

## STUDIES IN MONODOMINANT FORESTS IN EASTERN MATO GROSSO, BRAZIL: II. A FOREST IN THE AREÕES XAVANTE INDIAN RESERVE

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The floristic composition, structure, soil fertility and leaf nutrient concentrations were analysed in a monodominant forest of *Brosimum rubescens* Taub. located in the Areões Xavante Indigenous Reserve (14°34'S, 51°58'W). The area lies in the ecotone between Amazonian forest and cerrado in the municipality of Água Boa, Mato Grosso State, Brazil. Sixty nested plots (10 × 10m each) were located in a representative portion of the forest, giving a total sampling area of 0.6ha (40 × 150m). A total of 609 trees ≥ 5cm dbh belonging to 57 species, 46 genera and 32 families were present. The most important family was *Moraceae*, with *B. rubescens* as the dominant species with a relative dominance of 59%. The diameter distribution of *B. rubescens* was unbalanced, indicating an episodic recruitment that could lead to future changes in the forest structure. The high basal area per hectare of *B. rubescens* indicates the possibility of sustainable logging for commercial exploitation. Analysis of composite soil samples collected from the surface layer (0–10cm) of each of the 60 plots did not indicate any significant gradients in fertility within the area sampled. Mean soil pH was 4.6 and the availability of essential nutrients was very low (0.22cmol(+) kg<sup>-1</sup> K, 0.048cmol(+) kg<sup>-1</sup> Ca, 0.167cmol(+) kg<sup>-1</sup> Mg, and 1.5mg kg<sup>-1</sup> P). The higher availability of Mg in the soils in comparison with Ca was a feature observed in other monodominant forests in the Amazon region, as well as in other parts of the world. Analysis of foliar samples showed that the dominant species, *B. rubescens*, maintained higher foliar concentrations of K, Ca and Mg than other species in the forest. This probably indicates a competitive advantage for this species. Also, the higher concentrations of Mg in the soil did not affect its uptake of Ca or K.

*Keywords.* Amazonian forest, *Brosimum rubescens*, cerrado, phytosociology, plant nutrition, soil fertility.

### INTRODUCTION

Ecologists have been seeking information on the mechanisms maintaining high species diversity in tropical forests for a considerable time (Richards, 1996). A number of explanations have been suggested for the coexistence of many species, e.g. 'the regeneration niche' (Grubb, 1977), 'assembly rules' (Wilson *et al.*, 1996), and the role of gaps in creating different levels of light intensity in the understorey (Brokaw, 1982; Clark & Clark, 1987; Hartshorn, 1989).

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Most tropical forests contain many woody species, with the most abundant accounting for less than 10% of all individuals (Felfili, 1994, 1997; Richards, 1996). However, there exist so-called monodominant forests where a single species represents 50–100% of total individuals (Connell & Lowman, 1989; Hart *et al.*, 1989; Hart, 1990). Such forests have been reported from several tropical countries including Brazil (Davis & Richards, 1934; Eggeling, 1947; Martijena & Bullock, 1994; Read *et al.*, 1995; Marimon & Felfili, 1997; Nascimento *et al.*, 1997; Felfili *et al.*, 1998). There is, however, no clear understanding as yet of the processes responsible for the dominance of a single species in such forests.

The main objective of the present study was the characterization of the structure, floristic composition, soil properties and foliar nutrient status of a monodominant forest dominated by *Brosimum rubescens* Taub. (*Moraceae*) in an area of transition between the Amazonian forests and the cerrado (savanna) vegetation in the valley of the Araguaia river in Mato Grosso State, Brazil.

#### STUDY SITE

The study area (14°34'S, 51°58'W) was located in the Xavante Indigenous Reserve at Areões, in the municipality of Água Boa, Mato Grosso, Brazil (Fig. 1). It is in the transition zone between the two largest vegetation formations of Brazil, the Amazonian forest and the cerrado (savanna woodlands). Experimental plots were located in an undisturbed patch of forest where the local indigenous population usually collects fruits and other plant material and hunts wild animals. The climate of the region is *Aw* according to the Köppen classification, with eight months of rain, annual precipitation from 1300 to 1400mm, and a mean monthly temperature of 23.5°C (Camargo, 1963; Fig. 2 shows data from the nearest station with long-term records).

#### METHODS

The fieldwork was conducted from July 1996 to July 1997. The sampling of vegetation was systematic (Philip, 1994). Sixty nested 10 × 10m plots were located in a representative portion of the forest, giving a total sampling area of 0.6ha (40 × 150m). Diameter at breast height (dbh), height, and identification to species or morphospecies level were recorded for all trees ≥ 5cm dbh. Herbarium specimens were deposited at UB (Universidade de Brasília, Brasília) and the James Alexander Ratter Collection at the Nova Xavantina campus of the University of Mato Grosso State.

Phytosociological parameters (Curtis & McIntosh, 1950, 1951) and diameter distribution were calculated. Shannon's ( $H' = -\sum(p_i \ln p_i)$ ) and Simpson's ( $\lambda = \sum[n_i(n_i - 1)]/[n(n - 1)]$ ) indices were used to evaluate species diversity. Pielou's evenness index ( $J' = H'/\ln S$ ) was also calculated (Magurran, 1988).

Height and diameter distribution were evaluated. The class intervals for the forest and its main species (those with at least 20 individuals recorded) were calculated



according to Spiegel's (1976) formulae, which minimize the number of classes that would have no members:  $nc = 1 + 3.3 \log(n)$ , where  $nc$  = number of classes,  $n$  = number of trees;  $IC = A/nc$ , where amplitude  $A$  = maximum value (of either diameter or height) – minimum value; lower limit of class distribution  $I$  = minimum value –  $IC/2$ . The 'q' quotient was calculated to determine whether the diameter distribution was balanced (Meyer, 1952). This model, based on geometric progression, assumes that in mixed natural forests where equilibrium between mortality and recruitment exists, the ratio between the number of trees in successive diameter classes should be constant. The ratio is obtained by dividing the number of individuals in one class by the number in the previous.

Four surface soil samples (0–10cm depth) were collected at random from each  $10 \times 10$  m plot, and mixed together to form a composite sample for chemical analysis. The samples were air-dried and sieved through a 2mm mesh. Soil pH was measured in a 1:2.5 soil–water suspension and in 1M KCl. Exchangeable Ca, Mg and Al were determined in 1M KCl and available P, K, Fe, Mn, Cu and Zn in Mehlich's solution (0.0125M  $H_2SO_4$  + 0.05M HCl).

To determine the nutritional status of the dominant species and to compare it with others of the community, composite leaf samples were collected from each of four to six individuals of *Brosimum rubescens*, *Amaioua intermedia* var. *brasiliiana*, *Protium pilosissimum*, *Inga thibaudiana*, *Vitex panshiniana* and *Licania blackii*. Each sample consisted of a minimum of 10 fully expanded mature leaves, without signs of herbivory or damage by insects and diseases, taken from trees with a minimum dbh of 10cm. Leaf samples were digested using a tri-acid mixture of sulphuric, nitric and perchloric acids and nutrient concentrations determined in the extract. Phosphorus was determined by colorimetry and other elements by atomic absorption or emission spectroscopy (Allen, 1974).

## RESULTS

A total of 609 individuals belonging to 57 species, 46 genera and 32 families were found in the study site, plus one morphospecies (Table 1). Dead trees accounted for 3.45% of the total number of individuals.

The families with the greatest number of species were *Chrysobalanaceae* with six and *Euphorbiaceae* with four. The eight most important families accounted for 72% of the total importance value index (IVI) and 73% of the total density (number of individuals) of the whole community (Fig. 3). There were two species belonging to *Moraceae*: the dominant species, *Brosimum rubescens*, and *Sorocea guilleminiana* with only one individual in the whole sampling area. The most important genera were *Licania* with four species, *Inga* with three, and *Protium*, *Hirtella*, *Coccoloba* and *Erythroxylum* with two each. For individuals with  $dbh \geq 5$ cm, Shannon's diversity index ( $H'$ ) was 3.12 nats/ind. and Simpson's ( $1/D_s$ ) index 11.94. Pielou's evenness ( $J'$ ) was 0.77. For individuals with  $dbh \geq 10$ cm,  $H' = 2.62$ ,  $1/D_s = 5.65$  and  $J' = 0.7$ .

The most abundant species was *B. rubescens*, comprising 23% of all individuals

with dbh  $\geq 5$ cm and 40.3% of those with dbh  $\geq 10$ cm. It accounted for 66.2% of all individuals with dbh  $\geq 20$ cm and 83.1% with dbh  $\geq 30$ cm. The second most abundant species was *Protium pilosissimum*, with only one third of the density (i.e. number of individuals)  $\geq 5$ cm dbh of *B. rubescens*. The basal area per hectare amounted to 24.73m<sup>2</sup>, of which 58.9% belonged to *B. rubescens*. The relative dominance (% basal area) of *B. rubescens* increased in higher dbh categories: 63.6% for dbh  $\geq 10$ cm, 72.0% for dbh  $\geq 20$ cm, 81.37% for dbh  $\geq 30$ cm.

The highest importance values (out of a total figure of 300) were recorded for *B. rubescens* (93.8), *Protium pilosissimum* (21.2), *Inga* sp. (18.3), *Ephedranthus parviflorus* (13.1) and *Amaioua intermedia* var. *brasiliensis* (11.6), which together represented 53% of the total IVI. Dead trees accounted for 2.98%. *Brosimum rubescens* alone accounted for 31.3% of the total IVI, and was the most frequent species (present in 82% of the plots). Besides *B. rubescens*, only *P. pilosissimum* and *Inga* sp. showed frequencies greater than 50%. All other species were present in less than 25% of the plots; 17 were present only in one plot. The seven species of lianas sampled (*Dicranostyles ampla*, *Coccoloba glaziovii*, *Odontadenia puncticulosa*, *Anthodon decussatum*, liana (indet.), a Malpighiaceae liana and *Callichlamys* sp.) represented 7.06% of the total number of individuals and 1.21% of the basal area.

The majority of the individuals of the dominant species, *B. rubescens*, was concentrated in the three higher height classes between 16.4 and 25.3m (Fig. 4). Three storeys could be distinguished in the forest. The understory, composed of individuals with heights between 1.3 and 10m, included species such as *Siparuna guianensis*, *Alibertia verrucosa*, *Erythroxylum daphnites* and *Tapura amazonica*. The intermediate storey, composed of individuals with heights between 10 and 20m, included *Protium pilosissimum*, *Amaioua intermedia* var. *brasiliensis*, *Micropholis venulosa* and *Coccoloba* sp. The upper storey, formed by all individuals taller than 20m, included *B. rubescens*, *Hymenaea courbaril* var. *stilbocarpa*, *Dicranostyles ampla* and a Malpighiaceae liana.

The diameter distribution of individuals with dbh  $\geq 5$ cm showed a reversed-J shape, with 51.9% of all individuals in the 5–10cm dbh class (Fig. 5). The distribution of dead trees also followed the same tendency. The values of 'q' quotient for the individuals were variable from the third class, indicating an imbalance between successive classes (Fig. 5).

The diameter distribution of seven species with at least 20 individuals in the experimental plots is shown in Fig. 6. Among these, *Protium pilosissimum* and *Inga* sp., restricted to the understory, showed a straightforward decline with decreasing diameter class distribution. *Amaioua intermedia* and *Ephedranthus parviflorus* also showed similar diameter class distributions but with a more gradual decrease after the first class. The other species showed irregular distributions. *Licania blackii* and *Nectandra cuspidata* had fewer individuals in the first class than the second. *Brosimum rubescens* showed an almost trimodal distribution, probably implying an episodic nature of regeneration. Observations of the regeneration on the forest floor indicated an absolute dominance of *B. rubescens* seedlings.

TABLE 1. Phytosociological parameters for the monodominant *B. rubescens* forest in the Indigenous Reserve at Areões

Species	Family	Density		Dominance		Frequency		
		AD	RD	ADo	RDo	AF	RF	IVI
1. <i>Brosimum rubescens</i> Taub.	<i>Moraceae</i>	233.3	22.99	14.557	58.85	81.67	11.95	93.79
2. <i>Protium pilosissimum</i> Engl.	<i>Burseraceae</i>	101.7	10.02	0.483	1.95	63.33	9.27	21.24
3. <i>Inga</i> sp.	<i>Mimosaceae</i>	90.0	8.87	0.405	1.64	53.33	7.80	18.31
4. <i>Ephedranthus parviflorus</i> S. Moore	<i>Annonaceae</i>	55.0	5.42	0.519	2.10	38.33	5.61	13.13
5. <i>Amaioua intermedia</i> Mart. var. <i>brasiliana</i> (A. Rich.) Steyerem.	<i>Rubiaceae</i>	51.7	5.09	0.393	1.59	33.33	4.88	11.56
6. <i>Chaetocarpus echinocarpus</i> (Baill.) Ducke	<i>Euphorbiaceae</i>	31.7	3.12	0.828	3.35	26.67	3.90	10.37
7. <i>Licania blackii</i> Prance	<i>Chrysobalanaceae</i>	36.7	3.61	0.696	2.81	26.67	3.90	10.33
8. <i>Nectandra cuspidata</i> Nees	<i>Lauraceae</i>	40.0	3.94	0.494	2.00	26.67	3.90	9.84
9. Dead trees		35.0	3.45	0.333	1.35	28.33	4.15	8.94
10. <i>Vitex panshiniana</i> Mold.	<i>Verbenaceae</i>	16.7	1.64	0.819	3.31	13.33	1.95	6.91
11. <i>Inga heterophylla</i> Willd.	<i>Mimosaceae</i>	20.0	1.97	0.301	1.22	18.33	2.68	5.87
12. <i>Dicranostyles ampla</i> Ducke	<i>Convolvulaceae</i>	23.3	2.30	0.098	0.40	18.33	2.68	5.38
13. <i>Mouriri apiranga</i> Spruce ex Triana	<i>Melastomataceae</i>	20.0	1.97	0.110	0.44	16.67	2.44	4.85
14. <i>Micropholis venulosa</i> (Mart. & Eichl.) Pierre	<i>Sapotaceae</i>	10.0	0.99	0.457	1.85	10.00	1.46	4.30
15. <i>Siparuna guianensis</i> Aubl.	<i>Monimiaceae</i>	16.7	1.64	0.048	0.19	16.67	2.44	4.28
16. <i>Hymenaea courbaril</i> L. var. <i>stilbocarpa</i> (Hayne) Lee & Lang.	<i>Caesalpiniaceae</i>	5.0	0.49	0.724	3.00	5.00	0.73	4.23
17. <i>Coccoloba glaziovii</i> Lindan	<i>Polygonaceae</i>	16.7	1.64	0.076	0.31	15.00	2.20	4.14
18. <i>Minquartia guianensis</i> Aubl.	<i>Olacaceae</i>	11.7	1.15	0.291	1.18	11.67	1.71	4.04
19. <i>Inga thibaudiana</i> DC.	<i>Mimosaceae</i>	16.7	1.64	0.099	0.40	13.33	1.95	3.99
20. <i>Odontadenia puncticulosa</i> (A. Rich.) Pulle	<i>Apocynaceae</i>	15.0	1.48	0.048	0.19	11.67	1.71	3.38
21. <i>Mabea fistulifera</i> Mart.	<i>Euphorbiaceae</i>	13.3	1.31	0.209	0.85	8.33	1.22	3.38
22. <i>Sclerobium paniculatum</i> Vog.	<i>Caesalpiniaceae</i>	8.3	0.82	0.325	1.31	8.33	1.22	3.35
23. <i>Pouteria cuspidata</i> (A. DC.) Baehni	<i>Sapotaceae</i>	6.7	0.66	0.422	1.71	6.67	0.98	3.34
24. <i>Xylopia sericea</i> A. St. Hil.	<i>Annonaceae</i>	10.0	0.99	0.116	0.47	10.00	1.46	2.92
25. <i>Hirtella glandulosa</i> Spreng.	<i>Chrysobalanaceae</i>	10.0	0.99	0.065	0.26	10.00	1.46	2.71
26. <i>Miconia holosericea</i> (L.) DC	<i>Melastomataceae</i>	10.0	0.99	0.057	0.23	10.00	1.46	2.68
27. <i>Casearia arborea</i> (L.C. Richard) Urban	<i>Flacourtiaceae</i>	10.0	0.99	0.037	0.15	10.00	1.46	2.60
28. <i>Alibertia verrucosa</i> S. Moore	<i>Rubiaceae</i>	11.7	1.15	0.046	0.19	8.33	1.22	2.56
29. <i>Simarouba amara</i> Aubl.	<i>Simaroubaceae</i>	5.0	0.49	0.313	1.26	5.00	0.73	2.49
30. <i>Diospyros sericea</i> A. DC.	<i>Ebenaceae</i>	5.0	0.49	0.180	0.73	5.00	0.73	1.95

TABLE 1. (Cont'd)

Species	Family	Density		Dominance		Frequency		IVI
		AD	RD	ADo	RDo	AF	RF	
31. <i>Sloanea sinemariensis</i> Aubl.	<i>Elaeocarpaceae</i>	8.3	0.82	0.095	0.38	5.00	0.73	1.94
32. <i>Anthodon decussatum</i> Ruiz & Pav.	<i>Hippocrateaceae</i>	6.7	0.66	0.037	0.15	6.67	0.98	1.78
33. <i>Buchenavia capitata</i> (Vahl.) Eich.	<i>Combretaceae</i>	5.0	0.49	0.136	0.55	5.00	0.73	1.77
34. <i>Schefflera morototoni</i> (Aubl.) B. Mag., Steyerm. & D.G. Frodin	<i>Araliaceae</i>	3.3	0.33	0.210	0.85	3.33	0.49	1.67
35. <i>Protium heptaphyllum</i> (Aubl.) E.K. Marchal	<i>Burseraceae</i>	5.0	0.49	0.021	0.09	5.00	0.73	1.31
36. <i>Pera coccinea</i> (Benth.) Muell. Arg.	<i>Euphorbiaceae</i>	3.3	0.33	0.091	0.37	3.33	0.49	1.18
37. <i>Himatanthus bracteatus</i> (A. DC.) R.E. Woodson	<i>Apocynaceae</i>	3.3	0.33	0.112	0.45	1.67	0.14	1.02
38. <i>Maprounea guianensis</i> Aubl.	<i>Euphorbiaceae</i>	3.3	0.33	0.045	0.18	3.33	0.49	1.00
39. <i>Coccoloba</i> sp.	<i>Polygonaceae</i>	3.3	0.33	0.033	0.13	3.33	0.49	0.95
40. Liana (indet.)	Indeterminate	3.3	0.33	0.016	0.07	3.33	0.49	0.88
41. <i>Callichlamys</i> sp.	<i>Bignoniaceae</i>	3.3	0.33	0.013	0.05	3.33	0.49	0.87
42. Liana – <i>Malpighiaceae</i>	<i>Malpighiaceae</i>	3.3	0.33	0.012	0.05	3.33	0.49	0.87
43. <i>Jacaranda copaia</i> (Aubl.) D. Don	<i>Bignoniaceae</i>	1.7	0.16	0.087	0.35	1.67	0.24	0.76
44. <i>Aspidosperma quirandy</i> Hassler	<i>Apocynaceae</i>	1.7	0.16	0.058	0.24	1.67	0.24	0.64
45. <i>Agonandra brasiliensis</i> Miers ex Bentham	<i>Opiliaceae</i>	1.7	0.16	0.033	0.14	1.67	0.24	0.54
46. <i>Platypodium elegans</i> Vog.	<i>Fabaceae</i>	1.7	0.16	0.032	0.13	1.67	0.24	0.54
47. <i>Hirtella gracilipes</i> (Hook. f.) Prance	<i>Chrysobalanaceae</i>	1.7	0.16	0.029	0.12	1.67	0.24	0.53
48. <i>Licania gardneri</i> (Hook. f.) Fritsch.	<i>Chrysobalanaceae</i>	1.7	0.16	0.023	0.09	1.67	0.24	0.50
49. <i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	<i>Bombacaceae</i>	1.7	0.16	0.014	0.06	1.67	0.24	0.47
50. <i>Cecropia</i> sp.	<i>Cecropiaceae</i>	1.7	0.16	0.013	0.06	1.67	0.24	0.46
51. <i>Sorocea guilleminiana</i> Gaud.	<i>Moraceae</i>	1.7	0.16	0.011	0.05	1.67	0.24	0.45
52. <i>Licania</i> sp.	<i>Chrysobalanaceae</i>	1.7	0.16	0.008	0.03	1.67	0.24	0.44
53. <i>Erythroxylum citrifolium</i> A. St. Hil.	<i>Erythroxylaceae</i>	1.7	0.16	0.007	0.03	1.67	0.24	0.44
54. <i>Licania apetala</i> (E. Mey.) Fritsch.	<i>Chrysobalanaceae</i>	1.7	0.16	0.007	0.03	1.67	0.24	0.44
55. <i>Erythroxylum daphnites</i> Mart.	<i>Erythroxylaceae</i>	1.7	0.16	0.005	0.02	1.67	0.24	0.43
56. <i>Dipteryx alata</i> Vog.	<i>Fabaceae</i>	1.7	0.16	0.005	0.02	1.67	0.24	0.43
57. <i>Tapura amazonica</i> Poepp. & Endl.	<i>Dichapetalaceae</i>	1.7	0.16	0.004	0.02	1.67	0.24	0.43
58. <i>Tabebuia roseo-alba</i> (Ridley) Sandw.	<i>Bignoniaceae</i>	1.7	0.16	0.004	0.02	1.67	0.24	0.42
Total		1015	100	24.731	100	683.30	100	300

AD, absolute density, number of trees ha<sup>-1</sup>; RD, relative density; ADo, absolute dominance, basal area, m<sup>2</sup> ha<sup>-1</sup>; RDo, relative dominance; AF, absolute frequency, %; RF, relative frequency; IVI, importance value index. Confidence interval ( $P=0.95$ ): density=(933–1097) and dominance=(20.74–28.71).



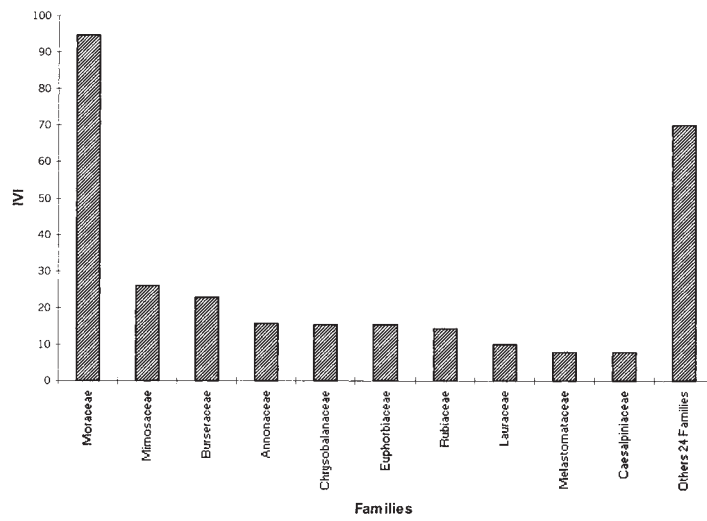


FIG. 3. Importance value indices (IVI) of the most important families.

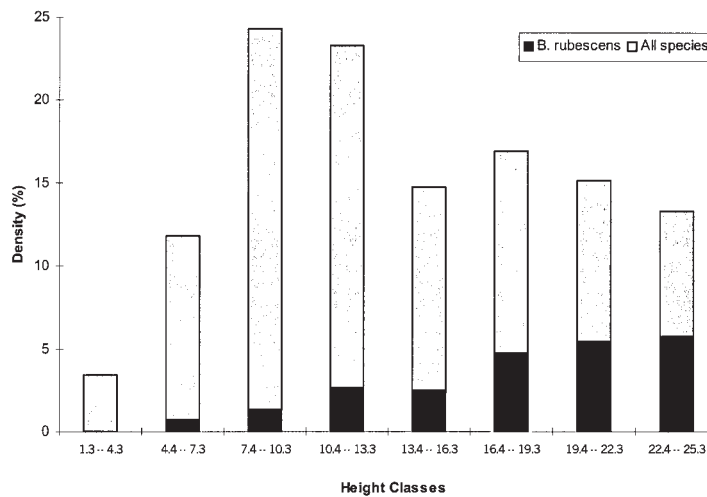


FIG. 4. Comparison of the height distribution of the dominant species *B. rubescens* and of all species.

The soil of the forest was a gravelly dark red latosol with low soil pH, high levels of exchangeable Al, and low levels of available Ca. One of the distinguishing features was the higher availability of Mg than Ca in the soil, with Mg/Ca ratios above 3 (Table 2). The foliar nutrient concentrations in *B. rubescens* and five other species are given in Table 3. These values are within the range usually reported for native tree species on dystrophic soils in the Amazon and cerrado regions of central Brazil (Haridasan, 1992).



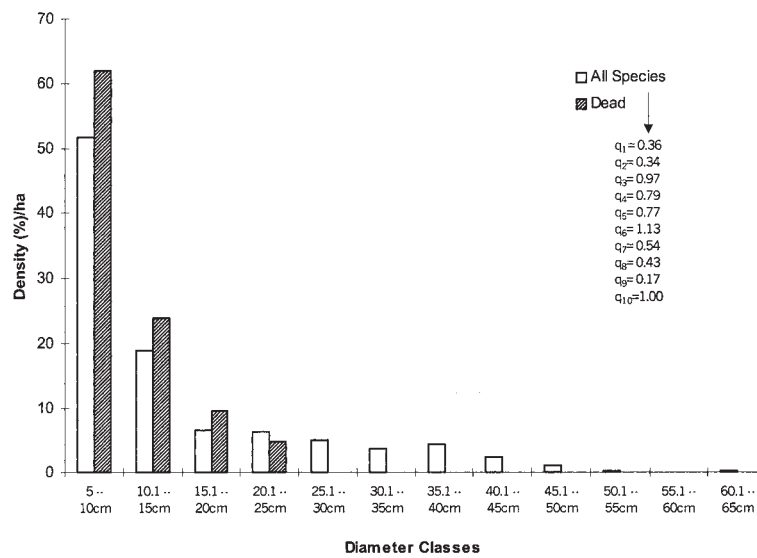


FIG. 5. Diameter distribution and correspondent 'q' quotient ratio of all live ( $n=588$ ) and dead individuals ( $n=21$ ).

#### DISCUSSION

The *Brosimum rubescens* forest shows lower indices of species richness and evenness when compared with other tropical forests in Brazil (Felfili & Silva Júnior, 1992; Felfili, 1994; Nascimento *et al.*, 1997). The diversity indices reported here ( $H'=2.62$  and  $J=0.71$ ,  $DAP \geq 10\text{cm}$ ) are comparable with those of other monodominant forests in Brazil and elsewhere (Davis & Richards, 1934; Eggeling, 1947; Connell & Lowman, 1989; Martijena & Bullock, 1994; Nascimento *et al.*, 1997). According to Connell & Lowman (1989), the greater the dominance of the main species the less diverse is the monodominant forest. This pattern was found when the monodominant *B. rubescens* forests of Fazenda Eldorado (Marimon *et al.*, 2001) and the present forest were compared. There was 46% of common species between these two monodominant forests. The present forest was richer and more diverse in species than that of Fazenda Eldorado, and it would be interesting to investigate if these forests are stable or if they are in a successional stage.

*Brosimum rubescens* accounted for 58.9% of the relative dominance for  $dbh \geq 5\text{cm}$  and 63.6% for  $dbh \geq 10\text{cm}$ . These values are somewhat lower than those reported by Marimon & Felfili (1997) for the monodominant forest of *B. rubescens* at Fazenda Eldorado in Nova Xavantina, Mato Grosso, Brazil (71% for  $dbh \geq 5\text{cm}$ ). The greater dominance of *B. rubescens* in the higher  $dbh$  classes (i.e. as a large tree) is a feature noted for other dominant species in monodominant forests elsewhere (Martijena & Bullock, 1994; Isaacs *et al.*, 1996). A similar pattern of stratification has been reported in other monodominant (Eggeling, 1947; Nascimento *et al.*, 1997; Marimon *et al.*, 2001) and mixed forests (Ratter *et al.*, 1973; Felfili, 1997).

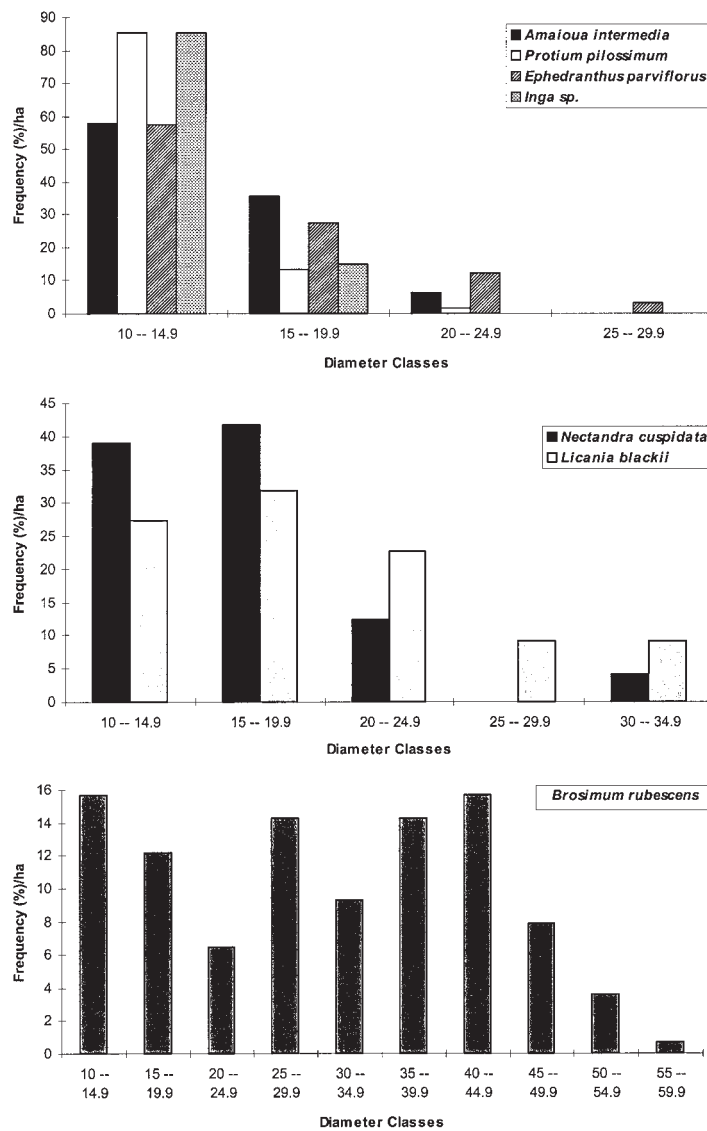


FIG. 6. Diameter distributions of the species with at least 20 individuals sampled.

The relative density of the dominant species *B. rubescens* reported here (40.3% for dbh  $\geq 10$ cm) was higher than the values for the dominant *Peltogyne gracilipes* reported by Nascimento *et al.* (1997) in a monodominant forest in Amazonia, and for dominant *Mora excelsa* by Davis & Richards (1934) in the Guyanas. *Brosimum rubescens* ranked first in IVI because of the much higher values in all three phytosociological parameters added to calculate this parameter: relative density, relative dominance and relative frequency, followed by *Protium pilosissimum*, *Inga sp.*,

TABLE 2. Soil pH and availability of nutrients (sample size,  $n=60$ ) in a monodominant forest in Areões Xavante Indian Reserve

Soil properties	Mean (SD)
pH in KCl	3.7 (0.12)
pH in H <sub>2</sub> O	4.6 (0.14)
Exchangeable cations (cmol(+) kg <sup>-1</sup> )	
Al	1.3 (0.31)
K	0.218 (0.062)
Ca	0.048 (0.018)
Mg	0.167 (0.057)
Available P (mg kg <sup>-1</sup> )	1.5 (1.5)
Micronutrients (mg kg <sup>-1</sup> )	
Fe	117 (16)
Mn	24.6 (7.2)
Zn	2.4 (2.1)
Cu	1.1 (0.4)

SD, standard deviation.

TABLE 3. Concentration of leaf nutrients (mg kg<sup>-1</sup>,  $n=4$ ) in species found in a monodominant forest in Areões Xavante Indian Reserve

Species	P	K	Ca	Mg	Fe	Mn	Zn	Cu	Al
<i>Brosimum rubescens</i>	0.076	0.429	0.416	0.236	54	321	13.6	6.6	141
<i>Inga thibaudiana</i>	0.105	0.261	0.315	0.150	77	70	17	11.5	142
<i>Vitex panshiniana</i>	0.087	0.429	0.191	0.208	91	105	13	9.5	230
<i>Licania blackii</i>	0.055	0.306	0.213	0.190	55	293	9	8.6	119
<i>Amaioua intermedia</i> var. <i>brasiliانا</i>	0.050	0.228	0.344	0.209	64	44	9.6	7.3	156
<i>Protium pilosissimum</i>	0.077	0.236	0.218	0.164	119	30	13.8	7.4	186
Mean of spp. other than <i>B. rubescens</i>	0.075	0.292	0.256	0.184	81	108	12	9	167

*Ephedranthus parviflorus* and *Amaioua intermedia* var. *brasiliانا*. The dead trees, as a group, were ninth in ranking. Others have reported similar rankings for dead trees in native forests (Felfili & Silva Júnior, 1992). With a basal area above 24m<sup>2</sup> ha<sup>-1</sup>, the forest could be classified as dense according to criteria suggested by Pires & Prance (1985) for the Amazon forests, with the possibility of sustainable logging, particularly for *B. rubescens*.

The 'q' quotient (Meyer, 1952; Leak, 1964; Osmaston, 1968) was around 0.35 between the first and second class, and the second and third class, which contained together 77% of the individuals, and then became variable. Leak (1964) suggested that it is common to find an imbalance in the higher diameter classes that contain few individuals.

Figure 6 shows the distribution of diameter classes for seven species. *Brosimum rubescens* has an almost trimodal distribution, suggesting more than one pulse of

regeneration in its history with an episodic recruitment as described by other authors for some species (Clark & Clark, 1987; Bongers *et al.*, 1988). This pattern is probably related to temporal variations in light level at the forest floor. Several authors have already noted that gap size (Brokaw, 1982) influences recruitment, and sometimes increases the dominance of some species (Wilson, 1988). The diameter distribution of the monodominant forest of Fazenda Eldorado (Marimon *et al.*, 2001) suggested one pulse of regeneration while the curve in this forest suggested more than one pulse.

Seedlings of *B. rubescens* occur in massive numbers under the adult trees, that are close to each other in this forest. Therefore, the Janzen-Connell model (Schupp, 1992), which indicates that recruitment is inhibited near to the mother tree, does not apply here. Burkey (1994) found a similar pattern for *Brosimum alicastrum* in Mexico. Therefore this forest can be considered as Type I according to Connell & Lowman's (1989) classification for monodominant forests. To fit this classification the dominant species should remain in the forest for more than one generation and its seedlings should persist in the understorey under shade.

*Protium pilosissimum* reached only a small size, and seems to complete its life cycle in the forest understorey. *Inga* sp., a heliophilous species, presented a decreasing distribution with a strong decline from the first to the second class. *Licania blackii* and *Nectandra cuspidata* lack individuals in the smaller classes, probably because of unfavourable conditions for their recruitment in the recent past as suggested by some authors (Felfili, 1997) for species that presented this sort of pattern. Felfili (1997) suggested that only a small group of species presents a reversed-J shape in tropical forests, whilst most species show an intermediate pattern. Such imbalances over time cause fluctuations in forest structure.

The high soil acidity, high exchangeable Al and higher availability of Mg as compared with Ca encountered in this study seem to be a common feature of other monodominant tropical forests in Brazil and elsewhere (Read *et al.*, 1995; Nascimento *et al.*, 1997; Villela, 1997). The last of these factors may be significant because most soils of Amazonian forests and of the cerrado region show lower concentrations of available Mg than Ca (Haridasan, 1992; Thompson *et al.*, 1992). However, there is no conclusive evidence yet that monodominance in tropical forests is related to soil factors.

The levels of nutrients in the leaves reported in this study reflect generally the poor fertility of the native soil. However, *B. rubescens*, the dominant species, with its higher concentrations of major nutrients K, Ca and Mg as compared with other species of the community, seems to have a competitive edge in its capacity for cation uptake. The levels of K, Ca and Mg in the dominant species are generally higher than in other species. Another important factor appears to be its ability to maintain high uptake of K and Ca despite possible antagonistic effects of high Mg levels in the soil. The ratio of concentrations of Ca/Mg in the leaves varied from 0.55 to 1.57 among the species, with *B. rubescens* showing values of 1.34 despite the higher availability of Mg as compared with Ca in the soil. Whether the relative proportions of these cations in the leaves are in the optimum range for each species can be

determined only by more comparisons under natural conditions or by fertilizer trials, adding these nutrients to the soil in different proportions. Such comparisons would also help to determine whether *B. rubescens* has any competitive advantage under the edaphic conditions reported in this study. The high levels of Mn in the leaves of *B. rubescens* and *Licania blackii* would qualify them as Mn accumulator species (Gauch, 1972).

#### CONCLUSIONS

The *Brosimum rubescens* forest in the Areões Indigenous Reserve fits into the category of Type I monodominance postulated by Connell & Lowman (1989) and shows one of the lowest records of diversity for tropical forests. The high acidity and poor soil fertility of the forest are comparable with those of most Amazonian forests and with cerrado vegetation on dystrophic soils. However, the higher availability of Mg than of Ca in the soil is a feature that it shares with other monodominant tropical forests. The higher foliar concentrations of cations in *B. rubescens* than in other species could indicate a competitive advantage responsible for monodominance under high availability of Mg in the soil.

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