

THE VEGETATION OF A SEASONAL VÁRZEA FOREST IN THE LOWER SOLIMÕES RIVER, BRAZILIAN AMAZONIA.

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ABSTRACT — The species composition of the seasonal várzea forest growing on a bank of the Ilha de Marchantaria / lower Solimões-Amazonas River, Brazil was studied in an area of slightly less than one hectare. Two biomass plots were harvested. Forty-seven arboreal species representing 46 genera in 25 families were recorded. Tree density was 1086 per hectare. Total basal area was 45 m² ha⁻¹. Mean species density was 6.5 ± 1.98 per 100 m². The most abundant species were *Crataeva benthamii* (Capparidaceae), *Laetia corymbulosa* (Flacourtiaceae) and *Vitex cymosa* (Verbenaceae). The highest basal area per species was 10.2 m² for *Pseudobombax munguba* (Bombacaceae). The common species are known to be typical floristic elements of the seasonal varzea forest. Above ground dry biomass was equal to 97 and 255 t ha⁻¹, respectively. Its chemical composition is characterized by comparatively high bioelement contents equal to 2.4 percent on the average. Calcium was the most important bioelement. Structure of the forest and age datings of trees allow the successional classification of the stands.

Key words: Amazon, bioelements, biomass, floodplain, seasonal varzea forest, species composition, structure

A Vegetação de uma Floresta Sazonal de Várzea no Baixo Rio Solimões, Região Amazônica Brasileira.

RESUMO — Estudou-se numa área de pouco menos de um hectare, a composição de espécies de uma floresta sazonal de várzea, a qual cresce numa elevação da Ilha de Marchantaria / baixo rio Solimões-Amazonas. Fez-se colheita de duas parcelas de biomassa. Registrou-se 47 espécies arbóreas, representando 46 gêneros em 25 famílias. A densidade arbórea foi de 1086 por hectare. A área basal total foi de 45 m² ha⁻¹. A densidade média de espécies foi de 6,5 ± 1,38 por 100 m². As espécies mais abundantes e frequentes foram *Crataeva benthamii* (Capparidaceae), *Laetia corymbulosa* (Flacourtiaceae) e *Vitex cymosa* (Verbenaceae). A maior área basal por espécie foi de 10,2 m² para *Pseudobombax munguba* (Bombacaceae). As espécies comuns são conhecidas como elementos florísticos típicos da floresta sazonal de várzea. A biomassa acima do chão foi de 97 e 255 t ha⁻¹, respectivamente. A composição química é caracterizada por um conteúdo de bioelementos relativamente alto, igual a 2,4% na média. Cálcio foi o bioelemento mais importante. A estrutura da floresta e a datação da idade das árvores permite a classificação sucessional das formações arbóreas.

Palavras-chaves: Amazônia, bioelementos, biomassa, várzea, floresta sazonal de várzea, composição de espécies, estrutura

INTRODUCTION

Amazonian floodplain forests were first classified by PRANCE (1979, 1989) as seasonal várzea (whitewater) and seasonal igapó (black- and clearwater) forests based on the water quality of the flooding rivers. A bioelement study of foliage,

bark and wood from a variety of arboreal species sampled in both, seasonal várzea and seasonal igapó forests (KLINGE *et al.*, 1983; 1984; KLINGE, 1986; KLINGE & FURCH, 1991), yielded biogeochemical arguments which supported that classification. (For water and soil chemistry see K. FURCH *et al.*, 1983).

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The second important characteristic of seasonal várzea and igapó forests is the monomodal flood pulse (PRANCE, 1979; JUNK *et al.*, 1989; KLINGE *et al.*, 1990) which, due to its intensity, effects a distinct seasonality along the Amazon and its main tributaries. This becomes visible as many tree species of the várzea floodplain shed their leaves during the submersion phase (WORBES, 1983) and form annual rings in the wood (WORBES, 1985; 1986; WORBES & JUNK, 1989).

According to both the importance and the rapid development of the Amazonian várzea, the Tropical Working Group of the Max-Planck-Institute for Limnology at Plön in cooperation with the National Institute for Amazonian Research (INPA), Manaus, increased their research activities in the last ten years and focussed on a seasonal várzea forest at Ilha de Marchantaria. Forest related investigations were carried out on morphology and chlorophyll content of tree leaves (B. FURCH, 1984), root respiration (SCHLÜTER, 1989), mycorrhiza of trees (MEYER, 1991), wood decomposition (MARTIUS, 1989), and litter fall (KLINGE *et al.*, unpubl.).

This basic investigation on structure and species composition of some floristically different forest stands was carried out to complete the picture of the seasonal várzea forest ecosystem.

Study Area

The present study describes the species composition of a seasonal várzea forest, growing on the southern-

most bank of Ilha de Marchantaria. The forest of the embankment measures, at most, 35 m in width. In the south, the bank is delimited by Lago Camaleão. The large island is situated in the lower Solimões River, approximately 15 km above its confluence with the Negro River (3°15'S, 58°58'W). The island consists of river-born sediments of the Solimões River (IRION *et al.*, 1983).

MATERIAL AND METHODS

A line was run in October 1982 from the eastern point of Ilha de Marchantaria to the west on the highest part of the embankment, over a distance of 1882 m. Trees and climbers growing up to two meters on either side of the line were mapped, enumerated and identified to species level. L. Coelho, an experienced tree spotter of INPA, identified most species in the field. Unidentifiable plants were checked in INPA's herbarium. The circumference of all living trees and woody climbers was recorded on an area of 7528 m². 75 subplots of 4 x 25 m size were established. The plot No. 76 measured only 4 x 7 m in area, since after 7 m the line touched the forest plot established by J. Adis. In his rectangular plot, 1500 m² in area and named plot A, he surveyed the forest vegetation in fifteen 10 x 10 m subplots in the same manner as we did in the line transect. Top height of smaller trees in plot A was estimated using a pole of known length. Top height of taller trees was estimated by aid of gas-filled balloons, tied to a previously marked string of 30 m length.

In all cases, the lower dbh-limit was established at 5 cm, since during reconnaissance work it was found to be almost completely lacking in smaller trees.

Family Importance Values (FIV) (MORI *et al.*, 1983) and relative Species Importance Values (SIV; equal to the sum of relative abundance, relative frequency and relative basal area) were computed. Dry weight of biomass samples was estimated and chemical analyses were carried out as described in KLINGE *et al.* (1983).

Two biomass plots, which were each 96 m² and separated by meters, were established near to the eastern starting point outside of the transect.

RESULTS

Floristic composition

Plant families

Twenty-five plant families were recorded in the study area (Tab. 1). Leguminosae *sensu lato* (including Mimosaceae, Caesalpinaceae, and Fabaceae) was richest in species. Six of the leguminous species belonged to the Caesalpinaceae and three each to the Fabaceae and Mimosaceae. The Annonaceae, Euphorbiaceae, Flacourtiaceae and Moraceae *sensu lato* (including Cecropiaceae) were also represented by three species per family. Seven families were represented by two species per family, and 13 families by a single species each.

The Leguminosae *sensu lato* ranked highest, according to their Family Importance Values (FIV) equal to 45

(cf. MORI *et al.*, 1983). They were followed (in decreasing order of FIV, see Tab. 1) by the Cappariaceae, Flacourtiaceae, Bombacaceae, Verbenaceae, Moraceae *sensu lato*, Lauraceae, Tiliaceae, and Euphorbiaceae. The remaining 16 families had low Family Importance Values which varied between 2 and 8.

Comparing the floristic composition of the forest in plot A with the transect, it was observed that eleven families (Tab. 1) were recorded exclusively in the transect and two families exclusively in plot A.

Plant species

Forty-seven woody plant species representing 46 genera were recorded in the study area (Tab. 2; Fig. 1). The total number of living trees was 980 (1086 per ha). Species Importance Values of *Crataeva benthamii* and *Laetia corymbulosa* were particularly high. These two species were both very abundant and very frequent. *Pseudobombax munguba* had the highest basal area (10.2 m²) of all species. Each of the last eight species in Table 2 was represented by a single individual.

The average species density of plot A was 1.1 species per 100 m². Species density in the transect varied between 2 and 10 species per 100 m². The mean species density was 6.46 ± 1.985 species per 100 m² (N = 76). Species number per 100 stems is 4.8 in the transect and 14.8 in plot A.

Palms (Arecaceae) contributed insignificantly to the composition of the seasonal várzea forest under study. There were two species represented by

Table 1. Plant families of the study area (9028 m²) in the Plot A (ADIS, unpubl.) in a seasonal várzea forest, Ilha de Marchantaria.

Plant family	Number of species	Relative tree density	Relative basal area	FIV
Caesalpiniaceae	6	4.19	6.51	22.46
x Fabaceae	3	5.92	216	13.96
Mimosaceae	3	1.46	1.00	8.34
Leguminosae sensu lato	12	11.57	9.67	44.76
Flacourtiaceae		19.23	9.35	34.46
Moraceae sensu lato ¹⁾		6.11	5.58	17.57
Euphorbiaceae	1 3 each	6.75	1.13	13.76
Annonaceae		1.64	0.70	8.22
Subtotal 1	12	41.11	19.92	96.31
Lauraceae		2.55	9.74	16.21
Polygonaceae		0.82	3.29	8.03
x Lecythidaceae		1.55	0.26	5.73
Myrtaceae	2 each	1.37	0.14	5.43
Bignoniaceae		0.91	0.46	5.29
Areaceae		0.82	0.41	5.15
x Sapotaceae		0.64	0.19	4.75
Subtotal 1	14	8.66	14.49	50.59
Capparidaceae		25.52	8.95	36.43
Bombacaceae		3.37	25.57	27.90
Verbenaceae		8.57	8.20	18.73
x Tiliaceae		2.64	11.13	15.73
x Boraginaceae		1.73	4.22	7.91
x Polygalaceae		2.00	0.26	4.22
x Apocynaceae	1 each	1.28	0.10	3.34
xx Aquifoliaceae		0.36	0.31	2.69
x Araliaceae		0.09	0.24	2.29
x Sterculiaceae		0.18	0.01	2.15
x Guttiferae		0.09	0.07	2.12
x Sapindaceae		0.09	0.01	2.06
xx Simaroubaceae		0.09	0.01	2.06
Subtotal	13	46.01	59.08	127.63
Total	51	99.97	100.00	296.99

1) including the Cecropiaceae

x observed exclusively in the transect

xx observed exclusively in plot A

Table 2. Species composition in 9028 m² of a seasonal várzea forest, Ilha de Marchantaria, Solimões River. Number of subplots in which species occurred (No. S.P.), number of individuals with dbh 5 cm or more (No. Tr.), basal area (B.A.) and relative species Importance Values Index (SIV). SIV is calculated for trees and shrubs only.

Species	No. S. P.	NO. Tr.	B. A. (m ²)	SIV
<i>Crataeva bentharii</i> Eichl. in Mart.	76	268	4.37	54.41
<i>Laetia corymbulosa</i> Spruce ex Benth.	67	152	3.48	38.47
<i>Pseudobombax munguba</i> (Mart. & Zucc.) Dugand	18	36	10.17	32.59
<i>Vitex cymosa</i> Bert. ex Spreng.	40	84	3.13	24.86
<i>Luehea</i> sp.	24	29	4.64	19.53
<i>Cecropia latiloba</i> Miq.	23	55	2.19	15.95
<i>Nectandra amazonum</i> Nees	19	27	3.52	15.51
<i>Macrolobium acaciifolium</i> Benth.	21	38	2.40	14.29
<i>Pterocarpus amazonum</i> (M. ex Benth.) Amsh.	24	56	0.79	12.81
<i>Alchornea discolor</i> Endl. & Poepp.	21	61	0.40	11.71
<i>Casearia aculeata</i> Jacq.	29	39	0.17	10.63
<i>Cordia</i> sp.	10	19	1.76	8.41
<i>Triplaris surinamensis</i> Cham.	7	7	1.24	5.27
<i>Pseudoxandra leiophylla</i> (Diels) R. E. Fries	10	13	0.24	4.07
<i>Tabernaemontana</i> sp.	10	13	0.03	3.55
<i>Pithecellobium jupunba</i> (Willd.) Urb.	6	8	0.27	2.76
<i>Eugenia</i> sp.	8	8	0.05	2.64
<i>Annona</i> sp.	4	4	0.42	2.29
<i>Crescentia amazonica</i> Ducke	4	7	0.08	1.77
<i>Piranhea trifoliata</i> Baill.	5	5	0.07	1.74
<i>Gustavia augusta</i> L.	3	6	0.07	1.44
<i>Bactris</i> sp.	4	5	0.01	1.41
<i>Astrocaryum jauary</i> Mart.	3	3	0.15	1.33
<i>Tabebuia barbata</i> (E. Mey.) Sandw.	3	3	0.11	1.23
<i>Neolabatia cuprea</i> (Huber) W. A. Rodr. & J. M. Pires	3	4	0.04	1.15
<i>Chlorophora tinctoria</i> (L.) Gaudich	3	3	0.07	1.12
<i>Copaifera</i> sp.	2	3	0.11	1.01
<i>Ilex inundata</i> Poepp. ex Reiss.	1	4	0.13	0.94
<i>Cassia leiandra</i> Benth.	2	2	0.07	0.81
<i>Labatia glomerata</i> (Pohl ex Miq.) Radlk.	2	2	0.02	0.68
<i>Byttneria</i> sp.	2	2	0.01	0.64
<i>Schefflera</i> sp.	1	1	0.10	0.57
<i>Crudia amazonica</i> Spruce ex Benth.	1	1	0.07	0.50
<i>Alchornea castaneifolia</i> (Willd.) Juss.	1	2	0.01	0.45
<i>Psidium acutangulum</i> A. DC.	1	2	0.01	0.43
<i>Inga</i> sp.	1	1	0.04	0.42
<i>Sorocea duckei</i> W. Burger	1	1	0.04	0.41
<i>Tachigalia</i> sp.	1	1	0.03	0.40
<i>Calophyllum brasiliense</i> Camb.	1	1	0.03	0.39
<i>Acosmium</i> sp.	1	1	0.03	0.39
<i>Homalium</i> sp.	1	1	0.01	0.33
<i>Simaba guianensis</i> Aubl.	1	1	0.01	0.33
<i>Licania armenica</i> (Nees) Kosterm.	1	1	0.01	0.33

Lianas:

Polygalaceae 1
Machearium sp.
Dalbergia sp.
Paullinia sp.

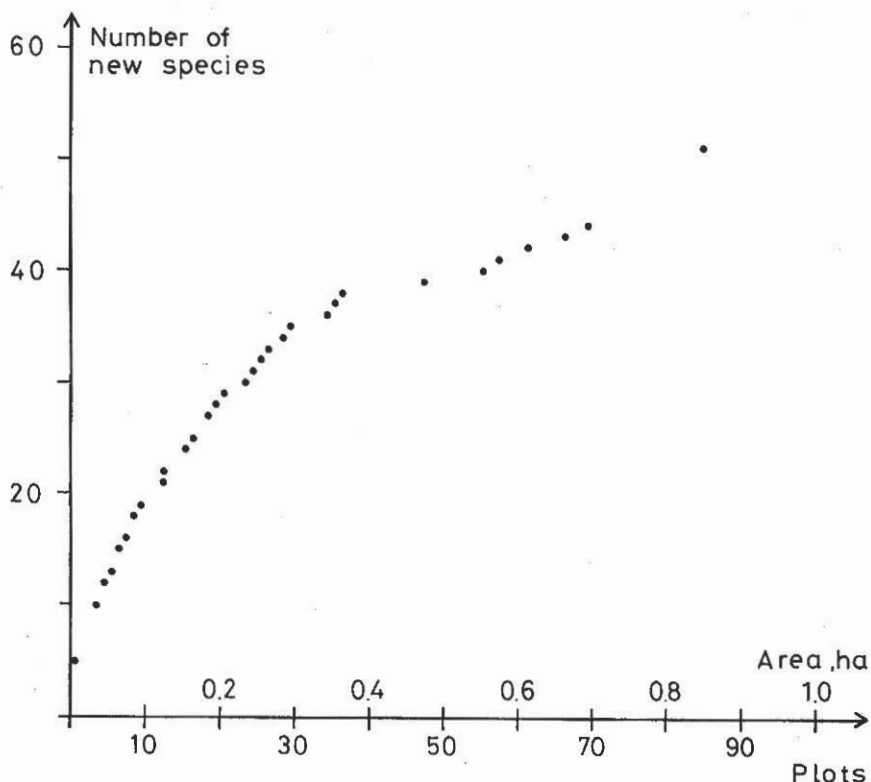


Figure 1. Number of additional species found by adding an additional 100 m² quadrat to the sample size, seasonal várzea forest, Ilha de Marchantaria.

less than 1 percent of the individuals. Woody climbers were represented by four species. Climbers were conspicuous at the forest floor, as they occasionally formed dense tangles, which were not supported by a tree. Epiphytes in the canopy/trunk area were rare and mostly represented by Orchidaceae.

Forest structure

Diameter at breast height and top height of trees

Maximum diameter at breast height (dbh) was 103.8 cm for a *Pseudobombax munguba* tree growing

in the transect. Other species represented by big trees were *Luehea* sp., *Nectandra amazonum*, *Cordia* sp., *Triplaris surinamensis*, and *Macrolobium acaciifolium*.

The distribution of the dbh size classes illustrated a typical J-shaped curve (Fig. 2), as shown for various other tropical forests (CAMPBELL *et al.*, 1986; LAMPRECHT, 1986)

Basal area varied between 8 and 131 m² ha⁻¹ in the 76 plots of the transect and was 65 m² ha⁻¹ in plot A. The value of the study area was 45 m² ha⁻¹. The basal area of Amazonian forests rarely surpasses 40 m² per ha (PIRES, 1984). LAMPRECHT (1972)

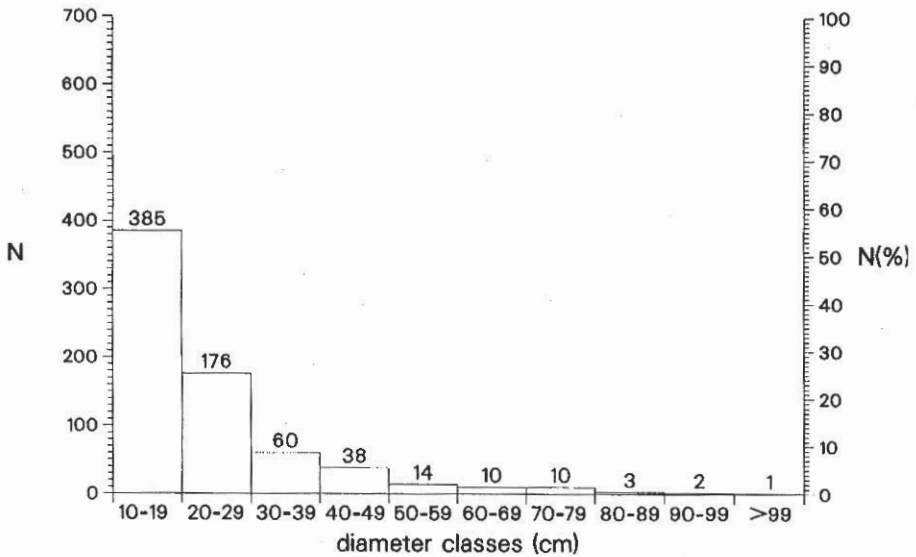


Figure 2. dbh-class distribution of 699 trees (dbh > 10 cm) sampled in the study area of a seasonal várzea forest, Ilha de Marchantaria.

reported basal area values between 40 and 60 m² per ha for mountain forests of South America.

Measurements of top height of trees existed for 385 trees from plots A and W (the latter established in the central part of the island by WORBES, 1983), and the two biomass plots. This casual selection of the total sample represented some 39 species. Species represented by at least nine individuals for which top height and dbh data were available, are depicted in Figure 3.

Maximum top height of trees was 28 m. In plot W this height was reached by several *Pseudobombax munguba* trees, forming the canopy roof (Tab. 3). Tallest *P. munguba* in plot A, also forming the canopy roof, reached only 25 m in height. *P. munguba* is a light demanding species, which does not regenerate in a closed forest. This is deduced from the obser-

vation that there was no representative below 14 m in height and smaller than 15 cm in dbh (see Fig. 3). Single individuals of *Pterocarpus amazonum* and *Crataeva benthamii* reached top heights of about 25 m.

C. benthamii was, however, mostly represented by considerably lower trees. There were relatively few species (like *Casearia aculeata* or *Tabernaemontana* sp.), which as single trees occurred only below 5 m in height. The majority of the species forming the main canopy was intermediate in height (Tab. 3). *Crataeva benthamii* and *Laetia corymbulosa* mostly composed the lower canopy. *Luehea* sp., *Macrolobium acaciifolium*, *Nectandra amazonum*, and *Pterocarpus amazonum* represented the upper canopy.

Cecropia latiloba presented a special case. Usually it formed pure stands or was dominant, as in biomass

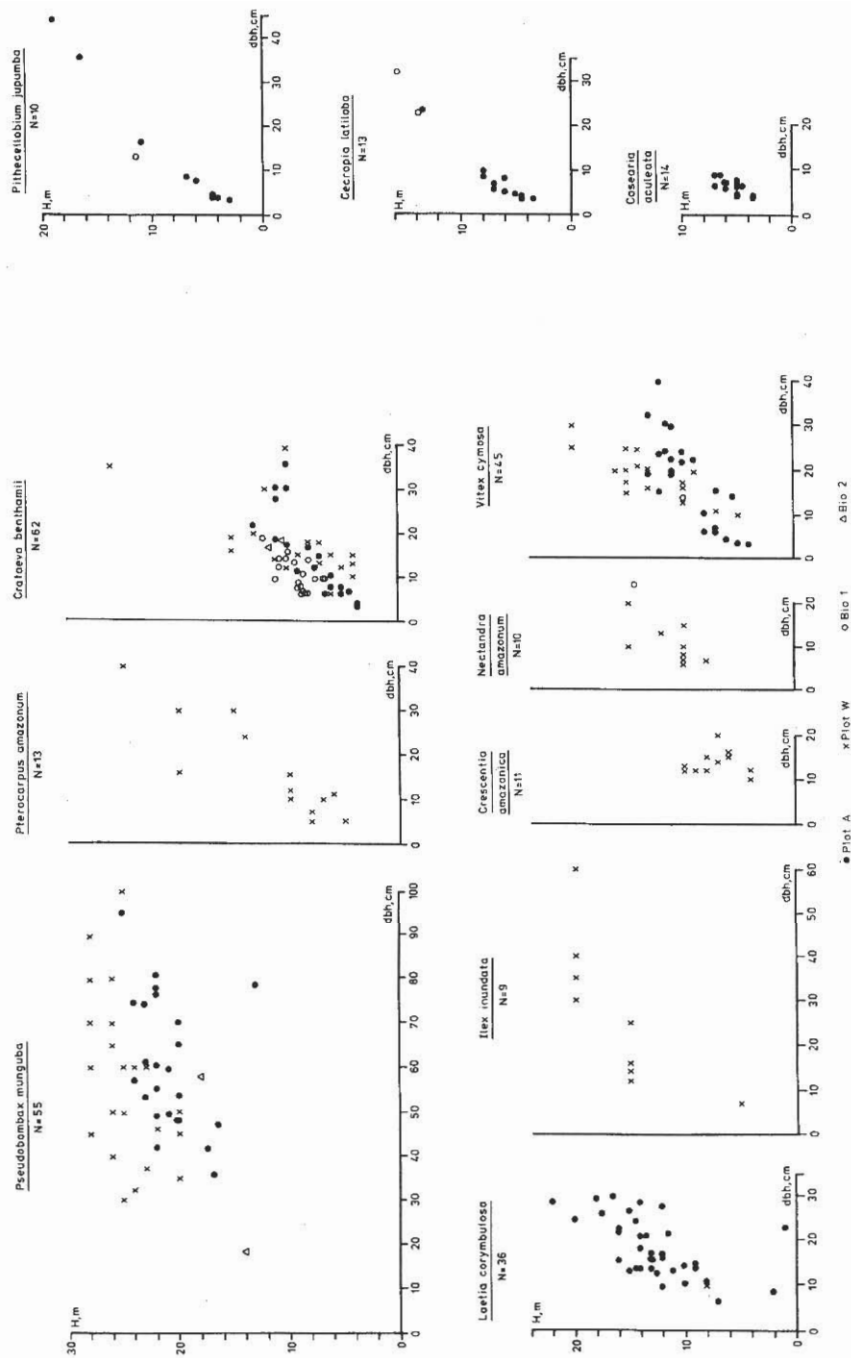


Figure 3. Tree height of eleven species sampled on Ilha de Marchantaria, plotted against their dbh.

plot 1. Occasionally this species was represented by isolated and relatively small trees under the closed canopy of the forest. More often, it occurred in groups outside the forest or at the forest fringe, where the ground was not covered by grasses.

There was a simple structured stand dominated by *Cecropia latiloba* forming the canopy roof at a height of 15 m, under which a dense vegetation composed almost exclusively by *Crataeva benthamii* had developed (biomass plot 1, Tab. 4). Biomass plot 2 represented a stand type from which *Cecropia latiloba* was absent. The canopy roof was encountered at about 20 m height (Tab. 5). Although less dense, the stand was richer in species. The lower canopy was composed exclusively by *Crataeva benthamii*.

Plot W represented a stand clearly dominated by *Pseudobombax munguba*. This species formed the canopy roof at a height of 28 m (WORBES, 1986). The vertical sections beneath this canopy were dominated by different species (*Laetia corymbulosa* the section 15-20 m above ground, *Vitex cymosa* the section 10-15 m above ground, and casually *Crataeva benthamii* the two sections).

The space in the three stands from ground level to 3 m above ground was free of tree crowns as it was in the forest, except for the few low growing species like *Tabernaemontana* sp. and *Casearia aculeata*.

Above ground biomass and bole volume

Species contribution to above ground biomass and bole volume of two small plots is given in Tables 4 and 5. The

taller stand (biomass plot 2) with fewer but bigger trees had a basal area of 95.7 m² ha⁻¹, which was 2.5 times greater than in the other plot. Its above ground biomass of 257.6 t ha⁻¹ was 2.4 times larger. Its bole volume was 4.35 times larger.

In biomass plot 1, the upper canopy was composed exclusively of *Cecropia latiloba*. While contributing about one third to both basal area and above ground biomass, this species contributed about 50 per cent to the total bole volume. *Crataeva benthamii* dominated the lower canopy, contributing about two thirds to both basal area and above ground biomass, and about 50 per cent to the total bole volume. *Vitex cymosa* and *Copaifera* sp. contributed insignificantly to the totals of the stand.

East of this plot a pure stand of *Cecropia latiloba* occurred.

In biomass plot 2 *Luehea* sp. and *Pseudobombax munguba*, which composed the upper canopy, together contributed about three quarters to the basal area, the above ground biomass and the bole volume. *Crataeva benthamii*, a member of the lower canopy, contributed comparatively more to the total stand than the other four species.

The vegetation of plots A and W, which was dominated by big trees of *Pseudobombax munguba*, had a bole volume of 554 and 696 m³ ha⁻¹, respectively.

Bioelements of the above ground biomass

The average bioelement content of the dry above ground biomass of both biomass plots is given in Table 6.

The bioelement contents of both plots differed slightly, due to their different species composition. Calcium

Table 3. Vertical classification of tree species in biomass plots 1 and 2, Plot A and in Plot W in the central part of the island (cf. WORBES, 1983).

< 10m	10-20m	20-25m	> 25m
Alchornea castaneifolia (Willd.) Juss.	Annona sp. I	Eschweilera sp.	Pseudobombax munguba (Mart. & Zucc.) Dugand
Casearia aculeata Jacq.	Annona sp. II	Labatia glomerata (Pohl ex Miq.) Radlk.	
Copaifera sp.	Casearia aculeata Jacq.	Laeia corymbulosa Spruce ex Benth.	
Crescentia amazonica Ducke	Cecropia latiloba Miq.	Luehea sp.	
Gustavia augusta L.	Crataeva bentharii Eichl. in Mart.	Piranhea trifoliata Baill.	
Mollia sp.	Elaeoluma glabrescens (Mart. & Eichl. ex Miq.) Aubr.	Pterocarpus amazonum (M. ex Benth.) Amsh.	
Pithecellobium inaequale (H.B.K.) Benth.	Ilex inundata Poepp. ex Reiss.	Swartzia sp.	
Pseudoxandra polyphleba R.E. Fries	Luehea sp.	Triplaris surinamensis Cham.	
Psidium acutangulum A. DC.	Macrobium acacifolium Benth.		
Simaba guianensis Aubl.	Matayba macrolepis Radlk.		
Tabebuia barbata (E. Mey.) Sandw.	Mouriri guianensis DC.		
Tabernaemontana sp.	Nectandra amazonum Ness.		
Trichilia singularis C. DC.	Pithecellobium jupunba (Willd.) Urb.		
Zanthoxylum compactum (Huber ex Abuq.) Waterm.	Rourea sp.		
	Sorocea duckei W. Burger		
	Vitex cymosa Bert. ex Spreng.		

was the most abundant bioelement. Potassium followed next. Nitrogen ranked third and magnesium fourth. The least abundant bioelement was phosphorus. Among the alkali- and alkali-earth metals calcium was dominant, followed by potassium. The nitrogen/ phosphorus ratio was below 20:1.

DISCUSSION

According to the classification of Amazonian inundation forests (PRANCE, 1979; 1989; KLINGE & FURCH, 1991), the forest under study is easily identified as seasonal várzea forest. The annual flooding by the whitewater of the Solimões-Amazon River has two major consequences which differentiate this biotope from a non-flooded Amazonian "terra firme" forest:

1) The monomodal flood pulse (JUNK *et al.*, 1989) causes, in a distinct seasonality, an annual change between favorable and poor growth conditions for the tree vegetation. Tree species settling in the floodplains require the ability to adapt to prolonged inundations (cf. JUNK, 1989);

2) The flooding by the nutrient rich whitewater (FURCH *et al.*, 1983) and the annual sedimentation result in a comparable high soil fertility (WORBES, 1986) and a high bioelement content in all compartments of the trees (Tab. 6). The bioelement content of the várzea vegetation exceeds those from the Amazonian terra firme considerably and reaches values of tree stands in Panama (KLINGE, 1976).

Differences between terra firme and floodplain forests are visible in species composition and appearance of dominant families. In the Amazonian terra firme forest the leading families are Bombacaceae, Burseraceae, Chrysobalanaceae, Lauraceae, Lecythidaceae, Leguminosae *sensu lato*, Moraceae, Sapotaceae, and Vochysiaceae (BALSLEV *et al.*, 1986; KLINGE *et al.*, 1975; PRANCE *et al.*, 1976). Myrtaceae is the dominant family of the Bahian terra firme forest (MORI *et al.*, 1983). Of the mentioned families, the Burseraceae, Chrysobalanaceae and Vochysiaceae apparently play no major role in the seasonal várzea forest of the lower Solimões River. Arecaceae are mentioned as dominant in both the tidal várzea forest and the floodplain forest. The abundance of palms in tidal várzea forest has been stressed by HUECK (1966), PIRES (1976) and PIRES & PRANCE (1985). In the seasonal várzea under study, forest palms are an insignificant floristic element. Among the leading families of this forest type are the Capparidaceae and Flacourtiaceae, families little represented in Amazonian terra firme forest.

According to DUCKE & BLACK (1954), HUECK (1966), GESSNER (1968), BRAGA (1979), PRANCE (1979, 1989), and PIRES & PRANCE (1985) typical floristic elements of the seasonal várzea forest are, among others, *Pseudobombax munguba*, *Vitex cymosa*, *Piranhea trifoliata*, *Crescentia amazonica*, *Nectandra amazonum*, *Gustavia augusta*, and *Crataeva benthamii*. All

Table 4. Species contribution to above ground biomass, bole volume and basal area of a seasonal várzea forest (biomass plot 1), Ilha de Marchantaria.

Height class, m	Species	Above ground biomass.		% of totals per ha					
		(dry matter), t ha ⁻¹	97.52	Foliage	Branch	Biomass	Bole	Above ground	Bole volume
		Bole volume, m ³ ha ⁻¹	201.4	0.56	9.73	15.95	26.24	46.54	33.91
		Basal area, m ² ha ⁻¹	38.25	2.86	38.60	26.26	67.72	48.24	60.11
		Leaf area, m ² m ⁻²	4.2	0.22	1.29	2.11	3.62	3.83	4.01
				0.06	0.94	1.41	2.41	1.40	1.97
10-15	<i>Cecropia latiloba</i>			3.14	40.83	29.78	73.75	53.47	66.09
3-10	<i>Crataeva benthameii</i>			3.70	50.56	45.73	99.99	100.01	100.00
	<i>Vitex cymosa</i>								
	<i>Copaifera</i> sp.								
	Subtotal								
	Total								

Table 5. Species contribution to above ground biomass, bole volume and basal area of a seasonal várzea forest (biomass plot 2), Ilha de Marchantania.

Above ground biomass. (dry matter), t ha ⁻¹	Bole volume, m ³ ha ⁻¹	Basal area, m ² ha ⁻¹	Leaf area, m ² m ⁻²	Height class, m	Species	Biomass			% of totals per ha		
						Foliage	Branch	Bole	Above ground	Bole volume	Basal area
257.6	876.8	95.7	3.3	15-20	Luehea sp.	0.21	25.76	26.24	52.21	54.82	47.83
					Pseudobombax munguba	0.09	6.34	9.57	16.00	29.40	28.36
					Polygalaceae (climber)	0.08	1.23	0.84	2.15	n.d.	0.55
					Subtotal	0.38	33.33	36.65	70.36	84.22	76.74
				10-15	Nectandra amazonum	0.11	6.87	2.55	9.53	4.06	5.13
					Annona sp.	0.27	3.87	0.72	4.86	2.17	3.32
					Maclobium acaciifolium	0.11	0.35	3.10	3.56	2.04	2.44
					Pithecellobium jupunba	0.07	0.55	1.43	2.05	0.96	1.53
					Pseudobombax munguba	0	0.16	1.19	1.35	2.14	2.80
					Subtotal	0.56	11.80	8.99	21.35	11.37	15.22
				3-10	Crataeva bentharii	0.22	5.00	3.08	8.30	4.39	8.03
					Total	1.16	50.13	48.72	100.01	99.98	99.99

these species have been recorded in our study area.

Species which were recorded on the terra firme (CAMPBELL *et al.*, 1986) and in the present study are *Gustavia augusta* and *Piranhea trifoliata*. However, studies on terra firme and adjacent floodplain forests in the Amazon region show concurrences of 18% (BALSLEV *et al.*, 1986) and 45% (CAMPBELL *et al.*, 1986) on species level.

The effects of flood pulse and soil fertility may explain the comparable low species diversity of the várzea floodplain (BONGERS *et al.*, 1988). Not more than 250-300 tree species are presently recorded from the region of the lower Solimões River (KLINGE *et al.*, 1983; REVILLA, 1991; WORBES, 1983; this study). This number of species can be found in one hectare or less on the terra firme. In terms of species per 100 stems, the investigated transect shows the lowest figure of 12 studies from Amazonian forests (Tab. 7).

Whereas diversity and density values range at the lower limits of pantropical means for lowland rain forests, basal area, however, is comparably high (BONGERS *et al.*, 1988).

Distribution by dbh for trees > 10 cm dbh of all plots did not differ considerably from results in other tropical forests. Often observed is a distribution of more than 60% trees with dbh 10-20 cm, about 20% with dbh 20-30 cm, 10% with dbh 30-40 cm and low percentages of the remaining diameter classes (CAMPBELL *et al.*, 1986, LAMPRECHT, 1986).

Interesting differences offer the addition of trees below 10 cm dbh and the splitting into 5 by 5 cm classes (Fig. 4). This shows a development from plots with a high percentage of low diameter classes to a relatively homogeneous distribution in the order of biomass plot 1, biomass plot 2, the transect, Plot A and Plot W. In the same order, an increase of the above ground biomass is observed: 97.5 t ha⁻¹ in biomass plot 1, 257.6 t ha⁻¹ in biomass plot 2, MARTIUS (1989) calculated a mean figure of 260 t ha⁻¹ for a stand close to our forest and 107-402 t ha⁻¹ are calculated for different subplots of Plot W (WORBES, unpubl. data).

Age dating of trees from the different locations on Ilha de Marchantaria (WORBES, 1989) gives an age of less than 20 years for biomass plot 1, about 40 years for biomass plot 2, the transect and the MARTIUS (1989) stand, and about 80 years for Plot W. The increasing age of the different stands goes along with a decreasing accessibility from the banks of the island (biomass plots 1 and 2, transect) to the center (Plot W). Local inhabitants report jute was cultivated in the region of the transect forest during the early 40s, and the field was later abandoned. This alone explains the differences of the described trends in size class distribution, tree height, above ground biomass and diversity.

Structural analysis and age dating point out that the investigated stands are equal to young successional stages. According to the classification of BUDOWSKI (1961) biomass plot 1 represents an early secondary forest;

Table 6. Bioelements in dry above ground biomass of a seasonal várzea forest (biomass plot 1 and 2), Ilha de Marchantaria.

	Bio 1		Bio 2		Ratio Bio 2/Bio 1	
	kg ha ⁻¹	% of total	kg ha ⁻¹	% of total	kg ha ⁻¹	% of total
Biomass	97500		254600		2.61	
Nitrogen	387.1	18.46	1107.2	16.98	2.86	0.92
Phosphorus	31.5	1.50	67.1	1.03	2.13	0.69
Potassium	665.6	31.75	1806.2	27.70	2.71	0.87
Calcium	805.75	38.43	2988.2	45.98	3.71	1.20
Magnesium	163.0	7.77	341.7	5.24	2.10	0.67
Sodium	43.4	2.07	200.45	3.07	4.62	1.48
Total	2096.35	99.98	6520.85	100.0	3.11	1.19
Ca+Mg+K+Na	1677.75	80.03	5346.55	81.99	3.19	1.02
Ca %	48.03		56.08		1.17	
K %	39.67		33.78		0.85	
Mg %	9.71		6.39		0.66	
Na %	2.59		3.75		1.45	
N/P	12.29		16.50			

Table 7. Comparative structural data of selected Amazonian inundation and terra firme forests.

Forest type and locality	Plot size		dbh-limit, cm	Tree density, N per ha		Basal area, m ² ha ⁻¹	N species per plot	N species per 100 stems	leading plant family	N species % of Individuals	Arecaceae	Source
	m ²	ha		N	per 100 stems							
Seasonal várzea forest												
- Ilha de Marchantaria	2100 m ²		5	830	60	30	17.8	Bombacaceae	0		Worbes, 1983	
- Ilha de Marchantaria			5	1217	41	44	4.8	Leguminosae sensu lato	2	< 1	This study	
= Transect	7528 m ²		5	813	65	18	14.8	Bombacaceae	1	< 1	This study	
= Plot A	1500 m ²			1086	45	48	4.9	Leguminosae sensu lato	1		This study	
= Total study area	9028 m ²			325 - 1270	24 - 58	69 - 127	8.6 - 24.3		1		Revilla, 1991	
- Lower Solimões	1 ha		5						1	1		
											(15 replicates)	
Tidal várzea forest												
- Guama river/Pará	1 ha		5	539	n.d.	53	9.8	Arecaceae	4	54	Pires & Koury, 1959	
	3.8 ha		10	483	n.d.	107	5.8		7	32	Pires & Koury, 1959	
- Guama river/Pará	500 m ²		2)	5020	n.d.	53	21.1	Arecaceae	2	29	Aubréville, 1961	
- Ilha das Onças	2500 m ²		5	1376	40	51	12.9	Arecaceae	1	60	Anderson et al., 1985	
Floodplain forest												
- Napo river/Ecuador	1)		10	417	35	149	35.5	Arecaceae	5	30	Balslev et al., 1986	
Terra firme forest												
- Manaus	1 ha		8	735	n.d.	75	10	Lecythidaceae	3	2	Lechthaler, 1956	
- Manaus	27 ha		25	102	n.d.	431	15.6	Celastraceae			Rodrigues, 1967	
- Manaus	1 ha		15	358	n.d.	179	50	Lecythidaceae	1	< 1	Prance et al., 1976	
- Manaus	2000 m ²			1.5 m height	10220	37	24.6				Klinge et al., 1975	
- San Carlos de Rio Negro/Venezuela	1300 m ²		1	1361	32	130	8.8	Euphorbiaceae	2	< 1	Klinge & Herrera, 1983	

1) Point-centered quarter method 2) All plants sampled n.d. = no data

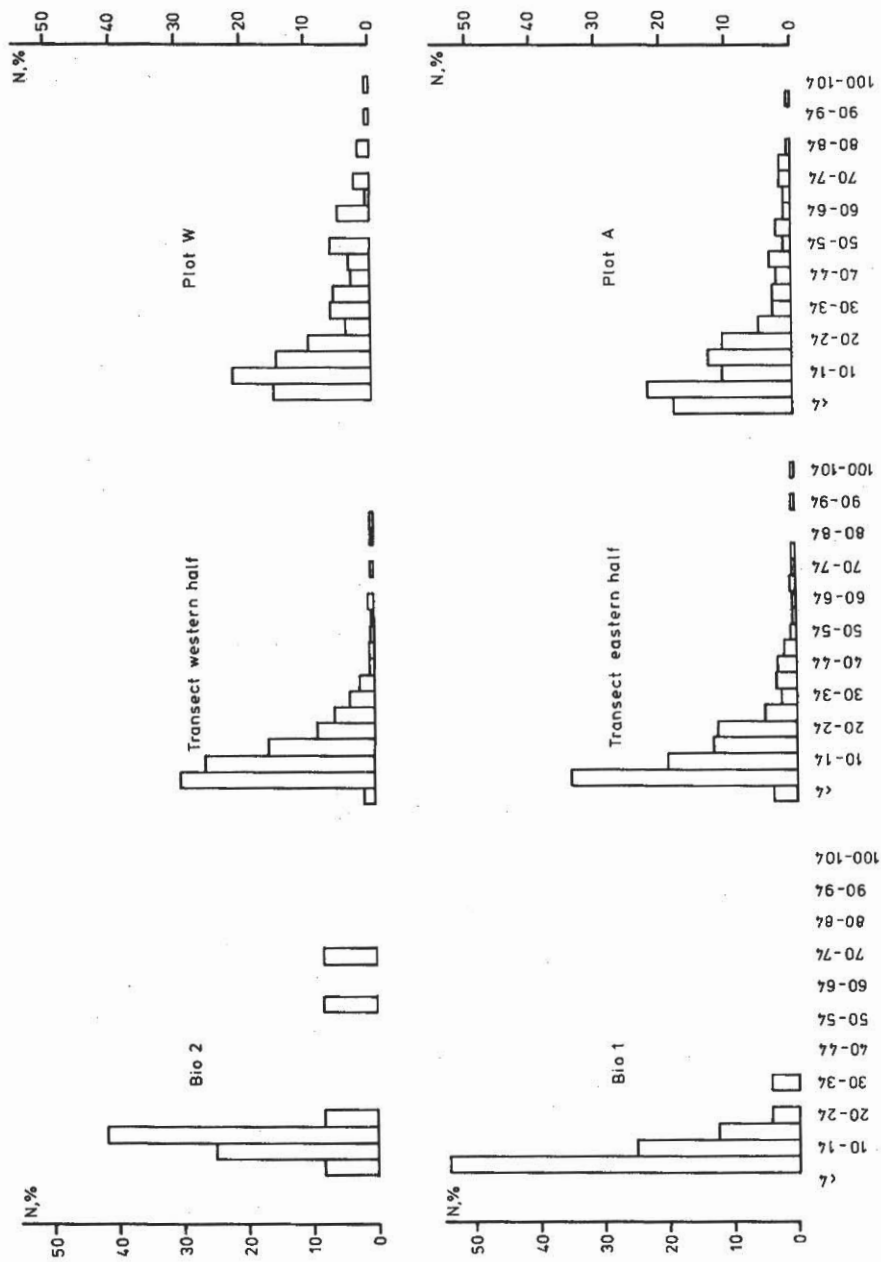


Figure 4. Relative tree density in 5 by 5 cm dbh-classes of the study area of a seasonal várzea forest, Ilha de Marchantaria.

the transect and Plot W are late secondary forests. The rapid development to a relatively high diversity and to a homogenous structure in Plot A and Plot W can be traced back to often observed dynamical mechanisms on fertile soils (MAAREL, 1988). The presented study should be seen on the background of a worldwide deforestation in the tropics, which requires an increase of knowledge about reforestation and dynamical processes in tropical forests.

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