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TREE SPECIES DIVERSITY OF A PREMONTANE RAIN FOREST IN THE CORDILLERA DE TILARAN, COSTA RICA

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Resumen. La diversidad de las especies de árboles en un bosque muy húmedo premontano fue investigado en la Reserva Forestal de San Ramón, Costa Rica. Se han encontrado 94 especies de árboles de 40 familias desde 10 cm de diametro (DBH). La parcela de investigación se encuentra a 1000 m de altitud, mide una hectárea y encierra 25 subparcelas de 20 por 20 metros. La cantidad de especies corresponde a la cantidad de especies de bosques muy húmedos de las zonas bajas. La relación entre las especies de árboles y el tamaño de la parcela indica que el tamaño de una hectárea no es suficiente para un inventario completo. Más que un tercio de las especies existe con un sólo individuo en la parcela. Casi no existen árboles dominantes. La dominancia y abundancia de especies es tema de discusión en este artículo.

Abstract. Tree species diversity was studied in a premontane wet forest area in the Reserva Forestal de San Ramón (40 km North of San Ramón, Alajuela, Costa Rica). About 94 species of trees (DBH ≥ 10 cm) from 40 families of Angiosperms were found. The study plot consisted of 25 squares of 20 x 20 m, located at an altitude of about 1000 m. Species number is in the same range as that of lowland rain forests, but the species-area relationship indicates that the 1 ha study plot is not sufficient for a complete inventory. About one third of the tree species are represented by a single individual only. Dominant species are almost lacking. Dominance and abundance of tree species is critically discussed. *Accepted 21 March 1995.*

Key words: Costa Rica, premontane wet forest, tree species diversity, tree dominance.

INTRODUCTION

Tropical rain forests are complex ecosystems which are especially rich in species. They are distinguished from all other terrestrial ecosystems by a very high diversity on many levels (species, life-forms, etc.). Although they cover less than 10% of the world's land surface they contain considerably more than half of the world's living species (Wilson 1988). This is even more the case for plants, since at least two thirds of the assumed 250.000 cormophyte species grow in the tropics (Kubitzki 1985, Whitmore 1993). Not only is the total diversity in the various tropical forests impressive, also a high diversity level can be seen on a local scale, e.g., 233 different cormophytes grow in only 100 m^2 in a lowland wet forest in Costa Rica (Whitmore *et al.* 1985). Most taxa (mosses, ferns, orchids, etc.) or lifeforms (epiphytes, lianas, etc.), and especially trees, exhibit a similar diversification on a local scale.

There are some tree species lists from tropical areas which demonstrate that lowland rain forests are often dominated by a few tree species (e.g., *Pentaclethra macroloba* in La Selva), but still many other tree species are present in very low numbers (Lieberman & Lieberman 1987). In some montane, or cloud forests, tree species diversity seems to be extrordinarily high. The record is held by two areas of lower and higher fertility, with about 289 and 300 tree species per hectare, as shown by Gentry (1988a, 1988b) for Yanamono close to Iquitos in Peru (Terborgh 1992). Since data on tree species diversity, dominance and abundance from lower montane forests in the tropics are almost lacking (Swaine *et al.* 1987), we have chosen a premontane study site in the Cordillera de Tilarán.

Floristic inventories can be used later on as a basis for biogeographical evaluations. Furthermore, floristic inventories are basic requirements for ecological studies relating to altitudinal gradients as well as to future studies on ecosystem structure and processes at the study site.

STUDY AREA

The study was carried out during August 1992 and March 1994 in the Reserva Forestal de San Ramón (RFSR) (since 1994 Reserva Biológica Alberto Brenes). The RFSR (founded 1975) is located in the province of Alajuela in north-central Costa Rica (10° 13'N, 84° 37'W) and forms part of the Caribbean slope of the Cordillera de Tilarán. 7800 ha of almost undisturbed primary forest cover this protected area. The relief is very mountainous with inclinations of up to 25°–30° over more than 80% of the whole area (Cruz 1989, Ortiz Vargas 1991a).

The soils developed from volcanic ashes. They are dark, deep and rich in organic matter, well drained and fairly rich in nutrients. They can be classified as andosols (Pérez *et al.* 1978). With altitudes ranging between 800-1500 m and an average annual rainfall up to 4000 mm, the RFSR can be classified as part of the Orobiome I (Walter & Breckle 1983, 1991), forming a premontane wet forest following the life-zone system of Holdridge *et al.* (1971). The study site is located on the south-eastern slope of the Río San Lorencito valley near the Biological Station of the RFSR. The altitude ranges between 910 and 950 m with a mean inclination of 14°.

Altitudinal aspects

The Reserva Forestal de San Ramón provides at an intermediate altitudinal level of about 1000 m forest significantly different from wet evergreen lowland forests in Costa Rica such as in La Selva, (< 100 m) or montane forests as in Monteverde (1400-1700 m). The forest canopy reaches a height of 30-40 m but does not appear very dense, the different canopy layers contain numerous small and medium-sized gaps and permit a well-developed herbaceous layer at the ground. Based on the interesting mixture of lowland and highland species which covers the RFSR, this forest can be interpreted as a transition forest (Burger 1991).

Local floristics

Besides common lowland and montane species, several unusual and endemic species can be found in the RFSR, like the highly dispersed passion flower tree *Passiflora tica* or an unusual new genus of the Lauraceae *Povedadaphne* (Burger 1991, Gómez Laurito & Ortiz Vargas 1991). Even a new endemic tree family, Ticodendraceae *(Ticodendron incognitum)*, has been discovered (Gómez Laurito & Gómez 1989). Further endemic trees, like the Myrtaceae *Plinia salticola* are known (Sprenger 1992).

A considerable number of tree species exists with extremely low density, and in an ample region only single individuals were found. Additionally no tree species dominance seems to be apparent.

METHODS

One hectare of forest area, apparently homogenous with respect to physiognomy, was selected, marked out and subdivided in 25 sub-plots of 400 m^2 each. All trunks (including the palms and the tree ferns) with 10 cm diameter at breast height (DBH) and more were counted, tagged, and the trees identified. The trees which could not be identified in the field by examination with binoculars were inspected at the Herbario Nacional de Costa Rica by means of collected specimens. Additionally the trees were measured in height and DBH and were mapped to the nearest 50 cm.

The abundance and dominance values (total and proportional) of each tree species were calculated from the inventory data. Total abundance (TA) represents the trunk number per area of each species, the proportional abundance (PA) means their percentage of the total trunk number per area. The basal area of tree species provides a more reliable instrument for biomass estimations than do trunk numbers, therefore tree species dominance values (TD) are represented by their basal area, calculated from DBH (Hoheisel 1976, Lamprecht 1986). The proportional dominance (PD) is equivalent to the percentage of each tree species' value of the total basal area in the study plot.

The distribution of the tree species' frequency values indicates the homogeneity level of a forest stand (*sensu* Lamprecht 1986). The frequency (F) of the tree species was examined by evaluation of the tree positions within the plot. If a species occurs in all subplots (n=25) it is represented in 100% of the plots and is well dispersed. The occurrence in only one sub-plot corresponds in the present investigation to a minimum frequency of 4% and indicates rareness. The frequency values have been subdivided into 5 classes: category I corresponds to occurrence of a tree species in 1–20% of the sub-plots, following by category II with 21–40% up to category V or occurrence in 81–100% of all sub-plots.

RESULTS

General findings

In the one hectare study plot a total of 436 living trees with at least 10 cm DBH (including the palms) were found, belonging to 94 species and 40 families. Only two species of the diverse palm flora of the RFSR exceed the minimum DBH level of 10 cm, contributing 13.9% to the total trunk number, and 6.11% to the basal area of the plot. Considering the area occupied, the number of the tree ferns with at least 10 cm DBH is also noteworthy, with 83 individuals (15.6% of all stems) they comprise a basal area at breast height of 1.27 m², which corresponds to a proportional dominance of 2.94% (Table 1).

Another striking aspect can be seen in Table 1: the dominance (TD) and the abundance values (TA) of the tree species diverge widely. The most abundant tree species are not the most dominant; the palm *Iriartea deltoidea* is present with 66 individuals and a dominance value of 2.44 m² or 5.68%, while the 3 most dominant tree species *Elaegia uxpanapensis*, *Ficus jimenesis* and *Weinmannia pinnata* comprise a total of

TABLE 1. Total and proportional abundance (TA, PA), total and proportional dominance (TD, PD) and the frequency (F) of the tree species in the one hectare study plot. TA represents the trunk number per species per hectare, PA is the percentage per species of all trunks. TD represents the basal area, unit is m². PD represents the percentage of each tree species of the total TD-value. F indicates the occurrence of the tree species in percent of all sub-plots (n = 25, area of each plot = 400 m²). All trees in the one hectare study site with a DBH ≥ 10 cm were included. The tree species were arranged by the TA-value in declining order.

No.	Tree species	Family	TA N	PA %	TD m2	PD %	F %
1	*Iriartea deltoidea* Ruíz Lopez & Pavón	Arecaceae	66	12,7	2,44	5,68	92
2	*Plinia salticola* Mc Vaugh	Myrtaceae	40	7,7	0,49	1,14	72
3	*Inga leonis* Zamora	Mimosaceae	17	3,3	0,53	1,24	44
4	*Guarea glabra* M. Vahl	Meliaceae	15	2,9	2,33	5,42	44
5	*Sloanea faginea* Standley	Elaeocarpaceae	13	2,5	1,22	2,84	40
6 (1)	*Elaegia uxpanapensis* Lorence ined.	Rubiaceae	13	2,5	12,18	28,36	40
7	*Cupania macrophylla* A. Rich.	Sapindaceae	12	2,2	0,85	1,97	36
8	*Calatola costaricensis* Standley	Icacinaceae	11	2,3	0,40	0,94	32
9	*Pseudelmedia oxyphyllaria* J. D. Smith	Moraceae	10	1,9	0,29	0,67	28
10	*Clethra mexicana* A. DC.	Clethraceae	9	1,7	0,65	1,52	20
11	*Brosimum costaricanum* Liebm.	Moraceae	9	1,7	0,42	0,99	28
12	*Cestrum scandens* Vahl	Solanaceae	8	1,5	0,09	0,22	16
13	*Protium costaricense* (Rose) Engl.	Burseraceae	8	1,5	0,27	0,64	20
14	*Lonchocarpus pentaphyllus* (Poiret) DC.	Papilionaceae	8	1,5	0,32	0,74	32
15	*Conostegia micrantha* Standley	Melastomataceae	8	1,5	0,31	0,18	32
16	*Ruagea glabra* Triana & Planchon	Meliaceae	7	1,3	0,57	1,34	20
17	*Trophis mexicana* (Liebm.) Bureau	Moraceae	7	1,3	0,17	0,39	24
18	*Euterpe macrospadix* Oersted	Arecaceae	6	1,2	0,18	0,43	24
19	*Perrottetia longistylis* Rose	Celastraceae	6	1,2	0,38	0,90	12
20	*Alchornea* sp.	Euphorbiaceae	6	1,2	0,56	1,29	16
21	*Sapium oligoneurum* Schumann & Pittier	Euphorbiaceae	6	1,2	2,09	4,86	24
22	*Inga barbourii* Standley	Mimosaceae	6	1,2	0,34	0,80	24
23	*Hernandia stenura* Standley	Hernandiaceae	6	1,2	0,62	1,45	20
24	*Elaegia auriculata* Hemsley	Rubiaceae	5	1,0	0,08	0,18	16
25	*Cordia lucidula* J.M. Johnston	Boraginaceae	5	1,0	0,27	0,14	20
26	*Erythrina gibbosa* Cuf.	Papilionaceae	5	1,0	0,09	0,20	16
27	*Helicostylis tovarensis* (Klotzsch & Karsten) C.C. Berg	Moraceae	5	1,0	0,06	0,13	20
28	*Mortoniodendron anisophyllum* (Standley) Standley & Steyerm.	Tiliaceae	5	1,0	0,37	0,86	20
29	*Ocotea insularis* (Meissner) Mez	Lauraceae	4	0,8	0,10	0,24	12
30	*Conostegia setifera* Standley	Melastomataceae	4	0,8	0,05	0,11	12
31	*Marlieria mesoamericana* P.E. Sanchez	Myrtaceae	4	0,8	0,26	0,61	16
32	*Pouteria austin-smithii* (Standley) Cronq.	Sapotaceae	4	0,8	0,06	0,15	16
33	*Pachira aquatica* Aublet	Bombacaceae	3	0,6	0,08	0,19	12
34	*Alchornea glandulosa* Poeppig var. *pittieri* (Pax) Pax	Euphorbiaceae	3	0,6	0,10	0,24	8
35	*Hyeronima oblonga* (Tul.) Muell. Arg.	Euphorbiaceae	3	0,6	0,21	0,49	12
36	*Pithecellobium brenesii* Standley	Mimosaceae	3	0,6	0,03	0,08	12
37	*Miconia brenesii* Standley	Melastomataceae	3	0,6	0,04	0,10	12
38 (2)	*Ficus jimenesis* Standley	Moraceae	3	0,6	5,13	11,96	12
39	*Otoba novogranatensis* Mold.	Myristicaceae	3	0,6	0,08	0,18	12
40	*Eugenia valerii* Standley	Myrtaceae	3	0,6	0,09	0,21	12

No.	Tree species	Family	TA N	PA %	TD m2	PD %	F %
41	*Allophyllus psilospermus* Radlk.	Sapindaceae	3	0,6	0,04	0,09	8
42	*Heliocarpus apendiculatus* Turcz.	Tiliaceae	3	0,6	0,09	0,20	8
43	*Cecropia insignis* Liebm.	Cecropiaceae	2	0,4	0,16	0,36	8
44 (3)	*Weinmannia pinnata* L.	Cunoniaceae	2	0,4	3,17	7,39	8
45	*Erythroxylum macrophyllum* Cav.	Erythroxylaceae	2	0,4	0,04	0,09	4
46	*Inga punctata* Willd.	Mimosaceae	2	0,4	0,03	0,08	8
47	*Pterocarpus hayesii* Hemsley	Papilionaceae	2	0,4	0,33	0,77	8
48	*Alfaroa costaricensis* Standley	Juglandaceae	2	0,4	0,10	0,23	8
49	*Ocotea babosa* Allen	Lauraceae	2	0,4	0,05	0,12	8
50	*Ocotea gomezii* W. Burger	Lauraceae	2	0,4	0,02	0,06	4
51	*Ocotea tenera* Mez & J.D. Smith ex Mez	Lauraceae	2	0,4	0,02	0,05	8
52	*Povedadaphne quadriporata* W.Burger	Lauraceae	2	0,4	0,66	1,53	4
53	*Conostegia* sp.	Melastomataceae	2	0,4	0,02	0,04	8
54	*Naucleopsis naga* Pittier	Moraceae	2	0,4	0,09	0,22	8
55	*Sorocea trophoides* W.Burger	Moraceae	2	0,4	0,08	0,18	8
56	*Virola guatemalensis* (Hemsley) Warb.	Myristicaceae	2	0,4	0,04	0,08	8
57	*Neea* sp.	Nyctaginaceae	2	0,4	0,04	0,10	8
58	*Chimarrhis parviflora* Standley	Rubiaceae	2	0,4	0,06	0,14	8
59	*Randia calycosa* Standley	Rubiaceae	2	0,4	0,02	0,06	8
60	*Turpinia occidentalis* (Sw.) Don	Staphyllaceae	2	0,4	0,08	0,18	8
61	*Xylopia bocatorena* Schery	Annonaceae	1	0,2	0,03	0,06	4
62	*Hirtella triandra* Sw.	Chrysobalanaceae	1	0,2	0,05	0,12	4
63	*Licania hypoleuca* Benth.	Chrysobalanaceae	1	0,2	0,27	0,64	4
64	*Licania kallunkii* Prance	Chrysobalanaceae	1	0,2	0,02	0,04	4
65	*Coussapoa parviceps* Standley	Cecropiaceae	1	0,2	0,23	0,53	4
66	*Dichapetalum donnell-smithii* Engl.	Dichapetalaceae	1	0,2	0,03	0,07	4
67	*Alchornea latifolia* Sw.	Euphorbiaceae	1	0,2	0,01	0,02	4
68	*Tetrorchidium europhyllum* Standley	Euphorbiaceae	1	0,2	0,08	0,18	4
69	*Inga oerstediana* Benth. ex Seemann	Mimosaceae	1	0,2	0,01	0,02	4
70	*Hasseltia floribunda* Kunth.	Flacourtiaceae	1	0,2	0,07	0,16	4
71	*Xylosma hispidula* Standley	Flacourtiaceae	1	0,2	0,05	0,11	4
72	*Billia colombiana* Planch. et Lindl.	Hippocastanaceae	1	0,2	0,05	0,12	4
73	*Salacia petenensis* Lundell	Hippocrateaceae	1	0,2	0,03	0,07	4
74	*Ocotea whitei* Woodson	Lauraceae	1	0,2	0,02	0,04	4
75	*Ocotea* sp.	Lauraceae	1	0,2	0,06	0,14	4
76	*Eschweilera neei* S Mori	Lecythydaceae	1	0,2	0,01	0,02	4
77	*Bunchosia veluticarpa* W.R. Anderson ined.	Malpigiaceae	1	0,2	0,02	0,05	4
78	*Conostegia oerstediana* O. Berg ex Triana	Melastomataceae	1	0,2	0,01	0,03	4
79	*Miconia theaezans* Bonpl. Cogn.	Melastomataceae	1	0,2	0,03	0,08	4
80	*Clidemia densiflora* (Standley) Gleason	Melastomataceae	1	0,2	0,01	0,03	4
81	*Guarea rhopalocarpa* Radlk.	Meliaceae	1	0,2	0,02	0,04	4
82	*Ficus costaricana* (Liebm.) Miq.	Moraceae	1	0,2	0,26	0,61	4
83	*Ficus* sp.	Moraceae	1	0,2	0,13	0,29	4
84	*Maquira costaricana* (Standley) C.C. Berg	Moraceae	1	0,2	0,02	0,05	4
85	*Ardisia* sp.	Myrsinaceae	1	0,2	0,01	0,02	4
86	*Eugenia austin-smithii* Standley	Myrtaceae	1	0,2	0,01	0,02	4
87	*Neea amplifolia* J.D.Smith	Nyctaginaceae	1	0,2	0,01	0,03	4
88	*Neea popenoei* P.Allen	Nyctaginaceae	1	0,2	0,06	0,13	4
89	*Coccoloba tuerkheimii* J.D. Smith	Polygonaceae	1	0,2	0,35	0,82	4
90	*Guettarda crispiflora* M. Vahl	Rubiaceae	1	0,2	0,07	0,16	4
91	*Coussarea caroliana* Standley	Rubiaceae	1	0,2	0,01	0,02	4
92	*Meliosma vernicosa* (Liebm.) Griseb.	Sabiaceae	1	0,2	0,07	0,15	4
93	*Cupania glabra* S.W.	Sapindaceae	1	0,2	0,03	0,08	4
94	*Hybanthus guanacastensis* Standley	Violaceae	1	0,2	0,01	0,02	4
	Total tree species		436	84,4	41,67	97,06	100
	Tree ferns		83	15,6	1,27	2,94	92
	Total individuals		519	100	42,94	100	100

20.48 m^2 or 47.71% of the dominance value with only 18 individuals. The total basal area of all trunks is 42.94 m^2 (see Table 1).

Floristic structure

The canopy of the study-plot reaches a height of 40 m, but only 2,5% of all trees constitute the highest layer between 30 and 40 m. The mightiest canopy layer is formed at medium height between 10 and 20 m by 55% of all trees. More than a third of all trees have a height of between 5 and 10 m while 10% reaches 5 m (Fig. 1).

A more striking distribution has been found at the measured DBH's of all trees, which range between 10 and 210 cm. 85% of all trees measure between 10 and 30 cm DBH. 8% of the trees still remain between 30 and 50 cm DBH, and the upper range between 50 and 210 cm DBH is represented alltogether by only 7% (Fig. 2).

Species-area relationship

Fig. 3 shows the steady increase in tree species number while adding the areas of the sub-plots (with 400 m^2 size each) up to n = 25, equivalent to the whole one hectare study-plot. Summing the first 6 sub-plot areas the species number increases steeply as expected, while with further summation the increase declines slightly. But even by adding the areas of the final sub-plots a notable increase in species number still can be observed. This species-area relationship clearly indicates that the minimum area of the classical phytosociological approach is not yet reached within the 1 ha study plot.

Tree species dispersion

More than a third of the tree species are represented by only one individual in the whole study-plot; they are highly dispersed (see Table 1). The frequency values (F) of the more abundant tree species indicate

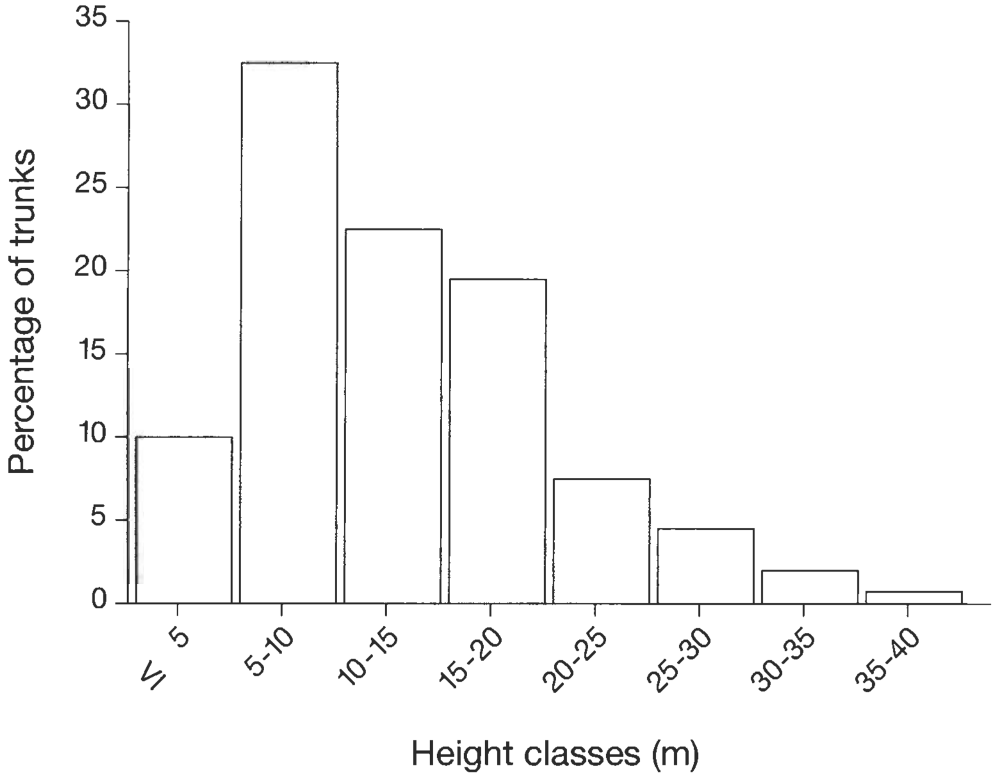

FIG. 1. Percentage distribution of individual trees (≥10 cm DBH) within trunk height classes (m). Minimum height was 2.70 m, maximum height 40 m.

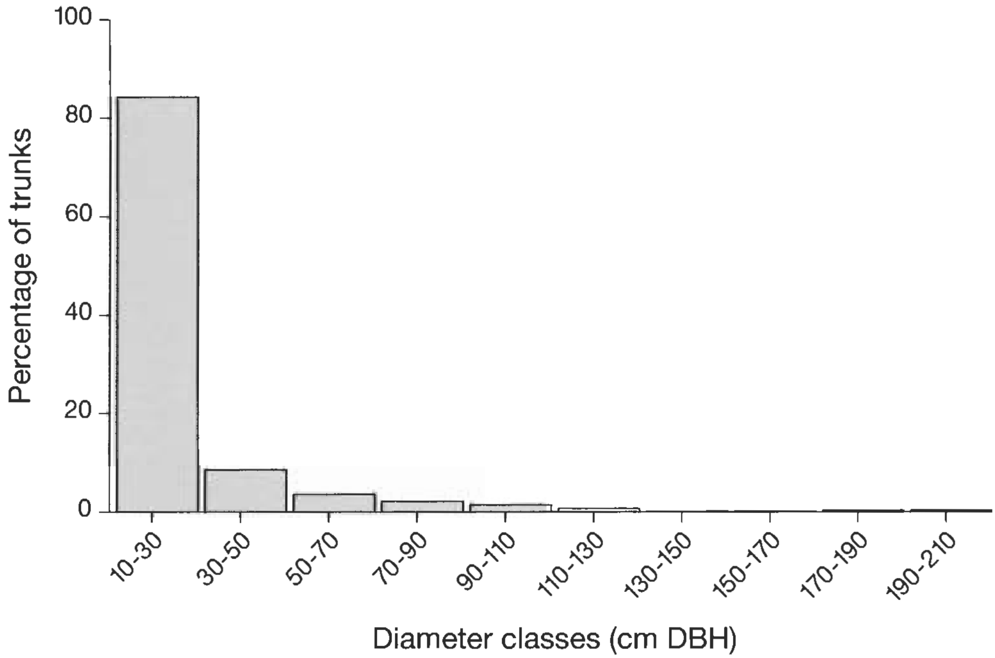

FIG. 2. Percentage distribution of individual trees within trunk diameter classes (DBH). Maximum diameter was 210 cm.

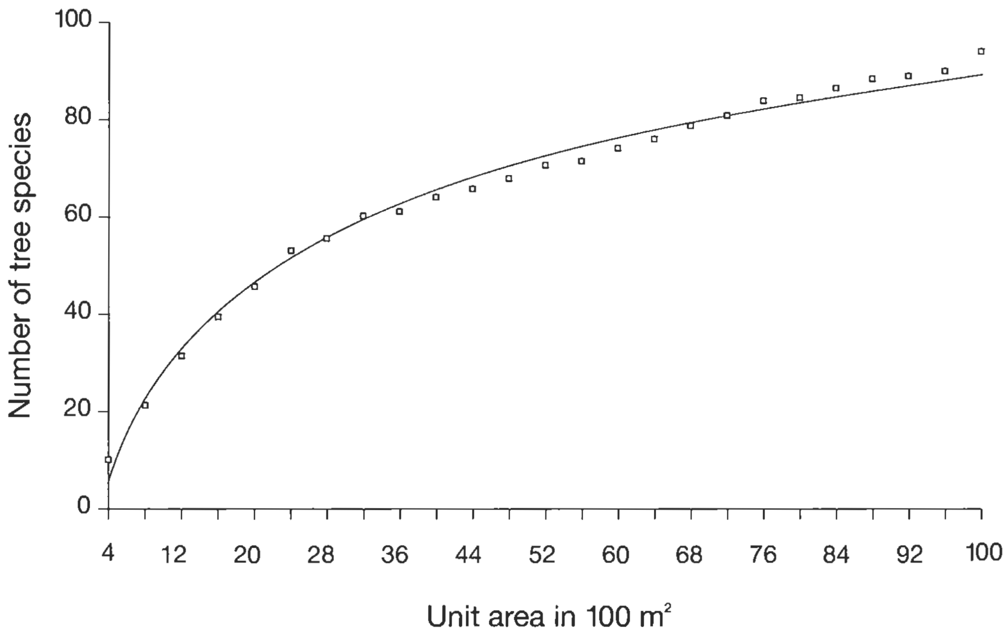

FIG. 3. Species number per unit area; increasing number of species with increasing number of sub-plots (n=25), area of each plot = 400 m^2.

an almost even distribution throughout the plot, no clumping was observed. The horizontal distribution of all abundant tree species in the study-plot is indicated in Fig. 4. It is very obvious that 82% of all species can be found in frequency category I, they appear only in 20% of the sub-plots; only 10% grow in 40% of the plots. The remaining 8% of tree species occur in more than 40 % of the plots. The typical frequent tree species with regular occurrence in more than 4/5 of the plots are very rare.

DISCUSSION

Tree species inventories at defined study sites and in minimum diameter classes give a reliable instrument to indicate the diversity level of a study site. Habitat diversity gradients can be used to examine biogeographic relationships.

The tree species inventory in the one hectare study-plot in the Reserva Forestal de San Ramón shows a high species richness. The 94 tree species per ha which have been found reached the same magnitude of tree species numbers (79–107 species per ha) found by Lieberman & Lieberman (1987) in lowland forests in Costa Rica.

The San Ramón figure is lower than the 125 species per ha counted in Suriname by Maas (1971) and the 144 species per ha by Cain *et al.* (1956) and Pires *et al.* (1953), both in Brazil, as well as the 153 species per ha found by Korning & Thomsen (1987) in Venezuela.

But also notably less species rates than in the RFSR have been recorded from several lowland sites cited in Lamprecht (1986), who reports species numbers with a range between 42 and 85 tree species per ha in lowland forests in Venezuela. In the Dominican Republic 31 species per ha at about 500 m (Ankewitz & Collbey 1992) were counted. Though several studies have shown a decline in tree species richness with increasing altitude (Flenley 1979, Jacobs 1981, Lamprecht 1986, Heaney & Proctor 1990) this is not the case with our study site: even at an altitude of

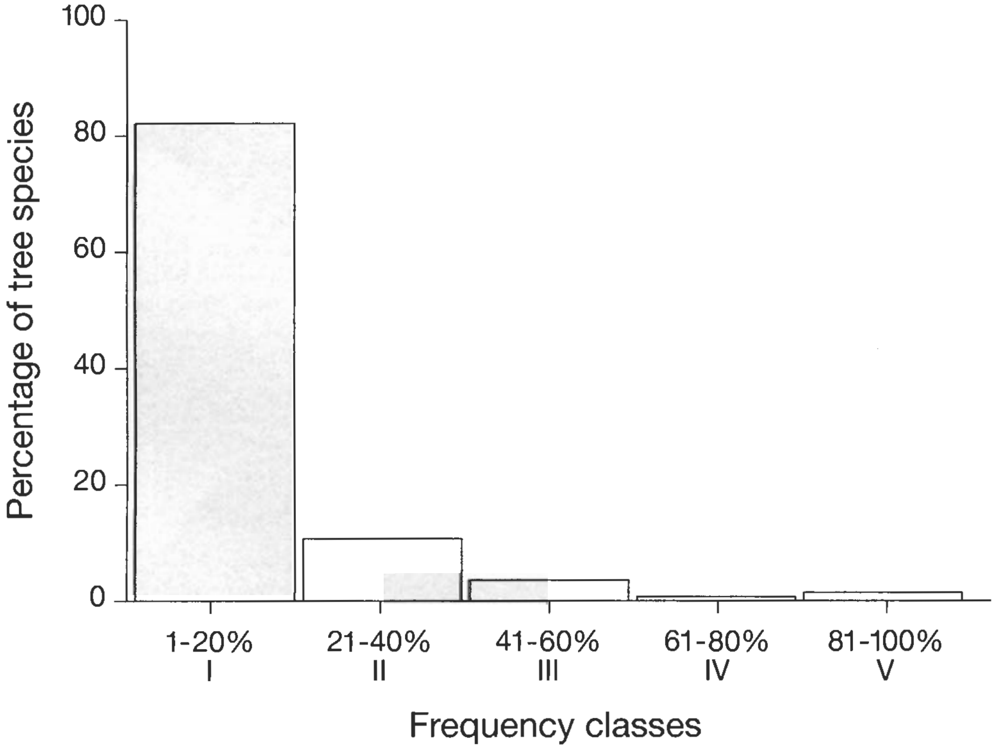

FIG. 4. Distribution of tree species within different frequency classes. Category I corresponds to occurrence in 1–20% of the sub-plots, category II to 21–40%, up to category V, *i.e.*, occurrence in 81–100% of the subplots (number of sub-plots = 25, area of each plot = 400 m^2).

about 1000 m it still maintains this high species number. Some montane locations also seem to contradict this reported general observation as was shown by Gentry (1988) for Yanamono in Peru. Certainly not only elevation-dependent factors control tree species diversity. Responsible factors among others may be the high annual rainfall of up to 4000 mm without a real dry period, and the sufficient but not too rich nutrient availability of the andosols, which exclude some other biodiversity limiting factors (Burger 1980). Gentry (1982, 1992) found a close correlation between increasing forest diversity and higher rainfall and the equal distribution of rainfall throughout the year.

The low dominance values of the tree species contribute considerably to tree species richness (Tilman 1982). The most dominant tree species which was found was *Elaegia uxpanapensis*, which comprised nearly a third (28.4%) of the total basal area but has only 2.5% of the trunk abundance. In spite of the high PD-value *Elaegia uxpanapensis* is not a noticeably dominant tree in comparison to *Pentaclethra macroloba* of lowland forest in La Selva (Lieberman & Lieberman 1987) with a percentage basal area (=PD) of 36% and 13.7% of all trunks. The dominance of *Pentaclethra macroloba* is obvious because of high PD- and high PA-values. We suggest indicating dominance of a tree species by the mean value of the proportional dominance (PD) and proportional abundance (PA). If dominance values are calculated in this way, *Elaegia uxpanapensis* would have a value of 15.5%, better reflecting the apparent dominance level.

The widely diverging TA and TD values of the different tree species *Elaegia uxpanapensis, Ficus jimenesis* and *Weinmannia pinnata* indicate their highly differing DBHs. Of course, the three most dominant tree species exhibit the highest DBH values.

The height and DBH measurements are in agreement with observations by Bernhardt (1991) and Hartshorn (1991) of a premontane wet forest, where the upper layer of the canopy reaches 30-40 m. Canopy heights of tropical wet forests decline with increasing altitude (Jacobs 1981, Whitmore 1975). The lower layer is compact, with numerous slim trees between 15 and 25 m in height (Hartshorn 1991).

The numerically high abundance of tree ferns is quite characteristic for wet forests at higher altitudes (Hartshorn 1991, Lamprecht 1986, Whitmore 1975), their percentage of basal area rising with increasing altitude as shown by Heaney & Proctor (1990). High trunk numbers of palms are in the same way characteristic for this altitudinal level (Hartshorn 1991), but they are only half as abundant as in lowland sites in La Selva (Lieberman & Lieberman 1987).

The tree density of 436 per ha in the RFSR ranges between tree densities of other study sites in the Neotropics. 395-593 trees per ha ($\geq$ 10 cm DBH) have been counted, but the basal area of 41.67 m^2 (without the tree ferns) is noteably higher than the measured basal areas of between 29.0-35.7 m^2 of the above mentioned study-plots (overview in Swaine *et al.* 1987). Ankewitz & Collbey (1992) observed 744 trees per ha (10 cm DBH) with a basal area of 42.96 m^2 at the Quita Espuela (Dominican Republic) at about 500 m a.s.l. Tree height at this wind-exposed site was rather low (10-15 m). Both references indicate the occurrence of more trees in higher diameter classes in the RFSR than in the aforementioned study-sites.

The tree species/unit area relationship in Fig. 1 suggests an even higher tree species rate in this premontane wet forest because of its still relatively steeply increasing species value when the final sub-plots are summed. The selected study area of 1 hectare seems to be insufficient to represent the whole forest stand. The high percentage (36%) of tree species which are represented by only one individual per hectare supports the previous observation of highly dispersed tree species and the high percentage of 82% of species in frequency class I (see Fig. 4). It indicates a high heterogeneity level of the forest stand (Lamprecht 1986) and supports the assumption of noteably increasing species rates by extending the study-plot in the RFSR.

The high diversity and low abundance of tree species raises the question of specific reproduction strategies as well as of tree population structure, which should be and will be tackled more intensively in future research.

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