AMAZONIANA	XI	1	91 – 116	Kiel, Oktober 1989

From cooperation between Max-Planck-Institute for Limnology, Working Group Tropical Ecology, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus/Amazonas (INPA), Brazil

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

Nutrient dynamics of decomposing leaves from Amazonian floodplain forest species in water*

by

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(accepted for publication: October 1989)

Abstract

Decomposition experiments were performed in freshwater tanks using fresh leaves of four Amazonian tree species from blackwater and whitewater floodplain forests. Weight loss, loss of the major elements, Na, K, Mg, Ca, N and P from the leaves, and release of these elements into the water were studied during a four month period. Based on the nutrient contents of fresh multispecies leaf litter and data on the shedding of this litter, nutrient inputs from leaves into bodies of blackwater and whitewater in the forests during flood period were calculated. The input of dissolved inorganic N, P and K may be as great or even greater than input from river water, indicating the importance of the floodplain forest as nutrient pump from sediments into the water.

Keywords: **Decomposition, leaf litter, Amazon, Negro, nutrients.**

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*) This study is dedicated to Dr. Hans Klinge to commemorate his 60th birthday.

Introduction

The nutrient flux within Amazonian forest ecosystems is determined to a large extent by the decomposition and remineralization of leaf material and the reincorporation of the liberated nutrients. Decomposition processes are favoured by high temperature and humidity (SWIFT et al. 1979; BRINSON et al. 1981; DAY 1983; LUIZAO & SCHUBART 1986; WEBSTER & BENFIELD 1986). Amazonian floodplain forests are strongly influenced by the annual flood pulse, caused by the periodically rising water level in the large rivers (JUNK et al. 1989). The floor of the floodplain forest along the Amazon River (várzea) and the Negro River (igapó) is flooded as long as seven months a year. Thus litter decomposition takes place under terrestrial as well as under aquatic conditions.

Decomposition of aquatic plant material exposed to longterm submergence has often been studied (HOWARD-WILLIAMS & JUNK 1976; GODSHALK & WETZEL 1978; HOWARD-WILLIAMS & HOWARD-WILLIAMS 1978; BASTARDO 1979; ESTEVES & BARBIERI 1983; FURCH & JUNK 1985; GAUR et al. 1989; JUNK & FURCH 1990) but there have been few investigations on terrestrial plants (KAUSHIK & HYNES 1971; WETZEL & MANNY 1972; FURCH et al. 1988; STEWART & DAVIES 1989; THOMPSON & BÄRLOCHER 1989), since under natural conditions, this leaf litter is seldom submerged.

Most studies of terrestrial and aquatic decomposition focus on dry weight loss and the loss of mineral nutrients from the organic material (e.g. O'CONNELL & MENAGE 1983; KLEMMEDSON & BLASER 1988; O'CONNELL 1988; REDDY & VENKATAIAH 1989). Studies are scarce on the release of nutrients, including the amount of solutes directly delivered to the aquatic environment by the decomposing biomass (PLANTER 1970; KISTRITZ 1978; BASTARDO 1979; FURCH & JUNK 1985; HELBING et al. 1986; SILVA & MORAES 1986; FURCH et al. 1988). However, in floodplains with periodic alterations between aquatic and terrestrial conditions, decomposition of terrestrial plant material in the water plays an important role in nutrient enrichment of the water while the river level is rising, and nutrient loss while it is falling (IRMLER 1979; FURCH et al. 1988; JUNK et al. 1989).

In this study, decomposition experiments on tree leaves from Amazonian floodplain forests were carried out under aquatic conditions to determine the fate of the elements Na, K, Mg, Ca, N and P lost from the leaf material and to estimate their impact on the nutrient budget of the ecosystem.

Material and Methods

The plant material used for the decomposition experiments were fresh, fully developed leaves of four common tree species from two different Amazonian floodplain forests. *Cecropia latiloba, Salix humboldtiana* and *Pseudobombax munguba* are species of the Amazon floodplain or "várzea" forest. Their leaves were sampled on Ilha de Marchantaria (03° 15'S, 58° 58'W), the first island in the Amazon River upstream from the confluence with the Negro River. *Aldina latifolia* is a species of the Negro River floodplain or "igapó" forest. Its leaves were sampled at Tarumã Mirím (03° 02'S, 60° 17'W), a tributary of the Negro River near its confluence with the Amazon River.

Table 1: Characterization of the leaf material used for the decomposition experiments. *KLINGE et al. (1983), S.L.A. = specific leaf areal.

	C. latiloba	*S. humboldt.*	*P. munguba*	*A. latifolia*
Locality	várzea	várzea	várzea	igapó
Nutrient content	high	high	high	low
Leaf size (cm^2)	817*	28	75*	52*
S.L.A. (cm^2 g^{-1})	164.9	80.8	84.3	114
Leaf hardness	soft	soft	medium	hard
Water content (%)	71.4	59.1	67.4	65.9
Fresh weight (g)	4400	4000	4000	4000
Dry weight (g)	1258	1636	1304	1364

From three of the tree species a total of 4.0 kg of fresh leaf material was collected, but from *Cecropia latiloba*, 4.4 kg was taken. This corresponded to a dry weight between 1.3 and 1.6 kg (Table 1). The leaves of the four species were exposed for about four months to 700 l ground water, acid (pH 4.21) and poor in electrolytes (Table 2), in one freshwater tank each kept at ambient air temperature between 27 and 30 °C. Some of the fresh leaves were divided into 100 g subsamples in litter bags made of 2 mm mesh. The water was not aerated during the study period, and the leaves were kept in the dark to surpress primary production by algae and thus to exclude this factor from the element cycling. Samples of water and leaf material were removed at intervals of 5 to 12 days.

Table 2: Chemical qualities of the ground water used for the decomposition experiments. Values are given in mg l^{-1}, except for specific conductance at 25 °C (K_{25}), given in μS cm^{-1}.

H	K_{25}	Na	K	Mg	Ca
0.06	24.0	1.06	0.34	0.08	0.20
HCO_3	SO_4	Cl	PO_4-P	NO_5-N	NH_4-N
<0.61	0.22	1.69	0.01	1.17	0.04

Subsamples of leaf material were dried at 105 °C and analyzed for nitrogen, phosphorus, sodium, potassium, magnesium and calcium. N was determined by the Kjeldahl method, P by the molybdate blue method, and Na, K, Mg, and Ca spectrometrically (AAS). Further details are given by HOWARD-WILLIAMS & JUNK (1976). The following analytical methods were used: a glass electrode for pH; a platinum electrode for specific conductance; AAS for sodium, potassium, magnesium, and calcium; titration with $AgNO_3$ using K_2CrO_4 as an indicator, according to HÖLL (1970) for chloride; the molybdate blue and indophenol blue methods for phosphate and ammonium, respectively (FURCH 1975); potentiometric titration with 0.01 N HCl for alkalinity; the turbimetric method using a Technicon Autoanalyzer for sulfate; reduction to nitrite and photometric analysis with sulphanilamide for nitrate (GRASSHOFF 1976). Further details are given by FURCH (1984a). The chemical qualities of the ground water used for the experiments are shown in Table 2.

Results

1. Dry weight loss and changes in O_2, pH and conductance of the water

There are marked differences among the tree species in the decomposition rates of their leaves in water as a percentage of dry weight loss (Figs. 1 and 2). Decomposition of *Cecropia* and *Salix* leaves is very quick, and after about ten weeks, they have lost about 85 % and 75 % of their dry weight, respectively. The decomposition of *Pseudobombax* leaves is much slower and the corresponding loss is about 45 %. *Aldina* leaves decompose very slowly with only about a 10 % dry weight loss.

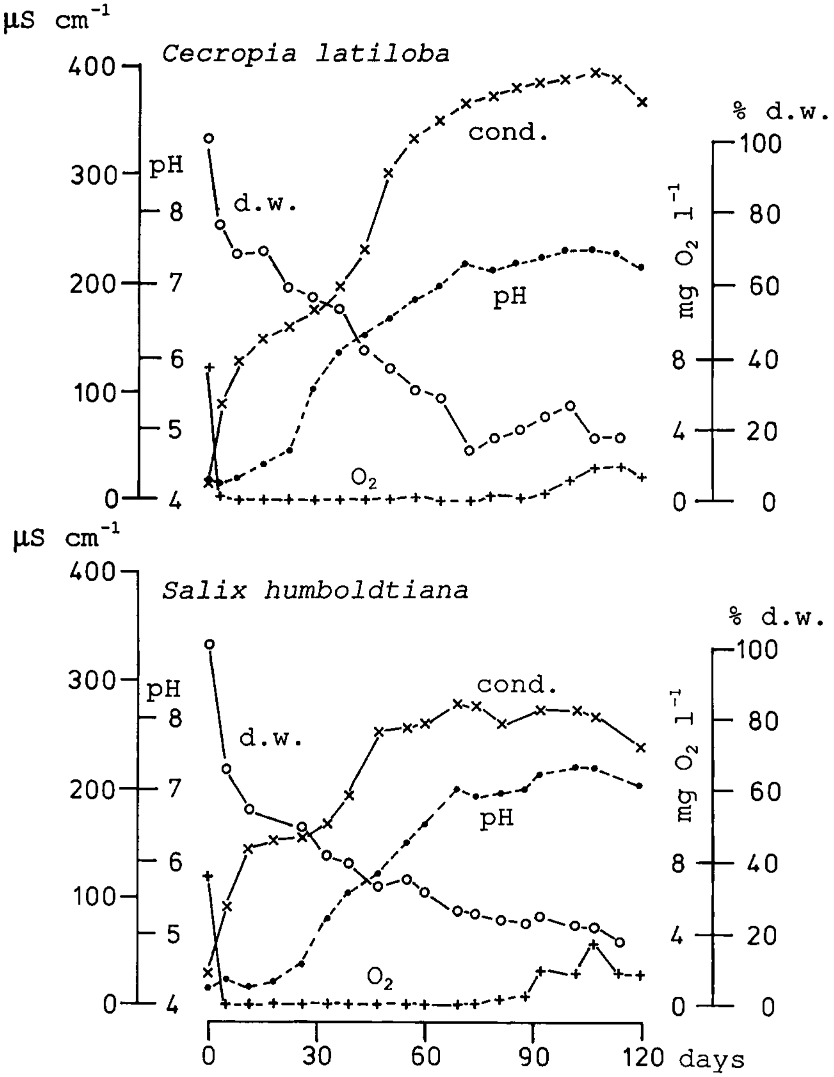

Fig. 1:
Dry weight (d.w.) loss from leaf material and change of pH, specific conductance at 25 °C (cond.), and O_2 content of the water during decomposition of fresh leaves of *Cecropia latiloba* (1.3 kg dry weight) and *Salix humboldtiana* (1.6 kg dry weight) in water (700 l).

Leaf decomposition is accompanied by drastic changes in water chemistry. Oxygen content abruptly decreases to zero, indicating a high oxidation rate of organic substances. Specific conductance and pH strongly increase due to high liberation rates of electrolytes and basic substances resulting in a subsequent increase in buffer capacity (FURCH & JUNK 1985; FURCH et al. 1988).

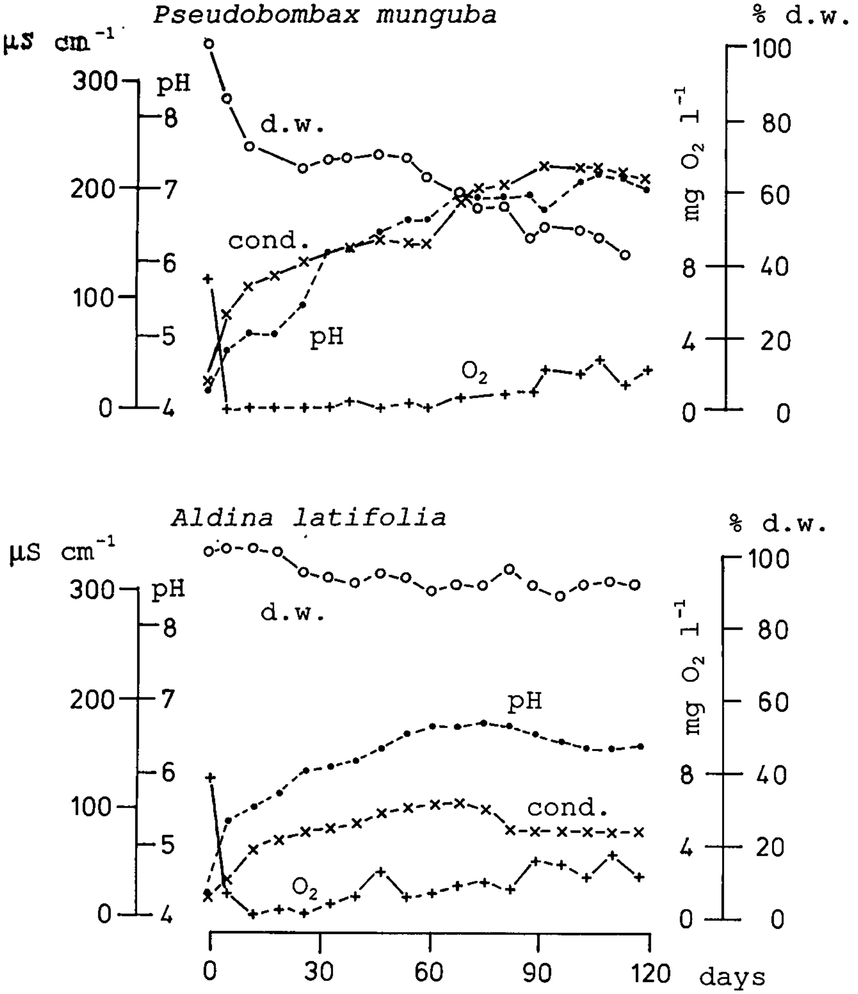

Fig. 2:
Dry weight (d.w.) loss from leaf material and change of pH, specific conductance at 25 °C (cond.), and O_2 content of the water during decomposition of fresh leaves of *Pseudobombax munguba* (1.3 kg dry weight) and *Aldina latifolia* (1.4 kg dry weight) in water (700 l).

The decomposition rate of várzea tree leaves is positively correlated with their N content (Table 3), as observed by MELIN (1930), KAUSHIK & HYNES (1971), HART & HOWMILLER (1975), WEBSTER & BENFIELD (1986) and DENICH (1989). This is not true for leaves from the igapó tree, *Aldina latifolia*, which is very poor in mineral nutrients. In spite of a relatively large nitrogen content (Table 3), they decompose very slowly.

Table 3: The elemental content of samples fresh tree leaves (n = 3). Those in parenthesis were provided by KLINGE et al. (1983). Concentrations are given in g kg^{-1} dry weight.

	C. latiloba	*S. humboldt.*	*P. munguba*	*A. latifolia*
Na	0.10 ± 0.06	0.90 ± 0.08	0.03 ± 0.00	0.03 ± 0.01
	(0.06)	(–)	(0.04)	(0.02)
K	12.22 ± 1.40	14.16 ± 0.70	13.64 ± 3.13	8.98 ± 0.67
	(15.51)	(–)	(22.28)	(3.57)
Mg	3.41 ± 0.79	2.26 ± 0.06	8.14 ± 0.76	1.01 ± 0.01
	(4.17)	(–)	(5.09)	(1.24)
Ca	10.01 ± 2.10	14.40 ± 0.90	18.18 ± 0.46	1.90 ± 0.10
	(15.13)	(–)	(7.11)	(1.13)
N	29.45 ± 0.76	23.60 ± 0.96	18.97 ± 0.15	22.13 ± 0.10
	(33.95)	(–)	(28.30)	(24.30)
P	2.16 ± 0.11	1.55 ± 0.16	2.08 ± 0.12	1.28 ± 0.03
	(1.98)	(–)	(2.40)	(0.44)

The increases in pH and specific conductance and the duration of the anaerobic conditions in the water are positively related with the decomposition rate. Small differences in the water content of the fresh leaves (Table 1), do not affect these general trends.

2. Nutrient release from leaves into the water

All experiments in this study show that K is quickly released in large quantities (Figs. 3 - 6). Within a period of 11 days between 7.2 and 10.5 g K per kg dry weight are detected in the water. This corresponds to a release rate between 80 % and 86 % of the initial K amount. Therefore, among plant nutrients, K may be the best indicator for leaching intensity during decomposition. The amounts of calcium ions released from decomposing leaves may be great, too (Figs. 3 - 6). However, the liberation rate of Ca is far lower than that of K, and differences between species are considerable. Within the first 14 days of decomposition, between 0.2 and 3.7 g Ca per kg dry weight are released into the water. This corresponds to between 8 % and 37 % of the initial Ca amount. These amounts increase after about six weeks to between 0.5 and 7.1 g Ca, corresponding to a release rate between 28 % and 71 % of the initial Ca amount. However, there is no relationship between the amount of Ca initially stored in the leaf material and the amount released during decomposition.

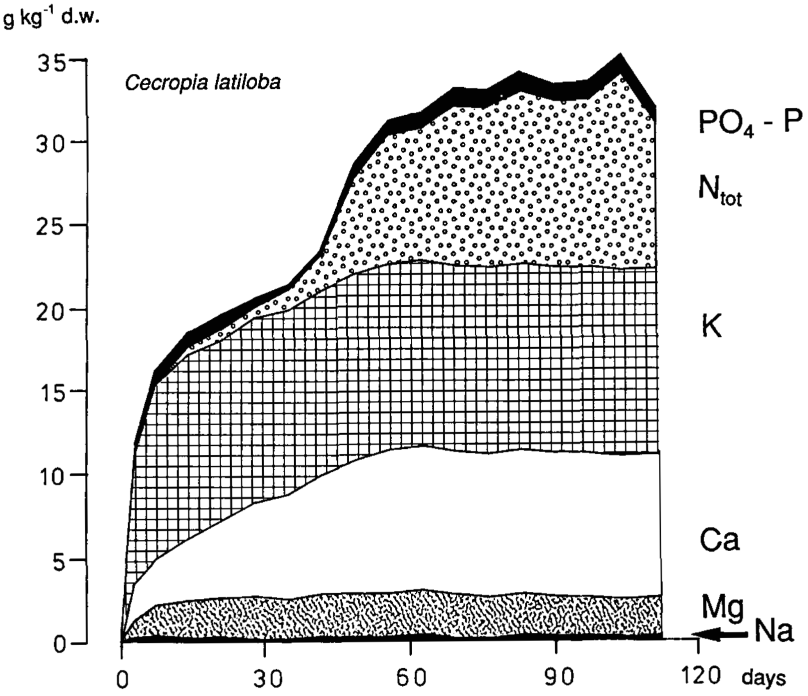

Fig. 3:
Amounts (g) of dissolved nutrient elements (Na, K, Mg, Ca, N and P) released into the water during decomposition of 1 kg of dry leaf biomass from *Cecropia latiloba*. $N_{tot} = NO_3 - N + NO_2 - N + NH_4 - N$.

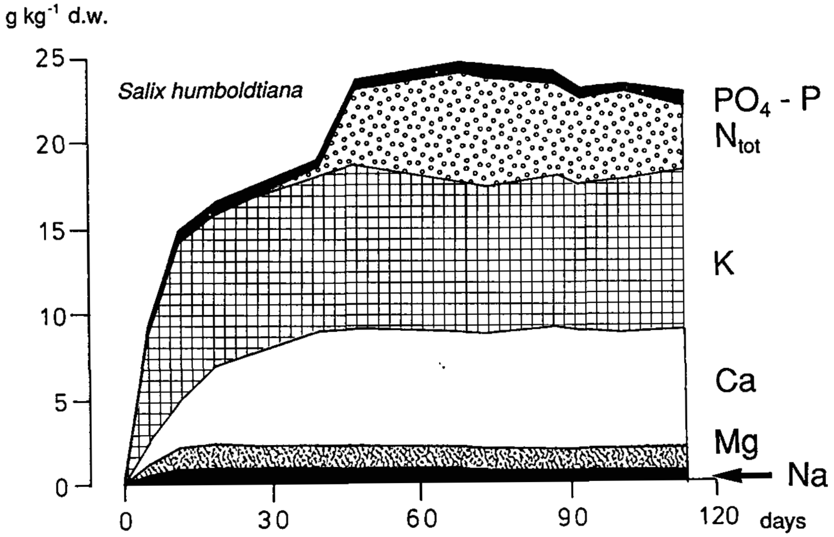

Fig. 4:
Amounts (g) of dissolved nutrient elements (Na, K, Mg, Ca, N and P) released into the water during decomposition of 1 kg of dry leaf biomass from *Salix humboldtiana*. $N_{tot} = NO_3 - N + NO_2 - N + NH_4 - N$.

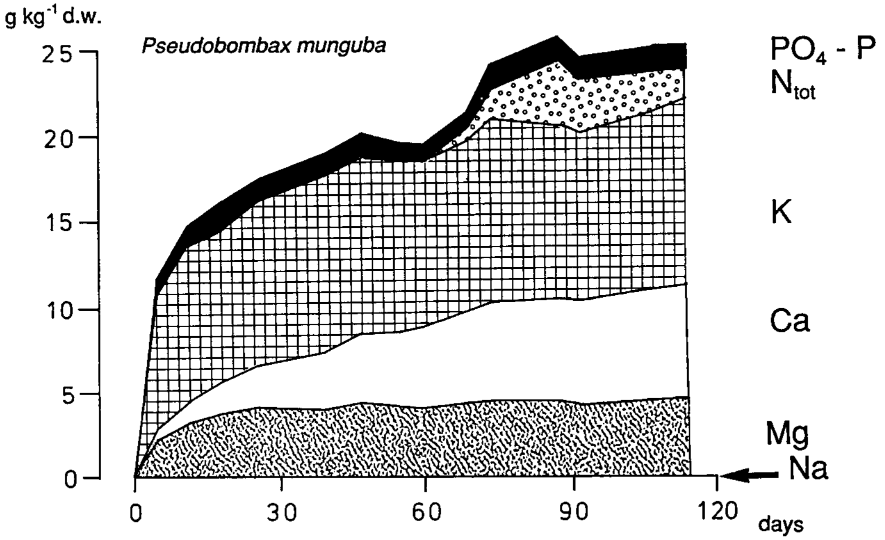

Fig. 5:
Amounts (g) of dissolved nutrient elements (Na, K, Mg, Ca, N and P) released into the water during decomposition of 1 kg of dry leaf biomass from *Pseudobombax munguba*. $N_{tot} = NO_3 - N + NO_2 - N + NH_4 - N$.

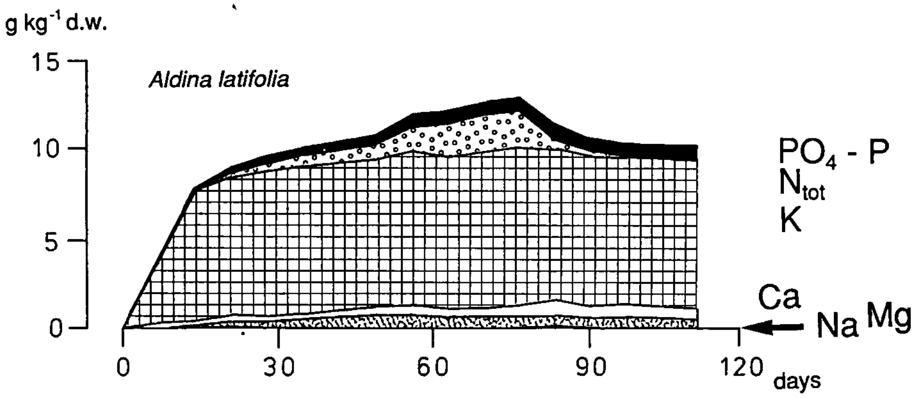

Fig. 6:
Amounts (g) of dissolved nutrient elements (Na, K, Mg, Ca, N and P) released into the water during decomposition of 1 kg of dry leaf biomass from *Aldina latifolia*. $N_{tot} = NO_3 - N + NO_2 - N + NH_4 - N$.

Table 4: Sequences of maximum release of elements by decomposing tree leaves during a four month period.

Amount (g/kg)		% of initial amount
K > N > Ca > Mg > P	*C. latiloba*	K > Ca > Mg > P > N
K > Ca > N > Mg > P	*S. humboltiana*	K > P > Mg > Ca > N
K > Ca > Mg > N > P	*P. munguba*	K > P > Mg > Ca > N
K > N > Ca > P > Mg	*A. latifolia*	K > Mg > P > Ca > N

Generally less Mg is released into the water than Ca, and the release is positively related with the initial amount. PO_4-P quantities released are relatively small (Figs. 3 - 6), and there are no marked correlations with the initial amounts. Na quantities released are almost too low to be depicted in the Figures 3 - 6, except from *Salix* leaves. Na will therefore not be considered in detail.

The greatest differences among tree species are shown in the quantity and liberation dynamics of inorganic nitrogen, in the form of NH_4, NO_2, and NO_3. Nitrogen is present mainly in the form of NH_4 in the water. The concentrations of NO_2 and NO_3 are negligibly low during the main period of decomposition. The várzea species show a positive relationship between the initial N content of the leaves and the amount released during decomposition (Table 3). The igapó species, *Aldina latifolia,* with a relatively large N content in its leaves releases only small quantities into the water. Since in the first stages of decomposition, dissolved inorganic N generally fails to appear in notable quantities, it is assumed that N liberation is less a result of leaching processes than a result of microbial attack on organic N compounds, mainly proteins.

Sequences of the release of elements into the water, shown in Table 4, reveal differences among tree species. Identical release patterns are only observed for potassium, the quantities of which are greatest, considering both the absolute amount and the percentage of the initial amount, and for nitrogen, for which the quantities are smallest in terms of the percentage of the initial amount.

3. Loss of nutrients from leaf material

Nutrient losses are calculated from weight loss and the nutrient content of the leaf material in the litter bags. A comparison between the amount of nutrients released into the water (Figs. 3 - 6) and that lost from leaf biomass (Figs. 7 - 10) reveals different patterns. The amounts of K and Mg lost from the leaf biomass are similar to those released into the water. Those of P and Ca, but especially N, are much greater. Thus sequences of nutrient losses from decomposing leaf material are different from those of nutrient release (Table 5). It is noteworthy that losses of nutrients expressed as percentages of the initial amount show the same sequences for all tree species, in spite of remarkable differences in the initial concentrations.

Table 5: Sequences of maximum loss of elements from decomposing tree leaves during a four month period.

Amount (g/kg)		% of initial amount
N > K > Ca > Mg > P	*C. latiloba*	K > Mg > P > Ca > N
N > K > Ca > Mg > P	*S. humboldtiana*	K > Mg > P > Ca > N
Ca > K > N > Mg > P	*P. munguba*	K > Mg > P > Ca > N
K > N > P > Mg > Ca	*A. latifolia*	K > Mg = P > Ca > N

The initial nutrient content and the maximum amounts of nutrients released and lost from decomposing tree leaves within a four month period are summarized in Table 6.

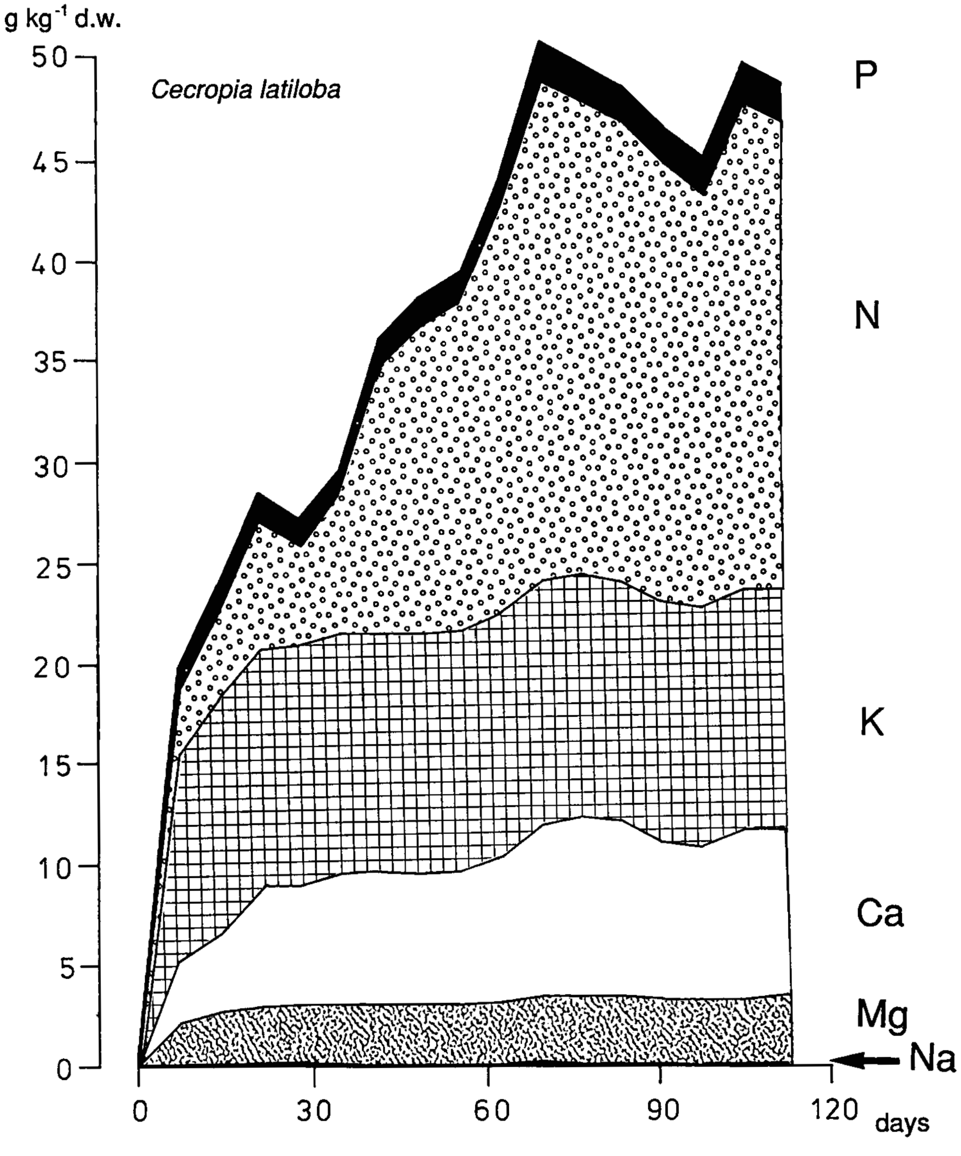

Fig. 7:
Amounts (g) of nutrient elements (Na, K, Mg, Ca, N and P) lost from 1 kg of dry leaf biomass from *Cecropia latiloba* during decomposition in water.

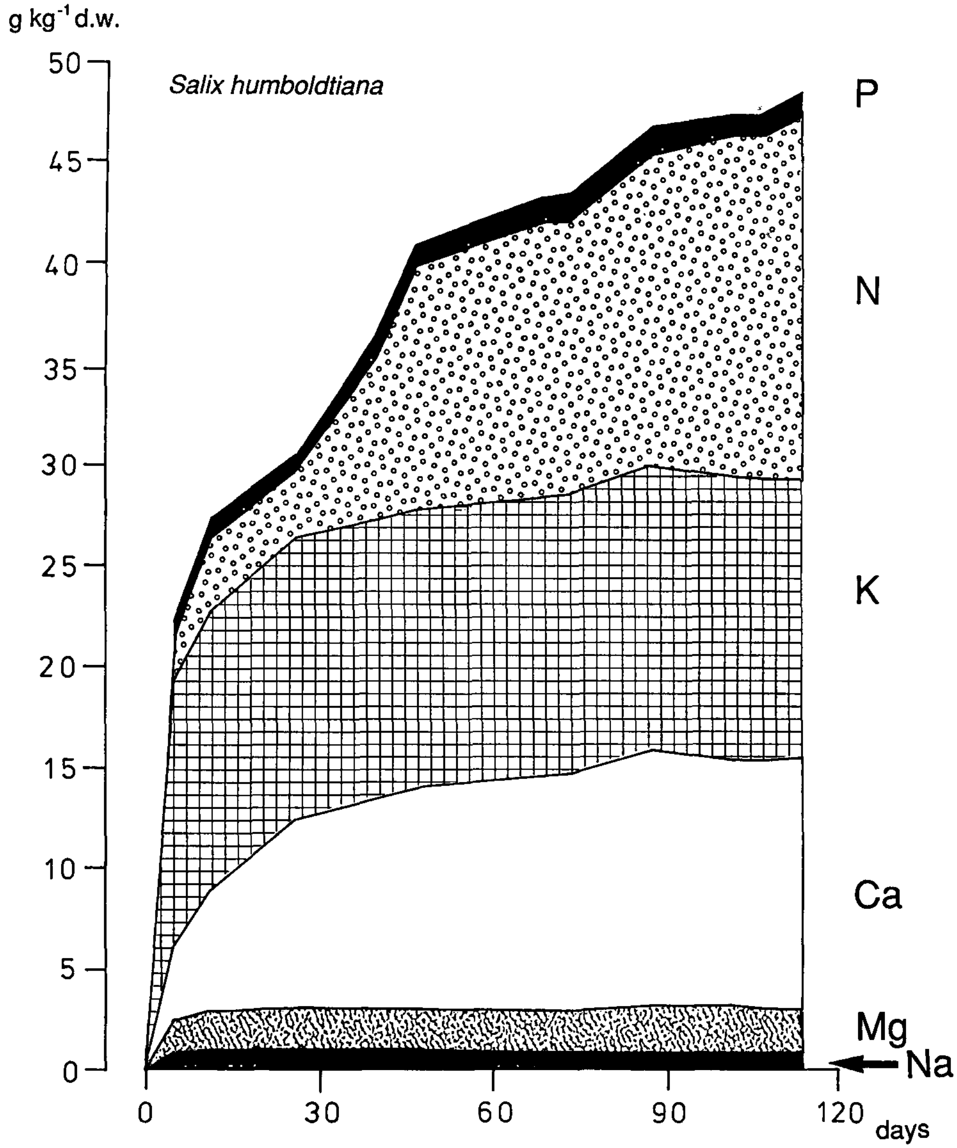

Fig. 8:
Amounts (g) of nutrient elements (Na, K, Mg, Ca, N and P) lost from 1 kg of dry leaf biomass from *Salix humboldtiana* during decomposition in water.

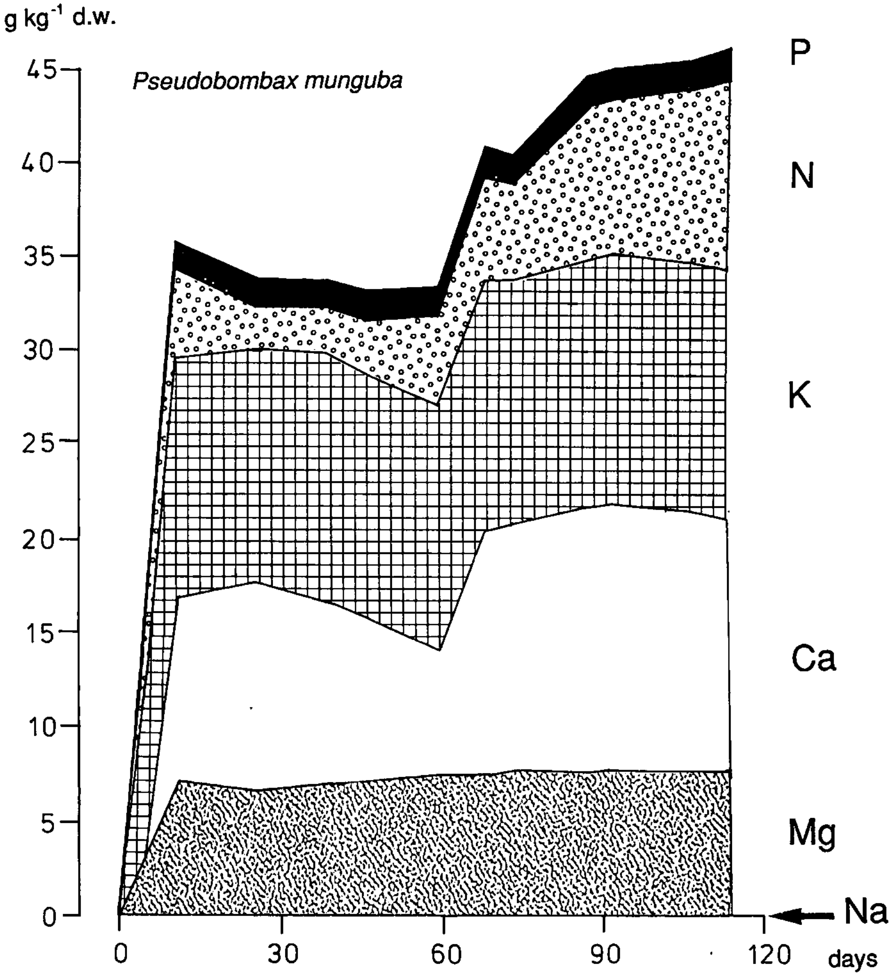

Fig. 9:
Amounts (g) of nutrient elements (Na, K, Mg, Ca, N and P) lost from 1 kg of dry leaf biomass from *Pseudobombax munguba* during decomposition in water.

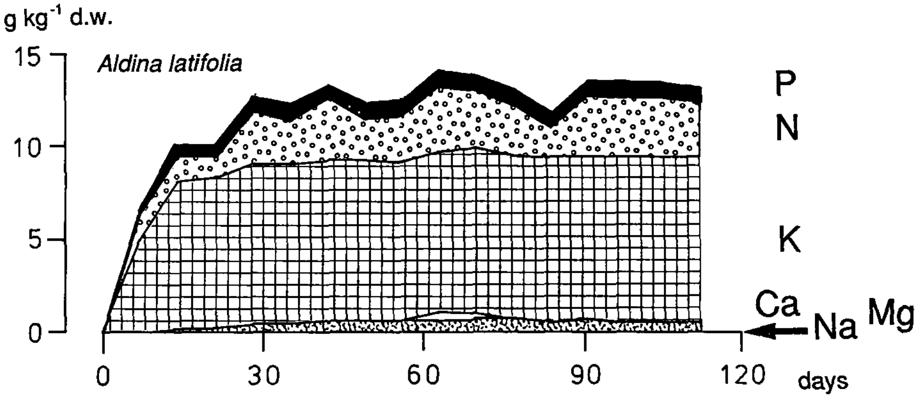

Fig. 10:
Amounts (g) of nutrient elements (Na, K, Mg, Ca, N and P) lost from 1 kg of dry leaf biomass from *Aldina latifolia* during decomposition in water.

Table 6: Maximum weight loss (% dry weight), initial content of K, Mg, Ca, N, and P in the leaves of four tree species from Amazonian floodplain forests (g kg^{-1} dry weight), and maximum amounts of these elements (g) released into the water (rel.) and lost (loss) from 1 kg dry weight of leaves during a four month period of decomposition in the water. K_r : ratio of the maximum amount released to the initial amount, K_1 : ratio of the maximum amount lost to the initial amount. Sodium was not considered due to its extremely low proportion in the leaf biomass (Table 3).
* The strange relationship between the released and lost amounts of Ca is explained by methodological problems due to the extremely low Ca concentrations in leaves of *Aldina latifolia*. $N_{tot} = NO_3 - N + NO_2 - N + NH_4 - N$.

		C. latiloba	*S. humboldt.*	*P. munguba*	*A. latifolia*
Weight loss (%)		86.0	82.6	58.5	11.9
Initial (g kg^{-1})		12.22	14.16	13.64	8.98
Rel. (K_r)	K	11.10 (0.91)	9.20 (0.65)	10.94 (0.80)	8.67 (0.97)
Loss (K_1)		12.07 (0.99)	14.01 (0.99)	13.24 (0.97)	8.85 (0.99)
Initial (g kg^{-1})		3.41	2.26	8.14	1.01
Rel. (K_r)	Mg	2.67 (0.78)	1.30 (0.58)	4.54 (0.56)	0.65 (0.64)
Loss (K_1)		3.25 (0.95)	2.17 (0.96)	7.57 (0.93)	0.66 (0.65)
Initial (g kg^{-1})		10.01	14.40	18.18	1.90
Rel. (K_r)	Ca	8.60 (0.86)	7.07 (0.49)	6.68 (0.37)	0.92 (0.48*)
Loss (K_1)		8.90 (0.89)	12.76 (0.89)	14.19 (0.78)	0.50 (0.26*)
Initial (g kg^{-1})		29.45	23.60	18.97	22.10
Rel. (K_r)	N_{tot}	10.42 (0.35)	6.40 (0.27)	3.95 (0.21)	2.08 (0.09)
Loss (K_1)		24.87 (0.84)	17.79 (0.75)	9.90 (0.52)	3.61 (0.16)
Initial (g kg^{-1})		2.16	1.55	2.08	1.28
Rel. (K_r)	P	1.10 (0.51)	0.91 (0.59)	1.51 (0.73)	0.80 (0.63)
Loss (K_1)		1.97 (0.91)	1.46 (0.94)	1.69 (0.81)	0.83 (0.65)
Initial (g kg^{-1})		57.25	55.97	61.01	35.27
Rel. (K_r)	sum	33.89 (0.59)	24.88 (0.44)	27.62 (0.45)	13.12 (0.37)
Loss (K_1)		51.06 (0.89)	48.19 (0.86)	46.59 (0.76)	14.45 (0.41)

4. Fate of the elements

The initial total amount of nutrients and their distribution in water and leaf material at different stages of decomposition are shown in Figures 11 - 14. Potassium accounts for the largest portion of all dissolved nutrients during the first stages of decomposition. Later on, calcium and nitrogen become more dominant, while the amounts of phosphorus and magnesium generally do not exceed more than 7.5 % and 12.2 % of all nutrients, respectively. In *Pseudobombax* leaves, relative amount of Mg, 22.2 %, is unusually high. The percentage of K released from *Aldina* leaves is extremely high, corresponding to 94.4 % of all dissolved nutrients at any stage of decomposition.

Of the nutrients remaining in the plant material, nitrogen is the most abundant. Calcium can account for up to 32 %, while the amounts of K, P, and Mg generally are very small, not exceeding more than 4.4 %, 3.6 % and 5.5 %, respectively. Marked changes in the relationships among the nutrients occur only at the beginning of the decomposition (Figs. 11 - 14).

A comparison between nutrients detected in the water and those lost from the remaining detritus shows that there are considerable discrepancies (Figs. 11 - 14, bottom rows), which are due to the following:

- Loss of fine detritus particles from the litter bags;
- Fixation by consumer organisms, such as bacteria and fungi;
- Dissolution of organic compounds, which are not analyzed;
- Losses to the atmosphere.

The identities and amounts of those nutrients not located vary according to the species. For example, up to 52 % of the not located nutrients are Ca in the experiment with *Pseudobombax* leaves, only 25 % in the experiment with *Salix* leaves, and 2 % in that with *Cecropia* leaves (Figs. 11 - 14).

5. Chemical composition of fresh multispecies leaf litter

Fresh leaves from individual tree species were used in the experiments because they are more homogeneous than mixed leaf litter, in which the leaves vary in age, water content, and chemical composition. However, fresh multispecies leaf litter is a more realistic basis for quantitative estimates of nutrient fluxes during decomposition. Therefore, mixed samples of fresh leaves and fresh leaf litter from 20 tree species from the várzea and 20 from the igapó floodplain forest were collected and analyzed (Table 7).

Compared with fresh leaves, fresh leaf litter is impoverished in its total nutrient content, mainly due to the marked reduction of K, N, and P content. The elimination of K and N was more pronounced from the várzea leaf litter than from the igapó leaf litter (Table 7). However, fresh leaf litter is enriched in Ca, and, to a lesser extent, in Mg and Na. Comparing the nutrient content of the mixed samples with the data of KLINGE et al. (1983) for fully developed leaves and those of ADIS et al. (1979) for fresh leaf litter, considerable similarity is apparent (Table 7).

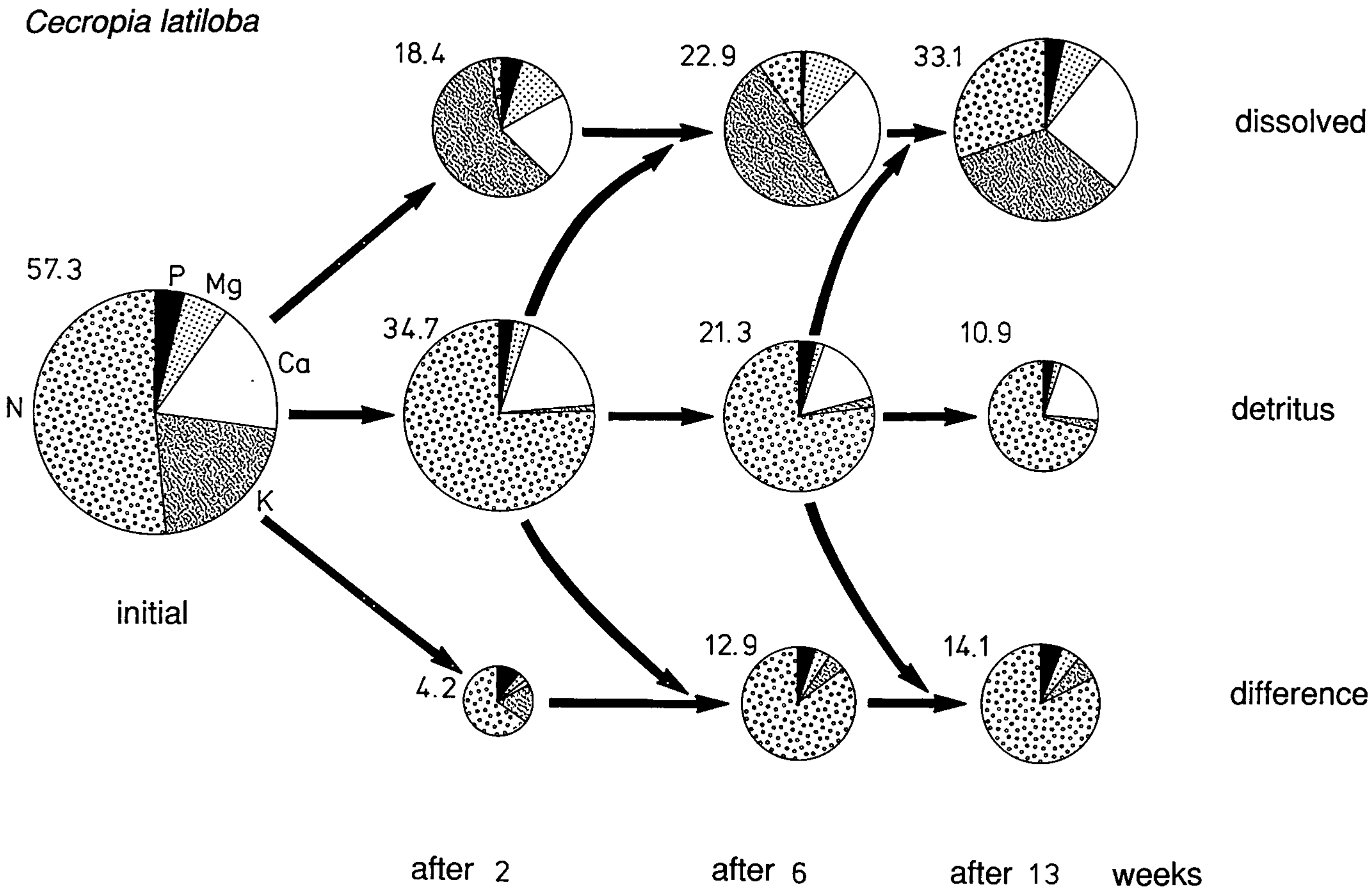

Fig. 11:
Distribution of the leaf nutrients K, Mg, Ca, N and P at different stages of decomposition of 1 kg of dry leaves from *Cecropia latiloba* in water. The circle area is proportional to the sum of the five nutrients, given in g as numbers to the left of the circles. Upper row: nutrients released into the water; middle row: nutrients stored in the detritus; bottom row: nutrients distributed elsewhere, calculated as the difference between the initial nutrient amount and the amount of nutrients released plus nutrients stored in the detritus.

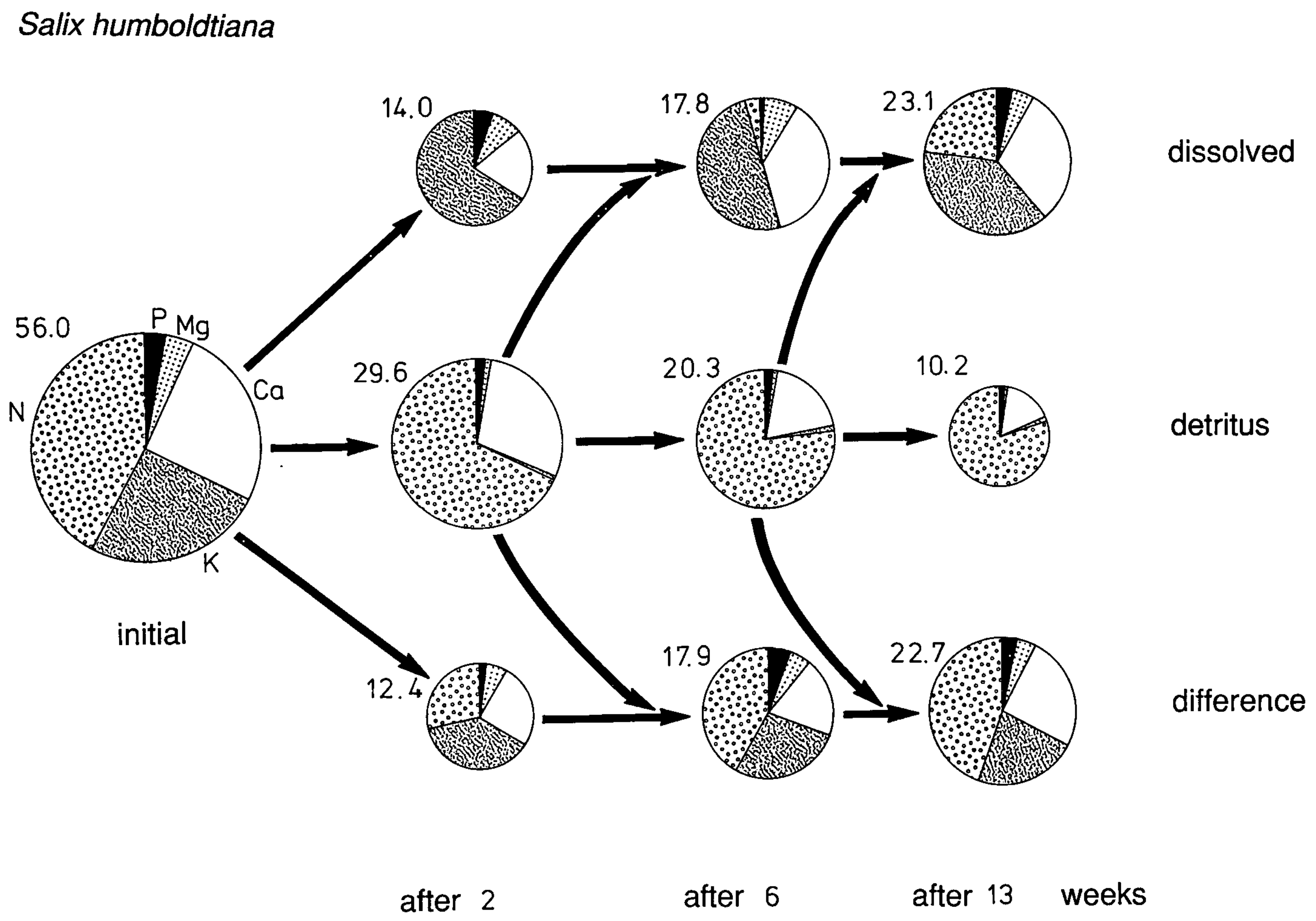

Fig. 12:
Distribution of the leaf nutrients K, Mg, Ca, N and P at different stages of decomposition of 1 kg of dry leaves from *Salix humboldtiana* in water. For further explanations, see Figure 11.

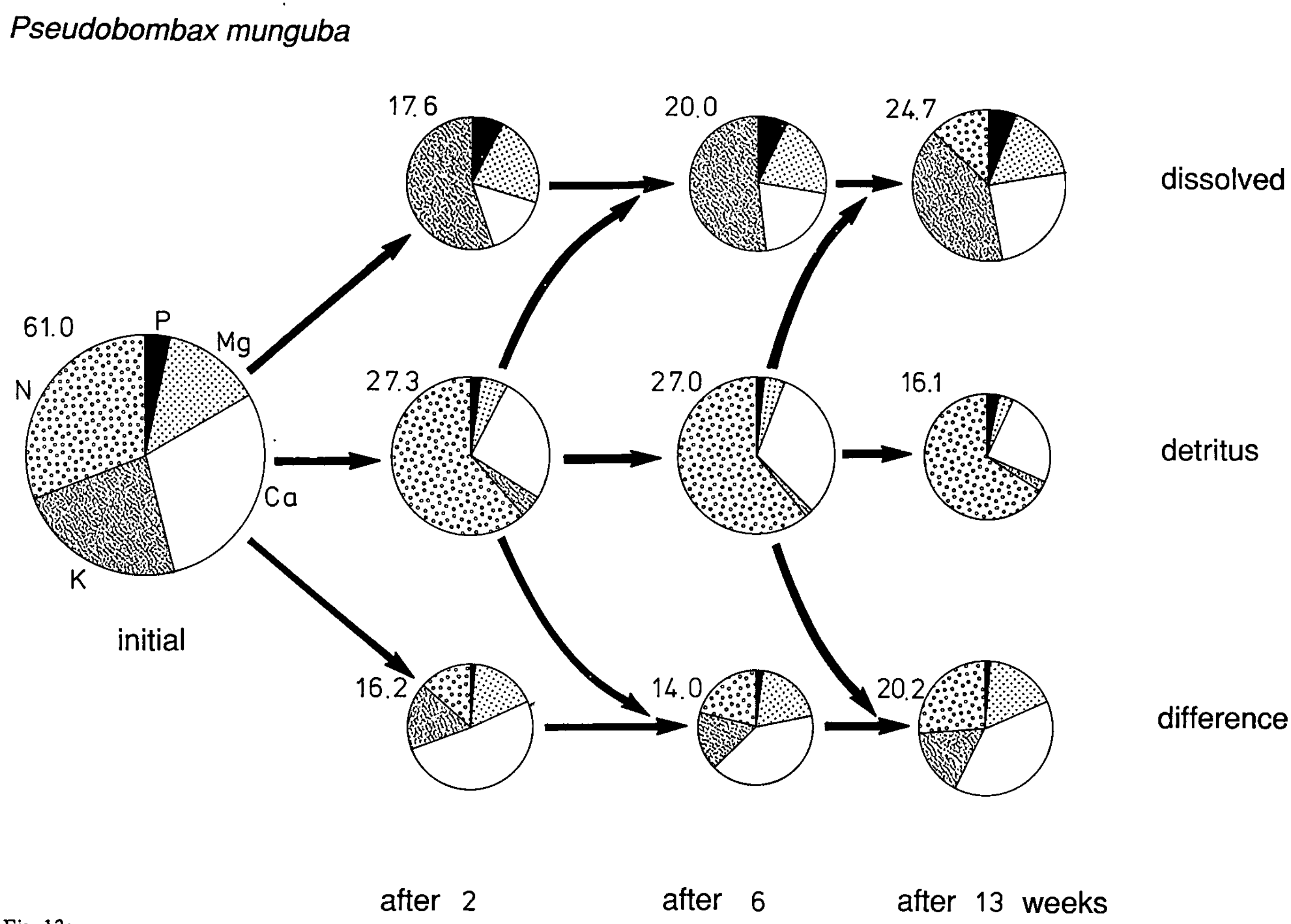

Fig. 13:
Distribution of the leaf nutrients K, Mg, Ca, N and P at different stages of decomposition of 1 kg of dry leaves from *Pseudobombax munguba* in water. For further explanations, see Figure 11.

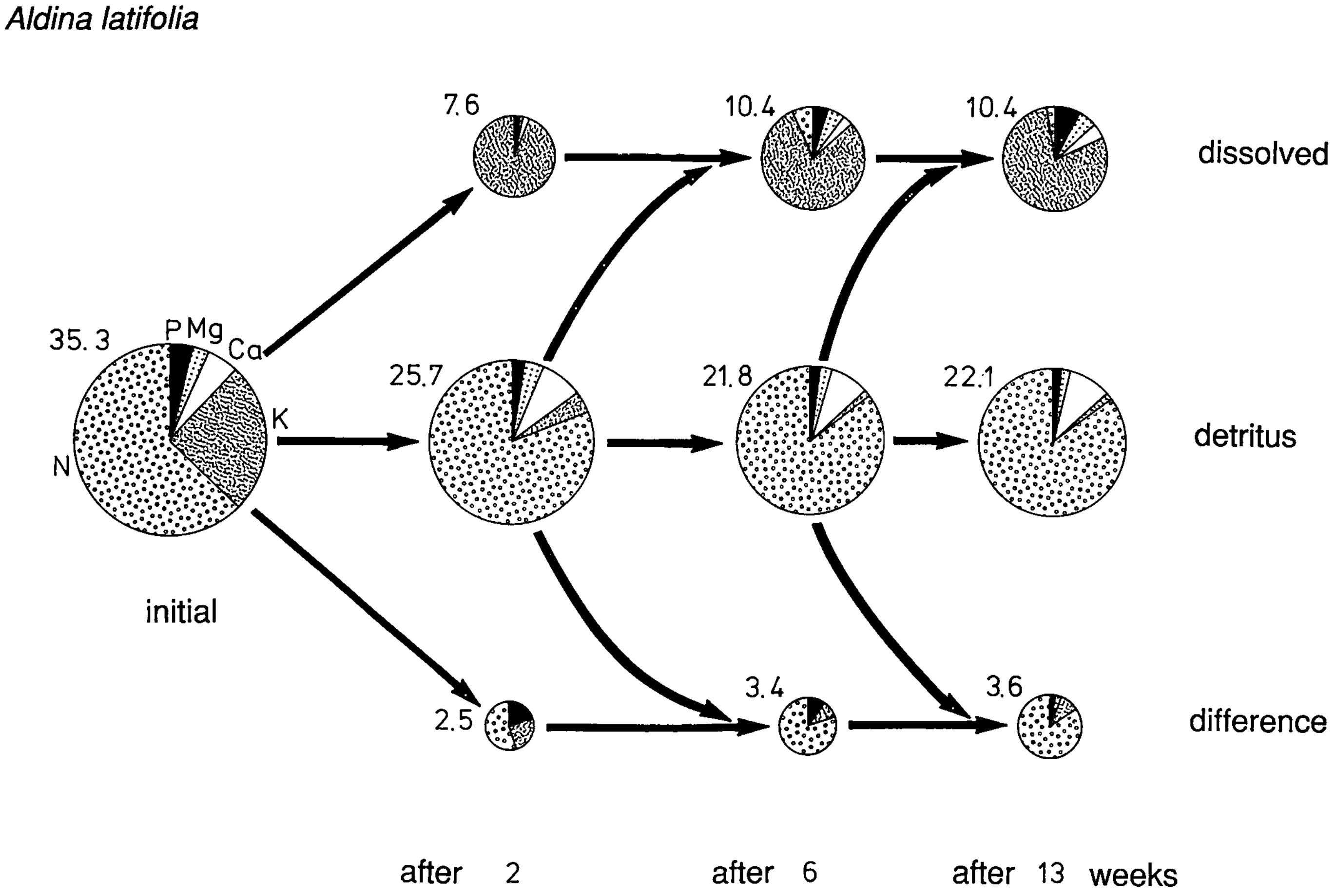

Fig. 14:
Distribution of the leaf nutrients K, Mg, Ca, N and P at different stages of decomposition of 1 kg of dry leaves from *Aldina latifolia* in water. For further explanations, see Figure 11.

Table 7: Nutrient element content (g kg^{-1} dry weight) in mixed samples of fresh leaves and fresh leaf litter from 20 tree species from the floodplain forests igapó (Anavilhanas) and 20 from the várzea (Ilha de Marchantaria).

1) Mean concentrations of elements in fully developed leaves from the várzea (Ilha de Marchantaria, n = 31) and from the igapó (Praia Grande, n = 21) reported by KLINGE et al. (1983).

2) Mean concentrations (g kg^{-1} dry weight) in fresh leaf litter reported by ADIS et al. (1979).

	Várzea		**Igapó**	
	Fresh leaves	Leaf litter	Fresh leaves	Leaf litter
Na	0.06 (0.20 ± 0.27)[1]	0.18 (0.09 ± 0.03)[2]	0.04 (0.25 ± 0.44)[1]	0.07 (0.06 ± 0.01)[2]
K	9.00 (13.18 ± 6.84)[1]	4.33 (4.90 ± 0.70)[2]	6.40 (6.33 ± 2.62)[1]	4.68 (3.00 ± 0.50)[2]
Mg	2.84 (3.98 ± 1.85)[1]	3.02 (3.20 ± 0.80)[2]	1.56 (1.22 ± 0.58)[1]	1.68 (1.28 ± 0.10)[2]
Ca	13.75 (19.14 ± 8.31)[1]	18.58 (15.40 ± 3.60)[2]	4.20 (2.51 ± 2.04)[2]	5.77 (5.00 ± 0.60)[2]
N	22.30 (25.87 ± 5.31)[1]	13.50 (21.00 ± 0.40)[2]	15.60 (17.31 ± 4.04)[1]	11.70 (14.30 ± 0.90)[2]
P	1.56 (1.76 ± 0.43)[1]	1.02 (0.78 ± 0.06)[2]	0.84 (0.62 ± 0.26)[1]	0.45 (0.18 ± 0.02)[2]
sum	49.51 (64.13)	40.63 (45.37)	28.64 (28.24)	24.35 (23.82)

Discussion

The Amazonian floodplain várzea and igapó forests, although influenced by the same climatic and hydrological regime, strongly contrast in their biogeochemical conditions. Amazon River water, flooding the várzea, is far richer in nutrients and sediment than the Negro River water, which floods the igapó (SIOLI 1950, 1965, 1968; KLINGE & OHLE 1964; ANONYMOUS 1972; SCHMIDT 1972; FURCH et al. 1982; FURCH 1984a; JUNK & FURCH 1985; FURCH & KLINGE 1989). The vegetation of the várzea shows considerable higher nutrient levels than that of the igapó (KLINGE et al. 1983, 1984; KLINGE 1985, 1986; FURCH & KLINGE 1989). The species growing in the várzea and the igapó forests are different (PRANCE 1979), and litter production by the várzea forest is about double that of the igapó forest (ADIS et al. 1979; FURCH & KLINGE 1989).

Differences between the várzea and igapó are also apparent in the leaf decomposition dynamics under aquatic conditions. The dynamics of decomposition and the liberation of nutrients are dependent on the physical and chemical quality of the leaves from the different tree species (WEBSTER & BENFIELD 1986; NICOLAI 1988; DENICH 1989). While our knowledge of the physical structure of the leaves is poor (KLINGE et al. 1983), their composition in terms of the chemical elements is better known (KLINGE et al. 1983; KLINGE 1985, 1986; FURCH & KLINGE 1989).

Large dry weight losses are observed from leaves of the three várzea forest species, which are rich in nutrient elements. Their decomposition rates are nearly as high as those observed for herbaceous plants under similar conditions (HOWARD-WILLIAMS & JUNK 1976; FURCH & JUNK 1985; HELBING et al. 1986; MURTY & SESHAVATHARAM 1989; JUNK & FURCH 1990). Leaves of the igapó species, which are poor in nutrient elements, decompose more slowly. This phenomenon has also been observed in other tropical rainforests that are poor in nutrient elements (KLINGE 1977).

The decomposition of várzea tree leaves is accompanied by high liberation rates of solutes into the water, mainly K, Mg, Ca, and NH_4, while from decomposing igapó tree leaves, only K ions are released in considerable amounts.

Loss rates of nutrient elements are remarkably higher from the leaves of the three várzea tree species than from those of the igapó tree species. For várzea species, loss rates are generally higher than the release rates, especially for the elements N, Ca and Mg. For the igapó species, *Aldina latifolia*, the loss and release rates are more similar. It is suggested that the differences in decomposition between várzea and igapó species are due to the slower microbial activity in the hard leaves from *Aldina latifolia*, which are poor in nutrient elements.

Fresh multispecies leaf litter from várzea and igapó species is generally poorer in nutrient elements than fresh leaves from the same trees. This is most apparent for N, P and K, while Ca is more abundant in the litter (IRMLER 1979; IRMLER & FURCH 1980; MEDINA 1984), as found in temperate regions, as well (MONK 1971; BAUMEISTER & ERNST 1978; MENGEL & KIRKBY 1978). Fresh leaf litter from the várzea generally is richer in nutrient elements, except for K, than that from the igapó.

To estimate the impact of fresh decomposing leaf litter on the nutrient budget of both floodplain forest types, calculations were made for the flood period using the following assumptions:

– Annual leaf fall in the várzea and igapó forest equals 1.057 kg m^{-2} (KLINGE pers. comm.) and 0.532 kg m^{-2} (ADIS et al. 1979), respectively, of which 50 % is produced during a four month period of flooding (ADIS et al. 1979, KLINGE pers. comm.).

– The nutrient content of the litter corresponds to the values for the mixed leaf litter samples (Table 7).

– Nutrient loss and release rates correspond to the maximum values obtained in the decomposition experiments with fresh leaves (see K_l and K_r in Table 6). For the three várzea species average values are used.

– The impact on the ecosystem is calculated by comparing the nutrient input from fresh leaf litter with the nutrient concentrations in the Amazon and Negro River water, assuming a water depth of 4 m.

The following equation is used:

$$C = \frac{c_1 \cdot a \cdot d_{1,2,3} \cdot b}{100 \cdot h}$$

where

C = calculated element input to the river water (mg l^{-1})
c_1 = element concentration in fresh leaf litter (g kg^{-1})
a = annual leaf litter fall (kg m^{-2})
b = leaf litter fall during the period of the high water level, April - July (% of annual)
d_1 = maximum element release rate during a four month decomposition period (ratio K_r, see Table 6)
d_2 = maximum element loss rate during a four month decomposition period (ratio K_1, see Table 6)
d_3 = total element input from leaf litter during the period of the high water level, April - July (ratio = 1:1)
h = the level of the river water above the forest floor (m).

Table 8: Chemical composition of the Amazon River and Negro River water. a: in the main channels near Manaus; monthly average for 1981 in the Amazon and a two year average for 1975 - 1976 in the Negro (FURCH 1984a, * ANONYMOUS 1972); b: the calculated input of dissolved nutrients released from decomposing fresh leaf litter; c: the calculated input of nutrients lost from decomposing fresh leaf litter; and d: the calculated input of total nutrients from fresh leaf litter during a four month period of high water. The input as % of river water concentration is shown in parentheses. N_{tot} = sum of NO_2 - N, NO_3 - N and NH_4 - N. For further explanations, see text.

		a	b	c	d
	Amazon River		(%)	(%)	(%)
Na	(mg l^{-1})	2.99	0.024 (+ 1)	0.024 (+ 1)	0.024 (+ 1)
K	(mg l^{-1})	0.87	0.452 (+ 52)	0.561 (+ 64)	0.572 (+ 66)
Mg	(mg l^{-1})	1.35	0.240 (+ 18)	0.356 (+ 26)	0.375 (+ 28)
Ca	(mg l^{-1})	9.72	1.399 (+ 14)	2.087 (+ 21)	2.455 (+ 25)
N_{tot}	(μg l^{-1})	155	499 (+ 322)	1249 (+ 806)	1784 (+1152)
PO_4-P	(μg l^{-1})	26	82 (+ 315)	120 (+ 462)	135 (+ 529)
	Negro River				
Na	(μg l^{-1})	380	5 (+ 1)	5 (+ 1)	5 (+ 1)
K	(μg l^{-1})	327	302 (+ 92)	308 (+ 94)	311 (+ 95)
Mg	(μg l^{-1})	114	71 (+ 62)	73 (+ 64)	112 (+ 98)
Ca	(μg l^{-1})	212	184 (+ 87)	100 (+ 47)	384 (+ 181)
N_{tot}	(μg l^{-1})*	72	70 (+ 97)	124 (+ 173)	778 (+1081)
PO_4-P	(μg l^{-1})*	6	19 (+ 317)	19 (+ 317)	30 (+ 500)

The data in Table 8 show that there is a strong input of nutrients into the system from leaf litter, which is especially pronounced in the cases of the basic nutrients N, P, and K, and in blackwater, Ca and Mg as well. The decomposition experiments show that a considerable proportion of these nutrients enters the water in the form of dissolved inorganic compounds, and they are therefore directly available for uptake by aquatic consumers, especially primary producers. Since the trees in the floodplain forests extract most of their nutrients from the sediment, litter production can be considered a powerful nutrient pump from sediment to water. This is especially important for the blackwater of the Negro River, where nutrients are extremely scarce (ANONYMOUS 1972; FURCH et al. 1982; FURCH 1984a). The relatively large release of alkali earth metals into the blackwater may be of special biological importance since these elements are found only in unusually low quantities (FURCH 1976; FURCH & KLINGE 1978; FURCH et al. 1982). While biogenic enrichment in nutrient elements has already been demonstrated for várzea lakes (FURCH et al. 1983; FURCH 1984a, b; FURCH & JUNK 1985), proof of this is still lacking for the blackwater in the igapó. It is suggested that in blackwaters, the nutrient elements are rapidly taken up by aquatic consumers since the nutrient deficit is generally high.

Summary

Fresh leaves of *Cecropia latiloba, Salix humboldtiana* and *Pseudobombax munguba*, common tree species of the Amazon River floodplain forest (várzea), and *Aldina latifolia*, a common tree species of the Negro River floodplain forest (igapó), were exposed in litter bags in freshwater tanks filled with ground water for decomposition studies. Changes in dry weight and in the chemical composition of the leaves and water were recorded for a period of about four months.

Great nutrient and dry weight losses from the nutrient rich leaves of the three várzea tree species were observed. The leaves had lost up to 86 % of their initial biomass and up to 89 % of the initial amount of total nutrients, determined as the sum of Na, K, Mg, Ca, N and P. The loss of K was greatest, between 97 and 99 % of the initial amount, and loss of N was the least, between 52 and 84 % of the initial amount. Due to the differences in the loss rates for the individual elements, the nutrient composition of the leaf material changed during decomposition.

The nutrient-poor leaves from the igapó tree species, *Aldina latifolia*, decomposed much more slowly. The leaves lost only about 10 % of their initial biomass, and the total nutrients diminished to about 60 % of the initial amount. Only the loss of K was as high as that from decomposing leaves of the várzea species, 99 % of the initial amount, while the loss of N was slight, 16 % of the initial amount. Since the loss of total nutrients was far greater than the corresponding dry weight loss, the nutrient content of the leaf material can be said to have diminished rapidly during decomposition.

A large portion of the total nutrients lost from the leaves, between 44 and 59 % from várzea tree leaves and 37 % from igapó tree leaves, was detected in the water in the form of inorganic ions. Consequently, the acid and electrolyte-poor ground water used for the experiments had changed to a well buffered water, rich in electrolytes. In the water with decomposing várzea tree leaves, K and later, Ca and NH_4 became the dominant cations. In the experiment with *Aldina* leaves, only K appeared in high quantities in the water; NH_4 and Ca concentrations remained very low. In all experiments, HCO_3 was the dominant anion, responsible for the increase in the buffer capacity of the water.

A calculation of the input of nutrients from mixed leaf litter during flooding was made, assuming 5 and 2.7 t ha^{-1} leaf fall in the várzea forest and the igapó forest, respectively, during the four month period of flooding. The following quantities (kg ha^{-1}) were released into the water of the várzea forest: Na: 0.94, K: 18.08, Mg: 9.61, Ca: 55.97, N: 19.98 and P: 3.29. In the igapó forest, the values were Na: 0.19, K: 12.08, Mg: 2.86, Ca: 7.37, N: 2.80 and P: 0.76. The total nutrient input into the system is considerably greater because annual litter fall is double that during the period of flooding, and there are large amounts of nutrients left in the remaining detritus.

Resumo

Folhas frescas de *Cecropia latiloba, Salix humboldtiana* e *Pseudobombax munguba*, espécies arbóreas comuns de floresta de planicie de inundação ("várzea") do Amazonas, e *Aldina latifolia*, uma espécie arbórea da floresta de inundação ("igapó") do Rio Negro, foram expostas em sacos de liteira, em tanques enchidos com água freática, para estudos da decomposição. Seguiram-se as mudanças no peso seco e na composição química das folhas e respectivamente da água durante um período de 4 meses.

Constataram-se altas perdas de nutrientes e de peso seco das folhas ricas em nutrientes, das três espécies arbóreas da várzea. A biomassa das folhas perdeu até 86 % do peso inicial, e até 89 % do conteúdo inicial em nutrientes totais (soma de Na, K, Mg, Ca, N e P). A perda de K era a mais alta (entre 97 e 99 % do conteúdo inicial), e a perda de N era a mais baixa (entre 52 e 84 % do conteúdo inicial). Devido a estas quotas de perda diferentes para os elementos individuais, a composição em nutrientes do material de folhas mudara durante a decomposição.

As folhas pobres em nutrientes da espécie arbórea de igapó, *Aldina latifolia*, decompuzeram-se muito mais lentamente. A biomassa das folhas perdeu somente mais ou menos 10 % do peso inicial dela, e os nutrientes totais diminuiram a mais ou menos 60 % do teór inicial. Unicamente a perda de K era tão alta como a nas folhas em decomposição das espécies de várzea (99 % do teór inicial), enquanto que a perda de N era baixa (16 % do teór inicial). Sendo que a perda de nutrientes totais era, com muito, mais alta do que a respectiva perda de peso seco, o conteúdo em nutrientes do material de folhas ficou fortemente reduzido durante a decomposição.

Uma porção grande dos nutrientes totais desprendidos da biomassa das folhas (entre 44 e 59 % para as folhas das árvores de várzea, e 37 % para as folhas das árvores de igapó) reencontraram-se na água em forma de ions inorgânicos. Consequentemente, a água freática ácida e pobre em eletrólitos, transformou-se a uma água bem tamponada, rica em eletrólitos. Na água contida as folhas de árvores de várzea em decomposição, K, e mais tarde Ca e NH_4, tornaram-se os cátions dominantes. No experimento com folhas de *Aldina,* havia somente K que apareceu na água em quantidades altas, enquento que as concentrações de NH_4 e especialmente Ca permaneceram muito baixas. Em todos os experimentos era HCO_3 que se tornou o ánion dominante, cuja formação causou o aumento da capacidade de tampão da água.

Calculou-se a quantidade de nutrientes desprendidos da liteira mista de folha durante a inundação pelos rios, avaliada em 5 e 2.7 toneladas/hectare de folhas caidas na floresta de várzea resp. na de igapó, durante um período de inundação 4 meses por ano. As seguintes quantidades (em Kg $\cdot$ ha^{-1}) foram desprendidas à água: Na 0.94, K 18.08, Mg 9.61, Ca 55.97, N 19.98 e P 3.29 na floresta de várzea, respectivamente Na 0.19, K 12.08, Mg 2.86, Ca 7.37, N 2.80 e P 0.76 na floresta de igapó. A introdução total de nutrientes no sistema de fato é considerevalmente maior porque a queda de liteira foliácea anual é o dobro da durante a época de inundação, ficando grandes quantidades de nutrientes retidos no detrito remanescente.

Acknowledgments

We are grateful to the Deutsche Forschungsgemeinschaft, Bonn-Bad Godesberg, for funding this study, and to S. Bartel for realization of chemical analyses.

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