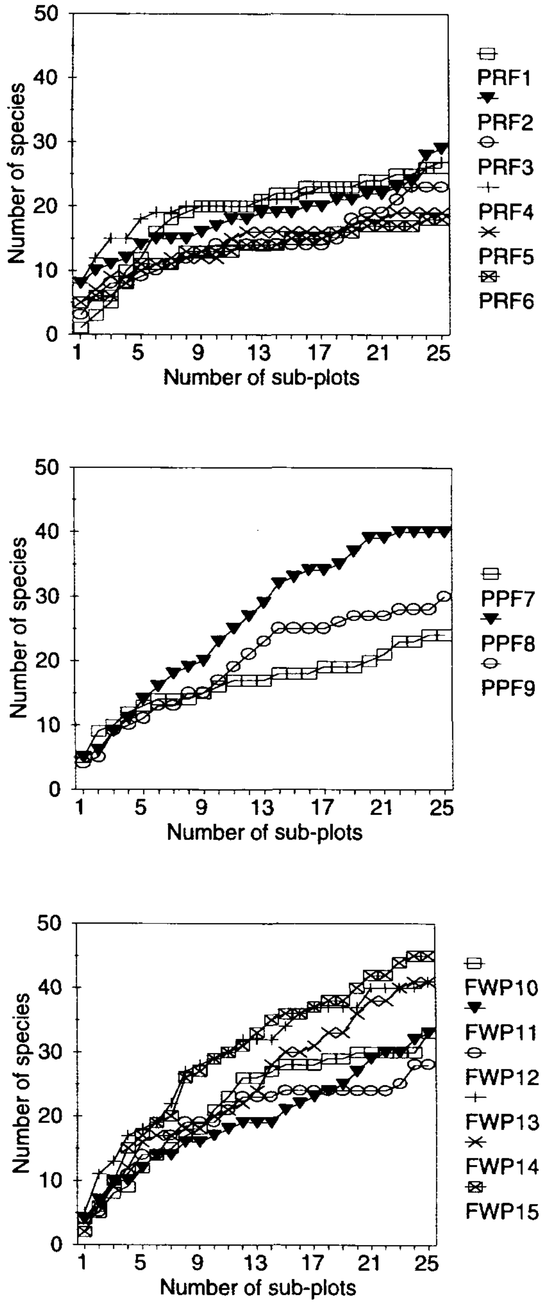


FIG. 8. Species-area curves for trees (≥ 10cm) on each study plot in PRF, PPF and FWP. Each curve follows the order of enumeration of the twenty-five 10m × 10m subplots.

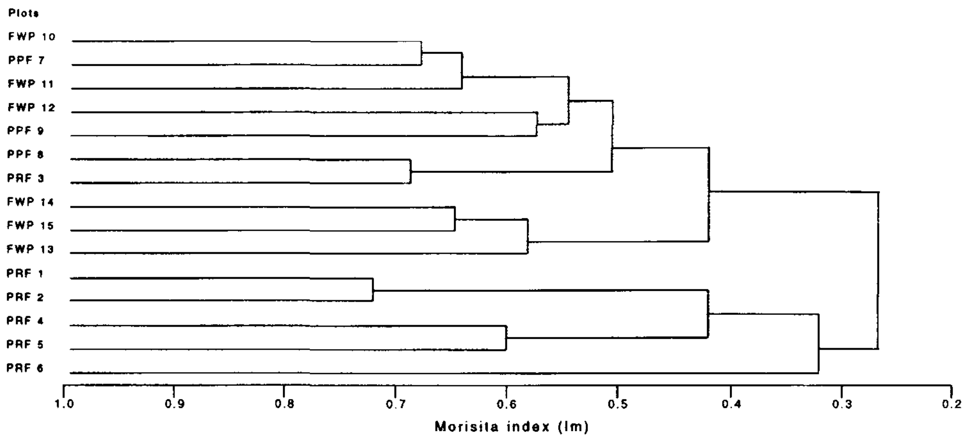


FIG. 9. Dendrogram produced by applying group average clustering to the species similarity data between plots for trees ≥10cm dbh from three different forest types on Maracá Island, Brazil.

et al. (1988), Ratter et al. (1973, 1978) and Thompson et al. (1994) that deciduous forests are associated with more nutrient-rich soils.

Vertical structure. The height of the canopy of the Maracá forests (20–35m tall, with emergents reaching 40m or more) is similar to that normally found for *terra firme* forest on the fringe of the Amazonian forest (Ratter et al., 1973, 1978; Uhl, 1982), but lower than values found for canopy height (30–40m) in central (Takeuchi, 1961; Prance et al., 1976) and eastern Amazonia (Almeida et al., 1994). Although PRF showed a higher and more closed canopy than most of the forest types at the eastern part of the island, including the other two types of semi-evergreen forest studied by Thompson et al. (1994) and Milliken & Ratter (1989), a similar value for canopy height was found by Thompson et al. (1992a) for the FWPb.

Tree density. The Maracá forest plots 1–15 have values of tree density (≥10cm dbh) ranging from 295 to 463ha^{-1} (Table 4), with the lowest value for FWPa at the eastern part of Maracá and the highest one for the PRF in the central area of the island. Milliken & Ratter (1989) found density values equivalent to 453ha^{-1} and 677ha^{-1} using a point-centred quarter (PCQ) method in other PRFs on Maracá and 527ha^{-1} in a FWP at the western end of the island. These values fall into the ranges of 285–859 trees ha^{-1} reported by Campbell et al. (1986), Gentry (1987) and Gentry (1988) for Amazonian forests. PRF values (401–677 trees ha^{-1}) are similar to those found for gallery forests in southern (416ha^{-1}, Gibbs et al., 1980) and central Brazil (650ha^{-1}, Felfili, 1994) and for lowland rainforests in Africa (471ha^{-1}, Gartlan et al., 1986; 477ha^{-1}, Hart et al., 1989) and in south-east Asia (470ha^{-1}, Newbery et al., 1992). However, they are, in most of the cases, lower than the values reported by Proctor et al. (1983) for four sites in south-east Asia

(615–778 trees ha^{-1}). The highest value (778 trees ha^{-1}) reported in the last work was for a large-stature heath forest.

Basal area. The basal areas for trees ≥10cm dbh of the PRF sites in this study (PRFa, mean $32.8m^2$ ha^{-1}, range 25.2–38.3; PRFb, mean $39.1m^2$ ha^{-1}, range 36.7–43.1) were generally higher than those of the other forest types studied, although the PPF showed marginally higher figures than PRFa (Table 3). Similarly Milliken & Ratter (1989) using the PCQ survey method also found high basal area values in forests dominated by *Peltogyne* (e.g. $44.7m^2$ ha^{-1} on their Transect 14A and $40.4m^2$ ha^{-1} on Transect 16A). These values for PRF fall into or come close to the ≥ $40m^2$ ha^{-1} given for 'exceptionally large forests' by Pires & Prance (1985) in their description of vegetation types of the Brazilian Amazon, and sometimes exceed Lamprecht's (1972) figure of $30–40m^2$ ha^{-1} for lowland rainforests in northern South America. They are also high compared with the range ($23–37m^2$ ha^{-1}) for lowland rainforests in Africa (Dawkins, 1959).

Milliken & Ratter (1989) have described other 'exceptionally large forests' in areas without *Peltogyne* at the east end of the island ($41.1m^2$ ha^{-1} on Transect 2A and $54.5m^2$ ha^{-1} on Transect 7A – see their discussion on forest biomass and species diversity), but nevertheless the PRFs in general tend to be larger than FWPs. Most of the latter fall into the 'dense forest' category ($24–40m^2$ ha^{-1}) of Pires & Prance (1985) but some into the smaller 'open or vine forests' ($18–24m^2$ ha^{-1}).

Lianas. The results (Table 7) do not support Milliken & Ratter's (1989) view that the *Peltogyne* forest has a lack of lianas and that the occurrence of lianas on the smooth bark of *Peltogyne* is rare. In our study about 50% of *Peltogyne* trees supported at least one liana. Our values showing PRFa with 40% of trees with lianas, PPF (34%) and FWPa (22%) are lower than those found by Balslev et al. (1987) (53%) for a tropical evergreen lowland rainforest in Ecuadorian Amazônia, Campbell & Newbery (1993) (57%) for a lowland rainforest in Sabah, Malaysia, and Putz et al. (1985) (44, 47 and 54%) for three other lowland rainforest sites in Sarawak, Malaysia. However, other authors have found similar proportions of trees supporting lianas to those found for our PRF and PPF: Balslev et al. (1987) (31%) for a flooded Amazonian forest in Ecuador, Mori et al. (1983) (37.5%) for a moist forest in eastern Brazil, and Putz & Chai (1987) (33%) for a lowland rainforest at Lambir, Sarawak, Malaysia. However, our value for FWPa (22%) seems to be the lowest reported for lowland tropical rainforests.

Floristics

Family composition. The main difference at the family level between PRF and FWP is that the Caesalpiniaceae are the most important family in the former, and are poorly represented both in species and in number of individuals in the latter. The Sapotaceae were the second most important family in the PRF and the first in the FWP. The Sapotaceae were second to the Moraceae in the FWPb when data for all six plots of Thompson et al. (1992a) were used. Three of these plots were later felled and the data for the remaining plots, those used in this paper, have Sapotaceae ranked first. These results are in agreement with Milliken & Ratter's (1989) data for forests at the eastern tip of Maracá. Other important features of the PRF are the rarity or absence of some families that are important in the other forest types on Maracá, such as the Annonaceae, Burseraceae, Chrysobalanaceae and Moraceae. Those families are in the list of the 11 most important families in the central Amazonian forest (Prance, 1990). It is also noteworthy that families such as the Apocynaceae, Chrysobalanaceae, Lecythidaceae and Palmae that were abundant in forests along the station trail system at the eastern end of the island, including PRFa, were rare or did not occur at all in the PRFb in the more western Casa Maracá area. Despite this difference, Milliken & Ratter (1989) considered that the *Peltogyne* forests at the southern end of the Preguiça trail (near to the PRFb plots) have a floristic composition similar to the eastern FWP forests.

Although forest is continuous in the Amazon basin, family importance varies from area to area, with the Leguminosae the most important family in Amapá and Pará (Campbell et al., 1986), Leguminosae and Moraceae in Amazonian Ecuador (Valencia et al., 1994), Lecythidaceae in Manaus (Prance et al., 1976; Rankin-de-Merona et al., 1992), Moraceae and Myristicaceae in Beni, Bolivia (Boom, 1986), Myristicaceae and Euphorbiaceae in Acre (Campbell et al., 1986), Euphorbiaceae at the western end and Moraceae and Sapotaceae at the eastern end of Maracá (Milliken & Ratter, 1989; Thompson et al., 1992a). Thompson et al. (1992a) emphasized that the Lecythidaceae, Leguminosae (*sensu lato*), Myristicaceae and Euphorbiaceae did not contribute a high proportion of the species in their Maracá plots. However, in this study the plots in PRFa, PRFb, PPF and FWPa always showed the Lecythidaceae as the third or fourth most important family with the Caesalpiniaceae as the most important family in the PRF, due in the main to the presence of *Peltogyne gracilipes* itself.

Species composition. The values of species similarity within groups of plots were usually high (Fig. 9). However, in PRFa the species similarity between plots PRFa 3 and PRFa 1 was 0.40 and between PRFa 3 and PRFa 2 was 0.45, while the value between PRFa 1 and PRFa 2 was higher (0.73). The relatively low values of species similarity for PRFa 3 may be related to its position close to the margin of the PRFa area. For the PRFb the low values found between plots PRFb 6 and PRFb 4 (0.38) and PRFb 5 (0.36) can also be related to the location of PRFb 6 on a small island. However, Campbell (1994) also found low values of similarity between transects in Amazonian forests, with a maximum similarity of 0.21 in terra firme plots and 0.47 in the várzea forests. According to him, these values indicate that there is probably no such thing as a 'representative' small sample for any Amazonian forest.

Ecclinusa guianensis, *Lecythis corrugata*, *Licania kunthiana*, *Maximiliana maripa*, *Pradosia surinamensis*, *Simarouba amara* and *Tetragastris panamensis* are among the most important species in Maracá forests. However, *Peltogyne* showed the highest relative dominance values (62%) reported for Amazonian lowland forests. According to Milliken & Ratter (1989), *Pradosia surinamensis* is one of the most important species in the forests at the eastern tip of Maracá. It is noteworthy that species such as *Licania kunthiana* and *Tetragastris panamensis*, very common in PPF and FWP, occur with low density and dominance in PRF. Another important point is the number of palms in PRF in relation to the FWP. In the former forest type, no palms occurred in the Casa Maracá plots, while in PRFa, 28 individuals were recorded. However, most of these tree palms were located in plot PRFa 1 ($n=17$) suggesting that it might have suffered more disturbance. High densities of palm species such as *Astrocaryum aculeatum*, *Maximiliana maripa* and *Oenocarpus bacaba* may be the result of higher degree of disturbance in these areas, since they are frequent and form dense populations in secondary forests (Kahn & Granville, 1992). Proctor & Miller (pers. comm.) list eight tree species that are known to be favoured by human disturbance (*Apeiba schomburgkii*, *Astrocaryum aculeatum*, *Genipa americana*, *Guazuma ulmifolia*, *Jacaranda copaia*, *Lindackeria paludosa*, *Maximiliana maripa* and *Simarouba amara*). Most of these species occur in PPF (six out of eight) and FWP (six out of eight, FWPa), while only three of these species occurred in PRFa and one in PRFb. However, no archaeological evidence or signs of charcoal or charred logs were found on the soil surface of plots, other than those of FWPb, although charcoal was found in all plots at 25cm depth or more. Therefore, it is difficult to infer whether these communities are a result of human disturbance or are natural.

The number of species (a total of 135 for trees and lianas $\geq$ 10cm dbh) found in 3.75ha (total of all the plots studied) on Maracá, and the records for 0.75ha of 49 species in PRF, 52 (PPF) and 56 (FWP), show that the Maracá forests, especially the PRF, are in the lower range of the species richness for Amazonian lowland forests (range 60–300 species per ha, Campbell et al., 1986 and Gentry, 1988). Campbell et al. (1986) also found relatively low species richness in a lowland forest in the south-eastern border of Amazonia (1500–1700mm annual rainfall) with a range from 118 to 162 species per hectare. According to them these values are lower than the mean (174 species) for the 10 comparable phytosociological studies conducted in Amazonia. They pointed out that their 1ha transect would not have been sufficient to sample the species richness, since the species-area curve (all the transects combined) began to level off after about 1.5ha and approached an asymptote at 3ha. For the PRF, PPF and FWP, the species-area curves (Fig. 8) suggest that the low species-richness is not a reflection of the insufficient area sampled. Other authors (Black et al., 1950; Ratter et al., 1973, 1978; Boom, 1986; Gentry, 1988) have also recorded low values for lowland Amazonian forests located on the fringe of the Amazonia, but the species-richness of the PRF seems to be the lowest of the values yet reported for a lowland rainforest in Amazonia.

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APPENDIX 1

Soil chemical analysis techniques

Loss-on-ignition was determined in oven-dried samples after heating at 375°C for 16h. The pH was measured in a 1:2 soil:deionized water mix which was stirred and allowed to stand for 1h. Total nitrogen and phosphorus were extracted from 1g subsamples of soil digested in a mixture of 4.4ml of the mixed digestion reagent (420ml of concentrated sulphuric acid, containing 0.1% selenium as a catalyst, and 350ml of '100 volume' hydrogen peroxide). They were measured colorimetrically by a FIAstar 5010 flow injection auto-analyser using the gas diffusion method (FIAstar application sheet no. 50-03/84) for nitrogen and the stannous chloride-ammonium molybdate method (FIAstar application sheet no. 60-02/83) for phosphorus. For analysis of exchangeable cations (Allen, 1989), 10g subsamples of soil were extracted by 10 successive additions of 10ml of 1M ammonium acetate solution adjusted (by the addition of acetic acid) to pH 4.9 and were determined on a Varian AA-575 Atomic Absorption Spectrophotometer using an air-acetylene flame for sodium and potassium and a nitrous oxide-acetylene flame for calcium and magnesium. Total acidity and exchangeable aluminium were analysed by titration after 10g subsamples of soil were leached by 10 successive additions of 10ml of 1M potassium chloride solution. Total acidity was measured by titration with NaOH using phenolphthalein as the indicator. Another titration with 5mM hydrochloric acid was carried out for exchangeable aluminium, after adding 10ml of 1M potassium fluoride to the titration solution. Hydrogen was estimated as the difference of the total acidity and aluminium. The sum of total exchangeable cations plus total acidity were calculated to determine the values of cation exchange capacity. Particle-size composition was measured using the hydrometer method (EMBRAPA, 1979) on 50g soil samples from each soil pit sample.

For extractable nitrogen, 10g subsamples of 10 randomly selected fresh samples of soil (0–10cm) were each extracted with 50ml of 1.5M potassium chloride containing 1mg l^{-1} mercuric chloride to retard microbial action (Robertson, 1984). Each solution was shaken, allowed to equilibrate for 8h and filtered, before analysis. Ammonium ions were analysed by the indophenol blue method (Gine et al., 1980), and nitrate (with nitrate) ions by the cadmium reduction method (Henriksen & Selmer-Olsen, 1970), using a FIA (flow injection analysis) system. Phosphorus was extracted from 5g subsamples of the same fresh soil samples using 50ml 0.025N sulphuric acid and 0.05N hydrochloric acid – the Mehlich method (EMBRAPA, 1979). Each solution was shaken, allowed to equilibrate for 12h, then filtered. The extracted solutions were analysed colorimetrically by the reduction of orthophosphate by ascorbic acid using a molybdate reagent (Allen, 1989).

APPENDIX 2

List of tree species occurring in the three forest types studied

	Family	Forest types		
Abuta grandifolia (Mart.) Sandw.	Menispermaceae	PRF	PPF	
Acosmium tomentellum (Mohl.) Yakovl.	Fabaceae		PPF	
Agonandra silvatica Ducke	Opiliaceae			FWP
Alexa canaracunensis Pittier	Fabaceae	PRF		
Alseis longifolia Ducke	Rubiaceae	PRF	PPF	FWP
Amaioua corymbosa Kunth	Rubiaceae		PPF	FWP
Ampelocera edentula Kuhlm.	Ulmaceae		PPF	FWP
Aniba hostmanniana (Nees) Mez	Lauraceae			FWP
Apeiba schomburgkii Szysz.	Tiliaceae	PRF	PPF	FWP
Arrabidea conjugata (Vell.) Mart.	Bignoniaceae			FWP
Aspidosperma eteanum Mgf.	Apocynaceae			FWP
Aspidosperma nitidum Benth.	Apocynaceae	PRF	PPF	
Astrocaryum aculeatum G.F.W. Mey	Palmae	PRF	PPF	FWP
Astronium lecointei Ducke	Anacardiaceae			FWP
Bauhinia ungulata L.	Caesalpiniaceae	PRF		
Bauhinia sp.	Caesalpiniaceae	PRF		
Brosimum lactescens (Moore) C.C. Berg	Moraceae		PPF	FWP
Byrsonima schomburgkiana Benth.	Malpighiaceae			FWP
Casearia sylvestris Sw. var. *sylvestris*	Flacourtiaceae			FWP
Casearia ulmifolia Vahl ex Vent.	Flacourtiaceae	PRF		
Cassia moschata Kunth	Caesalpiniaceae			FWP
Clarisia racemosa R. & P.	Moraceae			FWP
Cecropia sp.	Moraceae			FWP
Chaunochiton kappleri (Sagot & Egl.) Ducke	Olacaceae	PRF		
Cheiloclinium cognatum (Miers.) A.C. Smith	Hippocrateaceae		PPF	
Chomelia barbellata Standl.	Rubiaceae	PRF	PPF	
Chrysophyllum argenteum Jacq.	Sapotaceae		PPF	
Chrysophyllum sparsiflorum Kl. ex Miq.	Sapotaceae			FWP
Combretum sp.	Combretaceae	PRF		
Cordia sellowiana Cham.	Boraginaceae	PRF		
Couepia paraensis (Mart. & Zucc.) Benth subsp. *glaucescens* (Spr. ex Hook.) Prance	Chrysobalanaceae	PRF	PPF	
Couratari multiflora (J.E. Smith) Eyma	Lecythidaceae		PPF	FWP
Cupania sp.	Sapindaceae			FWP
Crepidospermum goudotianum (Tul.) Tr. & Pl.	Burseraceae	PRF	PPF	FWP
Dialium guianense (Aubl.) Sandw.	Caesalpiniaceae			FWP
Didymopanax morototoni Decne. & Planch.	Araliaceae			FWP
Drypetes variabilis Vitt.	Euphorbiaceae	PRF	PPF	FWP

	Family	Forest types		
Duguetia lucida Urb.	Annonaceae		PPF	FWP
Duroia eriopila L.f.	Rubiaceae	PRF	PPF	FWP
Ecclinusa guianensis Eyma	Sapotaceae	PRF	PPF	FWP
Enterolobium schomburgkii Benth.	Mimosaceae	PRF	PPF	FWP
Erythroxylum anguifugum Mart.	Erythroxylaceae	PRF		
Eschweilera pedicellata (Richard) Mori	Lecythidaceae		PPF	
Eugenia cupulata Amsh.	Myrtaceae	PRF	PPF	FWP
Eugenia sp.	Myrtaceae	PRF		
Exellodendron barbatum (Ducke) Prance	Chrysobalanaceae		PPF	FWP
Faramea crassiloba Benth.	Rubiaceae	PRF		FWP
Faramea sp. 1	Rubiaceae			FWP
Ficus sp.	Moraceae	PRF		
Ficus sp. 1	Moraceae	PRF		
Genipa americana L.	Rubiaceae	PRF		
Guatteria schomburgkiana Mart.	Annonaceae	PRF	PPF	FWP
Guatteria sp.	Annonaceae			FWP
Guettarda spruceana M. Arg.	Rubiaceae			FWP
Gustavia augusta L.	Lecythidaceae		PPF	
Himatanthus articulatus (Vahl) Woods.	Apocynaceae	PRF	PPF	FWP
Hymenaea courbaril L.	Caesalpiniaceae			FWP
Hippocratea volubilis L.	Hippocrateaceae			FWP
Inga sp. 1	Mimosaceae			FWP
Inga sp. 2	Mimosaceae	PRF		
Inga sp. 3	Mimosaceae		PPF	
Lecythis corrugata Poit.	Lecythidaceae	PRF	PPF	FWP
Licania apetala (E. Mey.) Fritsch	Chrysobalanaceae		PPF	
Licania kunthiana Hook.f.	Chrysobalanaceae	PRF	PPF	FWP
Lindackeria paludosa (Benth.) Gilg.	Flacourtiaceae		PPF	FWP
Lonchocarpus sp.	Fabaceae	PRF		
Lueheopsis duckeana Bussett	Tiliaceae	PRF	PPF	FWP
Machaerium sp.	Fabaceae	PRF	PPF	FWP
Maprounea guianensis Aubl.	Euphorbiaceae			FWP
Maximiliana maripa (Correa) Drude	Palmae	PRF	PPF	FWP
Maytenus guianensis Kl.	Celastraceae			FWP
Mezilaurus itauba (Taub.) ex Mez	Lauraceae		PPF	
Myrcia splendens (Sw.) DC.	Myrtaceae			FWP
Ocotea fasciculata (Nees) Mez	Lauraceae		PPF	FWP
Ocotea sandwithii Kostermans	Lauraceae			FWP
Oenocarpus bacaba Mart.	Palmae		PPF	FWP
Ormosia coarotada Jacks.	Fabaceae			FWP
Ormosia smithii Rudd	Fabaceae			FWP
Ormosia sp.	Fabaceae			FWP
Ormosia sp. 1	Fabaceae	PRF		
Ouratea castaneaefolia (DC.) Engl.	Ochnaceae		PPF	FWP
Peltogyne gracilipes Ducke	Caesalpiniaceae	PRF	PPF	
Peltogyne paniculata (Aubl.) Sandw. subsp. *pubescens* (Benth.) M.F. da Silva	Caesalpiniaceae	PRF		
Picramnia spruceana Engl.	Simaroubaceae	PRF	PPF	
Pinzona coriacea Mart. & Zucc.	Dilleniaceae			FWP
Pouteria cladantha Sandw.	Sapotaceae	PRF	PPF	

	Family	Forest types		
Pouteria hispida Eyma agg.	Sapotaceae	PRF	PPF	FWP
Pouteria reticulata (Engl.) Eyma subsp. *reticulata*	Sapotaceae	PRF	PPF	FWP
Pouteria surumuensis Baehni	Sapotaceae	PRF	PPF	FWP
Pouteria ? torta (Mart.) Radlk.	Sapotaceae			FWP
Pouteria venosa (Mart.) Baehni subsp. *amazonica* Penn.	Sapotaceae		PPF	FWP
Pradosia surinamensis (Eyma) Penn.	Sapotaceae	PRF	PPF	FWP
Protium tenuifolium (Engl.) Engl. subsp. *tenuifolium*	Burseraceae			FWP
Quiina rhytidopus Tul.	Quiinaceae			FWP
Rinorea brevipes (Benth.) Blake	Violaceae	PRF		
Rollinia exsucca (Dun.) A. DC.	Annonaceae			FWP
Rudgea crassiloba (Benth.) Rob.	Rubiaceae			FWP
Ryania speciosa Vahl var. *bicolor* DC.	Flacourtiaceae		PPF	FWP
Simarouba amara Aubl.	Simaroubaceae	PRF	PPF	FWP
Sloanea garckeana K. Schum. vel sp. aff.	Elaeocarpaceae			FWP
Sloanea guianensis Aubl.	Elaeocarpaceae			FWP
Sloanea sp.	Elaeocarpaceae			FWP
Swartzia dipetala Willd. ex Benth.	Fabaceae			FWP
Swartzia grandifolia Bong. ex Benth.	Fabaceae	PRF		
Tabebuia uleana (Kranzl.) Gentry	Bignoniaceae	PRF	PPF	FWP
Tetragastris panamensis (Engl.) Kuntze	Burseraceae		PPF	FWP
Trichilia cipo (A. Juss) C. DC.	Meliaceae		PPF	
Trichilia sp.	Meliaceae			FWP
Virola cf. *sebifera* Aubl.	Myristicaceae			FWP
Vitex schomburgkiana Schauer	Verbenaceae	PRF		
Xanthoxylum rigidum H. & B.	Rutaceae	PRF		
Xylopia frutescens Aubl.	Annonaceae			FWP
Zollernia grandifolia Schery	Fabaceae	PRF		
Zygia sp. 1	Mimosaceae	PRF		
Zygia sp. 2	Mimosaceae	PRF		
DS 177				FWP
DS 180				FWP
DS 210				FWP
DS 453	Rubiaceae			FWP
DS 535				FWP
DS 628				FWP
MTN 17		PRF		
MTN 224		PRF		
MTN 225		PRF		
MTN 342		PRF		
MTN 389,433		PRF		
MTN 414		PRF		
MTN 3141				FWP
MTN 3499			PPF	
MTN 3834	Rubiaceae	PRF		
MTN 3923		PRF	PPF	FWP
MTN 3733		PRF	PPF	
MTN 3973		PRF		
R 5645				FWP