AMAZONIANA	VIII	1	19 – 45	Kiel, September 1983

From cooperation between Max-Planck-Institute for Limnology, Working group "Tropical Ecology", Plön, West Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus–Amazonas, Brazil

Da cooperação entre Max-Planck-Institut für Limnologie, Arbeitsgruppe Tropenökologie, Plön, Alemanha Oc., e Instituto Nacional de Pesquisas da Amazônia, Manaus–Amazonas, Brasil

Foliar nutrient levels of native tree species from Central Amazonia. 1. Inundation forests

by

H. Klinge, K. Furch, E. Harms and J. Revilla*

Max-Planck-Institute for Limnology, Working group "Tropical Ecology", Plön, W.-Germany
*Instituto Nacional de Pesquisas da Amazônia (INPA)

Introduction

Two fundamentally different forest categories are represented in the Amazon region: the terra firme forest and the inundation forest. The latter includes várzea forest and igapó forest (DUCKE and BLACK 1953; AUBRÉVILLE 1961; HUECK 1966; WILLIAMS et al. 1972; IRMLER 1977, 1978a).

The terminology of Amazon inundation forest has been confusing until PRANCE (1979, 1980) proposed to exclusively apply the term várzea forest to communities exposed to flooding by rivers like the Solimões/Amazonas or Madeira carrying turbid water. Such water is relatively rich chemically, Ca^{++} being the dominant cation (FURCH et al. 1982). The term igapó forest is retained by PRANCE for forest communities exposed to flooding by rivers like the Tapajós carrying clear water or like the Rio Negro carrying black-water (SIOLI 1954; KLINGE 1967). Rio Negro water is extremely poor chemically, the dominant cation being H^+ followed by Na^+ (FURCH in press). Using hydrological criteria, both inundation forest types are subdivided further (PRANCE loc. cit.), and lists of typical tree species demonstrate the obvious floristic differences between them.

From the compilation of the literature on Amazon forests (KLINGE in press a, b) it is evident that floristic inventories were carried out relatively frequently in the terra firme forest which is rich in species. There are a few studies of its biomass and nutrient store carried out in terra firme forest near Manaus/Brazil (FITTKAU and KLINGE 1973; KLINGE and RODRIGUES 1973, 1974; KLINGE 1976; GOLLEY et al. 1980a). Studies of bio-

0065-6755 / 1983 / 019 / © MPI für Limnologie, AG Tropenökologie, Plön; INPA, Manaus

mass, nutrient store and ecosystem functioning were also carried out in terra firme forests of the upper Rio Negro in Venezuela (JORDAN and UHL 1978; HERRERA et al. 1978, 1981, in press; GOLLEY et al. 1980b; BONGERS et al. in press; KLINGE and HERRERA 1978, in press).

Floristic studies in the less species rich inundation forests are scarce (WORBES 1983). Biomass and nutrient studies do not exist.*) Várzea forests (acc. to PRANCE' classification) were studied floristically by PIRES and KOURY (1959), AUBRÉVILLE (1961), PIRES and PRANCE (1977) and WORBES (1983, in prep.), while such studies in igapó forests are due to RODRIGUES (1961a, b), TAKEUCHI (1962), KEEL and PRANCE (1979) and REVILLA (1981).

IRMLER (1975, 1978a, b, 1981) studying the invertebrate fauna of Amazon inundation forests developed a model of the inundation forest ecosystem (IRMLER 1979). JUNK (1980) contributed models of the nutrient cycling and the food-web, while IRMLER (1982) described the nitrogen turnover in the igapó forest ecosystem. Invertebrates in Amazon inundation forests are being studied also by BECK (1972, 1976), ADIS (1981), ADIS and FUNKE (1982) and ERWIN and ADIS (1982).

The present study was undertaken to compare the leaf size and foliar levels of N, P, K, Ca, Mg and Na of different inundation forests (várzea forests at Marchantaria and Iranduba, igapó forest at Praia Grande) in Central Amazonia *sensu* FITTKAU (1971). The study is related to a comprehensive ecological study of a várzea island in the lower Solimões. It is carried out in co-operation between Instituto Nacional de Pesquisas da Amazônia (I.N.P.A.) at Manaus/Brazil and the Working Group of the Department of Tropical Ecology of the Max-Planck-Institute of Limnology at Plön (KLINGE 1982).

Tree species sampled in inundation forests

Altogether, 45 trees of 39 species (32 genera, 26 families) were sampled in 1981, in the two várzea sites. 22 additional trees of 22 species (18 genera, 13 families) were sampled in the igapó site.

Healthy leaves from 32 trees representing 28 species in 24 genera (20 families) were sampled in the várzea forest on the Marchantaria island in the lower Solimões (Table 1, see Fig. 1 IRION et al. 1983). The island is built-up entirely by Solimões sediments (IRION et al. 1983). The forest vegetation forming about 15 m wide elongated bands occupying low ridges, is considered to be late successional. The sampling site is the same one on which ADIS et al. (in prep.) are measuring the fine litter fall.

---

*) A biomass and nutrient inventory of várzea forest was started in 1982 by KLINGE et al.

Table 1: Species sampled in three inundation forests, their leaf area and weight, and levels of N, P, K, Ca, Mg and Na, in adult leaves

Family	Species	Leaf size cm^2	Specific leaf area (S.L.A.) $cm^2 g^{-1}$	Specific leaf weight (S.L.W.) $g\ m^{-2}$	ppm N	ppm P	ppm K	ppm Ca	ppm Mg	ppm Na
I. Várzea forest on the Marchantaria island										
Anacardiaceae	?	164.8	166.0	60.3	31800	2350	23051	19975	4373	121
Apocynaceae	*Anacampta* sp.	88.0	112.1	89.2	19200	1380	12622	15265	3167	117
Bignoniaceae	*Tabebuia barbata* (E. Mey.) Sandw.	61.5	113.2	88.3	21500	2230	12846	19888	3342	143
	Crescentia amazonica Ducke	72.7	199.1	50.2	23600	1270	14326	15885	5969	229
Bombacaceae	*Pseudobombax munguba* L.*)	74.8	89.0	112.4	28300	2400	22280	7113	5089	39
Boraginaceae	?	91.7	295.2	33.9	35000	2260	31286	15887	3992	156
Capparidaceae	*Crataeva benthamii* Eichl.	45.9	74.9	133.5	26800	1790	9605	38741	7315	169
Euphorbiaceae	*Alchornea discolor* (Endl.) Poepp.	123.8	182.2	54.9	22900	2080	6168	24797	3160	204
	A. castaneifolia (Will.) Juss.	32.0	91.8	108.9	26800	2130	11006	7709	1854	83
Flacourtiaceae	*Laetia corymbulosa* Spr. ex Benth.	42.8	126.9	78.9	28067	2043	23708	22063	4632	117
	Casearia aculeata Jacq.	24.3	176.9	56.5	26600	2120	16691	36591	8426	1376
Guttiferae	*Rheedia brasiliensis* (Mart.) Pl. et Tr.	173.3	82.6	121.1	14600	1510	13732	13934	2433	58
Lauraceae	*Nectandra amazonum* Nees	50.7	109.4	91.4	20300	2210	11212	8133	1909	104
Lecythidaceae	*Gustavia augusta* L.	104.3	125.0	80.0	28000	2150	8715	18066	5522	69
Leguminosae	*Mimosa* sp.	5.3	206.7	48.4	29000	1970	15506	18706	2484	212
	Pithecellobium multiflorum (H.B.K.) Benth.	13.0	135.8	73.6	31100	1540	10301	2359	1038	122
	P. inaequale (H.B.K.) Benth.	59.4	118.2	84.6	27400	1510	7908	8630	1754	70
	Inga strigillosa Spr. ex Benth.	45.5	102.4	97.7	28800	970	4744	23687	2363	57
	I. sp. 2	136.3	150.5	66.7	35500	1600	8463	23702	2876	107
	I. sp. 3	43.8	88.6	112.9	25500	1170	3472	21368	2128	928
Meliaceae	*Trichilia* sp.	100.9	73.9	135.3	17800	1720	6688	26417	6716	35
Moraceae	*Cecropia latiloba* Miq.	816.9	60.4	210.6	33950	1980	15505	15132	4172	63
Myrtaceae	*Psidium* sp.	19.2	95.9	104.3	19000	1050	8075	31776	4142	170
Polygonaceae	*Ruprechtia tenuiflora* Bth.	24.4	156.8	63.8	23900	960	8058	25452	5396	230
Rubiaceae	*Genipa* sp.	263.0	108.0	92.6	19900	2210	23797	11834	6202	117
Sapotaceae	*Labatia glomerata* (Miq.) Radlk.	61.3	125.3	81.6	23950	1580	10135	13865	3001	124
Tiliaceae	*Mollia* sp.	165.0	175.0	57.1	21300	1650	9782	20265	5921	326
?	?	15.0	131.5	76.1	25500	1320	8216	20134	2708	87

Table 1: (cont.)

Family	Species	Leaf size	Specific leaf area (S.L.A.)	Specific leaf weight (S.L.W.)	ppm					
		cm^2	$cm^2\ g^{-1}$	$g\ m^{-2}$	N	P	K	Ca	Mg	Na
II. Várzea forest at Iranduba										
Annonaceae	*Duguetia quitarensis* Benth.	59.6	149.6	66.8	26700	1270	11750	7099	2124	130
	Unonopsis guatterioides (A.Dc.) R.E. Fries	85.1	95.8	104.4	18700	300	4210	6271	1919	45
Apocynaceae	*Malouetia furfuracea* Benth.	94.1	166.9	59.9	20600	1000	4117	19913	4935	20
Combretaceae	*Buchenavia* sp.	17.1	85.3	117.2	16800	430	4982	24062	3047	48
Flacourtiaceae	*Casearia aculeata* Jacq.	20.0	211.7	47.2	47300	1280	16513	25788	7342	219
Leguminosae	*Swartzia auriculata* Poepp.	84.3	122.1	81.9	28500	330	3946	17236	3156	41
	Cassia leiandra Benth.	10.3	179.0	55.9	17200	510	3308	12447	4534	73
Olacaceae	*Dulacia candida* (Poepp.) O. Kuntze	29.3	122.6	81.6	38200	1790	25480	22762	6396	87
Polygonaceae	*Symmeria paniculata* Benth.	166.9	101.1	98.9	25500	1080	7444	13237	4173	53
	Ruprechtia tenuiflora Bth.	31.0	97.4	102.7	18800	810	10699	11863	2640	133
Sapindaceae	*Talisia* sp.	176.7	90.1	111.0	15200	770	2552	30728	4628	62
Simarubaceae	*Picramnia spruceana* Engl.	26.3	311.4	32.1	31100	600	5891	9251	3432	96
Verbenaceae	*Vitex cymosa* Bert.	100.2	195.0	51.3	19200	1150	11031	11420	4054	92

Table 1: (cont.)

Family	Species	Leaf size	Specific leaf area (S.L.A.)	Specific leaf weight (S.L.W.)	ppm					
		cm^2	cm^2 g^{-1}	g m^{-2}	N	P	K	Ca	Mg	Na
III. Igapó forest at Praia Grande										
Chrysobalanaceae	*Licania apetala* var. *apetala* (E. Mey.) Fritsch**)	49.7	114.5	87.3	16800	430	4512	1572	2864	237
Combretaceae	*Buchenavia oxycarpa* Eichl.	12.9	72.9	137.2	16100	500	6374	2204	1299	121
	B. ochroprumna Eichl.	10.5	75.7	132.2	13100	500	4707	1832	316	229
Humiriaceae	*Humiria balsamifera* (Aubl.) St. Hil.	39.9	54.0	185.2	13500	690	3052	2535	1322	1536
Lauraceae	*Mezilaurus synandra* (Mez.) Kosterm.	18.3	80.8	123.8	18700	940	5280	.656	1142	531
Lecythidaceae	*Eschweilera coreacea* (DC) Mart. ex Berg	64.9	91.9	109.8	15900	540	7005	2000	729	92
Leguminosae	*Sclerolobium hypoleuca* Benth. **)	37.0	144.3	69.3	21100	580	7621	2012	1348	46
	S. odorifera Spruce ex Benth.	41.6	49.4	202.4	15000	420	2994	598	718	55
	Aldina latifolia var. *latifolia* Spruce ex Benth. **)	51.5	116.0	86.2	24300	440	3565	1330	1236	20
	Parkia discolor Spruce ex Benth.	34.3	211.4	47.3	22200	1110	6131	7817	1783	48
	Swartzia laevicarpa Amsh.	63.2	78.5	127.4	19200	590	6666	2193	1207	35
	S. argentea Spruce ex Benth.	71.9	78.1	128.0	18200	510	8621	1152	435	75
	S. polyphylla A. DC.	24.3	80.6	124.1	22200	840	4200	6106	1114	74
	Macrolobium multijugum (DC) Benth.	13.1	186.7	53.6	25500	1100	9943	5497	2009	105
Malpighiaceae	*Byrsonima chrysophylla* H. B. K.	52.6	84.2	118.8	16500	860	4821	5856	1409	50
Ochnaceae	*Blastemanthus grandiflorus* Spruce **)	36.4	124.2	80.5	17500	360	9263	840	780	255
	Ouratea spruceana Engler	36.4	51.0	196.1	10200	690	3074	2226	1255	1518
Proteaceae	*Panopsis rubescens* (Pohl.) Pittier	47.8	122.2	81.1	16000	910	8885	1026	1229	35
Rubiaceae	*Duroia velutina* Hook & Schum. *)	111.4	85.9	116.4	16500	440	7196	2927	1707	60
Sapindaceae	*Matayba opaca* Radlk. *)	65.7	71.1	140.7	17800	1420	9098	1492	1592	135
Sapotaceae	*Franchetella crassifolia wawra* (Radlk.) J.M. Pires **)	28.9	77.1	129.8	12700	360	5794	660	372	41
Theaceae	*Ternstroemia candolleana*	18.5	77.3	129.4	12200	160	13129	1583	1310	65

*) New leaves only

**) Sampled on low lying, clayey ground

While most families are represented by a single species, the Bignoniaceae, Euphorbiaceae and Flacourtiaceae are represented by two species each. Six species (3 genera) belong to the Leguminosae.

Leaves of additional 13 trees were sampled in the várzea forest at Iranduba, on the left terra firme bank of the Solimões, south of Manaus. They represent 13 species in 13 genera (10 families). *Ruprechtia tenuiflora* and *Casearia aculeata* are also included in the Marchantaria sample. While Apocynaceae, Flacourtiaceae, Leguminosae and Polygonaceae occur in both várzea samples, the Annonaceae, Combretaceae, Olacaceae, Sapindaceae, Simarubaceae and Verbenaceae are restricted to the Iranduba site.

The third sampling locality is Praia Grande, on the right bank of the Rio Negro about 50 kms up river from Manaus. The forest has recently been analyzed phytosociologically by REVILLA (1981). Leaves were sampled from 22 trees representing 22 species (18 genera, 13 families). 6 species were observed on clayey ground away from the river, while the majority of species was sampled on a sand barrier immediately adjacent to the beach. Most families are again represented each by a single species, except for the Leguminosae with 8 species in 5 genera (Table 1). The genera *Buchenavia* (Combretaceae) and *Swartzia* (Leguminosae) were also sampled in the várzea forests, where they are represented by different species. Representatives of the Chrysobalanaceae, Humiriaceae, Malpighiaceae, Ochnaceae, Proteaceae and Theaceae were sampled exclusively at Praia Grande.

Samples of wood and bark of the species listed in table 1 were also taken. Their chemical data will be reported elsewhere (FURCH, HARMS and KLINGE in prep.).

Analytical methods

The leaves were wrapped in paper and dried in an oven, at I.N.P.A. In the laboratory at Plön, the petioles were cut and the leaf blade outlines were drawn on paper. By aid of a computer the area was measured. Leaves were not washed or cleaned otherwise (STEYN 1959). Leaves were then ground in a commercial mill. The powder was dried at 105 °C. Nitrogen was estimated using the Kjeldahl technique. After ashing at 450 °C the samples were treated with conc. HCl. Ca, Mg, K and Na were estimated by flame atomic absorption (Perkin-Elmer AAS 300). P was estimated colorimetrically at 430 μm.

Results

1. Leaf area, specific leaf area, and specific leaf weight

Mesophyllous leaves (45 - 182.2 cm^2 in area, RAUNKIAER 1934) predominate in the three leaf samples (Fig. 1). While leaves of this size are observed among 50 - 60 % of the várzea trees, this leaf size is represented in the igapó forest by only 40 % of the trees.

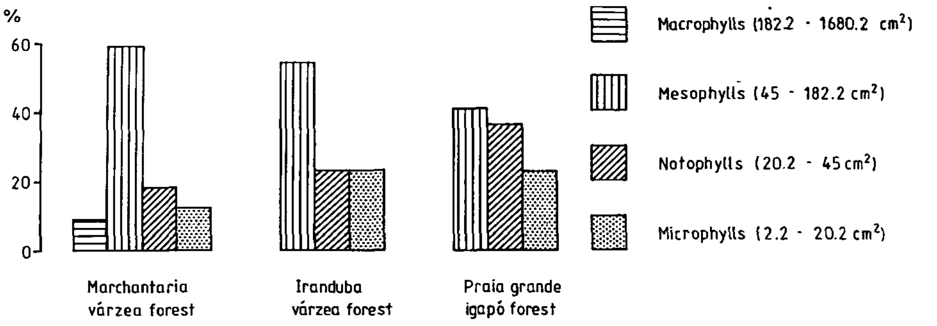

Fig. 1:
Leaf size spectra for three Central-Amazonian inundation forests

The proportion of notophylls (20.2 - 45 cm^2 in area, WEBB 1960) increases from 18 % in the Marchantaria forest to 23 % in the Iranduba forest and is 36 % in the igapó forest.

Microphylls (2.2 - 20.2 cm^2 in area) account for 23 % of the trees in both the Iranduba and Praia Grande leaf samples. Their percentage is considerably smaller in the Marchantaria forest, where macrophylls (182.2 - 1680.2 cm^2 in area) are observed exclusively in *Cecropia latiloba* and *Genipa* sp.

In addition to the decrease of the proportion of mesophylls from the várzea forest on the Marchantaria island towards the igapó forest at Praia Grande, the mean leaf area of the mesophylls in the várzea forests is 91 and 110 cm^2, respectively, while it is much smaller in the igapó forest (Table 2). The proportions of noto- and microphylls increase along with the decrease of the mesophyll proportion.

Table 2: Leaf area, specific leaf area (S.L.A.) and specific leaf weight (S.L.W.) in leaf size classes of inundation forests[1)]

Site	Leaf size class	n	Leaf area (cm^2)	S.L.A. ($cm^2 g^{-1}$)	S.L.W. (gm^{-2})
Marchantaria	macrophylls	3	632.3 ± 329.7	76.2 ± 39.1	171.2 ± 118.6
várzea	mesophylls	19	91.0 ± 67.5 a	124.8 ± 54.0 a	83.8 ± 27.9 a
	notophylls	6	33.4 ± 9.0 e	126.7 ± 35.0 b	84.1 ± 23.0 b
	microphylls	4	13.1 ± 5.8 c	167.5 ± 54.7 c	75.6 ± 22.9 c
Iranduba	mesophylls	7	109.6 ± 44.4 a	131.5 ± 40.0 a	73.5 ± 25.2 a
várzea	notophylls	3	28.9 ± 2.4 b	177.1 ± 117.0 b	72.1 ± 36.2 b
	microphylls	3	15.8 ± 5.0 c	158.7 ± 65.6 c	73.4 ± 38.2 c
Praia Grande	mesophylls	9	64.3 ± 19.6 d	93.6 ± 19.0 d	110.7 ± 21.1 d*)
igapó	notophylls	8	34.9 ± 5.7 e	99.0 ± 57.2 b	129.3 ± 60.5 b
	microphylls	5	14.7 ± 3.6 c	98.7 ± 49.3 c	115.2 ± 34.8 c

1) In each column, figures followed by the same letter are not statistically different (t - test, P > 5 %)

*) Significance level at P < 1 %

The values of the specific leaf area (S.L.A.) of the igapó trees are considerably smaller than those of the two várzea forests (Table 2), the igapó leaves being heavier (see specific leaf weight, S.L.W., table 2).

The comparatively low specific leaf area and high specific leaf weight of the macrophylls in *Cecropia* is due to their exceptionally strong leaf veins (MEDINA, pers. comm. 1982). Such veins are needed to stabilize the very large leaf blades (Table 1).

2. Foliar nutrient levels

The foliar concentrations of N, P, K, Ca, Mg and Na (in ppm) vary very widely (Table 1). The ranges are particularly wide for calcium and sodium (Table 3). They are much smaller for magnesium, phosphorus and potassium. The smallest range is observed for nitrogen.

Table 3: Ranges of the foliar concentrations of Ca, Na, Mg, P, K and N (n = 67)

Element	Range (ppm)	Maximum / Minimum
Calcium	478 - 38 741	81 : 1
Sodium	20 - 1 536	77 : 1
Magnesium	316 - 8 426	27 : 1
Phosphorus	160 - 2 420	15 : 1
Potassium	2 552 - 31 652	12 : 1
Nitrogen	10 200 - 47 300	5 : 1

2.1. Impact of leaf size

Minor differences of the mean elemental concentrations in ppm between the leaf size classes within each leaf sample are observed in table 4. The differences are not significant statistically, except for the calcium concentrations of macrophylls and mesophylls of the Marchantaria sample ($P < 5$ %).

Major differences are observed when comparing the foliar levels of the leaf size classes from different sites. The concentrations of the three leaf size classes of the igapó sample are lower than those fo the two várzea samples, except for sodium.

Table 4: Foliar levels of N, P, K, Ca, Mg and Na in leaf size classes [1]

		ppm									
		Marchantaria				Iranduba			Praia Grande		
		Macro-	Meso-	Noto-	Micro-	Meso-	Noto-	Micro-	Meso-	Noto-	Micro-
n		3	19	6	4	7	3	3	9	8	5
N	$\bar{x}$	29267	25253	26233	26150	22057	29367	27100	17911	16800	17120
	±S.D.	8445	5633a	1680b	5297c	4890ad	9815be	17438cf	2634d**	4657e**	5342f
P	$\bar{x}$	2057	1815	1710	1470	843	1067	740	682	631	640
	±S.D.	266	424a	535b	389c	392d**f	635b	469eh	329f**	260g**	554h
K	$\bar{x}$	18269	13232	13774	10525	6436	14023	8268	6708	5266	7886
	±S.D.	4816	7453a	7103b	3697c	3753d*e	10209bf	7190c	2022e*	2347f	3567c
Ca	$\bar{x}$	14033	18939	20929	18244	15129	14625	20766	2172	2849	2354
	±S.D.	1905	8432a	9967b	12100c	8475a	7161b	2295c	1502d**	2683e**h	1847f
Mg	$\bar{x}$	4849	4073	4370	2593	3570	4156	4974	1379	1086	1215
	±S.D.	1947	1691a	2407b	1275c	1195a	1980b	2181c	684d**	444e*	605c
Na	$\bar{x}$	81	125	479	148	63	105	113	82	447	210
	±S.D.	31	72a	543b	55c	37d*e	24b	92c	68ae	671b	189c

[1] In each row, figures followed by the same letter are not statistically different. Letters without stars $P < 5$ %,
* $P < 1$ %, ** $P < 0.1$ %.

2.2. Impact of leaf age

The chief variable of the chemical composition of leaves of a given species is leaf age (GRUBB 1977; MEDINA in press). Among the inundation forest tree leaves, this is made evident for two species each in Marchantaria várzea forest and Praia Grande igapó forest (Table 5). These species presented at the time of sampling (April 1981) young and adult leaves simultaneously. A third species had young leaves only. The exact age of all leaves is unknown. It is therefore probably that age differences among the adult leaves account for some of the reported variability of their foliar elemental concentrations.

Table 5: Elemental concentrations in leaves of different age from Marchantaria várzea forest and Praia Grande igapó forest species

		ppm					
Species	Leaf age	N	P	K	Ca	Mg	Na
Marchantaria várzea forest							
Genipa sp.	adult	19 900	2 210	23.797	11 834	6 202	117
	young	41 500	2 420	31 652	1 916	4 828	163
Trichilia sp.	adult	17 800	1 720	6 688	26 417	6 716	35
	young	21 000	2 200	24 010	9 046	2 693	83
Pseudobombax munguba	young	28 300	2 400	22 288	7 113	5 089	39
Praia Grande igapó forest							
Swartzia laevicarpa	adult	19 200	590	6 666	2 193	1 207	35
	young	17 100	900	11 168	478	917	39
S. polyphylla	adult	22 200	1 100	6 131	7 817	1 783	48
	young	19 700	990	15 247	1 118	840	48
Matayba opaca	young	17 800	1 420	9 098	1 492	1 592	135

Adult leaves are generally higher in calcium (SPECTOR 1956; GRUBB 1977; BOWEN 1979; CHAPIN 1980). This is also true for the species listed in table 5. Their adult leaves are also richer in magnesium. Young leaves are much richer in potassium and, sometimes, also in nitrogen, phosphorus and sodium.

2.3. Variation of foliar elemental concentrations among individuals of the same species, sampled at different localities

Three species of the Marchantaria várzea forest were sampled in replicates, and two additional species were sampled in both várzea sites. Their foliar elemental concentrations are reported in table 6.

Table 6: Variability of foliar elemental concentrations among replicates in 5 species from different sites in várzea forests

Species			N	P	K (ppm)	Ca	Mg	Na
Marchantaria várzea forest								
Laetia corymbulosa		$\bar{x}$	28 067	2 043	23 708	22 063	4 632	117
(n = 3)	S.D.	%	6.1	15.0	17.7	41.6	16.2	36.8
Cecropia latiloba		$\bar{x}$	33 950	1 980	15 505	15 132	4 172	63
(n = 2)	S.D.	%	9.8	16.4	4.8	0.5	52.8	1.6
Labatia glomerata		$\bar{x}$	23 950	1 580	10 135	13 865	3 001	124
(n = 2)	S.D.	%	9.7	23.3	15.7	16.8	126.5	33.1
Várzea forests of Marchantaria and Iranduba								
Casearia aculeata		$\bar{x}$	36 950	1 700	16 602	31 189	7 884	797
(n = 2)	S.D.	%	39.6	34.9	0.8	24.5	9.7	102.6
Ruprechtia tenuiflora		$\bar{x}$	21 350	885	9 378	18 657	4 018	181
(n = 2)	S.D.	%	16.9	12.0	19.9	51.5	48.5	38.1

The observed coefficients of variation are relatively low for phosphorus and potassium. They vary greatly for the other elements. There is no clear tendency of a greater variability between individuals from distant contrasting sites (Marchantaria and Iranduba) than between those from less distant sites on the Marchantaria island.

The number of both species and replicates is small. It does not allow for firm conclusions on the variability of the foliar elemental concentrations between individuals from different sites.

2.4. Between-species variability of the foliar elemental concentrations among adult leaves

Comparative data of foliar concentrations of the six elements from other Amazon inundation forest species do not exist, except for *Crudia amazonica* (Leguminosae). Leaves of this species were sampled by WILLIAMS et al. (1972) in both a Rio Negro igapó forest and a Rio Branco várzea forest. Leaves from the latter site yielded much higher concentrations of nitrogen, phosphorus, potassium, sulfur and magnesium than leaves from the Rio Negro igapó. *C. amazonica* leaves from the Rio Negro igapó are considerably richer in nitrogen, calcium, magnesium and phosphorus than the leaves of the species we have collected in the Praia Grande igapó.

In order to obtain a relative scale for a classification of the species according to their foliar concentrations of the six elements studied, we divided the elemental ranges of each sampling locality into four equal portions (Table 7). The means for the species sampled in replicates were used. The four partial ranges are termed 'very rich'$^{(+++++++)}$, 'rich'$^{(+++++)}$, 'low'$^{(+++)}$ and 'very low'$^{(+)}$.

Table 7: Subdivision of total ranges of N, P, K, Ca, Mg and Na

Element	Site	Class (ppm) Very low(+)	Low(+++)	Rich(+++++)	Very rich(+++++++)
Nitrogen	Marchantaria	14 600 - 19 825	19 826 - 25 050	25 051 - 30 275	30 276 - 35 500
	Iranduba	15 200 - 23 225	23 226 - 31 250	31 251 - 39 275	39 276 - 47 300
	Praia Grande	10 200 - 14 025	14 026 - 17 850	17 851 - 21 675	21 676 - 25 500
Phosphorus	Marchantaria	960 - 1 320	1 321 - 1 680	1 681 - 2 040	2 041 - 2 400
	Iranduba	300 - 673	674 - 1 045	1 046 - 1 418	1 419 - 1 790
	Praia Grande	160 - 475	476 - 790	791 - 1 105	1 106 - 1 420
Potassium	Marchantaria	3 472 - 10 426	10 427 - 17 379	17 380 - 24 333	24 334 - 31 286
	Iranduba	2 552 - 8 284	8 285 - 14 016	14 017 - 19 748	19 749 - 25 480
	Praia Grande	2 994 - 5 528	5 529 - 8 062	8 063 - 10 595	10 596 - 13 129
Calcium	Marchantaria	2 359 - 11 455	11 456 - 20 550	20 551 - 29 646	29 647 - 38 741
	Iranduba	6 271 - 12 385	12 386 - 18 500	18 501 - 24 614	24 615 - 30 728
	Praia Grande	598 - 2 403	2 404 - 4 208	4 209 - 6 012	6 013 - 7 817
Magnesium	Marchantaria	1 038 - 2 885	2 886 - 4 732	4 733 - 6 579	6 580 - 8 426
	Iranduba	1 919 - 3 275	3 276 - 4 631	4 632 - 5 986	5 987 - 7 342
	Praia Grande	316 - 953	954 - 1 590	1 591 - 2 227	2 228 - 2 864
Sodium	Marchantaria	35 - 370	371 - 706	707 - 1 041	1 042 - 1 376
	Iranduba	20 - 70	71 - 120	121 - 169	170 - 219
	Praia Grande	20 - 399	400 - 778	779 - 1 157	1 158 - 1 536

While the four concentration classes of the two várzea forests (Marchantaria and Iranduba) resemble each other, those of the igapó forest at Praia Grande are mostly below the várzea classes. This is however not true for sodium which is generally lower in the Iranduba leaves.

Replacing the absolute concentrations by the symbols allows to classify the species of each site according to the pattern of symbols and to establish groups of species with a similar pattern (Table 8).

The established groups comprise mostly two to three species and, at most, six species. At the family level, the Leguminosae tend to have high nitrogen concentrations, while the representatives of the Myrtaceae and Theaceae present low levels of nitrogen, phosphorus and/or potassium (GRUBB 1977). The mostly very low sodium concentrations vary little. The pattern of species in the genera *Alchornea, Inga* and *Pithecellobium* of the Marchantaria forest, and *Sclerolobium* and *Swartzia* in the Praia Grande forest may differ considerably. It is thus quite probable that each species is characterized by its individual pattern of foliar concentrations of N, P, K, Ca, Mg and Na.

Table 8: Concentration pattern of N, P, K, Ca, Mg and Na of adult leaves from three distinct inundation forests

					ppm		
Species	Family	N	P	K	Ca	Mg	Na
Marchantaria várzea forest							
1. Rich to very rich in N, P, Ca and Mg							
Casearia aculeata	Flacourtiaceae	+++++	+++++++	+++	+++++++	+++++++	+++++++
Crataeva benthamii	Capparidaceae	+++++	+++++	+	+++++++	+++++++	+
2. Rich to very rich in N, P and K, mostly low to very low in Ca, Mg and Na							
?	Boraginaceae	+++++++	+++++++	+++++++	+++	+++	+
?	Anacardiaceae	+++++++	+++++++	+++++	+++	+++	+
Laetia corymbulosa	Flacourtiaceae	+++++	+++++++	+++++	+++++	+++	+
3. Rich to very rich in N and P, mostly low to very low in K, Ca, Mg and Na							
Cecropia latiloba	Moraceae	+++++++	+++++	+++	+++	+++	+
Alchornea castaneifolia	Euphorbiaceae	+++++	+++++++	+++	+	+	+
Mimosa sp.	Leguminosae	+++++	+++++	+++	+++	+	+
Gustavia augusta	Lecythidaceae	+++++	+++++++	+	+++	+++++	+
4. Low to very low in all elements							
Rheedia brasiliensis	Guttiferae	+	+++	+++	+++	+	+
Anacampta sp.	Apocynaceae	+	+++	+++	+++	+++	+
Labatia glomerata	Sapotaceae	+++	+++	+	+++	+++	+
5. Low to very low in N, P and K, rich to very rich in Ca and/or Mg							
Psidium sp.	Myrtaceae	+	+	+	+++++++	+++	+
Crescentia amazonica	Bignoniaceae	+++	+	+++	+++	+++++	+
Ruprechtia tenuiflora	Polygonaceae	+++	+	+	+++++	+++++	+
Mollia sp.	Tiliaceae	+++	+++	+	+++	+++++	+
6. Rich to very rich in N and Ca, mostly low to very low in P, K and Mg							
Inga strigillosa	Leguminosae	+++++	+	+	+++++	+	+
Inga sp. 2	Leguminosae	+++++++	+++	+	+++++	+	+
Inga sp. 3	Leguminosae	+++++	+	+	+++++	+	+++++
7. Rich to very rich in P and K or Ca and Mg, respectively, low in N							
Alchornea discolor	Euphorbiaceae	+++	+++++++	+	+++++	+++	+
Genipa sp.	Rubiaceae	+++	+++++++	+++++	+++	+++++	+
Trichilia sp.	Meliaceae	+	+++++	+	+++++	+++++++	+
8. Rich to very rich in N or P, low to very low in K, Ca, Mg and Na							
Pithecellobium inaequale	Leguminosae	+++++	+++	+	+	+	+
?	?	+++++	+	+	+++	+	+
P. multiflorum	Leguminosae	+++++++	+++	+	+	+	+
Tabebuia barbata	Bignoniaceae	+++	+++++++	+++	+++	+++	+
Nectandra amazonum	Lauraceae	+++	+++++++	+++	+	+	+

Table 8: (cont.)

Species	Family	N	P	K	Ca	Mg	Na
					ppm		
Iranduba várzea forest							
1. Rich to very rich in most elements							
Casearia aculeata	Flacourtiaceae	+++++++	+++++	+++++	+++++++	+++++++	+++++++
Dulacia candida	Olacaceae	+++++	+++++++	+++++++	+++++	+++++++	+++
2. Low to very low in all elements							
Unonopsis guatterioides	Annonaceae	+	+	+	+	+	+
Ruprechtia tenuiflora	Polygonaceae	+	+++	+++	+	+	+++++
Cassia leiandra	Leguminosae	+	+	+	+++	+++	+++
Swartzia auriculata	Leguminosae	+++	+	+	+++	+	+
Picramnia spruceana	Simarubaceae	+++	+	+	+	+++	+++
3. Rich in P							
Vitex cymosa	Verbenaceae	+	+++++	+++	+	+++	+++
Symmeria paniculata	Polygonaceae	+++	+++++	+	+++	+++	+
Duguetia quitarensis	Annonaceae	+++	+++++	+++	+	+	+++++
4. Rich to very rich in Ca							
Talisia sp.	Sapindaceae	+	+++	+	+++++++	+++	+
Malouetia furfuracea	Apocynaceae	+	+++	+	+++++	+++++	+
Buchenavia sp.	Combretaceae	+	+	+	+++++	+	+
Praia Grande igapó forest							
1. Rich to very rich in most elements							
Macrolobium multijugum	Leguminosae	+++++++	+++++	+++++	+++++	+++++	+
Parkia discolor	Leguminosae	+++++++	+++++++	+++	+++++++	+++++	+
2. Rich to very rich in N and P, mostly low to very low in K and Mg							
Swartzia polyphylla	Leguminosae	+++++++	+++++	+	+++++++	+++	+
Mezilaurus synandra	Lauraceae	+++++	+++++	+	+	+++	+++
3. Rich to very rich in N, low in other elements							
Aldina latifolia	Leguminosae	+++++++	+	+	+	+++	+
Sclerolobium hypoleuca	Leguminosae	+++++	+++	+++	+	+++	+
Swartzia laevicarpa	Leguminosae	+++++	+++	+++	+	+++	+
4. Rich to very rich in K, mostly low to very low in N, P, Ca and Mg							
Ternstroemia candida	Theaceae	+	+	+++++++	+	+++	+
Panopsis rubescens	Proteaceae	+++	+++++	+++++	+	+++	+
Blastemanthus grandiflorus	Ochnaceae	+++	+	+++++	+	+	+
Swartzia argentea	Leguminosae	+++++	+++	+++++	+	+	+
5. Rich to very rich in Ca or Mg							
Licania apetala	Chrysobalanaceae	+++	+	+	+	+++++++	+
Byrsonima chrysophylla	Malpighiaceae	+++	+++++	+	+++++	+++	+
Duroia velutina	Rubiaceae	+++	+	+++	+++	+++++	+

Table 8: (cont.)

Species	Family	N	P	K	Ca	Mg	Na
				ppm			
6. Low to very low in most elements							
Franchetella crassifolia	Sapotaceae	+	+	+++	+	+	+
Buchenavia ochroprumna	Combretaceae	+	+++	+	+	+	+
Eschweilera coreacea	Lecythidaceae	+++	+++	+++	+	+	+
Sclerolobium odoratissi.	Leguminosae	+++	+	+	+	+	+
Buchenavia oxycarpa	Combretaceae	+++	+++	+++	+	+++	+
Ouratea spruceana	Ochnaceae	+	+++	+	+	+++	+++++++
Humiria balsamifera	Humiriaceae	+	+++	+	+++	+++	+++++++

2.5. Ratios N/P, K/Ca, Ca/Mg, K/Na, and relative N content

The N/P ratios vary between 9:1 and 86 : 1 (Table 9). The Marchantaria leaves are characterized by values below 20 : 1 (82 %). The ratios are much higher for leaves from both Iranduba (15 % below 20 : 1) and Praia Grande (29 % below 20 : 1).

The K/Ca ratios vary less (0.2 : 1 - 11.0 : 1). Those of the Marchantaria leaves are mostly below 2 : 1 (7 % above 2 : 1). All Iranduba leaves have K/Ca ratios below 2 : 1, while in the Praia Grande leaves 71 % have ratios above 2 : 1.

The Ca/Mg ratios vary between 1 : 1 and 10 ; 1. While at Marchantaria 39 % of the leaves present values above 5 : 1, this percentage is 23 % at Iranduba and 10 % at Praia Grande.

The K/Na ratios vary between 2 : 1 and 571 : 1. 54 % of the Marchantaria leaves are characterized by values below 100 : 1. The respective values are 62 % for both Praia Grande and Iranduba.

When studying the macro-element composition of both its leaf litter and fresh foliage of the Manaus terra firme forest (KLINGE and RODRIGUES 1968a, b) it was observed that the leaves are relatively rich in nitrogen, when compared to other forests (KLINGE 1976). MEDINA (1981) concluded from these and own data that nitrogen is the most abundant element in lowland tropical forest on nutrient-poor soil. The ratio N % (N + P + K + Ca + Mg + Na) (Table 1) in the várzea foliage is 42 % (Marchantaria) and 47 % (Iranduba), while it is 61 % in the igapó foliage. The difference between both várzea leaf samples not being significantly different ($P > 5$ %), the value for the igapó foliage is highly significant different from the várzea values ($P < 0.1$ %). This finding confirms the above observation that nitrogen is the most abundant element, even in chemically poor forest like the igapó at Praia Grande.

Table 9: N/P, K/Ca, Ca/Mg and K/Na ratios[1)]

		N/P		K/Ca		Ca/Mg		K/Na	
	n	Range	$\bar{x} \pm 1$ S. D.	Range	$\bar{x} \pm 1$ S. D.	Range	$\bar{x} \pm 1$ S. D.	Range	$\bar{x} \pm 1$ S. D.
Marchantaria	28	9.0 - 29.7	15.7 ± 5.1ac	0.2 - 4.4	1.0 ± 0.9ac	1.4 - 10.0	5.1 ± 2.0a	3.7 - 571.5	124.8 ± 110.9a
Iranduba	13	19.7 - 86.4	35.1 ± 20.7b*	0.1 - 1.7	0.7 ± 0.5a	2.7 - 7.9	4.1 ± 1.6a	41.2 - 292.9	111.3 ± 69.5a
Praia Grande	21	12.5 - 70.3	31.7 ± 14.8abd**	0.7 - 11.0	4.3 ± 3.2b**d**	0.6 - 5.8	2.2 ± 1.6b*	2.0 - 253.9	91.3 ± 71.4a

1) In each column, figures followed by the same letter are not significantly different ($P > 5$ %).
Letters without stars $P < 5$ %, *$P < 1$ %, **$P < 0.1$ %.

2.6. Average concentrations of the inundation forest leaves

The mean concentrations and standard deviations for the six elements in adult leaves were calculated separately for each site (Table 10). Substantial differences are observed, the lowest means of nitrogen, phosphorus, potassium, calcium and magnesium are observed for the leaves of the Praia Grande igapó, and the highest means of the elements, except magnesium, for the leaves from the Marchantaria várzea forest. The igapó leaves when compared to the Marchantaria leaves, are particularly low in calcium, less so in magnesium, phosphorus and potassium, while they are similar in nitrogen and sodium.

The observed standard deviations are generally high, due to the composition of the samples by many species and to age differences even among the adult leaves.

Table 10: Mean concentration (ppm) of Ca, Mg, P, K, N and Na in adult leaves from three inundation forests of Central Amazonia [1)]

	Várzea forest		Igapó forest	Ratio
Element (ppm)	Marchantaria (31 individuals in 27 species)	Iranduba (13 individuals in 13 species)	Praia Grande (21 individuals in 21 species)	$\bar{x}_M : \bar{x}_I : \bar{x}_{PG}$
Calcium	19 141 ± 8 312ac	16 314 ± 7 729a	2 506 ± 2 041b**d**	7.64 : 6.51 : 1
Magnesium	3 982 ± 1 850ac	4 029 ± 2 447a	1 218 ± 584b**d**	3.27 : 3.31 : 1
Phosphorus	1 755 ± 430ac	871 ± 442b	618 ± 256bd**	2.87 : 1.41 : 1
Potassium	13 183 ± 6 840ac	8 609 ± 6 552b	6 325 ± 2 617bd**	2.08 : 1.36 : 1
Nitrogen	25 865 ± 5 307ac	24 908 ± 146a	17 305 ± 4 042b**d**	1.50 : 1.44 : 1
Sodium	195 ± 270ac	85 ± 53b	249 ± 441bc	0.78 : 0.34 : 1

1) Figures in each row followed by the same letter are not different statistically.
** Significance level at $P < 0.1$ %.

The unexpected differences between the chemical composition of the leaves from the two várzea forests are supposed to be due to soil differences of both sites. While the soils of the Marchantaria island have developed exclusively from sediments laid down by the Solimões river, those at Iranduba are assumed to have developed from soft terra firme rocks low in phosphorus (ANON. 1969; KLINGE 1976) superficially covered by Solimões sediments.

2.7. Foliar levels of N, P, K, Ca, Mg and Na per leaf unit area

Reflecting the differences in specific leaf area and specific leaf weight, phosphorus, potassium, calcium per unit leaf area are significantly lower in the Praia Grande igapó (Table 11). While the nitrogen content in the leaves from the three sampling locality does not differ significantly, specifically the low concentrations of phosphorus and calcium in the blackwater of the Rio Negro igapó are reflected by extraordinarily low contents of these elements in adult leaves from the Praia Grande site. These leaves are also remarkably rich in sodium. The Iranduba leaves resemble more the igapó leaves considering phosphorus and potassium, while they are similar to the Marchantaria leaves in the contents of calcium and magnesium.

Table 11: Mean foliar levels of N, P, K, Ca, Mg and Na ($\mu g\ cm^{-2}$) in inundation forests (adult leaves)[1)]

		$\mu g\ cm^{-2}$	
	Nitrogen	Phosphorus	Potassium
Marchantaria	217.6 ± 91.2a	15.1 ± 6.6a**	105.6 ± 60.6a
Iranduba	182.4 ± 116.7a	6.5 ± 3.6b**	63.8 ± 51.4b
Praia Grande	192.8 ± 52.7a	7.6 ± 4.3c**	70.1 ± 31.5b
	Calcium	Magnesium	Sodium
Marchantaria	161.5 ± 210.7ac	34.6 ± 22.4ac	1.57 ± 2.22ac
Iranduba	131.9 ± 91.7a	29.9 ± 12.8a	0.61 ± 0.33b
Praia Grande	26.9 ± 19.3b**d*	14.2 ± 6.7b**c	3.96 ± 8.48bc

[1)] In each column, figures followed by the same letter are not statistically different (t-test, $P > 5$ %).

* Significance level at $P < 1$ %, ** at < 0.01 %.

3. Foliar levels of alkali-earth and alkali metals, in comparison with these metals in natural waters associated with the inundation forest sites

FITTKAU (1971), FURCH and KLINGE (1978), FURCH and JUNK (1980), FURCH et al. (1982) and FURCH (in press) have convincingly shown that the portion of the Amazon basin which is flooded by the Solimões, is geochemically much richer than the remaining areas, i. e., the terra firme and the igapó areas. This conclusion is primarily based on chemical water analyses. As shown in the preceding section, these regional differences are also reflected by the foliage of the inundation forests.

Since the geochemical reasoning of the mentioned authors is based on the relative contribution of the elements sodium, potassium, magnesium and calcium in natural waters, the proportions of these elements in the leaves from the three sampling sites were calculated and compared to those reported by FURCH (loc. cit.) for the respective associated natural waters (várzea - Solimões, igapó - Rio Negro) (Fig. 2).

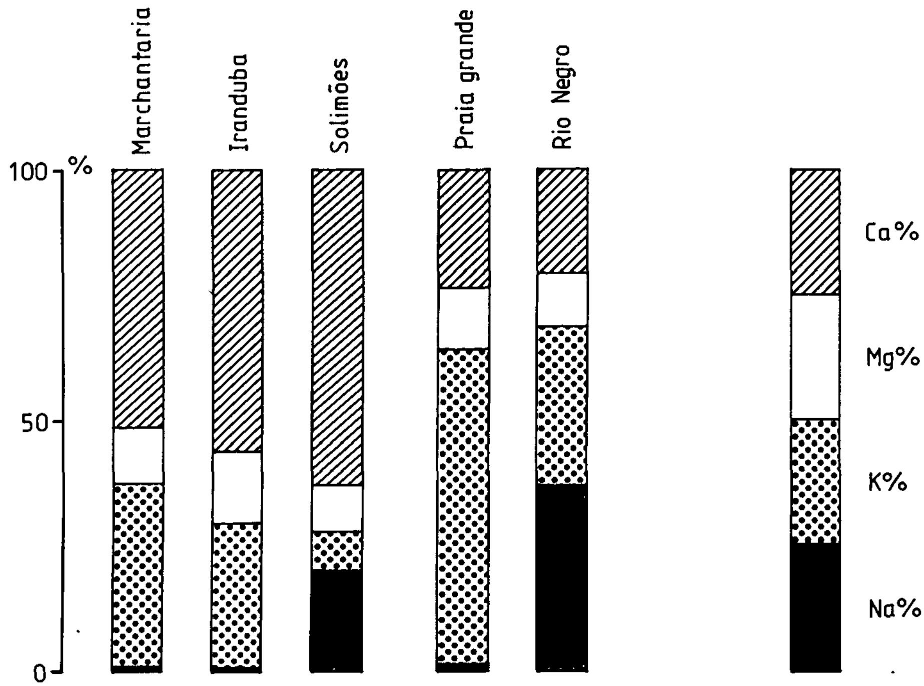

Fig. 2:
Relative composition of the foliage of three Central-Amazonian inundation forests, and of the water of Solimões and Rio Negro, by calcium, magnesium, potassium and sodium

A striking similarity between the relative composition of the várzea tree leaves and the Solimões water is observed. The alkali-earth metals represent a much higher proportion than the alkali metals, because of a high calcium contribution varying between 52 and 62 %. While in the Solimões water there is a relatively high sodium proportion, it is extremely low in the foliage.

A much lower Ca + Mg contribution is observed in both the igapó foliage and the Rio Negro water, mainly due to a low calcium proportion. While potassium contributes more than the three other elements in the igapó foliage, there is a considerable sodium contribution in the Rio Negro water.

Looking into the relative contribution of these elements in aquatic macrophytes growing on the várzea (HOWARD-WILLIAMS and JUNK 1977), their leaves are much richer in potassium than the tree leaves.

The observed differences in the relative composition by the alkali and alkali-earth metals are connected with differences in the absolute amounts of these elements and of phosphorus in the foliage and the water. The amounts of these elements in both foliage and water of the várzea are considerably greater than in the igapó (Table 12).

Table 12: P, K, Mg, Ca and Na (g kg^{-1}) in the foliage of inundation forests and in the water of Solimões and Rio Negro, and the concentration factors

Element	Várzea				
	Solimões water	Foliage, g kg^{-1}		Concentration factor	
	10^{-3} g kg^{-1}	Marchantaria	Iranduba	Marchantaria	Iranduba
P	0.105	1.755	0.871	16714	8295
K	0.9	13.183	8.609	14648	9566
Mg	1.1	3.982	4.029	3620	3663
Ca	7.2	19.141	16.314	2653	2266
Na	2.3	0.195	0.085	85	37
Sum	10.605	38.256	29.908		

Element	Igapó		
	Rio Negro water	Foliage, g kg^{-1}	Concentration factor
	10^{-3} g kg^{-1}	Praia Grande	
P	0.025	0.618	24720
K	0.33	6.325	19167
Mg	0.11	1.218	11073
Ca	0.21	2.506	11933
Na	0.38	0.249	655
Sum	1.055	10.916	

Comparing the amounts of the foliage and the water within each inundation ecosystem (várzea, igapó), differences in the accumulation of the elements in the leaves are observed. Speaking generally, the igapó trees concentrate much more strongly calcium and magnesium in their foliage than do the várzea trees which live in a chemically richer environment than the igapó trees. The concentration factors of essential nutrients and sodium may also be interpreted in terms of energy the plants invest in assimilating the nutrients from the water.

Final remarks

It has been shown that the várzea tree foliage is richer in chemical elements than the igapó foliage. In connection with the water chemists' observation that the Amazon basin presents geochemically poor conditions in its areas of terra firme and igapó, the question may be asked whether the richness of the várzea foliage in nutrients is only a relative one or also an absolute richness.

In order to find an answer to this question we have compiled chemical data for a number of tropical forests. The data refer to the foliage of primary forests or primary forest species mostly in the neotropics. They were found in STARK (1970, 1971), KLINGE (1976), GRUBB (1977), TANNER (1977), HERRERA (1979), GOLLEY et al. (1980a, b), OHLER (1980), SOBRADO and MEDINA (1980), GRIMM and FASSBENDER (1981), MEDINA et al. (1981), PEACE and MACDONALD (1981). The obtained absolute ranges of N, P, K, Ca, Mg and Na in tropical foliage are depicted in fig. 3. The average concentrations for the three inundation forests we have studied (Table 10 refers), are also indicated in this graph.

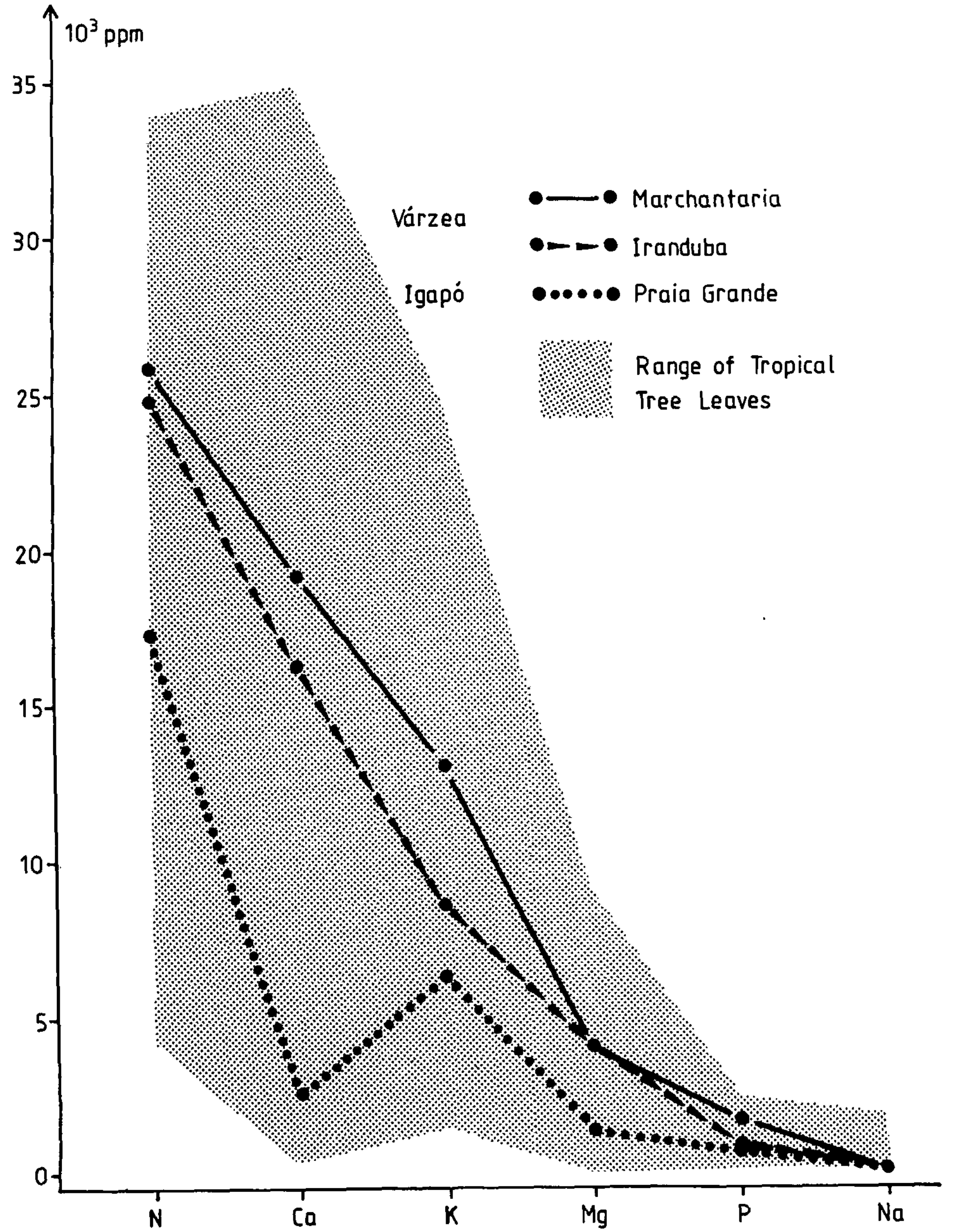

Fig. 3:
Average levels of nitrogen, calcium, potassium, magnesium, phosphorus and sodium in the foliage of three Central-Amazonian inundation forests, in comparison with the ranges of these elements in tropical forest foliage

It is evident that the foliar concentrations of the igapó foliage are low also by tropical standards, while those of the várzea are high.

Although much lower than the várzea foliage, the igapó foliage is relatively rich in nitrogen, when compared to the mean of tropical forest foliage in general. Thus, nitrogen is an abundant element also in the generally nutrient-poor igapó ecosystem (KLINGE 1976; MEDINA 1981).

The soil and its chemical composition, jointly with the chemical quality of the water flooding the soil, are factors which govern the nutrient conditions of the plants growing on these soils. The soil of good nutrient conditions of the Marchantaria island therefore provides the trees growing on it with much nutrients so that the foliage is rich in them, both by Amazonian and tropical standards. The igapó soil consisting primarily of quartz sand, supports trees with a foliage low in nutrients. One might therefore expect to find a richer foliage among igapó trees growing on better quality igapó soil. ADIS and IRION (pers. comm. 1982) studied the clayey ground at Praia Grande off the river, where we have sampled 6 species. Acc. to these authors, the clay sediment is derived from the Solimões being therefore a várzea sediment which is older than the Rio Negro sand at the beach where we have sampled the majority of igapó species. For both groups of species, the average concentrations are reported in table 13. The foliage of species growing on the Rio Negro sand is richer in phosphorus, calcium and sodium, but lower in the other elements. The observed differences however are not significant statistically, except for phosphorus ($P < 0.1$ %). Thus, there are no major differences between the foliar elemental contents from sandy and clayey substrate, both exposed since unknown time, to the chemically extremely poor Rio Negro water.

Table 13: Foliar elemental concentrations of igapó leaves at Praia Grande, from different soils

	ppm		
Element	Clay soil (old várzea sediment) 6 species	Sandy soil (Rio Negro sand) 14 species	Ratio $\bar{x}_C : \bar{x}_S$
Magnesium	1 385 ± 861	1 069 ± 471	1.30 : 1
Potassium	6 325 ± 2 110	5 840 ± 2 238	1.08 : 1
Nitrogen	18 150 ± 4 030	17 307 ± 4 068	1.05 : 1
Phosphorus	435 ± 67	729 ± 231	0.60 : 1
Calcium	1 557 ± 831	2 978 ± 2 325	0.52 : 1
Sodium	110 ± 106	322 ± 527	0.34 : 1

WORBES (1983) studying a more mature stand of the Marchantaria inundation forest in comparison with a Rio Negro igapó, pointed out that the Marchantaria forest contains a number of deciduous tree species mainly in the upper canopy, while the Rio Negro igapó is apparently an evergreen community (REVILLA 1981). While in the scarce botanical literature on Amazon inundation forests (see reviews by KLINGE, in press a, b) there is hardly any reference to the evergreen or deciduous nature of igapó and várzea forests, GESSNER (1968) remarked that certain igapó species retain their green foliage during the inundation (B. FURCH, in prep.). MONK (1966) interpreted the preference given by evergreen species to nutrient-poor soil in terms of nutrient conservancy. LOVELESS (1961, 1962) described the foliage of evergreens as sclerophyllous, and MEDINA (1981) reported that deciduous neotropical trees contain in their leaves more than 1000 ppm P and over 15000 ppm N, neotropical evergreen species presenting concentrations below these values. The same author reported that the deciduous species have larger leaf blades of relatively low weight, while the opposite is true for the evergreens.

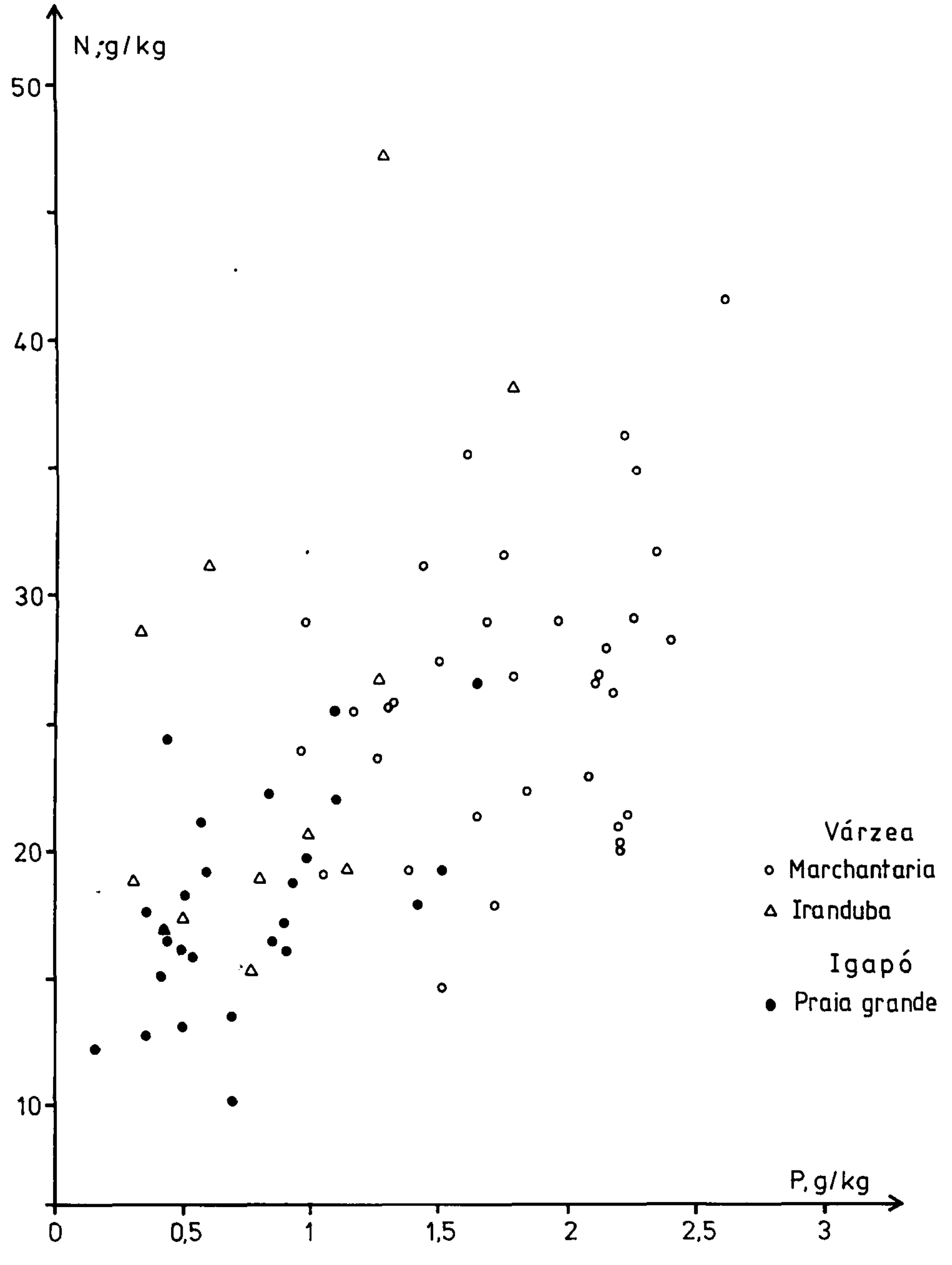

Fig. 4:
Nitrogen and phosphorus in the leaves of three Central-Amazonian inundation forests

Plotting the nitrogen concentrations against the phosphorus values both in ppm for the leaves from the three sampling sites in inundation forests (Fig. 4) it is observed that almost all várzea leaves have concentrations above 19000 ppm N and 1000 ppm P, respectively. Only twenty percent of the igapó leaves present nitrogen and phosphorus concentrations above these values. A wide N/P ratio indicating a low P-availability in the soil (MEDINA 1981; MEDINA et al. 1981), this ratio is near 15 in Marchantaria leaves, while for both Iranduba and Praia Grande it is between 25 and 30 (Tables 9 and 12 refer). Thus, the leaf size and chemical characteristics of the Praia Grande igapó leaves correspond to evergreen species (WORBES 1983). This however does not apply to every individual species, as evident from the considerable between-species variability of the data.

If the igapó species really are evergreen, their leaves can be expected to be sclerophyllous. Anatomical studies and estimation of the water content can confirm this assumption.

Summary

The study of the leaf size spectra and foliar concentrations of N, P, K, Ca, Mg and Na of 52 species sampled in three Central-Amazon inundation forests (2 várzea sites, 1 igapó site) yielded significant differences between várzea and igapó forests. The várzea foliage consists of larger and less heavy leaves with elemental concentrations being high even by tropical standards. The igapó foliage consists of relatively small leaves which are heavier, but much lower in the studied elements. The igapó leaves are supposed to be sclerophyllous and evergreen.

Resumo

O estudo sobre o espectro do tamanho de folhas e concentrações foliares de N, P, K, Ca, Mg e Na em 52 espécies de folhas coletadas em tres florestas inundáveis da Amazônia Central (2 áreas na várzea, 1 área no igapó), revelaram diferenças significantes entre as florestas da várzea e do igapó. A folhagem da várzea consiste de folhas maiores e menos pesadas com concentrações altas de elementos, mesmo sob o ponto de vista de normas tropicais. A folhagem do igapó, consiste de folhas relativamente pequenas, as quais são mais pesadas porém mais baixas nos elementos estudados. As folhas do igapó são consideradas esclerófilas e sempre verde.

References

ADIS, J. (1981): Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian inundation forests.- Amazoniana 7: 87 - 173.

ADIS, J. und W. FUNKE (1982): Jahresperiodische Vertikalwanderungen von Arthropoden in Überschwemmungswäldern Zentralamazoniens.- Verh. Ges. Ökol. 10: (in press).

ANONYMOUS (1969): Os solos da área Manaus – Itacoatiara.- Estudos e Ensaios 1: 1 - 117.

AUBRÉVILLE, A. (1961): Etude écologique des principales formations végétales du Brésil et contribution a la connaissance des forêts de l'Amazonie brésilienne.- Centre Technique Forestier Tropical, Nogent-sur-Marne, 268 p.

BECK, L. (1972): Der Einfluß jahreszeitlicher Überflutung auf den Massenwechsel der Bodenarthropoden im zentral-amazonischen Regenwaldgebiet.- Pedobiologia 12: 133 - 148.

BECK, L. (1976): Zum Massenwechsel der Makro-Arthropodenfauna des Bodens in Überschwemmungswäldern des zentralen Amazonasgebietes.- Amazoniana 6: 1 - 20.

BONGERS, F., ENGELEN, D. and H. KLINGE (in press): Phytomass structure of natural plant communities on spodosols in southern Venezuela. Bana woodland.- Vegetatio.

BOWEN, H. J. M. (1979): Environmental Chemistry.- Academic Press, London - New York - Toronto - Sydney - San Francisco, 333 p.

CHAPIN, F. S. (1980): The mineral nutrition of wild plants.- Ann. Rev. Ecol. Syst. 11: 233 - 260.

DUCKE, A. and G.A. BLACK (1953): Phytogeographical notes on the Brazilian Amazon.- An. Acad. bras. Ciencias 25: 1 - 46.

ERWIN, T. L. and J. ADIS (1982): Amazonian inundation forests. Their role as short-term refuges and generators of species richness and taxon pulses.- In: G. T. Prance (ed.) Biological diversification in the tropics. Columbia University Press, New York, 358 - 371.

FITTKAU, E. J. (1971): Ökologische Gliederung des Amazonas-Gebietes auf geochemischer Grundlage.- Münster. Forsch. Fortschr. 20/21: 35 - 50.
FITTKAU, E. J. and H. KLINGE (1973): On biomass and trophic structure of the Central Amazonian rain forest ecosystem.- Biotropica 5: 2 - 14.
FURCH, K. (in press): Amazon water chemistry: Rules of distribution of chemical properties among freshwaters.- In: H. Sioli (ed.) The Amazon.
FURCH, K. and W. J. JUNK (1980): Water chemistry and macrophytes of creeks and rivers in southern Amazonia and the Central Brazilian shield.- In: J. I. Furtado (ed.) Tropical Ecology and Development, Kuala Lumpur, 771 - 796.
FURCH, K., JUNK, W. J. and H. KLINGE (1982): Unusual water chemistry of natural waters from the Amazon region.- Acta cient. venez. 33: 269 - 273.
FURCH, K. and H. KLINGE (1978): Towards a regional characterization of the biogeochemistry of alkali and alkali-earth metals in northern South America.- Acta cient. venez. 29: 434 - 444.
GESSNER, F. (1968): Zur ökologischen Problematik der Überschwemmungswälder des Amazonas.- Int. Rev. ges. Hydrobiol. 53: 525 - 547.
GOLLEY, F. B., YANTKO, J., RICHARDSON, Th. and H. KLINGE (1980a): Biogeochemistry of tropical forests. 1. The frequency distribution and mean concentration of selected elements in a forest near Manaus/Brazil.- Trop. Ecol. 21: 59 - 70.
GOLLEY, F. B., YANTKO, J. and C. JORDAN (1980b): Biogeochemistry of tropical forests. 2. The frequency distribution and mean concentration of selected elements near San Carlos de Rio Negro.- Trop. Ecol. 21: 71 - 81.
GRIMM, U. et H. W. FASSBENDER (1981): Ciclos biogeoquímicos en un ecosistema forestal de los Andes Occidentales de Venezuela. 1.- Turrialba 31: 27 - 37.
GRUBB, P. J. (1977): Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition.- Ann. Rev. Ecol. Syst. 8: 83 - 107.
HERRERA, R. (1979): Nutrient distribution and cycling in an Amazon Caatinga forest on spodosols in southern Venezuela.- Unpubl. Ph. D. Thesis, University of Reading, 241 p.
HERRERA, R., JORDAN, C. F., KLINGE, H. and E. MEDINA (1978): Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients.- Interciencia 3: 223 - 232.
HERRERA, R., JORDAN, C. F., MEDINA, E. and H. KLINGE (1981): How human activites disturb the nutrient cycles of a tropical rainforest in Amazonia.- Ambio 10: 109 - 114.
HERRERA, R., MEDINA, E., KLINGE, H., JORDAN, C. F. and C. UHL (in press): Nutrient retention mechanisms in tropical forests: The Amazon Caatinga, San Carlos pilot project, Venezuela. In: F. di Castri, F. W. G. Baker and M. Hadley (Eds.) Ecology in Practice: Establishing a scientific basis for land management. Tycooly, Dublin.
HOWARD-WILLIAMS, C. and W. J. JUNK (1977): The chemical composition of Central Amazonian aquatic macrophytes with special reference to their role in the ecosystem.- Arch. Hydrobiol. 79: 446 - 464.
HUECK, K. (1976): Die Wälder Südamerikas.- Fischer, Stuttgart, 422 p.
IRION, G., ADIS, J., JUNK, W. J. and F. WUNDERLICH (1983): Sedimentological studies of the "Ilha de Marchantaria" in the Solimões/Amazon River near Manaus.- Amazoniana 8 (1): 1 - 19.
IRMLER, U. (1975): Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazonia.- Amazoniana 5: 337 - 409.
IRMLER, U. (1977): Inundation-forest types in the vicinity of Manaus.- Biogeographica 8: 17 - 29.
IRMLER, U. (1978a): Matas de inundação da Amazônia Central em comparação entre águas brancas e pretas.- Ciência e Cultura 30: 813 - 821.
IRMLER, U. (1978b): Die Struktur der Carabiden- und Staphylinidengesellschaften in zentralamazonischen Überschwemmungswäldern.- Amazoniana 6: 301 - 326.
IRMLER, U. (1979): Considerations on structure and function of the Central-Amazonian Inundation Forest Ecosystem with particular emphasis on selected soil animals.- Oecologia (Berl.) 43: 1 - 18.
IRMLER, U. (1981): Überlebensstrategien von Tieren im saisonal überfluteten amazonischen Überschwemmungswald.- Zool. Anzeiger, Jena 206: 26 - 38.

IRMLER, U. (1982): Litterfall and nitrogen turnover in an Amazonian blackwater inundation forest.- Plant and Soil 67: 355 - 358.
JORDAN, C. F. and C. UHL (1978): Biomass of a "tierra firme" forest of the Amazon basin.- Oecologia Plantarum 13: 387 - 400.
JUNK, W. J. (1980): Areas inundáveis - um desafio para limnologia.- Acta Amazonica 10: 775 - 795.
KEEL, S. H. K. and G. T. PRANCE (1979): Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil).- Acta Amazonia 9: 645 - 655.
KLINGE, H. (1967): Podzol soils: A source of blackwater rivers in Amazonia.- Atas simpósio Biota Amazónica 3: 117 - 125.
KLINGE, H. (1976): Bilanzierung von Hauptnährstoffen im Ökosystem tropischer Regenwald (Manaus) – vorläufige Daten.- Biogeographica 7: 59 - 77.
KLINGE, H. (1982): Biologisch-ökologische Probleme Südamerikas.- MPG Spiegel 5: 12 - 15.
KLINGE, H. (in press, a): Was wissen wir von den Wäldern und Waldökosystemen Amazoniens? - Spixiana, München.
KLINGE, H. (in press, b): Forest structure.- Proc. I.U.C.N. workshop Sao Carlos/S. P., 1982.
KLINGE, H. and R. HERRERA (1978): Biomass studies in Amazon Caatinga forest in southern Venezuela. 1.- Trop. Ecol. 19: 93 - 110.
KLINGE, H. and R. HERRERA (in press): Phytomass structure of natural plant communities on spodosols in southern Venezuela: Tall Amazon Caatinga.- Vegetatio.
KLINGE, H. and W. A. RODRIGUES (1968a): Litter production in an area of Amazonian terra firme forest. 1.- Amazoniana 1: 287 - 302.
KLINGE, H. and W. A. RODRIGUES (1968b): Litter production in an area of Amazonian terra firme forest. 2.- Amazoniana 1: 303 - 310.
KLINGE, H. and W. A. RODRIGUES (1973): Biomass estimation in a Central Amazonian rain forest.- Acta cient. venez. 24: 225 - 237.
KLINGE, H. and W. A. RODRIGUES (1974): Phytomass estimation in a Central Amazonian rain forest.- In: H. A. Young (ed.) Forest Biomass Studies, Maine University Press, Orono, 339 - 350.
LOVELESS, A. R. (1962): Further evidence to support a nutritional interpretation of sclerophylly.- Ann. Bot. 26: 551 - 461.
MEDINA, E. (1981): Nitrogen content, leaf structure and photosynthesis in higher plants: a report to the UNEP study group on photosynthesis and bioproductivity, London.
MEDINA, E. (in press): Significación ecológica del contenido foliar de nutrientes y él área foliar especifica en ecosistemas tropicales.- Proc. IInd Congr. Latinamer. Bot., Brasilia 1978.
MEDINA, E. CUEVAS, E. et P. I. WEAVER (1981): Composición foliar y transpiración de especies leñosas de Pico del Este, Sierra de Luquillo, Puerto Rico.- Acta cient. venez. 32: 159 - 165.
MONK, C. D. (1966): An ecological significance of evergreenness.- Ecology 47: 504 - 505.
OHLER, F. M. J. (1980): Phytomass and mineral content in untouched forest.- CELOS rapporten 132: 1 - 43.
PEACE, W. J. H. and F. D. MACDONALD (1981): An investigation of the leaf anatomy, foliar mineral levels, and water relations of trees of a Sarawak forest.- Biotropica 13: 100 - 109.
PIRES, J. M. e H. M. KOURY (1959): Estudo de um trecho de mata de várzea próximo a Belém.- Bolm téc. Inst. Agron. Norte 36: 3 - 44.
PIRES, J. M. and G. T. PRANCE (1977): The Amazon forest: A natural heritage to be preserved.- In: G. T. Prance and T. S. Elias (eds.) Extinction is forever. Bronx, 158 - 194.
PRANCE, G. T. (1979): Notes on the vegetation of Amazonia. III.- Brittonia 31: 26 - 38.
PRANCE, G. T. (1980): A terminologia dos tipos de florestas amazónicas sujeitas a inundação.- Acta Amazonica 10: 495 - 504.
RAUNKIAER, C. (1934): The life-forms of plants and statistical plant geography.- Oxford, Clarendon, 632 p.
REVILLA, J. (1981): Aspectos florísticos a fitossociológicos da floresta inundável (igapó) Praia Grande, Rio Negro, Amazonas, Brasil.- Tese, Universidade do Amazonas e I.N.P.A., 129 p.
RODRIGUES, W. A. (1961a): Estudo preliminar de mata de várzea alta de uma ilha do baixo de Rio Negro de sólo argiloso e úmido.- I.N.P.A. Publ. Bot. 10: 1 - 50.

RODRIGUES, W. A. (1961b): Aspects phytosociologiques des pseudocatingas et forêst de varzea du Rio Negro.- In: A. Aubréville (loc. cit.), 209 - 265.
SIOLI, H. (1954): Gewässerchemie und Vorgänge in den Böden im Amazonasgebiet.- Naturwissenschaften 41: 456 - 457.
SOBRADO, M. and E. MEDINA (1981): General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'Bana' vegetation of Amazonas.- Oecologia (Berl.) 45: 341 - 345.
SPECTOR, W. S. (1956): In: W. B. Saunder (ed.) Handbook of biological data.- Cited after Bowen 1979.
STARK, N. (1970): The nutrient content of plants and soils from Brazil and Surinam.- Biotropica 2: 51 - 60.
STARK, N. (1971): Nutrient cycling: 1. Nutrient distribution in some Amazonian soils.- Trop. Ecol. 12: 24 - 50.
STEYN, W. J. A. (1959): Leaf analysis. Errors involved in the preparative phase.- Agric. Food Chemistry 7: 344 - 348.
TAKEUCHI, M. (1962): The structure of the Amazonian vegetation. VI. Igapó.- Jl Fac. Sci., Univ. Tokyo, Sect. III, Bot. 8: 297 - 304.
TANNER, E. V. J. (1977): Four montane rain forests of Jamaica.- J. Ecol. 65: 883 - 918.
WEBB, L. J. (1960): A new attempt to classify Australian rain forests.- Silva fennica 187: 103 - 106.
WILLIAMS, W. A., LOOMIS, R. S. and P. DE T. ALVIM (1972): Environments of evergreen rain forests on the lower Rio Negro, Brazil.- Trop. Ecol. 13: 65 - 78.
WORBES, M. (1983): Vegetationskundliche Untersuchungen zweier Überschwemmungswälder in Zentralamazonien – vorläufige Ergebnisse.- Amazoniana 8 (1): 47 - 65.

Author's addresses:

Dr. Hans Klinge
Dr. Karin Furch
Elke Harms
Max-Planck-Institut für Limnologie,
Arbeitsgruppe Tropenökologie
Postfach 165
D - 2320 Plön/Holstein
West Germany

Dr. J. Revilla C.
Instituto Nacional de Pesquisas
da Amazônia (INPA)
Caixa postal 478
69.000 Manaus/Amazonas
Brazil

Accepted for publication in January 1983