| AMAZONIANA | IX | 3 | 281 – 295 | Kiel, Dezember 1985 |
| --- | --- | --- | --- | --- |

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. 2. Campina

by

Hans Klinge

Dr. Hans Klinge, Max-Planck-Institut für Limnologie, Arbeitsgruppe Tropenökologie, Postfach 165, D - 2320 Plön/Holstein, West Germany.
(accepted for publication: December 1984)

**Abstract**

Adult leaves of 14 woody species were sampled in the campina at km 62 of the road Manaus – Caracaraí. The lamina were classified as to their size and analysed for N, P, K, Ca, Mg and Na.

Comparing the foliar levels of the bioelements to relevant data for other neotropical woody vegetation, they are much below those of forests from geochemically richer areas (Amazon várzea and certain other floodplains, volcanic areas) and resemble the foliar bioelement levels of terra firme vegetation.

Keywords: **foliar bioelements, campina, Amazon region, leaf size, tropical forest classification.**

## Resumen

Se han recolectado hojas adultas de 14 espécies leñosas de la campina en el kilómetro 62 de la carretera Manaus – Caracaraí. Las láminas han sido clasificadas según su tamaño. Seguidamente se las han analisado para N, P, K, Ca, Mg y Na.

Comparando los niveles foliares de bioelementos con datos relativos de otros tipos de vegetación leñosa neotropical, los de la campina son muy inferiores a aquellos de bosques de áreas geoquimicamente más ricas (area de inundación amazónica (várzea) y extra-amazónicas, áreas volcánicas). Son muy semejantes a los niveles foliares de bioelementos de la vegetación de tierra firme.

---

This study is dedicated to Prof. Dr. Harald Sioli to commemorate his 75th birthday.

---

0065-6755 / 1985 / 281 / © MPI für Limnologie, AG Tropenökologie, Plön; INPA, Manaus

## Introduction

Campina is a low sclerophyllous vegetation growing on 'white sands' (STARK 1970; BRAGA & BRAGA 1975; LISBÔA 1975; KLINGE & MEDINA 1979; ANDERSON 1981). PRANCE & SCHUBART (1978) assume that campina is an old secondary vegetation occupying sites of former white sand forest. Campina is surrounded by campinarana (campina forest, LISBÔA 1975). Campina comprises open or sun campina and closed or shade campina. The difference between these campina types is given by the extent of patches of vegetation separated by barren white sand areas and by the percentage of canopy coverage of the islands (ANDERSON et al. 1975). Each campina type has its own microclimatic characteristics (RIBEIRO & SANTOS 1975). The hydraulic conductivity of the sand is high (REICHARDT et al. 1975). Groundwater and streams draining campina sites are often of the blackwater type (KLINGE 1967; KLINGE & MEDINA 1979; BRINKMANN 1981; St. JOHN & ANDERSON 1982).

In the companion paper KLINGE et al. (1983) have demonstrated that the mean foliar concentrations of N, P, K, Ca, Mg and Na of trees from two stands of várzea forest sensu PRANCE (1979) of the lower Solimões are – also by tropical standards – relatively high. The mean foliar concentrations of the species from an igapó forest sensu PRANCE (1979) of the lower Rio Negro are much lower. The differences between várzea- and igapó foliage are confirmed by the results of chemical analyses of bark and wood samples from the same trees sampled for foliar analysis (KLINGE et al. 1984). A comparison of neotropical foliage chemistry of terra firme forests and of forest growing in floodplains (várzea) has revealed that the former forests in general have rather low foliar bioelement concentrations (KLINGE 1984).

In the present paper foliar concentrations of N, P, K, Ca, Mg and Na of 14 woody species sampled in a campina near Manaus are presented. Their means are compared to other tropical forests.

## Material and Methods

The leaves were sampled in the Campina Biological Reserve INPA/SUFRAMA at km 62 of the road Manaus – Caracaraí from Manaus, in the morning of October 12, 1982.

The list of plant species of that campina comprises 45 species in 35 families (ANDERSON et al. 1975). We sampled 14 species of which according to these authors 7 are common ones, 2 are occasional species, and 3 are rare ones (Table 3). Two species were not classified as to their frequency by ANDERSON et al. *Glycoxylon inophyllum* being dominant in the campina (ANDERSON et al. 1975; LISBÕA 1975) is the only species which was not sampled in the campina proper, but in the transition from campina to campinarana. Ten of the 14 species are included in a study of the dispersal mechanisms of campina species (MACEDO & PRANCE 1978).

The leaves were wrapped in paper and oven-dried at Manaus. The petioles were cut and the leaf blade outlines were drawn on paper, at Plön. By aid of a computer the leaf area was measured. Leaves were not washed or cleaned otherwise prior to chemical analysis. After grinding the powder was oven-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 spectroscopy (Perkin-Elmer AAS 300). P was estimated colorimetrically.

## Results and Discussion

### 1. Leaf size, Specific leaf area (SLA) and Specific leaf weight (SLW)

Six species (43 %) with leaves between 20.2 and 45 $cm^2$ in area are notophylls (WEBB 1960, Table 1). Leaves of four species (29 %) measuring between 45 and 182.2 $cm^2$ are mesophylls. Four additional species with leaves between 2.2 and 20.2 $cm^2$ are microphylls (RAUNKIAER 1934). The notophyll percentage of the campina is greater than in the igapó forest (KLINGE et al. 1983). An elevated percentage of notophylls was reported by BRUNIG (1974) for kerangas (Heath) forests in East Malaysia, also growing on low nutrient sandy soils. Notophylls are dominant in the bana, South Venezuela (BONGERS et al., in press; CUEVAS & KLINGE, in prep.), the soils being classified as Spodosols (FAO-Unesco 1971 - 1981). They are exposed to drought alternating with waterlogging.

Table 1: Mean specific leaf area (SLA) per leaf size class of 3 Amazon forests.

| | | Mesophylls (45 - 182.2 $cm^2$) | | Notophylls (20.2 - 45 $cm^2$) | | Microphylls (2.2 - 20.2 $cm^2$) | Average |
|---|---|---|---|---|---|---|---|
| Forest type | n | $cm^2/g$ (1 s.d.) | n | $cm^2/g$ (1 s.d.) | n | $cm^2/g$ (1 s.d.) | $cm^2/g$ |
| Várzea forest[1)] | 19 | 124.8 (54.0)a | 6 | 126.7 (35.0)ac | 4 | 167.5 (54.7)ac | 139.7 |
| Igapó forest[1)] | 9 | 93.6 (19.0)$b^x$ | 8 | 99.0 (57.2)ab | 5 | 98.7 (49.3)ab | 97.1 |
| Campina[2)] | 4 | 59.4 ( 9.2)$c^{xx}$ | 6 | 57.2 ( 7.8)$b^{xxx}$ | 4 | 63.2 (24.6)$b^x$ | 59.9 |

[1)]KLINGE et al. 1983 [2)]This study

In each column, figures followed by the same letter are not statistically different (t-test, $p > 0.05$)
$p < 0.05^x$ $p < 0.01^{xx}$ $p < 0.001^{xxx}$

Acc. to MEDINA (1984) tropical plants growing in highly leached, acid soils low in nutrients have a leaf anatomy characterized by a coriaceous texture, thick cell walls and cuticules, and a compact mesophyll. Their SLA ($cm^2/g$) is lower than the SLA of species growing in more favourable habitats (MEDINA & KLINGE 1983). The mean SLA of the campina species in the three leaf size classes is very low and even lower than in the igapó species growing in low nutrient quartz sand flooded for several month by the Rio Negro (Table 1). The differences between the leaf size classes of each forest are not significant statistically. MEDINA (1984) reported even lower SLA values for bana species (SOBRADO & MEDINA 1980).

The SLW ($g/m^2$) of evergreen species is much greater than of deciduous species (MEDINA 1984). The average SLW values in table 2 increase from 80 $g/m^2$ in the várzea forest with a relatively high proportion of deciduous trees (WORBES 1983) to 175 $g/m^2$ in the evergreen campina. The differences between the leaf size classes of each forest again are not significant statistically.

Table 2: Mean specific leaf weight (SLW) per leaf size class of 3 Amazon forests.

| | | Mesophylls | | Notophylls | | Microphylls | Average |
|---|---|---|---|---|---|---|---|
| Forest type | n | $g/m^2$ (1 s.d.) | n | $g/m^2$ (1 s.d.) | n | $g/m^2$ (1 s.d.) | $g/m^2$ |
| Várzea forest[1)] | 19 | 83.8 (27.9)a | 6 | 84.1 (23.0)a | 4 | 75.6 (22.9)a | 81.2 |
| Igapó forest[1)] | 9 | 110.7 (21.2)b$^{xx}$ | 8 | 129.3 (60.5)ab | 5 | 115.2 (34.8)ab | 118.4 |
| Campina[2)] | 4 | 171.6 (27.4)c$^{xxx}$ d$^{xx}$ | 6 | 177.9 (26.7)b$^{xxx}$ | 4 | 179.6 (73.3)b$^{x}$ | 176.4 |

1)KLINGE et al. 1983 2)This study For statistical differences see note in table 1.

## 2. Foliar levels of N, P, K, Ca, Mg and Na

### 2.1. Concentrations per unit dry weight

The foliar concentrations of N, P, K, Ca, Mg and Na of the campina species are tabulated in table 3. The species are arranged acc. to their leaf size. There is no statistically significant difference between the means of the leaf size classes, except for Ca. The mean Ca concentration of the mesophylls is significantly higher than is the mean concentration of Ca in the notophylls.

The variability of all elements within the mesophylls is relatively low. This is shown by the coefficient of variation. It is relatively small in the mesophylls, increases considerably among the notophylls, and is usually highest in the microphylls.

### 2.2. Content per unit leaf area

The foliar bioelement contents expressed as $g/m^2$ are tabulated in table 4. While there is no statistical difference between the contents of N, P, K and Mg of the three leaf size classes, the Ca content of the mesophylls is significantly higher than in both other leaf size classes, and the Na content of the notophylls is significantly higher than the Na content of the mesophylls. The coefficient of variation also increases from the mesophylls towards the microphylls, but the increase is usually not as strong as in the absolute concentrations (Table 3).

Comparing the nitrogen and phosphorus contents of the campina species to those reported by MEDINA (1984) for deciduous (1.6 g $N/m^2$, 0.12 g $P/m^2$) and evergreen species (4.3 g $N/m^2$, 0.23 g $P/m^2$), of a dry tropical forest the campina species (1.9 g $N/m^2$, 0.1 g $P/m^2$) resemble the deciduous species.

### 2.3. N/P ratio

High N/P ratios are indicative of a restricted soil phosphorus supply (MEDINA 1984). Only four campina species present N/P ratios below 20 : 1 (Table 4). The same small proportion of low N/P ratios was observed in the igapó community (KLINGE et al. 1983). Because of the high standard deviation of the mean N/P ratio of the campina species it is not significantly different from the mean N/P ratio of the várzea forest with much higher foliar bioelement concentrations and with smaller N/P ratios than both the campina and the igapó, respectively.

### 2.4. Foliar alkali- and alkali-earth metals

Hydrochemical research in the Amazon region (FURCH 1976, 1984; FURCH & KLINGE 1978; FURCH et al. 1982; JUNK & FURCH 1980) has revealed that chemically poor waters present a dominance of alkali metals over the alkali-earth metals. In the chemically richer Solimões water, however, the ratio between both elemental groups is reversed. In the comparative study of foliage chemistry of inundation forests in Central Amazonia (KLINGE et al. 1983) corresponding differences between tree species from both inundation forest types were observed.

The concentrations of alkali-earth- and alkali metals in the campina foliage, together with the relative contribution of these elements to their sum, are presented in table 5. A general dominance of the alkali- over the alkali-earth metals is observed. The ratio of both groups of elements, however, is only 1.1 : 1 in the mesophylls, while it is 2 : 1 in the notophylls and microphylls, respectively.

There is a single species (*Miconia* sp.) whose foliage is dominated by Ca. 57 % of the species present a dominance of foliar potassium, while 36 % of the species present a dominance of foliar sodium.

The mean concentration of foliar sodium of the campina is surprisingly high (Table 3). It is even 2.4 times higher than the already high foliar Na concentration of the Low bush savanna in Surinam (1800 ppm, STARK 1970). It is noteworthy that the foliage of the mixed terra firme forest at Manaus is also high in Na (1146 ± 827 ppm, GOLLEY et al. 1980). Although extremly high the foliar Na concentration of the campina does by far not reach the Na concentration of halophytes (25000 - 154000 ppm, FLOWER & LÄUCHLI 1983) or of grasses and herbs (up to 8400 ppm, BAUMEISTER & ERNST 1978). Since it cannot be excluded with certainty that the campina leaves were contaminated by sweat during the sampling (October 12, 1982 was a very hot and sunny day) the potential impact of sweat was checked. We assumed two drops of sweat per each leaf. Acc. to RÖMPP (1975) sweat usually contains over 0.5 % NaCl. Two drops of sweat (0.1 ml) containing then 0.4 mg Na were assumed to have contaminated each leaf sampled. The calculations, separately for the three leaf size classes, however, show that, if contamination by sweat occurred, it accounts for only a minor portion of the Na concentration of the campina leaves and cannot explain the observed foliar Na concentration in the order of 1000 to 18000 ppm Na (Table 3).

## 3. Foliar bioelements of the campina, in comparison with other tropical forests

Comparing the mean values of the six foliar elements of the campina vegetation to those of other tropical forests (Table 6), it can be expected from the outset that the várzea foliage or the foliage of forests growing on chemically rich soils is richer in bioelements than the campina. This expectation is realized by the data for the várzea forest and the Moist Tropical Forest of Panama (Table 6). The dry forest and partially the semideciduous forest, too, have also higher foliar bioelement concentrations.

The forests listed below the campina, although differing in one or another foliar bioelement from the campina, are much similar to the latter and their relatively low foliar bioelement concentrations contrast markedly to those of the first four examples in table 6.

Tab. 3: Concentration of foliar bioelements of 14 campina species.

| | Species | Family | Abundance[1)] | Dispersal mechanism[2)] | | ppm Nitrogen | Phosphorus | Potassium | Calcium | Magnesium | Sodium |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mesophylls | *Miconia* sp. | Melastomataceae | ? | | | 9300 | 410 | 4150 | 5270 | 3140 | 1160 |
| | *Clusia* sp. | Clusiaceae | ? | | | 10400 | 680 | 8890 | 7990 | 2580 | 3370 |
| | *Glycoxylon inophyllum* (Mart. e Miq.) Ducke | Sapotaceae | +++ | O | | 8900 | 590 | 9160 | 4570 | 3130 | 3010 |
| | *Macrolobium arenarium* Ducke | Leguminosae | (+) | | | 13000 | 380 | 7320 | 5570 | 1870 | 1940 |
| | | | | | Mean | 10400 | 515 | 7380 | 5850 | 2680 | 2370 |
| | | | | | s.d. | 584 a | 144 a | 2301 a | 1595 a | 600 a | 1010 a |
| | | | | | s.d. % | 5.6 | 28.0 | 31.2 | 27.3 | 22.4 | 42.6 |
| Notophylls | *Pagamea duckei* Standl. | Rubiaceae | +++ | O | | 10900 | 470 | 8650 | 3780 | 3240 | 2550 |
| | *Ouratea spruceana* Engl. | Ochnaceae | +++ | O | | 8300 | 380 | 6666 | 1590 | 2310 | 2210 |
| | *Manilkara amazonica* (Huber) Standl. | Sapotaceae | + | | | 9000 | 520 | 3380 | 1200 | 1680 | 5160 |
| | *Mouriri nervosa* Pilg. | Melastomataceae | (+) | O | | 10700 | 450 | 3110 | 1100 | 2230 | 5890 |
| | *Hirtella racemosa* Lam. var. *racemosa* | Chrysobalanaceae | +++ | O | | 9400 | 300 | 3840 | 4840 | 2800 | 6490 |
| | *Mabea occidentalis* Benth. | Euphorbiaceae | +++ | Au | | 13600 | 840 | 8290 | 1800 | 1740 | 2910 |
| | | | | | Mean | 10317 | 493 | 5656 | 2385 | 2333 | 4202 |
| | | | | | s.d. | 1893 a | 186 a | 2682 a | 1549 b[x] | 605 a | 1864 a |
| | | | | | s.d. % | 18.3 | 37.7 | 47.4 | 64.9 | 25.9 | 44.4 |
| Microphylls | *Sandemania hoehnei* (Cogn.) Wurdack | Melastomataceae | +++ | O | | 7900 | 380 | 4610 | 2340 | 3430 | 210 |
| | *Tabernamontana rupicola* Benth. | Apocynaceae | +++ | Au | | 13500 | 110 | 4660 | 1990 | 3010 | 3210 |
| | *Eugenia patrisii* Vahl | Myrtaceae | (+) | D | | 6100 | 300 | 3940 | 2980 | 1630 | 3640 |
| | *Vernonia grisea* Baker | Compositae | + | An | | 24300 | 900 | 15470 | 6740 | 4230 | 18580 |
| | | | | | Mean | 12950 | 423 | 7170 | 3513 | 3075 | 6410 |
| | | | | | s.d. | 8197 a | 338 a | 5543 a | 2190 ab | 1088 a | 8256 a |
| | | | | | s.d. % | 63.3 | 79.9 | 77.3 | 62.3 | 35.4 | 128.8 |

For statistical differences see note in Table 1

1) Acc. to ANDERSON et al. (1975): common +++; occasional +; rare (+)

2) Acc. to MACEDO & PRANCE (1978): Anemochory An; Autochory Au; Dyszoochory D; Ornithochory O

Tab. 4: Foliar contents of N, P, K, Ca, Mg and Na ($g/m^2$) in 14 campina species.

| | | $g/m^2$ | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Species | N | P | K | Ca | Mg | Na | N : P |
| Mesophylls | *Miconia* sp. | 1.403 | 0.062 | 0.626 | 0.795 | 0.474 | 0.175 | 22.6 |
| | *Clusia* sp. | 1.537 | 0.101 | 1.314 | 1.181 | 0.381 | 0.498 | 15.2 |
| | *Glycoxylon inophyllum* | 1.830 | 0.121 | 1.505 | 1.145 | 0.384 | 0.399 | 15.1 |
| | *Macrolobium arenarium* | 2.366 | 0.069 | 1.332 | 1.014 | 0.340 | 0.353 | 34.3 |
| | Mean | 1.784 | 0.088 | 1.194 | 1.034 | 0.395 | 0.356 | 21.8 |
| | s.d. | 0.427 a | 0.028 a | 0.388 a | 0.175 a | 0.057 a | 0.135 a | 9.0 a |
| | s.d. % | 23.9 | 31.8 | 32.5 | 16.9 | 14.4 | 37.9 | 41.3 |
| Notophylls | *Pagamea duckei* | 1.687 | 0.073 | 1.339 | 0.585 | 0.502 | 0.395 | 23.1 |
| | *Ouratea spruceana* | 1.521 | 0.070 | 1.220 | 0.291 | 0.423 | 0.405 | 21.7 |
| | *Manilkara amazonica* | 2.022 | 0.117 | 0.759 | 0.270 | 0.377 | 1.159 | 17.3 |
| | *Mouriri nervosa* | 2.018 | 0.085 | 0.587 | 0.207 | 0.421 | 1.111 | 23.7 |
| | *Hirtella racemosa* | 1.755 | 0.056 | 0.717 | 0.904 | 0.523 | 1.212 | 31.3 |
| | *Mabea occidentalis* | 2.119 | 0.131 | 1.292 | 0.280 | 0.271 | 0.453 | 16.2 |
| | Mean | 1.854 | 0.087 | 0.986 | 0.423 | 0.420 | 0.789 | 22.2 |
| | s.d. | 0.234 a | 0.029 a | 0.333 a | 0.270 $b^{xx}$ | 0.091 a | 0.409 $b^{x}$ | 5.4 a |
| | s.d. % | 12.6 | 33.3 | 33.8 | 63.8 | 21.7 | 51.8 | 24.3 |
| Microphylls | *Sandemania hoehnei* | 1.689 | 0.081 | 2.138 | 0.500 | 0.733 | 0.045 | 20.9 |
| | *Tabernamontana rupicola* | 1.566 | 0.013 | 0.541 | 0.231 | 0.349 | 0.372 | 120.5 |
| | *Eugenia patrisii* | 1.626 | 0.080 | 1.050 | 0.794 | 0.435 | 0.970 | 20.3 |
| | *Vernonia grisea* | 2.960 | 0.110 | 1.884 | 0.821 | 0.515 | 2.263 | 26.9 |
| | Mean | 1.960 | 0.071 | 1.403 | 0.587 | 0.508 | 0.913 | 47.2 |
| | s.d. | 0.668 a | 0.041 a | 0.739 a | 0.278 $bd^{xx}$ | 0.165 a | 0.978 ab | 49.0 a |
| | s.d. % | 34.1 | 57.7 | 52.7 | 47.4 | 32.5 | 107.1 | 103.8 |
| | Overall mean | 1.864 | 0.084 | 1.165 | 0.644 | 0.438 | 0.701 | 29.2 |
| | s.d. | 0.414 | 0.031 | 0.486 | 0.351 | 0.111 | 0.586 | 26.9 |
| | s.d. % | 22.0 | 36.9 | 41.7 | 54.5 | 25.3 | 83.6 | 92.1 |

For statistical differences see note in Table 1

Tab. 5: Concentrations of foliar alkali-earth- and alkali metals and the proportions of Ca, Mg, K and Na.

| | | ppm | K + Na | % | | | |
|---|---|---|---|---|---|---|---|
| | Species | Ca + Mg + K + Na | Ca + Mg | Ca | Mg | K | Na |
| Mesophylls | *Miconia* sp. | 13720 | 0.63 : 1 | 38.4 | 22.9 | 30.2 | 8.5 |
| | *Clusia* sp. | 22830 | 1.16 : 1 | 35.0 | 11.3 | 38.9 | 14.9 |
| | *Glycoxylon inophyllum* | 19870 | 1.58 : 1 | 23.0 | 15.8 | 46.1 | 15.1 |
| | *Macrolobium arenarium* | 16700 | 1.24 : 1 | 33.4 | 11.2 | 43.8 | 11.6 |
| | Mean | 18280 | 1.14 : 1 | 32.5 | 15.3 | 39.8 | 12.5 |
| | s.d. | 3938 A | | 6.6 ACa | 5.5 Ab$^{xx}$c | 7.0 Aad$^{xx}$e | 6.9 Ab$^{xx}$f$^{xx}$ |
| Notophylls | *Pagamea duckei* | 18220 | 1.60 : 1 | 20.7 | 17.8 | 47.5 | 14.0 |
| | *Ouratea spruceana* | 12776 | 2.28 : 1 | 12.5 | 18.1 | 52.2 | 17.3 |
| | *Manilkara amazonica* | 11420 | 2.97 : 1 | 10.5 | 14.7 | 29.6 | 45.2 |
| | *Mouriri nervosa* | 12330 | 2.70 : 1 | 8.9 | 18.1 | 25.2 | 47.8 |
| | *Hirtella racemosa* | 17970 | 1.35 : 1 | 26.9 | 15.6 | 21.4 | 36.1 |
| | *Mabea occidentalis* | 14740 | 3.16 : 1 | 12.2 | 11.8 | 56.2 | 19.7 |
| | Mean | 14576 | 2.09 : 1 | 15.3 | 16.0 | 38.7 | 30.0 |
| | s.d. | 2935 A | | 7.0 B$^{xx}$a | 2.5 Aac | 15.0 Ab$^{x}$de | 14.9 B$^{x}$ae |
| Microphylls | *Sandemania hoehnei* | 10590 | 0.84 : 1 | 22.1 | 32.4 | 43.5 | 2.0 |
| | *Tabernamontana rupicola* | 12870 | 1.57 : 1 | 15.5 | 23.4 | 36.2 | 24.9 |
| | *Eugenia patrisii* | 12190 | 1.64 : 1 | 24.4 | 13.4 | 32.3 | 29.9 |
| | *Vernonia grisea* | 45020 | 3.10 : 1 | 15.0 | 9.4 | 34.3 | 41.3 |
| | Mean | 20168 | 2.06 : 1 | 19.3 | 19.7 | 36.6 | 24.5 |
| | s.d. | 16596 A | | 4.7 B$^{x}$Da | 10.3 Aac | 4.9 Ab$^{xx}$d$^{x}$ | 16.5 ABad |
| | Overall mean | 17232 | 1.71 : 1 | 21.3 | 16.9 | 38.4 | 23.4 |
| | s,d. | 8581 | | 9.5 | 6.1 | 10.3 | 14.4 |

For statistical differences see note in Table 1

Mayuscules refer to columns, minuscules to rows

## 4. Tentative classification of tropical forest based on foliar bioelements

In search for a scale of a classification of foliar bioelement concentrations, the absolute ranges of foliar N, P, K, Ca, Mg and Na of Amazon inundation forests were divided in four equal portions. Each species was then compared to the respective four concentration classes, and species with a similar bioelement pattern were identified (KLINGE et al. 1983). For example, species with concentrations of foliar N, P, and K in both upper concentration classes, but with foliar Ca, Mg and Na in the lower concentration classes were classified as 'rich to very rich in foliar N, P, and K, and low to very low in foliar Ca, Mg and Na'.

The next step was to compile chemical foliage data of tropical forests. The obtained ranges of the various foliar bioelements were considered as the respective tropical standards against which individual data were measured. This allowed to classify the várzea forests as 'relatively rich by tropical standards' in foliar bioelements, while the igapó forest was classified as 'relatively poor in these elements by tropical standards' (KLINGE et al. 1983).

In a study of exclusively neotropical forests with a majority of examples from Amazonia (KLINGE 1984), two chemical groups of forest foliage were established. One group had significantly higher concentrations of foliar N, P, K, Ca and Mg than the other one. The group with lower concentrations comprised terra firme forests and also the igapó forest. The group with higher concentrations was composed by várzea forests and a few extra-Amazonian forests in Panama and western Venezuela. Both areas are geochemically richer than most of the Amazon region (FITTKAU 1971), the minor portion of Amazonia which is geochemically relatively rich, being the várzea. Comparing the foliar means of both groups to the tropical foliar standards subdivided in three equal sections (upper portion termed 'rich by tropical standards', middle portion accordingly as 'medium by tropical standards', and lower portion as 'poor by tropical standards') (Fig. 1), it is evident that even the group with higher foliar concentrations has mean concentrations of foliar Ca, K, Mg and P which are 'medium by tropical standards', while the group of lower concentrations is in these elements 'poor by tropical standards'. The mean foliar nitrogen concentration of the group of higher concentrations, however, is identified as 'rich in foliar N, by tropical standards', and the mean nitrogen concentration of the other group as 'medium in this bioelement, by tropical standards'.

In Fig. 2, the foliar concentrations of the sixteen stands (Table 6 refers) are presented graphically. They are compared, individually for each element, to both the levels of foliar concentrations of the groups of higher and lower concentrations, and to the respective tropical standards. While most forests including the campina are in all elements, except for sodium, in the lower portion of the tropical ranges, the first three forests of table 6 fall in the middle portion in the cases of foliar Ca, K and Mg. The foliar N concentration of the várzea forests falls in the upper portion of the tropical range and is accompanied by the foliar N concentration of the Brazilian podzol vegetation (no. 15, Table 6). The Tall Caatinga and the Low bush savanna have foliar Mg concentrations classified as 'medium by tropical standards' while they are classified as 'poor by tropical standards' in the remaining foliar elements. There are also some additional exceptions from the general rule which are not mentioned specifically.

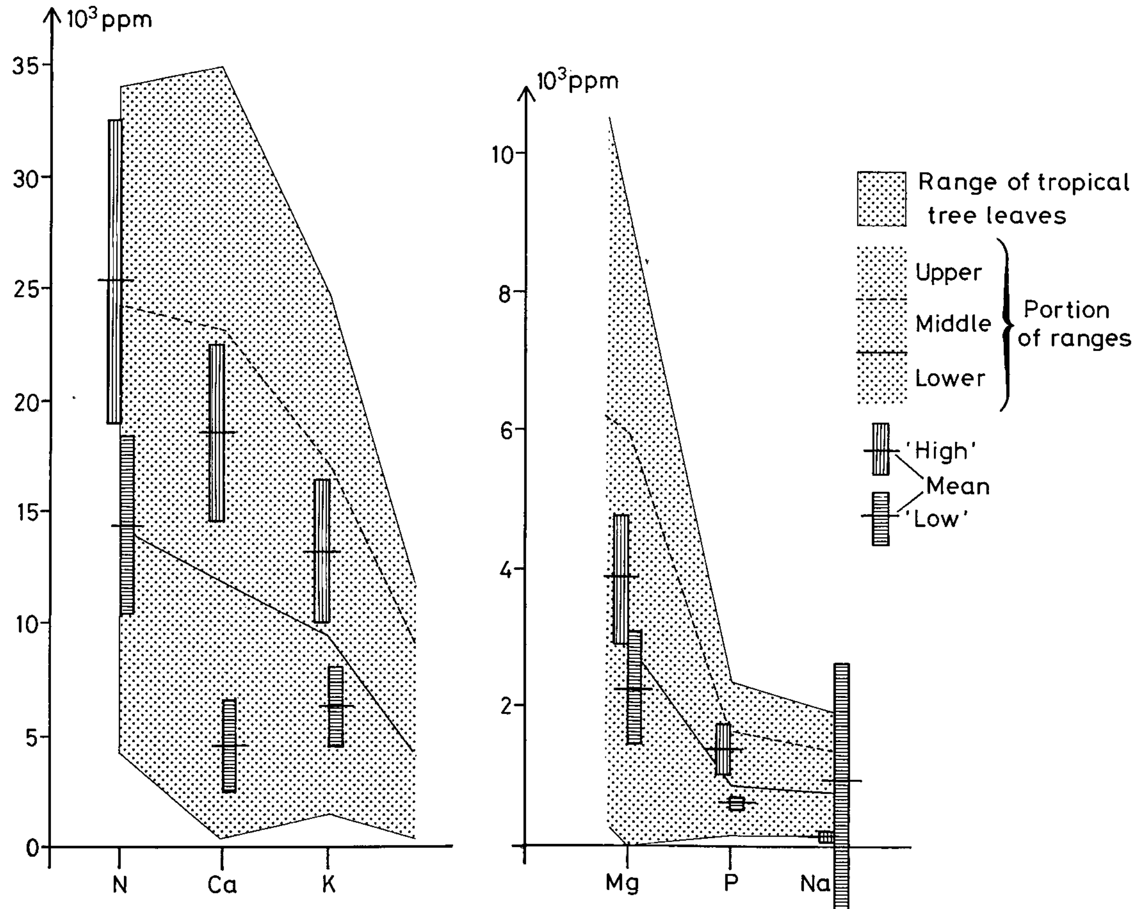


Fig. 1:
'High' and 'low' mean foliar concentrations of N, P, K, Ca, Mg and Na of neotropical (mostly Amazonian) forests, in comparison with the ranges of these elements in tropical tree foliage subdivided in three equal sections (upper, middle and lower ones, defined as – by tropical standards – 'rich', 'medium' and 'poor').

Tab. 6: Average foliar bioelement levels of selected tropical forest stands.

| | Forest type | N of species | N | P | K | Ca | Mg | Na | Source |
|---|---|---|---|---|---|---|---|---|---|
| | | | ppm (1 s.d.) | | | | | | |
| 1.[1] | Várzea forest Marchantaria | 28 | 25865 (5307) $b^{xxx}$ | 1755 (430) $b^{xxx}$ | 13183 (6840) $b^{xxx}$ | 19141 (8312) $b^{xxx}$ | 3982 (1850) $b^{xx}$ | 195 (270) $b^{xx}$ | KLINGE et al. 1983 |
| 2. | Moist tropical f. Panama | ? | 14000 | 1500 (931) $c^{xx}$ | 15300 (6230) $c^{xxx}$ | 22900 (1824) $c^{xxx}$ | 2575 (340) a | 225 (126) $c^{xx}$ | GOLLEY et al. 1975 |
| | Dry forest | | | | | | | | |
| 3. | Deciduous sp. | 7 | 21000 (2700) $c^{xxx}$ | 1580 (300) $d^{xxx}$ | 17000 (8100) $d^{xxx}$ | 15800 (8800) $d^{xxx}$ | 3600 (1800) a | n.d. | MEDINA 1984 |
| 4. | Evergreen sp. | 4 | 11800 (1600) a | 710 (70) $e^{xx}$ | | | | | MEDINA 1984 |
| | Semideciduous f | | | | | | | | |
| 5. | Deciduous sp. | 4 | 17100 (2200) $d^{xx}$ | 1150 (460) $f^{x}$ [1] | 6500 (2900) a | 7700 (3600) $e^{x}$ | 2900 (1600) a | n.d. | MEDINA 1984 |
| 6. | Evergreen sp. | 9 | 12100 (4700) a | 570 (200) a | | | | | MEDINA 1984 |
| 7. | Campina (BS) | 14 | 11093 (4376) a | 479 (216) a | 6581 (3386) a | 3697 (2184) a | 2644 (774) a | 4309 (4436) a | This study |
| 8. | Montane forests | 21 | 11730 (1850) a | 660 (143) $g^{xx}$ | 5133 (351) a | 7230 (825) $f^{xxx}$ | 1960 (551) $c^{xx}$ | n.d. | MEDINA 1984 |
| 9. | Amazon forest | 27 | 10560 (2800) a | 610 (115) $h^{x}$ | 5730 (987) a | 4030 (1976) a | 1300 (265) $d^{xxx}$ | n.d. | MEDINA 1984 |
| 10. | Heath forest (BS) | 9 | 8702 (1373) a | 219 (62) $i^{xxx}$ | 3507 (1484) $e^{xx}$ | 7497 (5082) $g^{x}$ | 1995 (2222) a | n.d. | PEACE & MacDONALD 1981 |
| 11. | Igapó forest (BS) | 22 | 17305 (4042) $e^{xxx}$ | 618 (256) a | 6325 (2617) a | 2506 (2041) a | 1218 (584) $e^{xxx}$ | 249 (441) $d^{xx}$ | KLINGE et al. 1983 |
| 12. | Tall Caatinga (BS) | 40 | 10820 (4090) a | 560 (180) a | 5830 (2820) a | 5280 (3830) a | 3560 (1560) $f^{xx}$ | n.d. | HERRERA 1979 |
| 13. | Dimorphandra f. Surinam (BS) | 1 | 20410 | 1375 | 1548 | 8000 | 2400 | 500 | STARK 1970 |
| 14. | Low bush sand savanna (BS) | ? | 5050 | 625 | 1547 | 6800 | 3750 | 1800 | STARK 1970 |
| 15. | Brazil podzols (BS) | ? | 28200 | 2500 | 6500 | 2500 | 2200 | 240 | STARK 1970 |
| 16. | Bana (BS) | 12 | 8350 (3452) a | 440 (174) a | 6950 (3512) a | 3510 (1575) a | n.d. | n.d. | SOBRADO & MEDINA 1980 |

[1] Numbers refer to Fig. 2

BS = Bleached sand and similar extremely low nutrient soils, partly classified as Spodosols

For statistical differences see note in Table 1

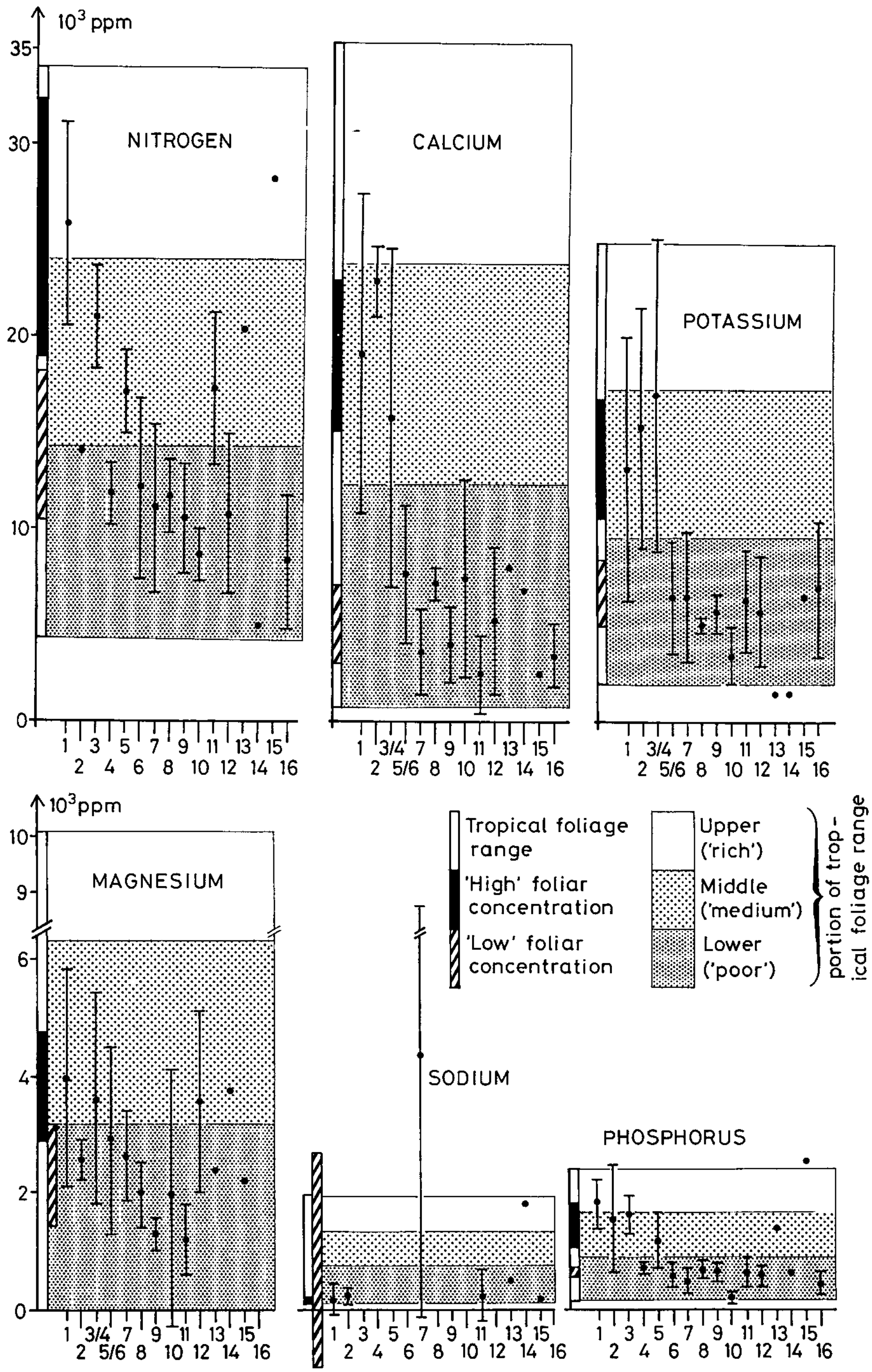


Fig. 2:
Mean foliar concentrations of N, P, K, Ca, Mg and Na of 16 tropical forests identified in table 6, in comparison with both the respective tropical ranges subdivided in three equal portions (upper or 'rich', middle or 'medium', lower or 'poor'), and 'high' and 'low' mean foliar concentration of neotropical forests (see Fig. 1).

## Final remarks

Oligotrophic bleached quartz sands whether or not classified as Spodosols are widespread in the humid tropics of particularly South America and Southeast Asia (KLINGE 1968). The Rio Negro basin in northern South America is one of the centres of distribution of these soils (KLINGE 1966).

One pecularity of these soils is that they carry a vegetation which regarding floristics and structure differs strikingly from the surrounding forest on heavier textured soils (SPRUCE 1908; DUCKE & BLACK 1953; STEENIS 1935; RICHARDS 1954; BRUNIG 1974). This curious vegetation is intimately related to the 'heath' vegetation (SPECHT 1979).

SIOLI (1954) assumed that the peculiar vegetation of bleached quartz sands is the cause of humic-stained streams of the blackwater-type. Not being a terrestrial ecologist he invited me 25 years ago to join the group of scientists he had gathered in the Max-Planck-Institut at Plön, in order to develop research about the vinculation of land and water, specifically the Amazon blackwaters and their terrestrial environment in which these waters were assumed to rise. Being very grateful for this unique opportunity this paper is dedicated to Harald Sioli at the occasion of his 75th birthday.

## Acknowledgments

We are grateful to Dr. S. Renner, University of Hamburg for assistance in sampling and identification of the species; to Dr. H. J. Krambeck, Plön, for measuring the leaf areas, and to D. Albrecht, J. Dieterich, E. Harms, D. Lemcke, all at Plön, and I. Ploog, Schuby, for skillful technical assistance.

## References

ANDERSON, A. B. (1981): White-sand vegetation of Brazilian Amazonia.- Biotropica 13: 199 - 210.

ANDERSON, A. B., PRANCE, G. T. & B. W. P. DE ALBUQUERQUE (1975): A vegetação lenhosa da Campina da Reserva Biológica INPA-SUFRAMA (Manaus - Caracaraí, km 62).- Acta Amazonica 5: 225 - 246.

BAUMEISTER, W. & W. ERNST (1978): Mineralstoffwechsel und Pflanzenwachstum.- Fischer, Stuttgart, p. 139 - 141.

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

BRAGA, M. N. & P. I. S. BRAGA (1975): Estudos ecológicos da campina da Reserva Biológica INPA-SUFRAMA (Manaus - Caracaraí, km 62).- Acta Amazonica 5: 247 - 260.

BRINKMANN, W. L. F. (1981): Zum Chemismus von Schwarzwässern in Zentralamazonien.- Beitr. Hydrol., Sonderheft 2: 121 - 135.

BRUNIG, E. F. (1974): Ecological studies in the Kerangas forests of Sarawak and Brunei. Kuching, Sarawak Forest Department, 237 p.

CUEVAS, E. & H. KLINGE (in prep.): Bana: biomass, nutrient content, litter fall and decomposition.-

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

FAO-Unesco (1971 - 1981): Soil map of the world.- Paris, Unesco.

FLOWER, T. J. & A. LÄUCHLI (1983): Sodium versus potassium: substitution and compartmentation.- In: O. L. LANGE et al. (eds.) Encyclopedia of Plant Physiology, N. S., Berlin - Heidelberg - New York, Springer, 15B: 651 - 681.

FITTKAU, E. J. (1971): Ökologische Gliederung des Amazonasgebietes auf geochemischer Grundlage.- Münster. Forsch. Geol. Paläontol. **20/21:** 35 - 50.
FURCH, K. (1976): Haupt- und Spurenmetallgehalte zentralamazonischer Gewässertypen (erste Ergebnisse).- Biogeographica **7:** 27 - 43.
FURCH, K. (1984): Water chemistry of the Amazon basin: The distribution of chemical elements among freshwaters.- In: H. SIOLI (ed.) The Amazon. Junk, Dordrecht, p. 167 - 199.
FURCH, K., JUNK, W. J. & H. KLINGE (1982): Unusual chemistry of natural waters from the Amazon region.- Acta cient. venez. **33:** 269 - 273.
FURCH, K. & 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.
GOLLEY, F. B., McGINNIS, J. T., CLEMENTS, R. G., CHILD, G. I. & M. J. DUEVER (1975): Mineral cycling in a Tropical Moist Forest ecosystem.- Athens, University of Georgia Press, 248 pp.
GOLLEY, F. B., YANTKO, J., RICHARDSON, Th. & H. KLINGE (1980): Biogeochemistry of tropical forests. 1.- Trop. Ecol. **21:** 59 - 70.
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.
JUNK, W. J. & K. FURCH (1980): Quimica da água e macrófitas aquáticas de rios e igarapés na Bacia Amazônica e nas áreas adjacentes.- Acta Amazonica **10:** 611 - 633.
KLINGE, H. (1966): Verbreitung tropischer Tieflandspodsole.- Naturwiss. **53:** 442 - 443.
KLINGE, H. (1967): Podzol soils: a source of blackwater rivers in Amazonia.- Atas Simpósio Biota Amazonica, Belém 1966, **3:** 117 - 125.
KLINGE, H. (1968): Report on tropical podzols. 1st draft.- FAO, Rome, 88 pp.
KLINGE, H. (1984): Lowland Amazon forests, bioelements and geochemistry.- EMBRAPA-CPATU, 1st Symposium on the Humid tropics, Belém 1984.
KLINGE, H., FURCH, K. & E. HARMS (1984): Selected bioelements in bark and wood of native tree species from Central-Amazonian inundation forests.- Amazoniana 9 (1): 105 - 117.
KLINGE, H., FURCH, K., HARMS, E. & J. REVILLA (1983): Foliar nutrient levels of native tree species from Central Amazonia. 1.- Amazoniana **8:** 19 - 45.
KLINGE, H. & E. MEDINA (1979): Rio Negro Caatingas and Campinas, Amazonas States of Venezuela and Brazil.- In: R. L. SPECHT (ed.) Heathlands and related shrublands. Ecosystems of the world **9A:** 483 - 488.
LISBÔA, P. L. (1975): Observações gerais e revisão bibliográfica sobre as campinas amazônicas de areia branca.- Acta Amazonica **5:** 211 - 223.
MACEDO, M. & G. T. PRANCE (1978): Notes on the vegetation of Amazonia II.- Brittonia **30:** 203 - 215.
MEDINA, E. (1984): Nutrient balance and physiological processes at the leaf level.- In: E. MEDINA, H. A. MOONEY & C. VÁZQUEZ-YANES (eds.) Physiological ecology of plants of the wet tropics. The Hague, Junk, 139 - 154.
MEDINA, E. & H. KLINGE (1983): Productivity of tropical forests and tropical woodlands.- In: O. E. LANGE et al. (eds.) Encyclopedia of Plant Physiology, N. S., Berlin - Heidelberg - New York **12D:** 281 - 303.
PEACE, W. J. H. & 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.
PRANCE, G. T. (1979): Notes on the vegetation of Amazonia III.- Brittonia **31:** 26 - 38.
PRANCE, G. T. & H. O. R. SCHUBART (1978): Notes on the vegetation of Amazonia I.- Brittonia **30:** 60 - 63.
RAUNKIAER, C. (1934): The life-forms of plants and statistical plant geography.- Oxford, Clarendon, 632 p.
REICHARDT, K., SANTOS, A. DOS, NASCIMENTO, V. F. DO & O. O. S. BACCHI (1975): Movimento de água subterrânea em ecossistema Campina Amazônica.- Acta Amazonica **5:** 287 - 290.
RIBEIRO, M. DE N. G. & A. DOS SANTOS (1975): Observações microclimáticas no ecossistema Campina amazônica.- Acta Amazonica **5:** 183 - 189.
RICHARDS, P. W. (1954): The tropical rain forest. University Press, Cambridge, 450 pp.
RÖMPP's Chemie-Lexikon (1975).- Stuttgart, Franckh, 7. ed. p. 3140.

SIOLI, H. (1954): Gewässerchemie und Vorgänge in den Böden im Amazonasgebiet.- Naturwissenschaften **19:** 456 - 457.
SOBRADO, M. & E. MEDINA (1980): General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'bana' vegetation of Amazonas.- Oecologia (Berl.) **45:** 341 - 345.
SPECHT, R. L. (1979): Heathlands and related shrublands of the world.- In: R. L. SPECHT (ed.) Heathlands and related shrublands.- Ecosystems of the world **9A:** 1 - 18.
SPRUCE, R. (1908): Notes of a botanist on the Amazon and the Andes.- MacMillan, London, vols. 1 and **2:** 518 pp and 542 pp.
STARK, N. (1970): The nutrient content of plants and soils from Brazil and Surinam.- Biotropica **2:** 51 - 60.
STEENIS, C. G. G. J. VAN (1935): Maleische vegetatieschetsen.- Tidschr. k. Ned. Ardrijkse. Genootschap, 2nd Ser., Part **52:** 171 - 203.
St. JOHN, T. V. & A. B. ANDERSON (1982): A re-examination of plant phenolics as a source of tropical black water rivers.- Trop. Ecol. **23:** 151 - 154.
WEBB, L. J. (1960): A new attempt to classify Australian rain forests.- Silva fennica **187:** 103 - 106.
WORBES, M. (1983): Vegetationskundliche Untersuchungen zweier Überschwemmungswälder in Zentralamazonien.- Amazoniana **8:** 47 - 65.