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Beiträge zur tropenökologischen Forschung in Costa Rica

Contributions
to Tropical Ecology
Research in Costa Rica

Herausgegeben von
I. Wattenberg & S.-W. Breckle

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PREFACE

Tropical rain forests belong to the most complex and most species rich ecosystems of the world. But the existence of these ecosystems is threatened by massive exploitation. Huge areas of tropical forests have already been destroyed irreversibly without knowing almost nothing about the genetic resources of the species composition and their ecological importance. It can be supposed that a high number of endemic species is getting permanently lost while exploiting tropical primary forests.

Since only a few decades tropical forest ecosystems are the focus of intensive studies worldwide to work against their rapid destruction. A better knowledge about these ecosystems is a basic requirement to develop adequate utilization and reforestation concepts to protect the remaining primary forests as well as possible.

The Department of Ecology within the Faculty of Biology of the University Bielefeld has established a new focal point of research in Costa Rica to contribute to a better knowledge of Tropical Rainforest Ecosystems. This was possible thanks to the cooperation with the Biological Station at the Reserva Forestal de San Ramón, now the Reserva Biológica Alberto M. Brenes, which was initiated by Prof. St. Vogel (Mainz, now Vienna). We were able to help to improve the infrastructure of the station considerably, so also other German groups were doing research there and it was possible to intensify steadily the cooperation of the University of Bielefeld and the University of Costa Rica, Sede Occidente in San Ramón. One of these results is an agreement of a cooperation treaty between both universities.

The Research-Projects were financed by various sources. We express our thanks especially to the Deutsche Forschungsgemeinschaft (DFG) and the E. u. H. Walter-Stiftung that helped us essentially with their financial support for this research work.

The present edition of "Bielefelder Ökologische Beiträge" presents some results of the preceding six years of intensive ecological research in the Biological Reserve "Reserva Biológica Alberto Manuel Brenes" in Costa Rica. The study area was supposed to be a species rich ecosystem and this led us to select this area as our study site. We wish to thank the Director of the Reserve for his logistical support, the scientific cooperation and, above all, for his friendship all over the years, that has grown during the research work in Costa Rica. We also wish to thank Victor Mora and Hugo Perez Z. vicariously for all contributers who have enabled us to do our research work under frequently difficult conditions of a recently established Biological Station in a real wet climate. Further more we wish to thank the University of Costa Rica (UCR) for the permission of using their facilities and all persons for their support to feel at home in a foreign country. We do hope that this volume may enhance more cooperative research between both partners and may also be a mean for students to decide to do research in fascinating primary forest to understand at least a small portion of the complex structure and the manyfold functions of such a forest in order to help to preserve these areas for future generations.

Ingrid Wattenberg & Siegmar-W. Breckle

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SOIL CONDITIONS WITHIN THE RIO LORENCITO VALLEY (RESERVA BIOLÓGICA ALBERTO BRENES, SAN RAMÓN, SIERRA DE TILARÁN, COSTA RICA)

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ABSTRACT

The soil conditions of the Rio Lorencito Area are described by typical soil profiles. It seems to be evident, that in most parts of the valley the soil conditions are very similar. The soils are of volcanic origin, they are mostly rather coarse, but also rich in clay-minerals. The upper humus horizons are indistinct and shallow. Some of the ecologically important soil parameters are listed. pH is almost always between 4 and 5, potential acidity being rather high. Nutrient availability is low, but apparently not deficient for normal growth.

GEOGRAPHICAL SITUATION

The Biological Station within the Biological Reserve is located close to the Rio Lorencito creek. The Rio Lorencito valley stretches from west to east. The valley of the Rio Lorenco stretches almost parallel only about a few kilometers south. Both rivers join about 15 km north-east and discharge to the Caribbean side (see map, Fig. 1; BRECKLE & BRECKLE 1996).

GEOMORPHOLOGICAL SITUATION

Along the creek and within the creek of the Rio Lorencito there are large boulders of basaltic origin accumulated. Along the steep slopes on both sides of the valley there are very loose soils developed which are highly susceptible to erosion. Steep slopes and narrow ravines demonstrate that the erosion activity is very strong. Rather often parts of slopes, together with smaller or larger trees fell down.

The trail to the station crosses some parts of such a steep slope and some narrow ravines. The efforts to construct a small road to the station, so that the station could be reached by 4-W-D-vehicles, was already 2 or 3 times unsuccessful. Strong rains during the long rainy period (between May and December, see BRECKLE & ORTIZ 1997) made it impossible to construct a durable road.

In some of the narrow ravines stones, boulders, tree and plant material slowly croaches down to the Rio Lorencito, making the ravines inaccessible.

Along the river only narrow stripes are part of the riverbed and may be inundated during strong rains. The Auwald is thus not very well developed. Flat and horizontal plains are missing. The relief energy is very high.

Some smaller areas with a size of only a few square meters, which are formed by the creek during the rain period and covered with sediments, are the places where annuals (mainly *Impatiens wallichii*) and small shrubs rapidly invade.

METHODS USED

Mainly the data from two sites (A and B) will be given and be compared with other sites. Both sites are located on the same slope, facing North, above the Biological Station. Site A is from the lower slope (950mNN) and Site B from the same slope but almost near the crest (1070mNN). The sites (A and B) are indicated on the map (Fig. 1). The profiles were dig out, so that the whole profiles were visible. Samples along the profiles were taken as mixed samples at the following depths (cm): 0-1; 1-2; 2-5; 5-10; 10-15; 15-20; 20-25; 30-35; 40-45; 50-55; 60-65; 70-75; 80-85 in march, 1995.

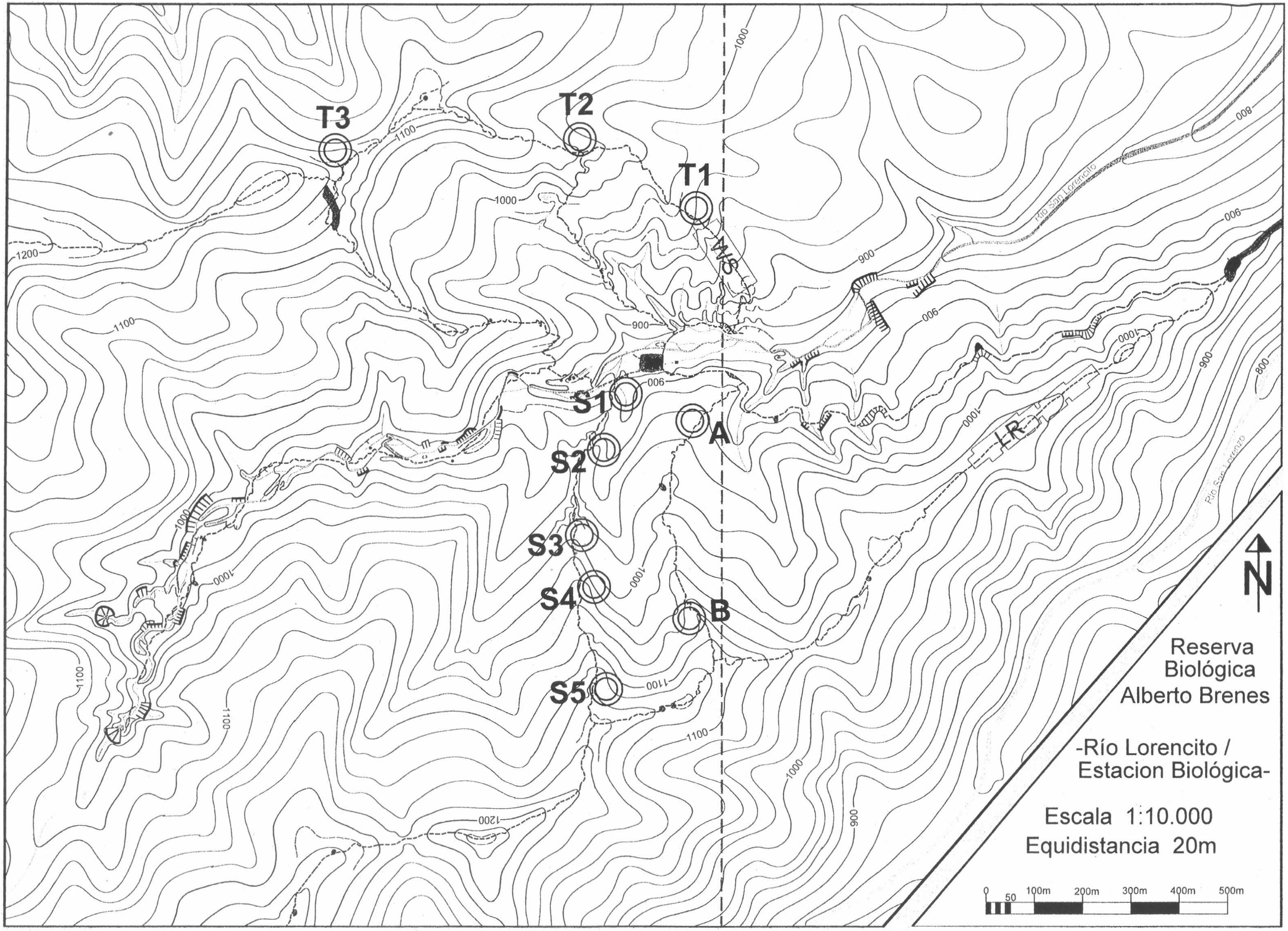
Samples from Site S1-S5 and T1-T3 were taken by WEINAND in march and april 1995.

pH was measured in suspensions of soil and water (1 : 2,5) or soil and KCl-solution (1M; 1 : 2,5).

Soil nutrients were measured by extraction of soil samples with Ammonium-Acetate (0,1 M NH_4 $OOC.CH_3$). By definition we call this the plant-available fraction (STEUBING & FANGMEYER 1992).

Measurements were made by atomic absorption (flame technique: Perkin Elmer 380, or by graphite furnace technique PE 5100).

Fig.1 (see next page) : Map of the close vicinity of the Biological Station within the Rio Lorencito Valley (Reserva Biológica Alberto Brenes, San Ramón, Sierra de Tilaran, Costa Rica). Soil Profiles were investigated at Site A and B until 85cm (BRECKLE); at Site S1-S5 and T1-T3 soil samples were taken by WEINAND. **LR**: 1 ha-Plot "Leyers-Römich"; **WS**: 1-ha-Plot "Wattenberg-Sprenger"



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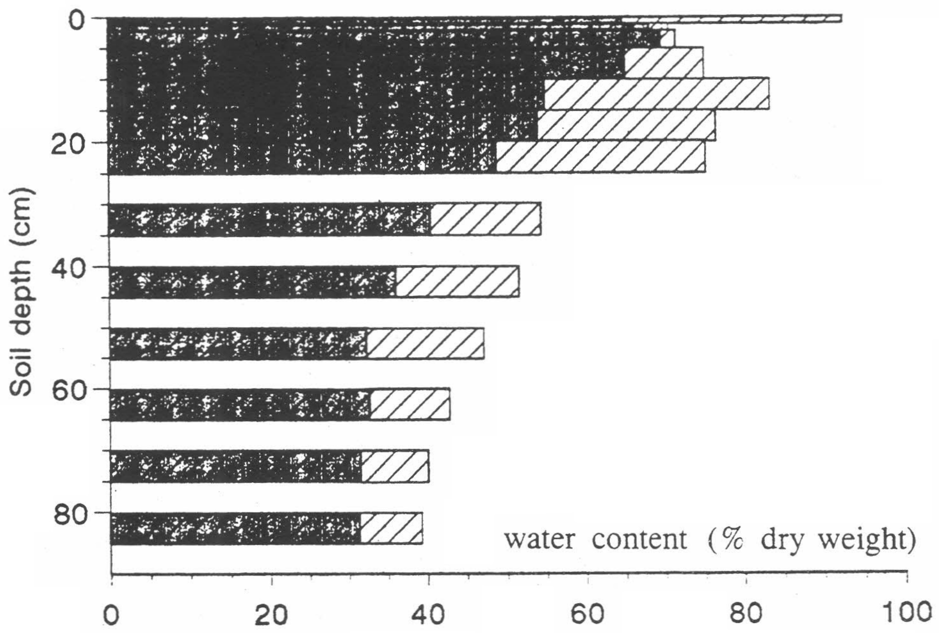

Fig. 2: Water content (% dry weight) along the soil profile at sampling sites A and B

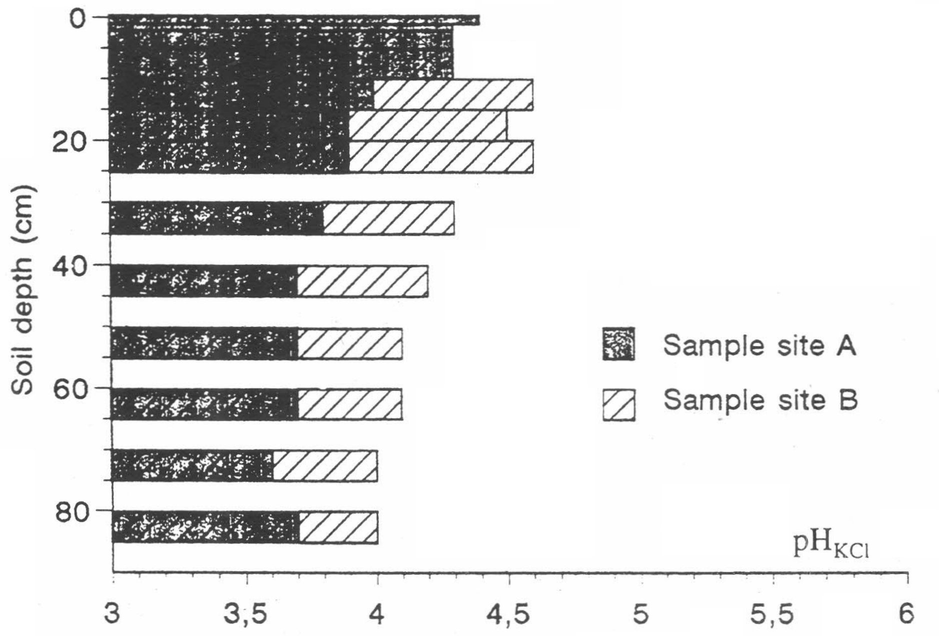

Fig. 3: pH_{H2O} along the soil profile at sampling sites A and B

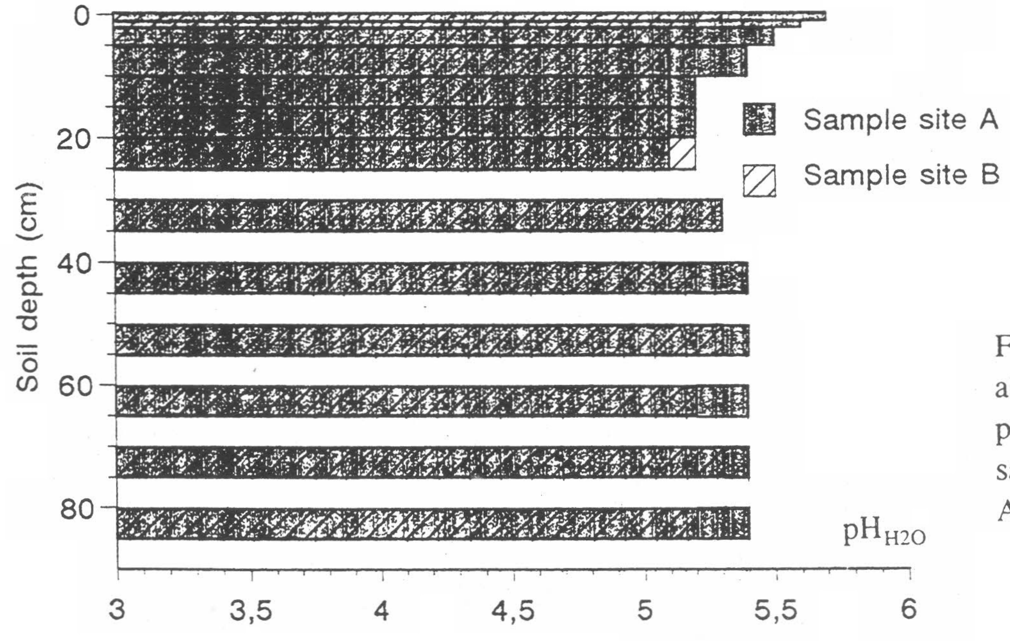

Fig. 4: pH_{KCl} along the soil profile at sampling sites A and B

Chloride was measured by potentiometry with the Marius-Micro-Chlor-Counter with the silver-electrode.

Organic C was measured by ashing soil samples in the oven at 500°C. Since the Carbonate-Content is negligible this method is accurate enough.

SOIL SITUATION

The soil profile can be described as follows, see Table 1:

Table 1: description of the various soil characters at Site A with increasing depth along the soil profile. The soil profile at Site B was less densely rooted, colours and structure along depth were very similar.

horizon/ depth (cm)	colour	structure	rooting
0 - 1 cm	dark brown, few green leaves	remnants of leaves, partly mineralized, organic	some fine roots and mycelia
1 - 2 cm	dark brown	organic, fine material	some roots and mycelia
2 - 5 cm	dark brown	sandy and fine material	many fine roots, clumped mycelia
5 - 10 cm	deep brown	sandy and fine material	many fine, some coarse roots
10 - 15 cm	brown	rather sandy and fine material	fine and coarse roots
15 - 20 cm	brown	sandy and fine material	mainly coarse roots
20 - 25 cm	reddish brown	fine material, sandy	some coarse roots
30 - 35 cm	slightly reddish pale brown	fine material, few coarse pieces	few coarse roots
40 - 45 cm	pale to reddish grey-brown	fine material, sandy, coarse stones	few coarse roots
50 - 55 cm	reddish grey-brown	sandy and coarse stones	few coarse, one thick root'
60 - 65 cm	grey brown	sandy and coarse stones	very few coarse roots
70 - 75 cm	grey brown	sandy and many stones	very few roots
80 - 85 cm	grey brown	sandy and many stones of different sizes	almost no roots

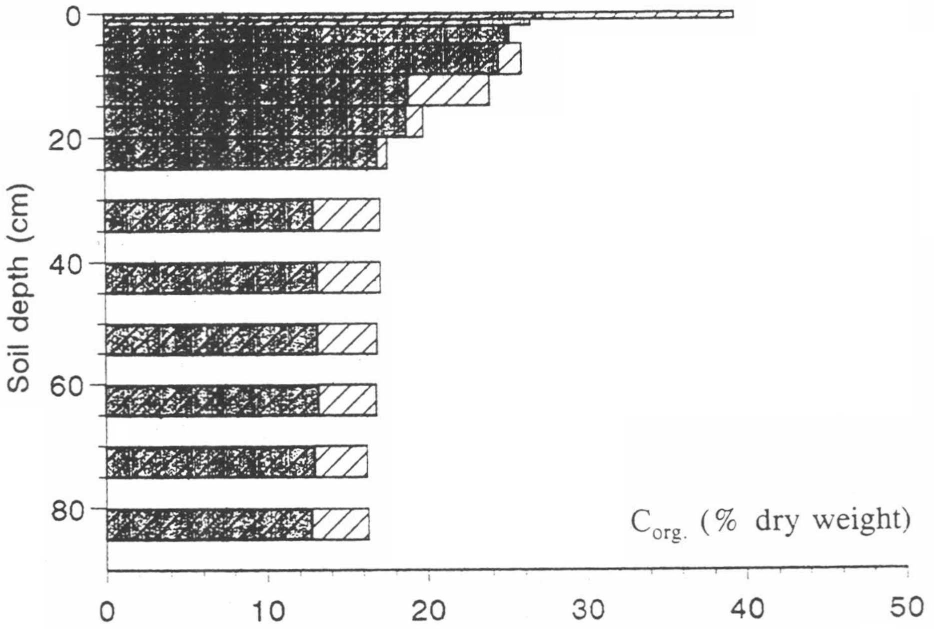

Fig. 5: Content of organic carbon (% dry weight) along soil profile at sampling sites A and B

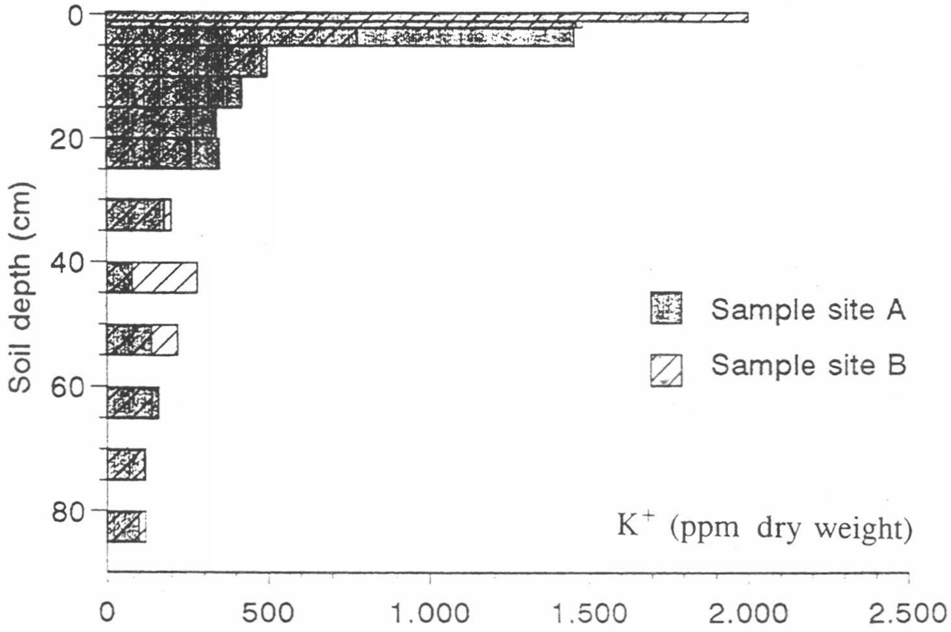

Fig. 6: K^+-content along soil profile at sampling sites A and B

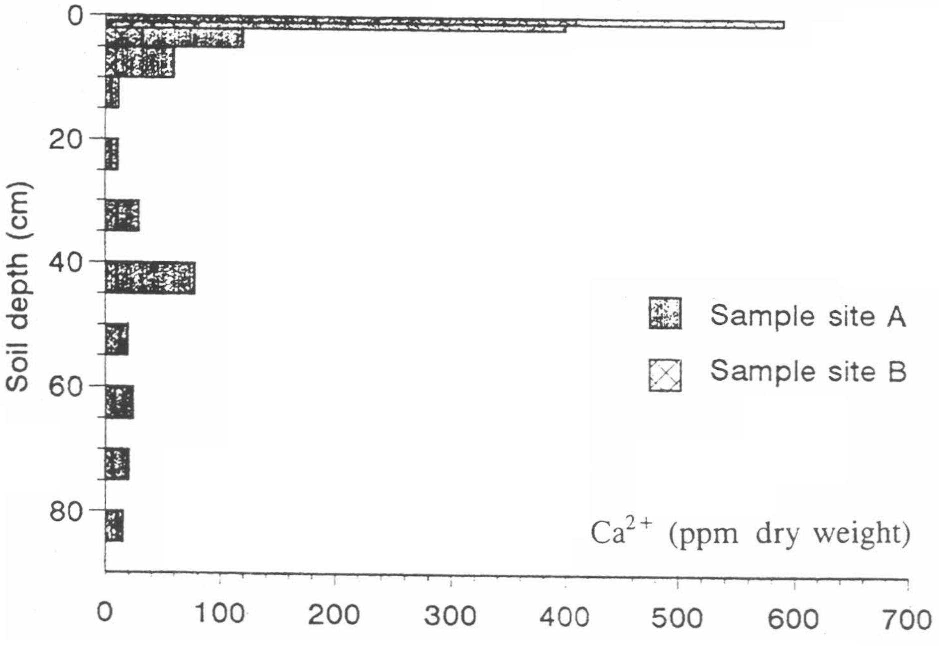

Fig. 7: Ca^{2+}-content along soil profile at sampling sites A and B

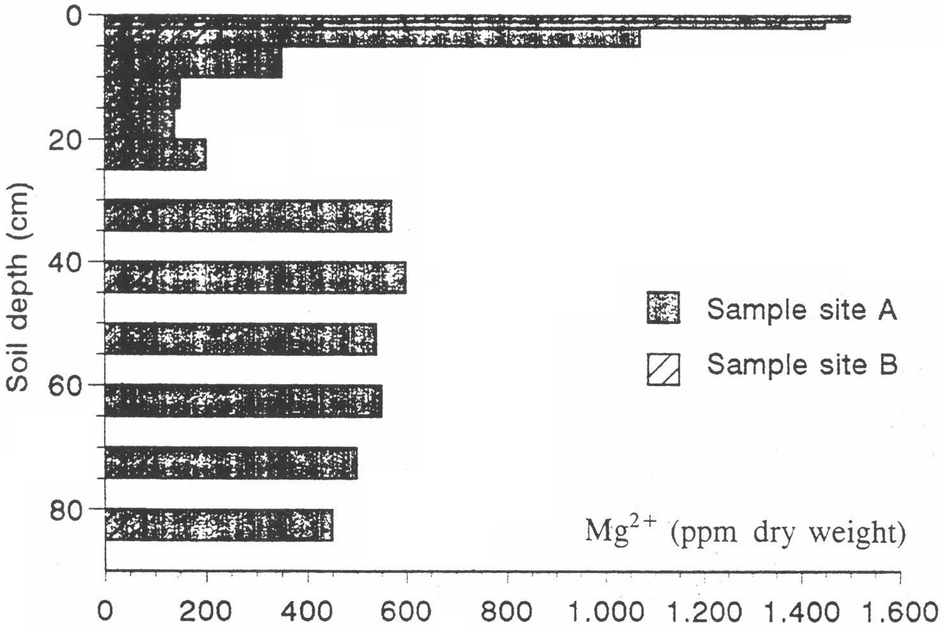

Fig. 8: Content of Mg^{2+} along soil profile at sampling sites A and B

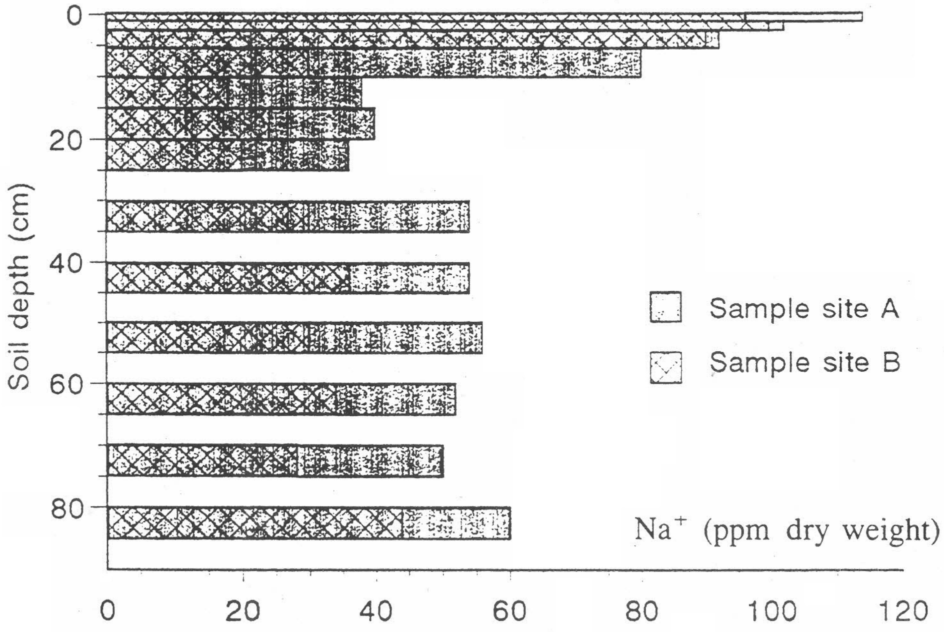

Fig. 9: Content of Na^{+} and Cl^{-} along soil profile at sampling sites A and B

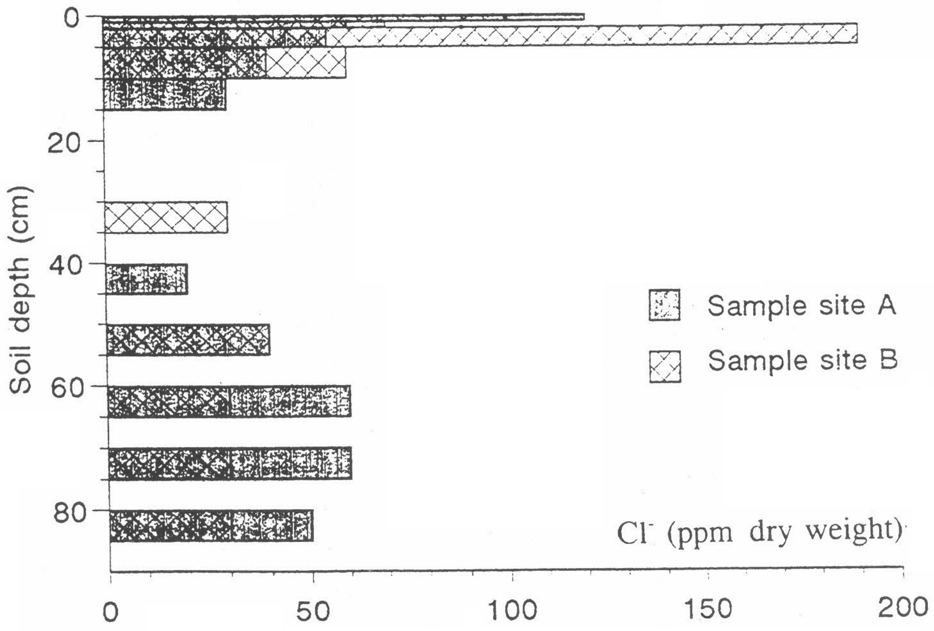

Fig. 10: Content of Cl^{-} along soil profile at sampling sites A and B

As an example the analytical data from the 2 soil profiles (Site A and B) are given in Fig. 2 - 10.

The pH between the 2 sites (Fig. 3 and 4) differs only slightly and is somewhat less acidic in the upper horizons. The difference between the p_HH_2O and the p_HKCl is larger in Site A than in Site B, especially in the lower horizons. This indicates that the potential acidity is higher in the lower slope soils.

A slight change is visible above 30cm, these upper horizons are richer in $C_{org.}$ (Fig. 5), they are less coarse, their water holding capacity is higher (Fig. 2).

The rooting density is not shown. It was noted, however, that it was distinctly higher in the upper 30cm in comparison to the lower parts of both profiles. The soil colour did not indicate very distinct horizons. The colour changes from the upper darker brown horizon to somewhat brighter and slightly more reddish-brownish horizons below half a meter.

The nutrient contents are relatively low. Ca_{2+} is shown in Fig. 7, it is accumulated only with the litter layer, this is parallel in both sites. Below 5 cm soil depth it is less than 100 ppm plant available calcium.

The behaviour of magnesium is surprisingly different (Fig. 8). It is distinctly higher than Ca, and has a minimum within the 10-30cm horizon, but is also accumulated with the litter layers (0-1cm, 1-2cm). In both ions site A is distinctly richer than Site B, this indicates an accumulation process downslope.

The rather strong accumulation of potassium in the upper horizons is indicated in Fig. 6 for both sites rather equally. Chloride was (with the used method) close to the detection limit (Fig. 10). Similar to K^+ and also to Na^+ (Fig. 9) it is accumulated with the litter layers.

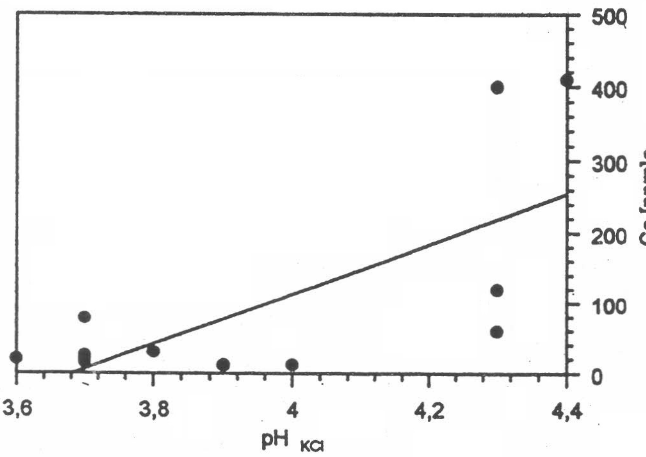

Fig. 11: Correlation between Ca^{2+} and pH at Site A (r = 0.71)

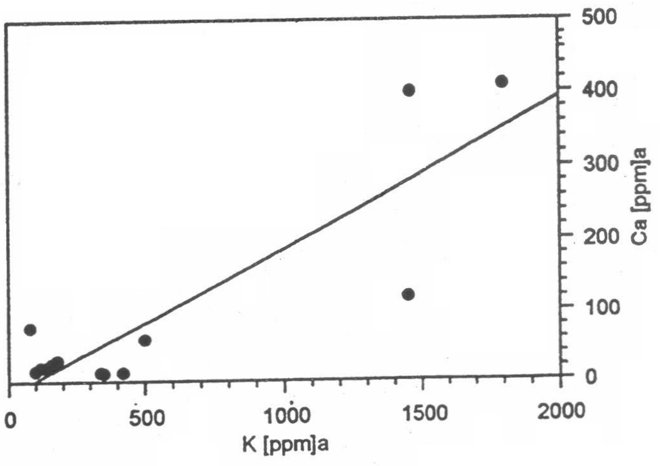

Fig. 12: Correlation between K^+ and Ca^{2+} at Site A (r = 0.87)

A slight correlation between Ca^{2+} and p_H is shown in Fig. 11 (the regression coeffizient being r = 0.71), and between K^+ and C^{2+} (r = 0.87) (Fig. 12).

On other sites also soil samples were investigated: WEINAND checked nutrient content at 8 sites (S1-S5 and T1-T3, see map, Fig. 1). The results indicate almost no differences between sites of one slope. The average values therefore are given in Table 2 for the north facing slope (S1-5) and for the south facing slope (T1-3).

Table 2: Content of Na^+, K^+, Mn^{2+} and Mg^{2+} (extract with Ammoniumacetate = "plant available fraction") along the soil profile at sampling sites S1 - S5 at the north-facing slope (first figure) and from the south-facing slope (second figure)at sampling sites T1 - T3 (see map, Fig. 1), Rio Lorencito, (means, mmol per kg dry soil), data from WEINAND.

soil depth (cm)	K north//south	Na north//south	Mg north//south	Mn north//south
0 - 1	4,8//5,4	2,6//2,6	4,5//4,2	0,5//0,45
1 - 2	3,6//3,0	2,5//2,2	2,6//2,0	0,3//0,2
2 - 5	2,8//1,9	2,5//2,7	1,7//1,4	0,4//0,4
5 - 10	2,2//2,7	2,0//2,6	0,9//0,6	0,25//0,25
10 - 20	2,3//1,4	2,3//2,4	0,75//0,3	0,15//0,1
20 - 30	1,6//1,3	2,4//2,0	0,8//0,3	0,12//0,05
30 - 40	1,1//1,1	2,5//2,3	0,83//0,4	0,1//0.02
40 - 50	1,3//1,7	2,0//2,0	1,05//0,35	0,08/0,015
50 - 60	2,2//1,6	1,8//1,9	1,45//0,45	0,05//0,01
60 - 70	1,3//1,9	2,1//1,7	0,52//0,5	0,03//0,01

From Site S5 (almost near to the crest) also lead (Pb) was measured. It exhibits rather high values of about 15-30ppm (per dry matter) (Table 3).

Table 3: Content of Pb along the soil profile at sampling site S5 at the north-facing slope close to the crest (total content, ppm, dry weight)

soil depth (cm)	0-1	1-2	2-5	5-10	10-20	20-30	30-40	40-50	50-60
Pb	18	19	20	22	18	23	26	32	17

In contrast to the other checked elements it is obvious that Pb has another pattern of distribution within the soil profile, the lower horizons have a higher content.

At other localities within the Rio Lorencito valley soil samples were analyzed by several diploma candidates, too, and Table 4 gives a list of the particle size fractions and some other characteristics of soils from 3 localities (sites see map, Fig. 1).

Table 4 : Particle fractions and horizons from soil profiles from the Rio Lorencito valley (data modified, from BULJOVCIC , 1994)

horizon		depth (cm)	description	sand %	silt %	clay %
H0	WS	0-2	old leaves, twigs, fine roots	-	-	-
	LR	0-1	dto.	-	-	-
	T2	0-2,5	dto.	-	-	-
H1	WS	1,5-3	almost black, loose, many fine roots	84	14	2
	LR	1-4	dto.	78	20	2
	T2	1,5-4	dto.	86	11	3
H2	WS	7-15	dark, soft, many fine roots	82	16	2
	LR	7-10	dark brown, many fine roots	89	8	3
	T2	7-10	very dark, moist, some fine roots	87	11	2
H3	WS	17-33	brown, some fine, some thick roots	89	9	2
	LR	18-20	brown, loamy, some fine roots	87	12	1
	T2	20-25	light brown, moist, sticky, few roots	79	19	2
H4	WS	30-45	brown, some stones, strong roots	89	9	2
	LR	33-50	brown, loose, no stones, thick roots	65	17	18
	T2	60-65	brown, loamy, no stones	78	19	3
H5	WS	>46	bright brown, loamy clumps, stones	67	11	22
	LR	>50	bright brown, sticky, large stones	57	20	23
	T2	>65	bright brown, loamy, large stones	74	18	8

The nutrient content from the various horizons are shown in Table 5. It is very obvious that the shallow upper horizon with the fast mineralization of litter in terms of chemical characteristics differs from the other, deeper horizons very significantly. From the 10cm depth the nutrient content during the wet season and the dry season from 5 localities are shown in Table 6.

Table 5 : Means of nutrient contents and standard-deviation (n = 5 in H1-H4) from 5 horizons of various soil samples from the Rio Lorencito Valley (acc. to Buljovcic 1994; exact localities and soil depths are not indicated).

horizon	K	Ca	Mg	Mn	Zn	PO_4
H1	272 ± 218	1000 ± 399	190 ± 74	28 ± 6	0,46 ± 0,21	37 ± 15
H2	118 ± 158	384 ± 498	85 ± 98	11 ± 6	0,23 ± 0,12	25 ± 7
H3	56 ± 70	80 ± 58	22 ± 18	7 ± 5	0,50 ± 0,35	16 ± 8
H4	39 ± 49	13 ± 28	15 ± 8	4 ± 2	0,38 ± 0,16	8 ± 2
H5	21	35	13	3	-	8

Table 6 : Nutrient contents from 5 different localities within the Rio Lorencito area during the dry season (dry s.; march+april 1992) and during the wet season (wet s.; june/july 1992) from 10cm soil depth (localities see map, fig. 1: **LR**; **WR**; **±T2** = close to T2; **T1/2** = between T1 and T2; **±S1** = close to S1, valley site) (acc. to BULJOVCIC 1994).

site		K	Ca	Mg	Mn	Zn	PO_4
LR	dry s.	42± 8	111± 46	41±22	10,4±3,4	0,27±0,16	31,3±10,3
	wet s.	54±14	123± 60	43±12	6,9±1,9	0,31±0,12	36,6±10,7
WR	dry s.	44±41	122± 81	36±30	8,9±3,6	0,29±0,34	20,4± 6,2
	wet s.	63±58	153± 99	41±28	8,7±5,6	0,20±0,08	25,0± 3,8
T1/2	dry s.	48±21	172±164	25± 9	8,9±5,0	0,52±0,38	24,6±11,9
	wet s.	---	---	---	---	---	---
±T2	dry s.	31± 8	44±21	20± 8	3,3±0,6	0,21±0,24	50,3±25,8
	wet s.	35± 4	44±16	21± 6	2,9±0,5	0,76±0,32	53,4±16,1
±S1	dry s.	194±112	896±733	167±107	23,7±11,3	0,57±0,18	13,4± 4,4
	wet s.	204± 73	1032±958	182±145	16,9± 7,1	0,26±0,09	16,8± 5,0

Again it is interesting to note that the higher values of K-, Mg-, Ca- and Mn-content could be found at the valley site (S1), whereas the slopes exhibit lower values. At the crest (T2) those nutrients are the lowest, comparably. Almost the opposite behaviour is to be seen with the P-values. Zn is not significantly different at the various sites. Only slightly significant are the differences between dry and wet season. K, Mg and Ca values are somewhat lower during the wet season, Mn slightly higher.

The trace element situation is currently checked by SCHEFFER and will be published later.

DISCUSSION

Since there are few values from similar sites of primary forests in literature, we can only compare those values with data from cultivated plants and agricultural soils.

However, rather often the applied methods differ and the variability of plant cover, the climatic conditions as well as the soil processes are so different between sites, that comparisons are often impossible.

Soils derived from volcanic rocks are found in many tropical areas. From the Volcan Barva area GRIEVE et al. (1990) gave data which indicate a rather similar low range of nutrients. Slightly differing are the data from MARTINI & SUAREZ (1975) from various other localities in Costa Rica, and much higher are those from alluvial soils near Turrialba, analyzed by MARTINI & MOSQUERA (1972). They indicate the same trend as with the valley site (S1) in the Rio Lorencito Valley, where additional sediments and organic material is accumulating.

The potential cation exchange capacity was measured by BULJOVCIC (1994) with ca. 60 mequ/100g (CEC_{pot}) and the actual CEC was about 17 mequ./100g (CEC_{act}) in the upper soil horizon. This is a rather low fertility when compared with agricultural soils (BERTSCH 1987).

The Zn values indicate a very low availability, and with agricultural crops it would be a deficiency situation, as it was shown already by SNEDACKER & GAMBLE (1965) in Panama.

The Phosphate-situation is more complicated, since the applied extraction methods in various countries differ tremendously and rather often it is not clear what really the plant available fraction of PO_4 would be. In comparison with the data from GRIEVE et al (1990) from the Volcan Barva area (1,3 - 13,6 ppm) the values from San Ramón are almost double (26 - 40 ppm). This means the Phosphate-situation in San Ramon is rather good.

The pH-values between 4 and 6 (pH_{H2O}) are the common range of pH-values in many tropical forest soils from low to montane situations.

ACKNOWLEDGEMENTS

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CITED LITERATURE

AMBERGER, A. 1983 Pflanzenernährung. Ökologische und physiologische Grundlagen; Dynamik und Stoffwechsel der Nährelemente.- Ulmer/Stuttgart

BERTSCH, F. 1987 Manual pra interpretar la fertilidad de los suelos de Costa Rica. 2nd ed. in ACEDO, D.M. & QUIRÓS A.D.(eds.) Oficina de Publ. de la Univ. de CR, San José, CR

BIRKELBACH, J. 1995 Mineralstoffakkumulation von fünf Baumarten in einem prämontanen Regenwald in Costa Rica.- Diplomarbeit Universität Bielefeld

BIRKELBACH, J., BRECKLE, S.-W. & R. ORTIZ V. 1996: Element contents of soil and leaves and their correlation in five tree species in an area of the Reserva Biológica Alberto Brenes, Costa Rica.- Memoría Investigación Res. Biol. Alb. Ml. Brenes, San Ramon, Revista Pensamiento Actual, vol.2: 53-59

BRECKLE, S.-W. 1995: Canopy structure, ecosystem function and diversity in a montane tropical primary forest in Costa Rica.- in BRECKLE, S.-W. & Y. WAISEL (ed.): Bielefelder Ökologische Beiträge (BÖB), Band 8. Beiträge des israelisch-deutschen workshop "Structure and function on all levels" im April 1994 in Tel Aviv; 97-111

BRECKLE, S.-W. & BRECKLE,R. 1996 Mapping geomorphology and trails around the Biological Station at the Reserva Biológica Alberto Brenes (Sierra de Tilaran), Costa Rica.- Memoría Investigación Res. Biol. Alb. Ml. Brenes, San Ramon, Revista Pensamiento Actual, vol.2: 5-10

BRECKLE, S.-W. & R. ORTIZ V. 1997 Climate and ecological conditions at the Reserva Biológica de San Ramón / Costa Rica (this volume)

BULJOVCIC, Z. 1994 Nährstoffgehalte in den Blättern von *Plinia salticola* L. (Myrtaceae) und *Elaeagia auriculata* Hemsl. (Rubiaceae) sowie im Boden eines prämontanen Regenwaldes in Costa Rica.- Diplomarbeit Universität Bielefeld

EPSTEIN, E. 1971 Mineral nutrition in plants: principles and perspectives.- New York

FASSBENDER, H.W. 1972 Chemisches Verhalten der Hauptnährstoffe in Böden der Tropen, insbesondere in Lateinamerika.- Gött. Bodenkundliche Berichte, Bd. 23

GRIEVE,I.C., PROCTOR J. & COUSINS,S.A. 1990 Soil variation with altitude on volcan Barva, Costa Rica.- Catena 17, 525-534

GRUBB, P.J. & EDWARDS, P.J. 1982 Studies of mineral cycling in a montane rain forest in New Guinea III. The distribution of mineral elements in the above-ground material.- J. Ecol. 70 : 623-648

KINZEL, H. 1982 Pflanzenökologie und Mineralstoffwechsel.- Ulmer/Stuttgart

MARTINI,J.A. & MOSQUERA,L. 1972 Properties of five tropepts in a toposequence of the humid tropics in Costa Rica.- Proc. Soil Sci. Soc. Amer. 36, 473-478

MARTINI,J.A. & SUAREZ,A. 1975 Potassium status of some Costa Rican latosols and andosols and their response to potassium fertilization under greenhouse conditions.- Proc. Soil Sci. Soc. Amer. 39, 74-80

MOSER, P. 1994 Vergleichende Untersuchungen zu den Mineralstoffverhältnissen in Bestandeslücken (gaps) und im Bestand des prämontanen Regenwaldes der Sierra de Tiaran de Costa Rica.- Diplomarbeit Bielefeld/Oldenburg

SCHEFFER, A. 1997 Untersuchungen zu den Spurenelementgehalten im montanen tropischen Regenwald in der Reserva Biológica Alberto Brenes des San Ramón, Costa Rica.- Diplomarbeit Univ. Bielefeld (in preparation)

SNEDACKER,S.C. & GAMBLE,J.F. 1965 Compositional analysis of selected second-growth species from lowland Guatemala and Panama.- BioScience 19, 536-538

STEUBING, L. & FANGMEIER, A. 1992 Pflanzenökologisches Praktikum.- Ulmer/Stuttgart

TANNER, E.V.J. 1985 Jamaican montane forests: Nutrient capital and cost of growth.- J. Ecol. 73 : 553-568

WATTENBERG, I. & BRECKLE, S.-W. 1995: Tree species diversity of a premontane rain forest in the Cordillera de Tilaran, Costa Rica.- Ecotropica 1: 21 - 30

WATTENBERG, I., BRECKLE, S.-W. & R. ORTIZ V. 1996: La diversidad de especies de arboles y la estructura de un Bosque muy Humedo Premontano en la Reserva Biológica Alberto Brenes (Sierra de Tilaran), Costa Rica.- Memoria Investigación Res. Biol. Alb. Ml. Brenes, San Ramon, Revista Pensamiento Actual, vol.2: 11-19

WEBER, C. 1994 Mineralstoffverhältnisse bei Baumfarnen in einem prämontanen Regenwald Costa Ricas.- Diplomarbeit Bielefeld/Oldenburg

WEBER, C., HERRERA B.,O., BRECKLE, S.-W. & R. ORTIZ V. 1996: Las relaciones de los nutrientes en las hojas de los Helechos Arborescentes en la Reserva Biológica Alberto Brenes.- Memoria Investigación Res. Biol. Alb. Ml. Brenes, San Ramon, Revista Pensamiento Actual, vol.2: 33-41

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INVESTIGATION OF IMPORTANT MINERAL NUTRIENTS IN LEAVES OF TWO TREE SPECIES IN A PREMONTANE WET FOREST IN COSTA RICA

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INTRODUCTION

Everybody is fascinated by the biodiversity and the high biomass to be found in tropical forests. One might imagine that a high nutrient content in the tropical soils could account for this. However, in this respect tropical soils are extremly diverse. An example of a paradox is the Amazon Basin where a high species richness and biomass in the primary forest is found despite the extremely nutrient-poor soil. So the question arises as to whether the nutrient contents in the soil and the plant correspond.

In Costa Rica there was and is vulcanic activity accounting for relatively nutrient rich soils. In a primary premontane wet forest the nutrient conditions were investigated. In order to examine these conditions, leaves of two tree species and soil samples were collected as indicators of the nutritional status of trees (VAN DEN DRIESSCHE, 1974) and soils respectively.

LOCATION & EXPERIMENTAL OBJECTIVE

The area of investigation is situated in the Cordillera de Tillarán, in the Reserva Biológica Alberto Brenes (former Reserva Forestal de San Ramon). The Biological station is located at 895 m above sea level. The annual rainfall reaches about 5500 mm (CRUZ, 1989) and the average temperature varies from 19 to 23 °C. The forest is classified as a tropical premontane evergreen rainforest (GÓMEZ, 1986). The soils are Inceptisols of vulcanic origin (TAXONOMÍA DE SUELOS, SMSS,1982); they are sandy but contain a high amount of organic material (10-20% OM).

In this work the macro-nutrient (Ca, K, Mg, P) and micro-nutrient (Mn, Zn) contents in the leaves of two moderatly distributed tree species and the surrounding soil were analyzed.

QUESTIONS OF INTEREST

- What influence does leaf age have on the nutrient content of the leaves?
- Are there any differences between the nutrient contents of the leaves of the two tree species?
- Do the nutrient contents of the leaves and soil correspond?
- How are the nutrients distributed in the soil profile?

MATERIALS & METHODS

During the dry season (March/April) young (same size as mature but light geen and at the end of the twig) and mature leaves (all leaves dark green) were collected. One leaf sample of *Plinia salticola* (Myrtaceae) included 30 leaves and one of *Elaeagia auriculata* (Rubiaceae) included 15 leaves because the latter were much bigger. Altogether 25 individual trees of *P. salticola* and 23 of *E. auriculata* were examined. The soil samples were taken arround the trees to a depth of 10 and 15 cm (A-Horizon). To analyze the contents of the macro-nutrients (Ca, K, Mg and P) and the micro-nutrients (Mn, Zn) the leaves were dried at 70°C and the milled leaf material was treated according to HEINRICHS *et al.* (1986). The soil samples were extracted by ammonium acetate (pH 7, FAO-Unesco, 1990; US-SOIL-TAXONOMY, 1990) in order to determine the content of exchangable cations.

The cations were analyzed by flame atomic absorbtion spectrometry. The contents of phosphorus in the plants were determined by photometry by staining the leaf samples with ammonium molybdate and -vanadate and the soil samples were treated according to the Ca-lactat method (STEUBING & FANGMEIER, 1992).

RESULTS

The nutrient concentrations in the leaves are in agreement with the data for crop plants and trees (MARSCHNER, 1990; BERGMANN, 1992; MENGEL, 1991) with the exception of manganese and phosphorus (Table 1&2) . The concentration of manganese, expecially in *Plinia salticola*, was higher than is usual in plants. Conversely the phosphorus concentration in both species was very low (<0,1% dm, Table 1&2).

The content of exchangable nutrients in the soils is shown in Table 3 and 4. The pH(H_2O) is between 4,7 and 6,1 (4,0-5,1 in 0,1 M KCl) with no differences between the sites.

A correlation analysis did not show any significant connections between the nutrient contents of leaves and soil samples using the described extraction. But there was a statistical difference between the nutrient contents of young and mature leaves. Higher concentrations of Ca, Mg and Mn were found in mature leaves and P and K concentrations were higher in young leaves. For Zinc there was no clear difference between the concentrations of young and mature leaves. However, in general there was a very low Zn concentration in the soil and the plants.

Also, between the tree species there was a difference in the elemetal concentrations. Ca and Mn concentrations were higher in *P. salticola* leaves while the opposite was shown for K, P and Zn which were higher in *E. auriculata* leaves. Both species had a similar Mg concentration.

From analysis of the soil profile (ca. 1m depth) it was clearly shown that the minerals Ca, Mg, K and Mn reached the highest concentration in the upper soil layer (0-15 cm, H-Horizon and A-Horizon).

Table 1: Concentrations of macro-elements in the leaves of *Plinia salticola* and *Elaeagia auriculata*

macro-minerals	**mature leaves**		**young leaves**	
	% dm	**sd**	**% dm**	**sd**
P				
Plinia salticola	0,44	0,05	0,62	0,11
Elaeagia auriculata	0,58	0,10	0,75	0,18
K				
Plinia salticola	5,59	1,69	9,77	2,91
Elaeagia auriculata	9,76	2,95	13,07	3,67
Mg				
Plinia salticola	2,66	0,44	1,88	0,41
Elaeagia auriculata	2,66	0,70	2,02	0,50
Ca				
Plinia salticola	12,12	1,95	7,49	2,50
Elaeagia auriculata	6,64	2,43	4,20	1,77

Table 2: Concentrations of micro-elements in the leaves of *Plinia salticola* and *Elaeagia auriculata*

micro-minerals	**mature leaves**		**young leaves**	
	mg/kg dm	**sd**	**mg/kg dm**	**sd**
Mn				
Plinia salticola	713	252	367	168
Elaeagia auriculata	281	107	205	131
Zn				
Plinia salticola	18	3	20	6
Elaeagia auriculata	34	8	30	9

Table 3: Concentrations of macro-elements in the soil on sites of *Plinia salticola* and *Elaeagia auriculata*

macro-minerals	**10 cm deep**		**20 cm deep**	
	mg/kg dm	**sd**	**mg/kg dm**	**sd**
P				
Plinia salticola	27,9	18,7	15,2	7,7
Elaeagia auriculata	26	10,6	13,9	4,9
K				
Plinia salticola	55	42	40	41
Elaeagia auriculata	67	85	43	57
Mg				
Plinia salticola	50,6	69,2	42,8	74,1
Elaeagia auriculata	46,6	45,7	26,3	18,9
Ca				
Plinia salticola	246	450	223	469
Elaeagia auriculata	190	195	120	86

Table 4: Concentrations of micro-elements in the soil on sites of *Plinia salticola* and *Elaeagia auriculata*

micro-minerals	**10 cm deep**		**20 cm deep**	
	mg/kg dm	**sd**	**mg/kg dm**	**sd**
Mn				
Plinia salticola	8,9	5,6	6,7	3,8
Elaeagia auriculata	12,2	8,2	8,2	5,5
Zn				
Plinia salticola	0,34	0,28	0,27	0,15
Elaeagia auriculata	0,40	0,34	0,27	0,20

Table 5: Concentrations of the six elements Ca, K, Mg, Mn, P, Zn [mg/kg dry matter] in tree leaves from eight different rainforests

investigated area	**Ca**	**K**	**Mg**	**Mn**	**P**	**Zn**	**comments**
rainforest near San Carlos, Venezuela (GOLLEY *et al.*, 1980b)	1090 ± 681	3799 ± 1316	1054 ± 419	153 ± 89	570 ± 132	11 ± 3	average (28 species)
„terrà firme“ forest in brazil (GOLLEY *et al.*, 1980a)	4537	6567	3855	87	469	13	Myrtaceae
	6576	4043	4201	154	450	15	Rubiaceae
central amazone, brazil (KLINGE, 1985)	1000-7000	2000-9000	1500-3500	-	300-900	-	depending on trees-species (altogether 14 species)
mountain rain forest in New Guinea (GRUBB & EDWARDS, 1982a)	15000 ± 1500	7700 ± 700	3100 ± 400	-	860 ± 40	-	average of 8 tree species
rainforest in NO Columbia (GOLLEY *et al.*, 1978)	3905	1210	3175	31	593	229	canopy leaves
	3550	11520	5630	27	561	125 (high!)	brushwood
secondary forests in Guatemala and Panama (SNEDAKER & GAMBLE, 1969)	1000-20000	1000-20000	3000-13000 (high)	10-200	100-200	20-50	depending on tree-species (18 species, including brushes)
mountain rainforests on Jamaica (TANNER, 1977) „mull ridge forest“	15300	23300	6700	610	900	-	*Palivourea alpina*
	5100	9500	2100	60	800		*Eugenia virgultosa*
premontane wet forest in Costa Rica (own results)	5390 ± 2430	11490 ± 3700	2320 ± 670	243 ± 124	667 ± 167	30 ± 8	*Elaeagia auriculata*
	9700 ± 3230	7780 ± 3180	2250 ± 570	536 ± 273	531 ± 126	19 ± 5	*Plinia salticola*

DISCUSSION

The nutrient content in the leaves of the two tree species were in a similar range compared with data of crop plants and trees in other tropical forests (Table 5 and Table 5.4.13 in BERGMANN, 1992). The lack of connection between the nutrient concentrations in the soil and the leaves, determined in this work, can be interpreted in different ways: The trees are well supplied with nutrients and capable to storing these and/or the concentrations in the soil lie above the minimum requirement of the plants and/or the extraction methods for the soil are not able to mimic plant uptake. The latter point is always a problem for plant analyses. GLASER & DRECHSEL (1991) for example screened different phosphorus extraction methods in soils and looked for a correlation with P-concentrations in plants. They found no correlation between P-concentration in soil and leaves when measured with the Ca-lactat method. Also GOLLEY *et al.* (1978) found no connection between these parameters in their investigation in Colombia.

In the detected pH range most plant nutrients are easily available and aluminium toxicity should not be a serious problem. And according to BERTSCH (1987) the content of exchangable cations in the soil can be described as moderately fertile.The high content of organic material in the upper soil layer contributes to the high binding capacity and this is probably the reason for the accumulation of minerals in that soil profile and the latter causes the high root density.

It is not clear as to whether the low P-content in the leaves indicates a deficiency as the trees showed no visible P-deficiency symptoms and the soil was well supplied with P. Leaves of trees in other rain forests have similar low P-concentrations (Table 5). It is reasonable to assume that these tropical trees are adapted to this low P-concentration. Conversely the element Mn is highly concentrated in the leaves of *P.salticola* and possibly this species is an Mn-accumulator or even Mn-tolerant.

From the literature, K, Mg and P are known to be mobile in the phloem but Zinc and Ca are not, while Mn seems to have limited mobility. From our results we conclude that K and P are remobilized from older to younger leaves and that these elements are perhaps growth limiting. This is in aggreement with findings of GRUBB & EDWARDS (1982a) in New Guinea; TANNER (1977) in Jamaica and VENEKLAAS (1991) in Colombia who found a high remobilization of K into younger leaves and CHAPIN (1980) who found a high remobilzation of P before abscission. Mg is not supposed to be a limiting factor. Because the two species are not specific for location, pH or soil nutrient content there are probably other factors which contribute to the difference in nutrient concentrations, like competition for light, space or physiological differences.

LITERATURE

BERGMANN, W. (1992) *Ernährungsstörungen bei Kulturpflanzen, Entstehung, visuelle und analytische Diagnose*. 3. Aufl. Fischer, Stuttgart

BERTSCH F (1987) *Manual para interpretar la fertilidad de los suelos de Costa Rica*. 2nd. ed. Eds. Acedo DM & Quirós AD. Oficina de Publicaciones de la Universidad de Costa Rica. San José, Costa Rica

CRUZ DG (1989) Nuestras Reservas Forestales y Zonas Protectoras. Ministerio des Recursos Naturales, Energía y Minas. Costa Rica

FAO-UNESCO (1990) *Soil Map of the world*. Food and agricultural organization of the United Nations. United Nations educational, scientific and cultural organization. International soil reference and information centre. World Soil Resource Report. Revised Legend. FAO, Rome

GLASER B & DRECHSEL P (1991) Beziehungen zwischen "verfügbarem" Bodenphosphat und den Phosphatblattgehalten von *Tectona grandis* (Teak) in Westafrika. *Z Pflanzenernähr Bodenk* **155**, 115-119

GOLLEY FB, RICHARDSON T & CLEMENTS RG (1978) Elemental Concentrations in Tropical Forests and Soil of Northwestern Colombia. *Biotropica* **10**, 144-151

GOLLEY FB, YANTKO J, RICHARDSON T & KLINGE H (1980a) Biochemistry of tropical forests: 1. The frequency distribution and mean concentration of selected elements in a forest near Manaus, Brasil. *Trop Ecol* **21**, 63-70

GOLLEY FB, YANTKO J & JORDAN C (1980b) Biochemistry of tropical forests: 2. The frequency distri-bution and mean concentration of selected elements near San Carlos de Rio Negro, Venezuela. *Trop Ecol* **21**, 70-80

GÓMEZ LD (1986) *Vegetación de Costa Rica*. San José, Costa Rica

GRUBB PJ & EDWARDS PJ (1982a) Studies of mineral cycling in a montane rain forest in New Guinea. III. The distribution of mineral elements in the above-ground material. *J Ecol* **70**, 623-648

GRUBB PJ & EDWARDS PJ (1982b) Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil characteristics and the division of mineral elements between the vegetation and soil. *J Ecol* **70**, 649-666

HEINRICHS H, BRUMSACK H-J, LOFTFIELD N & KÖNIG N (1986) Verbessertes Druckaufschlußsystem für biologische und anorganische Materialien. *Z Pflanzenernähr Bodenk* **149**, 350-353

KLINGE H (1985) Foliar nutrient levels of native tree species from Central Amazonia. 2. Campina. *Amazoniana* **9**, 281-297

MARSCHNER H (1990) *Mineral Nutrition of Higher Plants*. 4th ed. Academic Press, London

MENGEL K 1991. *Ernährung und Stoffwechsel der Pflanze*. 7. Aufl. Fischer, Jena

SNEDAKER SC & GAMBLE JF (1969) Compositional Analysis of Selected Second-Growth Species from Lowland Guatemala and Panama. *BioScience* **19**, 536-538

STEUBING L & FANGMEIER A (1992) *Pflanzenökologisches Praktikum.* Ulmer, Stuttgart

TANNER EVJ 1977. Four montane rain forests of Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J Ecol* **65**, 883-918

TAXONOMÍA DE SUELOS (1982) Un sistema básico de clasificación de suelos para hacer e interpretar Reconocimientos de suelos. Soil Management Support Services SMSS. Technical Monograph No. 5

US-SOIL-TAXONOMY (1990) Soil Survey Stuff. Keys to Soil Taxonomy. 4th ed. Soil Management Support Services SMSS. Blacksburg, Virginia. Technical Monograph No. 19

VAN DEN DRIESSCHE R (1974) Prediction of mineral nutrient status of trees by foliar analysis. *Bot Rev* **40**, 347-394

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COMPARATIVE INVESTIGATIONS OF MINERAL SUBSTANCE RELATIONSHIPS IN GAPS AND IN THE FOREST STAND OF THE PREMONTANE RAINFOREST OF THE SIERRA DE TILARÁN COSTA RICA

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1. INTRODUCTION

1.1. BASIS FOR THE CHOICE OF TOPIC

In the framework of the dissertation "The importance of gap structure for the maintenance of diversity of tree species of a montane rainforest region in Costa Rica", it was of interest to collect data about the mineral substance relationships in the gaps and in the forest stand chosen for investigation. Comparative investigations of mineral substance relationships in gaps and in forest stand have already been carried out in La Selva (C. UHL, K. CLARK, N. DEZZEO, P. MAQUIRINO, not published) in an evergreen, tropical lowland rain forest. In this study, no change in nutrient content of nitrogen, potassium and calcium in comparison with the adjacent stand could be demonstrated. As the three rainforest types (evergreen, tropical lowland rainforest, foliage shedding, rain-green tropical rain forests and tropical mountain or drizzling forest) are greatly distinguished by their altitude, species diversity and species number, as well as height and the range of trees, the results obtained in one type of forest cannot be transferred to the others. For this reason, it appeared to be sensible to carry out an independent study with the delimited theme "Comparative investigations of the mineral relationships in gaps and in the stand of the premontane rainforest of the Sierra de Costa Rica in the montane rainforest region of Costa Rica". In the investigation of the mineral substance relationship the heterogeneity of the nutrition composition occuring in the soil of the gaps could also serve as an attempt at an explanation of the preferential establishment of individual species. The last-mentioned possible results of this study can only be discussed within the context of the dissertation by I. WATTENBERG.

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1.2. DEFINITION OF A GAP AND THE BASIS OF GAP RESEARCH.

For the study presented, the term gap is defined as follows: "A clearing in a stand caused by different natural causes, which are limited to the following five in the 14 selected gaps: withered tree (1), fallen-down crown of the tree (2), uprooted tree (3), standing withered tree (4), individual fallen-down boughs (5) (Classification of causes after WATTENBERG 1993)".

In an article about gaps and species diversity by JULIE SLOAN DENSLOW (1987), the general interest in gap research is summarized as follows. With the help of gap research, an answer to the question "How did the enormous species diversity in tropical rain forest develop - as a result of highly specific users of niches or by chance in the course gene drift coevolution?" could be found. This formulation of the statement of the problem has drawn particular interest in the past few years, as the increasing deforestation of the rainforests makes the necessity of reforestation increasingly more obvious. The effect of the 'senseless' exploitation of rainforests, of their potential for mineral raw materials, fine wood and energy capacity demonstrates itself in the form of erosion, nutrient impoverishment of the soil, changes in climate, reduction in species and the dying out of species, as well as the threat to the primitive peoples and their culture through the destruction of their habitat (M. SOMMER 1990). With the help of knowledge about the composition of species, species establishment, as well as knowledge about abiotic factors the individual species require, it would be possible to commence reforestation projects justified by the location in order to diminish the already ensuing results of the destruction of the rainforest.

2. LOCATION OF THE INVESTIGATION

All investigations were carried out in the Reserva Forestal de San Ramón (RFSR). The reserve was recently upgraded to Reserva Biologica Brenes (RB) and covers a total area of 8000 ha.

2.1. GEOGRAPHICAL LOCATION OF THE RESRVA BIOLOGICA ALBERTO BRENES

The reserve lies in the middle north of Costa Rica in the province Alajuela, approximately 40 km north-west of the town of San Ramón. It belongs to the caribean slope of the Cordillera de Tilarán and shows a mountain relief out of steep slopes with slope gradients of 25-30%, as well as deep V-shaped valleys (ORTIZ 1991). The biological station lies close to the border of the Reserva Biologica Alberto Brenes, directly at Rio San Lorencito.

2.2. VEGETATION

Following the system developed by L. HOLDRIDGE, the Reserva Alberto Brenes is a submontane, perhumid rainforest. The forest extends over a range of altitude from 800 m to 1500 m NN. It is exclusively a primary forest, which is subdivided into three levels. The highest level constitutes a large number of tree species at a height of 30-40 m, followed by a shrub layer in which, at a height of 2-8 m, shadow-tolerating plants grow. The third layer constitutes a partly soil-covering herbaceous plant layer, in which no lignified plants are to be found (VARGAS 1991). In addition, the forest is characterized by a large quantity of epiphyte vegetation, on the tree trunk as well as in the crown region. From a bird´s eye view, the crown roof can be recognized by a space in the stand (gaps) structure, which has arisen from the uprooted, chopped down and withered trees, fallen-down crown regions or individual fallen-down boughs (WATTENBERG 1993). The gaps vary in size between 30 and 200 m^2, according to their cause of occurence.

2.3. SOIL

The soil within the RB belongs to the andosoles. Andosoles (Japanese an shoko do = dark-coloured soil) are dark, deep, nutrient-rich soils which derive from vulcanic ashes. The upper soil of the andosole is mostly very loose and dark coloured, as a result of a high humic acid content. The shining red-brown clay-rich B horizon clearly stands out against the layer (O horizon) and the A horizon. It possesses a large porous volume and a high water capacity, which distinguishes it as a favourable plant location (SCHEFFER/SCHACHTSSCHABEL 1992). In the case of the soils investigated, it is orchic andosoles, which consist of an orchic A horizon and a cambic B horizon of sticky consistency (MAPA DE SUBGRUPOS DE SUELOS DE COSTA RICA).

3. METHODS AND MEASUREMENT TECHNIQUES

3.1. FIELDWORK

A representative number of 14 gaps were selected which differ according to the following criteria:

Topography (elevation, slope gradient and direction), size, age and cause.

The sample size per gap varied in relation to the gap size ($32\text{-}200^2$) between 10 and 36 samples. In total, 248 samples were taken.

The gaps were subdivided by I. WATTENBERG into subplots (2 m x 2 m). This subdivision into subplots was undertaken measuring from the middle point of the gaps in all directions. For the taking of soil samples, the subplot scheme was adopted. Starting from the formulation of the question of the study, the subplot raster was continued starting from the edge of the gap for the taking of stand samples. In each subplot, two mixed probes were taken: one from the A horizon (0-10 cm) and one from the B horizon (10-40 cm).

3.2. DRYING OF SAMPLES

The drying to constant weight took place in a drying cabinet in San José (Costa Rica) at a constant temperature of 40 °C (J.M. ANDERSON/J.S.I. INGRAM 1989). The relative level of humidity as a result of an annual precipitation of 1500-2000 mm in San José (Costa Rica: Datos e Indicadores Basicos 1992) does not allow an exclusive air-drying. Following complete drying, the soil samples were sealed in a plastic bag for transport.

3.3. LABORATORY METHODS

3.3.1. Elution and filtration

100 ml distilled H_2O was added to 10 g of the dry substance soil in a ground-glass stoppered flask and eluted for 24 h on a circular vibrator. Then, the samples were filtered twice (method standard procedure). Following the second filtration, the eluate was filled in 100 ml PE (polyethylene) bottles and kept in a fridge at 4 °C. The addition of a salt for faster elution (e.g. NH_4Cl) was dispensed with, as the anion concentration of the eluate should be determined by ion chromatography and additional ions would have burdened the column.

3.3.2. Measurement techniques

Before the determination of the concentrations of individual selected minerals from the soil, the pH value and the conductivity of all samples was determined.

The measurement of the cations available to the plant was carried out using AES (atom emission spectrometry) with ICP (inductively coupled plasma). The advantage of the AES with ICP in comparison with the flame AAS (atom absorption spectroscopy) lies in the simultaneous multi-element determination, the resulting speed of the method and the directly linked up, computer-controlled evaluation. The concentrations of the macro-elements calcium, magnesium and sodium, as well as the trace elements manganese and zinc were measured. The measurement of anions available to the plants was carried out using ion chromatography by means of column chromatography. The concentrations of chloride, nitrate and sulphate were measured.

4. RESULTS

4.1. DESCRIPTION OF GAPS AND ALTITUDE MEASUREMENTS

Table 1: 1 = broken off tree, 2 = fallen-down crown section, 3 = uprooted tree, 4 = standing withered tree, 5 = individual, fallen-down boughs (I. Wattenberg).

Location	Gap[1]	Altitude in m NN	Size m^2	Number of samples	Cause	Comments
Northern slope	29	935	154	36	1	Collection of moisture in northern direction
	31	935	190	25	1	see 29
	9	1040	127	15	2	Gap 9 and 28 border one another
	28	1040	85	12	2	Extreme slope slant in an easterly direction
	26	1105	49	16	5	Gaps 26, 19 and 20 border one another
	19	1105	85	20	3	Sample taking during heavy rain
	20	1105	77	10	3	
South slope	21	955	183	16	3	
	13	995	43	12	4	In sum very dark, as the gap tree still standing
	12	985	83	20	1	
	11	995	45	18	4	A large part of the gap floor covered with crowns of the gap trees
	10	1005	200	20	1	Herbaceous plant layer already 1.5 m high
	14	1005	91	14	2	
	33	1095	32	20	2	Came into being January 1993

4.2. MEASUREMENT OF THE PH VALUES

The values for the current acidity lie in the A horizon, distinguished by gaps, between pH 3.99 and pH 5.16; the values of potential acidity between pH 3.44 and 4.53 (Fig. 1). The potential acidity is, in the middle, 0.6 pH units lower, in which the trend can be recognized that differences in relation to the current values vary: at a lower $^{pH}H_2O$, the difference from $^{pH}CaCl_2$ is smaller than in the case of a higher $^{pH}H_2O$. On comparison of the horizons, it is clear that the values in the A horizon are, with one exception (gap 10),

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[1] The numbering of the gaps was adopted from I.Wattenberg

lower. In addition, it can be inferred from the graph that the greater the value in the A horizon, the smaller are the differences between A and B horizons.

The comparison of measurements of the samples from gap and stand produced, for all gaps and stands, average values differently distributed mineral substance contents. In half of the groups, the values are higher in the stand and, in the other half, in the gap.

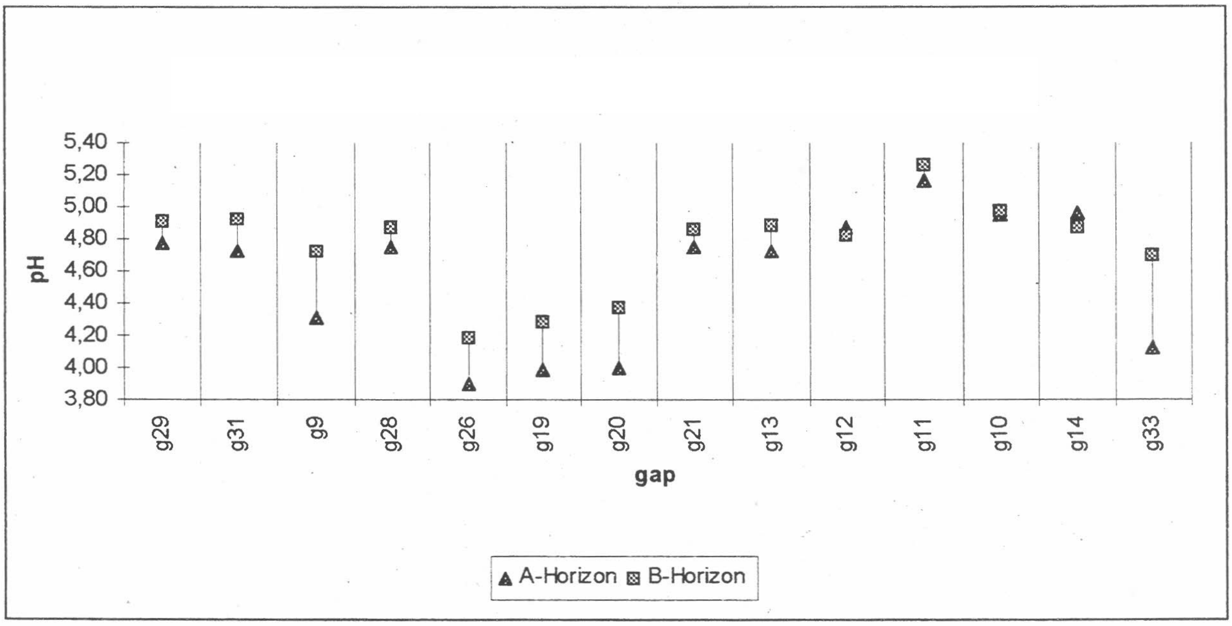

Fig. 1: Comparison of the pH_{H_2O} values in A and B horizons:

4.3. MEASUREMENT OF THE CATIONIC MACROMINERAL SUBSTANCES (CA^{2+}, K^+, MG^{2+}, NA^+)

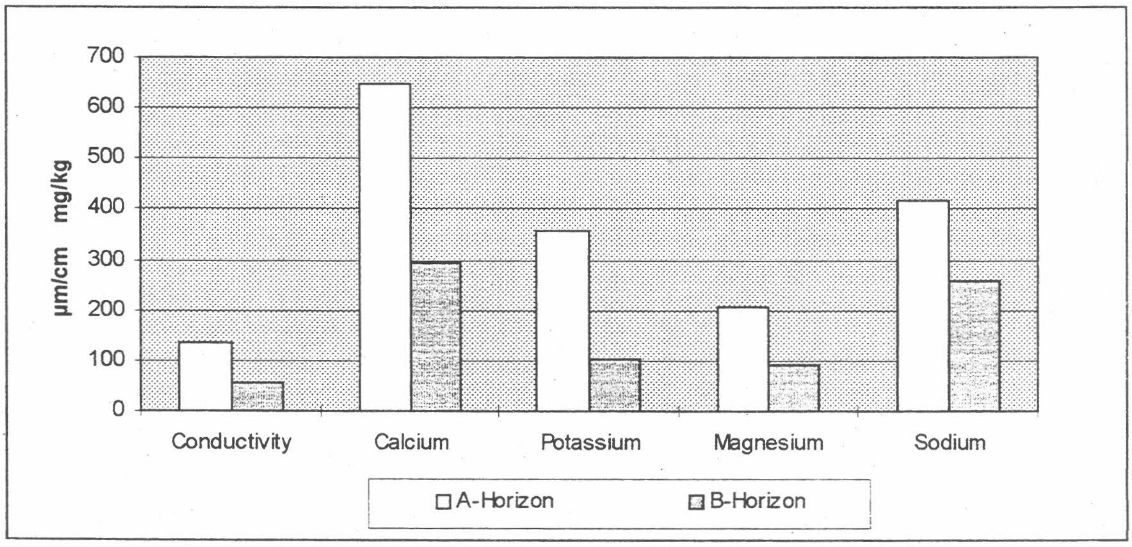

Fig. 2: Averages of the total samples separated according to A and B horizons:

The values for conductivity (in µS/cm) as well as those of the cationic macro elements (in g/kg) lie in the A horizon on average 45% higher than in the B horizon.

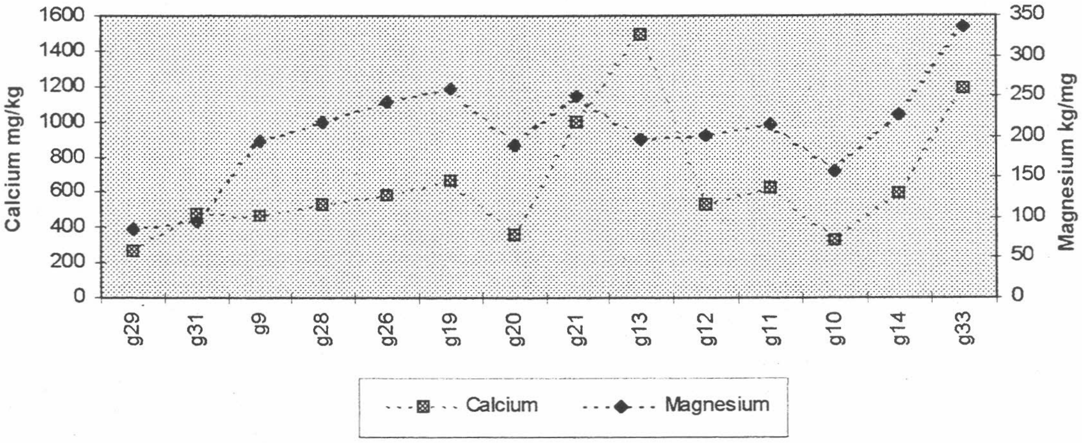

Fig. 3: Comparison of the average of Ca^{2+} and Mg^{2+} in the A horizons:

Figure 3 shows a clear parallelism of the nutrient content of calcium and magnesium with reference to the individual gaps. The calcium concentrations lie, on average, a factor of three higher. One such dependence can also be demonstrated for magnesium and potassium with a ratio of 1:2. The clearly deviating value for gap 13 is certainly based on the size of the gap, as well as also the cause of the gap. Gap 13 is very small and, due to the still existing tree, altogether very dark.The taking of samples could only be undertaken, in each case, in one subplot in each direction, therefore all samples derive from the direct root region of the gap tree. This fact creates a large inhomogeneity in the samples, and consequently a greater variance in the values.

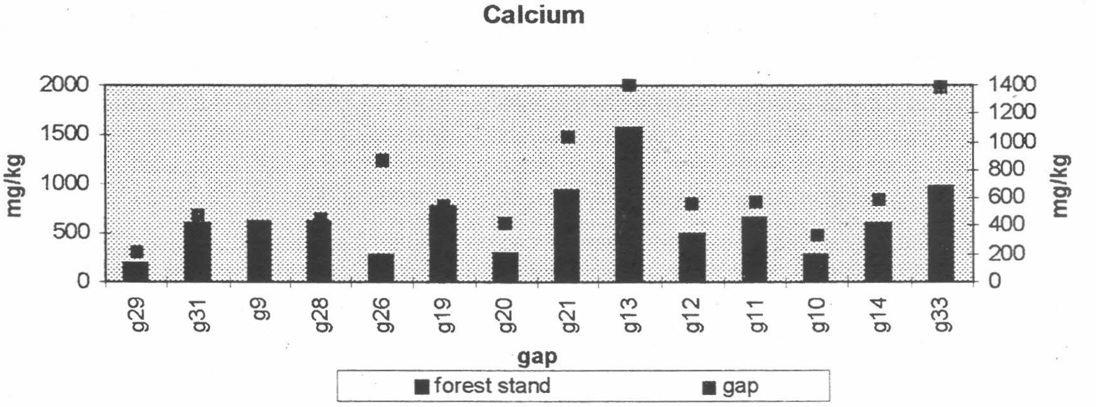

Fig.4: Comparison of gap and stock in relation to calcium content in the A horizon:

In total, the same statement can be made for the investigations of cationic macroelements as was made for the pH and conductivity measurements: no differences in the amounts of nutrients with reference to the location of sampling, gap and forest stand, appear. In the case of the results for calcium and magnesium gap 13, as in Fig. 3, is conspicuous. To what extent the additional observations made in gaps 19 and 11 (see Table 1), in the case of the calcium and magnesium values, have led to the extreme differences in gap and forest stand, cannot be answered without the additional collection of data.

4.3. MEASUREMENT OF THE ANIONS (CL^-, NO_3^{2-}, SO_4^{2-})

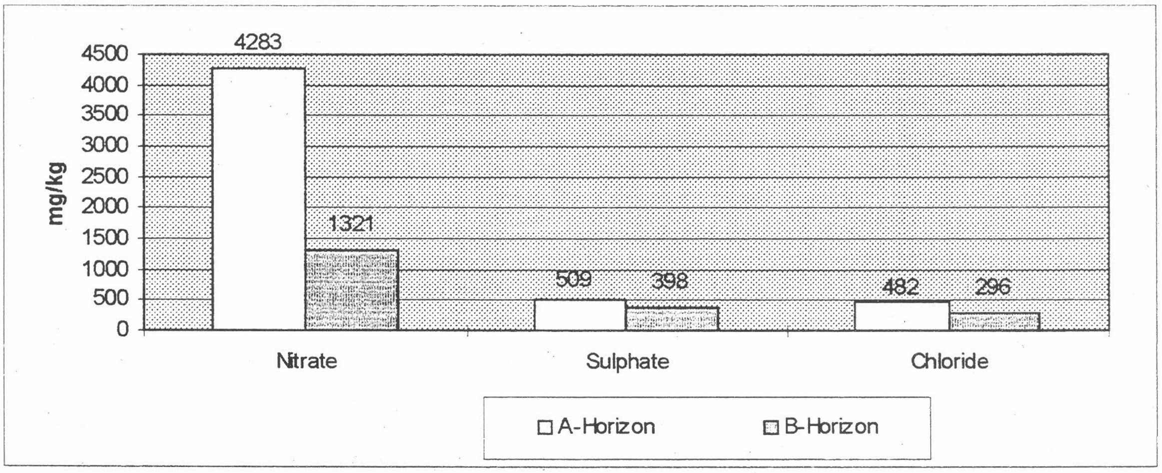

Fig. 5:Averages of the anion measurements distinguished in relation to A and B horizons:

In the case of the anions, similar concentration ratios are shown in relation to the A and B horizons as in the case of the cations. On comparison of the measured anion macroelements no proportionalities, as for calcium and magnesium values, can be demonstrated.

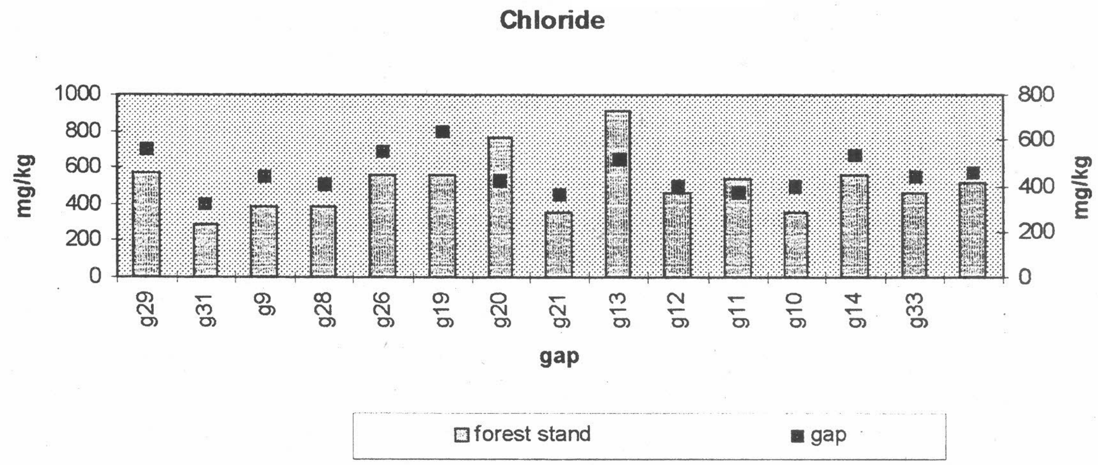

Fig. 6: Comparison of gap and forest stand with reference to chloride concentration in the A horizon:

In the case of the anionic macroelements, the same picture is shown as for the cationic macroelements. There are no clear tendencies in relation to the location of sample taking in a gap or in a forest stand.

4.5. DEGREE OF CROWN COVER

In addition to mineral substance concentration in gap and forest stand, the degree of crown cover over both areas was assessed separately and compared (Data from A. SPRENGER, C. LEYERS AND I. WATTENBERG).

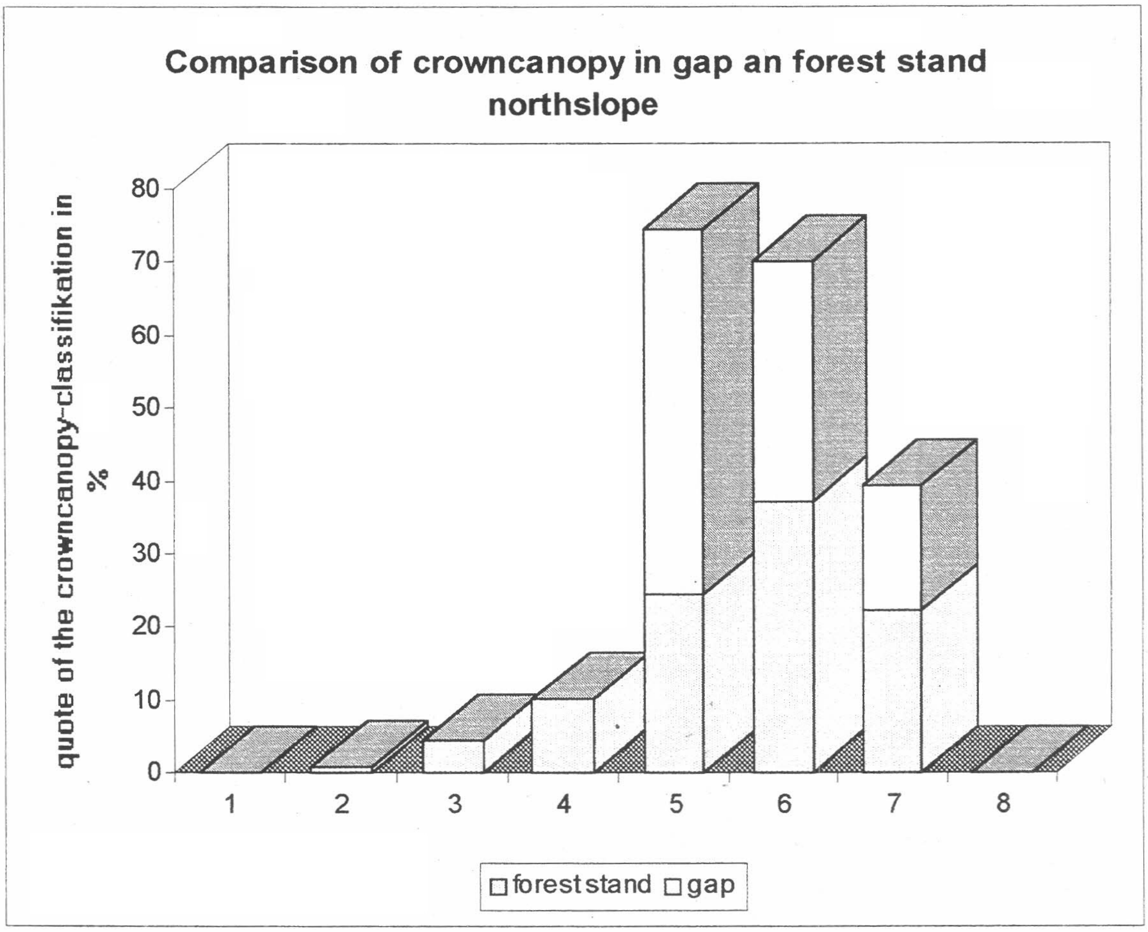

Fig. 7:Northern slope (degree of crown cover classes: 1 = 61-65%, 2 = 66-70%, 3 = 71-75%, 4 = 76-80%, 4 = 76-80%, 5 = 81-85%, 6 = 86-90%, 7 = 91-95%, 8 = 96 -100%)

The major part of the slope shows a degree of cover corresponding to classes 5-7. Most gaps can be ascribed to crown cover class 5; in the case of the forest stand, class 6. From this it can be concluded that solar radiation in the gaps is only insignificantly higher than in the forest stand.

5. DISCUSSION OF THE RESULTS

5.1. COMPARISON OF THE MINERAL SUBSTANCE RATIO GAP/FOREST STAND

At the centrepoint of the study was answering the question "Do differences exist in the mineral configuration in gaps in comparison with the neighbouring forest stand?"

No uniform differences in the mineral configuration were found, in the investigation presented, between gap and forest stand. In some gaps, the values were higher in the gaps, in others in the forest stand. In the following, the possible causes of this result are discussed.

In this study, only one of four factors that have an effect on cap and forest stand were considered in more detail. Mineral substance ratios but not, however, light, temperature and water relationships were investigated. These factors are very closely linked, e.g. the amount of precipitation that falls on gap soil is higher than in the forest stand, as interception by the crown cover is omitted. However, this is also again equalised by the increased rate of evaporation as a result of the additional amount of radiation which falls in the gap. From this example, it is made clear how complex the correlations are. For this reason, all four factors are taken up in the discussion, as well as including data from other investigations.

The increased amount of radiation which falls onto the ground through the crown cover gave rise to the suspiscion that the rate of mineralisation, as a result of the ground temperature in the gap, is higher than in the neighbouring forest stand. This thesis could not be completey dispelled by the study presented as, on the one hand, no increased amount of minerals in the gap substrate could be demonstrated and, on the other hand, this fact in turn could depend on on the increased intake of nutrients by the seedlings in the gaps. However, the increase in the soil temperature in the gap should not be overrated. In an investigation of this factor in La Selva (C. UHL, K. CLARK, N. DEZZEO, P. MAQUIRINO, not published) in small gaps (> 500 m^2), only an increase in the soil temperature by 2.0 °C in comparison with the neighbouring forest stand was established . The smaller size of the gaps (32-200 m^2) leads to the quantity of radiation which falls on the gap soil, in the case of these gaps, being only insignificantly higher in comparison with the stand, due to the constantly unfavourable angle of irradiation. The smaller gap size of the gap selected by I. Wattenberg resulted not from a special selection of smaller gaps, but represented the average gap size in the Reserva Biologica Alberto Brenes. The appearance of small gaps in the RB was established in the extreme gradient of slope of 20-35%. This factor is the reason why the trees do not reach such a height and extent as in a typical lowland rainforest (La Selva), which stretches over an area with only insignificant differences in height. The rain forest stand looses, in a mountanous relief, its foothold and is overthrown (=>gap). In addition, sloping locations are more endangered by windbreak, as the area of assault by the wind on exposed, sloping locations is larger. In the area of investigation of the Reserva Biologica Alberto Brenes, therefore, no such 'Giant trees', with several metres of spread, are to be found which then, on falling down, leave correspondingly large gaps behind.

A basic difficulty of this study was the establishment of the border between gap and forest stand. To a large extent the boundaries drawn by I. WATTENBERG were taken over. In older gaps, in which the degree of crown cover had already increased through advancing regeneration, the borders were further displaced in the direction of the centre of the gap. Due to the fact that the relative fast crown cover termination over a gap not only reduces the amount of radiation falling on the soil (=> increase in soil temperature, PAR = photopsynthetically active radiation), but also the amount of water diminishes, as the greater part is lost due to interception in the crown cover. On closer consideration of the problem of the border of gap and forest stand, there was the consideration of undertaking a classification according to age and, consequently, of gaining an additional differentiation criterion or further correlation factors. This classification was, on the basis of different causes of gaps, not possible. Gaps with the following causes: standing dying tree, crown sections that had fallen down and individual fallen-down boughs are subject to a spontaneous dynamic, therefore the situation in these gaps changes constantly due to additionally falling-down boughs, parts of the crown or through the falling of the standing dead tree (gap tree). Because of this dynamic, which leads to an increase in the gap, or at least runs toward the regeneration dynamic, it is not possible with a selection of 14 gaps with five different causes, to form age groups and to draw correlative comparisons. These two opposing dynamics have more stronger effects in the case of smaller gaps, as the error in drawing the border between gap and forest stand, in the case of smaller gaps with a correspondingly smaller sample size, has a greater weight. The effect of the inaccuracy of smaller sample sizes in the gaps with fewer subplots can be readily recognized from gap 13.

The comparison of the degree of crown cover in gap and forest stand (Fig. 7) confirmed the thesis that, in the case of smaller gaps, the additional amount of incident radiation in comparison with the forest stand is only insignificantly higher. In a study from Denslow (1987) in La Selva, this was specified with values for the rate of irradiation. Consequently, 20-35% of the total sunlight falls on the soil of a gap with an area of 400 m^2, and with an area of 200 m^2 it is still only 9%, and in the forest stand 1-2%.

The measurement of height of the gaps was not only carried out for the purpose of a more precise determination of the gaps, but also drawn into consideration as a possible influence of importance on gap regeneration. The maximal difference in height between gaps was 200 m, therefore the temperature difference was, according to Mapa de Unidades Bióticas de Costa Rica (1993), on average 0.5 °C at a height of 100 metres. The difference in height of 200 m following comparison of the gaps was not sufficient to demonstrate differences based on this magnitude of influence.

Overall, it could be shown that, in the case of all discussed magnitudes of influence, the smaller sizes of the gaps was the proposition-restricting factor. The objective of gap research, mentioned at the beginning, namely, to carry out basic research for reforestation is, with this study, not possible. Certainly, also in lowland rain forest, no information about the necessary soil conditions for reforestation were gained since, as a result of deforesting, a large amount of nutrients are withdrawn from circulation. For this reason, artificial gaps are being made in La Selva by deforestation and their regeneration observed. This type of gap research on artificial gaps comes close to the situation of deforesting and, with that, of an interrupted nutrient cycle.

As already mentioned in the introduction, these results are linked with a study which is concerned with the diversity of tree species, therefore the discussion of the results obtained is very limited. The fact that no significant differences in amounts of mineral substances in gap and forest stand were found can certainly be discussed once more in relation to the establishment of species and species dominance.

5.2. GENERAL ASSESSMENT OF THE SOIL

The following assessment of the soil in relation to its mineral configuration was made exclusively on the basis, in the treatment of the subject, of the measured values in comparison with values from the litterature deriving from "Bookers Soil Manual".

All values determined for the A horizon lie below a pH of 5.5, which is classified as low. This low pH value has naturally an influence on the availability of nutrient. The microbial breakdown by acidophobic bacteria is limited and the ion solution, as well as ion exchange, are influenced to different extents according to element. Acidophylic mycorrhiza bacteria enable the trees to directly take in nutrients from the soil layer (walter/Breckle 1991). The extent of this circulation of material is specific to the type of forest and, overall, not yet sufficiently researched. It is, however, certain that the "main work of destruction" in a soil with a pH value of less than 5.5 rests with the fungi.

The availability of the phosphate ions decreases very quickly at low pH values, as the free ions then preferentially enter into insoluble complex combinations with Al^{3+} or Fe^{2+}. This fact has the consequence that, with the method chosen of ion chromatography (limit of detectability 0.1 mg/l), the phosphate content could not be determined. A reduction in availability is also observed for Ca^{2+}, Mg^{2+} and K^{+}, the values for Mg^{2+} and K^{+} can be classified as average, whereas the values for Ca^{2+} must be assigned to the low category. The ratio of the macroelements with 3:1 for Ca^{2+} and Mg^{2+}, as well as 1:2 for Mg^{2+} and K+ likewise range within an average limit. For most of the microelements, the opposite phenomenon is to be observed at low pH, therefore the availability increases with decreasing pH, which is easy to understand from the Mn values measured. A relatively low pH therefore excludes a deficiency of microelements for all micronutrients except molybdenum.

For nitrogen and sulphur, on the basis of the measured values, no nutrient balance is made available. The nitrate content was greatly changed as a result of drying, and the sulphate content alone reflect all the S sources not available to the plants, as S can also be taken in in the form of SO_2 by the plant from the air. The sodium content of the soil does not play any role for the plants in this soil, as the Na^{2+} is not an essential macroelement and is only problematical for the plant when it occurs in large amounts, as a competitor to the other macroelements.

6. SUMMARY

The object of this study was to compare the relative mineral content in clearings with those in areas of denser growth. A number of important macronutritional and micronutritional elements were selected as examples and mixed samples from two horizons were analysed separately according to sampling location (i.e. clearings/areas of denser growth). The samples showed no differences in relation to their pH values, conductivity and nutritional content. These results allow the conclusion that it is not a particular quantity of the nutritional elements or their diversity that is responsible for the fast regeneration of such clearings. These results are limited in their general validity since, on the one hand, the tests were carried out in a very limited area and, on the other, the clearings selected were all > 200 m^3 and, therefore, the prevailing light and temperature conditions differ only slightly from those in the areas of denser growth. In this size of clearings, both the crown and the root region will probably be taken over very quickly by the tree population in the adjacent areas of denser growth. How and in what form the seeds, seed banks and possibly the shoots, which are permanently present in the forest soil, become established, is the subject of the investigations carried out by I. Wattenberg whose study is appendixed as a supplement.

7. LITERATURE

ANDERSON, J.M. & INGRAM, J.S.I. 1989: Tropical Soil Biology and Fertility: A Handbook of Methods. Wallingford C. A. B. International

BORNEMISZA, E. 1990: Problemas del azufre en suelos de cultivos de Mesoamerica. San Jose, Editorial de la Universidad de Costa Rica

BRUNIJNZEEL, L. A. 1991: Nutrient input-output budgets of tropical forest ecosystems: a review. Journal of Tropical Ecology 7: 1-24

BURINGH, P. 1979: Indroduction to the study of soils in tropical and subtropical regions. Centre for Agricultural Publishing and Documentation Wageningen

Costa Rica 1992: Datos e Indicadores Basicos. San José, Costa Rica

DENSLOW, J.S. 1987: Tropical Rainforest Gaps and Tree Species Diversity. Ann. Rev. Ecol. Syst. 18: 431-451

DENSLOW, J. S.et al. 1987: Bioassays of nutrient limitation in a tropical rain forest soil. Oecologia 74: 370-376

GANSSEN, R. 1972: Bodengeographie. Stuttgart, K.F. Koehler Verlag

GIANI, L. 1992: Ökologisches Fortgeschrittenenpraktikum Bodenkunde, SS 1992. Abt. Bodenkunde Universität Oldenburg

GOLIGHTLY, D.W. & AKBAR 1992: Inductively Coupled Plasma in Analytical Spectrometry. VCH Publishers, Inc.

HUSTON, M. 1980: Soil nutrients and tree richness in Costa Rican forests. Journal of Biogeography 7: 147-157

JANZEN, D. H. (ED.) 1983: Costa Rican National History. Chicago, University of Chicago Press

JORDAN,C.F. 1985: Nutrient Cycling in Tropical Forest Ecosystems. Chichester, John Wiley & Sons Ltd.

KUNZE, U. R. 1990: Grundlagen der quantitativen Analyse. Stuttgart, Thieme Verlag

MOHR E.C.J. et al. 1972: Tropical Soils. Niederlande, Geuze Dordrecht

NYE, P.H.& GRENNLAND, D.J. 1964: Changes in the soil after clearing Tropical Forest. Plant and Soil XI, (No.1)1: 101-112

REICHHOLF, J.H. 1990: Der Tropische Regenwald. dtv München

SANCHEZ, P.A. 1976: Properties and Managment of soils in the Tropics. New York, John Wiley & Sons

SCHAPENSEEL, H.W., SCHOMAKER, M. & AYOUB, A. 1990: Soils on a warmer earth. Amsterdam, Elsevier Sience Publishers B.V.

SCHEFFER, F. 1992: Lehrbuch der Bodenkunde. Stuttgart, Enke- Verlag

SOMMER, M. 1990: Countdown für den Dschungel. Stuttgart, Schmetterling Verlag

STÜBEN, P. E. (Hrsg.) 1985: Kahlschlag im Paradies. Giessen, Focus Verlag

TERBORGH, J. 1993: Lebensraum Regenwald: Zentrum der biologischen Vielfalt. Heidelberg, Spektrum Akademischer Verlag

VALERIO, C. E. 1991: La Diversidad Biologiça de Costa Rica. San Jose, Editorial Heliconia

VARESCHI, V. 1980: Vegetationsökölogie der Tropen. Stuttgart, Ulmer Verlag

WALTER H. & BRECKLE S.-W. 1991: Spezielle Ökölogie der tropischen und Subtropischen Zone, 2. unveränd. Aufl.. Stuttgart, G. Fischer Verlag

WEISCHET W. 1984: Schwierigkeiten tropischer Bodenkultur. Spektrum der Wissenschaft, 112-122

WHITEMORE, T. C. ET AL. 1983: Tropical Rain Forest: Ecology and Managment. Oxford, Blackwell Scientific Publications

YOUNG, A. 1976: Tropical soils and soil survey. Cambridge, Cambridge University Press

BIELEFELDER ÖKOLOGISCHE BEITRÄGE 11: 37-45, 1997

DISTRIBUCIÓN ALTITUDINAL DE LOS HELECHOS ARBORESCENTES EN LA RESERVA BIOLÓGICA ALBERTO BRENES, CORDILLERA DE TILARÁN

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Esta investigación se realizó como parte del convenio entre la Universidad de Costa Rica y la Universidad de Ulm, Alemania entre setiembre 1992 y setiembre 1993 en la Reserva Biológica Alberto Brenes. El terreno estudiado se extiende sobre las zonas de vida del bosque pluvial premontano, del bosque pluvial montano bajo y del bosque pluvial montano (según Holdridge 1967).

Se analizó la distribución altitudinal de ocho especies de helechos arborescentes (Cyatheaceae y Dicksoniaceae) a lo largo de un transecto desde 875 m hasta 1475 m de elevación, considerando los factores ecológicos. Las distintas especies se distribuyen de manera característica. Para cada una se observó un nivel máximo de distribución en una altitud determinada y un límite inferior o superior. La distribución de especies depende de la humedad relativa, de la temperatura y también de las condiciones de luz.

Hasta la fecha existe poco conocimiento sobre la ecología de los helechos arborescentes. Las investigaciones de Bittner & Breckle (1995) informan sobre el índice del crecimiento anual. La distribución de especies observada en la reserva se puede comparar a las resultados de Nisman (1965), Lee et al. (1986) y Gómez (1991).

METODOLOGÍA

TAXONOMÍA

Para la identificación de las especies se usaron las claves de Lellinger (1989) y Moran (1991), además la colección del Herbario Nacional de Costa Rica. Las especies investigadas se distribuyen geográficamente entre México y los Andes argentinos y en consecuencia no son endémicas (Tryon & Gastony 1975; Tryon & Tryon 1982; Lellinger 1989, Moran 1991). Muestras de las especies colectadas se encuentran en el Herbario Nacional de Costa Rica (CR) y en el herbario de la Universidad de Costa Rica (UCR). Se trata de:

Alsophila erinacea (H. Karst.) Conant, var. *erinacea*
Alsophila polystichoides H. Christ
Cyathea caracasana var. *maxonii* (Underw. in Maxon) Tryon
Cyathea delgadii Sternb.
Cyathea fulva (M. Martens & Galeotti) Fee
Cyathea nigripes (C. Chr.) Domin
Cyathea pinnula (H. Christ) Domin
Dicksona gigantea H. Karst.

La siguiente clave del campo se creó exclusivamente para la identificación de las ocho especies representadas en el transecto.

1 Tronco y pecíolos sin escamas, con tricomas largas, soros en el márgen de los segmentos, hojas secas permaneciendo en el tronco
Dicksonia gigantea

1 Tronco o pecíolos con escamas, con espinas, soros en las venas del segmento 2

2 Espinas peciolares agudas, negras, brillantes, las pinnas frequentemente más largas que 60 cm 3

2 Espinas peciolares poco marcadas, las pinnas hasta 60 cm de largo 4

3 Pinnulas pinnadas, soros en grupos, indusios oscuros y perennes
Alsophila erinacea

3 Pinnulas bipinnadas, soros en filas, indusios de color claro, no perennes
Alsophila polystichoides

4 Soros con indusios envolventes 5

4 Indusios ausentes 7

5 Hojas pubescentes en el envéz, escamas anaranjadas, en dos filas en el márgen del pecíolo, también en la superficie del tronco,base del pecíolo negro
Cyathea delgadii

5 Hojas lisas en el envéz, escamas en toda la superficie del pecíolo 6

6 Pinnulas sésiles, escamas de color melado, poco densas en el pecíolo, pecíolo verde
Cyathea fulva

6 Pinnulas basales pecioladas hasta 3 mm, escamas y pecíolo de color café, escamas muy densas en la base del pecíolo
Cyathea caracasana

7 Escamas negras en el tronco, ausentes en el pecíolo, pecíolo negro y liso, las pinnulas pecioladas (2 - 4 mm), tronco hasta 10 cm de ancho y 10 m de altura
Cyathea nigripes

7 Escamas de color café con márgenes rojizos en la base del pecíolo, las pinnulas sésiles, tronco delgado alcanzando como máximo los 2 m de altura
Cyathea pinnula

Las especies *Alsophila firma* (Baker) Conant y *Cyathea trichiata* (Maxon) Domin también crecen dentro de la reserva pero no aparecen en el transecto.

TRANSECTO

La metodología fue modificada según el manual de Van der Hammen et al. (1989). Se instaló un transecto altitudinal de 875 m a 1475 m de elevación, siguiendo el sendero al Volcán Muerto, atrás de la estación biológica. El transecto tiene exposición al Norte. La área investigada con 6 m de ancho, 2500 m de largo y una distancia altitudinal de 600 m se divide en seis zonas de 100 m altitudinales. Se determinó la elevación exacta por 28 puntos fijos, usando un altímetro barométrico.

El clima fue observado en mediciones mensuales de la precipitación y de la temperatura del suelo en cada zona altitudinal. Adicional se instaló termómetros especiales para medir las temperaturas máximas y mínimas del aire en 1230 m y 1475 m de elevación. Todos helechos arborescentes presentados en el transecto se clasificó por especie, tamaño del tronco y fertilidad. En cada sitio de crecimiento se medió tanto la inclinación como la cobertura relativa de copas de árboles, usando un densiómetro de espejo. Los datos de abundancia o frecuencia se refieren a helechos por hectárea.

RESULTADOS

CLIMA

Durante el año que duró esta investigación, se midió un total de 3660 mm de precipita-ción a 875 m de altitud. La estación seca dura de enero a abril. Se eleva la temperatura media anual a 19,5 °C (mínima 17,2 °C en enero, máxima 20,8 °C en mayo). A partir de 875 m de altura aumenta la cantidad de lluvias en 30%, mientras que la temperatura baja unos 3 °C hasta la cumbre del Volcán Muerto a 1475 m (Tab. 1). A 1230 m de elevación la temperatura del aire varía entre 12 °C y 29 °C dentro de la vegetación. Generalmente se encuentra el límite inferior del estrato de nubes a 1100 m de altura determinando el límite del bosque premontano. Durante la estación seca baja la niebla hasta cerca de 800 m. El microclima del bosque premontano se caracteriza por condiciones constantes de alta humedad relativa, mientras que el bosque montano se ve afectado por periodos de sequía esporádicos.

Tab. 1: Datos mensuales de precipitación [mm] y de temperatura [°C] en distintas alturas

més	elevación		
	875 m snm	**1230 m snm**	**1475 m snm**
	mm / °C	mm / °C	mm / °C
set. 92	306		
oct. 92	613		
nov. 92	431 / 19,5	385 / 17,7	
dic. 92	148 / 18,9	204 / 17,4	
ene. 93	138 / 17,2	164 / 16,1	
feb. 93	69 / 18,5	79 / 16,8	
mar. 93	151 / 19,8	185 / 17,7	
abr. 93	55 / 20,3	66 / 18,6	104 / 17,3
mayo 93	331 / 20,8	358 / 19,1	457 / 17,9
jun. 93	477 / 20,2	552 / 18,7	605 / 17,6
jul./ago. 93	944 / 20,0	951 / 18,7	980 / 17,5

DISTRIBUCIÓN ALTITUDINAL

Entre 1100 y 1200 m de elevación se observó la mayor abundancia de helechos arborescentes dentro del estrato inferior de nubes. Por encima de los 1200 m se disminuye tanto la abundancia como la diversidad de especies (Tab. 2). A 1370 m se percibe un cambio de la flora. En la zona más elevada *Cyathea caracasana* aparece con frecuencia desplazando a tres especies de helechos arborescentes.

Tab. 2: Distribución altitudinal de helechos arborescentes a lo largo del transecto

zona	**elevación** [m snm]	**bosque**	**abundancia** [helechos / ha]	**especies**
1	875 - 969	premontano	590	5
2	970 - 1069	premontano	682	7
3	1070 - 1169	montano bajo	922	7
4	1170 - 1269	montano bajo	490	7
5	1270 - 1369	montano bajo	459	4
6	1370 - 1475	montano	468	3

Según la distribución altitudinal se pueden clasificar dos grupos de especies con distintas estrategias de vida: *Alsophila erinacea, Cyathea delgadii, C. nigripes* y *C. pinnula*, como especies premontanas aparecen con mayor frecuencia debajo de los 1100 m (Fig. 1). Se trata de helechos del sotobosque en bosques primarios con una gran tolerancia de sombra. Las especies montanas *Alsophila polystichoides, Cyathea caracasana, C. fulva* y *Dicksonia gigantea* son más frecuentes por encima de 1100 m y se parecen más a las plantas pioneras.

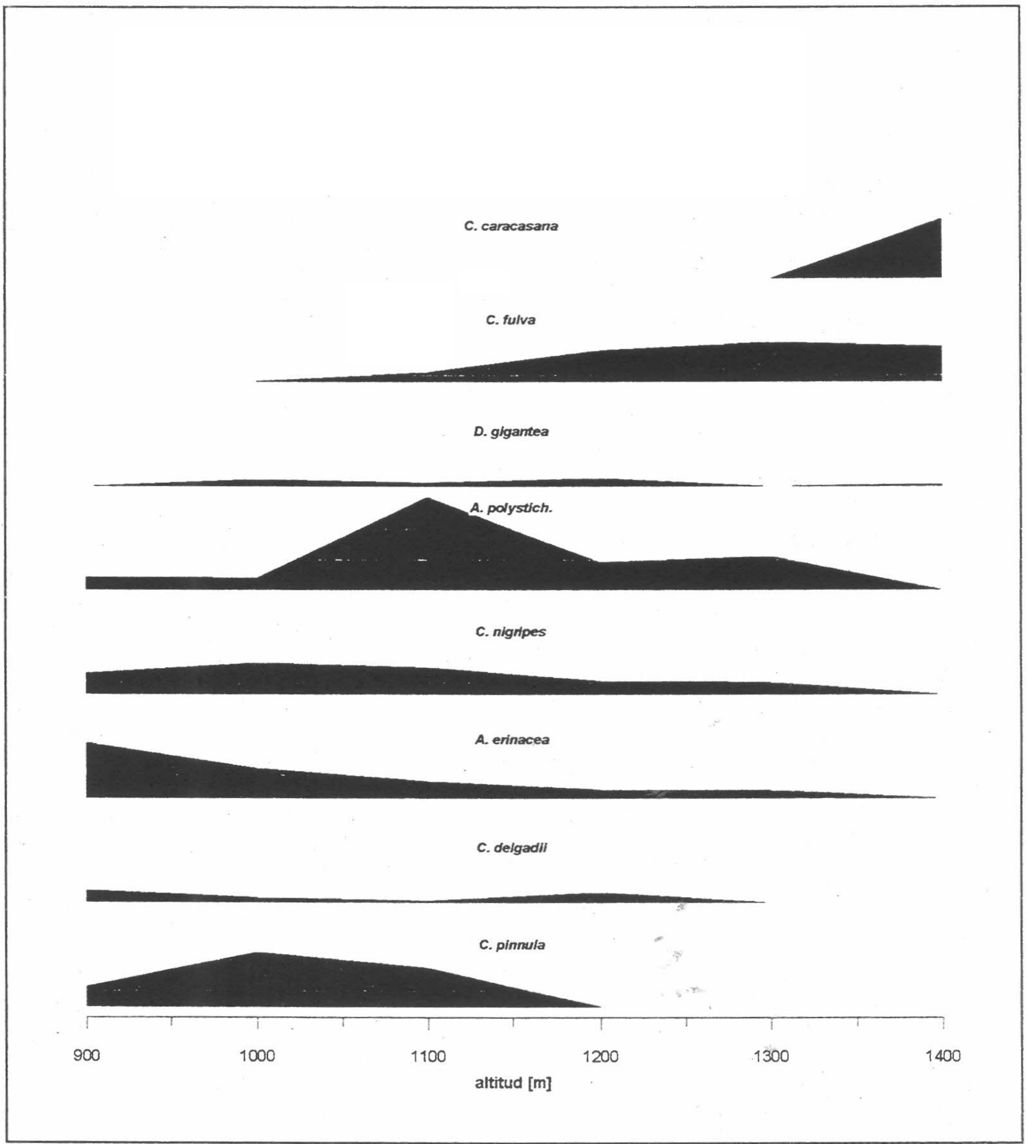


Fig. 1: Distribución altitudinal de ocho especies a lo largo del transecto. La extensión de las superficies negras indica la abundancia.

INCLINACIÓN

La mayor parte del área del transecto presenta inclinaciones entre 10° y 20°. El porcentaje de pendientes más inclinadas aumenta debajo de los 1000 m. En el transecto los helechos arborescentes colonizan todos sitios hasta 80° de pendiente. *Alsophila erinacea, Cyathea nigripes* y *C. pinnula* como especies premontanas crecen con mayor frecuencia en sitios con una inclinación superior a 20°. Las otras no tienen preferencias con respecto a la inclinación.

CONDICIONES DE LUZ

Debido a claros en las copas de los árboles, los helechos del bosque montano reciben mayor cantidad de luz que las especies premontanas. El promedio de la cobertura relativa de copas de árboles se eleva a 92% en 900 m y solamente a 63% en 1400 m de altura. En la Fig. 2 se ve comparada la distribución de especies según la cobertura relativa. Varios individuos de *Cyathea caracasana* y *C. fulva* aparecen en sitios completamente expuestos al sol.

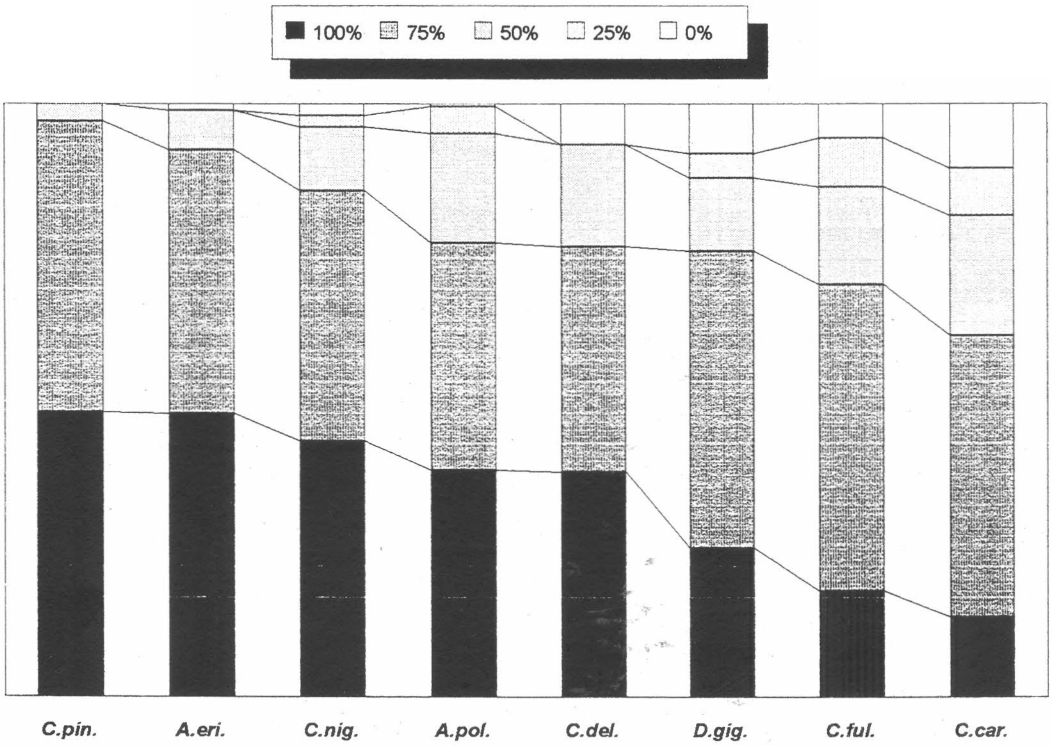


Fig. 2: Distribución de especies según la cobertura relativa, clasificada en 5 categorías de cobertura entre 0 y 100%.

Los claros desempeñan un papel importante en la germinación y la reproducción de los helechos arborescentes por las condiciones favorables de una temperatura más alta y una mayor cantidad de luz. Se extienden los claros con 10 m de diámetro o más a 7% del área del transecto. Los helechos con menos de 0,75 m de tamaño, designados como plantas juveniles, se encuentran con doble abundancia dentro de los claros (excepto a *Alsophila polystichoides*). *Cyathea pinnula* se ha adaptado completamente a la vida en los claros.

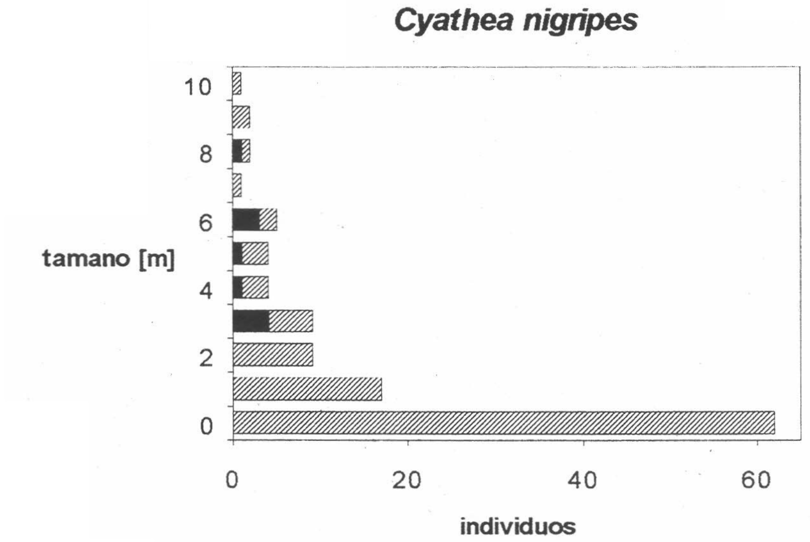
LUZ Y CRECIMIENTO

El crecimiento de los helechos arborescentes se ve beneficiado por el aumento de luz. Se examinó la relación entre la cobertura relativa y las dimensiones de 36 individuos de *Cyathea fulva*. Fue posible demostrar estadísticamente, que los individuos que obtuvieron una mayor cantidad de luz, se caracterizaron por una mayor superficie de hojas, por un mayor diámetro del tronco y por un tronco más prolongado. El porcentaje de individuos fértiles es elevado en sitios más iluminados.

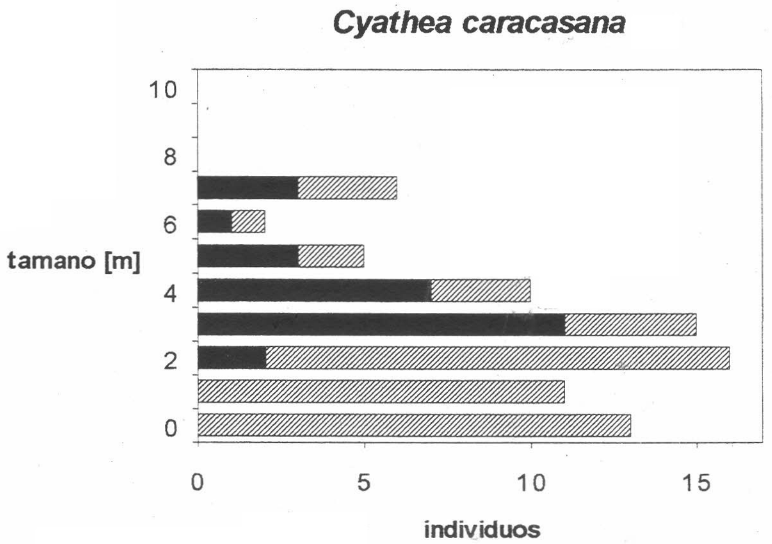
ESTRUCTURA DE POBLACIÓN

Parecido a la distribución altitudinal se pueden agrupar las especies en dos categorías. En las poblaciones premontanas, primero en *Cyathea nigripes* y *Alsophila erinacea*, las plantas juveniles menor de 0,75 m de tamaño forman la mayor parte (Fig. 3). Solo pocos ejemplares alcanzan la madurez. El índice del crecimiento anual es pequeño (Bittner & Breckle 1995). *C. caracasana* y *C. fulva* en tanto que especies montanas se caracterizan por poblaciones homogéneas. Ejemplares de todos tamaños están representados por igual (Fig. 3). La parte de individuos fértiles se eleva a 37% de la población de *C. caracasana*. Similares estructuras de poblaciones se percibe con frecuencia en plantas pioneras (Whitmore 1990).

Cyathea pinnula se ha adaptado mejor a las condiciones prevalecientes en los claros. Este helecho produce esporas después de poco tiempo, alcanzando como máximo los 2 m de tamaño. Termina su desarrollo después de pocos años y se ve substituido por otras especies.



Cyathea nigripes



Cyathea caracasana

Fig. 3: Estructura de población en dos especies típicas, clasificada en 11 categorías de tamaño del tronco entre 0 y 10 m. Individuos fértiles indicados por columnas negras.

LITERATURA CITADA

BITTNER, J., BRECKLE S.-W. 1995: The growth rate and age of tree fern trunks in relation to habitats. Am. Fern J. 85: 37-42.

GÓMEZ, L.D. 1991: Cyatheaceae y Dicksoniaceae (Pteridophyta). En: Janzen, D.H., Historia natural de Costa Rica. Edit. de la UCR, San José, Costa Rica, 822 p.

HOLDRIDGE, L.R. 1967: Life zone ecology. Centro Científico Tropical, San José, Costa Rica, 206 p.

LEE, M.A.B., BURROWES, P.A., FAUTH, J.E., KOELLA, J.C., PETERSON, S.M. 1986: The distribution of tree ferns along an altitudinal gradient in Monteverde, Costa Rica. Brenesia 25/26: 45-50.

LELLINGER, D.B. 1989: The ferns and fern-allies of Costa Rica, Panamá and the Chocó (Part 1). Dept. of Botany, Smithonian Institution, Washington D.C., 364 p.

MORAN, R.C. 1991: Eight new species of tree ferns (*Cyathea*, Cyatheaceae) from the American tropics and three new combinations. Novon 1: 88-104.

NISMAN, C. 1965: Estudio taxonomico y ecológico de los helechos arborescentes de Costa Rica. Tesis, Universidad de Costa Rica, San José, Costa Rica.

TRYON, R.M., GASTONY, G.J. 1975: The biogeography of endemism in the Cyatheaceae. Fern Gaz. 11: 73-79.

TRYON, R.M., TRYON, A.F. 1982: Ferns and allied plants with special reference to tropical America. Springer, New York, 857 p.

VAN DER HAMMEN, T., MUELLER-DOMBOIS, D., LITTLE, M.A. 1989: Manual of methods for mountain transect studies. International Union of Biological Sciences, Paris, 66 p.

WHITMORE, T.C. 1990: An introduction to tropical rain forests. Oxford University, Oxford.

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COMPARATIVE STUDIES ON POPULATION ECOLOGY OF *IRIARTEA DELTOIDEA*, *ELAEAGIA UXPANAPENSIS* AND *CALATOLA COSTARICENSIS* IN A TROPICAL PREMONTANE RAIN FOREST IN THE CORDILLERA DE TILARÁN, COSTA RICA

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INTRODUCTION

High tree species diversity is a characteristic of tropical rain forests and has been well documented for several sites in Costa Rica (HEANEY & PROCTOR 1990, WATTENBERG & BRECKLE 1995, LIEBERMAN & LIEBERMAN 1987, 1994, HARTSHORN 1991). Numbers of 79 - 135 tree species with a diameter of ≥ 10 cm at breast height (DBH) per hectare were counted. The study site comprise of 94 tree species (≥10 cm DBH) per hectare (WATTENBERG & BRECKLE 1995, WATTENBERG ET AL. 1996, WATTENBERG 1996).

Less extinction rates and higher differentiation rates in the tropics may have lead to the development of high tropical biodiversity but how can so many species coexist actually? Apart from tree species numbers and abundances there is not much known about the ecology of most of the existing tree species at the study site. A first approach to understand the maintenance of high tree species diversity is to investigate some aspects of population ecology of tree species and the ecological behaviour of juvenile trees.

This paper presents the findings from three years of investigation of two abundant tree species and one arborescent palm species of the study area for population distribution and for establishment, mortality and growth rates of the juveniles with some respect to different light levels.

STUDY AREA

The study was carried out in the Reserva Biológica Alberto Manuel Brenes (RBAMB, until 1994 Reserva Forestal de San Ramón) near the Biological Station. The coordinates are 10° 13' N and 84° 37'. The RBAMB forms a part of the Carribian slope of the Cordillera de Tilarán and is located in the province of Alajuela in north-central Costa Rica. This protected area of 7800 ha is covered by almost undisturbed primary forest.

The relief is mainly mountainous with inclinations between 25 and 30° (VARGAS 1991, ORTIZ V. 1991) and ranges between 800 an 1500 m of altitude. The soils developed from volcanic ashs, they are rich in organic matter and well drained, they can be classified as andosols (NUHN 1978, VARGAS 1991). Climatic data of the RBAMB are available only for a few years, mean annual rainfall of the available data was 3750 mm without a real dry period during the year. Mean temperatures per month ranged between 18° and 21° during the year (unpublished data of BRECKLE 1996).

According to the altitude and the climatic conditions the RBAMB can be classified as a tropical premontane wet forest following the life-zone system of HOLDRIDGE et al. (1971). The forest canopy reaches a height of 30-40 m containing numerous small and medium-sized gaps which permit a well-dedeveloped herbaceous layer on the ground (WATTENBERG & BRECKLE 1995).

STUDY SPECIES

The species were selected according to different criteria. First criterion was their assumed status as non-pioneer species. In the present study the definition of a pioneer species is strongly following the definition of SWAINE & WHITMORE (1988) which depends on the restricted germinating ability of a species only under sunlight conditions. The idea was to investigate the different ecological behaviour of non-pioneer species, because they are much less known than pioneers but numerically predominant. Second criterion was the representative sample size, we focus on abundant species of both, of juveniles up to the height of 400 cm and of adults about 10 cm DBH. Further criteria were the obvious differences in their appearance and distribution.

***Iriartea deltoidea* Ruíz Lopez & Pavón (Arecaceae)**

Iriartea deltoidea is one of two large palm species in the study area reaching the canopy. This palm tree is very frequent on the study site. According to HOLDRIDGE & POVEDA (1975) *Iriartea deltoidea* is an endemic species in Costa Rica. *Iriartea deltoidea* is also known as a subcanopy species from the lowland sites of La Selva and Corcovado, Costa Rica (HARTSHORN 1991).

***Elaeagia uxpanapensis* Lorence ined. (Rubiaceae)**

Elaeagia uxpanapensis is a frequent tree species of the canopy on the study site. It is only known from the Carribian slope of the Cordillera de Tilarán and from South Mexico (BURGER & TAYLOR 1993).

***Calatola costaricensis* Standley (Icacinaceae)**

Calatola costaricensis is a frequent tree species of the subcanopy on the study site. It is the only tree species of the Icacinaceae. *Calatola costaricensis* is growing up to an altitude of 2000 m. In Costa Rica, *Calatola costaricensis* is also known from the lowland site in Corcovado and the cloud forest of Monteverde, on both sites only as a rare tree species (HARTSHORN 1991).

METHODS

To investigate the population structure of the adults (≥ 10 cm DBH) of the study species one hectare of forest area was selected and marked out. All individuals (≥ 10 cm DBH) within the study plot were counted and the study species were measured in height and diameter at breast height. The abundance values of the study species were calculated from the inventory data of all trees (≥ 10 cm DBH). Total abundance of the adults (TA/A) is the number of trunks per species per hectare, relative abundance (RA/A) means the study species percentage of the total trunk number of the study plot.

The juveniles were investigated at different study plots. With respect to the planned analysis of the ecological behaviour under different light conditions the study plots were mainly selected as gaps within the forest. A gap was defined as a disturbed area on the forest floor under a light gap in the canopy caused by branch or tree fall with minimum area of 25 m² (WATTENBERG 1996). 30 gaps of different sizes were investigated. For comparative studies 4 completly overcrowned study plots have been selected additionly. These 34 study plots have been subdivided into transects of subplots with an area of 4 m² each. The total investigated area was 1088 m². All juvenile trees (including the large palm species) up to the height of 400 cm were tagged, identified and measured in height. Total abundance of the juveniles (TA/J) was the total stem number of the study species per 1088 m². Relative abundance (RA/J) means the percentage of trunks of each species of the total number of inventoried juveniles.

Juvenile establishment and mortality and juvenile height growth was measured over a period of three years, height growth was measured at intervals of one year.

The different light conditions were measured vicariously by determining the impermeability of light through the canopy as crown density. Crown density was measured with a sperical densiometer (Model A, LEMMON 1957). This instrument measures the amount of overhead cover as percentage of the obstructed sky. Crown density values were measured for each individual subplot.

RESULTS

DISTRIBUTION OF THE STUDY SPECIES

Iriartea deltoidea dispose of 66 individuals (≥ 10 cm DBH) per hectare which corresponds to a relative abundance of 12.7% (see table 1). *Iriartea deltoidea* can be found with a height up to 35 m but most individuals are distributed in the height classes between 5 and 20 m (see fig. 1). As a monocotyledone species the DBH of *Iriartea deltoidea* does not exceed 30 cm, 60% of *Iriartea deltoidea* are provided with a DBH between 20 and 30 cm (see fig. 4). The abundance values of the juvenile palms do not reflect the abundance values of the adults. The juveniles of *Iriartea deltoidea* contribute with only 2.3% of all inventoried juveniles (see tab. 1). The distribution of the juvenile palms indicates the highest percentage of 77% of the individuals in the lowest height class up to 50 cm, with declining tendency while rising height (see fig. 7).

Elaeagia uxpanapensis is less frequent, this species contributes with an RA/A value of only 2.5% to all inventoried trunks (see tab. 1). With a maximum height of 35 m *Elaeagia uxpanapensis* also reaches the canopy (see fig. 2) but as a tree species *Elaeagia uxpanapensis* appears completely different. *Elaeagia uxpanapensis* is nearly evenly distributed over a wide range of DBH-classes up to a maximum DBH of 210 cm (see fig. 5). The juvenile tree distribution in different height classes corresponds nearly to the distribution of *Iriartea deltoidea* (see fig. 8).

Calatola costaricensis is also less frequent with a low RA/A-value of 2.3% (see tab. 1). *Calatola costaricensis* only reaches the subcanopy with a maximum height of 25 m (see fig. 3). The low maximum DBH of 40 cm is related to the appearance of *Calatola costaricensis* as a subcanopy tree species (see fig. 6). Among the juvenile trees investigated, *Calatola costaricensis* is the most abundant species, 73 counted individuals in the area of 1088 m², represent 5% of all inventoried juvenile trees (see tab. 1). The height class distribution of the juveniles of *Calatola costaricensis* is similar to the distribution of *Iriartea deltoidea* and *Elaeagia uxpanapensis* (see fig. 9).

Table 1: Total and relative abundance of adult and juvenile trees of the study species. TA/A represents the trunk number (≥ 10 cm DBH) per species per hectare, RA/A is the percentage per species of all trunks (≥ 10 cm DBH). TA/J means the trunk number per species per 1088 m² of the juvenile trees, RA/J is the percentage of trunks per species of all juvenile trees.

	Trees (≥ 10cm DBH)		Juvenile trees	
Tree species	**TA/A (N)**	**RA/A (%)**	**TA/J (N)**	**RA/J (%)**
Iriartea deltoidea Ruíz Lopez & Pavón	66	12.7	34	2.3
Elaeagia uxpanapensis Lorence ined.	13	2.5	55	3.7
Calatola costaricensis Standley	11	2.3	73	5.0

JUVENILE ESTABLISHMENT AND MORTALITY

Among the study species *Elaeagia uxpanapensis* showed the greatest establishment of new juveniles over the three year period, nearly 75% of all inventoried juveniles appeared during the investigation period, while mortality was very low with a rate of 9.1%. Establishment and mortality of *Calatola costaricensis* was nearly balanced at a dynamic rate of 42.4% of establishment and 46.6% of mortality. The relation of establishment and mortality of *Iriartea deltoidea* was also nearly balanced but less dynamic with 17.6% of mortality and 20.6% of establishment (see fig. 10).

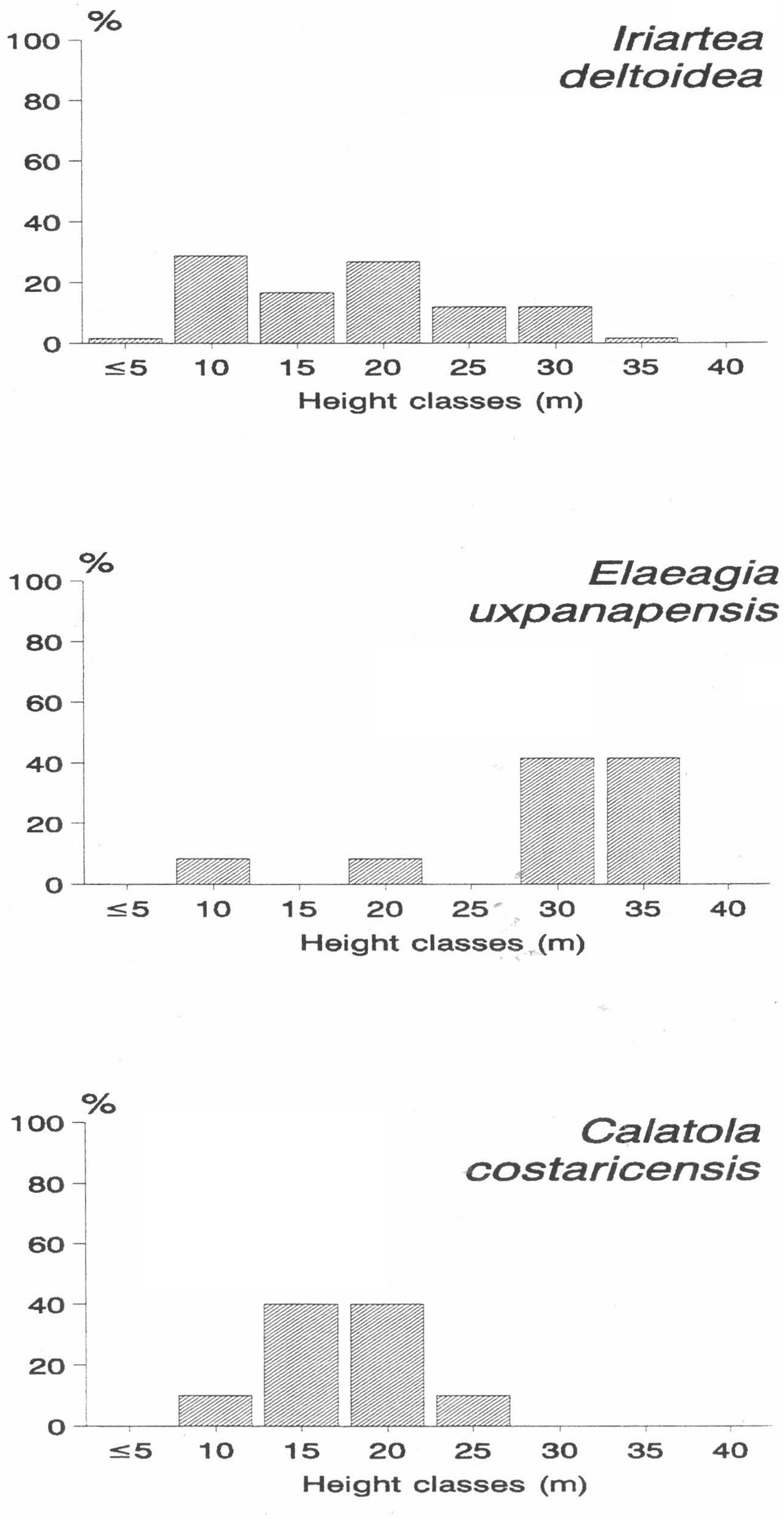

Figure 1-3: Percentage distribution of the study species (≥ 10 cm DBH) within trunk height classes (only the upper class limits are indicated)

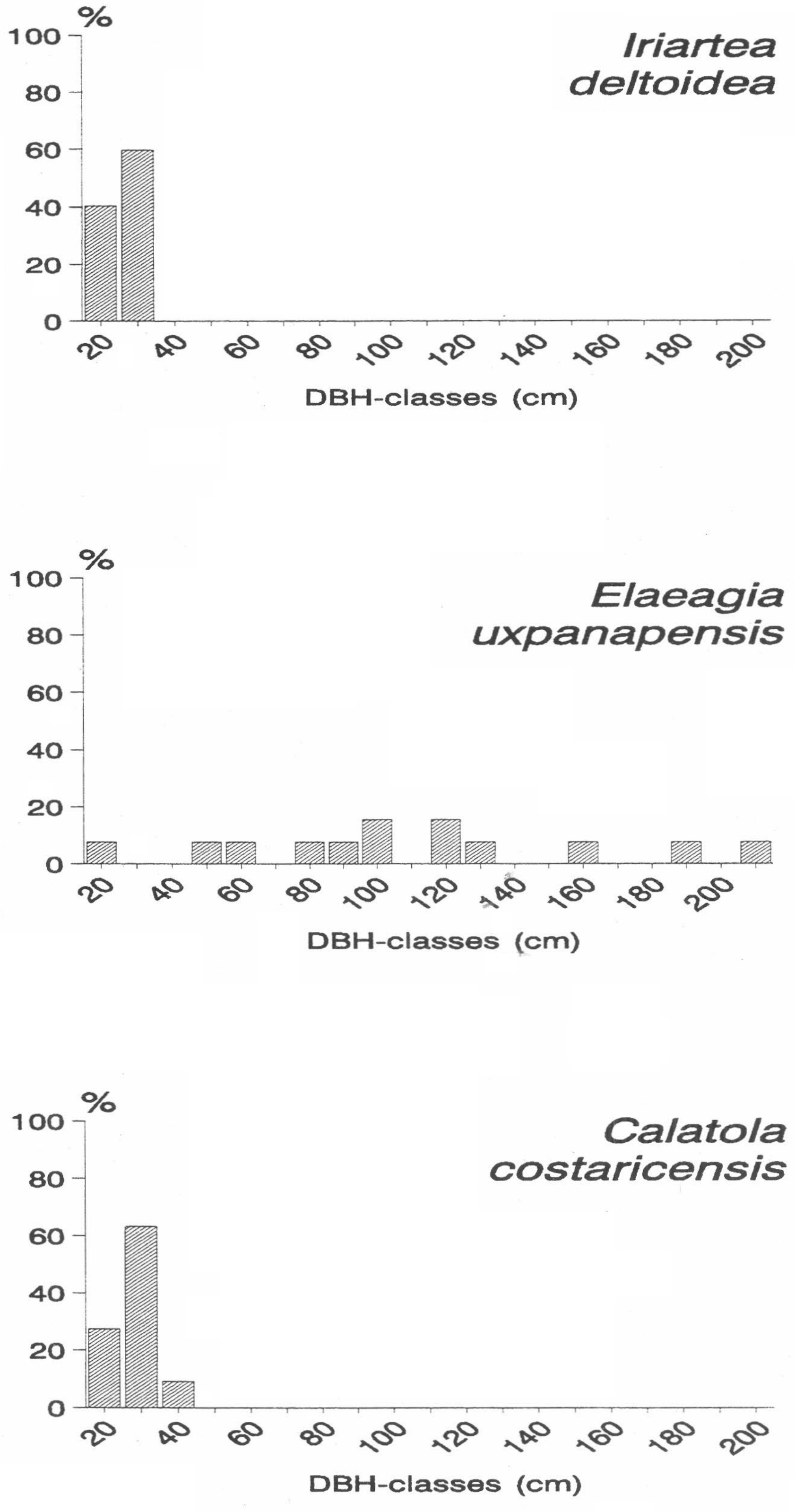

Figure 4-6: Percentage distribution of the study species (≥ 10 cm DBH) within DBH classes (only the upper class limits are indicated)

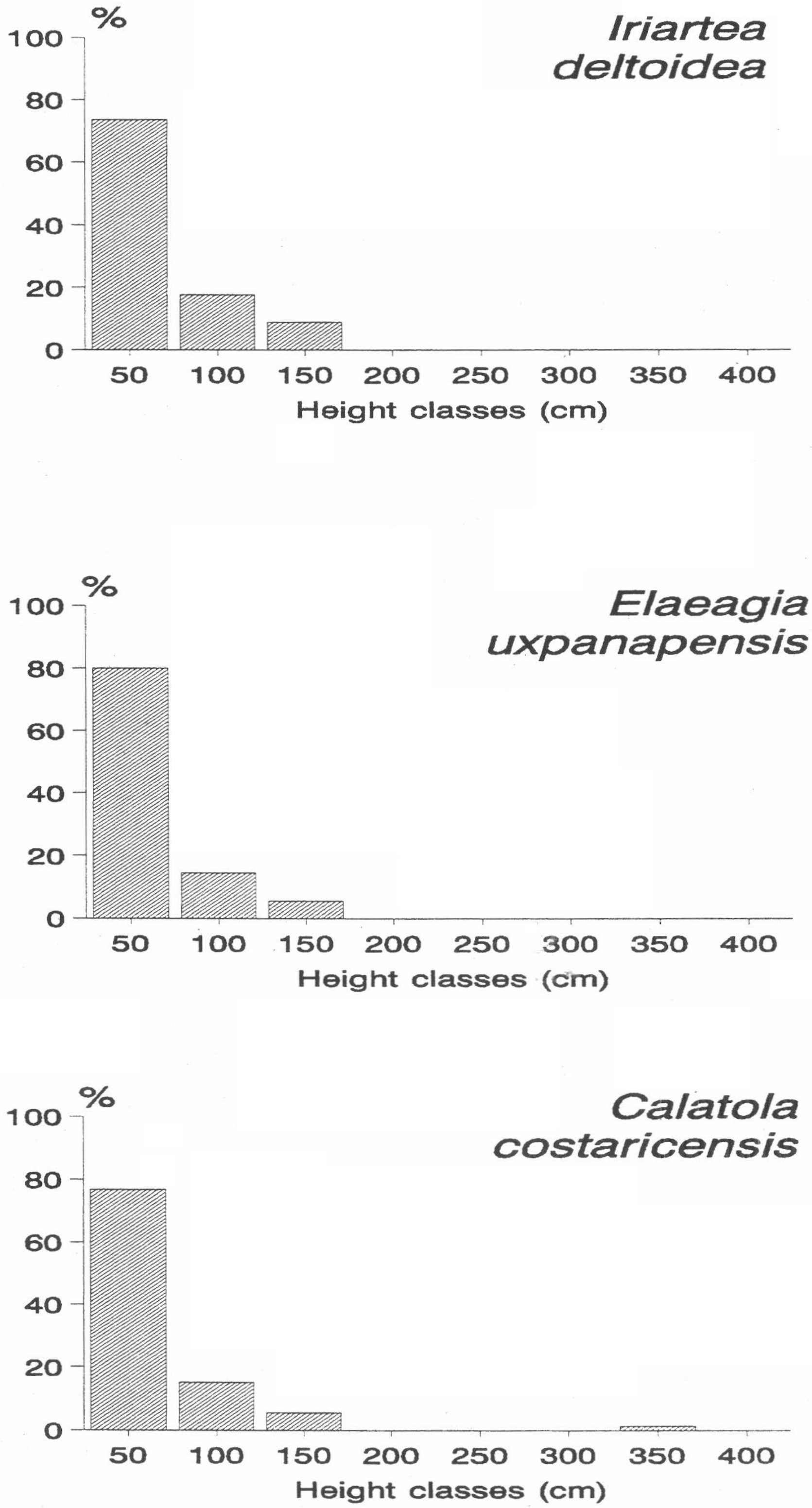

Figure 7-9: Percentage distribution of the juvenile trees of the study species (≤ 400 cm height) withinheight classes (only the upper class limits are indicated)

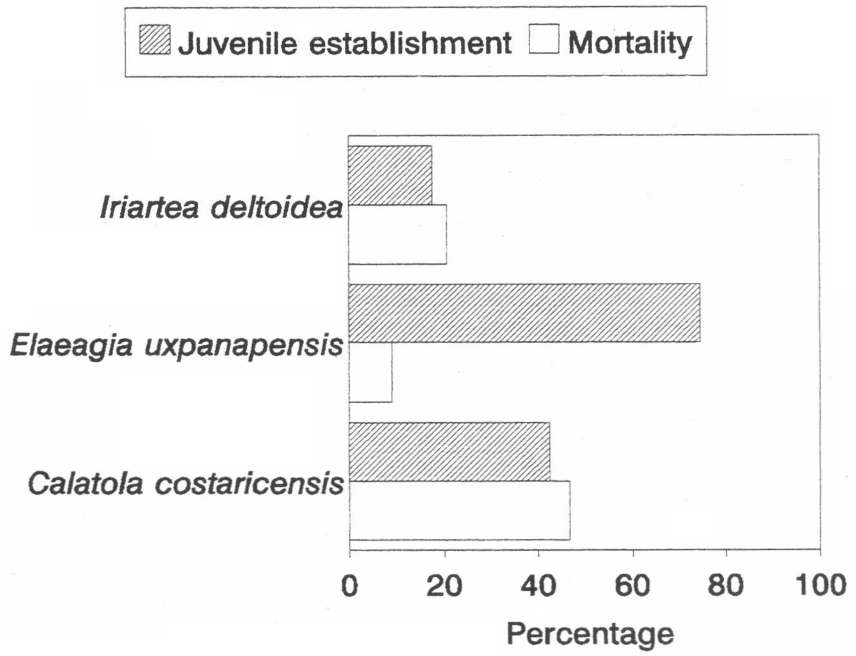

Fig. 10: Percentage of juvenile establishment and mortality of the study species over a three year period

GROWTH RATES OF THE JUVENILES

Highest growth rates per year among the study species exhibited the juveniles of *Elaeagia uxpanapensis*: 18 cm of height growth per year were measured as the median value. Height growth differences within the species amounted up to nearly 40 cm per year. Excluding the 5% of highest values, the maximum height growth was 49.4 cm per year. Median height growth per year of *Calatola costaricensis* was lowest at 7.5 cm. Maximum growth at the 95% level of values was 39.5 cm per year. Median height growth of *Iriartea deltoidea* was 12 cm per year, maximum growth at the 95% level of values was 46.8 cm per year.

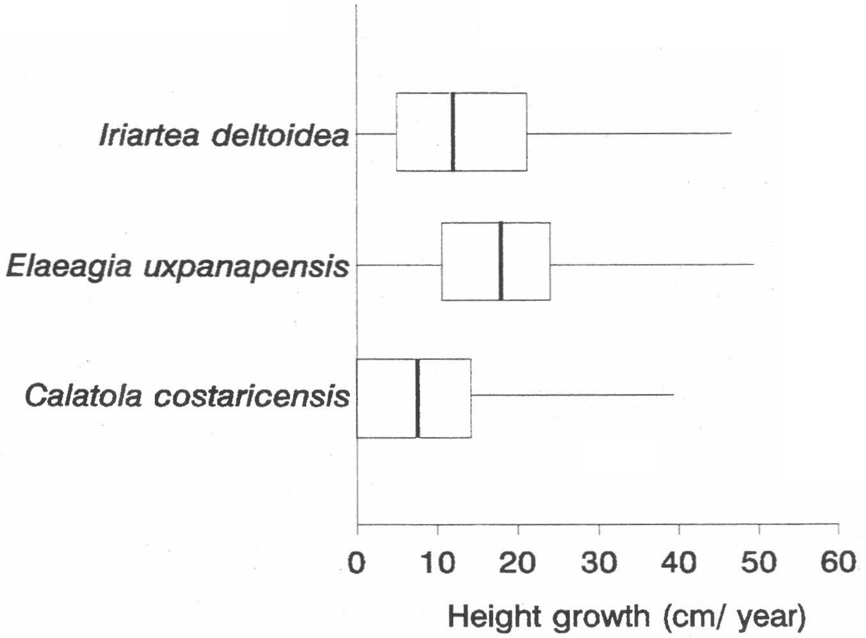

Fig. 11: Distribution of juvenile height growth per year among the study species (Thick vertical lines indicate the median of values, the rectangles represent the central 50% of the values and the total extension represent the central 90% of the values)

DISTRIBUTION UNDER DIFFERENT CROWN DENSITY LEVELS

For determining the distribution of the study species under different light levels the position of each juvenile in the different subplots and their accompanying crown density values have been combined. The distribution of the crown density values was selected vicariously to indicate the juvenile distribution of the study species under different light levels. For a better comparison the total distribution of all crown density values received, were additionally represented (see fig. 12).

The median crown density values of the study species was only differing between 83% as the lowest value for *Elaeagia uxpanapensis* and 88% as the highest value for *Calatola costaricensis*. The median of the total measured crown density values was found within this range at 84%. Within the central 95% of values none of the study species was found at a crown density level lower than 70%, the highest value was 93%.

The growth rates of the study species also have been analysed under the different light levels. The growth rates of *Iriartea deltoidea* and *Calatola costaricensis* did not differ significantly under the different light levels according to the nonparametric statistical test according to Kruskal-Wallis. *Elaeagia uxpanapensis* could not be tested because of insufficient parallels available.

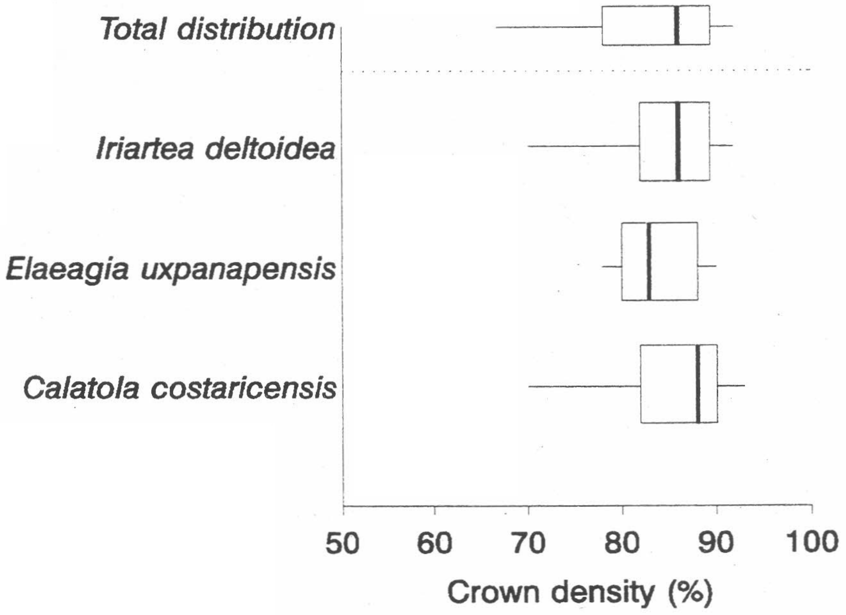

Fig. 12: Total distribution of the crown density values and distribution of the juveniles of the study species along the crown density gradient (Thick vertical lines indicate the median of values, the rectangles represent the central 50% of the values and the total extension represent the central 90% of the values)

DISCUSSION

The RA/A-value of *Iriartea deltoidea* of 12.7% is the highest available value on the one hectare study plot *Iriartea deltoidea* is the most frequent species (≥ 10cm DBH). *Elaeagia uxpanapensis* holds the 6. position and *Calatola costaricensis* the 8. position. Most species are rare, 36% of all 94 tree species (≥ 10 cm DBH, including palm trees) are represented only with one individual tree per hectare (WATTENBERG 1996).

But this high abundance of *Iriartea deltoidea* can not be found in general on the study site, according to observations of LEYERS (1993) *Iriartea deltoidea* is by far less abundant on wind exposed ridge sites. Among all inventoried juveniles *Iriartea deltoidea* is comparatively rare, this species holds only the 8. position. This low number of juveniles may result from the prefered gap study sites because they are mainly growing on non-gap sites (WATTENBERG 1996). According to LEYERS (1993), juveniles of *Iriartea deltoidea* are numerous on the study site. Furtheron, the distribution of the *Iriartea deltoidea* juveniles along the crown density gradient indicates no preference of more luminated sites which supports the assumption of *Iriartea deltoidea* as a non-pioneer species, which can persist and rejuvenite beyond the canopy. The height class distribution of the adults of *Iriartea deltoidea* and the numerous juveniles indicate a rejuvenating population with adequate offspring.

This is not the case with *Elaeagia uxpanapensis*. DBH-classes and height classes distribution of *Elaeagia uxpanapensis* (≥ 10 cm DBH) strongly indicate that the number of adolescents might not be enough to persist at this comparatively high abundance. Following LAMPRECHT (1986) the phenomenon of underrepresented adolescents within a tree species population is not an individual case. He hypothesises that this kind of distribution indicates a long living pioneer species within a late successional forest stand. At the initial stage of succession the prevalent light levels might have been sufficient for germinating which disappeared at later stages. Because this species can reach a considerable age they persist for a long time in the upper layer of the forest stand. This idea will be supported by the low fruit sizes of *Elaeagia uxpanapensis* of 2 mm, seeds have not been described yet (BURGER & TAYLOR 1993). The correlation between seed size and shade tolerance was mentioned several times (CLARK & CLARK 1992, FOSTER 1986, LAMPRECHT 1986, METCALFE & GRUBB 1995).

The distribution of the juveniles of *Elaeagia uxpanapensis* under different light levels represents the lowest median value of crown density among the study species. But even it is the lowest value, median crown density of 83% represents a low light level within the stand. On the other hand the mayority of the juveniles of *Elaeagia uxpanapensis* originate from vegetative resprouting and light requirements might be different. In this case nothing can be stated about the germinating ability of *Elaeagia uxpanapensis* as a requirement to determine the status of a pioneer or a non-pioneer tree species. The growth rates of *Elaeagia uxpanapensis* are highest among the study species, but beside species specific differences this might be the result of the slightly better light levels. In general, there is not much known about the ecology of *Elaeagia uxpanapensis* and further study will be required.

With its low maximum height and low DBH values *Calatola costaricensis* seems to be a typical shade tolerant subcanopy tree species which can persist in the shade under the closed canopy. Beyond that *Calatola costaricensis* dispose of large seeds with a weight of about 35 g which enables the species to persist for a long time as a seedling under lowest light levels (GENTRY 1993). On he whole study site seeds of *Calatola costaricensis* are frequent and present throughout the year. Seedlings can be found frequently at lowest light levels under the closed canopy with an appearent high vitality (WATTENBERG 1996). The distribution of the juveniles along the crown density gradient presents the highest crown density median value among the study species and support the assumption of *Calatola costaricensis* as a shadetolerant species. The establishment and mortality rate of *Calatola costaricensis* indicate high but balanced seedling dynamics.

The total abundances of the individuales (≥ 10 cm DBH) and of the juveniles of the study species can not be related because they originate from different study plots of different sizes. The growth rates of the study species are higher in comparison with findings of studies on other sites within the forest stands (CLARK & CLARK 1992, CLARK 1994), but this might be the consequence of better light conditions at gaps particularly selected study sites. The growth rates, however, are lower by far as the observed growth rates of *Heliocarpus appendiculatus* Turcz. or *Cecropia insignis* Liebm. which are known as real pioneer species, so that the presumption of the status of non-pioneer species has been supported.

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LITERATURE

BURGER, W. & TAYLOR, C.M. (1993): Flora costaricensis. Fam. 202 Rubiaceae. In: Fieldiana Botany Field Museum of Natural History, Chicago, S. 128.

CLARK, D.A. (1994): Plant Demography. In: Mc DADE, L.A. & BAWA, K.S., HESPENHEIDE, H.A. & HARTSHORN, G.S. (eds.): La Selva. Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, S. 90-105.

CLARK, D.A. & CLARK, D.B. (1992): Life history diversity of tropical trees. In: Ecological Monographs, Vol. 62, S. 315-344.

FOSTER, S. (1986): On the Adaptive Value of Large Seeds for Tropical Moist Forest Trees: A Review and Synthesis. In: The Botanical Review, Vol. 52, No. 3, S. 261-299.

GENTRY, A.H. (1993): A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru). With supplementary notes on herbaceous taxa. Conservation International, Washington, DC.

HARTSHORN, G.S. (1991): Plantas. In: JANZEN, D.H. (ed.): Historia Natural de Costa Rica. San José, S. 119-353.

HEANEY, A. & PROCTOR, J. (1990): Preliminary studies on forest structures and floristics on Volcan Barva, Costa Rica. In: Journal of Tropical Ecology, Vol. 6, S. 307-320.

HOLDRIDGE, L.R. & GRENKE, W.C., HATHEWAY, W.H., LANG, T. & TOSI (Jr.), J.A. (1971): Forest Environments in Tropical Life Zones. A pilot study. Pergamon Press.

HOLDRIDGE, L.R. & POVEDA, L.J. (1975): Arboles de Costa Rica. Palmas, otras monocotiledoneas arboreas y árboles con hojas compuestas o lobuladas. Centro Cientifico Tropical San José, Costa Rica.

LAMPRECHT, H. (1986): Waldbau in den Tropen. Verlag Paul Parey. Hamburg.

LEMMON, P.E. (1957): A spherical densiometer for estimating forest overstory density. In: Forest Science, Vol. 2, No. 1, S. 314-320.

LEYERS, C. (1993): Populationsökologische Untersuchung zweier Palmenarten im prämontanen Regenwald der Cordillera de Tilarán (Costa Rica). In: Diplomarbeit Universität Bielefeld.

LIEBERMAN, D: & LIEBERMAN, M. (1987): Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). In: Journal of Tropical Ecology, Vol. 3, S. 347-358.

LIEBERMAN, M. & LIEBERMAN, D. (1994): Patterns of Density and Dispersion of Forest Trees. In: Mc DADE, L.A. & BAWA, K.S., HESPENHEIDE, H.A., HARTSHORN, G.S. (eds.): La Selva. Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, S. 106-119.

METCALFE, D.J. & GRUBB, P.J. (1995): Seed mass and light requirements for regeneration in Southeast Asian rain forest. In: Can. J. Bot., Vol. 73, S. 817-826.

NUHN, H. (1978): Regionalisierung und Entwicklungsplanung in Costa Rica. In: NUHN, H. & SANDNER, G. & SPIELMANN H.O. (Hrsg.): Beiträge zur geographischen Regionalforschung in Lateinamerika. Universität Hamburg.

ORTIZ V., R. (1991): Informe técnico sobre la importancia biológica de la Reserva Forestal de San Ramón. Universidad de Costa Rica.

SWAINE, M.D. & WHITMORE, T.C. (1988): On the definition of ecological species groups in tropical rain forests. In: Vegetatio, Vol. 75, S. 81-86.

VARGAS, G. (1991): Algunas consideraciones geográficas, geológicas y ecológicas de la Cuenca del Río San Lorenzo, San Ramón, Alajuela, Costa Rica. In: ORTIZ V., R. (ed.): Memoria de Investigación Reserva Forestal de San Ramón. Universidad de Costa Rica. Serie Catedra Universitaria, S. 17-22.

WATTENBERG, I: (1996): Struktur, Diversität und Verjüngungsdynamik eines prämontanen Regenwaldes in der Cordillera de Tilarán in Costa Rica unter besonderer Berücksichtigung der Rolle der Gaps für die Aufrechterhaltung der Baumartendiversität. Dissertation Universität Bielefeld.

WATTENBERG, I. & BRECKLE, S.-W_ (1995): Tree species diversity of a premontane rain forest in the Cordillera de Tilarán, Costa Rica. In: Ecotropica, Vol. 1, S. 21-30.

WATTENBERG, I. & BRECKLE, S.-W. & ORTIZ V., R. (1996): La diversidad de especies de árboles de un bosque muy húmedo premontano en la Reserva Biológica Alberto Brenes. In: ORTIZ V., R. (ed.): Revista Pensamiento Actual. Memoría Investigación Reserva Biológica Alberto Ml. Brenes, San Ramón. Vol. 2. Universidad de Costa Rica, Sede de Occidente, S. 11-19.

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POPULATION STUDIES IN *ELAEAGIA AURICULATA* (RUBIACEAE) IN A PREMONTANE WET FOREST IN THE CORDILLERA DE TILARÁN, COSTA RICA

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INTRODUCTION

This study is part of the Schwerpunktprogramm "Mechanismen der Aufrechterhaltung tropischer Diversität" of the Deutsche Forschungsgemeinschaft (DFG). It is a population ecological study of the tree species *Elaeagia auriculata* (E.a.), which belongs to the family Rubiaceae. The study has been carried out on two different plots in the premontane wet forest of the Reserva Biológica Alberto Brenes (RBAB), Costa Rica. Former population ecological studies in the RBAB have considered the endemic tree *Plinia salticola* (Myrtaceae) (SPRENGER 1992), two palm species (LEYERS 1993), and two emergent trees (RÖMICH 1993). The palms and *Plinia salticola* are found frequently in the Reserva. C. Leyers, B. Römich, A. Sprenger and I. Wattenberg have already arranged the two plots. In contrast to the previous studies, the main interest of this investigation is the population structure, and the differences between the two plots, for a less frequent species. The species *Elaeagia auriculata* has been chosen since it is of major ecological importance in the RBAB (ORTIZ 1985).

STUDY AREA

The study was carried out during October 1994 and April 1995 in the Reserva Biológica Alberto Brenes (RBAB). The RBAB is located in the province of Alajuela in north-central Costa Rica (10°13'N, 84°37'W). It is 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 degrees over more than 80 % of the whole area (CRUZ 1989; ORTIZ 1991). With altitudes ranging between 800 and 1500 m, and an average rainfall up to 4000 mm, the RBAB can be classified as part of the Orobiome I (WALTER & BRECKLE 1983, 1991; WATTENBERG & BRECKLE 1995), forming a premontane wet forest following the life-zone system of HOLDRIGE ET AL. (1971).

Two sites near the biological station have been studied. The first one (Plot 1) is located along the line of the southern ridge of the Río San Lorencito valley. The altitude ranges between 1000 and 1040 m. The second site is on the south-eastern slope of the valley. Here the altitude ranges between 910 and 960 m with a mean inclination of 14 degrees (WATTENBERG & BRECKLE 1995).

STUDIED SPECIES

Elaeagia auriculata Hemsley (Rubiaceae) are trees of evergreen lower montane cloud forest and rain forest formations. The species ranges from Guatemala and Honduras to eastern Panama. In Costa Rica, it is found along the central highlands, from Volcán Tenorio in the Cordillera de Guanacaste to San Vito de Coto Brus, and on the Caribbean slope, in altitudes ranging from 350 to 1700 metres. The trees are up to 15 metres tall. They flower between November and March, and fruit between February and June (BURGER & TAYLOR 1993). The capsules open at the top, so that the up to 1 mm long seeds that have thin membranous wings at opposite ends (BURGER & TAYLOR 1993) can be distributed by the wind (anemochory). *Elaeagia auriculata* is also reproduced vegetatively, in particular by sprouting from fallen sticks (SCHROERS ET AL. 1996).

METHODS

Two hectars of forest area have been selected, marked out (LEYERS 1993; RÖMICH 1993; SPRENGER 1992; WATTENBERG & BRECKLE 1995), and subdivided into 100 squares of 10 x 10 m. On both plots the diameters at breast hight (DBH) of all trees, palms and tree ferns with DBH greater than 10 cm have been determined. For individuals with several trunks at the height of 1.30 m, the thickest trunk has been measured. The abundance and dominance values (total and proportional) of each group were calculated. The total abundance is the number of trunks per hectare of each group, the proportional abundance is the percentage with respect to the total trunk number per hectare. The basal area of trees provides a more reliable instrument for biomass estimation than do trunk numbers, therefore group dominance values are represented by their basal area, calculated from DBH (LAMPRECHT 1986; WATTENBERG & BRECKLE 1995). The proportional dominance is the percentage of each group value with respect to the total basal areas in the two study plots. The frequencies of *Elaeagia auriculata* have been examined by evaluation of the tree position within the 100 subplots on both study areas.

The position of all *Elaeagia auriculata* plants has been determined. For the sexual respectively vegetative juveniles of E.a. the following measurements have been carried out:

a) **Sexual juveniles**: The diameter of the stem (DS) has been measured with a sliding rule at the internode below the first leaf. Moreover, the height of the plants, i.e. the distance between the ground and the highest leaf, has been measured. All leaves have been counted.

With a spherical densiometer (Model A from LEMMON 1957) the shading has been determined. The densiometer has been held directly above the plants, which were not taller than one metre. It has been counted how many of the 96 quarter quadrats were at least half covered by higher vegetation. The resulting number has been multiplied by 1.04 to obtain a value for the percentage of shading, see (SCHROERS 1996) for details.

The calibration curve for the ideal leaf area (ILA) of E.a., i.e. including feeding on leaves, has been determined by measuring length, width and area of a limited number of leaves. It is given by

$$ILA = 0.59\,x + 2.21\,e^{-6}\,x^2 - 1.96\,e^{-11}\,x^3 + 6.21\,e^{-17}\,x^4$$

where x = length x width, r = 0.999, see (SCHROERS 1996).

Then the length and width of the largest leaf of each plant smaller than one metre have been measured, and the corresponding ILA has been calculated.

b) **Vegetative juveniles**: For each sprout from a (fallen) stick the same parameters as for the sexual juveniles have been measured. The height has now been measured from the beginning of the sprout. Shadowing and ILA have been determined whenever possible. Here no height limit of one metre has been set.

RESULTS AND DISCUSSION

Abundances and Dominances

A registration of the total standing of trees with DBH ≥ 10 cm on both plots had the following results (Table 1):

On Plot 1 there are 617 trunks, on Plot 2 only 469. The total abundance of Plot 1 coincides with the abundances of other tropical forest regions, see e.g. (GENTRY 1990; LIEBERMAN & LIEBERMAN 1987; MABBERLEY 1992), but the abundance of Plot 2 is smaller. In particular, the number of trunks that are neither palms nor tree ferns is much higher on Plot 1, whereas on Plot 2 there are more tree ferns than on Plot 1. The numbers of palms on both plots do not differ essentially, the numbers of E.a. trees is low on both plots. The frequency of E.a. is 7 % on Plot 1 and 5 % on Plot 2. The relative abundances of E.a. on both plots coincide, but because of the low total numbers of E.a. trees this is not a very significant statement.

WATTENBERG & BRECKLE (1995) showed that E.a. is only the 24th most frequent of the 93 tree species that are found on Plot 2. By the classification of HARTSHORN (1991), E.a. is *frequent* on this plot (WATTENBERG 1996), whereas in the near by montane region of Monteverde it only appears *occasionally* (HARTSHORN 1991).

The basal area is 37.5 m^2/ha on Plot 1, and 3.2 m^2/ha less on Plot 2. This is slightly higher than values from lowland rain forests that range between 28 and 33 m^2/ha (LAMPRECHT 1986). Again, in particular the dominance of other trees is higher on Plot 1 than on Plot 2, whereas tree trunks and palms have a higher dominance on Plot 2. The palms on Plot 1 are hence thinner. Since E.a. trees usually have small DBH, the relative dominance of E.a. is even less than its relative abundance. Results of DI STEFANO AND OTHERS (1995) state similar relative abundances and dominances on an other hectare of the RBAB.

A comparison with the study by RÖMICH (1993) shows, that the total number of trunks (without tree ferns) with DBH ≥ 10 cm on Plot 1 decreased by 15 between 1991 and 1994. In the same time the basal area increased by 1.1 m^2/ha. The major causes for the observed decrease of the abundance seem to be tree falls and fungal pathogens. The dominance increased nevertheless, because trees grew larger. The abundance of E.a. with DBH ≥ 10 cm increased from 5 to 7.

Since 1992, the total number of trunks with DBH ≥ 10 cm on Plot 2 decreased considerably. Compared to the study of SPRENGER (1992; Table 1) there are now 72 trunks less. In particular, the abundance of trees was reduced heavily (57 trunks less). The major cause seem to be tree falls. The decrease of the number of tree ferns by 16 individuals may be caused by different ways of counting the trunks, since often several trunks have connections with each other. The abundance of palms remained almost equal, and the number of E.a. individuals was constant as well (cp. WATTENBERG & BRECKLE 1995).

The basal area decreased since the 1992 study by 17.1 m^2/ha, i.e. by one third. The dominance of trees decreased by 17 m^2/ha. However, different methods of measuring thick trees in the study by Sprenger and in this study have to be taken in account. The dominance of tree ferns and palms did not change much. This means that in particular thick trees have fallen during the three years. There are now two new gaps on Plot 2.

Table 1: Total and proportional abundance, total and proportional dominance of palms, tree ferns and trees with DBH ≥ 10 cm in the two one hectare study plots. N stands for the trunk number, m^2 for the basal area per group and hectare. E.a.: *Elaeagia auriculata*.

		total	palms		tree ferns		E.a.		others	
Plot 1										
N	%	617	65	10.6	32	5.2	7	1.1	513	83.2
m^2	%	37.5	1.8	4.8	0.6	1.6	0.1	0.3	35.0	93.3
Plot 2										
N	%	469	67	14.3	69	14.7	5	1.1	328	69.9
m^2	%	34.3	2.4	7.0	1.2	3.5	0.1	0.3	30.6	89.2
Sprenger (1992)										
N	%	541	66	12.2	85	15.7	----	----	390	72.1
m^2	%	51.4	2.4	4.7	1.3	2.5	----	----	47.7	92.8

Elaeagia auriculata **population**

The *Elaeagia auriculata* plants are divided into groups of trees with DBH ≥ 5 cm, young trees with height of more than one metre and DBH < 5 cm, saplings with height less than one metre, and sprouts of vegetative juveniles.

There are more E.a. individuals on Plot 2 than on Plot 1 (Table 2; SCHROERS ET AL. 1996). E.a. hemiepiphytes grow on *Miconia* (Melastomataceae) and *Ficus* (Moraceae). One E.a. hemiepiphyte takes root around *Rondeletia* (Rubiaceae), which itself grows on *Ocotea* (Lauraceae).

Table 2: Numbers of *Elaeagia auriculata* plants on both plots.

	Plot 1	Plot 2
trees with DBH ≥ 5 cm	14	10
young trees with height > 1 m	25	41
saplings wiht height < 1 m	28	52
vegetative juveniles (sprouts)	27 (58)	89 (259)

Diameter of stems (DS)

- About 20 % of the E.a. saplings on Plot 1 have a DS of 0.1, 0.2, 0.3, 0.4, 0.5 cm respectively (Fig. 1). In contrast to this, on Plot 2 there are no saplings with DS less than 0.2 cm, and only 83 % of the saplings have DS ≤ 0.5 cm (Fig. 2). However, there is no significant difference between the two plots (U-Test).
- About 71 % of the young trees on Plot 2 have DS between 0.6 and 2.4 cm, whereas on Plot 1, about 56 % have a DS between 2.5 and 4.6 cm.
- The E.a. sprouts on both plots have DS between 1.3 and 2.8 cm. The percentage of sprouts with DS between 0.1 and 0.4 cm is 74 % on Plot 1, and 8 % less on Plot 2. Nevertheless, there is no significant difference (U-Test).

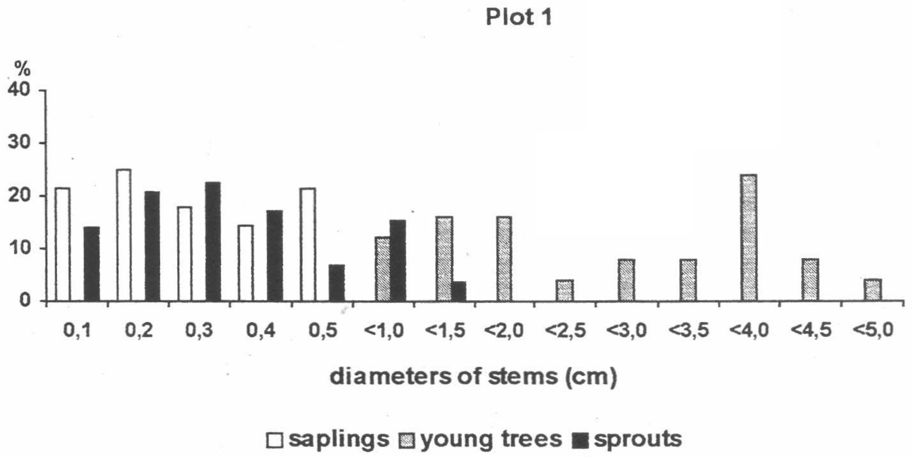

Fig. 1: Diameters of stems of *Elaeagia auriculata* juveniles on Plot 1.

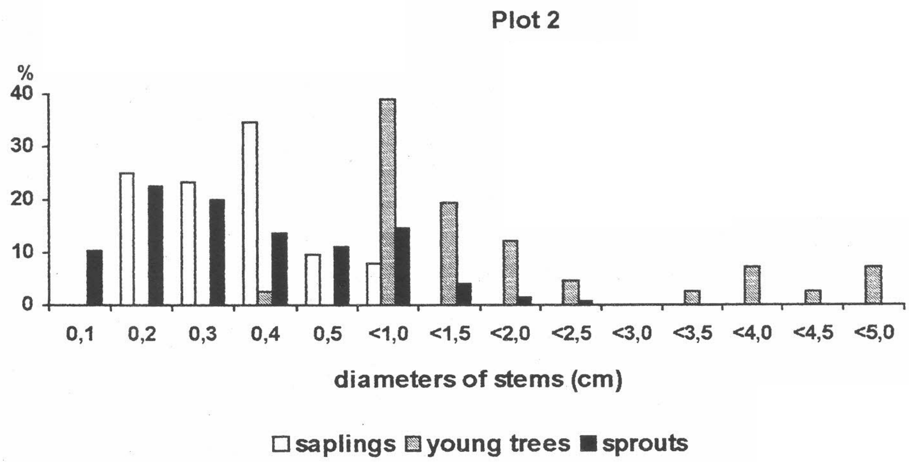

Fig. 2: Diameters of stems of *Elaeagia auriculata* juveniles on Plot 2.

Height

- The E.a. trees on both plots have heights less than 15 metres. Hence E.a. is part of the subcanopy.
- The E.a. saplings on Plot 1 have heights between 0.03 and 0.72 m (Fig. 3). The median is 0.25 m. About 40 % are smaller than 0.20 m. On Plot 2, the saplings have heights between 3 and 0.97 m, with a median of 0.39 m (Fig. 4). 37 % have heights between 0.20 and 0.40 m.
- The E.a. young trees on Plot 1 have heights between 1.0 and 7.5 m. The median is 3.19 m. 84 % of the trees have heights less than 5 metres, and between 1 and 5 m the heights are almost equally disributed. The situation is very different on Plot 2. Here 56 % (!) of the young trees have heights less than 2 metres. The heights vary between 1.07 and 8.00 m with a median of only 1.90 m.
- The E.a. sprouts on Plot 1 have heights between 0.02 and 2.0 m. Half of them are smaller than 0.2 m, and another quarter has heights between 0.2 and 0.4 m. The median is 0.2 m. The average sprout on Plot 2 is slightly higher. Here the heights range betweeen 0.01 and 3.70 m, only 36 % of the sprouts are smaller than 0.2 m, and another 20 % have heights between 0.2 and 0.4 m. The median is 0.33 m.

The difference between the heights of the young trees respectively the sprouts on both plots is significant, the corresponding difference between the heights of the saplings even highly significant (U-Test). On Plot 1 the young trees are higher than on Plot 2, whereas the saplings and the sprouts are higher on Plot 2. Moreover, the young trees on Plot 1 have larger DS than those on Plot 2. On Plot 1, there are more adult E.a. trees, and less young trees. Hence, the E.a. population on Plot 2 is probably "older" than that on Plot 1.

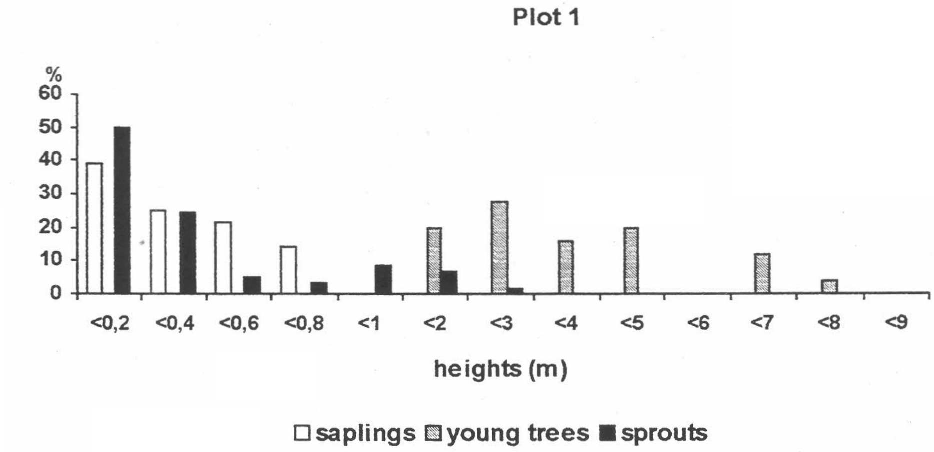

Fig. 3: Heights of *Elaeagia auriculata* juveniles on Plot 1.

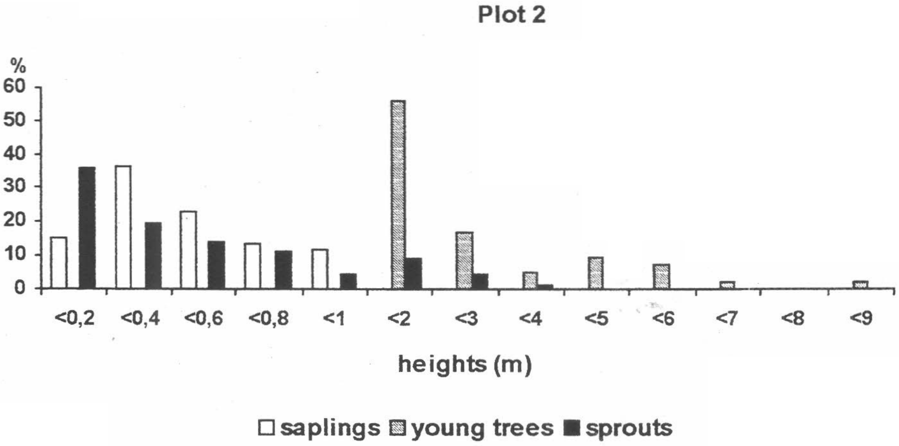

Fig. 4: Heights of *Elaeagia auriculata* juveniles on Plot 2.

Number of leaves

There is no significant difference concerning the number of leaves of the saplings, young trees respectively sprouts on both plots (U-Test). See SCHROERS (1996) for a description of the corresponding distributions.

Shading

- More than 80 % of the E.a. saplings on both plots are shaded for more than 95 %. There is no significant difference between the plots (U-Test). This fact, however, should not be overemphasized, since all the saplings on both plots are shaded for at least 85 %.
- More than 80 % of the sprouts on both plots are shaded for more than 95 %. Again there is no significant difference between the plots (U-Test).

- All the juveniles on both plots are shaded for the most part.

These results differ from those of WATTENBERG (1996). Wattenberg states that E.a. plants are found under relatively low crown roof densities. She concludes that E.a. prefers brighter places, although it is not a typical pioneer species in the sense of SWAINE & WHITMORE (1988). The regeneration of E.a. seems to be gap dependent.

Ideal leaf area (ILA)

- The E.a. saplings on Plot 1 have ILAs between 3 and 461 cm^2 (Fig. 5). Half of the leaves has an ILA of less than 50 cm^2. On Plot 2, only a third of the leaves has an ILA less than 50 cm^2. The ILAs range between 5 and 281 cm^2. However, there is no significant difference between the plots (U-Test).
- About half of the leaves of the sprouts on each plot have an ILA less than 50 cm^2. There is no significant difference between the plots (U-Test).

The leaves of higher or thicker saplings respectively sprouts have larger ILAs than those of smaller or thinner ones (SCHROERS 1996). Hence the leaves of "older" saplings and sprouts become larger. Moreover, the leaves of the sprouts tend to be larger for more shaded sprouts (SCHROERS 1996). Most of the higher E.a. plants have macrophyle leaf areas in the sense of RAUNKIAER (1934), i.e. leaf areas between 182 and 1640 cm^2. DOLPH & DIECHER (1980) showed that in Costa Rica there is a connection between macrophyle leaf areas and a mean annual biotemperature of 21-24° C. The RBAB has a mean annual temperature of about 20° C (BRECKLE 1996, unpublished data).

The large differences within the E.a. population with respect to the leaf areas of different plants cannot be explained by the used methods. Maybe the plant needs the different leaf areas in order to cope with the light anatomically and physiologically, and to use it for photosynthesis.

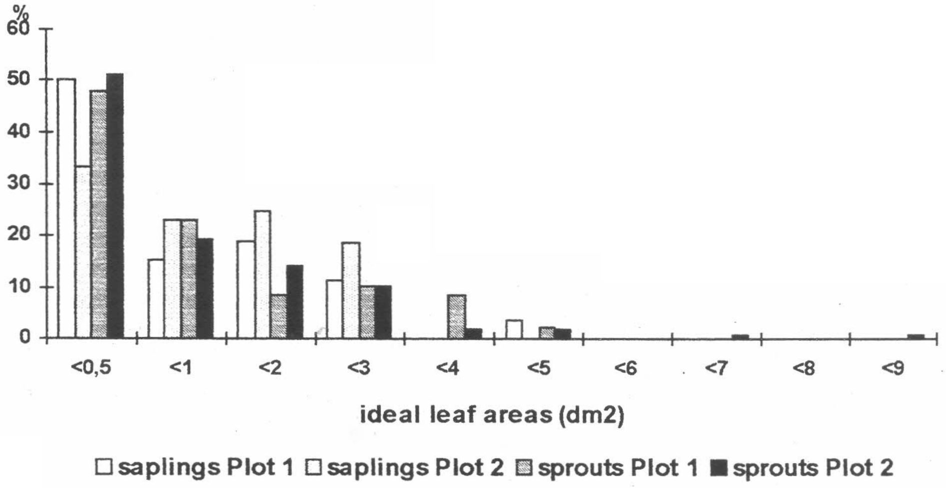

Fig. 5: Ideal leaf areas of *Elaeagia auriculata* juveniles on Plot 1 and 2.

Spatial distribution

There is a close connection between the pattern of spatial distribution of tropical tree species and the way the seeds are distributed (HUBBELL 1979). The pattern of population depends on the climatic conditions, since the winged E.a. seeds can be distributed by the wind. HAVEL (1971) shows that in a New Guinean forest winged seeds of a conifer are carried 60 metres in the direction of the monsoon wind but only 20 metres normal to the direction of the wind.

On the two plots studied here, the spatial distributions of E.a. are similar to each other. The whole population has a clumped pattern of distribution (χ^2-Test in the sense of FOWLER & COHEN 1990). *Plinia salticola* (- the most frequent tree species on Plot 2 -) and the two palm species *Iriatea deltoidea* and *Euterpe macrospadix* (- frequent on Plot 1 -) also have a clumped distribution (SPRENGER 1992; LEYERS 1993). Only the adult E.a. trees (DBH ≥ 7 cm) are randomly distributed, whereas E.a. saplings, young trees and vegetative juveniles have a clumped pattern of distribution. With increasing time the number of trees decreases, and the clumped distribution of the juveniles turns into the random distribution of the adult trees. This is consistent with results of WATTENBERG (1996) which state the high mortality of the E.a. juveniles. BARROS HENRIQUES AND GIRNOS DE SONSA (1989) also obtained a change from a clumped to a random distribution with increasing DBH.

The decrease of the number of individuals with growing age corresponds to the calculated minimal distances between neighbour E.a. plants (Fig. 6 and 7). On Plot 1, 71 % of the saplings have distances less than 2 metres from their nearest neighbour sapling. The median is 1.2 m. More than 60 % of the young trees have distances less than 6 m (median 4.6 m), whereas more than 80 % of the adult trees have distances between 8 and 12 m (median 8.5 m).

On Plot 2, 75 % of the saplings have distances less than 2 m (median 0.8 m), 75 % of the young trees have distances less than 6 m (median 2.8 m), whereas only 3 of the 8 adult trees on Plot 2 have distances less than 15 m (median 18.8 m).

The median of the distances between a sapling and the next adult tree (which is not necessarily the parent tree) is 11.4 m on Plot 1, and 4 metres more on Plot 2.

For *Plinia salticola*, SPRENGER (1992) also found the decrease of the number of individuals with growing age. However, here the mean distances of saplings are much larger (4.4 metres), whereas the mean distances of adults are smaller (7 metres).

Possible reasons for the decrease mentioned may be pathogens (AUGSPURGER 1983, 1984; AUGSPURGER & KELLY 1984), seed predation (JANZEN 1978; SCHUPP 1988; SCHUPP & FROST 1989), herbivores (JANZEN 1970; BAZZAZ 1987; CLARK & CLARK 1985), and competion for light and roots (BROKAW 1987; SCHMID 1991). For example, larvas of minierflies of the genus *Melanagromyza* can damage the epidermis of the leaves of E.a. juveniles.

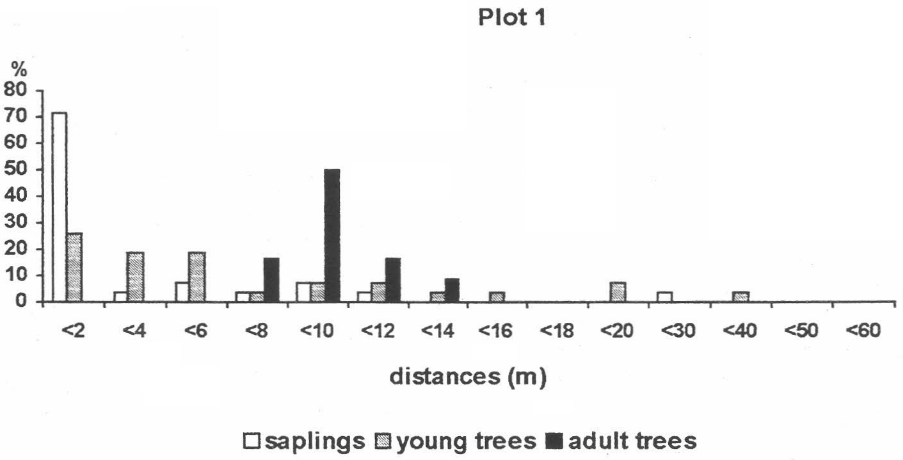

Fig. 6: Distances of *Elaeagia auriculata* plants on Plot 1.

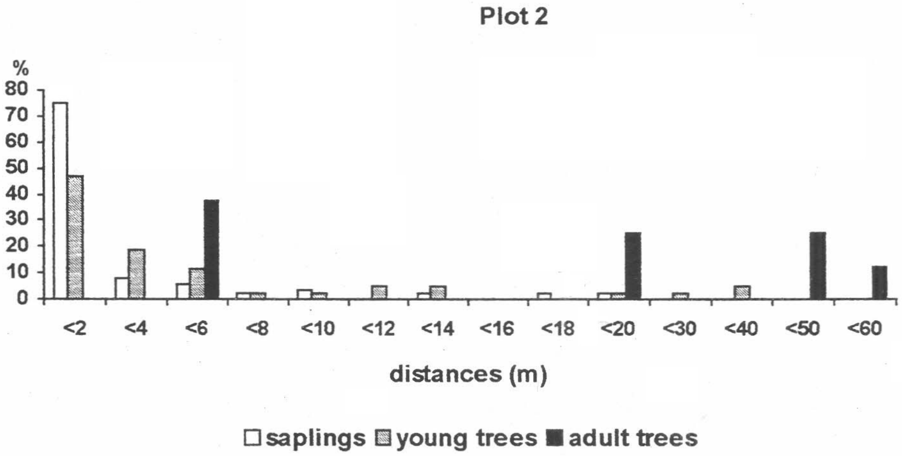

Fig. 7: Distances of *Elaeagia auriculata* plants on Plot 2.

Vegetative reproduction

The chance of survival of E.a. is increased by vegetative reproduction. A large part of the E.a. individuals is of vegetative origin. This part might be even larger, since it is not possible to distinguish the older young trees of vegetative origin from those of generative origin. This is confirmed by results of WATTENBERG (1996). In particular, in gaps in the RBAB, E.a. is the second most frequent species with sprouts from sticks, and the vegetative part is larger in gaps than in the closed stand of the forest. Furthermore, the height increase of vegetative juveniles is larger than that of generative juveniles (WATTENBERG 1996; HUNTER 1987). Hence the vegetative juveniles win the competion for light with the herbaceous vegetation at least during the first years (WATTENBERG 1996).

A crucial condition for a successful establishment of sprouts from sticks seem to be favourable climatic conditions. In the RBAB, there is less danger of dehydration by strong transpiration than in the lowlands. In fact, in the reserva there are few hours of sunshine and frequent fog, hence constantly high relative humidities and comparatively stable temperatures (WATTENBERG 1996). Experimental studies by BRENES & DI STEFANO (1996) confirm a high sensibility of *Elaeagia uxpanapensis* sprouts from sticks with respect to low relative humidity.

These researchers describe the advantages of vegetative reproduction in the following way:

In contrast to seed sources, there are permanently enough branches capable of reproduction. Once established, scions may grow very rapidly. In the case of extinction-prone tree species it is possible to increase the genetic pool in a comparatively short time.

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REFERENCES

AUGSPURGER, C.K. 1983. Seed dispersal of the tropical tree *Platypodium elegans* and the escape of its seedlings from fungal pathogens. Journal of Ecology 71: 759-771.

AUGSPURGER, C.K. 1984. Seedling survival of tropical tree species. Interactions of dispersal distance, light-gaps, and pathogens. Ecology 65 (6): 1705-1712.

AUGSPURGER, C.K. & C.K. KELLY 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia (Berlin) 61: 211-217.

BARROS HENRIQUES, R.P. & E.C. GIRNOS DE SONSA 1989. Population structure, dispersion and microhabitat regeneration of *Carapa guianensis* in northeastern Brazil. Biotropica 21 (3): 204-209.

BAZZAZ, F.A. 1984. Dynamics of wet tropical forests and their species strategies. In: Medina, E., Mooney, H.A. & C. Vazques-Yanes (eds). Physiological ecology of plants of the wet tropics. The Hague. Boston.

BRENES, L. & J.F. DI STEFANO G. 1996. Capacidad de propagación por estacas del árbol *Elaeagia uxpanapensis* D. Lorence, Rubiaceae. In: Revista de Biología Tropical Universidad de Costa Rica. In press.

BROKAW, N.V.L. 1987. Gap phase regeneration of three pioneer species in a tropical forest. Journal of Ecology 75: 9-19.

BURGER, Q. & C.M. TAYLOR 1993. Flora castaricensis. Fam. 202 Rubiaceae. In: Burger, W. Fieldiana Botany. Field Museum of Natural History. Chicago.

CLARK, D.B. & D.A. CLARK 1985. Seedling dynamics of a tropical tree. Impacts of herbivory and meristem damage. Ecology 66 (6): 1884-1892.

CRUZ, D.G. 1989. Nuestras Reservas Forestales y Zonas Protectoras. In: Ministerio de Recursos Naturales, Energía y Minas Costa Rica: 39-40.

DI STEFANO G., J.F., BRENES, L. & V. MORA 1995. Composición florística y estructura de un bosque primario del piso premontano pluvial, en San Ramón, Costa Rica. Rev. Biol. Trop. 43 (1-3): 67-73.

DOLPH, G.E. & D.L. DIECHER 1980. Variation in Leaf Size with Respect to Climate in Costa Rica. Biotropica 12 (2): 91-99.

FOWLER, J. & L. COHEN 1990. Practical Statistics for Field Biology. John Wiley & Sons. New York.

GENTRY, A. 1990. Four neotropical rainforests. Yale University. New Haven.

HARTSHORN, G.S. 1991. In: Janzen, D.H. (ed.). Historia Natural de Costa Rica. San José: 65-73.

HAVEL, J.J. 1971. The Araucaria forests of New Guines and their regenerative capacity. Journal of Ecology 59: 203-214.

HOLDRIDGE, L.R., GRENKE, W.C., HATHEWAY, W.H., LANG, T. & J.A.TOSI JR. 1971. Forest environments in tropical life zones. A pilot study.

HUBBELL, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-1309.

HUNTER, R.J. 1987. Reforestation with *Bombacopsis quinatum* (Jaq.) Dugand (Bombacaceae) in Costa Rica by means of vegetative reproduction. In: Revista Biología Tropical Vol. 35 No. 2: 195-201.

JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104: 501-528.

JANZEN, D.H. 1978. Seeding patterns of tropical trees. In: Tomlinson, P.B. & M.H. Zimmermann. Tropical trees as living systems. Cambridge University Press. Cambridge: 83-128.

LAMPRECHT, H. 1986. Waldbau in den Tropen. Verlag Paul Parey. Hamburg.

LEMMON, P.E. 1957. A spherical densiometer for estimating forest overstory density. In: Forest Science Vol. 2 No. 1: 314-320.

LEYERS, C. 1993. Populationsökologische Untersuchung zweier Palmenarten im prämontanen Regenwald der Cordillera de Tilarán (Costa Rica). Diplomarbeit. Universität Bielefeld.

LIEBERMAN, D. & M. LIEBERMAN 1987. Forest tree growth and dynamica at La Selva, Costa Rica. Journal of Tropical Ecology 3: 347-358.

MABBERLEY, D.J. 1992. Tropical rain forest ecology. Chapman & Hall. New York.

ORTIZ, R. 1985. Analysis ecológico de un bosque premontano muy humedo en la Reserva Forestal de San Ramón, Alajuela, Costa Rica. Cienc. Tec. 9: 59-71.

ORTIZ V., R. 1991. Memoria de Investigación, Reserva Forestal de San Ramón. Serie Cátedra Universitaria. Sede de Ocidente.

RAUNKIAER, C. 1934. The life-forms of plants and statistical plant geography. Oxford University Press. Oxford.

RÖMICH, B. 1993. Anlayse der Populationsstruktur und der Vebreitungsstrategie der Baumarten *Pterocarpus hayesii* und *Inga leonis* im prämontanen Regenwald der Reserva Forestal de San Ramón, Costa Rica. Diplomarbeit. Universität Bielefeld.

SCHMID, B. 1991. Konkurrenz bei Pflanzen. In: Schmid, B. & J. Stöcking (eds). Populationsbiologie der Pflanzen, Birkhäuser. Basel.

SCHROERS, S. 1996. Populationsökologische Untersuchung von *Elaeagia auriculata* (Rubiaceae) im Regenwald von Costa Rica. Examensarbeit. Universität Bielefeld.

SCHROERS, S., ORTIZ, R. & S.-W. BRECKLE 1996. Apuntes sobre *Elaeagia auriculata* (Rubiaceae).In: M.Sc. R. Ortiz (ed.). Revista Pensamiento Actual Vol. 2. Memoria Investigación Reserva Biológica Alberto Ml. Brenes, San Ramon: 41-43.

SCHUPP, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51: 71-78.

SCHUPP, E.W. & E.J. FROST 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and in the forest understory. Biotropica 21(3): 200-203.

SPRENGER, A. 1992. Populationsökologische Untersuchung von *Plinia salticola* (Myrtaceae) im prämontanen Regenwald der Cordillera de Tilarán (Costa Rica). Diplomarbeit. Universität Bielefeld.

SWAINE, M.D. &T.C. WHITMORE 1988. On the definition of ecological species groups in tropical rain forests. In: Vegetatio, Vol. 75: 81-86.

WALTER, H. & S.-W. BRECKLE 1983. Ökologie der Erde. Band 1: Ökologische Grundlagen in globaler Sicht. Stuttgart.

WALTER, H. & S.-W. BRECKLE 1991. Ökologie der Erde. Band 2 (2. Auflage): Spezielle Ökologie der Tropischen und Subtropischen Zonen. Stuttgart.

WATTENBERG, I. 1996. Struktur, Diversität und Verjüngungsdynamik eines prämontanen Regenwaldes in der Cordillera de Tilarán in Costa Rica. Dissertation. Universität Bielefeld.

WATTENBERG, I. & S.-W. BRECKLE 1995. Tree species diversity of a premontane rain forest in the Cordillera de Tilarán, Costa Rica. In: Ecotropica, Vol. 1: 21-30.

ASPECTOS DE LA AUTECOLOGIA DE *ELAEAGIA UXPANAPENSIS* D. LORENCE ESPECIE NATIVA CON VALOR FORESTAL (RESÚMEN DEL ANTEPROYECTO DE TESIS)

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La destrucción de los ecosistemas naturales en Costa Rica es acelerada. Sólo en deforestación se pierden alrededor de 60.000 Ha de bosque por año. La industria maderera fue subsidiada por esos bosques hasta la actualidad. Se proponen nuevas estrategias para el subsidio de la industria maderera, y entre ellas el uso de especies nativas en plantaciones se considera como una verdadera alternativa para nuestro País.

Algunos de los problemas por los que no se habían utilizado especies nativas en plantaciones forestales son: desconocimiento de la autecología de la especie, el manejo de la especie en el vivero, plagas, requerimientos edáficos y climaticos, fenología y biología reproductiva de especies forestales nativas (Comisión Nacional de Investigación en Conservación y Desarollo Forestal -CONIF-, 1993). Algunas de esas especies nativas maderables son endémicas, están esacasamente representadas en la composicíon florística del bosque, y muchas de las veces se han explotado, aunque se conoce poco o nada acerca de éstas.

Elaeagia uxpanapensis es un miembro de Rubiaceae y es conocida en Costa Rica sólo en la vertiente del Caribe de la Cordillera de Tilarán a unos 900 m.s.n.m., en el Valle del río Peñas Blancas, más bajo de Monteverde y en la Reserva Biológica Alberto Manuel Brenes (REBAMB) (Gómez Laurito 12065) en la provincia Alajuela. Esta especie es también conocida al sur de Mexico (BURGER & TAYLOR 1993).

Elaeagia uxpanapensis ha sido poco estudiada, ni siquiera existe una descripción de sus frutos y semillas (BURGER& TAYLOR 1993), a pesar de ser una especie conspicua en el bosque de la REBAMB, que alcanza el dosel y que ya ha sido explotada al menos a nivel regional para madera cuadro o piezas grandes, para construcción de casas y como postes de cerca. Estos árboles alcanzan alturas hasta de 40 m y su diámetros a la altura del pecho varían hasta 80 cm.

El objetivo general es investigar aspectos de la autecología de *Elaeagia uxpanapensis*, la germinación y la reproducción por estacas de la especie, para determinar su posible manejo con fines comerciales.

Objetivos específicos:

1. Describir las características generales de la parte vegetativa a parte reproductiva de la especie en estudio.

2. Investigar el comportamiento fenológico de *Elaeagia uxpanapensis*, en cuanto a caída de follaje, floración, fructificación y brotes.

3. Estudiar la distribución altitudinal de esta especie, en una porción de bosque premontano muy húmedo, en la REBAMB.

4. Determinar la regeneración natural de *Elaeagia uxpanapensis* en una porcion de bosque premontano muy húmedo.

5. Estudiar la germinación de semillas de esta especie, en condiciones de laboratorio.

6. Investigar si la especie es susceptible a reproducirse por medio de estacas, mediante el enraizamiento y aparición de brotes.

El trabajo se llevará a cabo en la REBAMB, ubicada 50 km al N.O: de San Ramón, provincia de Alajuela, en bosque premontano muy húmedo. Se procederá a la colecta de la parte vegetativa y reproductivas para su descripción. Para su fenología se empleará el método de FOURNIER (1974).

La distribución altitudinal será determinada mediante un sendero desde los 800 hasta los 1495 m.s.n.m.. En cada 100 m altitudinales se harán transectas de 10 x 50 m (divididas en subparcelas de 10 x 10), y cada individuo se le medirá la altura total y a la primer rama, así como el DAP. Se estimará la densidad, frecuencia y dominancia en cada estación altitudinal.

La regeneración natural se estudiará en 15 árboles semilleros, desde los que se trazarán cuadrículas a los 10, 20 y 30 m de 2 x 2 m, en dirección a los cuatro puntos cardinales. Se contarán las plantulas, brinzales y fustales. Las semillas se pondrán a germinar en caja Petri, y también se harán pruebas de 30 cm de largo y se sembrarán en condiciones de invernadero para determinar el grado de enraizamiento y aparición de brotes.

BIBLIOGRAFÍA

BURGER, W. & TAYLOR, C.M. (1993): Flora costaricensis. Fam. 202 Rubiaceae. In: Fieldiana Botany, New Series No. 33, Chicago Field Museum of Natural History. pp 129.

COMISIÓN NACIONAL DE INVESTIGACIÓN EN CONSERVACIÓN Y DESAROLLO FORESTAL (CONIF): 1993: Plan Nacional de Investigación en Conservación y Desarollo Forestal. Universidad Estatal a Distancia, San José, Costa Rica. 72 pp.

FOURNIER, L.A. 1974: Un método cuantitativo para medición de las carateristicas fenológicas en árboles. Turrialba 24 (4): 422-423.

FOURNIER, L.A. 1977: La sucesión ecológica como un método eficaz para la recuperación del bosque en Costa Rica. Agrn. Cost. 1 (1): 23-29

HOLDRIDGE, R.L. 1968: Ecología basada en zonas de vida. Centro Científico Tropical, San José, Costa Rica. 206 p.

BIELEFELDER ÖKOLOGISCHE BEITRÄGE 11: 77-88, 1997

ECOLOGICAL STUDIES IN A SUBMONTANE RAINFOREST IN COSTA RICA

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The field research for this study was carried out in the "Reserva Forestal de San Ramón" (now "Reserva Biológica Alberto Ml. Brenes", RBAMB) between august 1991 and may 1992. In 1 Ha of a submontane tropical primary rainforest of the "Cordillera de Tilarán" in Costa Rica, some autoecological characteristics, the distribution and the demographic structure of the understorey tree species *Plinia salticola* (Myrtaceae) have been investigated. The study site was located 10°12'40'' north and 84°36'20' west, on 870 m NN, with an annual rainfall of 3500 mm.

DESCRIPTION OF *PLINIA SALTICOLA*

Plinia salticola (MC VAUGH 1963) from the Myrtaceae family grows endemically in the RBAMB. It is a tree of the forest understorey, and grows up to 12 m. Its characteristic bark is white to light brown.

The evergreen, opposite, elliptic leaves of *Plinia salticola* are 11 to 17 cm long, and 3.5 to 5 cm wide. They are light green, brilliant and bald, with sharp pointed tips that are 8 to 10 mm long. Against daylight many oil bodies which are typical for Myrtaceae leaves are visible. The upper and under sides of young leaves are hairy.

Plinia salticola is cauliflor. The white flowers sit in fours directly on the tree stem or on older branches. The calyx and the corolla of the flowers consist of four leaves. The two outer leaves of the calyx are bigger than the two inner ones. The leaves of the corolla are grown together, 7 mm long and 5 mm wide. The round, orange- yellow ripe drupes have a diameter of 9 cm. The orange- brown, sweet pulp is about 1.5 cm thick and contains the heavy seed that is about 5 x 6 x 6 cm^3.

Fig. 1 shows bud, flower and leaf of *Plinia salticola*.

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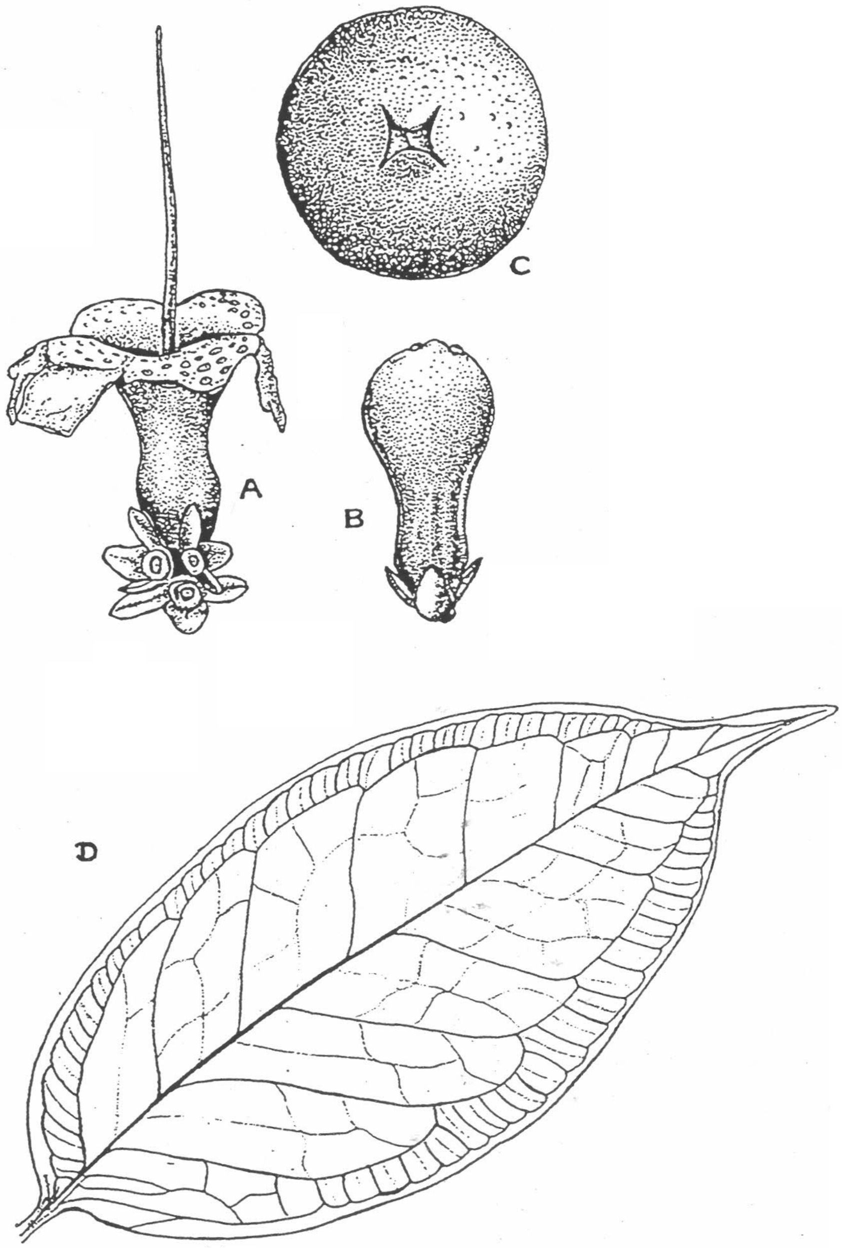


Fig. 1: *Plinia salticola*: flower (A), flower bud (B,C), leaf (D)

METHODS

In an area of 1 hectare the following parameters were measured:

- Study site: microclimate, topography, soil
- Structural parameters of the forest stock: breast diameters, stem area, canopy density (LAMPRECHT 1986)
- Structural parameters of *Plinia salticola*: vertical and horizontal position in the forest, tree height, canopy height, canopy diameter, canopy shape, canopy overshadowing, overgrowth with epiphytes and lianas, vitality (DAWKINS 1958, HALLE et al. 1978, SYNNOTT 1979)
- Phenological characteristics of *Plinia salticola*
- Rejuvenescence of *Plinia salticola*
- Spatial distribution of *Plinia salticola*

STUDY SITE

During the 10 months of investigation there was a precipitation of 3318 mm and an average temperature of 20.2 °C. A very rainy (august to december) and a dry season (january to march) were differentiated. The climatic measurements were carried out under the forest cover. Under open sky the conditions can be much more extreme. The area of investigation was very sloping. Strong rainfalls combined with steep slopes can favor the fall of trees. This formation of gaps creates changes in the light environment on the forest floor (JACOBS 1988). The soils in the study site were well drained and fertile. The high natural fertility that originates in the volcanic rocks can be an important factor for the high biodiversity of the forest (LAMPRECHT 1986, HART et al. 1989, MABBERLEY 1992).

STRUCTURAL PARAMETERS OF THE FOREST STAND

In the investigation area of 1 Ha 541 trees with breast diameters (BD) ò 10 cm were found. Compared to other rainforest areas this is an intermediate to low value (HOHEISEL 1976). The circular area of the stems was 51,4 m^2 ù Ha^{-1} which is an intermediate to high value (LAMPRECHT 1986). The distribution of the stem diameters of all trees formed an L-shaped curve (Fig. 2). This is typical for tropical primary forests (LAMPRECHT 1977). The average canopy density was 86 %.

STRUCTURAL PARAMETERS OF *PLINIA SALTICOLA*

Plinia salticola had a relative abundance of 7,4 % and therefore was a frequent tree species in the study site. Its dominance was less than 1 %. This low dominance proceeded from the small BD (on an average 10-11 cm, Fig. 3). *Plinia salticola* was up to 12 m high (Fig. 4) and belonged to the forest understorey (Fig. 5). It mostly was located on slopes where wind and erosion are very strong. Nevertheless understorey plants are more protected from these factors than canopy species. Generally light is a limiting factor in tropical forests (Jacobs 1988) and competition for light between plants especially in the understorey is very strong.

Table 1 shows the average slenderness ratio (tree height/BD), canopy height, and canopy diameter of the *Plinia salticola* individuals with BD ò 5 - < 10 cm and BD ò 10 cm.

Table 1: average measurements of the *Plinia salticola* stand

(cm)	BD ≥ 5 - <10 cm	vc*	BD ≥ 10 cm	vc*
tree height/ breast diameter	72	0.24	53	0.28
canopy height	296	0.5	342	0.43
canopy diameter	325	0.29	446	0.24

*: coefficient of variance

There was a strong linear correlation between the factors tree height and canopy height of all *Plinia salticola* trees with BD ò 5 cm, and also between BD and tree height of the trees with BD ò 5 - < 10 cm (Table 2).

Table 2: Pearson's coefficient of correlation between some parameters from *Plinia salticola*

parameters		BD ≥ 5 - < 10 cm	BD ≥ 10cm
BD	tree height	0.64	0.006
tree height	canopy height	0.82	0.77
BD	canopy diameter	0.24	0.20
tree height	canopy diameter	0.01	0.16
canopy height	canopy diameter	0.18	0.21

Fig. 6a-e shows the results from the measurements of the canopy shape, canopy over-shadowing, overgrowth with epiphytes, overgrowth with lianas, and vitality of the *Plinia salticola* trees.

PHENOLOGICAL CHARACTERISTICS OF *PLINIA SALTICOLA*

Fig. 7a,b shows the results from the phenological observations of *Plinia salticola*. Some phenological apparitions of the tree correlated with certain climatic conditions. The existence, duration, intensity and regularity of rainy and dry seasons can have an influence on the vegetation (Frankie et al., 1974). At the beginning of the dry season (january) the tree produced most of its leaves. In this period also fewer herbivore insects - which eat recently sprouted leaves with an high nutritive value and few secondary metabolites (Mori and Kallunki 1976) - have been found. At the end of the dry season (february) there was leaf fall. This loss of leaves probably was caused by the lack of water in this dry period. At the beginning of the dry season *Plinia salticola* also sprouted flower buds and the old flowers transformed into fruits. Flowering and fruiting periods of many tropical forest species depend on climatic factors and on the activities of pollinators and dispersing organisms. The flowers of *Plinia salticola* were pollinated by wasps, and the pulp of the fruits was eaten by bats. This caused the falling of the large seeds on the forest floor below the parent tree. All the trees of *Plinia salticola* in the study site produced their fruits a the same time. Many tropical trees with big seeds that are eaten by rodents show synchronous fruiting to guarantee a higher probability for the seeds to keep uninjured and to germinate (LIETH 1974). Periodically the *Plinia salticola* trees shed their outer bark from the trunk and the older branches. This periodical fall of the bark from the trunks and old branches was related to the sprouting of buds. With the bark the epiphytes also fell down and created space for the young cauliflor flowers. The results showed that phenological characteristics were related to climatic factors. Generally it can be assumed that the phenology of understorey plants depend less on climatic factors than the high canopy trees of the forest (FRANKIE et al. 1974).

REJUVENESCENCE OF *PLINIA SALTICOLA*

In september of 1991 157 individuals of *Plinia salticola* with BD < 5 cm were found in the area of investigation. From these 128 individuals were seedlings (stem height < 130 cm) and 29 young trees (stem height ≥ 130 cm). The position in the forest showed that *Plinia salticola* needs shade in its juvenile phase. No seedling was found in a gap. Light conditions play an important role in the germination and establishment of seedlings (TURNER 1990). Fig. 8a shows the distribution of the seedlings and Fig. 8b the distribution of the young trees to the height classes. Most of the seedlings were 30-55 cm, most of the young trees 200-250 cm high.

Besides the abiotic factors the biotic factors like rodents, herbivores, pathogens, lianas, competition for light, competition of roots and allelopathy also play an important role in tree establishment and growth (HOWE and SMALLWOOD 1982, AUGSPURGER 1984, CLARK and CLARK 1985, SCHUPP 1988). In this investigation the seedlings of *Plinia salticola* that had not grown during 5 months were more damaged by herbivores than seedlings which had increased in stem height (Fig. 9).

SPATIAL DISTRIBUTION OF *PLINIA SALTICOLA*

Fig. 10 shows the spatial distribution of the whole population of *Plinia salticola* in the 1 Ha forest plot. Accumulations of individuals are visible. Analyzing the different size classes - that is age classes - separately, only the saplings show an accumulated distribution whereas the trees with BD ≥ 10 cm were distributed casually. This transition from accumulated to casual distribution with increasing tree age has also been proved in demographic studies of different tropical tree species (BARROS HENRIQUES and GIRNOS DE SONSA 1989).

This investigation forms the basis to comprehend some complex interactions between abiotic and biotic factors on the demographic structure of the tropical understorey tree *Plinia salticola*. To get more information about the ecology of this species it is indispensable to study a large amount of parameters for the duration of various years.

Fig.2: number of stems on breast diameters of all the trees in 1 Ha with BD > 10 cm (half-logarithmic presentation)

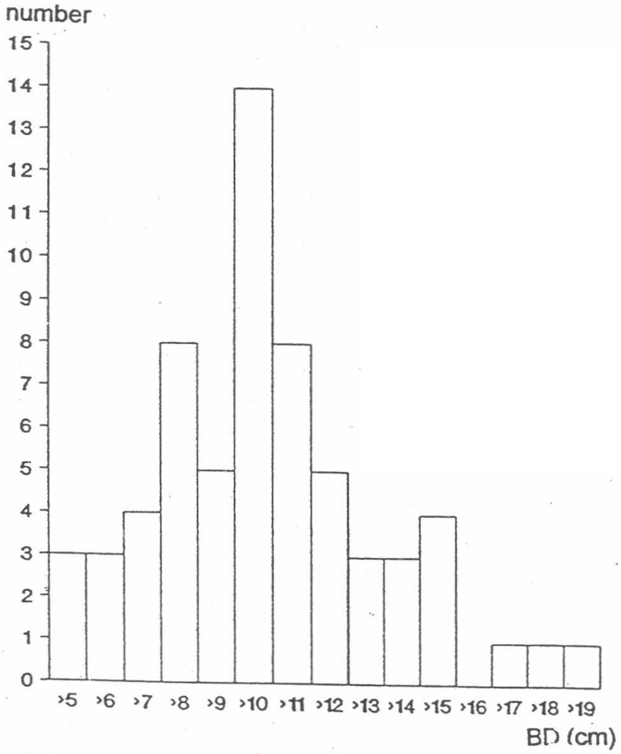


Fig.3: number of stems on breast diameters of *Plinia salticola* (BD ≥ 5 cm)

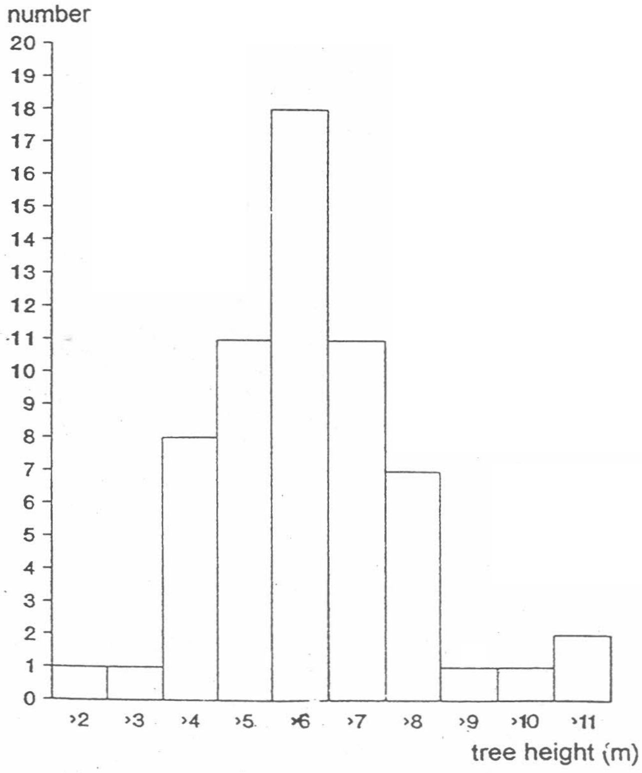
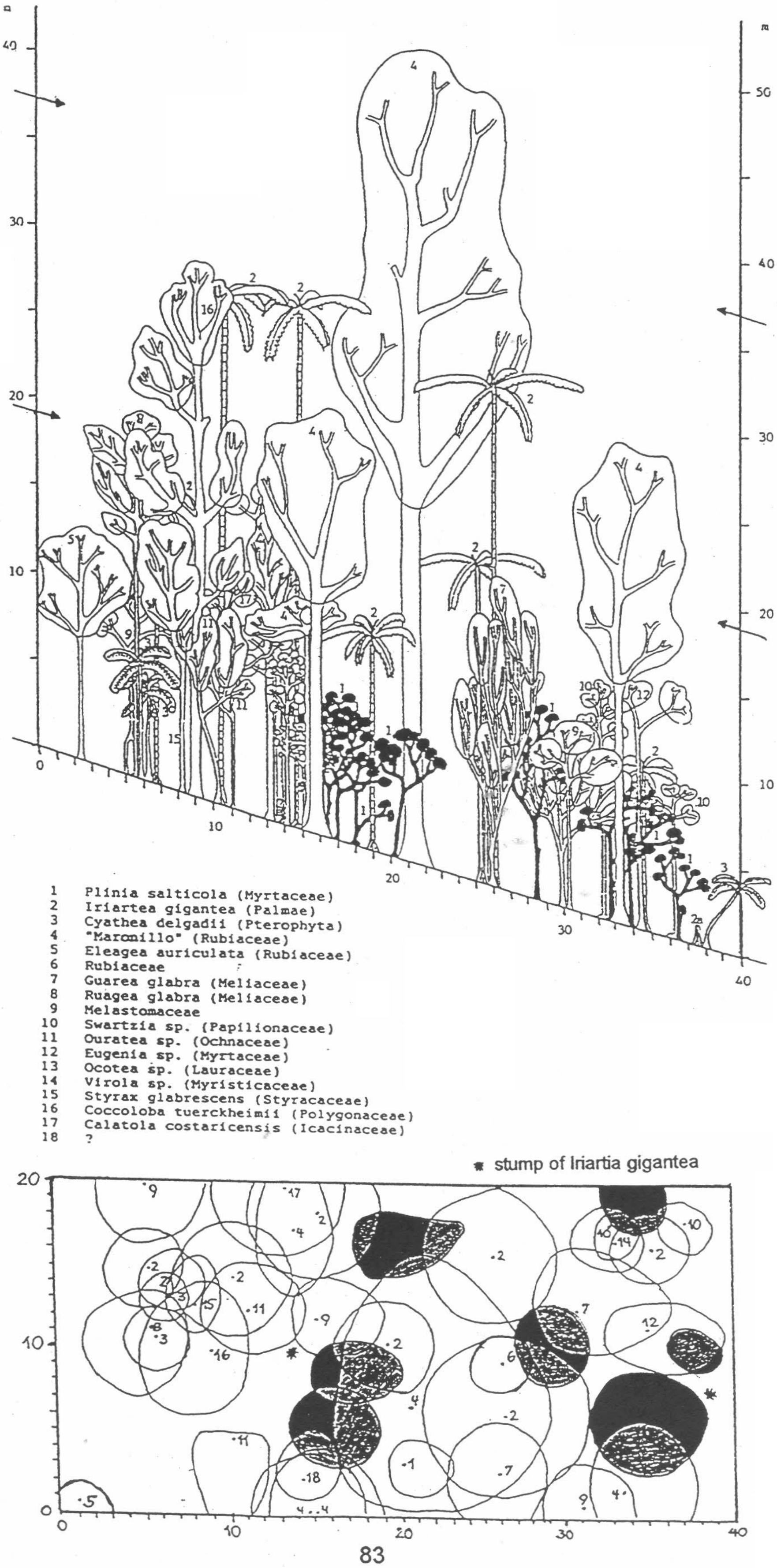


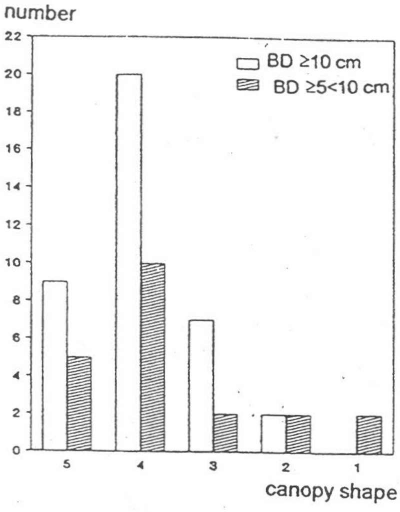
Fig.4: number of stems on tree heights of *Plinia salticola* (BD ≥ 5 cm)

Fig.5: section of the forest (40 x 20 m²), lateral view and topview, in black: *Plinia salticola*



1 Plinia salticola (Myrtaceae)
2 Iriartea gigantea (Palmae)
3 Cyathea delgadii (Pterophyta)
4 "Maronillo" (Rubiaceae)
5 Eleagea auriculata (Rubiaceae)
6 Rubiaceae
7 Guarea glabra (Meliaceae)
8 Ruagea glabra (Meliaceae)
9 Melastomaceae
10 Swartzia sp. (Papilionaceae)
11 Ouratea sp. (Ochnaceae)
12 Eugenia sp. (Myrtaceae)
13 Ocotea sp. (Lauraceae)
14 Virola sp. (Myristicaceae)
15 Styrax glabrescens (Styracaceae)
16 Coccoloba tuerckheimii (Polygonaceae)
17 Calatola costaricensis (Icacinaceae)
18 ?

* stump of Iriartia gigantea



5 - round and closed
4 - ±round and light
3 - ±round with gaps
2 - irregular and light
1 - irregular with gaps

Fig.6a: canopy shape

1 - without lianas
2 - less than half of the tree with lianas
3 - half of the tree with lianas
4 - more than half of the tree with lianas
5 - the entire tree with lianas

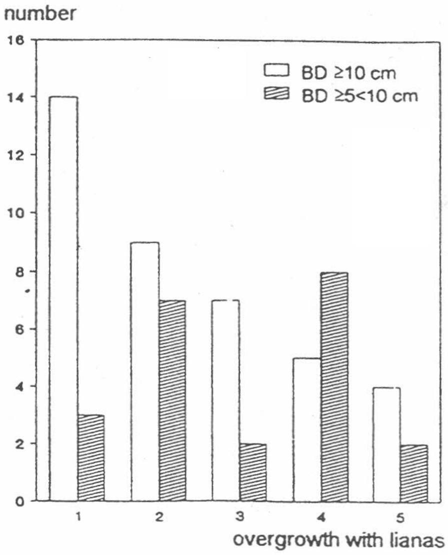
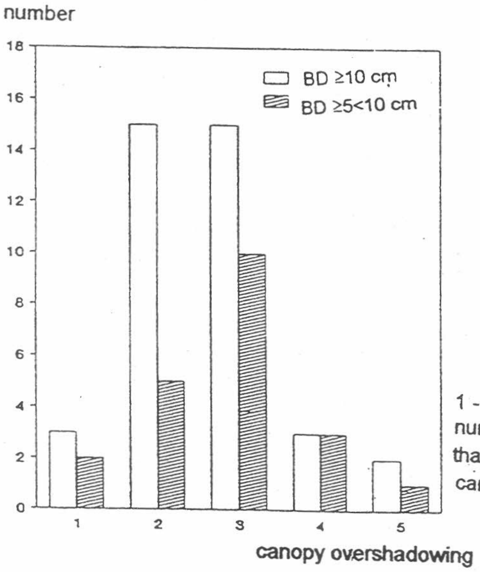


Fig.6d: overgrowth with lianas



1 - 5:
number of tree canopies that shade a *P.salticola* canopy

Fig.6b: canopy overshadowing

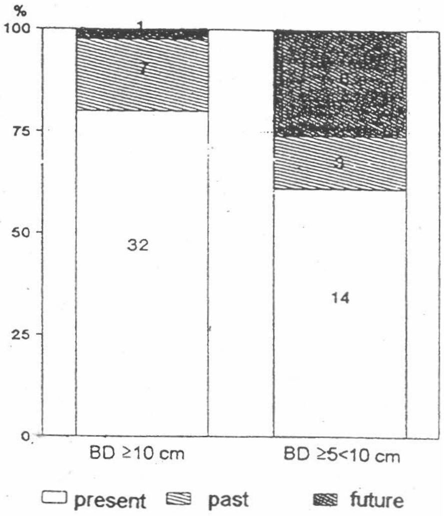
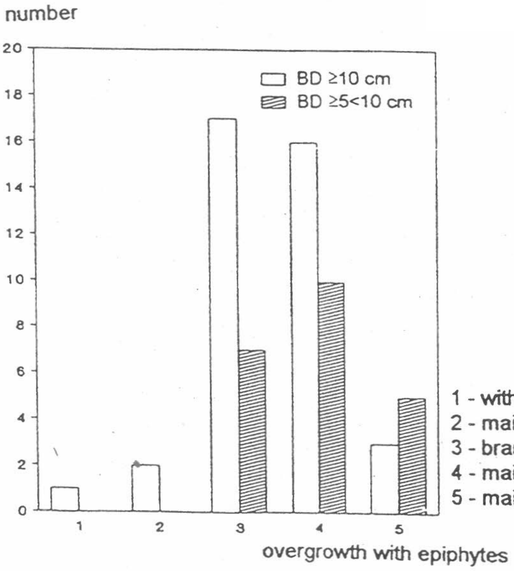


Fig.6e: vitality



1 - without epiphytes
2 - mainstem with, branches without epiphytes
3 - branches with, mainstem without epiphytes
4 - mainstem and older branches with epiphytes
5 - mainstem and all branches with epiphytes

Fig.6c: overgrowth with epiphytes

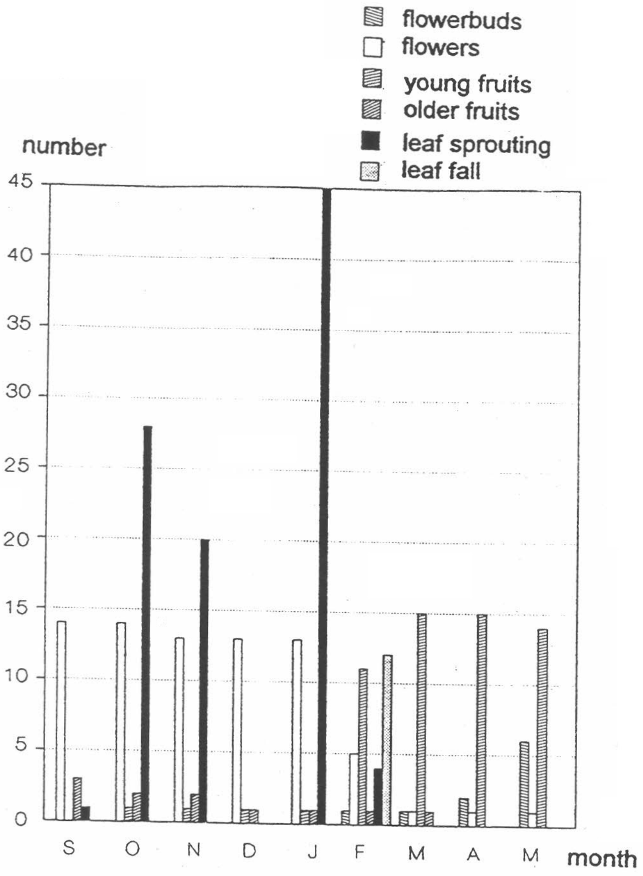


Fig.7a: some phenological characteristics of *Plinia salticola*

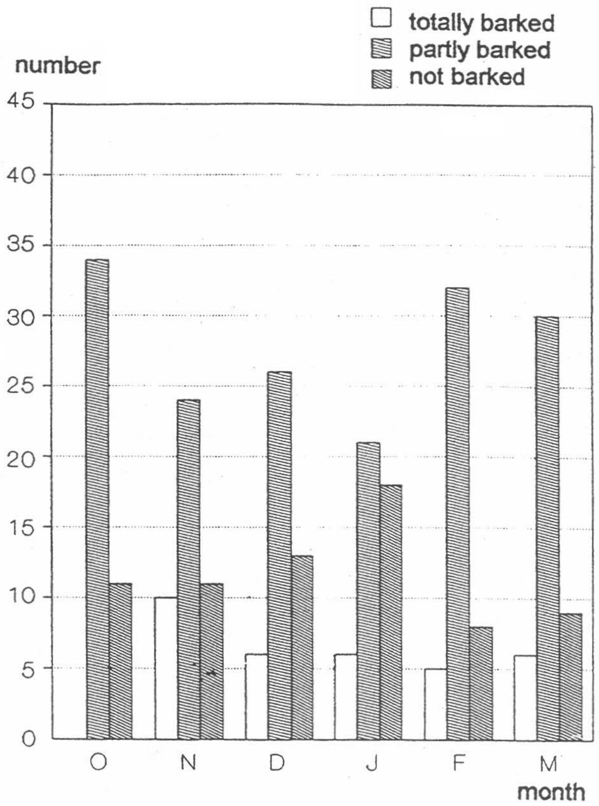


Fig.7b: barking of *Plinia salticola*

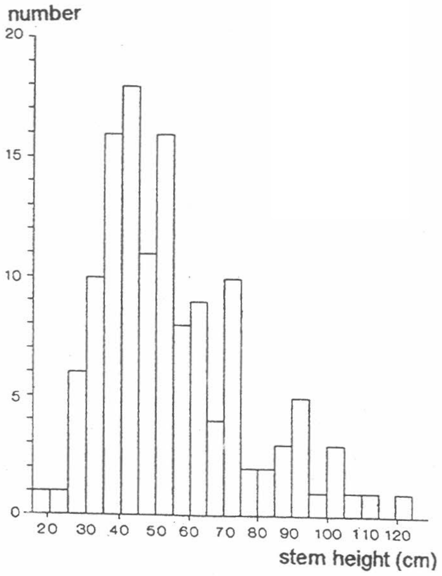


Fig.8a: stem height of seedlings of *Plinia salticola*

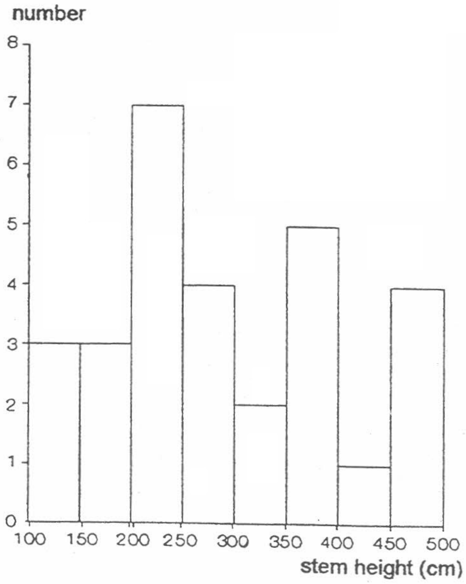


Fig.8b: stem height of young trees of *Plinia salticola*

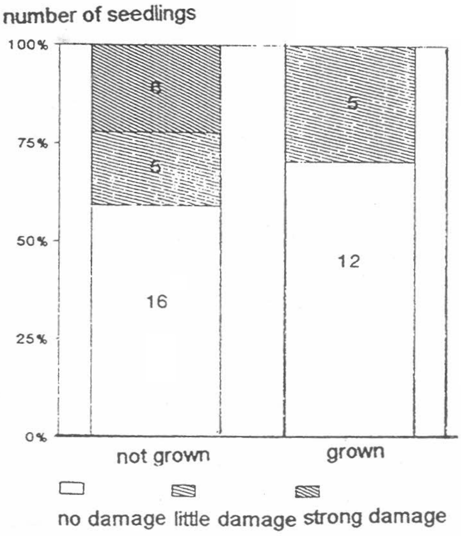
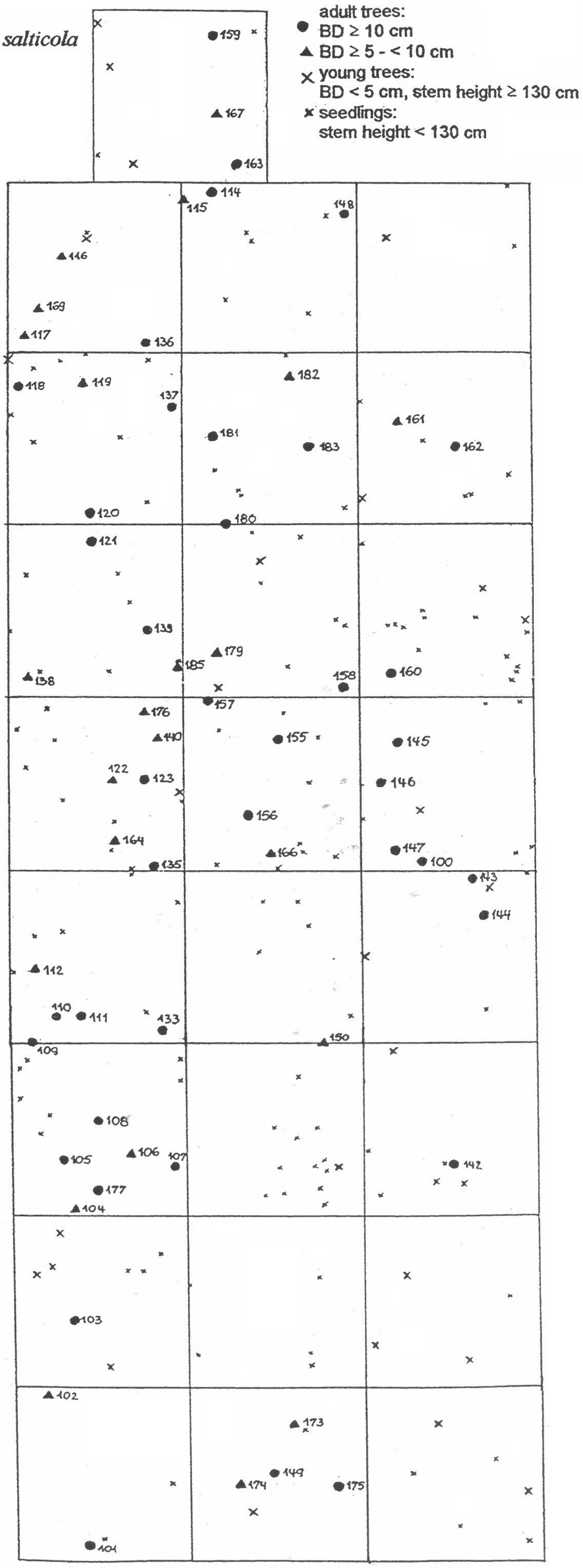


Fig.9: stem growth and damage of seedlings of *Plinia salticola* through herbivores

Fig.10: spatial distribution of *Plinia salticola* in 1 Ha of primary forest



LITERATURE

AUGSPURGER, C.K. (1984) : Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens.- Ecology 65(6): 1705-1712

BARROS HENRIQUES, R.P. and GIRNOS DE SONSA, E.C. (1989) : Population structure, dispersion and microhabitat regeneration of *Carapa guianensis* in northeastern Brazil.- Biotropica 21(3): 204-209

CLARK, D.B. and CLARK, D.A. (1985) : Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage.- Ecology 66(6): 1884-1892

DAWKINS, H.C. (1958) : The management of natural tropical high-forest with special reference to Uganda - Imperial Forestry Institute, University of Oxford, Paper No. 34

FRANKIE, G.W., BAKER, H.G. and OPLER, P.A. (1974) : Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica.- Journal of Ecology 62: 881-919

HALLÉ, F., OLDEMAN, R.A.A. and TOMLINSON, P.B. (1978) : Tropical trees and forests - an architectural analysis - Springer Verlag

HART, T.B., HART, J.A. and MURPHY, P.G. (1989) : Monodominant and species-rich forests of the humid tropics: causes for their cooccurrence.- The American Naturalist 133: 613-633

HOHEISEL, H. (1976) : Strukturanalyse und Waldtypengliederung im primären Wolkenwald "San Eusebio" in der Nordkordillere der venezolanischen Anden - Dissertation, Georg-August-Universität Göttingen

HOWE, H.F. and SMALLWOOD, J. (1982) : Ecology of seed dispersal.- Annual Review of Ecology and Systematics 13: 201-228

JACOBS, M. (1988) : The tropical rainforest - a first encounter - Springer Verlag

LAMPRECHT, H. (1977) : Structure and function of south american forests - in: MÜLLER, P. (ed.) : Ecosystem resarch in South America - Dr. W. Junk B.V. Publishers, The Hague, 151 p.

LAMPRECHT, H. (1986) : Waldbau in den Tropen.- Verlag Paul Parey

LIETH, H. (1974) : Phenology and seasonality modeling - Springer Verlag

MABBERLEY, D.J. (1992) : Tropical rain forest ecology.- Chapman & Hall, New York

MCVAUGH, R. (1963) : Tropical american Myrtaceae: a new species of *Plinia* L., from Costa Rica.- Fieldiana 29: 505-507

MORI, S. and KALLUNKI, J.A. (1976) : Phenology and floral biology of *Gustavia superba* (Lecythidaceae) in Central Panama.- Biotropica 8(3): 184-192

SCHUPP, E.W. (1988) : Seed and early seedling predation in the forest understory and in treefall gaps.- Oikos 51: 71-78

SYNNOTT, T.J. (1979) : A manual of permanent plot procedures for tropical rainforests - Tropical Forestry Papers, no.14 - Department of Forestry, Commonwealth Forestry Institute, University of Oxford, 67 p.

TURNER, I.M. (1990) : Tree seedling growth and survival in an Malaysian rain forest. Biotropica 22(2): 146-154

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THE HYMENOPHYLLACEAE IN THE RESERVA BIOLÓGICA ALBERTO BRENES

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The Reserva Biológica Alberto Brenes (RBAB) lies in Costa Rica in the Cordillera de Tilarán ranging between 800 m and 1500 m of altitude. The yearly rainfall is varying between 3500 and 4500 mm. In the terrain with rather steep slopes is growing a primary premontane forest allowing a microclimate of high humidity (up to 90%).

The Hymenophyllaceae, the filmy ferns, are so delicate that they need high humidity all over the year. They cannot bear neither a period of dryness nor disturbances in the forest. The family consists of epiphytic, epilithic, or terrestrial members with creeping, often hairy stems, less commonly erect. The fronds arranged distichously have a more or less long petiole and a simple to pinnately divided lamina of only one layer of cells between the veins. The expanded lamina, always without stomata, is glabrous or hairy with simple, stellate, or forked hairs. The rachis often is winged. The veins end free.

The solitary sori are standing terminal on veins with involucres either conical or bivalvate more or less to the base. The receptacle with the sporangia is formed by a marginal or extramarginal extension of the vein within the involucres.

The plants only have simple roots, in some species even none. They are poikilohydric. Water is absorbed by the laminae, too. When the air becomes drier, the fronds curl up as if dead, but by moistening they are able to unfold again as bryophytes do.

The family grows in tropical regions predominantly and also in southern temperate areas (in Europe 3 species). It includes 600 species in 7 genera (KRAMER & GREEN 1990) to more than 650 species in 34 genera (COPELAND 1947). LELLINGER (1989) to whom is referred here above all compiled all Hymenophyllaceae occurring in Costa Rica as far as known till now enumerating 73 species in only 2 genera: *Hymenophyllum* and *Trichomanes*. He distinguished them by the form of their involucres and the length of the receptacles. The genus of *Hymenophyllum* in this sense corresponds with 2 genera in KRAMER & GREEN (1990) and with 3-4 genera in COPELAND (1947) including neotropical species only, with COPELAND splitted *Trichomanes* in the sense of Lellinger into 6-7 genera and KRAMER & GREEN made up 2 genera of the neotropical species.

In *Hymenophyllum* the involucres are bivalved and the receptacles are short. LELLINGER divided the 31 species belonging to *Hymenophyllum* into 3 subgenera, *Trichomanes* with 42 species into 4 subgenera. The involucres of *Trichomanes* are long-conical with truncate, dilated, or slightly bilabiate mouth, the receptacles are long, overtoping the involucres in older stages.

In March 1992 21 species of Hymenophyllaceae were found in the Reserva Biológica Alberto Brenes, 8 ones belonging to the genus of *Hymenophyllum*. The figures oare copies of herbarium specimens.

Hymenophyllum fucoides (fig. 1) has toothed margins as characteristic of the subgenus of *Hymenophyllum*. The sori develop on the margins of the pinnae near rachis which nearly is exalate. The both othe subgenera of *Hymenophyllum* have entire margins and the sori generally develop on the tip of the pinnae. While the subgenus of *Mecodium* has glabrous laminae, those of *Leptocionium* are hairy. *Hymenophyllum myriocarpum* (fig. 2) only was found on branches of broken down trees in gaps. Probably this species grows on higher branches in the top and is able to bear more sun and dryness. LELLINGER reported this species in open ares as well as in forests. *Hymenophyllum hirsutum* (fig. 5) and *H. elegans* (fig. 8) have not only an alate rachis but also winged petioles. The longest fronds in *Hymenophyllum* of up to 20 cm occur in the species of *H. costaricanum* (fig. 3) and *H. microcarpum* (fig. 7), the smallest ones, fully developped, in *H. fragile* (fig. 6). All the species of the genus of *Hymenophyllum* found in the Reserva Biológica were growing epiphytically, in general on trunks.

The genus of *Trichomanes* is much more inhomogenous in form and habitat the *Hymenophyllum*. The subgenus of *Trichomanes* has the species withe the longest fronds up to 50 cm and the most robust petioles: *T. cf. rupestre* (fig. 9), *T. radicans* (fig. 10), and *T. collariatum* (fig. 11). While the petiole in *T. collariatum* is very short (1-6 cm), that of *T. radicans* obtains a length of up to 12 cm. The determination of *Trichomanes cf. rupestre* is not sure because sori are lacking, but it resembles best with its broad pinnae and long leaves. This species was not only found epiphytically growing but epilithically, while LELLINGER cited it epiphytical and terrestrial. Untypical for ferns looks *Trichomanes capillaceum* (fig. 15) because its laminae are reduced to the veins only with thickenings by the involucres. The fronds appear like hairs on the trunks of tree ferns where the plants exclusively were observed in the area.

The only species with an erect, short stem and well developped roots in the table is *Trichomanes rigidum* (fig. 16) of the subgenus of *Pachychaetum*, the single member of this subgenus found in the area. The fronds are arranged in a rosette nearly and the laminae have occluded luminae, they are not translucent because the cell-walls are thick and coarsely pitted (COPELAND 1947). As the growth indicates, the species is not epiphytic, but terrestrial in the Reserva Biológica.

The next subgenus, *Achomanes*, also is represented by one member in the table, *Trichomanes polypodioides* (fig. 17) with undivided, but regularly lobed leaves.

The fourth subgenus, *Didymoglossum*, comprises species generally without roots and with the smallest leaves of the Hymenophyllaceae listed here. While *Trichomanes reptans* (fig. 18) has pinnatifid leaves, those of *T. membranaceum* (fig. 19), *T. kapplerianum* (fig. 20), and *T. cf. pusillum* (fig. 21) are irregularly lobed to simple spathulate. The plants called *Trichomanes cf. pusillum* come nearest to *T. pusillum* according to LELLINGER, not completely, but other species fit less. At a first glance the "fronds" of *T. cf. pusillum* look like leaflets of a moss, f.e. *Mnium*, but they are recognized easily belonging to *Trichomanes* by a single conical sorus in the tip of most of the leaves.

Trichomanes membranaceum (fig. 19) has pale scale-like emergences on the margins of the sterile spathulate leaves, less on fertile ones which are irregularly lobed and distinctly less frequent.

The sori of *Trichomanes cf. rupestre, T. polyodioides*, and of the species of the subgenus of *Didymoglossum* develop on the tip of the pinnae, but on the margins below the tips of the pinnae in all the other species of *Trichomanes* listed here.

In general the species of the Hymenophyllaceae are epiphytic growing on trunks between mosse in dark humid places, where very little light passes through the canopy. Few of them are growing on branches, too. Only *Trichomanes cf. rupestre* and *T. pyxidiferum* (fig. 13) were found epilithic in the Reserva Biloógica and *Trichomanes chomanes rigidum* terrestrial as already mentioned. LELLINGER named 5 species to have an epilithic habitat in addition to the epiphytic one: *Trichomanes pyxidiferum*, and also *T. membranaceum, T. kapplerianum, Hymenophyllum fucoides,* and *H. microcarpum*. In the Reserva Biológica with its primary forest there are very few rocks free of soil, so that an epilithic habitat is rare.

The big number of species of the Hymenophyllaceae listed here indicates the worth and the richness of the forest of the Reserva Biológica Alberto Brenes.

LITERATURE

COPELAND, E.B. 1947: Genera Filicum. Annales Cryptogamici et Phytopathologici. Vol. V. Waltham/ Mass. (Chronica Botanica). 247 pp, 10 pl.

KRAMER, K.U. & P.S. GREEN (eds.) 1990: Pteridophytes and Gymnosperms. Berlin (Springer) 404 pp. In: KUBITZKI, K. (ed.), The Families and Genera of Vascular Plants. Vol. I.

LELLINGER, D.B. 1989: The Ferns and Fern-Allies of Costa Rica, Panama, and the Chocó. (Part 1: Psilotaceae through Dicksoniaceae). Pteridologia 2A. 364 pp.

Genus according	Subgenus to LELLINGER 1989	Species	Figures	Habitats in RBAB	Habitats according to LELLINGER 1989
Hymenophyllum	Hymenophyllum	H. fucoides	1	epiphytic	epiphytic, rarely epilithic
	Mecodium	H. myriocarpum	2	epiph.: branches	epiph.: forests and open areas
		H. costaricanum	3	epiphytic	epiphytic: trunks
		H. polyanthos	4	epiphytic	epiph.: trunks and branches
	Leptocionium	H. hirsutum	5	epiphytic	epiphytic: trunks
		H. fragile	6	epiphytic	epiphytic: trunks
		H. microcarpum	7	epiphytic	epiph.: trunks, rarely epilithic
		H. elegans	8	epiphytic	epiphytic
Trichomanes	Trichomanes	T. cf. rupestre	9	epiph., epilithic	epiph.: trunks, terrestrial
		T. radicans	10	epiphytic	epiphytic: trunks
		T. collariatum	11	epiphytic	epiphytic: trunks
		T. diaphanum	12	epiphytic	epiph.: trunks and branches
		T. pyxidiferum	13	epilithic	epiph.:trunks,branches, rarely epil.
		T. hymenophylloides	14	epiphytic	epiph.: trunks and branches
		T. capillaceum	15	epiph.: tree ferns	epiph.: trunks, often tree ferns
	Pachychaetum	T. rigidum	16	terrestrial	terrestrial
	Achomanes	T. polypodioides	17	epiphytic	epiph.: trunks, often tree ferns
	Didymoglossum	T. reptans	18	epiphytic	epiphytic: trunks, roots
		T. membranaceum	19	epiph.: trunks	epiphytic: trunks, epilithic
		T. kapplerianum	20	epiphytic	epiphytic: trunks, epilithic
		T. cf. pusillum	21	epiph.: trunks	epiphytic: trunks

Fig. 1 Hymenophyllum fucoides (Swartz) Swartz

Fig. 2 Hymenophyllum myriocarpum Hook.

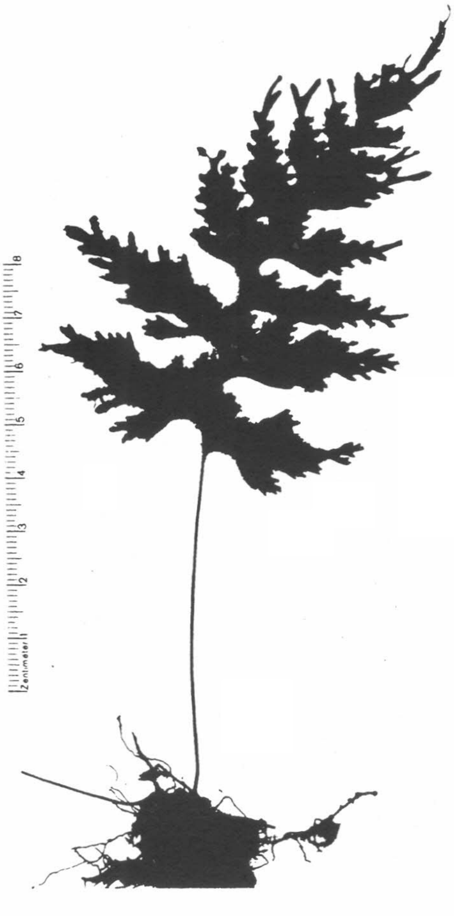

Fig. 3 Hymenophyllum costaricanum v.d.Bosch

Fig. 4 Hymenophyllum polyanthos (Swartz) Swartz

Fig. 5 Hymenophyllum hirsutum (L.) Swartz

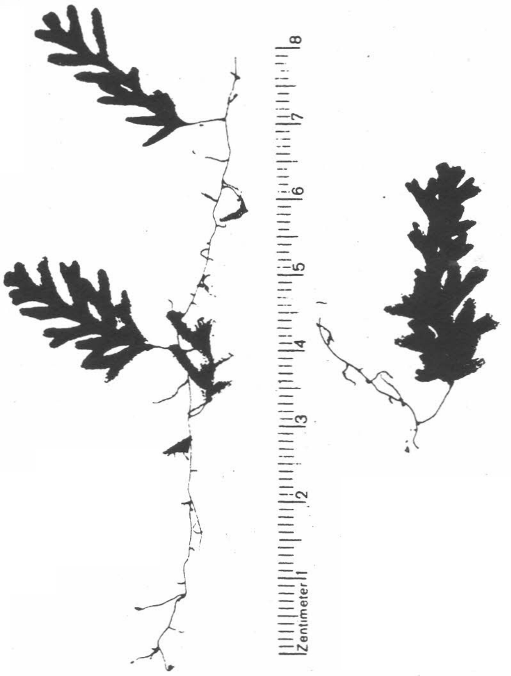

Fig. 6 Hymenophyllum fragile (Hedw.) Morton

Fig. 7 Hymenophyllum microcarpum Desv.

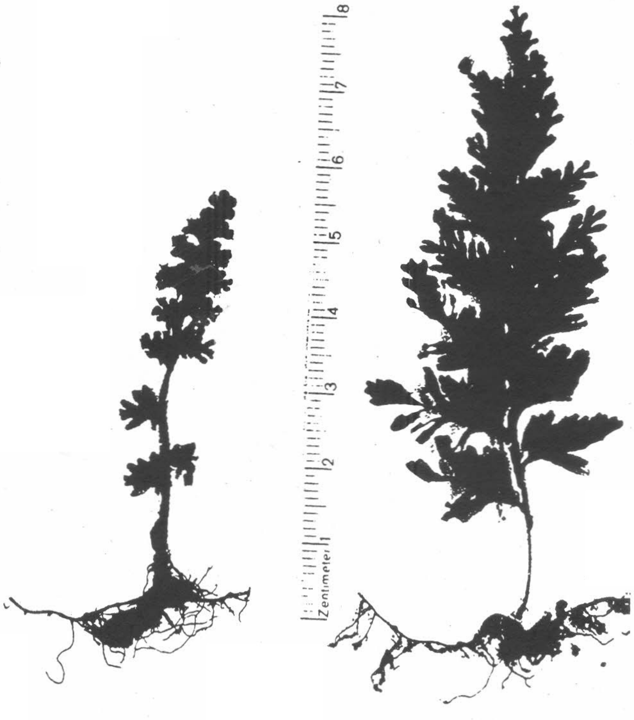

Fig. 8 Hymenophyllum elegans Spreng.

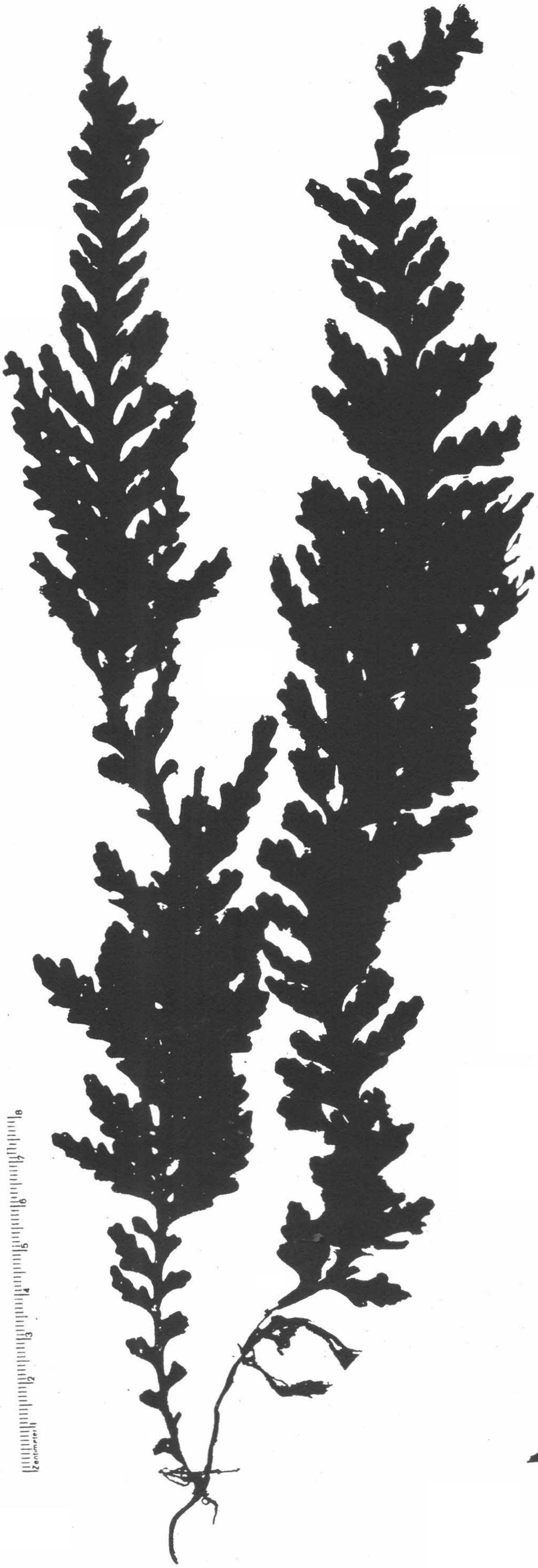

Fig. 9 Trichomanes
cf. rupestre (Raddi) v.d.Bosch

Fig. 10 Trichomanes
radicans Swartz

Fig. 11 Trichomanes collariatum v.d.Bosch

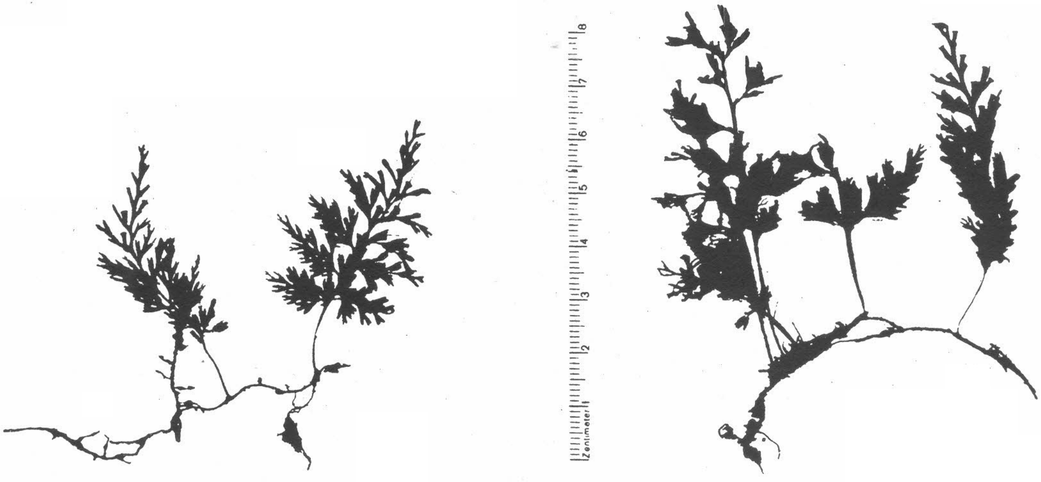

Fig. 12 Trichomanes diaphanum H.B.K.

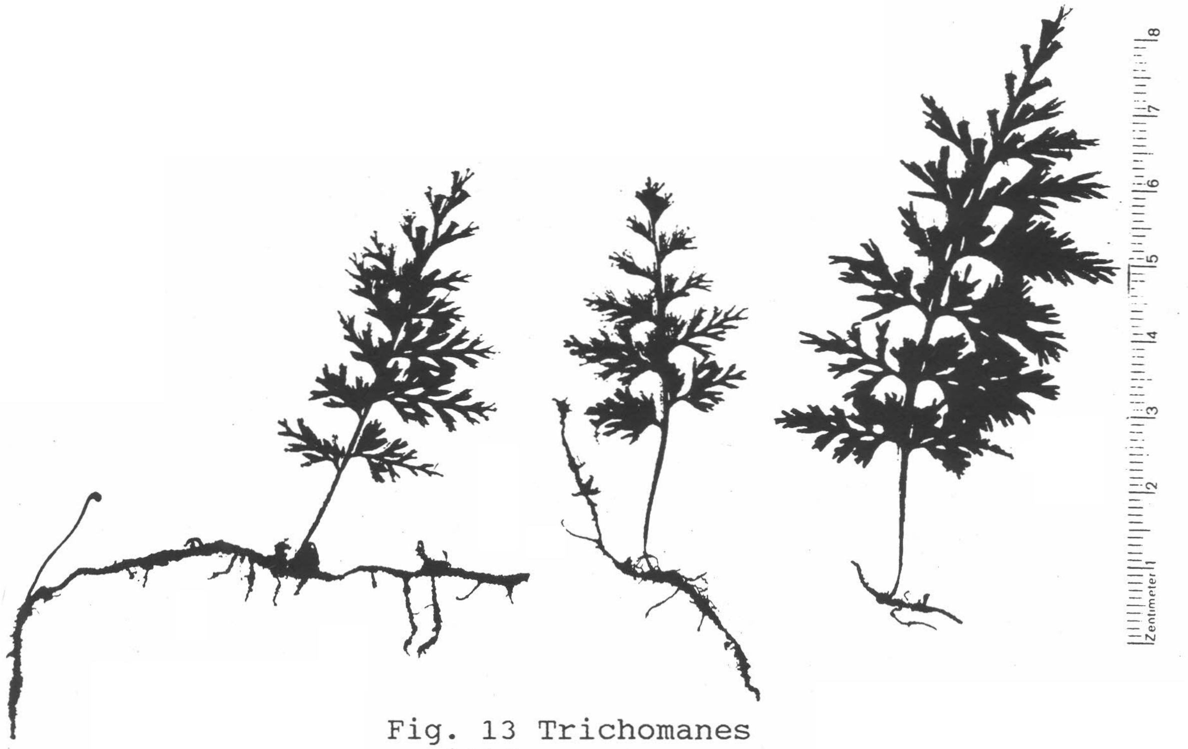

Fig. 13 Trichomanes
pyxidiferum L.

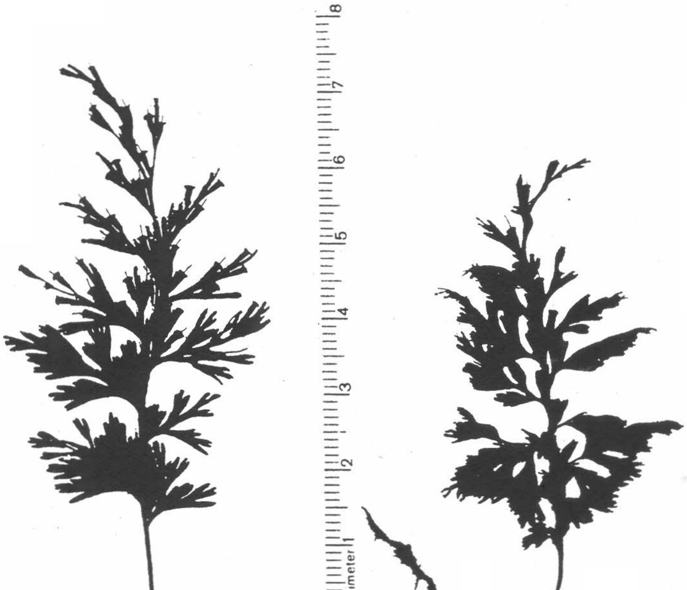

Fig. 14 Trichomanes
hymenophylloides v.d.Bosch

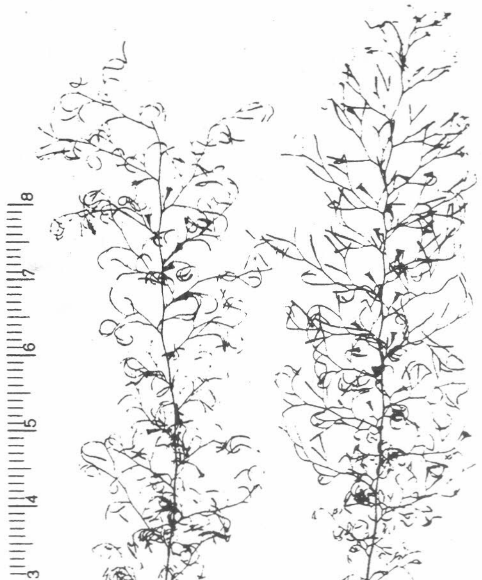

Fig. 15 Trichomanes
capillaceum L.

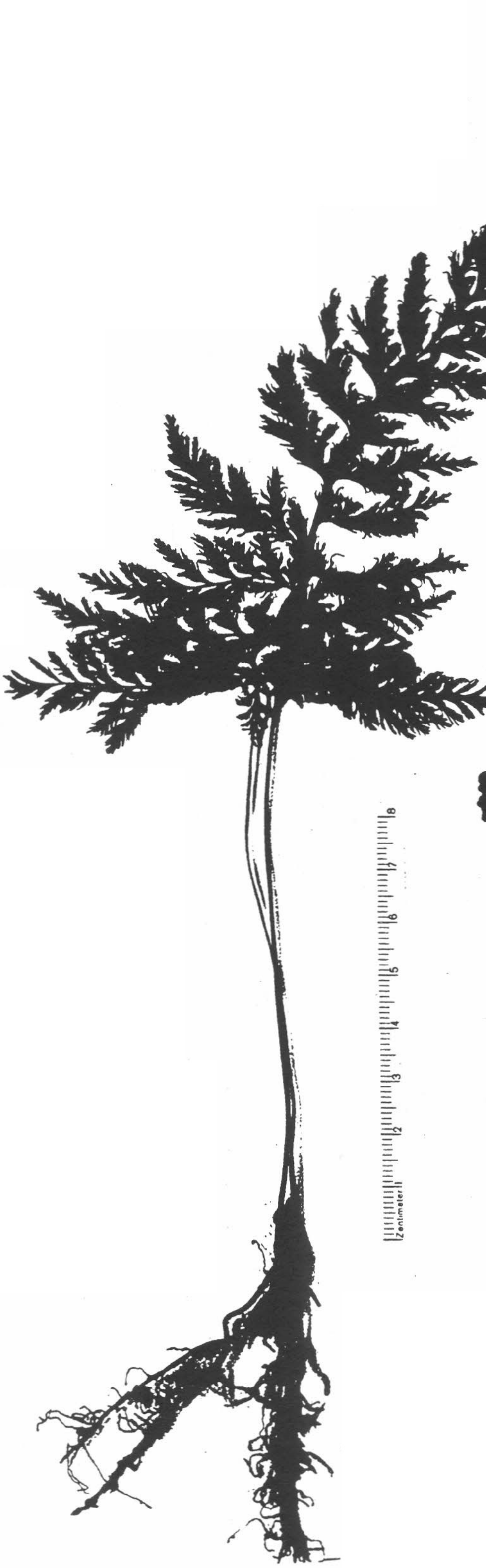

Fig. 16 Trichomanes rigidum Swartz

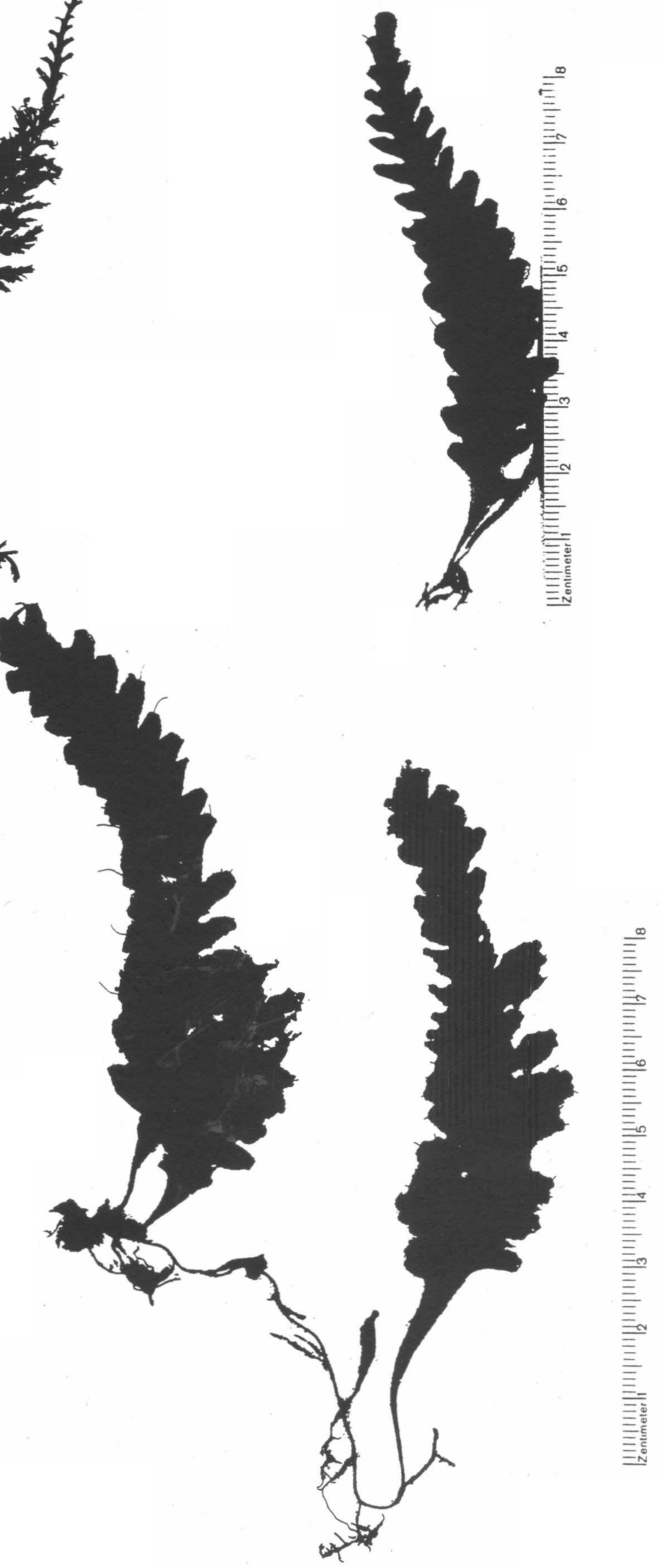

Fig. 17 Trichomanes polypodioides L.

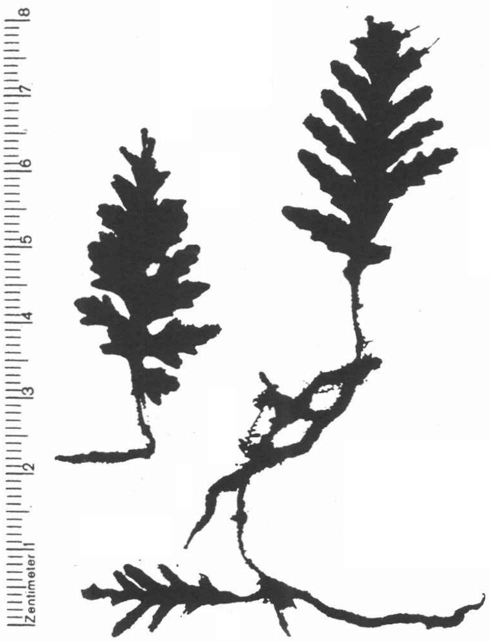

Fig. 18 Trichomanes reptans Swartz

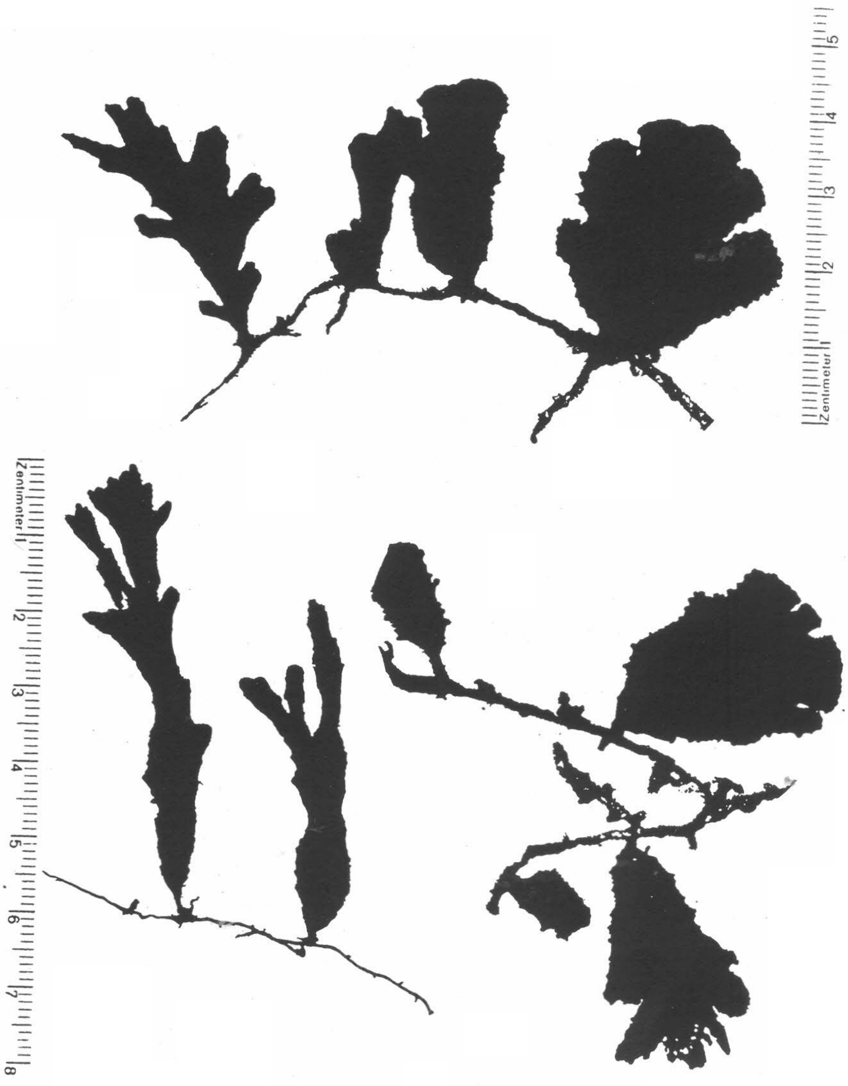

Fig. 19 Trichomanes membranaceum L.

Fig. 20 Trichomanes kapplerianum Sturm in Mart.

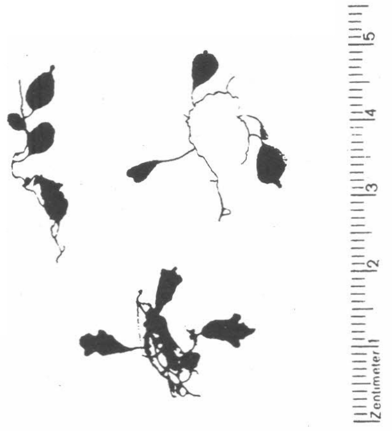

Fig. 21 Trichomanes cf. pusillum Swartz

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