

# Tree population studies in low-diversity forests, Guyana. I. Floristic composition and stand structure

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Studies were undertaken on the floristic composition and stand structure of four 1 hectare plots in the lowland forests of Kurupukari, Guyana. A total of 3897 trees, covering 153 species and 31 plant families were recorded at greater than 5 cm diameter at breast height (dbh). The number of species per hectare ranged from 61 to 84 (> 5.0 cm dbh) and 50–71 (>10.0 cm dbh). The total number of trees per hectare varied two-fold between study plots, with 45–50% of the trees within the 5–10 cm size-class. Mean total basal area varied from 32.39–34.63 m<sup>2</sup> per 100 m<sup>2</sup>. The four most dominant plant families represented 43.8% of the total number of trees, while representing only 11.2% of the species. No one plant family dominated in more than one of the four study plots, and all four plots held at least one plant family with more than 20% of the total number of trees. Although 14 tree species were common to all four plots, only 26%–35% of the species were represented by a single tree. Between three and seven species represented 50% of the trees within all size-classes, with species dominance occurring within the highest density plot.

These tropical forest types of central Guyana may represent some of the lowest diversity forests in the neotropics, whereby the total number of tree species is relatively limited, typically with six dominant canopy species, but the relative abundance of these species is highly variable between the forest types. Mechanisms influencing the competitive interactions associated with species dominance are discussed in relation to the importance of mycorrhizae and the persistence of species dominance.

*Keywords:* low-diversity forest; floristic composition; stand structure; species dominance; Guyana.

## Introduction

Tree population data from tropical forests has become widely available over the past decade, generating several comprehensive review papers (Swaine *et al.*, 1987; Gentry, 1988, 1990). However, many of these studies have concentrated on the relatively species-rich rather than the species-poor or species-dominant forest types (Connell and Lowman 1989; Hart, 1990) although species-poor forests have long been recognized (Davis and Richards, 1934, 1935. Species-poor or 'low-diversity' forest may be defined as a forest in which 50–80% of the canopy trees are represented by only one tree species (Connell and Lowman, 1989). Connell and Lowman (1989) recognized that two types of low-diversity forest may exist: persistent and non-persistent, and that mycorrhizae were likely to be the main factor providing a species with competitive superiority.

Mechanisms underlying species competitive interactions, and therefore the determinants of species dominance are central to the regulation of plant populations

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(Harper, 1977; Tilman, 1988; Crawley, 1990), and a range of theories have been suggested outlining the mechanisms by which species diversity may be maintained or species dominance suppressed (Grubb, 1977; Connell, 1979; Hubbell and Foster, 1986). However, mechanisms by which both species-rich and species-poor forest types may be maintained are less well understood. Whether different determinants of species dominance or suppression are at work within these different forest types needs to be addressed if a better understanding of tropical forest dynamics is to be developed. The lack of quantitative data on the distribution and abundance of tree species within low-diversity forests is likely to be one of the main limitations on this understanding.

Here we present data on the structure and composition of different forest types in central Guyana which may be defined as relatively low-diversity forests.

### Materials and methods

During 1992/93 four 1 hectare study plots were established at Kurupukari (4°34'51"N, 58°42'48"W) in central Guyana (see Fig. 1 and Box 1). Each study plot was situated within one of the forest types of the Kurupukari Sand Plateau recognized by Hawkes and Wall (1993). These plots were within the study area of the Commonwealth and Government of Guyana International Iwokrama Rainforest Programme, and this paper represents the first published quantitative floristic data from the area.

Each of the 1 hectare plots was divided into 10 × 10 m quadrats and each quadrat was then systematically surveyed by identifying, measuring and tagging all trees with a diameter at breast height (dbh) greater than 5.0 cm. Here data are presented at size thresholds of both 5.0 cm and 10.0 cm dbh in order to make comparisons with published literature. Where possible fertile voucher specimens were collected for each tree (when not possible non-fertile specimens were taken). Specimens were then identified by reference to collections housed at the University of Guyana herbarium and the Royal Botanic Gardens, Kew, where the specimens are currently stored. A full botanical list with voucher specimen numbers is provided in the Appendix. Trees were also named with assistance from Arawak and Macushi Amerindians of Kurupukari village, and after local names were agreed upon, specimens cross-referenced with available literature (Roosmalen, 1985; Mennega *et al.*; 1988; Tropenbos, 1993).

### Statistical analysis

One-way analysis of variance was used to determine any significant differences in species and tree composition between the four plots. The species richness exhibited normal distribution ( $S^2 < \text{mean}$ ), while tree densities closely exhibited a Poisson distribution ( $S^2 \approx \text{mean}$ ) and were square root transformed (with addition of 0.5 for values less than 10, Sokal and Rohlf, 1981). Basal area exhibited a negative binomial distribution and was log transformed. Linear regression was used to test for the significant differences in the relationship between total tree density and species richness per 100 m<sup>2</sup> covered by tree species for each of the four study plots. The Generalized Linear Interactive Model (GLIM) was used to examine significant differences in slope and intercept (see Crawley, 1993). Similarly, a log-log plot was used to examine significant differences in the species-area relationships and a log-normal plot for species abundance-rank curves for the four study plots. The species-area curves were constructed using sequential summing of

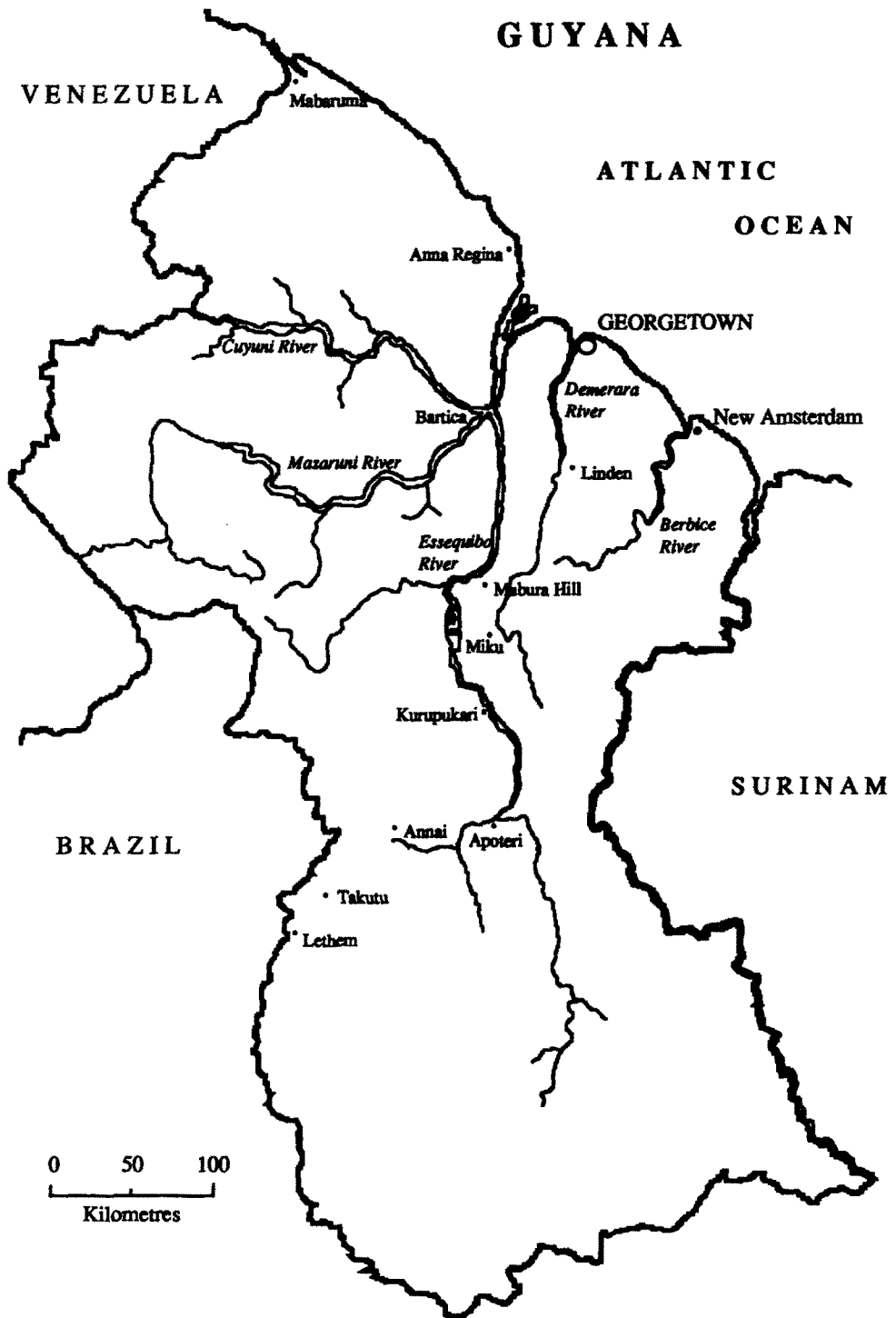


Figure 1. Map of Guyana.

**Box 1:** Description and location of the four study plots (see Fig. 2).

- Mora plot: – situated approximately 300 m from the Essequibo river,  
– dominated by Mora (*Mora excelsa* Caesalpinioideae),  
– upon alluvial soils (Hawkes and Wall, 1993).
- TA2 plot: – on forest transect at 0.2 km from the Guyana–Brazil highway,  
– dominated by Wallaba (*Eperua falcata* Caesalpinioideae),  
– a white sand forest type, *sensu* Davis and Richards (1934).
- TA12 plot: – situated on a forest transect, 1.2 km from the Guyana–Brazil highway,  
– mixed species forest type,  
– upon brown sand/loam soils.
- TA19 plot: – on forest transect at 1.9 km from the highway,  
– Greenheart (*Chlorocardium rodiaei* Lauraceae) – mixed species forest type,  
– upon brown sand/loam.

the 10 × 10 m (0.05 ha) quadrats. Frequency distributions for tree densities and species richness were analysed by fitting expected distributions and testing significance using  $\chi^2$  analysis (Sokal and Rohlf, 1981).

## Results

### *Species richness and tree densities*

Within all four study plots a total of 153 species and 31 plant families were recorded at greater than 5.0 cm dbh, representing 3897 individual trees. At a size threshold of 10.0 cm dbh, 120 species, 30 families and 2035 trees were recorded (Table 1, Appendix). Fifteen of the 31 families were represented by less than 1% of the total number of trees. The total number of species at 5.0 cm dbh in each plot varied from 61 in TA2 (50 species at 10 cm dbh also in TA2) to 84 in TA19 (71 at 10.0 cm dbh in TA12). Significant difference in mean species richness (number of species per 100 m<sup>2</sup>) was found for the Mora and TA12 plot, both of which were significantly lower in species richness than the other two plots (LSD = 0.435 at  $p = 0.05$ ; Table 1). The lack of significant differences between the TA19 and TA2 plots may be accounted for by the large variation in species richness between quadrats (scale of 100 m<sup>2</sup>).

There was a significant two-fold difference in tree density (at both 5.0 cm and 10.0 cm dbh thresholds, Table 1) between the low density Mora plot and the high density TA2 plot ( $F = 105.08$ , LSD = 0.10,  $df = 3$  and 396), although these two plots exhibited the lowest species richness at 10 cm dbh. Both TA12 and TA19 plots had similar tree densities (8.72 and 8.69 trees per 100 m<sup>2</sup> at 5.0 cm dbh, and 4.59 and 4.77 at 10.0 cm dbh respectively).

Variation in tree basal area between the four plots was small, with 32 to 35% of the total area covered by trees (Table 1), although after data transformation significant differences were detected between plots ( $F = 3.94$ ,  $df = 3$  and 396,  $p = 0.008$ ). However, this was accounted for by the significantly lower mean basal area in the TA2 plot (32.29 m<sup>2</sup> per 100 m<sup>2</sup>, LSD = 0.89), with no significant differences in mean basal area between the other three study plots.

A total of 230 trees from the four plots remain unidentified, this represented 5.5% of the

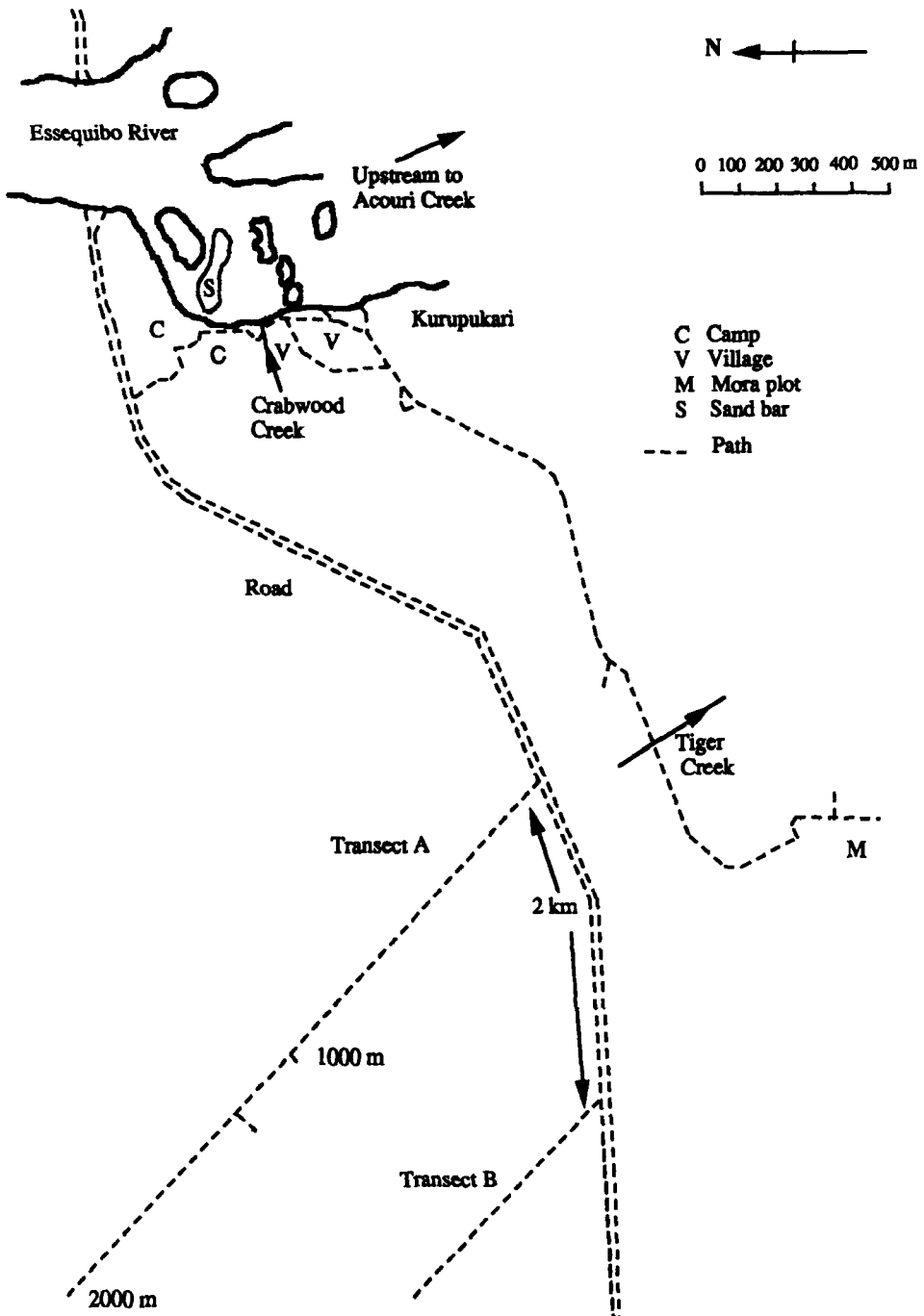


Figure 2. Map of Kurupukari, with forest plots situated at 0.2, 1.2 and 1.9 km along forest transect A from the Guyana–Brazil highway, and the Mora plot (M) situated 300 m from the Essequibo river.

**Table 1.** Summary of floristic composition of the four 1 ha study plots at Kurupukari, at 5.0 cm and 10.0 cm dbh thresholds. Note that the total number of species and trees includes unidentified species. See Appendix for full species list, and breakdown of identified and unidentified trees and species. Of the unidentified trees, 65.2% were represented by one species within plot TA2, which once identified would reduce the percentage of unidentified trees within any plot to less than 3.3%.

	Mora		TA12		TA19		TA2	
	5 cm dbh	10 cm dbh	5 cm dbh	10 cm dbh	5 cm dbh	10 cm dbh	5 cm dbh	10 cm dbh
Total no. of species	72	64	81	71	84	67	61	50
Total no. of families	23	23	25	23	26	23	23	23
Total no. of trees	716	357	872	459	869	477	1440	742
No. of unidentified trees (% total)	10 (1.3%)		8 (0.8%)		32 (3.3%)		180 (12.1%)	
No. of unidentified species	6		8		19		13	
Mean no. of trees per 100 m <sup>2</sup> (SE)	7.16 (0.26)	3.57 (0.18)	8.72 (0.26)	4.59 (0.23)	8.69 (0.29)	4.77 (0.21)	14.40 (0.36)	7.42 (0.27)
Mean no. of species per 100 m <sup>2</sup> (SE)	5.84 (0.19)	3.2 (0.17)	6.74 (0.19)	4.1 (0.20)	7.35 (0.21)	4.3 (0.18)	7.24 (0.18)	3.4 (0.16)
Mean basal area m <sup>2</sup> per 100 m <sup>2</sup> (SE)	34.63 (4.3)		34.18 (3.3)		34.55 (2.7)		32.29 (1.6)	

total number of trees recorded, which ranged from 0.9 to 12.5% within any given study plot (Table 2).

#### *Family composition and similarities between plots*

Species richness was predominantly attributed to four plant families (Lauraceae, Lecythidaceae, Leguminosae (Papilionoideae) and Chrysobalanaceae), which accounted for 32.9% (50 species) of the total number of species recorded from the four plots (Table 2).

Family dominance by tree density varied between the 5.0 cm and 10.0 cm size thresholds. At the 5.0 cm threshold three families dominated (Annonaceae, Lecythidaceae, and Leguminosae), which accounted for 41.4% of the total number of trees within all four study plots, but only 22.2% of the total number of species (Table 2). However, species of Annonaceae and Dichapetalaceae were mainly found within size-classes less than 10 cm dbh, accounting for less than 3.5% of the trees at size-classes greater than 10 cm dbh. At the higher size threshold the sub-family Caesalpinioideae, and families Chrysobalanaceae, Lecythidaceae and Bombacaceae dominated with 53.6% of the total number of trees.

No one plant family dominated all four study plots, although all four plots held at least one plant family which represented more than 20% of the total number of trees. In TA2 (at 10.0 cm threshold) Bombacaceae and Caesalpinioideae made up 52.2% of the total number of trees within the plot (Table 2). The Mora plot was dominated by Leguminosae (Caesalpinioideae and Mimosoideae) with 37.3% (27.2 and 10.1%). In TA19, 23.1% of the trees belonged to the family Chrysobalanaceae and 16.7% to the Lecythidaceae. In TA12, with the exception of Annonaceae (which was dominant at less than 10 cm dbh), family dominance was lower, with four families representing 12.6–16.3% of the total number of trees (Table 2).

Thirteen species at 5.0 cm dbh (11 at 10.0 cm dbh) were common to all four study plots.

**Table 2.** Percentage of trees by plant family for each of the four study plots at 5.0 cm and 10.0 cm size thresholds, and the number of species per family. Only those families with greater than 5.0% of the total number of trees in all any of the four plots are given.

Family	Mora		TA12		TA19		TA2		No. of sp.	
	5 cm	10 cm	5 cm	10 cm	5 cm	10 cm	5 cm	10 cm	5 cm	10 cm
Annonaceae	14.7	3.6	23.9	3.5	8.9	3.1	1.5	0.6	7	6
Lauraceae	1.1	1.7	4.3	6.9	8.4	12.3	6.5	6.6	11	10
Guttiferae	0.9	1.7	2.6	3.7	0.6	1.0	5.4	7.3	5	4
Bombacaceae	2.5	3.9	3.8	4.1	4.3	3.1	29.3	28.2	3	3
Lecythidaceae	3.7	8.1	8.6	16.3	13.6	16.7	0.1	0.1	9	9
Chrysobalanaceae	6.8	9.5	11.7	12.6	25.7	23.1	5.0	5.9	9	7
Leg. Caesalpinioideae	23.7	27.2	10.2	14.4	3.5	4.4	22.9	28.9	5	4
Leg. Papilionoideae	7.6	6.2	2.9	4.8	10.6	12.4	5.3	6.3	9	8
Leg. Mimosoideae	10.6	10.1	11.1	12.7	0.1	–	0.2	0.4	4	4
Myrtaceae	6.6	9.8	0.7	0.8	0.5	1.1	0.1	0.1	5	4
Dichapetalaceae	9.1	1.7	3.4	1.5	3.9	0.4	1.5	0.7	1	1
Other families	11.6	18.7	16.2	19.4	16.4	21.8	9.8	11.6	30	27
Unknowns	1.4	0.6	0.9	1.3	3.4	2.5	12.5	4.3	33	12
							Total no. of species		153	120

these species accounted for 39.0% of the total number of trees at 5.0 cm dbh (and 38.3% at 10.0 cm dbh). The most abundant of these species was *Catostemma fragrans* (Bombacaceae), which accounted for 12.7% of all trees. Plot TA2 exhibited the lowest number of species shared with the other three plots (18–24 species), with 13 species unique to that plot (Table 3). The number of species shared between the remaining three plots were 34–46 species, with 6–12 species unique to each plot (Table 3). At the generic level a similar pattern of plot-specificity was observed, with only two genera restricted to the Mora and TA12 plot, and four to TA19 and TA2 (two of these genera belonged to the Arecaceae). At the family level, only six were found in one of the four plots, with one species represented within each family. Two families were found only in TA2 (Icacinaceae, Melastomataceae), and one family each in TA19 (Olacaceae) and TA12 plot (Caryocaraceae). All plant families within the Mora plot were also present within at least one of the other three plots.

#### *Tree and species frequency distributions amongst size-classes*

Tree density and species richness frequency distributions for the four study plots are shown in Figure 3, for all individuals with dbh > 5 cm. Variation in tree density (variance/mean ratio ranged from 0.71 to 0.93) was higher than species richness (ratio from 0.49 to 0.62) in all four study plots (Fig. 3). Both tree densities and species richness were randomly distributed, demonstrated by a significant fit to a Poisson distribution in all study plots ( $\chi^2$ -values ranged from 4.59 to 23.02 for tree densities, and 9.92 to 22.38 for species richness). However, the variance/mean ratios for total basal area for the study plots were all greater than unity, with approximately a seven-fold difference between the four plots (7.93 in TA2 to 53.39 in the Mora plot), which indicated an aggregated distribution in basal area.

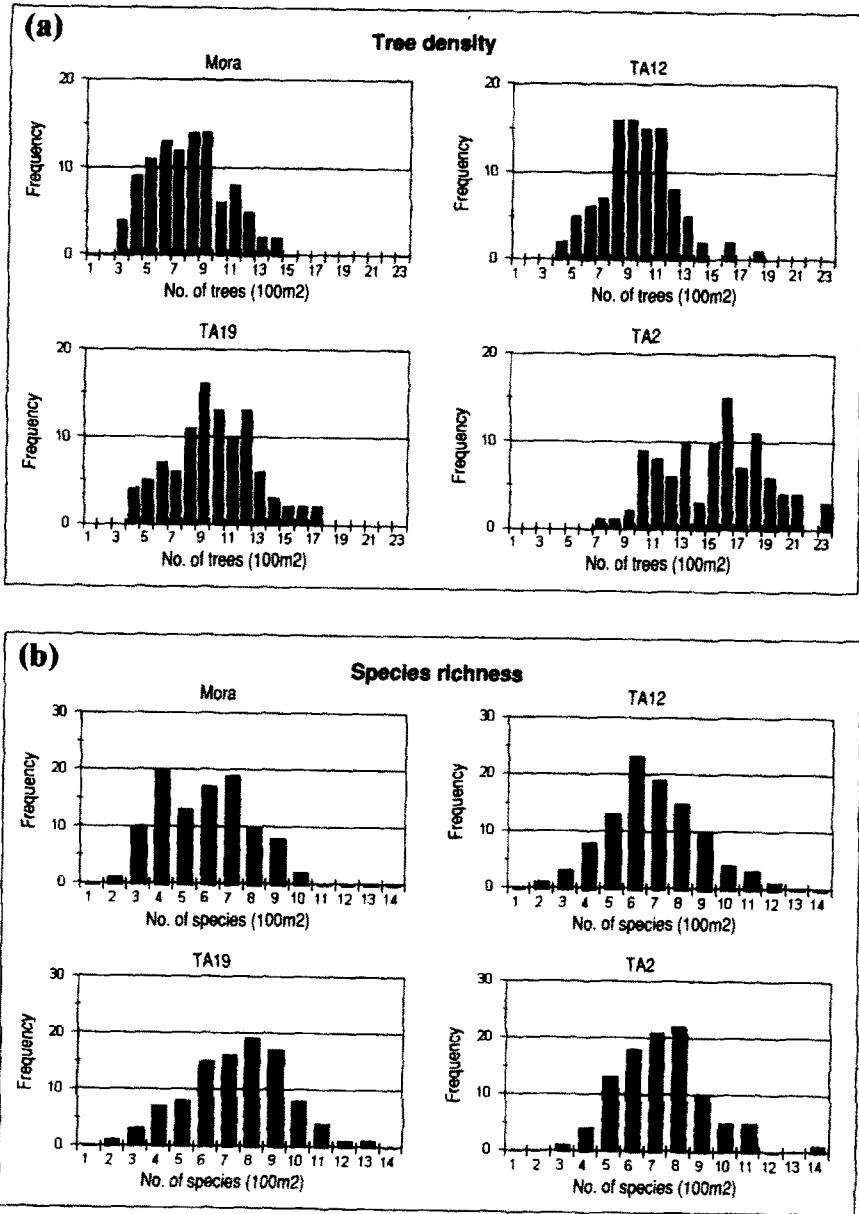
**Table 3.** Number of species common to the four study plots, with the total number of species given within the diagonal. The number of species, genera and families unique to each of the four plots is also given at 5.0 and 10.0 cm dbh thresholds. A total of 14 species were common to all four plots at the 5.0 cm dbh threshold, and 12 at the 10.0 cm threshold

		Mora	TA12	TA19	TA2
Mora		72	46	36	18
TA12			81	46	21
TA19				84	24
TA2					61
No. of species	@ 5 cm	6	8	12	13
	@ 10 cm	5	5	5	10
No. of genera	@ 5 cm	2	2	4	4
	@ 10 cm	1	1	1	4
No. of families	@ 5 cm	0	1	1	2
	@ 10 cm	0	1	0	2

Although the percentage of trees was relatively consistent between all four study plots in the 5–10 cm size-class (Table 4), significant differences in tree densities between all four study plots were found in the 5–10 cm size-class (Table 5,  $F = 32.08$ ), with between 45.1 and 50.1% of the trees recorded within this size-class (Table 5). The percentage of trees within the 10–15 cm size-class ranged from 18.1 to 24.1%. Significant differences in tree density between the four plots were detected for each size-class up to 35 cm, with tree densities in TA2 significantly higher than the other three plots (Table 5). However, in the 50+ cm size-class tree density was significantly lower for TA2 (1.4% of the number of trees) compared with the other three plots (6.3–7.4%). The variation in tree density between the size-classes showed no distinct pattern, with the variance/mean ratio ranging from 0.84 to 1.18.

#### *Species dominance and diversity*

Only six tree species (*Duguetia neglecta*, *Catostemma fragrans*, *Licania alba*, *L. heteromorpha*, *Eperua falcata* and *Mora excelsa*) represented 44.3% of the total number of trees recorded from all four plots (see Appendix). Species dominance was higher in plot TA2 where two species represented 51.7% at 5.0 cm dbh (56.1% at 5.0 cm dbh) of the trees (*C. fragrans* and *E. falcata*), with only 32 species representing 95% of the trees (Table 6). In the Mora plot, where *M. excelsa* accounted for 15.9% of the trees (at 5.0 cm dbh) and 20.2% (at 10.0 cm dbh), 34 species represented 95% of the trees. Similarly, 42 and 54 species in plots TA12 and TA19 represented 95% of the trees (Table 6). Although TA19 was shown to be the most species-rich plot, *L. alba* and *L. heteromorpha* did represent 25.2% of the trees. In comparison, in the TA12 plot only one canopy species dominated with more than 10% of the trees (*Pentaclethra macroloba* with 10.3% at 5.0 cm dbh and 11.1% at 10.0 cm dbh), although *D. neglecta* dominated the smaller size-class (5–10 cm dbh) with 20.7%. The number of species with only a single tree represented within any given plot were 34.9, 24.6, 35.1 and 25.3% of the total number of species recorded from the Mora, TA12, TA19 and TA2 plots respectively. Further details on species dominance



**Figure 3.** Frequency distributions for (a) tree densities (number of individual trees per 100 m<sup>2</sup>) and (b) species richness (number of species per 100 m<sup>2</sup>), using 5.0 cm dbh data. See text and Table 2 for further details. The variance/mean ratio for tree densities ranged from 0.71 to 0.93, and 0.49 to 0.62 for species richness, with a significant fit to a Poisson distribution at  $p < 0.05$ .

**Table 4.** Percentage of the total number of trees within ten size-classes from the four 1 ha study plots, at intervals of 5.0 cm dbh

Size-class	Mora	TA12	TA19	TA2
5–10 cm	50.1	47.3	45.1	48.4
10–15	20.1	24.1	22.6	19.1
15–20	10.1	8.2	9.0	12.5
20–25	4.3	4.4	5.7	5.8
25–30	2.5	2.5	3.6	5.0
30–35	1.9	2.1	2.8	3.7
35–40	1.4	1.9	2.5	2.6
40–45	1.2	1.7	1.2	1.0
45–50	1.0	1.4	1.2	0.5
50+	7.4	6.4	6.3	1.4
Total no. of trees	716	872	869	1440

**Table 5.** Mean tree densities per 100 m<sup>2</sup> within each of the ten size-classes for the four 1 ha study plots, with standard errors in brackets ( $n = 100$ ). F-statistic and LSD ( $p < 0.05$ ) values given with square-root transformation of data

Size class	Mora	TA12	TA19	TA2	Statistics
5–10 cm	4.40 (0.21)	5.12 (0.21)	5.47 (0.24)	7.91 (0.33)	F = 32.08 LSD = 0.11
10–15	1.32 (0.11)	1.89 (0.13)	1.45 (0.12)	2.59 (0.15)	F = 17.80 LSD = 0.09
15–20	0.66 (0.08)	0.66 (0.07)	0.81 (0.08)	1.60 (0.11)	F = 23.19 LSD = 0.08
20–25	0.30 (0.05)	0.40 (0.06)	0.47 (0.07)	1.10 (0.09)	F = 26.97 LSD = 0.07
25–30	0.19 (0.04)	0.22 (0.05)	0.34 (0.06)	0.83 (0.09)	F = 20.96 LSD = 0.06
30–35	0.10 (0.03)	0.20 (0.04)	0.28 (0.05)	0.34 (0.05)	F = 5.17 LSD = 0.05
35–40	0.08 (0.03)	0.17 (0.04)	0.15 (0.04)	0.15 (0.04)	F = 1.18 LSD = 0.04
40–45	0.09 (0.03)	0.13 (0.04)	0.12 (0.03)	0.12 (0.03)	F = 0.30 LSD = 0.04
45–50	0.05 (0.02)	0.08 (0.03)	0.13 (0.03)	0.01 (0.01)	F = 4.15 LSD = 0.03
50+	0.43 (0.06)	0.43 (0.07)	0.38 (0.06)	0.18 (0.04)	F = 3.95 LSD = 0.06

**Table 6.** Number of species represented by 25, 50, 90 and 95% of the total number of trees from each of the four study plots (see Fig. 5 for more detail)

% of trees	Mora	TA12	TA19	TA2
25	2	2	3	1
50	5	6	6	2
90	23	31	39	21
95	34	42	54	32

within different size-classes and the conservation implications will be dealt with elsewhere (Johnston and Gillman, in preparation).

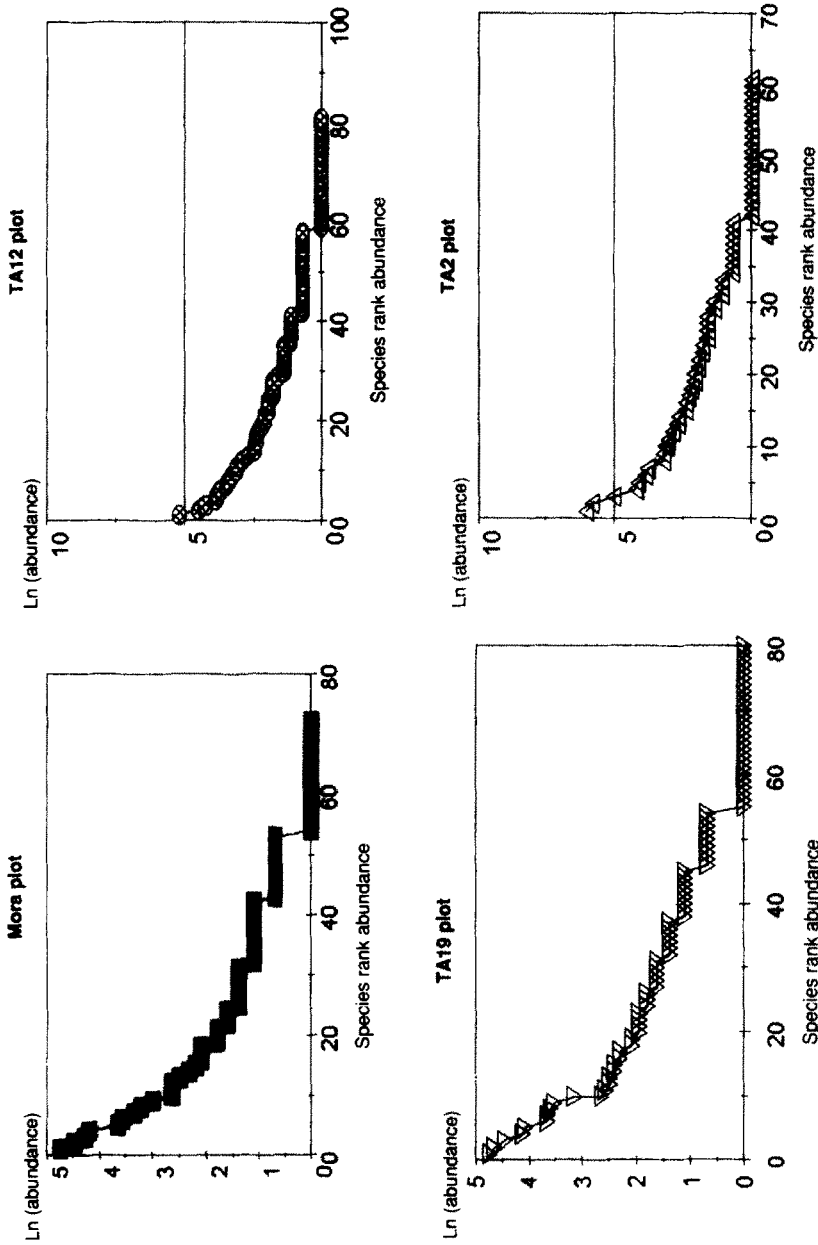
Curves of species abundance against rank abundance showed similar patterns in species dominance for all four plots (Fig. 4). No significant differences in rate of decline of species abundance with rank (slope of  $\ln(\text{species abundance})$  versus rank abundance) occurred between three of the plots ( $t < 1.96$ ; Mora, TA12 and T19). However, plot TA2 exhibited a significantly higher rate of change compared with the remaining three plots ( $t = 3.76$ ,  $df = 61$ , slope of  $-0.082$ , compared to a range of  $-0.051$  to  $-0.055$  for the remaining three plot curves).

The high species dominance was reflected throughout all the size-classes, where 3 to 7 species represented 50% of the trees which occurred within all four study plots for all ten size-classes (Fig. 5a), although TA2 did exhibit a consistently lower number of species at all size-classes. If the number of species which represent 95% of the trees is considered, noticeable differences between the plots only occurred at below 20 cm dbh (Fig. 5b). The higher species diversity in TA19 (Table 1) is shown to be accounted for by lower species dominance in the 5–10 cm size-class, in which 95% of the trees were represented by 54 species, compared with 34 to 42 in Mora and TA12 (Table 6). Likewise, the high species dominance in TA12 plot may be accounted for by the low number of species in the 5–10 cm and 50+ cm size-classes (Fig. 5b).

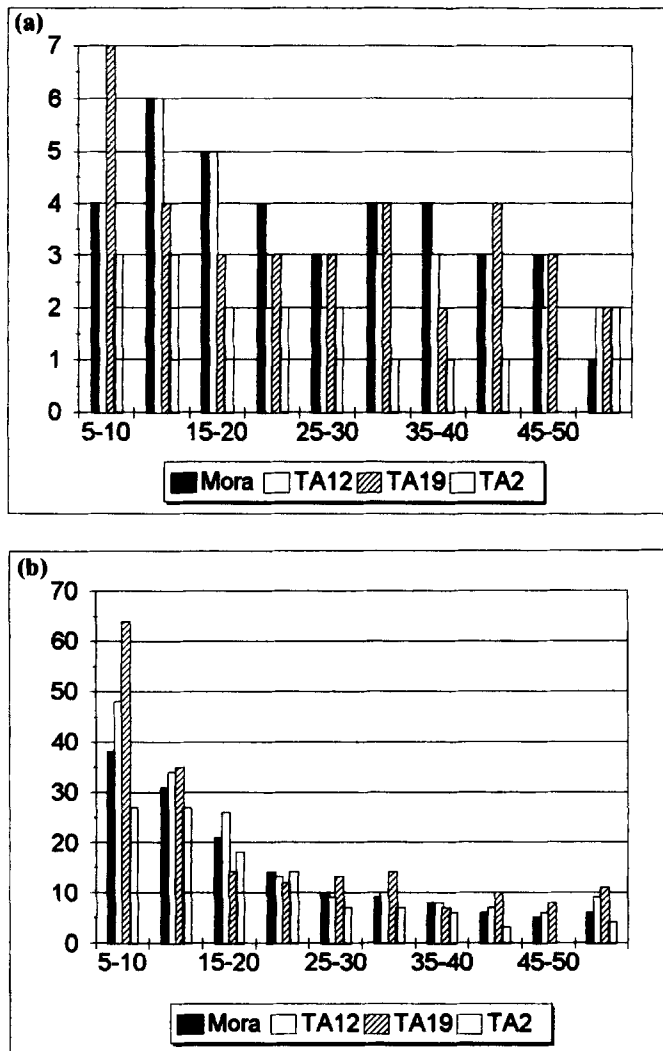
All four hectare study plots showed similar species-area curves where the number of species per hectare ranged from 61 to 84 species (Fig. 6). A log–log transformation of the species-area curves (Fig. 6,  $S = cA^b$ ) showed the rate of species increase with area ( $b$ ) for the four plots ranged from 0.37 (TA12) to 0.45 (TA19), with no significant differences between the four plots.

## Discussion

The forests of Kurupukari appear to be a mosaic of forest types, which comprise relatively few species in any one hectare and in which under specific conditions a particular species becomes dominant or set of species codominant. Substantial overlap may be seen between this locality and forests studied by Davis and Richards (1934) at Moraballi Creek, with Mora and Wallaba forest types represented at both localities. Tree density and species richness were slightly higher at Moraballi Creek (Table 7), although this may be accounted for a slightly larger study grid (1.2 ha instead of 1 ha). The number of species in the six most important families was similar, with an equal representation of Leguminosae and Chrysobalanaceae, but with a slightly greater representation of species in the families



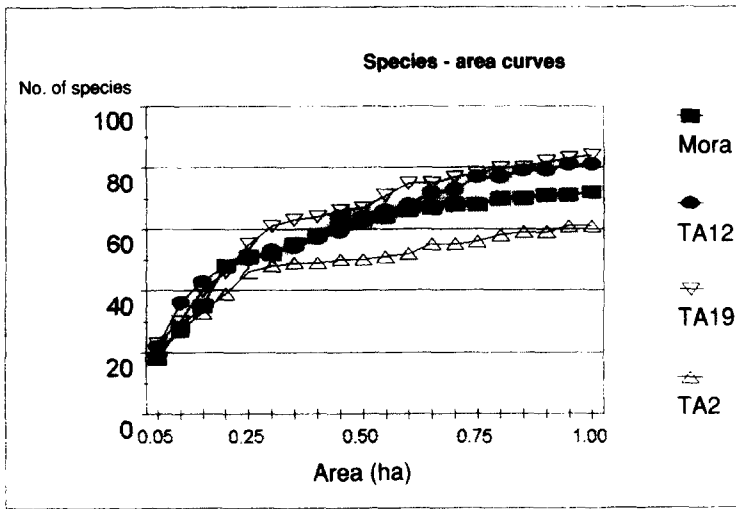
**Figure 4.** Species dominance curves for the four 1-ha study plots, illustrated as  $\ln(\text{species abundance})$  versus rank abundance. The intercepts were 3.31, 3.40, 3.44 and 4.07, and the slope coefficients  $-0.055$ ,  $-0.051$ ,  $-0.052$  and  $-0.082$  for the Mora, TA12, TA19 and TA2 plots respectively, with  $r^2$  ranging from 0.87 to 0.94.



**Figure 5.** Number of species represented by (a) 50% and (b) 95% of the trees within each of the ten size-classes, for each of the four study plots. Size class intervals at 5.0 cm, see Fig. 3 for further details.

Lecythidaceae, Lauraceae and Moraceae at Kurupukari. The only other lowland rain forest locality with high species dominance was studied by Lieberman and Lieberman (1987) in La Selva, Costa Rica, with forests dominated by *Pentaclethra macroloba* (Leguminosae, Mimosoideae), which had similar tree densities and approximately 20 more species per hectare (see Table 7).

The low-diversity forests at Moraballi Creek (Davis and Richard, 1934) and Kurupukari are clearly demonstrated when compared with other localities in Amazonia (Table 7). The number of species per hectare was typically 2–3 times higher in species-rich forest types (forest types in Brazil and Peru) compared with species-poor forest (Guyana and Costa



**Figure 6.** Species-area curves ( $S = cA^b$ ) for the four 1-ha study plots, with the number of species plotted against cumulative area of the study plot, at intervals of 0.05 ha, using 5.0 cm dbh threshold data. After log-log transformation of data ( $\log S = \log c + b \log A$ ) the intercept ( $\log c$ ) ranged from 1.02 to 1.14 and the slope coefficient ( $b$ ) 0.37 to 0.45,  $r^2$  ranged from 0.93 to 0.98 for all four study plots.

Rica). Differences in tree density were not so marked, although a 1.5 to 2-fold difference may be observed. The number of plant families in species-rich forest types is typically between 36 and 48, compared with less than 30 plant families in the species-poor forest types (Table 7).

From data available particular traits appear to make these forests at Kurupukari, and others classified as 'low-diversity', different from 'species-rich' forests:

- (i) Species richness in low-diversity forests is markedly less than 100 species per hectare at 10.0 cm dbh (Table 7).
- (ii) Species and family dominance within low-diversity forests is high, for example less than six species may account for over 50% of the individual trees at all size-classes (Table 7), with a single dominant species accounting for over 20% of the total number of trees.
- (iii) The number of families or species with only one individual tree in low-diversity forest is relatively low, representing less than 35% of the total number of species per ha. Gentry (1988) noted that in species-rich forest types, between 40% and 62% of species were represented by a single tree.
- (iv) High species dominance may occur in the understorey level (5 to 10 cm dbh), as defined in 'type II low-diversity' forest of Connell and Lowman (1989). However, tree data for size-classes below 10.0 cm are scarce, therefore the debate on understorey species dominance is inconclusive.
- (v) Species richness in low-diversity forests would appear to be predominantly accounted for within size-classes below 15 cm dbh, with little variation in species and tree densities in size-classes above 15 cm dbh (Tables 4 and 5).

Table 7. Comparisons of the floristic composition of 1 ha study plots at Kurupukari with selected neotropical study localities

	Kurupukari Guyana	Moraballi Cr. Guyana <sup>a</sup>	La Selva Costa Rica <sup>b</sup>	Cocha Cashu Peru <sup>c</sup>	Manaus Brazil <sup>c</sup>	Mishana Brazil <sup>c</sup>	Tambopata Peru <sup>c</sup>	Yanamono Peru <sup>c</sup>
No. of study plots	4	5	3	1	1	1	6	1
Size of study plot (ha)	1	1.2	4	1	1	1	1	1
Size threshold (cm dbh)	10.0	10.0	10.0	10.0	15.0	10.0	10.0	10.0
No. of species/ha	50-71	56-93	79-107	201	165	249	153-181	300
No. of plant families	23-26	23-30	-	47	36	43	41-46	48
No. of tree/ha	357-742	460-919	395-529	673	346	858	520-580	606
Species dominance <sup>d</sup>								
25% of trees	1-3	1-4	3	-	11	-	-	-
50%	2-7	4-8	12	-	-	-	-	-
95%	32-42	28-56	-	-	-	-	-	-
No. of species by family								
Leguminosae	6-11	8-11	28-30	27	19	37-38	19-28	42-44
Chrysobalanaceae	2-5	1-5	1-2	3	10	9	2-6	3
Lecthidaceae	2-8	1-6	3	1	18	5	2-4	7-9
Lauraceae	4-11	2-7	7-13	16	-	30	14-20	15
Bombacaceae	1-3	1-2	2-3	7	2	2	1-4	6
Moraceae	3-7	0-1	9-13	18	13	15	16-23	24

Data from <sup>a</sup>Davis and Richards (1934), <sup>b</sup>Lieberman and Lieberman (1987), <sup>c</sup>Gentry (1988, 1990); <sup>d</sup>species dominance taken as the number of species representing 25, 50 and 95% of the total number of trees.

### *Species richness and low-diversity forests*

The forest community at Kurupukari contained 14 tree species common to all four forest types, and a further 8–12 species abundant (species accounting for more than 10% of the total number of trees) within any given forest type. However, the relative abundance of these species varied considerably between the different forest types. A canopy tree species which was dominant within a given forest type was rarely dominant within another (although codominance between forest types was recorded, e.g. species of Lecythidaceae and Chrysobalanaceae). Typically one (e.g. *Mora excelsa*) or two (e.g. *Eperua falcata* and *Catostemma fragrans*) species were dominant within one particular area, but relatively scarce within another area, perhaps only 400–500 m from where that species was dominant.

It has often been noted that Leguminosae is the dominant family in neotropical forests (Gentry, 1988, 1990). For instance, Lieberman and Lieberman (1987) plots in Costa Rica, where Mimosoideae dominated, and *Pentaclethra macroloba* accounted for 13.7% of the trees. At Kurupukari Leguminosae represented 11.2% of the species, compared with 7.2, 7.2 and 6.6% of the Lauraceae, Lecythidaceae and Chrysobalanaceae respectively, the next most species-rich families. In comparison with species-rich forest types, a two to three-fold difference in the number of Leguminosae species per hectare is noticeable (Table 7). Gentry (1988) noted that 11 plant families (compared with eight at Kurupukari) contributed approximately half of the species richness of neotropical forests. These excluded Chrysobalanaceae and Lecythidaceae, both common and species-rich families at Kurupukari (notably in plot TA19).

The four plots at Kurupukari appeared to represent three types of 'low-diversity' forest, all of which exhibit a common characteristic of less than 100 species per hectare:

- (i) Single species dominant forest, *Mora excelsa* in the Mora plot, where one species represents between 50–80% of the canopy trees, or greater than 20% of the trees at all size-classes greater than 10.0 cm dbh.
- (ii) Two species dominant forest, *Eperua falcata* and *Catostemma fragrans* in TA2 plot, where two species represent more than 40% of the trees at all size-classes. High tree densities, typically greater than 500 trees per ha.
- (iii) Co-dominant forest, *Licania*/*Eschweilera*/*Pentaclethra* in TA12 plot, *Ocotea*/*Licania*/*Eschweilera* in TA19 plot, comprising two or three canopy species with any one species representing 10–20% of the trees, and species richness predominantly occurring at size-classes below 15 cm dbh.

Species dominance may be arbitrarily defined where a single species represents more than 20% of the total number of trees (at the 10.0 cm dbh threshold), and co-dominance when one or more species occurs, with each species representing 10 to 20% of the trees. Connell and Lowman (1989) recognized two types of low-diversity forest, differing in the persistence of the dominant (persistent dominant, Type I, and nonpersistent dominant forest, Type II). Connell and Lowman (1989) included both the *M. excelsa* and *E. falcata*/*C. fragrans* forest types (comparable with the Mora and TA2 plots presented here) of Davis and Richards (1934) as Type I low-diversity forests.

Both *M. excelsa* and *E. falcata*/*C. fragrans* forest types exhibit high seedling densities. In the TA2 plot (*Catostemma fragrans*) seedlings have been shown to include up to 80% of all individuals occurring below breast height. In contrast while *E. falcata* represented over 20% of the trees above 10 cm dbh, *E. falcata* seedlings were absent suggesting that the forest may shift towards single species dominance by *C. fragrans* (Johnston, in

preparation). Similar to *C. fragrans*, *M. excelsa* seedlings (individuals with a dbh < 1 cm) within the Mora-dominated forest represented up to 60% of the seedling-bank. While the Mora-dominated forests are considered to represent relatively established forest types (Davis and Richards, 1934; Beard, 1946), the remaining forest types (TA2, TA19, TA12) may represent forest ecotypes resulting from an interaction between soil type and successional stage. Hart (1990) proposed that high species dominance may be achieved during early and late successional stages, and co-dominance during mid-successional stages. The white sand forests dominated by *E. falcata*/*C. fragrans* may represent an early successional stage, which may be indicated by recent large-scale disturbance with the presence of charcoal in soil profiles (Hawkes and Wall, 1993), and the high densities and fast growth rates of *C. fragrans* seedlings (Johnston, in preparation). It is certainly likely that density-dependent processes during seedling/sapling recruitment are critical in determining species diversity and regulation of tree populations in both species-rich and species-poor forest types (Connell *et al.*, 1984; Hubbell *et al.*, 1990; Weldon, *et al.*, 1991; Condit *et al.*, 1992). However, the relative importance of succession in determining species dominance is currently impossible to assess without long-term monitoring of different forest types.

#### *Determinants of species dominance*

From these studies, six canopy dominant tree species (*E. falcata*, *C. fragrans*, *M. excelsa*, *Licania* sp., *E. sagotiana*, and *P. macroloba*) may be identified which exhibit a competitive advantage, under specific conditions, over other abundant tree species. Species dominance may be achieved by a species reducing the resource to the lowest rate of supply, so excluding all other species from utilizing that resource (Tilman, 1988). A mechanism by which such competitive advantage may be achieved is through the presence of mycorrhizae, as proposed by Connell and Lowman (1989), enabling that species to utilize a resource at levels previously limiting species dominance. However, evidence is lacking in support of Connell and Lowman (1989). Of the six species at Kurupukari, only *M. excelsa* and *P. macroloba* are definitely known to have an association with mycorrhizae (Connell and Lowman, 1989; Moyersoen, 1993). While *E. falcata* was considered by Connell and Lowman (1989) to be ectomycorrhizal, recent studies by Moyersoen (1993) in Caatinga forest of southern Venezuela have failed to show any such association. The presence of mycorrhizae may explain the high dominance of *M. excelsa* on alluvial soils, however, mycorrhizal associations are clearly not the only mechanism determining species dominance in low-diversity forest types, such as the dominance of *E. falcata*/*C. fragrans* on white sand soils. In order to assess the persistence of species dominance within these low-diversity forest types, and the mechanisms determining such dominance, it is essential that long-term manipulation experiments are conducted, which may then provide a better understanding of the dynamics of both species-poor and species-rich neotropical tree populations.

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Appendix 1. (Continued)

Family	Species	Voucher no.	Mora				TA19				TA2			
			5	10	5	10	5	10	5	10	5	10	5	10
Bombacaceae	<i>Catostemma fragrans</i>	102-92	14	10	32	18	38	15	414	202				
	<i>Catostemma</i> sp.	Obs.			1	1								
	<i>Bombax flaviflorum</i>	166-93	4	4				10	8					
Moraceae	<i>Brosimum guianense</i>	65-93	5	1	4	1	2	1	2	2				
	<i>Brosimum rubescens</i>	65b-93	4		4	2			3	2				
	<i>Ficus</i> sp. I	95-93	1	1	19	7	10	8						
	<i>Ficus</i> sp. II	95b-93	1				2							
	<i>Ficus</i> sp. III	Obs.					7	4	1	5				
	<i>Ficus</i> sp. IV	95c-93					3							
Cecropiaceae	<i>Cecropia</i> sp. I	Obs.	4	1	4	3		4						
	<i>Cecropia</i> sp. II	Obs.					1	1						
Lecythidaceae	<i>Eschweilera sagotiana</i>	7-92	6	6	69	69	86	63						
	<i>Eschweilera longipes</i>	78-93	3	5	2	2								
	<i>Eschweilera wachenheimii</i>	79-93	3	3	1	1	2	2						
	<i>Eschweilera grata</i>	120-93	3	3					1	1				
	<i>Lecythis zabucajo</i>	Obs.	3	3	1	1								
	<i>Lecythis corrugata</i>	105-92	8	8			12	5						
	<i>Lecythis confertiflora</i>	104-92	1	1	2	2		1						
Violaceae	<i>Couratari guianensis</i>	103-92					5	5	5	5				
	<i>Eschweilera</i> sp.	127-92					13	4						
	<i>Paypayrola longifolia</i>	6-93			1		11	3						
Sapotaceae	<i>Rinorea pubiflora</i>	82-92, 9-93	8	1	1	1	4	2						
	<i>Pouteria guianensis</i>	2-92			2	2	1	1						
	<i>Pouteria engleri</i>	75-93					4	3	5	3				
	Unk.	Obs.					2	5						

## Appendix 1. (Continued)

Family	Species	Voucher no. dbh	Mora			TA12			TA19			TA2		
			5	10	10	5	10	10	5	10	10	5	10	10
Chrysobalanaceae	<i>Licania alba</i>	3-92	20	6	27	46	27	105	53					
	<i>Licania persaudii</i>	4-92	2	2	7	7						25	12	
	<i>Licania heteromorpha</i>	11-92	10	10	23	48	23	114	57			11	9	
	<i>Licania cf. cuprea</i>	170-93										15	9	
	<i>Licania buxifolia</i>	171-93										14	14	
	<i>Parinari campestris</i>	86-92	3	2	1	1	1							
	<i>Licania sp. I</i>	Obs.	14	14										
	<i>Hirtella cf. silicea</i>	8-93						5					8	
<i>Licania sp. II</i>	Obs.													
Caesalpinioideae	<i>Eperua falcata</i>	110-92	35	13	33	40	33	1	1	1	331	215		
	<i>Eperua rubiginosa</i>	109-92	12	10										
	<i>Mora excelsa</i>	107-93	114	72	10	22	10	6	2					
	<i>Peltogyne sp.</i>	Obs.						1						
	<i>Sclerobium guianense</i>	14-92	8	2	23	27	23	23	18					
Papilionoideae	<i>Swartzia leiocalycina</i>	67-93	28	11	4	6	4	38	25					
	<i>Swartzia sp.</i>	Obs.	1	1							1	1		
	<i>Swartzia benthamiana</i>	160-93			2	2	2	10	5	5	25	14		
	<i>Clathrotropis</i>													
	<i>brachypetala</i>	45-92	25	10										
	<i>Clathrotropis macrocarpa</i>	150-93			8	8	8	36	25					
	<i>Diptotropis purpurea</i>	Obs.			1	1								
	<i>Ormosia coutinhoi</i>	159b-93			8	9	8	8	4		48	30		
<i>Unk. I</i>	127-93									1	1			
<i>Unk. II</i>	159a-93									1	1			
Mimosoideae	<i>Inga alba</i>	17-93	2	2	4	4	4	1			3	3		
	<i>Inga sp. I.</i>	89-92	2	2	3	3	3							
	<i>Inga sp. II.</i>	54-93	1	1										
	<i>Pentaclethra macroloba</i>	5-90	71	31	90	90	51							

Appendix 1. (Continued)

Family	Species	Voucher no.	Mora				TAI			
			dbh	5	10	10	5	10	5	10
Myrtaceae	<i>Eugenia patrisii</i>	Obs.	4	2	2	2	2	2	2	2
	<i>Marlierea</i> sp.	137-93	4	1	1	1	1	1	1	1
	<i>Myrcia phaeoclada</i>	97-93	38	3	1	1	2	2	2	2
	<i>Myrcia</i> sp. I.	121-93	1	1	1	1	1	1	1	1
	<i>Myrcia</i> sp. II	Obs.	1	1	1	1	1	1	1	1
Melastomataceae	Unk.	109-93								1
Olacaceae	<i>Heisteria cauliflora</i>	98-92				1	1	1	1	1
Ochnaceae	<i>Elvasia</i> sp.	20-92		2		1	1	1	1	1
Goupiaceae	<i>Goupia glabra</i>	19-92	9	11	6	3	3	3	3	3
Icacinaceae	<i>Emmotum</i> sp.	120-93								7
Dichapetalaceae	<i>Tapura guianensis</i>	65-92	65	6	7	34	34	2	22	5
Sapindaceae	<i>Talisia squarrosa</i>	169-93	3	1	7	4	6	4	11	3
	Unk.	2-93	3						5	5
Bursaceae	<i>Protium guianense</i>	37-93		4	4					
	<i>Protium sagotianum</i>	7-90		12	7	7	7	7	5	5
	<i>Protium decandrum</i>	28-92	4	2	2	6	6	6	6	6
	<i>Protium tenuifolium</i>	22-93				3	3	3	3	3
	<i>Protium</i> sp. I	Obs.	2	1		4	4	3	3	3
Anacardiaceae	<i>Protium</i> sp. II	Obs.				1	1	1	3	3
	<i>Tapirira marchandii</i>	23-92		2	2					
	<i>Tapirira guianensis</i>	59-93	3	3	3				6	4
	<i>Quassia simarouba</i>	Obs.	5	5	5	5	5	1	5	5
	<i>Quassia cedron</i>	136-93		6	5	7	7	3	5	5
Humiriaceae	<i>Humiria balsamifera</i>	Obs.		2	2				2	2
Araliaceae	<i>Schefflera decaphylla</i>	31-92	1	1	1				1	1
	<i>Tabernaemontana attenuata</i>	106-92	4	2						

## Appendix 1. (Continued)

Family	Species	Voucher no. dbh	Mora		TA12		TA19		TA2	
			5	10	5	10	5	10	5	10
	<i>Tabernaemontana undulata</i>	106b-92			1					
	<i>Aspidosperma oblongum</i>	8-92			3		7	2		
	<i>Aspidosperma</i> sp.	Obs.	2	2					2	2
	<i>Couma guianensis</i>	Obs.	1	1			2	2		
	<i>Parahancornia fasciculata</i>	Obs.	1	1					1	1
	Unk.	Obs.	1	1						
Boraginaceae	<i>Cordia nodosa</i>	9-92	5	4		7		2		
	<i>Cordia</i> cf. <i>alliodora</i>	15-92	1			6		3		
Bignoniaceae	<i>Jacaranda copaia</i>	Obs.	1	1		2	3	2		
Rubiaceae	<i>Duroia eriopila</i>	64-92	2	2		15	14	6	3	68
	<i>Duroia genipoides</i>	6-92	6	6		5		4		
	Unk.	39-93				2		2	2	
Arecaceae	<i>Oenocarpus bacaba</i>	22-92	1	1		2	4	2	4	
	<i>Bactris</i> sp.	Obs.				1				
	<i>Euterpe oleracea</i>	27-92				2		2		7
	<i>Astrocaryum sciophilum</i>	Obs.	3	3		3	5	3	5	
	<i>Socratea exorrhiza</i>	Obs.	3	3						
	No. of unidentified trees		10	2		8	32	6	12	180
	No. of unidentified species		6	2		8	19	6	8	13
	No. of identified trees		706	355		864	837	453	465	1260
	No. of identified species		66	62		73	65	65	59	48
	No. of identified families		23	23		25	26	23	23	23
	Total no. of trees		716	357		872	869	459	477	1440
	Total no. of species		72	64		81	84	71	67	61