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A CONTRIBUTION TO THE KNOWLEDGE OF THE BIOGEOCHEMISTRY OF AMAZON INUNDATION FORESTS.

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SUMMARY

Inundation forests from geochemically differing Amazon flood-plains are compared to forests from the Amazon terra firme growing on soils of different chemical quality, regarding the mean chemical composition by N, P, K, Ca, Mg and Na of their foliage, bark and wood.

The major findings are:

1º No commonality of the chemical structure of the inundation forests as opposed to the terra firme forests exists. But there is much commonality of inundation forests flooded by rivers relatively rich chemically (vārzea forests), on the one hand, and of terra firme and igapō inundation forests (non-vārzea forests) drained by chemically poor rivers, on the other hand.

2º The vārzea forests present total bioelement concentrations of at least 50000 ppm in both the foliage and the bark and of more than 13000 ppm in the wood. The non-vārzea forests present significantly lower levels of total bioelements.

3º The differences between the vārzea and non-vārzea forests are explained by differences of the geochemical conditions of the vārzea and non-vārzea segments of the Amazon land-scape, particularly regarding soil chemistry.

4º The most prominent difference between the vārzea and non-vārzea forests relates to the bioelements nitrogen and calcium. While the nitrogen proportion (expressed as per cent of the total bioelement content) of the vārzea forests is considerably lower in all biomass fractions than in the non-vārzea forests, the reserve is true for calcium. In addition, there is a remarkably high Na proportion of the foliage of non-varzea forests.

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UMA CONTRIBUIÇÃO AO CONHECIMENTO DA BIOGEOQUĪMICA DA BACIA AMAZŌNICA

RESUMO

As florestas de inundação das planīcies alagadas da Amazōnia, geoquimicamente diferentes, são comparadas ās florestas de terra firme da Amazōnia, que crescem sobre solos de qualidade quīmica diferente, considerando-se a composição quīmica mēdia pelo N, P, K, Ca, Mg e Na da folhagem, cōrtex e madeira.

Encontrou-se principalmente que:

1º Não existe nada em comum entre a estrutura quīmica das florestas de inundação em oposição ās florestas de terra firme. Entretanto, hā muito mais em comum entre as florestas de inundação, alagadas por rios relativamente ricos em produtos quīmicos (florestas de vārzea) por um lado, e por outro lado as florestas de terra firme e de igapō drenados por rios quimicamente pobres.

2º A concentração total de bioelementos em florestas de vārzea ē de pelo menos 50000 ppm tanto na folhagem como no cōrtex e de mais de 13000 ppm na madeira. As florestas de igapō e terra firme não apresentam nīvel significativamente menores do total de bioelementos.

3º As diferenças entre as florestas de vārzea e terra firme e igapō são explicadas pelas diferenças das condições geoquīmicas dos segmentos de vārzea, terra-firme e igapō da Amazōnia, especialmente com relação ā quīmica do solo.

4º A diferença mais notāvel entre as florestas de vārzea e terra-firme e igapō estā relacionada com os bioelementos nitrogēnio e cālcio. Enquanto a proporção do nitrogēnio (expressa em porcentagem do conteūdo total do bioelemento) das florestas de vārzea ē consideravelmente menor em todas as frações da biomassa do que nas florestas de terra-firme e igapō, com o cālcio dā-se o inverso. Alēm disso, hā uma proporção nitidamente elevada de Na na folhagem das florestas de terra-firme e igapō.

Present State-of-the-Art of Neotropical Forest Biogeochemistry

A comprehensive study of forest biogeochemistry requires to sample, in a given area or in a defined ecosystem, the major compartments, i.e., forest and faunal biomass, soil and soil parent material, aqueous and other fluxes within and between compartments, and to analyze the samples for chemical elements. Virtually all chemical elements of the periodic table should be estimated. This is, in addition to theoretical reasons, recommended by the surprising observation of the specific accumulation of chemical elements in fruits of certain species (Para-nut: barium, SEABER 1933; Couroupita guianensis: selenium, VARESCHI 1985).

Such a comprehensiveness is however not achieved in practice. Faunal biomass is only exceptionally analyzed and a selection of just a few chemical elements - mostly biologically important ones - is taken into account.

Considering the investment of labour, time and money in that kind of research, one might expect to find that tropical Third World forests are much less studied biogeochemically than forests of temperate developed countries. However, this is not true! Regarding lowland neotropical forests much relevant information is available in literature (Table 1); paleotropical forests are less studied in this respect.

Almost twenty different neotropical forests of the mainland's lowlands have been analyzed for at least the bioelements N, P, K, Ca, Mg and Na in the above ground biomass, by various authors (Table 1). The list is headed by a monograph of Panamanian forests. This first neotropical biogeochemical forest study published in 1975 by GOLLEY et al. was designed as a nutrient cycling study and is remarkably comprehensive. It deals with faunal and plant biomass, ecosystem fluxes and includes twenty different chemical elements.

Biogeochemical data of neotropical mountain forests can be found in FASSBENDER & GRIMM (1981), GRIMM & FASSBENDER (1981), GRUBB (1977), JORDAN (1977), MEDINA (1984), MEDINA et al. (1981), OVINGTON & OLSON (1970), and TANNER (1970).

The content of Table 1, when compared to the literature cited in 1967 by RODIN & BAZILEVICH, reflects the since then made impressive progress of neotropical forest biogeochemistry.

In spite of this progress only first steps into the field of biogeochemistry connecting geoscience and vegetation science were made. This becomes also evident from the subsequent presentation. In it, mean values of the concentrations of only six bioelements are being used. In a biogeochemical context, this is a legal way to describe the sampled ecological system. But in a biological-ecological context the chosen way is defective in that the mean values do not reflect the species diversity of the system.

Table 1 Publications covering bioelement inventories of the above ground biomass of neotropical lowland forest

Country	Forest type	Authors
1. Panama	Tropical Moist Forest	Golley et al. 1975
2. Panama	Same as 1, in addition Riverine, Mangrove and Mountain forests	Golley and Richardson 1977
3. Brazil	Amazon terra firme forest	Klinge 1976
4. Colombia	Tropical evergreen forest	Fölster et al. 1976
5. Venezuela	Amazon Caatinga forest	Herrera 1979
6. Brazil	Same as 3	Golley et al. 1980 a
7. Venezuela	Amazon terra firme forest	Golley et al. 1980 b
8. Surinam	Terra firme forest	Ohler 1980
9. Belize	Seasonally dry tropical hard-wood forest	Lambert et al. 1980
10. Venezuela	Semi-evergreen seasonal forest	Hase and Fölster 1982
11. Brazil	Vârzea- and igapõ forests	Klinge et al. 1983
12. Brazil	Neotropical forest comparison	Klinge 1984
13. Belize	Palm-dominated forest	Arnason et al. 1984
14. Brazil	Campina, in comparison with neo-tropical forests	Klinge 1985, in press
15. Brazil	Vârzea- and igapõ forests	Klinge et al., 1985, in press
16. Venezuela	Bana woodland	Cuevas and Klinge, unpubl.
17. Brazil	Vârzea forest	Klinge, unpubl.

Materials

The papers listed in Table 1 cover a wide geographical range from Belize in Central America down to the Amazon region of Brazil. They also cover a wide range of forest types. The majority of examples represents lowland forests not subject to flooding, i.e., upland or terra firme forests. According to the title of my presentation, it aims at describing biogeochemical features of Amazon inundation forests. Although inundation areas in general and tropical ones in particular were in the past much neglected by ecologists (JUNK 1980), four stands of such forests in the neotropics have been analyzed chemically.

The selected primary terra firme and inundation forest types to be discussed in this paper have in common a forest structure with a closed canopy at a height of 20-25 m above ground. In addition, they are floristically diverse and differ in species composition. They are exposed to drastically contrasting hydrological regimes. The terra firme forests are characterized by free vertical drainage of their soils; even in case of clayey soils in periods of heavy rainfall the drainage regime is not altered. The inundation forests are characterized by a hydroperiod of about six months during which the stands are flooded up to several meters; in this period there is a distinct O_2-deficit at the level of the root zone; many canopy trees then shedding their leaves indicate this period as one of low physiological activity. In the terra firme forest there is usually a short period of intensive leaf fall at times of lower precipitation. Because of the mentioned and other differences between terra firme and inundation forests (biogeochemical) differences between them may be expected to occur.

A. Biogeochemistry of Neotropical Primary Forests

1. Total Amounts of Bioelements

To calculate total bioelement contents of plant biomass is thought useful for a tentative ordination of vegetation types (HORAK & KINZEL 1971). However, the biological meaning of such values is probably very restricted. Contents of individual bioelements and their relations are certainly more informative biologically.

Total bioelement content here refers to the sum of solely P + K + Ca + Mg + Na, since nitrogen was not reported for bark and wood of one out of three terra firme stands.

In two stands each one among the terra firme and the inundation forest stands bark was not analyzed separately. Since, on a weight basis, bark contributes relatively little to the bole biomass, the bioelement content of wood samples "contaminated" by bark is assumed to differ little from that of pure wood tissue.

The total bioelement amounts of foliage, bark and wood vary considerably and represent apparently two part sections of the continuum theoretically to be expected (Figure 1), i.e., there is no intermediate section represented with amounts of 18000 - 30000 ppm in the foliage. Therefore, the seven stands cannot be assigned to one single group. There is one group with a mean foliar bioelement content of 35000 ppm, while the respective value of the second group is strikingly lower (12000 ppm). Even greater differences between both groups are observed for bark or wood. While the ratio is 2.85 : 1 for the foliage, it is 5.43 : 1 for bark, and 4.03 : 1 for wood. The means are statistically different at $p < 0.01$.

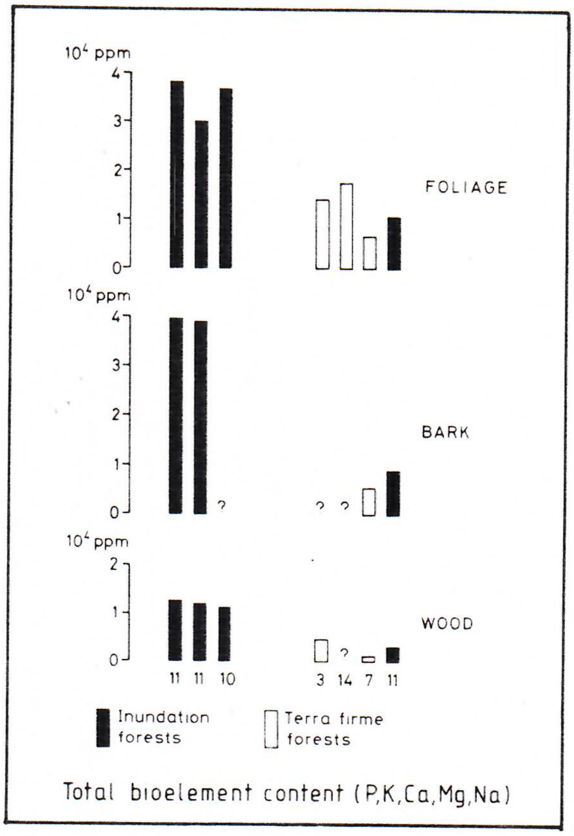

Figure 1 - Total bioelement content (P, K, Ca, Mg, Na in ppm) of foliage, bark and wood of seven neotropical forests. Numbers 3 to o4 refer to Table 1 giving the sources. ? = not analyzed

The total bioelement content of the wood is, as expected, lowest. The differences between biomass fractions are explained in terms of the physiological roles they play in the living tree.

The group of stands characterized by elevated bioelement contents is composed by two várzea stands[1] of the lower Solimões (Brazil) and one stand from the footzone of the Venezuelan Andes also subject to regular flooding. This group of stands will be referred to below as the "group of várzea stands", while the second group will be referred to as either "group of non-várzea stands" or "group of terra firme stands", although it is composed, in addition to three

[1] Classification of Amazon inundation forests acc. to PRANCE (1979)

terra firme stands, by one stand from the igapō inundation area[1].

The fact that chemical analyses of bark and wood yield results which agree with those obtained for foliage, point to the possibility of using analyses of any of the three biomass fractions to study the nutrient status of forest stands (BURG 1976).

Regarding the soils of both groups of neotropical forests, their chemical differences make understandable the chemical differences of the vegetation they support. The vārzea soils are listed as soils of much better chemical quality (FALESI 1984, WORBES 1985, FURCH, unpubl. data) than those of the terra firme and the igapō (COCHRANE & SANCHEZ 1982, COUTINHO & LAMBERTI 1971, MOORMANN & WANBEKE 1978, WAMBEKE 1978).

2. Individual Bioelement Contents

The individual contents of N, P, K, Ca, Mg and Na of foliage, bark and wood are depicted in Figure 2, separately for the seven stands.

The groups of vārzea stands and non-vārzea stands previously establishment on the basis of different total bioelement contents of the foliage, the bark and the wood, are recognizable in principle regarding the individual bioelement contents of the biomass fractions. This is particularly true for calcium in the foliage and the bark and for foliar sodium. The latter bioelement occurs at higher levels in the foliage of the group of terra firme forests than in the foliage of the group of vārzea forests, while the other five bioelements occur at lower levels in the group of terra firme forests.

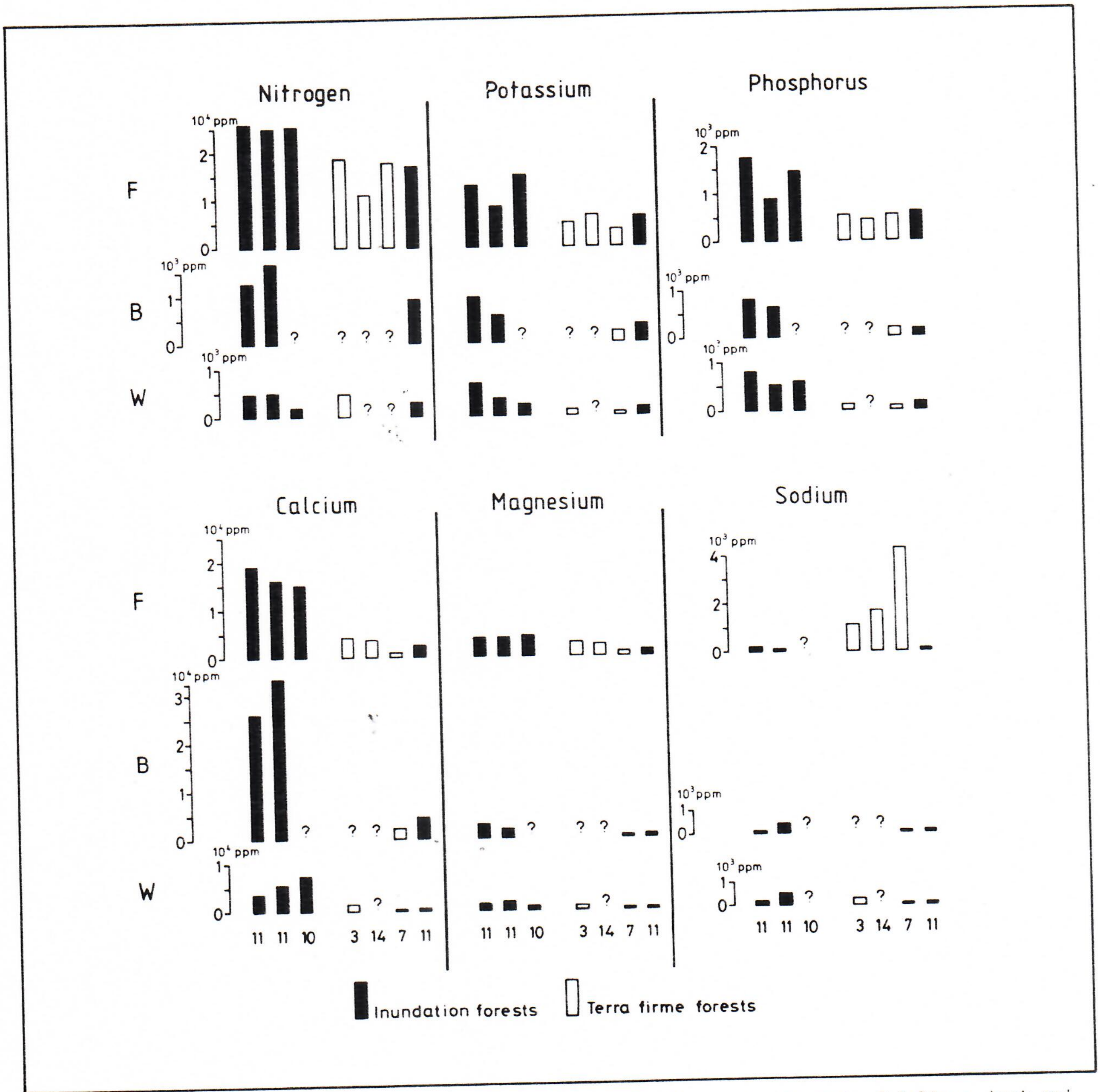

Figure 2 - Individual mean content of bioelements N, P, K, Ca, Mg and Na (in ppm) of foliage, bark and wood of same forests as in Figure 1.

3. Percentage Contribution of Individual Bioelements to Their Sum

The average percentages of the six individual bioelements on their sum of the foliage, the bark and the wood are graphically presented in Figure 3, separately for vārzea forests and non-vārzea forests.

The graph makes evident that the minor constituents are magnesium, phosphorus and sodium. The percentages of these bioelements vary between both the biomass fractions and the groups of forests, without any clear tendency.

Nitrogen, calcium and potassium are much more important bioelements. While the percentages of potassium are less variable than those of calcium and nitrogen, it is obvious that elevated nitrogen percentages of the non-vārzea forests correlate with lower total bioelement contents, and elevated calcium percentages are associated with higher total bioelement contents in case of the vārzea forests. This is true for the three biomass fractions.

The observed coupling of comparatively low total bioelement contents of the biomass of non-vārzea forests with a relatively high nitrogen accumulation reminds the observation of a higher relative N-content in the foliage of tropical woody vegetation growing on soils of comparatively low nutrient status, by KLINGE (1976).

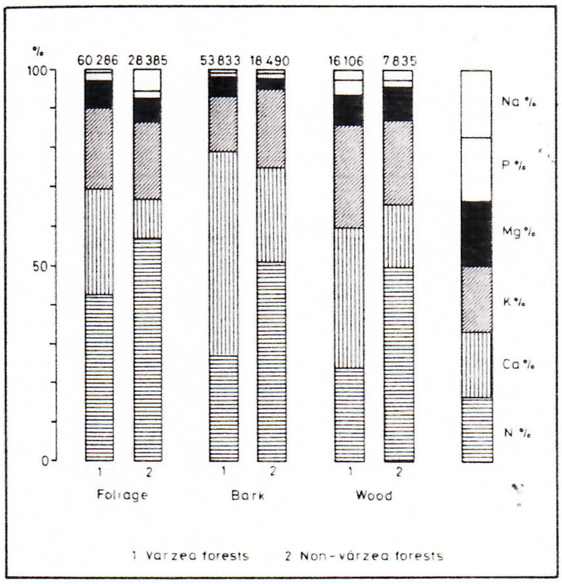

Figure 3 - Average content of N, P, K, Ca, Mg and Na, as percentages of the sum of these elements, for foliage, bark and wood of vārzea and non-vārzea forests. Numbers on top of bars are average total bioelement contents, in ppm.

4. Percentage Contribution of Individual Alkali- and Alkali-Earth Elements to Their Sum

Considering the average individual percentages of the alkali elements K and Na and the alkali-earth elements Ca and Mg in the above ground biomass of the vārzea and non-vārzea stands, in relation to the totals of these four bioelements (Figure 4), it is observed that the vārzea forests with higher total bioelement contents than the non-vārzea forests present a relative dominance of alkali-earth elements (60-80 %). This is due mainly to elevated Ca percentages. Among the non-vārzea forests the alkali percentages are by far greater than in the vārzea forests.

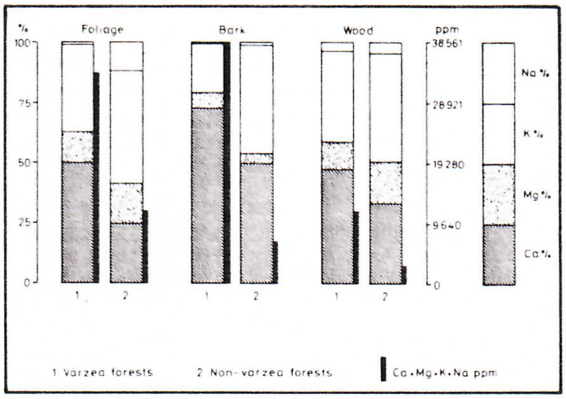

Figure 4 - Average content of alkali (Na, K) and alkali-earth (Ca, Mg) elements, as percentages of the sum of these four bioelements, in foliage, bark and wood of vārzea and non-vārzea forests.

This observation recalls the findings of hydrochemists studying Amazon freshwaters. They have observed a dominance of alkali-earth elements in the chemically richer waters of rivers of the vārzea; in chemically poorer waters of rivers draining the terra firme and the igapō, however, a dominance of alkali elements was found (FURCH 1976, 1984 a, 1984 b, 1985, FURCH & KLINGE 1978, FURCH et al. 1982, see also KLINGE et al. 1983).

Discussion and Conclusions

It has been shown that the studied groups of neotropical primary forests differ regarding the total bioelement content of their biomass fractions (foliage, bark and wood) and the proportions of nitrogen and calcium in these fractions.

Relatively high nitrogen percentages are coupled to comparatively low total bioelement contents. These characteristics are exhibited by the stands included in the group of terra firme or non-vārzea forests (terra firme forests proper and igapō forest). Comparatively high calcium percentages are associated with relatively high total bioelement contents. The latter characteristics are exhibited by the stands included in the group of vārzea forests.

The bioelement amounts encountered in the biomass being supplied by the soil, they reflect the strength of both that supply and the assimilative capacity of the trees.

1. Hydrological Versus Chemical Forest Classification

According to DUCKE & BLACK (1954), RICHARDS (1954) and HUECK (1966), among others, the distinction of inundation forests from terra firme forests is, from the ecological point of view, meaningful. From the chemical viewpoint, however, it is meaningless (Figure 5): There are at one hand inundation forests with an elevated total bioelement content and a relatively high calcium proportion, but a lower nitrogen proportion (vārzea forests). On the other hand there are forests with a relatively low bioelement content and high nitrogen, but low calcium proportions. These latter characteristics are exhibited by terra firme forests on compact soils, on bleached sands (campina/caatinga complex, KLINGE & MEDINA 1979), and by the inundation forest of the igapō type.

Further research is required to decide whether or not the chemical characteristics of the vārzea forests are restricted to them or also shared by primary terra firme forests supported by chemically rich soils.

The fact that inundation forests of elevated bioelement contents and higher Ca than N proportions grow in the vārzea, while inundation forests of low bioelement content with a higher N than Ca proportion grow in the igapō, agrees well with what is known about the geochemistry of these landscape elements. The vārzea rivers, for example, are, by world standards, relatively rich chemically and their most prominent cation is calcium. Rivers draining the igapō and the terra firme are, in contrast, chemically poor and usually do not present a dominance of calcium, but of alkali elements and H^+ (FURCH 1976, 1984a, 1984b, 1985, FURCH et al. 1982).

Equally important is that soil scientists have pointed out that oxisols and ultisols of low natural fertility prevail in the Amazon region of Brazil where they occupy the terra firme (COCHRANE 1984, COCHRANE & SANCHEZ 1972, MOORMANN & WAMBEKE 1978). The little studied igapō soils are extremely low in mineral nutrients (COUTINHO & LAMBERTI 1971, WORBES 1985). The vārzea soils, however, are listed as soils of much better chemical quality (FALESI 1984, WORBES 1985, FURCH unpubl. data) than those from the terra firme and the igapō.

2. Secondary Versus Primary Forests

When searching for chemical data of tropical vegetation growing on chemically rich soils we were unsuccessful as far as primary forests are concerned. But it was noticed that the total bioelement content of lowland secondary terra firme vegetation is often close to that of the group of vārzea forests.

Among the secondary vegetation there were two stands supported by limestone soils in Belize/Central America. One was dominated by the monocot *Orbignya cohune*, the other one was a mix of dicot species with some palms.

A strong dominance of calcium (45 %) separates the palm forest from other secondary forests and reflects the high Ca supply of the limestone soil (Table 2). Its Mg supply, however, is low, as indicated by extremely low Mg percentages of all trees and saplings. The high soil Ca supply is indicated by high Ca percentages of most trees and saplings. The

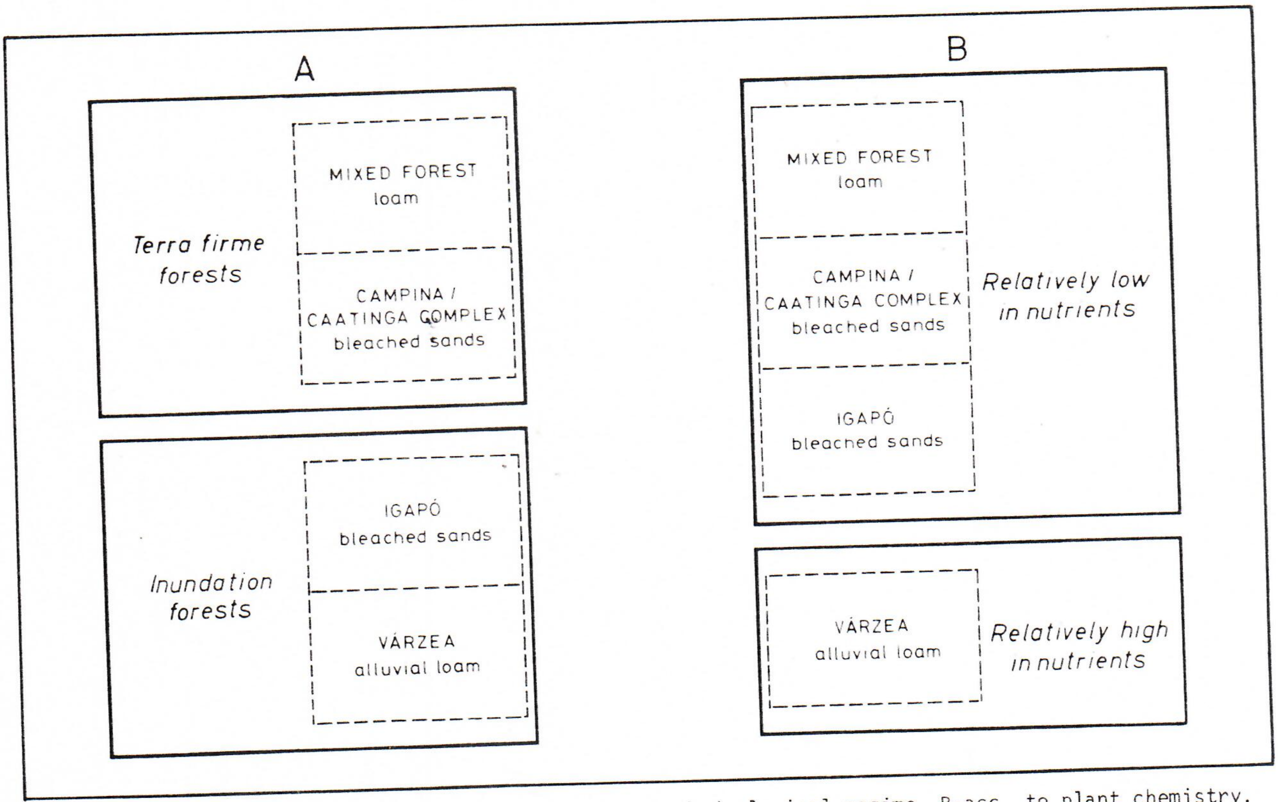

Figure 5 - Classification of Amazon forests. A-acc. to hydrological regime, B-acc. to plant chemistry.

Table 2 N, P, K, Ca and Mg of the foliage of secondary tropical vegetation, in comparison with primary vârzea and non-vârzea forests

	Group of primary vârzea forests		Secondary vegetation				Group of primary non-vârzea forests	
			Palm forests		Mixed forests			
	ppm	%	ppm	%	ppm	%	ppm	%
N	25404	42.2	18582	37.4	19075	43.1	16157	59.9
P	1362	2.3	1526	3.1	1264	2.85	551	2.0
K	12337	20.5	6422	12.9	14150	31.9	5424	20.1
Ca	16818	27.9	22214	44.7	6689	15.1	2881	10.7
Mg	4260	7.1	947	1.9	3115	7.0	1954	7.2
	60181	100.0	49691	100.0	44293	99.95	16967	99.9

strange thing is that the mixed community on limestone soils is lacking a high Ca %. Both trees and saplings are lacking it, while all of them have extremely low Mg percentages.

The elevated total bioelement content of secondary forests is, at least in part, due to the presence of fastgrowing species. STARK (1970) has pointed out that successional species present higher levels of certain bioelements than species of the primary forest. UHL et al. (1982) provided comparative data for successional species and sprouts of primary ones growing in the bleached sand area of San Carlos de Rio Negro (Table 3).

Successional species have a higher total bioelement content than sprout. In the cut + burn plots, i.e., plots fertilized by the ash of the former vegetation, both successional species and sprouts present higher total bioelement contents than the cut plots. Regarding the bioelement percentages the successional species have lower N percentages and higher Ca percentages than the sprouts.

From the above it is concluded that secondary vegetation should not be included in a comparison of primary forests.

3. Chemical Structrure of Forests

GOLLEY & RICHARDSON (1977) made the following statement: "All ecological systems have a chemical structure. This structure may be expressed in several ways. ... Presumably each ecosystem has a unique chemical composition, but would share common characteristics with systems of similar species composition, similar functions, and growing on similar chemical substrates". They found relatively little commonality between Panamanian types of forests, but much more between components of these forests. The results were obtained by applying the statistical technique of factor analysis.

Following GOLLEY & RICHARDSON the vãrzea and non-vãrzea forests of the present study will have a different chemical structure. The specific structural differences have been presented previously. Thinking in optically-oriented readers we decided to express the structures themselves by drawings of a type already used by other authors (RODIN & BAZILEVICH 1967, DENAYER-DE SMET 1973, ALVIM & CABALLA 1974).

The drawings were constructed using the absolute concentrations of the six bioelements (N, P, K, Ca, Mg, Na), separately for foliage and wood, and, in addition, six element ratios $(\frac{Ca}{Mg}, \frac{N}{P}, \frac{N}{Ca}, \frac{Ca + Mg}{K + Na}, \frac{100\ N}{N + P + K + Ca + Mg + Na}, \frac{100\ Ca}{N + P + K + Ca + Mg + Na})$. These twelve parameters were plotted on twelve axes starting from a central point under 30° degrees. By connecting the points on each axis a polygon is obtained. Commonality of systems is expressed by similarity of polygon shapes.

Two different types of polygons are obtained (Figure 6) which represent two principally different biogeochemical forest types. One type is characterized by long and broad arms extended in northern and southern directions (Ca and K concentrations, respectively, and Ca % and N/P ratios).

This type of polygon has also long, but fine arms extended in eastern and western directions (N and P concentrations, N% and Ca/Mg ratios, respectively). This type of polygon is representing the vãrzea forests from the Marchantaria island and from the left bank of the Solimões, respectively, both in the lower reaches of that river.

The other type of polygon represents the terra firme forest and the igapõ forest. It lacks the long and broad arms pointing to the north and the south. Instead it has short arms pointing to N 30° W and S 30° E formed by

Table 3 Foliar bioelements of 3-year old secondary growth on bleached sands at San Carlos de Rio Negro (acc. to UHL et al. 1982).

		cut		cut + burn		
		ppm	% total	ppm	% total	% cut
Tree sprouts						
	N	7440	35.7	8571	31.6	115.2
	P	670	3.2	1428	5.3	213.1
	K	5650	27.1	8571	31.6	151.7
	Ca	5490	26.3	7143	26.3	130.1
	Mg	1585	7.6	1428	5.3	90.1
	Total	20835	99.9	27141	100.1	130.3
Successional woody plants						
	N	7143	24.2	7273	19.3	101.8
	P	1428	4.8	1748	4.6	122.4
	K	6190	21.0	12028	32.0	194.3
	Ca	11905	40.3	14165	38.8	122.7
	Mg	2857	9.7	1958	5.2	68.5
	Total	29523	100.0	37622	99.9	127.4

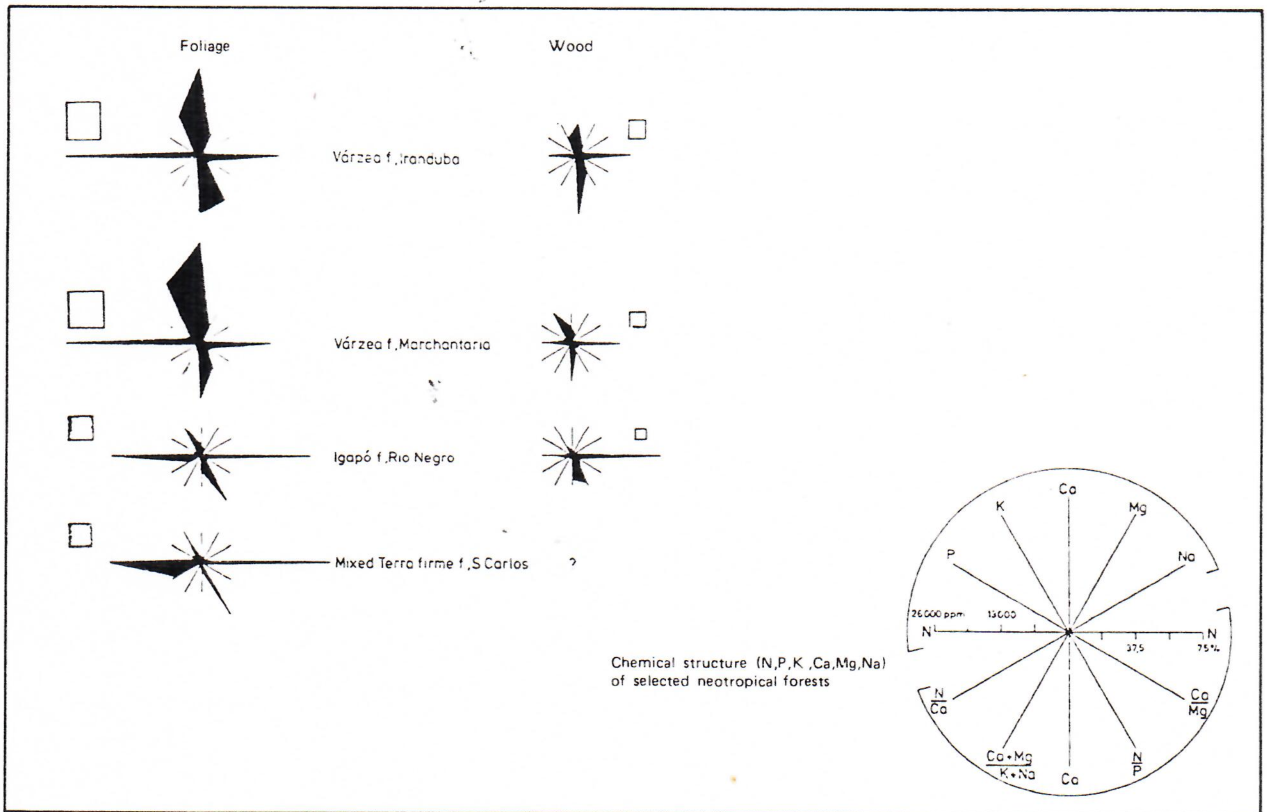

Figure 6 - Graphical representation of chemical structure of Amazon inundation and terra firme forest. Squares represent total bioelement content.

K and Ca concentrations, and Ca% and N/P ratios, respectively. It has long and relatively fine arms extending in eastern and western directions (N concentration and N/Ca ratios, and N % and Ca/Mg ratio, respectively).

In principle, the chemical structure of the wood resembles the foliage. One specific feature of the chemical structure of the vārzea and non-vārzea forests is not directly expressed by the polygons: the increase of the foliar Ca % and the decrease of the foliar N % towards the forests with an elevated total foliar bioelement content (Figure 7).

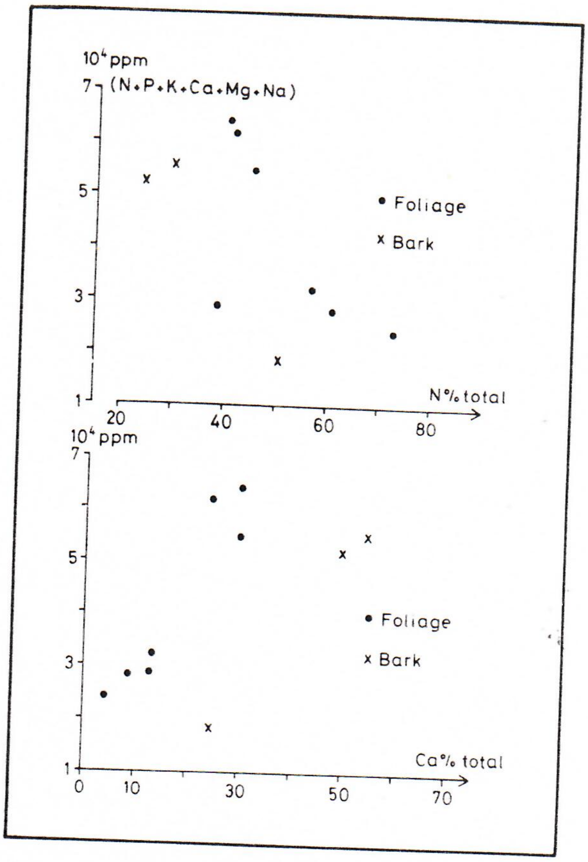

Figure 7 - Foliar calcium and nitrogen percentages of selected neo-tropical forests.

In this figure the individual percentages of both bioelements of the seven stands are plotted against the total foliar bioelement content. In Figure 8 the Ca % is plotted against the N %.

4. Chemical Structure and Nutrient Cycling

JORDAN & HERRERA (1981) proposed that there are two major types of nutrient cycling strategies of tropical forests which represent extremes of the nutrient gradient. One type is represented by forests growing on nutrient-poor soils where the system exhibits a number of nutrient conserving mechanisms (HERRERA et al. 1984). The other type is represented by forests growing on nutrient rich soils where there is no special need to develop nutrient conserving mechanisms.

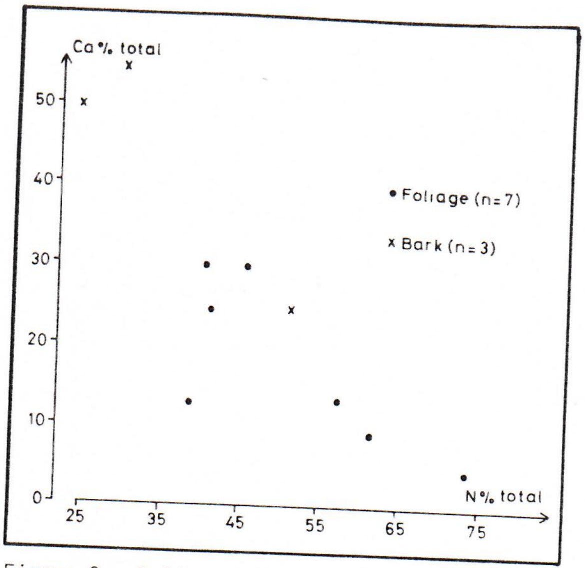

Figure 8 - Foliar calcium versus foliar nitrogen percentages of selected, neo-tropical forests.

Having in mind the groups of forests of different chemical structures we may assume that the forests of the terra firme and the igapō partly supported by bleached sands of low natural fertility represent ecological systems exhibiting nutrient conserving mechanisms. The vārzea forests most probably represent the opposite extreme of the nutrient gradient.

Comparing both types of systems it is astonishing how effective the nutrient conserving systems are in assimilating nutrients from low soil supplies.

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