

STUDIES IN MONODOMINANT FORESTS IN EASTERN MATO GROSSO, BRAZIL: I. A FOREST OF *BROSIMUM RUBESCENS* TAUB

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The occurrence of a monodominant tropical forest dominated by the tree species *Brosimum rubescens* Taub. (*Moraceae*) in the transition zone between the cerrado region and the Amazonian rain forests along the Araguaia valley in the state of Mato Grosso in Brazil is reported. A 6000m² (40 × 150m) area located in the central portion of a forest (14°50'47"S, 52°08'37"W) on the Eldorado Farm in Nova Xavantina was sampled to determine the structure, phytosociology and soil properties. A total of 44 tree species was found in the forest, with a Shannon diversity index (*H'*) of 2.37 and the Pielou evenness index (*J'*) of 0.63. These values were similar to those reported by other workers in an Amazonian monodominant forest dominated by *Peltogyne gracilipes*. Average tree density equal or greater than (\geq) 5cm dbh was 1066ha⁻¹ and basal area 37.46m² ha⁻¹. Dead standing individuals represented 7.03% of the total density and lianas 8.12%. The main families were *Moraceae*, *Rubiaceae*, *Burseraceae*, *Hippocrateaceae* and *Leguminosae*–*Caesalpinioideae*. The species with the highest importance value indices were *B. rubescens* (124.55), *Amaioua intermedia* var. *brasiliiana* (32.97), *Cheilochlinium cognatum* (22.41), *Tetragastris balsamifera* (19.58) and *Protium pilosissimum* (16.64). *Brosimum rubescens* alone accounted for 85.5% of the individuals \geq 30cm dbh, 80.35% of those \geq 20cm dbh, 57.33% of those \geq 10cm dbh, and 35.85% of those \geq 5cm dbh. The forest was composed of upper, middle and lower storeys. Diameter distribution was unbalanced for the community and for the main species, suggesting that establishment has been episodic. The surface soil was acid, with high exchangeable Al levels and low fertility, as is the case for most cerrados and Amazonian forests. The availability of K was in the range of adequacy, as compared with most native soils. However, concentrations of available Mg in the soil was higher than that of available Ca, with Mg/Ca ratios above three, unlike most cerrados and Amazonian forests, but similar to the soils of many monodominant tropical forests reported in the literature. Soils were characterized by high concentrations of available Fe. Besides the high Mg/Ca ratios, a high proportion of K as compared with the bivalent cations Ca and Mg, and toxicities of Fe and Mn due to strong acidity could be factors influencing the occurrence of species in this forest.

Keywords. Brazil, *Brosimum rubescens*, floristics, monodominant tropical forest, soils, structure.

INTRODUCTION

The high species diversity of tropical forests is well known (Richards, 1952; Gentry, 1982; Connell *et al.*, 1984) and the successional processes in these forests have been linked with gap dynamics (Denslow, 1980; Clark & Clark, 1992). Occurrence of

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many species with low relative densities is the main characteristic of such forests. The most abundant species constitute no more than 10% of the total number of individuals in various forest communities studied (Oliveira-Filho *et al.*, 1994; Felfili, 1995; Silva Júnior, 1995). However, there exist exceptions, where a single species shows 50–100% of dominance. Such monodominant forests have been reported from different continents (Davis & Richards, 1934; Beard, 1946; Connell & Lowman, 1989; Hart *et al.*, 1989; Milliken & Ratter, 1989, 1998; Hart, 1990; Johnston, 1992; Martijena & Bullock, 1994; Nascimento, 1994; Read *et al.*, 1995; Isaacs *et al.*, 1996; Nascimento *et al.*, 1997). An important question on the dynamics of these monodominant communities is whether they represent a successional stage or a climax.

The Araguaia Valley in eastern Mato Grosso state is an ecotonal region between the Amazonian forests and the cerrado (savanna) region of central Brazil, where a mosaic of phytophysionomies exist (Ratter *et al.*, 1973). The occurrence of a patch of a monodominant forest of *Brosimum rubescens* Taub. (*Moraceae*) on a lateritic soil in this region was reported by Felfili *et al.* (1988, 1998). The forest had a structure resembling a plantation, containing mostly even-sized, tall trees with straight boles.

Brosimum rubescens has been intensively logged in the region. Local people use the hardwood for buildings, furniture and fences. Its natural durability can reach 30 years. These forests are also important for the local Xavante Indians. The hardwood is used to make their traditional weapon, a heavy club called a *borduna*, and for crosses to mark graves. The fruits are eaten by the Indians and are important to them because they attract wildlife. The fruiting season of *B. rubescens* is considered to be the best time for hunting tapir and other game by the Xavantes.

The floristic composition and structure of this forest are described in this study. The availability of soil nutrients was investigated to determine whether soil fertility played a role in the dominance of a single species in this forest.

STUDY SITE

The study site (14°50'47"S, 52°08'37"W) was located within a 5000ha area of dry forest on the Eldorado Farm in the municipality of Nova Xavantina in eastern Mato Grosso, Brazil. Average altitude was 350m above sea level. The site was undisturbed although logging activities were starting nearby. The climate of the region is *Aw* in the Köppen classification (Camargo, 1963), with six to eight wet months per year; climatic data are given in Fig. 1.

The soil at the experimental site was a dystrophic tropofluent overlying consolidated and unconsolidated sediments belonging to the sedimentary cover of Bananal (RADAMBRASIL, 1981). The soil was deep, well drained and loamy in texture.

METHODS

The field-work was conducted from July 1996 to July 1997. The sampling of vegetation was systematic, following Philip (1994). A 40 × 150m grid containing sixty

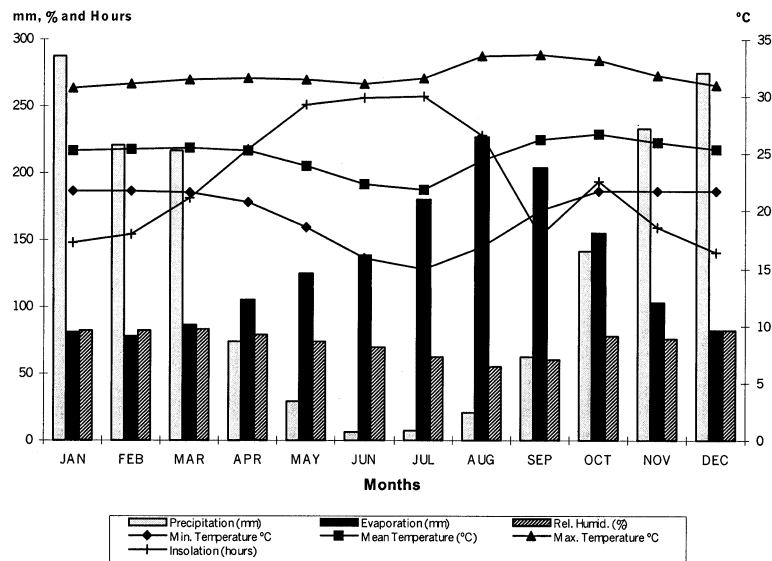


FIG. 1. Mean monthly precipitation, insolation, relative humidity, evaporation and temperatures for the Nova Xavantina region in Mato Grosso, Brazil (average of 30 years for the nearby Aragarças climatological station).

nested 10×10 m plots was located in a representative portion of the forest, giving a total sampling area of 0.6ha. All individuals ≥ 5 cm dbh (diameter at breast height) were identified to the species or morphospecies level and their dbh and height recorded. The dbh measurements were made with a calliper, and the height of trees up to 15m with a telescopic measuring rod; taller trees were measured with a Haga altimeter. Natural regeneration of *Brosimum rubescens* (individuals with dbh less than 5cm) was recorded in subplots located alongside the middle line of the sampled area. The size of these subplots varied according to the height of the individuals sampled: 1×1 m for those 0–30cm; 2×2 m, 31–60cm; 5×5 m, 61–200cm; 10×10 m, above 200cm. Voucher herbarium specimens were deposited at UB and IBGE.

Four surface soil samples (0–10cm) were collected at random from each 10×10 m plot, and mixed together to form a composite sample for chemical analyses. The soil samples were air-dried, sieved through a 2mm mesh sieve and the percentage gravel determined. Soil pH was measured in a 1:2.5 soil–water suspension as well as 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 $H_2SO_4 + 0.05$ M HCl).

Phytosociological parameters were calculated (Curtis & McIntosh, 1950, 1951). 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 distributions were evaluated. The class intervals (IC) for the forest and its main species (those with at least 10 individuals recorded) were

calculated according to Spiegel's (1976) formulae, which minimizes the number of classes that would have no members: $IC = A/nc$ and $nc = 1 + 3.3\log(n)$, where amplitude A = maximum value (of either diameter or height) – minimum value; nc = number of classes; n = number of trees. To determine the lower limit of class distribution (I): I = minimum value (of either diameter or height) – $IC/2$.

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 a class by the number in the preceding class.

RESULTS

Chemical characteristics of the soils and the percentage of gravel are presented in Table 1. The soil was strongly acidic and high in levels of available Al. The levels of available Ca and Mg were low. The level of K was intermediate. Iron concentrations were high.

Shannon's diversity index (H') was 2.37 and Pielou's evenness index (J') was 0.63 for all plants ≥ 5 cm dbh. These indices were 1.62 and 0.48, considering only the plants ≥ 10 cm dbh. Simpson's index (λ) was 0.36. Floristic composition and phytosociological parameters are given in Table 2.

The highest IVIs (Importance Value Index = relative density + relative dominance + relative frequency) were for *Moraceae*, *Rubiaceae*, *Burseraceae*, *Hippocrateaceae*, *Lauraceae* and *Leguminosae-Caesalpinioideae* (Fig. 2). These six families represented 83% of the total density and IVI of the forest and *Moraceae* with a single species, *Brosimum rubescens*, was by far the most important.

Brosimum rubescens was the most abundant species with 35.8% of all individuals, 57.3% of the individuals with dbh ≥ 10 cm, 80.4% of the individuals with dbh ≥ 20 cm, and 85.5% of the individuals with dbh ≥ 30 cm. The second most abundant species was *Amaioua intermedia* var. *brasiliiana* followed by *Cheilochinium cognatum* and *Tetragastris balsamifera*. The total basal area per ha was 37.46m², 71% of which was accounted for by *B. rubescens*.

The highest IVIs were for *B. rubescens* (124.6), *A. intermedia* var. *brasiliiana*

TABLE 1. Proportion of gravel and chemical properties of the soil of the monodominant *Brosimum rubescens* forest. Mean (and standard deviation) of 60 samples

| Gravel (%) | pH in KCl | pH in water | Al (cmol (+) kg ⁻¹) | Ca (cmol (+) kg ⁻¹) | Mg (cmol (+) kg ⁻¹) | K (cmol (+) kg ⁻¹) | P (mg kg ⁻¹) | Fe (mg kg ⁻¹) | Mn (mg kg ⁻¹) | Zn (mg kg ⁻¹) | Cu (mg kg ⁻¹) |
|----------------|----------------|----------------|---------------------------------|---------------------------------|---------------------------------|--------------------------------|--------------------------|---------------------------|---------------------------|---------------------------|---------------------------|
| 38.6 (19.0) | 3.68 (0.13) | 4.26 (0.10) | 2.20 (0.36) | 0.07 (0.07) | 0.21 (0.17) | 0.22 (0.06) | 2.88 (0.90) | 240.7 (25.3) | 16.9 (8.0) | 1.38 (0.33) | 3.46 (0.61) |

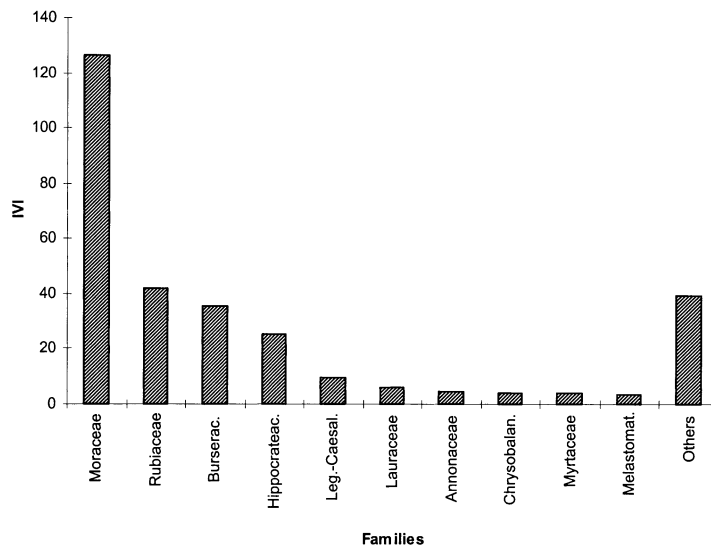


FIG. 2. Importance Value Indices of the most important families identified in the 0.6ha sampling area of the *Brosimum rubescens* forest.

(32.97), *C. cognatum* (22.41), *T. balsamifera* (19.58) and *P. pilosissimum* (16.64). These represented 72% of the total IVI and *B. rubescens* alone represented 41.5%. Dead standing trees represented 6.31% of the total (Table 2). Among the 44 species recorded, 17 had only one individual occurring in the sampling area and eight had only two individuals. *Hymenaea courbaril* had the largest individual in the sampling, measuring 105cm dbh.

The height distribution for *B. rubescens* and for the whole forest (all species) is shown in Fig. 3. Most of individuals of *B. rubescens* were in the higher classes with the maximum number between 22.3 and 25.2m. There is a distinct stratification in the forest. Trees of the upper storey (such as *Brosimum rubescens*, *Hymenaea courbaril* and *Jacaranda copaia*) reach about 28m, those of the middle storey (such as *Amaioua intermedia*, *Tetragastris balsamifera*, *Cheilochlinium cognatum* and *Protium pilosissimum*) 20m, while those of the lower storey (such as *Mouriri apiranga*, *Miconia holosericea*, *M. tomentosa*, *Siparuna guianensis* and *Tetragastris unifoliolata*) reach about 10m.

The diameter distribution of all individuals and the 'q' quotients are given in Fig. 4. Almost half of the individuals (41.41%) were in the first diameter class. The quotient 'q' varied among classes indicating that this is an unbalanced community. *Brosimum rubescens* distribution did not show the reversed-J shape expected for balanced populations, it was unimodal, with skewing to the right (Fig. 5). There were few individuals up to 20cm, a concentration between 20 and 40cm and a strong decrease above 40cm dbh. *Amaioua intermedia* var. *brasiliiana* had fewer individuals in the first class than in the second (q=1.13). Most of *T. balsamifera* individuals were up to 15cm dbh.

TABLE 2. Phytosociological parameters for the *Brosimum rubescens* forest. Absolute density (AD), relative density (RD), absolute dominance (ADo), relative dominance (RDo), absolute frequency (AF), relative frequency (RF) and importance value index (IVI). Species ranked by IVI

| Species | Density/ha | | Dominance/ha | | Frequency/ha | | IVI |
|--|------------|-------|--------------|-------|--------------|-------|--------|
| | AD | RD | ADo | RDo | AF | RF | |
| 1. <i>Brosimum rubescens</i> Taub. | 380.00 | 35.85 | 26.6183 | 71.25 | 98 | 17.46 | 124.55 |
| 2. <i>Amaioua intermedia</i> Mart. var. <i>brasiliiana</i> (A. Rich.) Steyerm. | 151.70 | 14.31 | 1.9972 | 5.35 | 75 | 13.31 | 32.97 |
| 3. <i>Cheilochlinium cognatum</i> (Miers) A. C. Smith | 103.30 | 9.75 | 0.6389 | 1.71 | 62 | 10.95 | 22.41 |
| 4. <i>Tetragastris balsamifera</i> (Swartz) O.K. | 68.30 | 6.45 | 1.7017 | 4.55 | 48 | 8.58 | 19.58 |
| 5. Dead individuals | 60.00 | 5.66 | 2.1953 | 5.88 | 42 | 7.40 | 18.93 |
| 6. <i>Protium pilosissimum</i> Engl. | 81.70 | 7.70 | 0.2416 | 0.65 | 47 | 8.28 | 16.64 |
| 7. Liana – <i>Malpighiaceae</i> | 45.00 | 4.25 | 0.2133 | 0.57 | 37 | 6.51 | 11.33 |
| 8. <i>Hymenaea courbaril</i> L. var. <i>stilbocarpa</i> (Hayne) Lee & Lang. | 5.00 | 0.47 | 1.5447 | 4.13 | 5 | 0.89 | 5.49 |
| 9. <i>Callichlamys</i> sp. | 15.00 | 1.42 | 0.0665 | 0.18 | 15 | 2.66 | 5.26 |
| 10. <i>Myrciaria floribunda</i> (West ex Willd.) Berg | 15.00 | 1.42 | 0.0727 | 0.19 | 13 | 2.37 | 3.98 |
| 11. <i>Anthodon decussatum</i> Ruiz & Pav. | 13.30 | 1.26 | 0.0657 | 0.18 | 13 | 2.37 | 3.80 |
| 12. <i>Nectandra cuspidata</i> Nees | 10.00 | 0.94 | 0.0808 | 0.22 | 10 | 1.78 | 2.93 |
| 13. <i>Ephedranthus parviflorus</i> S. Moore | 8.30 | 0.79 | 0.1328 | 0.36 | 8 | 1.48 | 2.62 |
| 14. <i>Nectandra hihua</i> (Ruiz & Pav.) Rohwer | 13.30 | 1.26 | 0.1544 | 0.41 | 5 | 0.89 | 2.56 |
| 15. Liana – <i>Rubiaceae</i> | 8.30 | 0.79 | 0.0506 | 0.14 | 8 | 1.48 | 2.40 |
| 16. <i>Jacaranda copaia</i> (Aubl.) D. Don | 3.30 | 0.31 | 0.2884 | 0.77 | 3 | 0.59 | 1.68 |
| 17. <i>Mouriri apiranga</i> Spruce ex Triana | 5.00 | 0.47 | 0.0221 | 0.06 | 5 | 0.89 | 1.42 |
| 18. <i>Micropholis venulosa</i> (Mart. ex Eichl.) Pierre | 3.30 | 0.31 | 0.1896 | 0.51 | 3 | 0.59 | 1.41 |
| 19. <i>Miconia holosericea</i> (L.) DC. | 5.00 | 0.47 | 0.0191 | 0.05 | 5 | 0.89 | 1.41 |
| 20. <i>Sloanea sinemariensis</i> Aubl. | 5.00 | 0.47 | 0.0108 | 0.03 | 5 | 0.89 | 1.39 |
| 21. <i>Inga heterophylla</i> Willd. | 6.70 | 0.63 | 0.0446 | 0.12 | 3 | 0.59 | 1.34 |
| 22. <i>Chaetocarpus echinocarpus</i> (Baill.) Ducke | 3.30 | 0.31 | 0.1148 | 0.31 | 3 | 0.59 | 1.21 |
| 23. <i>Caraipa</i> sp. | 5.00 | 0.47 | 0.0330 | 0.09 | 3 | 0.59 | 1.15 |
| 24. <i>Ouratea</i> sp. | 3.30 | 0.31 | 0.0503 | 0.13 | 3 | 0.59 | 1.04 |
| 25. <i>Sacoglottis guianensis</i> Benth. | 1.70 | 0.16 | 0.2136 | 0.57 | 2 | 0.30 | 1.02 |
| 26. <i>Aspidosperma discolor</i> A. DC. | 3.30 | 0.31 | 0.0421 | 0.11 | 3 | 0.59 | 1.02 |
| 27. <i>Apuleia leiocarpa</i> (Vog.) Macbr. | 1.70 | 0.16 | 0.1890 | 0.51 | 2 | 0.30 | 0.96 |

TABLE 2. (continued)

| Species | Density/ha | | Dominance/ha | | Frequency/ha | | IVI |
|--|------------|--------|-----------------|-----------------|--------------|--------|--------|
| | AD | RD | AD _o | RD _o | AF | RF | |
| 28. <i>Odontadenia puncticulosa</i> (Rich.) Pulle | 3.30 | 0.31 | 0.0084 | 0.02 | 3 | 0.59 | 0.93 |
| 29. <i>Miconia tomentosa</i> D. Don | 3.30 | 0.31 | 0.0071 | 0.02 | 3 | 0.59 | 0.93 |
| 30. <i>Unonopsis lindmanii</i> R. E. Fr. | 3.30 | 0.31 | 0.0065 | 0.02 | 3 | 0.59 | 0.92 |
| 31. <i>Licania apetala</i> (E. Meyer) Fritsch | 1.70 | 0.16 | 0.0899 | 0.24 | 2 | 0.30 | 0.69 |
| 32. <i>Licania kunthiana</i> Hook. f. | 1.70 | 0.16 | 0.0735 | 0.20 | 2 | 0.30 | 0.65 |
| 33. <i>Siparuna guianensis</i> Aubl. | 1.70 | 0.16 | 0.0577 | 0.15 | 2 | 0.30 | 0.61 |
| 34. <i>Physocalymma scaberrimum</i> Pohl | 1.70 | 0.16 | 0.0463 | 0.12 | 2 | 0.30 | 0.58 |
| 35. <i>Ormosia paraensis</i> Ducke | 1.70 | 0.16 | 0.0218 | 0.06 | 2 | 0.30 | 0.51 |
| 36. <i>Hirtella gracilipes</i> (Hook. f.) Prance | 1.70 | 0.16 | 0.0144 | 0.04 | 2 | 0.30 | 0.49 |
| 37. <i>Coccoloba glaziovii</i> Lindan | 1.70 | 0.16 | 0.0072 | 0.02 | 2 | 0.30 | 0.47 |
| 38. <i>Mabea fistulifera</i> Mart. | 1.70 | 0.16 | 0.0068 | 0.02 | 2 | 0.30 | 0.47 |
| 39. <i>Casearia arborea</i> Urban | 1.70 | 0.16 | 0.0052 | 0.01 | 2 | 0.30 | 0.47 |
| 40. <i>Xylopia sericea</i> A. St. Hil. | 1.70 | 0.16 | 0.0047 | 0.01 | 2 | 0.30 | 0.47 |
| 41. <i>Minuartia guianensis</i> Aubl. | 1.70 | 0.16 | 0.0044 | 0.01 | 2 | 0.30 | 0.46 |
| 42. <i>Duguetia marcgraviana</i> Mart. | 1.70 | 0.16 | 0.0040 | 0.01 | 2 | 0.30 | 0.46 |
| 43. <i>Pouteria</i> cf. <i>cuspidata</i> (A. DC.) Baehni | 1.70 | 0.16 | 0.0040 | 0.01 | 2 | 0.30 | 0.46 |
| 44. <i>Tetragastris unifoliolata</i> (Engl.) Cuatr. | 1.70 | 0.16 | 0.0037 | 0.01 | 2 | 0.30 | 0.46 |
| 45. <i>Erythroxylum squamatum</i> Swartz | 1.70 | 0.16 | 0.0035 | 0.01 | 2 | 0.30 | 0.46 |
| TOTAL | 1066.67 | 100.00 | 37.4639 | 100.00 | 570 | 100.00 | 300.00 |

Seedlings (0–30cm tall) of *B. rubescens* were abundant in the understorey of forest, averaging 14.13 plants m⁻², while seedlings 31–60cm tall averaged 2.59m⁻².

Figure 6 shows the high number of seedlings of *B. rubescens* in the lower height classes in comparison with other species, and this species practically disappeared after the 2m height class.

DISCUSSION

Diversity and evenness indices were much lower than in mixed tropical forests in Brazil which reach values of the order of 3–4 for Shannon index log e basis and 0.7–0.9 for evenness (Felfili, 1995; Walter, 1995). The values in our forest were lower than those found by Nascimento (1994) for a *Peltogyne gracilipes* monodominant forest in the Amazon (2.3–2.5 and 0.7–0.8). The Simpson index was similar to that

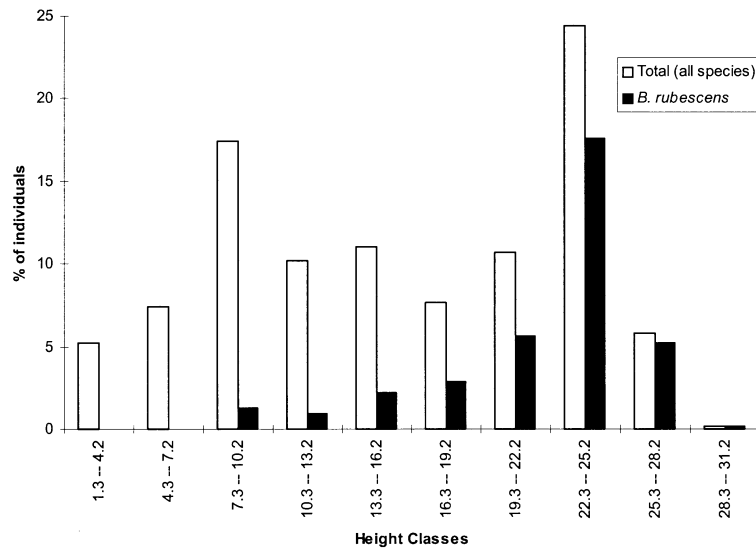


FIG. 3. Height distribution of trees in the 0.6ha sampling area.

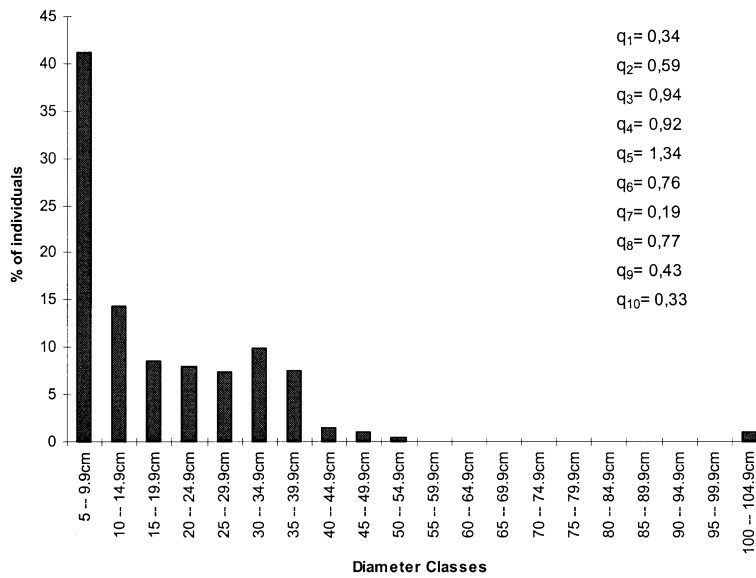


FIG. 4. Diameter distribution and corresponding 'q' quotient ratio of trees in the 0.6ha sampling area.

found by Hart *et al.* (1989) for a monodominant forest of *Gilbertiodendron* in Africa ($\lambda = 0.37$).

Several studies in Brazilian forests have shown that a few families contain a great proportion of the density, basal area and hence IVI (Felfili, 1995; Silva Júnior, 1995;

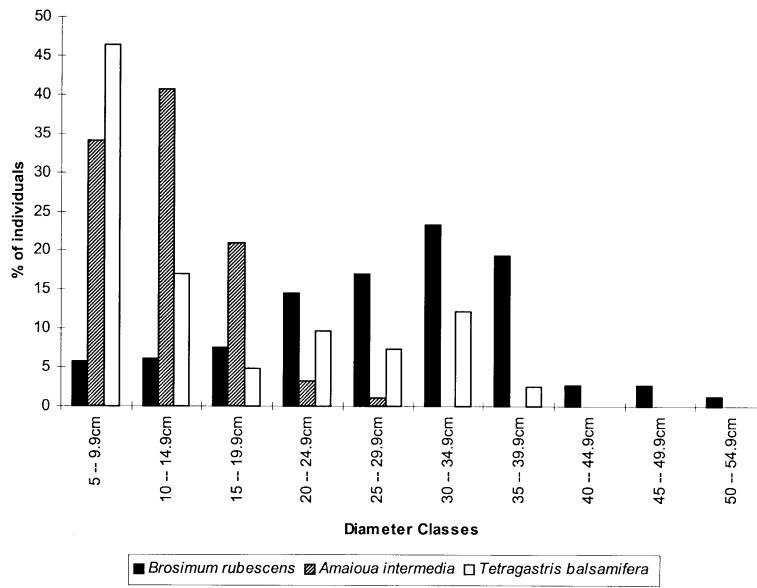


FIG. 5. Diameter distribution of *Brosimum rubescens*, *Amaioua intermedia* var. *brasiliana* and *Tetragastris balsamifera* in the 0.6ha sampling area.

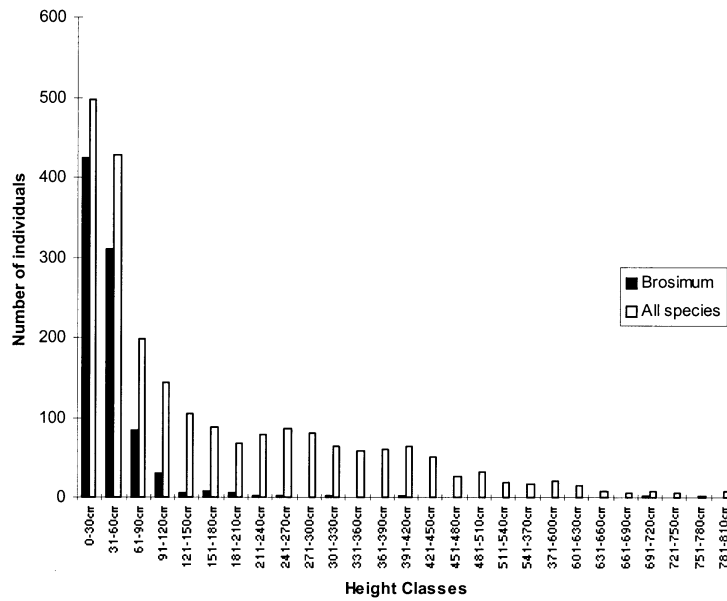


FIG. 6. Frequency distribution of the height of seedlings and saplings of *Brosimum rubescens* and other species.

Walter, 1995; Nascimento *et al.*, 1997), but the degree of dominance by just one species as well as the great concentration of individuals of the species in the higher diameter classes found in this forest is not common. It is comparable only with that found in other monodominant forests (Hart *et al.*, 1989; Martijena & Bullock, 1994; Read *et al.*, 1995; Isaacs *et al.*, 1996). A monodominant species (*Peltogyne gracilipes*) studied by Nascimento *et al.* (1997), on Maracá Island in the Amazonian forest, had 23% of all trees ≥ 10 cm dbh and 86% of those ≥ 30 cm dbh. The dominance of *Brosimum rubescens* in our forest is about three times greater than this for individuals ≥ 10 cm dbh. In fact, *B. rubescens* contained most of the total basal area of the forest, showing values and pattern for this parameter similar to that found for monodominant forests of *Celaenodendron mexicanum* Standl. ($28.8\text{m}^2 \text{ha}^{-1}$) in Mexico (Martijena & Bullock, 1994) and *Gilbertiodendron dewevrei* (De Wild.) Léonard in Africa (Hart *et al.*, 1989).

A large number of rare species (those with just one or two individuals in the sample) is also common in other Brazilian tropical forests such as a monodominant forest in the Amazon (Nascimento *et al.*, 1997), a gallery forest (Felfili, 1994), and a swampy gallery forest in Central Brazil (Walter, 1995).

The diameter distribution in our forest is unbalanced with the 'q' ratio between successive diameter classes inconstant, suggesting disequilibrium between mortality and recruitment (see Meyer *et al.*, 1961; Osmaston, 1968). Harper (1977) points out that most tropical forests do not have balanced diameter distributions although they tend towards it. The great disparity between the first and second diameter classes might indicate either high mortality of small individuals or a previous low recruitment of the seedlings into the first class, or both events. Felfili *et al.* (1988, 1998), studying a similar forest type, found the same diameter structure and suggested that the structure and composition of the forest might change in the future. Hubbell & Foster (1987) suggested that species with a similar pattern of diameter distribution to *B. rubescens* could be light-demanding or, at least, partially light-demanding, and mortality caused by low light levels was responsible for the pattern.

Hart *et al.* (1989), in a review of several works in tropical monodominant forests, suggested that such forests did seem to be characteristic of situations undisturbed for a long time. They concluded that the dominant species had characteristics in common, such as big seeds, persistent seedlings (with arrested development when shaded), and a low capacity for seed dispersion. *Brosimum rubescens* conforms to this in having big seeds (1cm diameter) and the presence in stands of many small woody seedlings (under 30cm tall) suggestive of the slow development found in persistent seedlings. The large quantity of seedlings under the mother trees also suggests a low dispersion capacity. Hart (1995) also noticed persistent seedlings in monodominant stands of *Gilbertiodendron dewevrei* in a forest in Zaire. After 10 years, half of the 123 *Gilbertiodendron* seedlings (<0.5m tall) tagged in 1981 were still alive but only one had reached 1m height. The *Brosimum* forest might present a similar pattern.

The high number of seedlings of *Brosimum* under 1m tall as opposed to the low

number greater than that height (and above 5cm diameter) suggests that light is conditioning their development. The few small trees occurring are in gaps, indicating that gaps play an important role in the succession. Brown & Whitmore (1992) described some species in a dipterocarp forest in Malaysia whose seedlings showed arrested development. They suggested that those small woody seedlings would have a better chance of survival when a gap occurred in the forest. Felfili *et al.* (1988, 1998) suggested the same for *B. rubescens* and Swaine & Whitmore (1988) reported this pattern for other species in tropical forests.

The absence or extreme paucity of *B. rubescens* seedlings and saplings above 1.2m tall could mean that this species might be replaced by co-occurring species and therefore the canopy would become increasingly species-rich. However, the high density of smaller seedlings of the species, together with the success of sapling growth in fortuitous gaps, suggests that establishment failure be caused by competition for light or nutrients. The apparent need for light for establishment of seedlings and saplings of *B. rubescens* suggests that the species might be reliant on infrequent disturbance to open up the canopy, creating gaps, to maintain its dominant status. Thus the establishment of *B. rubescens* is probably episodic. A similar recruitment situation was noted by Read *et al.* (1995) in a monodominant stand of *Nothofagus aequilateralis* in New Caledonia and they reached conclusions similar to ours.

Connell & Lowman (1989) classified monodominant forest into two categories based on the following criteria: (a) abundance of seedlings of the dominant species; (b) the degree of difficulty of their germination; and (c) the degree of disturbance of the community. If the seedlings tolerate shade and remain abundant under closed canopy, even though with arrested development, the species is classified as type I. This type persists beyond one generation. If the seedlings are absent under closed canopy and abundant in disturbed sites, the species is classified as type II. This type represents an initial successional stage and does not persist in the same site. Our evidence indicates the classification of *B. rubescens* as a type I monodominant species; all species previously suggested by Connell & Lowman (1989) as having type I strategy were *Leguminosae*.

The soils of the experimental plots were strongly acid, with high levels of exchangeable Al. Askew *et al.* (1971), comparing the dystrophic soils of the cerrado *sensu stricto* and the dry forests occurring in a broad vegetation zone between the cerrado plains of central Brazil and the Amazonian rain forests, reported mean values of soil pH of 4.33, which is close to the values reported in the present study. However, mean soil pH reported by Furley & Ratter (1988) was 5.0 for the cerrados in general. The pH values of the *B. rubescens* forest were similar to those reported in the literature for monodominant forests in British Guyana (Davis & Richards, 1934), equatorial Africa (Hart *et al.*, 1989), and Brazilian Amazon (Nascimento *et al.*, 1997).

The levels of available Ca and Mg in the *B. rubescens* forest were very low and comparable with the levels reported for dystrophic cerrados in central Brazil. However, unlike the situation in other cerrados (Haridasan, 1992), the levels of Ca

were lower than those of Mg with Mg/Ca ratios above 3.0. A similar pattern was reported by Nascimento *et al.* (1997) for the soils under monodominant stands of *Peltogyne gracilipes* in the Amazon and by Read *et al.* (1995) for soils in a *Nothofagus*-dominated forest in New Caledonia. However, the levels of Ca and Mg reported in the present study were much lower than the values reported by these authors.

The availability of K in the soil was in the range considered adequate in soil testing and higher than is commonly reported in the literature for mesophytic forests in central Brazil (RADAMBRASIL, 1981; Araújo & Haridasan, 1988; Felfili, 1994; Walter, 1995) or other monodominant forests (Read *et al.*, 1995; Nascimento *et al.*, 1997). However, Hart *et al.* (1989) have reported similar levels of K for a monodominant forest in equatorial Africa.

An important aspect of the soil properties of the experimental plots was the high percentage of gravel and high availability of Fe. Read *et al.* (1995) reported that the monodominance of *Nothofagus* species occurred predominantly on ultramafic soils with high concentrations of metals such as Ni, Cr and Mn and low concentrations of P, Ca and K. We did not determine the concentrations of Ni and Cr in the present study, nor did we determine the levels of nutrients at lower depths. Concentrations of Mn in the soil was high by soil testing standards and the very low soil pH could cause Mn toxicity in susceptible species and favour resistant ones.

CONCLUSIONS

The *Brosimum rubescens* forest studied fits into the category of type I monodominance of Connell & Lowman (1989). *Brosimum rubescens* dominated the upper forest storey but trunk diameter distribution was unimodal skewed to the right (larger dimensions), suggesting that establishment has been episodic. The maintenance of dominance seems linked to probably irregular disturbance-forming gaps that allow eventual establishment of some of the persistent seedlings. Soil nutrients might also play an important role in the dominance.

The soils of the forest showed higher availability of Mg than Ca, like many other monodominant tropical forests, although the levels of these nutrients in the surface layers were lower than those reported by other authors. Besides the high Mg/Ca ratios, high availability of K as compared with low availability of the bivalent ions, Ca and Mg, and toxicities of Fe and Mn resulting from the strong acidity of the soil could be factors influencing the distribution of species in this forest.

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