STRUCTURE AND FUNCTIONS OF A RAINFOREST IN THE INTERNATIONAL AMAZON ECOSYSTEM PROJECT: PRELIMINARY DATA ON GROWTH RATES AND NATURAL REGENERATION FROM A PILOT STUDY[1] /

J., HEUVELDOP*
M., NEUMANN*

Resumen

Se llevaron a cabo investigaciones básicas sobre la estructura florística y geométrica de los rodales, la forma de los árboles, los suelos y los microclimas en el área del proyecto internacional de investigación en ecosistemas del bosque pluvial, en San Carlos de Río Negro, Venezuela. La presente contribución se refiere a los sitios de asociaciones forestales que crecen sobre espodosoles.

En el proyecto se mantiene un sector de estudio permanente, en la que se limpiaron 13 lotes, de 10 x 10 m cada uno, para análisis de biomasa. Adyacentes a este sector, se establecieron 6 lotes experimentales de 50 x 100 m cada uno. Todos los lotes experimentales se limpiaron en diciembre de 1975 y tres de ellos fueron quemados en febrero de 1976.

En 1979 se hicieron nuevas mediciones en un área de 2 ha del sector de estudio no perturbado, en todos los lotes de biomasa, y en un lote experimental quemado y en otro no quemado. En las parcelas del bosque no perturbado se encontró que los incrementos diamétricos de los árboles con DAP superior a 13 cm eran relativamente bajos, alcanzando valores menores de 1 mm por año y muy variables, con una desviación estándar de ± 200%. Las tasas de crecimiento anual y los volumenes reducidos por mortalidad de árboles se igualaron, alcanzando aproximadamente 2.8 m^3 por ha, o sea 0.8% de la biomasa aérea verde. Se encontraron claros abiertos naturalmente 12 meses antes, a causa de la caída de algunos árboles. Los claros abiertos naturalmente 12 meses antes, a causa de la caída de algunos árboles. Los claros midieron un total del 0.5% del área ocupada por las 10 ha del sector de estudio permanente. De estas cifras se dedujo que el turno sería 190 años para los árboles emergentes y del dosel superior, y 60 años para los árboles de los estratos inferiores. Todas las especies emergentes y los del estrato superior se regeneran bajo el dosel cerrado.

En los lotes para análisis de biomasa y en los claros abiertos naturalmente se presentó una regeneración compuesta por las mismas especies, e inicialmente se había registrado una composición florística similar, sin embargo, los lotes para análisis de biomasa que habían recibido un tratamiento drástico, progresaron más lentamente y exhibieron una menor densidad que los claros naturales. La regeneración natural exhibió diferencias marcadas en composición, distribución y dominancia entre los lotes quemados y los no quemados, pero no hubo diferencias significativas del crecimiento promedio en altura. No se encontraron individuos de Cecropia *–especie pionera– en los claros naturales, y sólo unos pocos individuos en los lotes de biomasa, pero en los lotes quemados es la planta dominante. En los lotes que se limpiaron pero no se quemaron,* Cecropia *fue dominante solo durante los primeros 2–3 años y luego fue desplazada por otras especies; entre éstas se cuentan especies típicamente emergentes y las que van a ocupar tanto los estratos superiores como los inferiores, formando finalmente comunidades similares a los rodales originales.*

1 Received for publication in August 19, 1981.

* Proyecto Agroforestal GTZ/CATIE.
The Deutsche Forschungsgemeinschaft and the German Academic Exchange Service (DAAD) sponsored the remeasurement pilot project. The authors are grateful to Dr. E. Medina, Director of the project, and his staff at IVIC, Caracas, for providing all facilities during the stay in Venezuela and to Prof. Dr. E. F. Brünig, Drs C. Jordan and H. Klinge for suggestions and comments

Introduction

The most productive forest areas of the world are found in the tropics. Several publications which present recent and old records give an average net primary productivity of tropical forests of around 20 t/ha/y, ranging from 9 to 32 t/ha/ y (18, 29). This range reflects the large variety of site conditions and interactions between land communities and the enviroment. The San Carlos Research Project on the Amazon Rainforest Ecosystems is an international, interdisciplinary MAB Pilot Project which aims at better understanding the structures and functions of the tropical forest.

The project was designed and initiated in 1974. Among the major objectives of the project were the following: 1) To study the present floristic and geometric forest structure in order to determine any variation of structure which could be explained in physio-ecological terms similar to those previously determined in Borneo, and 2) to study the changes in forest structure by the repetition of initial measurements in order to determine rates of growth and regeneration. The initial measurements were made by Brunig and Klinge (12). The first remeasurement of the natural forest area was scheduled for 1985 because changes were expected to be slow and small, and therefore difficult to discern and prove with the simple methods to be adopted. In 1979 and unexpected opportunity arose for a pilot remeasurement of part of the plots, which was a good chance to obtain some preliminary information of changes and growth on the site. This pilot remeasurement was undertaken by the authors with financial support from the German Research Foundation (DFG) and sponsored by the German Academic Exchange Service (DAAD).

The organization and objectives of the San Carlos project are described by Medina *et al.* 34 and Brunig *et al.*, 11. A general description of the landscape and vegetation in the study site is given by Brunig and Heuveldop, 10 and Klinge *et al.*, 26. Herrera, 21 and Klinge *et al.*, 26 give information on the soils and terrain conditions. The climate is typical equatorial with a mean annual temperature of 26°C and an average rainfall of about 3600 mm year^{-1} (Heuveldop, subm. Amazoniana) (Figure 1). The forest formation class is natural weakly seasonal predominantly evergreen equatorial tropical lowland forest.

The research site includes a wide range of forest associations (Brunig *et al.*, 14) varying from a "tierra firme" forest (Jordan and Uhl, 25) through a so-called "high caatinga" forest (Klinge, 28), and finally to a low bana scrubland. The research plot includes altogether an area of 28 ha. Figure 2 shows a map of the plot lay-out. In this paper only the forest association groups K to N (Brunig *et al.*, 13), which vaguely correspond to Amazonian "high caatinga" forest, will be dealt with, and for the sake of simplicity be referred to as "the podzol site". The soils are podosols of sandy quartz mineralogy with varied drainage conditions (Klinge and Herrera, 27). Research work in the San Carlos Project is aimed at investigating the influence of ecological features on structures and functions of a natural rain forest ecosystem. Reviews of developments and preliminary results are given in Brunig (ed., 11) and Adisoemarto and Brunig (eds., 1). General goals are to quantify stand structure and function, stand developments and ecological consequences after different treatments, especially in regard to these extreme obligotrophic soils. Reported here are the results which focus on growth rates, mortality, and regeneration in a permanent, undisturbed observation area; and regeneration patterns in converted areas. These results were obtained from investigations and remeasurements carried out in 1979 by the authors and from the research reported in 1975 by Brunig and Klinge (Brunig *et al.*, 12) within the podzol site.

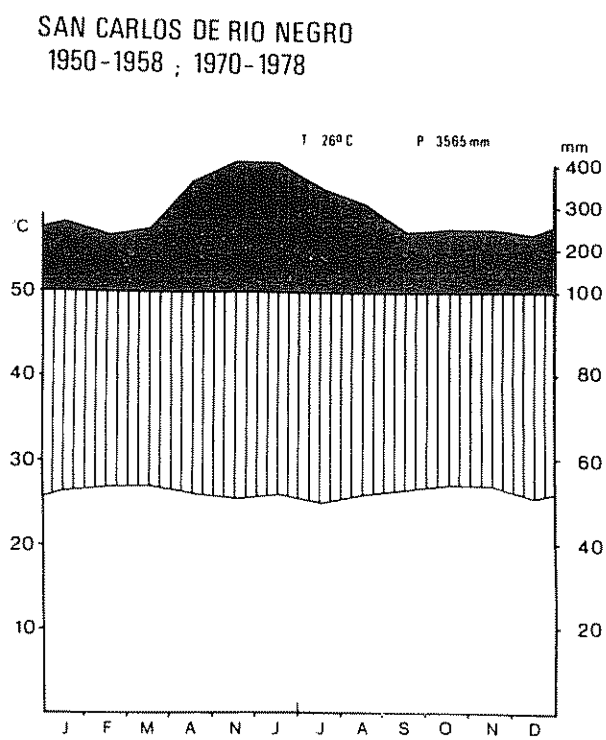

Fig. 1. Climate diagram for San Carlos de Rio Negro, Venezuela, according to LIETH. Data taken from Climate Station San Carlos 1950 to 1958 and 1970 to 1978 for intermediate time no data available.

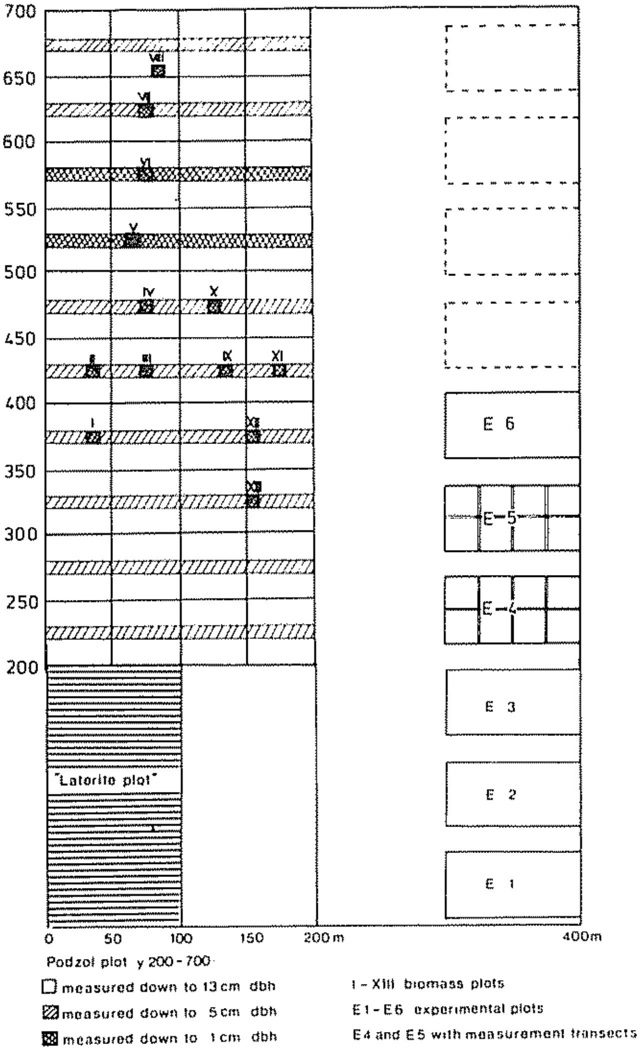

Fig. 2. Layout of the Natural forest research plot at San Carlos de Rio Negro, Venezuela for the amazonian ecosystem study.

Methods

The podzol site was divided into two parts, 10 ha each (see Figure 2), a permanent natural forest observation area (X = 0-200; Y = 200-700) and an adjoining area with experimental plots (X = 200-400; Y = 0-700). Brunig *et al*, 12, Brunig and Synnott, 13 and Synnott, 38 give a detailed description on the investigation methods used, some of which are described in the next paragraphs. For the initial study of tree dimensions, floristic and geometric stand structures, a coordinate grid was established in the 400 x 700 m area and field measurements were made within 10 x 10 m squares arranged continuously along 200 m long transects in the area X = 0-200 and Y = 200-700 (Figure 2). All trees exceeding certain minimum diameters were surveyed. The limits, determined after a trial survey, were set at 1 cm (2 transects, cross-hatched on the map, Figure 2), 5 m (8 transects, simply hatched) and 13 cm (40 transects, blank). Tree diameters were measured by using metal measuring tapes at breast height. All trees were recorded by species (local name and code number) and their location by decimeter co-ordinates of the trunk center at base in the X:Y-coordinate system. A topomap and map of all dead wood was drawn for each square.

Association and diversity patterns, along with stand characteristics of the natural forest observation area, were analysed by a number computer program previously described by Brunig *et al.*, 14. In the experimental plot area, trees above 13 cm diameter were measured in order to link the area to the vegetation classification in the natural forest area. The natural forest was subdivided at medium-scale level of variation into 10 association groups, H to Q. Variation at small scale proved exceedingly complex (Brunig, Alder and Smith, 13). Trees in thirteen subjectively distributed biomass plots (I – XIII, see Figure 2) and six experimental plots (El – E6, see Figure 2) were felled in 1975. Objectives and methods are described by Klinge and Herrera, 27, and Brunig *et al.*, 12.

The biomass plots (10 x 10 m) were completely clear felled and all phytomass removed in fractions between August (towards the end of the rainy season) and in December (in the middle of the dryer season).

Experimental plots E2, E3 and E4 were cut and burned without logging. The plots E1, E5 and E6 were only cut. In all plots stems remained unlogged. In early spring 1976 *Hevea* sp. was planted in the burned plots (4 x 4 m = 625 plants per ha). About one year after establishment of biomass and experimental plots, October 1976, Heuveldop and Herrera recorded natural regeneration in the 13 biomass plots (10 x 10 m) by counting all plants in a diagonal 1 m wide and 13 m long transect running from east to west in each plot. Since it was extremely difficult to ditinguish between species, these very small plants were classified by groups of tree seedlings, regrowth, *Monocotyledoneae, Selaginella,* palms and ferns. For technical reasons plot I was not registered.

Growth and regeneration measurements were made three and a half years later, in 1979, in an area covering 2 ha within the natural observation area by Heuveldop and Neumann. This remeasured part comprises 10 transects which, in accordance to the data analysis (Brunig *et al.*, 13), corresponds well to the average stand structures and species compositions of the whole study site. These 10 transects (Y = 500-600, X = 0-200) were selected because the area includes the two 1 cm transects established in 1975 for special intensive studies.

Some difficulties pertaining to growth rates arose from the fact that tree numbers and measurement points were not marked on the stems in 1975. Also, about 6% of the trees could not be located in the field in 1979 for some unknown reason. This may be connected to inaccuracies in 1975 or 1979, or with unrecorded removals in the intervening period. The errors in diameters, due to deviations of measurement height, may reach a magnitude of about 3% (Loetsch *et al.*, 31). Other sources of error, such as errors caused by different pulling strengths or tilting anges, are negligible. A small number of quite large measuring or recording errors were suspected because of very large differences and consequently all differences between diameter measurements in 1975 and in 1979 exceeding ± 1.5 cm were considered freaks and ignored in the calculations.

Natural regeneration was studied in 13 biomass plots within natural gaps (approx. at X = 10 – 20; Y = 560 – 570 and X = 170 – 180; Y = 540–550) and on the experimental plots E4 and E5 (50 x 100 m). In the biomass plots all trees of more than 0.2 m height were recorded (species and height) along the same diagonal transects as in 1976. In the first natural gap mentioned, the number of seedlings were estimated and all tree species above 0.2 m were recorded, while in the second gap only tree species above 1 m were recorded (species and height). These measurements were carried out along transects in the biomass plots. Regeneration was also studied in the experimental plots E4 and E5 along 1 m wide and one 100 m and three 50 m long transects in each plot. The transects were established as shown in Figure 2. Within these transects, all tree species reaching the height of at least 1 m were recorded (species and height). Not all of the six experimental plots were due to a limited amount of time. Plot E4 and plot E5 were selected because they are neighbouring and were treated differently in 1975, as mentioned above.

All species were documentated by an extensive sterile ecological reference collection and each by at least one fertile herbarium collection made by Brunig in 1975. Determinations were not yet completed at the Herbarium of Botanic Gardens, Caracas at the time of writing. Therefore, local vernacular names were used corresponding to the computing code numbers 1 to 410, 410 being a pool of more than 30 miscellaneous species.

Results

Stand data under natural conditions

Density, basal area and volume and stand tables were calculated for the whole 10 ha natural forest

Table 1. Structural stand parameters for tree 1 cm dbh, MAB Amazon Forest Ecosystem Project [Taken from Brünig, Alder and Smith (15)].

Forest association (code)	Number of stems ha⁻¹	Basal area ha⁻¹ m²	S.D.' (%)	Mean height tallest trees m	Tree volume m³	SD' %
(H)	11 634	38.3	60.0	32	421.9	61.0
(I)	8 361	37.5	61.3	33	426.3	60.0
(K)	12 011	41.9	51.6	29	374.7	63.4
(J)	16 385	38.4	55.8	27	292.8	66.2
(O)	10 000	33.5	46.8	27	344.4	44.9
(N)	9 485	39.7	44.3	24	362.1	40.9
(L)	11 128	34.7	39.3	24	286.4	33.0
(M)	8 119	38.2	43.0	21	328.0	36.9
(P)	10 000	30.8	55.1	14	228.2	52.2
(Q)	18 205	19.7	12.8	9	83.8	114.3
(H – Q)	11 533	35.6	m.c.		306.1	m.c

S D : standard deviation %
n.c. : not calculated
H, I : Yevaro-Hiua-Cunuri
K, J : Cunuri-Yevaro-Piapoco
O, N : Cunuri-Yaguacana-Tamacuari
L : Cunuri-Yucito-Piapoco
M : Cunuri-Yucito-Yaguacana
P : Cunuri-Yucito-Media luna
Q : Yucito-Cuncha marilla-Lengua vacca

Table 2. Number of stems, basal area and volume 13 cm dbh in the whole area (left) and in the 2 hectares selected for remeasurement in 1979, growing stock data relate to 1975 and are original data of Brunig, 1975.

Diameter breath height cm	Values for a 10 ha site (Y = 200-700, X = 200) Number of stems/ha N	%	Basal area/ha (m²)	Vol. above prod. (m³)	Values for a 2 ha site (Y = 500-600; X = 0-200) Number of stems/ha N	%	Basal area/ha (m²)	Vol. above prod. (m³)
1 – 4.9	8 681	79.5	3.53	9.8	8 640	81.9	3.44	9.6
5 – 9.9	1 292	11.8	5.02	24.6	950	9.0	3.73	22.9
10 – 12.9	324	3.0	3.23	22.2	295	2.8	2.93	24.2
13 – 14.9	144	1.3	2.18	16.6	126	1.2	1.90	17.1
15 – 19.9	224	2.1	5.19	44.2	214	2.0	5.01	48.6
20 – 29.9	190	1.7	8.49	85.8	221	2.1	10.07	110.3
30 – 39.9	52	0.5	4.57	52.6	78	0.7	6.43	76.1
40 – 49.9	12	0.1	1.81	22.4	16	0.2	2.48	32.8
50 – 59.9	4		0.89	12.2	8	0.1	1.90	25.6
60 –	2		0.95	12.9	6		2.33	31.8
total	10 925		35.86	303.3	10 554		40.22	399.0
d 13.0	628		24.08	246.7	669		30.12	342.3

study area and for each of the 10 association groups. A preliminary report is given by Brunig, Alder and Smith (15) and is reproduced in Table 1 for trees greater than 1 cm diameter at breast height (dbh). Mean basal area of trees above 1 cm dbh is 35.6 m^2 ha^{-1} for the whole area and 40.2 m^2 ha^{-1} for the remeasured 2 hectares in 1975. Corresponding tree volumes are about 303 m^3 ha^{-1} and 399 m^3 ha^{-1} respectively (calculated by an estimated form factor of 0.5), while the number of individuals trees amounted to 10 925 and 10 554. In comparison to the whole area, this means that somewhat larger trees were located in the selected area, proving logical when the association group map is consulted which shows a large bana area (groups P and W) outside the 2 hectares and a large proportion of Yevaro association (H and I) within the remeasured 2 hectares.

Mean number of individual trees and mean basal area for the 13 biomass plots are 11 446 ha^{-1} and 36.8 m^2 ha^{-1} (Klinge, 28).

The first results of the analyses of stand structure on the podzol site was presented by Brunig (Brunig *et al.*, 13 and 14). The association group classification program developed on precursors used earlier in Sarawak and Brunei is described in Adisoemarto and Brunig (eds., 1). The work on the structural analysis will be continued.

Development and growth in closed stands

Regeneration, growth and the resulting structural pattern of the forest are closely related to mortality and gap sizes (Ashton and Brunig, 3; Ashton, 4); these, in turn, are related to site characteristics, soil and time. Therefore, assessments of change are subject to a large variation between variables.

Mean diameter increments found in the San Carlos podzol sites are less than 1 mm $year^{-1}$ for all trees above 13 cm dbh, ranging from 0.2 m to 1.3 mm, depending on tree species. The increment of understory trees (1 cm to 13 cm dbh) is lower, averaging about 0.2 mm $year^{-1}$, while emergent trees (above 30 cm dbh) show a mean diameter increment of 0.9 mm $year^{-1}$. Table 3 gives some of the data obtained in 1975 and 1979. Basal area and number of trees above 13 mm dbh remains constant. Standard deviation of the average diameter increment is quite large, probably due to the large variation in growth rates among the very different social classes. Ingrowth in the class above 13 cm dbh compensates mortality with respect to the number of trees and species. Emergent trees on this site greater than 30 m in height, represent 2% of the total ingrowth. Main canopy trees, with heights between 20 and 30 m, amount to 25%, and the remaining 73% of total ingrowth are understory species.

The change in the number of stems is shown in Table 4. From 1975 to 1979, ingrowth in the 1 cm class was slightly higher than mortality in transects 520 – 530, compared to only 1% from the data in 1975 in transect 570 – 580. This indicates that there is hardly any change in species composition since almost all emergents and main canopy trees are able to regenerate in the shade of the forest stand without an intermediate gap phase

Table 3. Stand data per ha, development August 1975 – February 1979 in selected area (Y : 500-600; X = 0-200); for dbh 13 cm.

Parameter estimated	Data from 1975* living	Data from 1979 living	dead	increment	mortality (per % per year)	increment (% per year)
Basal area ($m^2 . ha^{-1}$)	30.12	30.09	0.87	0.84	0.8%	0.8%
Number of stems . ha^{-1}	669	667	37	35	5.5	5.2
dbh of b.a. mean – tree (cm)	23.94	24.18	17.3	0.24	–	0.3
Mean height (m)	22.7	n.c.[2]	23.1	n.c.[2]	–	–
Volume (m^3)	342.3	n.c.[2]	10.05	n.c.[2]	0.8	–

Source: *Brunig's fieldbook data.

[2] Not calculated, only diameter increment was measured in 1979.

Table 4. Ingrowth and mortality in the two 1 cm transects (X: 0-200; Y: 520-530 and X: 0-200; Y: 570-580).

Transect	N 1975[1] living dbh 1 cm	N 1979 living dbh 1 cm	Registered ingrowth in 1 cm class	Dead 1 cm dbh 13 cm	Dead dbh 13 cm
Y: 520 – 530 X: 0–200 (except biomass plot)	1 989	2 127	138	102	3
In % of all trees 1975		106	C.9	5.1	0.2
per ha	10 468	11.195	690	537	16
Y: 570 – 580 X: 0 – 200 (except biomass plot)	1 941	1 961	20	125	6
In % of all trees 1975		101.0	1.0	6.4	0.3
N per ha	10 216	10.321	100	653	32

1 Source Brunig's fieldbook data.

(Figure 3). The fact that the stand consists of a remarkable proportion of shade-bearing species might lead to the conclusion that they are in a late succession stage.

Mortality for all diameter classes averages 0.8% $year^{-1}$, which gives a calculated turnover rate of 123 years. However, mortality is unevenly distributed within the different storys (Table 4). Therefore, it seems reasonable to differentiate mortality in relation to tree layers. This will result in a turnover rate of about 60 years for understory trees and almost 190 years for emergents and main canopy trees.

The size of natural gaps amounting to 0.01 – 0.02 ha obviously originates from single tree falls.

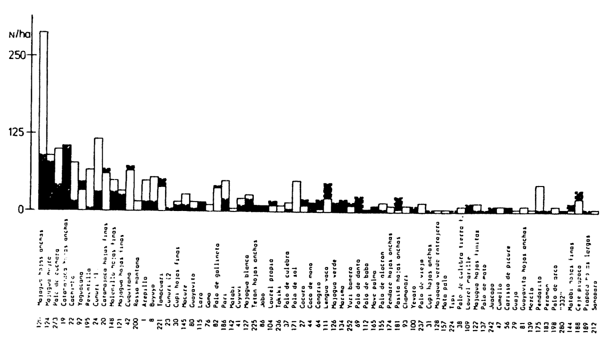

Fig. 3. Distribution of species under regeneration in two selected transects (10 x 200 m each) of the natural forest research plot at San Carlos de Río Negro, Venezuela, in decreasing order.

According to Brunig's investigations in 1975, the total area of one year old gaps comprises about 0.5% of the 10 ha site. Based on this data, turnover rates are calculated to be 200 years, which seems reasonable and corresponds to the results estimated by mortality rates.

REGENERATION IN CONVERTED AREAS

Biomass plots

The distribution of the 13 biomass plots is shown in Figure 2. These plots represent almost all association groups selected by the computer program excluding association I, which is located in an area dominated by *Eperua purpurea.* Table 5 gives some characteristics of the primary stands before cut and harvest. Number of individuals and species as well as basal area and tree volumes differ between the plots in relation to the variation in association groups. Species composition in and around the plots shows that the main canopy trees most common are Cunuri I (024), Yaguácana (092), Yévaro (100) and Piapoco (188). Before cutting, the understory in the plots were dominated by Tamacuari (221), Cunuri I (024), and Majagua hoja ancha (12). Therefore, there are some differences in species composition before and after harvest. On the other hand, regeneration in eleven plots shows that out of the most common four species, at least one is important in the mature stand before harvest or is important in the vicinity. Plot XII, especially, shows

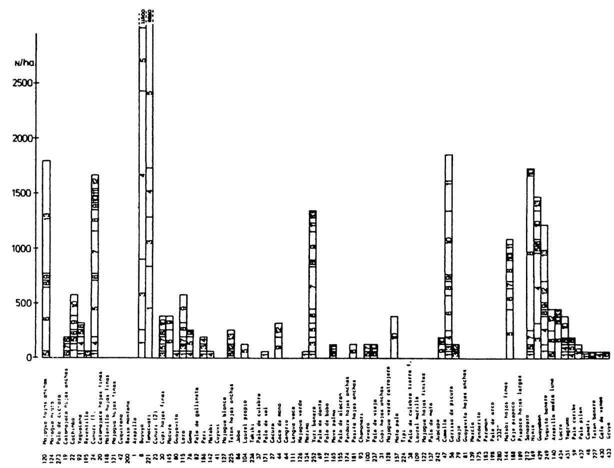

Fig. 4. The distribution of species under regeneration in the biomass plots Nos. 1-13 (10 x 10 m each) of the natural forest research plot at San Carlos de Rio Negro, Venezuela, ordered in accordance to the frequency distribution from the undisturbed transects (Fig. 3).

nearly the same species composition in the regeneration as in the surrounding mature stand. Figure 4 shows that the most common regeneration species in all plots is Buyuyo hormiga (008), which also exists sparsely in closed stands. In the larger gaps Yagrumo (431), *Cecropia* sp., and Lacre (434), a secondary succession species, appear frequently in only 2 plots (VI and XI). Considering the small but scattered regeneration area studied in all plots, (156 m^2 in total) it seems that species which are

Table 5. Some characteristics of the previous stand on the biomass plots in 1975 (for dbh 1 cm).

Plot No.	Number of stems* 100 m^{-1}	Number of species**	Basal area ha^{-1} ** m^2	Volume ha^{-1} ** m^3	McIntosh** index
I	62	15	31.00	282	0.7315
II	61	16	71.56	645	0.6783
III	94	39	33.48	254	0.8707
IV	98	28	34.47	272	0.7529
V	144	44	16.22	102	0.8584
VI	135	35	30.55	281	0.6882
VII	162	48	23.02	201	0.8279
VIII	130	26	51.00*	600*	0.6838
IX	113	37	35.18	261	0.8021
X	110	30	39.37	318	0.6979
XI	111	39	58.00	599	0.8505
XII	140	37	34.76	210	0.7414
XIII	191	36	26.91	98	0.8246
Average	119	33	37.35	317	

* From Klinge's biomass data.

** From Brunig's fieldbook data.

characteristic for the stands are also well represented in the biomass plots.

Mean height of all plants above 0.2 measured in 1979 is 0.47 m. This indicates an annual growth rate of more than 0.15 m, assuming germination immediately after treatment. In five plots, maximum height varies rather significantly and amounts to more than 1 m in five plots (IV, VI, VIII, IX and X). In four plots, maximum heights are 0.8 – 0.9 m, of Buyuyo (008). Fast growing species in the remaining plots are Catamajaca hoja ancha (019), Arepillo media luna (140), Macure (145), and *Cecropia*. The tallest tree, Catamaja h.a. (019) reaching a height of 3.5 m, is probably a coppice shoot. *Cecropia*, which does not occur in the closed stands, shows a dominant height of 2.9 m in one plot only (IV). Elsewhere (plots I, VI, VIII and XI), the average height is 1.1 m, which equals the heights measured for other species in the same plots.

In 1976 and 1979 the number of seedlings in the plots was estimated. Mortality was found to be 7% . Plot II had five times more seedlings in 1976 than the other plots. The reason is not exactly known yet. The average plant density for all plots was equal to or greater than 117 000 individuals per ha, 37 000 individuals having height greater than 0.2 m. Maximum and mean stem heights are positively correlated with the number of species (r = 0.71 and 0.66 respectively). Although these correlations are weak, there is a clear tendency of an increase in the number of species in all of the plots. Figure 5 shows mean heights in 1 m steps for all plots along the east-west transects and corresponding number of individuals. Obviously, the plot edges are occupied by less plants with lower mean heights on the east side than in the middle of the plots. There are no

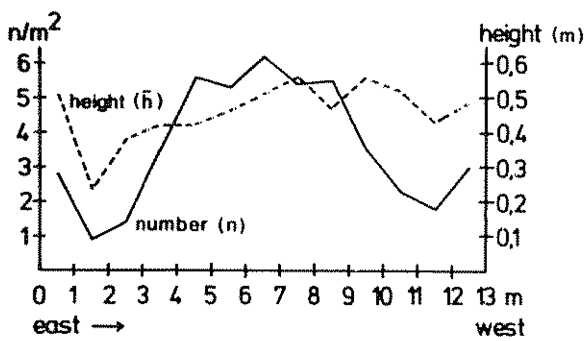

Fig. 5. Distribution of mean hight and number of individuals under regeneration in the biomass plots Nos. 1-13 (10 x 10 m each) of the natural forest research plot at San Carlos de Rio Negro, Venezuela. Measurements were taken in the 1 m wide east-west diagonals of each plot.

final conclusions on this picture yet. Possibly, the poor regeneration on the edges is connected to root competition, soil water status and temperature. Compared to natural gaps, regeneration on the biomass plots shows about 25% fewer individuals and about the same reduction in mean heights.

Regeneration on experimental plots

Adjacent to the study site, experimental plots (E1 – E6) were established in order to study the development of various natural and planted crops under clear cut, burned and unburned conditions (Brunig *et al.*, 12). For technical reasons the plots were not established as originally planned with exception for E3 and E5 where *Hevea* spp. was planted. Plot E5, which was clear cut only, can ecologically be regarded as a larger windthrow area. Clear cut and burned plot E4 resembles the initial situation in shifting cultivation areas or "conucos", which is the common land use form.

The original vegetation was investigated by Brunig in 1975. With respect to floristic aspects, the two plots E4 and E5 differ somewhat. Before clear cuts plot E4 (722 trees/ha above 13 cm dbh) corresponded closely to the intermediate areas of the study site, dominated by *Micranda spruceana* (association group L and M, simple structure, few species, rather low diversity, aerodynamically smooth). Plot E5 was more related to the *M. spruceana – Eperua leucantha* stand type (association group 0 and N, more complex, aerodynamically rougher and relatively rich in species). One year after cutting a similar secondary succession was found in both plots (E4 and E5). The dominating species was *Cecropia*. The ground vegetation in E4 was, practically, completely destroyed by the fire. In 1977, two years after treatments, *Cecropia* was well covering the burned area. On the contrary, in the unburned E5 the seed-

Table 6. Comparison of ecological (Motyka, M.) and ecological floristic (Srensen, S) smilarity and diversity index McIntosh, MI.) in experimental plots E4 (cut and burned and E5 (clear cut only) the decreasing similarity due to the different treatment and the lower MI on E4 in 1979.

	Original vegetation (above 12 cm dbh) 1975		Natural regeneration (above 1 m height) 1979	
M E4/E5	57.0		24.8	
S E4/E5	0.65		0.47	
	E4	E5	E4	E5
MI	0.627	0.611	0.492	0.815

lings pool remained more or less undisturbed. The plot showed, at the same time, increasing dominances of about 20 other species. The importance of *Cecropia* was distinctly diminished here. This tendency of increasing difference in species composition is continuing. In 1979 seventy-two species were found in E5 and twenty-five in E4 (Figure 6). Only two species, Lacre (434) and Café de venao (430), were found in the burned area E4, and did not occur in E5. The calculated density per hectare of all plants higher than 1 m was 29 800 in E4 and 10 800 in E5.

Similarities between both plots are quantified by application of the indices of Srensen, 37 and Motyka cited by Whittaker (4), based on original vegetation (1975) and on natural regeneration (1979). Diversities in both plots before and after treatments are characterized by the McIntosh-index (McIntosh, 33). Table 5 gives the results of these calculations. Before cutting, the plots showed close ecological and floristic similarities, while diversity in E4 was somewhat higher than in E5. Four years later, there is a decrease in all figures except for diversity in E5, which increased from MI 0.611 to MI 0.815 per 100 individuals.

In addition, average and maximum heights were measured on several occasions since plot establishment. *Cecropia,* the most numerous species on both plots during the first three years, showed differences in height growth as early as 1977. Measured mean heights of *Cecropia* in 1979 were 4 m in plot E4 and only 3 m in plot E5, while maximum heights

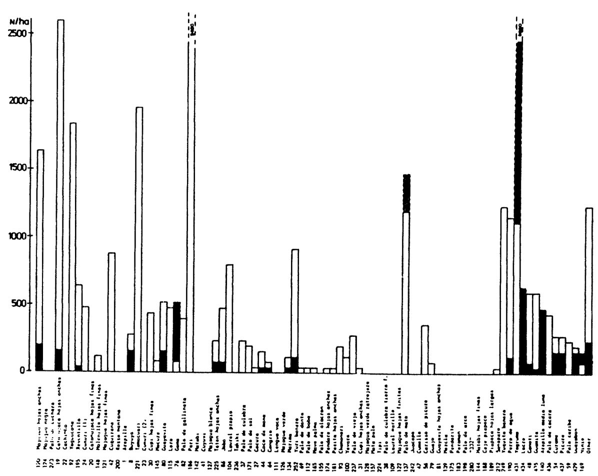

Fig. 6. The distribution of species under regeneration in two selected experimental plots (50 x 10 m each) of the natural forest research plot at San Carlos de Rio Negro, Venezuela, ordered in accordance to the frequency distribution from the undisturbed transects (Fig. 3).

amounted to 8.5 m in E4 and 5.0 m E5. Only in plot E5 was the maximum height equal to or exceeded by other species such as Guajo (079), reaching 12 m; Palo de dato (069), 10.5 m; Palo Brasil, (014) 6 m; and nine other species above 5 m.

A hybrid of *Hevea brasiliensis* was planted in plot E4 in April 1976. The plantation was carried out in 4 x 4 m (i.e. 625 plants per hectare). According to the inventory in 1979, thirteen living plants were found on the 250 m^2 sample plot area, which equals 520 individuals or 83% of the original number. The average height of each species was 1.8 m (i.e. below mean height of all individuals).

Differences in site conditions in regard to nutrient status have been investigated by Jordan and Uhl and are still under observation.

Discussion

The relatively small permanent study area of 10 ha comprises quite different stand types stratified into the mentioned 10 stand classification groups. Forest dynamics are affected by floristic and geometric structures, which change along gradients of time and site. The first resurvey in 1979, in one part of the study area after 3½ years, could not be expected to produce proof of significant structural changes. The data were analyzed, tentatively, as a guide to continued research. However, it seemed justified to produce the results of the analysis of the data of 1975 and 1979 in view of the scarcity of such measurements in natural and modified tropical rainforest.

The calculated variations of basal areas, volumes and stands are lower than the averages for tropical rain forest but agree to the general descriptions given for Kerangas and Kerapah in Sarawak and Brunei (Brunig, 9). It must be emphasized that the San Carlos data are yet quite insufficient from a biometrical point-of-view and that the standard deviation of the grand mean amounts to about 200% . This variation was not unexpected because single trees behave very differently in yearly increments according to their social position, age and condition. It seems correct not to use mean diameters and increment for determination of ages of trees because of the wide fluctuation in single values. But we feel justified to conclude that ingrowth and diameter growth equals losses by mortality resulting in an almost constant basal area.

Natural forests generally regenerate as a response to gaps in the upper canopy (Richards, 36; Ashton and Brunig, 3; Whitmore, 39; Halle *et al.*, 19). If the gaps in a sufficiently large are are well scattered, turn-over rates can be calculated (Ashton, 4). This is, however, valid only for uneven-aged primary forests. Murphy and Uhl, 35 found that in the adjacent tierra-firme forest 4.8% of the total area was in the gap phase with an estimated persistence of five years. The calculated turn-over rates amount to 104 years on this basis. Brunig (9c) showed from data in Sarawak that gap area and gap sites can be dependent on site and forest structure and the resulting covariances make any simple assessments rather dubious affairs. In the "caatinga" forest, on the podzol site, the area of 1-year old gaps was 0.5% of the total area in 1975 (see map in Brunig *et al.*, 14, and original field cards). Even if the resulting turn-over rate of around 200 years fits well to estimations based upon mortality rates, it has to be considered that, first, the interpretation of gap age is anything but reliable and, second, that if understory trees (seedlings and poles) with initial growth after windthrow in the upper canopy become suppressed after a couple of years, as in small gaps, the upper canopy closes from the sides. Possibly, because of this, estimated turn-over rates are exaggerated if calculations are based upon gap area only.

The remeasured part of the forest in the podzol site indicates a late successional stage as all important species regenerate in the closed stands without a particular gap phase. Whitmore, 39 found quite similar figures for dipterocarp stands in Malaya as we did in San Carlos, stating that 6%, 22% and 72% respectively of emergent, main canopy and understory trees are regenerating. On the contrary Hartshorn, 20 states that 75% out of 105 canopy tree species at La Selva, Costa Rica regenerate successfully only in gaps. Similar findings have been published by Aubreville, 5 and Richards, 36. However, comparisons of this kind are rather unsatisfactory because actual site and stand parameters differ greatly in time and, also, applied investigation methods vary within a rather wide range. Variabilities in stand architectures, species composition and seasonalities lead to differentiations in stand developments and dynamics which, in turn, interact with site factors and exchange processes.

In spite of this, comparisons provide, at least, an orientation which shows that biomass and productivity of the San Carlos stands are below average of tropical rain forests but well equal to stands under similar soil and environmental conditions in Borneo (Brunig, 7).

Richards, 36 and Brunig, 6 mention that natural regeneration is complex and is essentially dependent on interactions between nutrient, water supply and radiation components. Also, spectral distribution is one of the main factor affecting seed germination and, thus, determining survival and development of species. In regard to radiation quantities, similar effects are quoted by Evans *et al.*, 16; Gaterum *et al.*, 17 ; Hughes, 24; Loach, 30

Measurements on light distribution have been performed rather extensively in the San Carlos Project. It was found that relative light intensities at ground level average to 2 – 3%, which is more than previously expected. Longman and Jenik, 32 state that most results from investigations on light intensities in tropical rain forests show values lower than 1% of total light above canopy. Regeneration of almost all canopy species in the closed stands found in San Carlos on the podzol site, as well as on the laterite site (Murphy and Uhl, 35), may be due to this relatively high position of light penetration.

Light distribution seems to be more closely related to stand height than to any other stand parameters (Heuveldop, 22). The San Carlos stands are regarded as comparatively low, which is well in line with the average illumination rates at ground level. At the present stage of data evaluation, further correlations between radiation parameters and germination have not yet been quantified.

Differences in regenerating species and growth found between the 13 biomass plots may be due to variations in soil and drainage conditions, previous stand structure, floristic composition, nutrient status and seasonality of fructification. One year after treatment, regeneration was extremely poor in the number of individuals and height development. The 1979 inventory resulted in almost the same number of individuals as in 1976, with an average height of 47 cm for all plants above 20 cm. Compared to natural gaps, the biomass plots had no established regeneration at the time of canopy opening. After phytomass harvest the soils were bare, water holding capacity had decreased, the upper soil layers were compressed and no shading-under story trees were present. These heavy impacts have, probably, lead to the relatively low number of species which at an average is 12 per 13 m^2 (equal to 9230 per ha) for all 12 biomass plots recorded in 1979, values ranging from seven (5385 per ha) (plot XI and XII) to eighteen (13 846 per ha) (plot VIII). In the, more or less, equal sized natural gaps about four times more species were found. Typical pioneer species like *Cecropia* spp. occur only occasionally in the biomass plots. Climbers amounted to 12% in natural gaps and to about 15% of regenerating tree plants in the biomass plots. Plot size, in addition to conditions on these heavily treated biomass plots, did not distinctly favour specific pioneers.

On the other hand, no selective influence on species composition in the regeneration could be found in closed stands compared to the above mentioned natural gaps. An increase in light did not compensate for the changes in site conditions, as far as natural gap and biomass plot areas are concerned. Light quantities and qualities at ground level in the investigated closed stand seem sufficient for regeneration of all main species.

Evidently, an initial dominance of *Cecropia* spp. is possible only in the larger areas. As found in the clear cut and burned experimental plot E4, the significant dominance lasted for the first four years or more after treatment, while in the unburned plot E5, within two years after treament other species became dominant. This may be explained by higher root competition, and to changes in radiation pattern caused by the denser vegetation in the unburned plot, *Cecropia* decreasing in number and height after a couple of years. More research is needed in respect to species development, especially in correlation to microclimates, nutrients and water economy.

Within the total investigation site, twenty tree species representing 80% of all main canopy species, i.e. species of more than 20 m height, were selected for comparisons of regeneration in various plots (Table 7). These species amount to about 12% of all individuals in the main canopy. Under closed canopy 80% of all selected species were found representing 28% of all individuals within this layer.

Natural gaps and biomass plots show almost the same relative number of species, but a higher dominance than that found in regeneration under closed canopy. Compared to corresponding figures for the mature stand, dominance of the 20 selected species among all individuals is more than double under closed canopy and is about three times higher in gaps and biomass plots. Number of species in experimental plot E5 is well in line with the former plots, while the frequencies of other species are increasing. Plot E4 still shows heavy disturbances in 1979. It is noticeable that three years later 70% of the most frequent dominant species regenerate more or less independently of the treatments used (i.e. the area was not burned). Even after burning, 15% of the primary species occurred within this relatively short time, comprising 3% of all tree plants reaching more than 1 m in height.

Still the mechanisms controlling regeneration are widely unknown and further studies are needed to clarify the interdependent factors between forest structure, site, and forest dynamics. Supplementary studies of the physio-ecology and genetics of the major species are required.

The major remeasurements of the whole area, planned for 1985, will produce more reliable data on the dynamics of the natural stands and the recovery of the felled and burned plots. Studies of shifting cultivation plots nearby indicate that recovery seems to be more rapid than commonly supposed (Uhl, in Press). The pioneer species, *Cecropia,* is not found in the natural gaps, and on some biomass plots only single individuals are found, while this pioneer dominates on the burned experimental plot. On the clear cut and uburned plot *Cecropia* dominated only during the first 2 – 3 years and was then suppressed by other species. These are typical emergent and main canopy species as well as understory species, indicating the developing of a similar community as the previous stands.

Summary

In the international rainforest ecosystem research project at San Carlos de Rio Negro, Venezuela, basic investigations on floristic and geometric stand structure tree forms, soils and microclimates were carried out in 1975. The German contribution was focussed on the forest associations in the spodosol sites.

Table 7. Regeneration of 20 selected tree species, representing 80% of all individuals in the main canopy (tress above 20 m height), 1979.

Regeneration species	Closed stands	Natural gaps	Biomass plots	Unburned E5	Burned E4
In % of selected species	80	85	70	70	15
In % of all indiv in correspond layer	28	37	33	20	3

An area of 10 ha is kept as permanent study area, where 13 plots (10 x 10 m each) were clear cut for analysis of phytomass.

Six adjacent experimental plots were established, each measuring 50 x 100 m. All experimental plots were clear cut in December 1975, three of them additionally burned in February 1976.

Surveys were carried out in 1979 within a 2 ha area of the undisturbed study site, all biomass plots, one burned and one unburned experimental plot. Diameter increments in the mature stands for all trees above 13 cm dbh were found to be relatively low, with values less than 1 mm $year^{-1}$, and very variable with a standard deviation of ± 200%. Yearly growth rates and volumes reduced by mortalily, amount to about 2.8 m^3 ha^{-1} or 0.8% of above ground fresh phytomass. Natural 1-year-old gaps, caused by fallen single trees, comprise a total area of 0.5% within the 10 ha study site. Turn-over rates are calculated from these figures to be 190 years for emergent and main canopy trees, and 60 years for understory trees. All emergent and main canopy tree species regenerated under the closed canopy. On the biomass plots (10 x 10 m) and in the natural gaps the same regeneration species occur and similar floristic compositions are found as in the previous stands, though the heavily treated biomass areas develop slower and plant communities show less densities than the natural gaps. Regeneration in the clear cut, burned and unburned experimental plots show distinct differences in species, distribution and dominances but no significant differences in mean height growth. The pioneer species, *Cecropia,* is not found in the natural gaps and on some biomass plots only single individuals are found, while this pioneer dominates on the burned experimental plot. On the clear cut and unburned plot *Cecropia* dominated only during the first 2 – 3 years and was then suppressed by other species. These are typical emergent and main canopy species as well as understory species, indicating the developing of a similar community as the previous stands.

Literature cited

1. ADISOEMARTO S. and BRUNIG, E. F., eds. International MAB-IUFRO – Workshop on Tropical Rainforest Ecosystems Research, 2nd., Jakarta, 1978. Transactions. Special Report No 2. s l., s.e., 1979.

2. ALDER, D. *et al.* Strucktur und Funktion im Regenwald des internationalen Amazonas Okosystemorjektes. Vorläufige Mitteilung über Klassifikation der Bestände Variation der Bestandesstruktur und Niederschlogs-merkmale. **In** Symposium über biogeographische und landschaftsökologische Probleme Südamerikas: Wald und Wasser, 9th, Ploen. Amazoniana (Brasil) 4(4):423-444. 1979.

3. ASHTON, P. S. and BRUNIG, E. F. The variation of tropical moist forest in relation to environmental factors dual its relevance to land-use planning. Mitt. Bundesforsch. anst. Forst-Holwirtschaft 109:59-86. 1975.

4. ASHTON, P. S. and BRUNIG, E. F. The natural forest: plant biology, regeneration and tree growth. **In** Tropical Forest Ecosystems; a state of knowledge report. Paris, UNESCO/UNEP/FAO, 1978. pp. 180-215.

5. AUBREVILLE, A. Les forêts de l'Afrique occidental Française. Ann. Acad. Sci. Col. 9:1245. 1938.

6. BRUNIG, E. F. Forstliche Produktionslehre. Lang, Bern und Frankfurt, Europ. Hochschulschrift, 1971. 328 p.

7. BRUNIG, E. F. Biomass diversity and biomass sampling in tropical rain forest. **In** IUFRO Biomass Studies, IUFRO S.401. Orono, University of Maine, 1973. pp. 269-293.

8. BRUNIG, E. F. Some further evidence on the amount of damage attribute in lightning and wind-throw in Shorea albida forest in Sarawak. Commonwealth Forestry Review 52(3):260-265. 1973.

9. BRUNIG, E. F. Species richness and stand diversity in relation to site and succession of forests in Sarawak and Brunei. **In** Symposium on Biogeography and Landscape Research in South America, 3rd., Ploen, 1972. Amazonian (Brasil) 4(3):293-320. 1973.

10. BRUNIG, E. F. and HEUVELDOP, J. Structure and function in natural and man made forest in the humid tropics. **In** IUFRO World Congress, 16, Osb., 1976 s.n.t. pp. 500-511.

11. BRUNIG, E. F. and HEUVELDOP, J. ed. International MAB/IUFRO Workshop on Tropical Rainforest Ecosystems Research, Hamburg-Reinbek, 1977. Transactions. Special Report No. 1. s.l., s.e., 1977.

12. BRUNIG, E. F., HEUVELDOP, J. and KLINGE, H. San Carlos de Rio Negro: Ein Forschungsvorhaben des UNESCO-Programms. MAB als Beispiel internationaler Zusammenarbeit in problemorienfierter Grundlagen – forschung. Forstarchiv. 48(4): 71-74. 1977.

13. BRUNIG, E. F. *et al.* Structure and functions of a rainforest in the international amazon ecosystem project: floristic stratification and variation of some features of stand structure and precipitation. In Singh, J. S and Gopal, B., eds. Glimpses of ecology. Jaipur Prakash Publishers, 1978. pp. 129-144.

14. BRUNIG, E. F. *et al.* The International Amazon MAB Rainforest Ecosystem Pilot – Project at San Carlos de Rio Negro: Review of developments since the 1st. international workshop. In Adisoemarto, S. and Brunig, E. F., eds. International MAB-IUFRO Workshop on Tropical Rainforest Ecosystems Research. Chair of World Forestry, 2nd., Hamburg-Reinbek, 1979. Transactions. Special Report No. 2. s.n.t. pp. 47-66.

15. BRUNIG, E. F., ALDER, D. and SMITH, J. P. The International MAB Amazon-Rainforest Ecosystems Pilot-Project at San Carlos de Rio Negro: vegetation classification and structure. In MAB-IUFRO Workshop on Tropical Rainforest Ecosystems Research, 2nd., Hamburg-Reinbek, 1978. Transactions. Special Report No. 2. s.l., s.e., 1979.

16. EVANS, G. C., WHITMORE, T. C. and YOUNG, Y. K. The distribution of light reaching the ground vegetation in a tropical rainforest. Journal of Ecology 48:193-204. 1960.

17. GATERUM, G. E., McCOMB, A. L. and LOOMIS, W. E. Effects of light and soil moisture on forest tree seedling establishment. Iowa. Agricultural Experimental Station. Research Bulletin No 573. 1963. pp. 776-792.

18. GOLLEY, F. B. Gross and net primary production and growth parameters. In Tropical Forest Ecosystems; a state of knowledge. Paris, UNESCO/UNEP/FAO, Paris, 1978. pp. 233-248.

19. HALLE, F., OLDENAN, R. A. A. and TOMLINSON, P. B. Tropical trees and forests: an architectural analysis. Heindelberg, Springer, 1978. 441 p.

20. HARTSHORN, G. S. Tree falls and tropical forest dynamics. In Cabot Symposium, Tropical Trees as Living Systems, 4th., 1978. Cambridge, University Press, 1978. pp. 617-638.

21. HERRERA, R. Soil and terrain conditions in the San Carlos project study site: correlation with vegetation types. MitteiC. d. Bundesforsch. anst. f. Forst-u. Holzwirtsch (at press).

22. HEUVELDOP, J. Die amazonische Caatinga bei San Carlos de Rio Negro, Süd-Venezuela: Relative Beleuchtungsstärken im Bestand. Forstarchiv 48(8):148-154. 1977.

23. HEUVELDOP, J. Das Bioklima von San Carlos de Rio Negro, Venezuela. (Submitted to Amazoniana).

24. HUGHES, A. P. The importance of light compared with other factos affecting plant growth. In Light as an ecological factor. Oxford, Blackwell Scient. Publ., 1966. pp. 121-146.

25. JORDAN, C. and UHL, C. Biomass of a "tierra firme" forest of the Amazon basin calculated by a refined allometric relationship. Oecolgia Plantarum 13(4):387-400. 1973

26. KLINGE, H., MEDINA, E. and HERRERA, A. R. Studies on the ecology of Amazon Caatinga forest in the southern Venezuela. I. General features. Acta Científica Venezuela 28:270-276. 1977.

27. KLINGE, H. and HERRERA, R. Biomass studies in Amazon Caatinga forest in southern Venezuela. 1. Standing crop of composite root mass in selected stands. Tropical Ecology 19(1):93-110. 1978.

28. KLINGE, H. Studies on the ecology of the Amazon Caatinga forest in southern Venezuela. 2. Biomass dominance of selected tree species in the Amazon Caatinga near San Carlos de Rio Negro. Acta Científica Venezolana. 29:258-262. 1978.

29. LIETH, H. Basis und Grenzen für die Menschheitsentwicklung: Stoffproduktion der

Pflanzen. Umschau Wiss. Techn. 74(6): 169-174. 1974.

30. LOACH, K. Shade tolerance in tree seedlings. New Phytologist 66:607-621. 1967.

31. LOETSCH, F., ZOHRER, F. and HALLER, K. E. Forest inventory. Munchen-Bern-Wien, BLV Verlagsgesellsch, 1973. Vol. 2, 469 p.

32. LONGMAN, K. A. and JENIK, J. Tropical forest and its enviroment. London, Longman, 1974. 196 p.

33. McINTOSH, R. P. An index of diversity and the relation of certain concepts to diversity. Ecology 48:392-404. 1967.

34. MEDINA, E. *et al.* The Amazon project of the Venezuelan Institute for Scientific Research. Nature and Resources 13(3):4-6. 1977.

35. MURPHY, P. and UHL, C. Composition, structure, and regeneration of a tierra firme forest of the Amazon basin of Venezuela. In Annual Report on the study of nutrient dynamics of a tropical rainforest ecosystem and changes in the nutrient cycle due to cutting and burning. Athens, Univ. of Georgia, 1979.

36. RICHARDS, P. W. The tropical rain forest; an ecological study. Cambridge, University Press, 1976. 450 p.

37. SORENSON, T. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Det. Kong. Danske Vidensk. Seisk. Biol. Skr. 5(4):34. 1948.

38. SYNNOTT, T. J. A manual of permanent plot procedures for tropical rainforest. Oxford, Commonwealth Forestry Institute. Tropical Forestry Papers No. 14. 1979. 67 p.

39. WHITMORE, T. C. Tropical rainforest of the Far East. Oxford, Clarendon Press, 1975. 282 p.

41. WHITOMORE, T. C. Modes of variation in the composition of Tropical Lowland Evergreen Forest in the Southeast Asian archipielago and their correlation with the environment. Mitt. Bundesforsch. anst Forest-Holzwirtschaft 115:130-152. 1977.

41. WITTAKER, R. H. Communities and ecosystems. London, Macmillan, 1970. 162 p.