Nutrient dynamics of submersed decomposing Amazonian herbaceous plant species **Paspalum fasciculatum** *and* **Echinochloa polystachya** (1)

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Abstract

In the Amazon floodplain, decomposition of herbaceous plants occurs quickly during the flood period. Experiments with plant material of native terrestrial and aquatic grasses (Paspalum fasciculatum *and* Echinochloa polystachya) *in tanks, filled with groundwater, suggest that under mostly anaerobic conditions considerable amounts of Na, K, Ca, Mg, N, and P are lost from the exposed plant material during the first 2-4 weeks. Between 76 % and 100 % of the amounts of the individual elements lost from the plant material are found in soluble form in the water, excepting nitrogen, where the values obtained were 57 % for* Echinochloa *and 47 % for* Paspalum. *A budgeting of the various sources of bio-elements during the flood period in a hypothetical floodplain lake shows that inflowing river water is the main source for dissolved Na (99.5 %), Ca (93 %), and Mg (86.5 %). However, terrestrial herbaceous plants and the litter from the floodplain forest are by far the greatest sources for N (77.2 %), P (83.2 %), and K (60.7 %). The results point to the importance of terrestrial vegetation as a pump of nutrients from the sediments into the water and to its great contribution to the nutrient dynamics and productivity of floodplain systems.*

Key words : Decomposition — Herbaceous plants — Amazon — Floodplain — Nutrients — *Echinochloa polystachya* — *Paspalum fasciculatum* — Freshwaters — South America.

Résumé

Dynamique de la décomposition aquatique des plantes herbacées *Paspalum fasciculatum* et *Echinochloa polystachya*

Dans la plaine inondée de l'Amazone, la décomposition des plantes herbacées est très rapide durant la période d'inondation. Des expériences menées sur des plantes herbacées aquatiques et terrestres (Echinochloa polystachya *et* Paspalum fasciculatum) *dans des bassins remplis d'eau de source, suggèrent que de grandes quantités de bio-éléments (Na, K, Ca, Mg, N et P) sont perdues durant les 2 à 4 premières semaines d'exposition du matériel végétal. De 76 à 100 % des quantités totales d'éléments perdus par le matériel végétal se retrouvent sous forme soluble dans l'eau, à l'exception de l'azote pour lequel les valeurs obtenues sont de 57 % pour* Echinochloa polystachya *et 47 % pour* Paspalum fasciculatum. *Un bilan des diverses sources de bio-éléments durant la période d'inondation, dans un*

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hypothétique lac de la plaine inondée, montre que l'eau du fleuve est la plus importante source de Na (99.5 %), Ca (93 %) et Mg (86.5 %) sous forme dissoute. Cependant, les plantes herbacées terrestres et la litière de la forêt de la plaine inondée restent les plus importantes sources de N (77.2 %), P (83.2 %) et K (60.7 %). Ces résultats montrent l'importance de la végétation terrestre comme pompe à éléments des sédiments vers l'eau et sa grande contribution à la dynamique des éléments nutritifs et à la production des systèmes de plaine inondée.

MOTS CLÉS : Décomposition — Plantes herbacées — Plaine inondée — Amazone, Bilan des éléments nutritifs — *Echinochloa polystachya* — *Paspalum fasciculatum* — eau douce — Amérique du Sud.

INTRODUCTION

Herbaceous plant communities of Amazonian white-water river floodplains belong to the most productive plant communities on earth. PIEDADE *et al.*, (1991) indicate an annual net primary production of about 100 t ha^{-1} and maximum biomass values of 80 t ha^{-1} for the perennial C4-species *Echinochloa polystachya*, which has its main growth period during the aquatic phase. Values nearly as high are found for another C4-species in the same area, *Paspalum fasciculatum*, which has its main growth period during the terrestrial phase (JUNK, unpublished data). Both species are very successful in dealing with the annual change between dry and flood period (JUNK *et al.* 1989) and cover large areas of the Amazonian Várzea with monospecific stands. Annual species, most of them C3-plants, reach biomass values from 3 to 15 t ha^{-1} either during the dry period, or during the flood period (JUNK *et al.* 1989, JUNK, unpublished data).

Large biomass, high productivity and quick turnover suggest a possibly strong impact of herbaceous plant communities on the bio-element dynamics of the floodplain system. Most decomposition experiments with aquatic macrophytes focus on dry weight loss and the loss of bio-elements from the organic material (HOWARD-WILLIAMS & JUNK 1976, HOWARD-WILLIAMS & HOWARD-WILLIAMS 1978, ESTEVES & BARBIERI 1983, GOPAL 1984, GAUR *et al.* 1989, MORAN & HODSON 1989, JUNK & FURCH 1991, and others). However, loss of bio-elements from decomposing, material does not necessarily corresponds to their release into the water in soluble form. Such studies on the release of mineral solutes directly delivered to the water are less frequent (PLANTER 1970, GODSHALK & WETZEL 1978, KISTRITZ 1978, BASTARDO 1979, CARPENTER 1980, FURCH & JUNK 1985, HELBING *et al.* 1986, SILVA & MORAES 1986, TWILLEY *et al.* 1986, FURCH *et al.* 1988, 1989). However, the dynamics of the release of the bio-elements determine their availability in the system for new plant growth and are very important for the productivity of the whole floodplain system.

The following study attempts to determine the fate of the elements Na, K, Mg, Ca, N, P and C lost from *Echinochloa polystachya* and *Paspalum fasciculatum* plant material into the water and to estimate their impact on the nutrient budget of the ecosystem.

MATERIAL AND METHODS

The plant material used for the decomposition experiments was collected on Marchantaria island (03° 15′ S, 58° 58′ W), the first island upstream of the confluence of the Amazon River with the Negro River near Manaus. A mixture of leaves and stems of *Echinochloa polystachya* and *Paspalum fasciculatum* was placed in litter bags of 2 mm mesh size for about 4 months in tanks filled with 700 l groundwater, which was acidic and low in electrolyte content (Tab. I). The ambient air temperature ranged between 27 °C and 30 °C. Each bag contained 100 g fresh plant material, corresponding to 26.1 g dry weight for *Echinochloa polystachya* and 24.4 g for *Paspalum fasciculatum*. Total amount of exposed fresh material corresponded to 4 kg in each tank.

TABLE I

Chemical composition of the groundwater 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}) and pH
Composition chimique de l'eau de source utilisée pour les expériences de décomposition. Les valeurs sont présentées en mg l^{-1}, à l'exception de la conductivité spécifique à 25 °C (K_{25}, présentée en µS cm^{-1}) et du pH

pH :	4.20	HCO_3 :	0.61
K_{25} :	24.00	SO_4 :	0.22
Na :	1.06	Cl :	1.69
K :	0.34	PO_4 :	0.03
Mg :	0.08	NO_3 :	5.18
Ca :	0.20	NH_4 :	0.05

The water was not aerated during the study period and the experiments were performed in the dark to suppress primary production by algae and thus exclude interference with element cycling. Samples of water and leaf material were removed at weekly intervals.

Subsamples of leaf material were dried at 105 °C and analyzed for carbon, nitrogen, phosphorus, sodium, potassium, magnesium and calcium. C was analyzed after combustion at 1050 °C by acidimetry (C-analyzer, Fa. Wösthoff), 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 for the water analysis : a glass electrode for pH; a platinum electrode for specific conductance; the Winkler method for oxygen; AAS for sodium, potassium, magnesium, and calcium; the molybdate blue and indophenol blue methods for

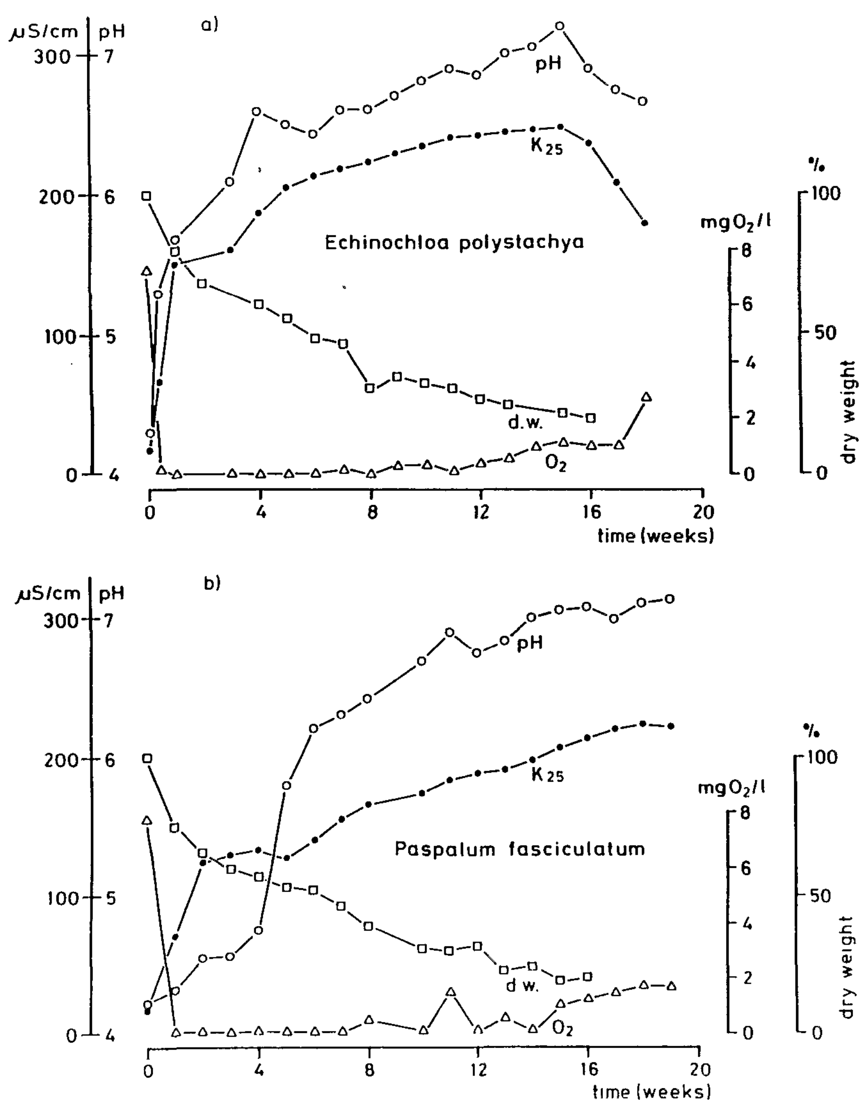

Fig. 1. — Dry weight loss (d. w.) and changes in pH, specific conductance at 25 °C (K_{25}) and content of O_2 in the water during decomposition of fresh biomass from *Echinochloa polystachya* (a) and *Paspalum fasciculatum* (b).
Perte de poids sec (d. w.), modifications du pH, conductivité spécifique à 25 °C (K_{25}) et concentration en O_2 de l'eau durant la décomposition de Echibochloa polystachya *(a) et* Paspalum fasciculatum *(b).*

phosphate and ammonium, respectively (Furch 1975); reduction to nitrite and photometric analysis with sulphanilamide for nitrate (Grasshoff 1976). Further details are given by Furch (1984a).

RESULTS

After one week of exposure in the water, biomass had lost 20 % of its initial dry weight for *Echinochloa polystachya* and 25 % for *Paspalum fasciculatum*, respectively, and after six weeks the loss was about 50 %. At the end of the study period (after sixteen weeks) about 20 % of the original dry weight remained (fig. 1a and 1b).

Weight loss of plant material was accompanied by drastic changes in water chemistry. Oxygen content abruptly decreased to zero and was followed by a long-term period of anaerobic conditions, which is a phenomenon frequently observed in Amazonian floodplains during rising and high water level (Junk 1984). The pH value increased more or less continuously from 4.2 to a maximum pH value of 7.1 for *Paspalum fasciculatum* and from 4.3 to 7.2 for *Echinochloa polystachya*. At the beginning of the experiment specific conductance of the electrolyte-poor water (about 20 µS cm^{-1}) showed a sharp increase, indicating a high leaching rate for the electrolytes. Later on, electrolyte content increased more slowly reaching maximum values of 220 and 240 µS cm^{-1} for *Paspalum fasciculatum* and *Echinochloa polystachya*, respectively.

After two weeks for *Echinochloa polystachya* and after three weeks for *Paspalum fasciculatum*, loss of magnesium, calcium and potassium was completed (fig. 2). This was equivalent to losses of initial amounts of approximately 97 % K, 93 % Mg and 90 % Ca for both species. Also amounts of nitrogen and phosphorus lost from the biomass are high after 2-3 weeks corresponding to 73 % P and 38 % N of the initial amounts for *Echinochloa polystachya* and 79 % P and 44 % N for *Paspalum fasciculatum*. Losses show an increase in the further stages of decomposition up to 85 % P and 79 % N for *Echinochloa polystachya* and 85 % P and 69 % N for *Paspalum fasciculatum*. Amounts of Mg, Ca and P lost from the biomass are quite similar for both species, i.e. up to 1.4, 2.8 and 1.8 g per kg dry weight, respectively, for *Echinochloa polystachya* and 1.5, 3.1 and 1.4 g per kg dry weight, respectively, for *Paspalum fasciculatum*. However, for *Echinochloa polystachya* amounts of K loss with max. 17.9 g per kg dry weight and N loss with 15.4 g per kg dry weight are

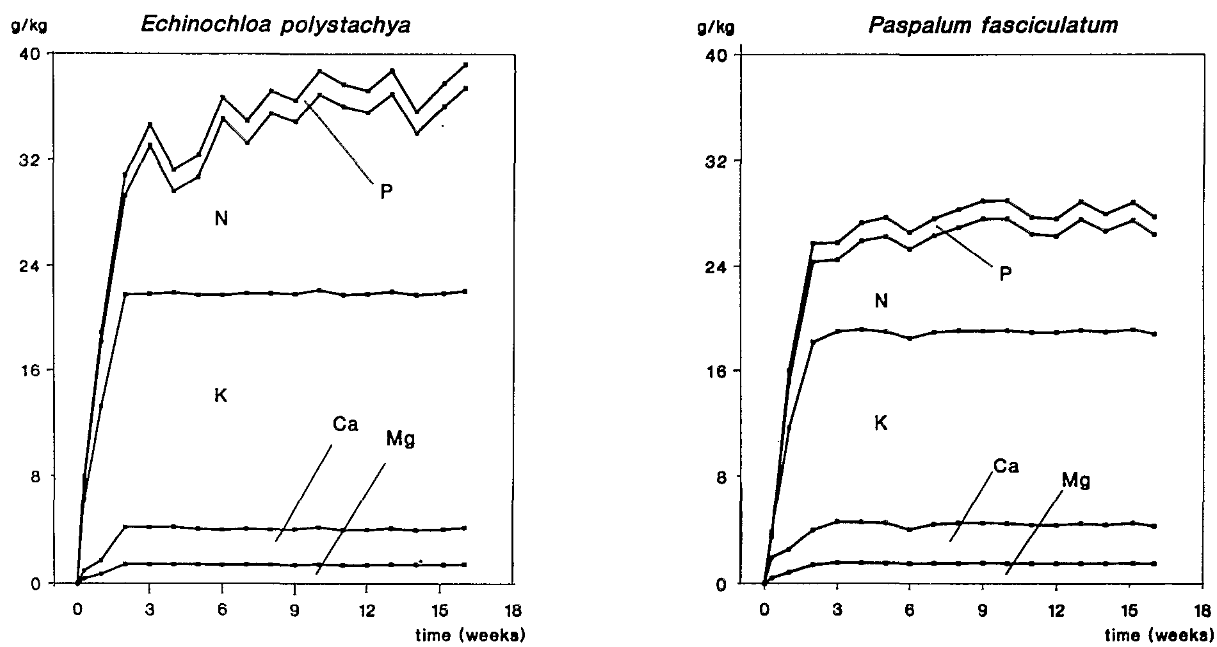

Fig. 2. — Cumulative amounts (g) of nutrient elements (Mg, Ca, K, N and P) lost from 1 kg of dry plant biomass from *Echinochloa polystachya* and *Paspalum fasciculatum* during decomposition in water.
Totaux cumulés (g) des éléments nutritifs (Mg, Ca, K, N et P) perdus à partir d'un kg de poids sec, de Echinochloa polystachya *et* Paspalum fasciculatum *durant la décomposition dans l'eau.*

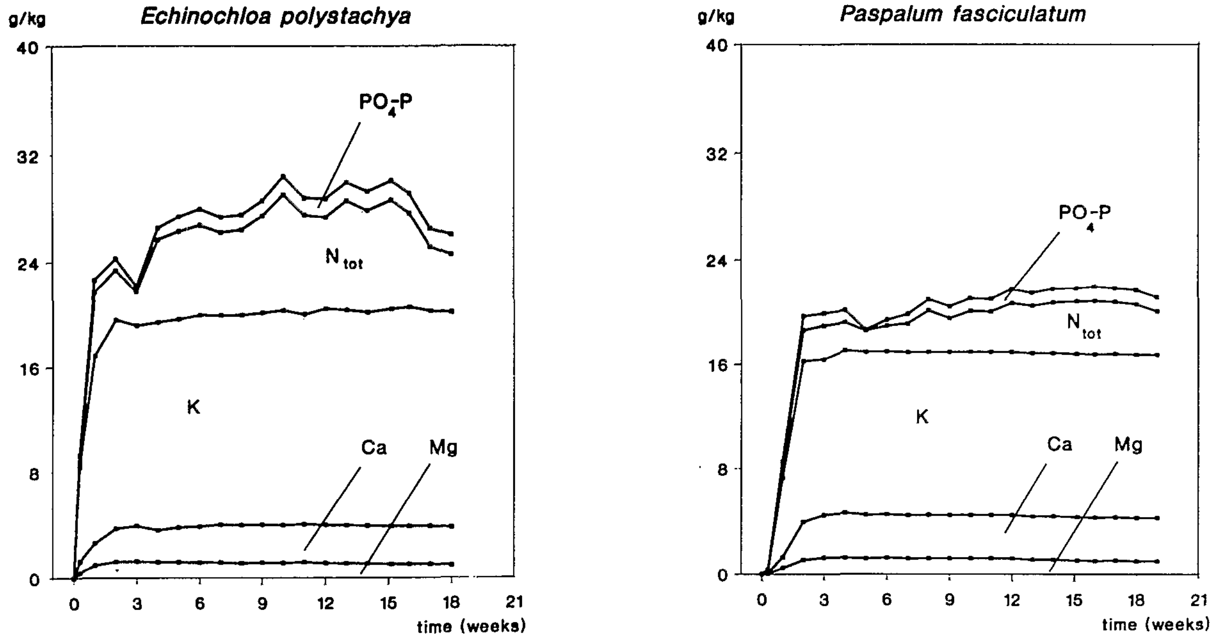

FIG. 3. — Cumulative amounts (g) of dissolved nutrient elements (Mg, Ca, K, N and P) released into the water during decomposition of 1 kg of dry plant biomass from *Echinochloa polystachya* and *Paspalum fasciculatum*. N_{tot} = sum of NH_4-N, NO_3-N, NO_2-N.
Totaux cumulés (g) des éléments nutritifs dissous (Mg, Ca, K, N et P) libérés dans l'eau durant la décomposition d'un kg de poids sec de Echinochloa polystachya *et* Paspalum fasciculatum. *N_{tot} = somme de NH_4-N, NO_3-N, NO_2-N.*

greater than for *Paspalum fasciculatum* with 14.5 and 8.6 g per kg dry weight, respectively. Amount of sodium loss corresponding to 0.06 g kg^{-1} was too low to be depicted in the figure.

Big portions of nutrients lost from the biomass (fig. 2) are found in the water as dissolved compounds as shown in fig. 3 (which looks very similar to fig. 2 except for nitrogen). Comparing data for maximum amounts lost from the biomass of *Echinochloa polystachya*, approximately 100 % Na, 98 % Ca, 93 % K, 90 % Mg, 83 % P, 57 % N are found dissolved in the water. The respective values are somewhat lower for *Paspalum fasciculatum* : approximately 100 % Na, 95 % Ca, 86 % K, 80 % Mg, 76 % P and 47 % N.

Changes of the bio-element content in the plant material show marked differences between the individual elements (figs. 4 and 5). While K content strongly decreases within the first two weeks and remains low for the rest of the decomposition period, N content increases after a slight depletion in the first weeks up to 125 % of its initial value for *Echinochloa polystachya* and up to 198 % for *Paspalum fasciculatum*. The fluctuations in N content of *Echinochloa polystachya* during the accumulation process cannot be explained. C contents do not change its initial level during the entire decomposition period (fig. 4).

Changes in Mg contents are similar to those of K contents (fig. 5) : a strong decrease within the first two weeks was followed by a slight but continuous increase. Ca and P concentrations showed a similarly strong decrease within the first 2-3 weeks. However, the decrease was followed by a strong increase, which continued to the end of the decomposition period without any indication that the accumulation phases for Ca and P were concluded by the end of the experiment. At this time Ca contents reach 57 % and 91 % and P contents reach 84 % and 110 % of the initial values for *Echinochloa polystachya* and *Paspalum fasciculatum*, respectively. Changes in Na contents are low for both species. Thus, nutrient impoverishment of plant material during decomposition is highest in the first 2-3 weeks. Afterwards the higher the dry weight loss the richer the residual material becomes in nutrients, especially in N, P and Ca (figs. 4 and 5).

The initial amounts of total nutrients (sum of N, P, K, Ca, Mg) and their distribution among different compartments are summarized in fig. 6 for selected stages of decomposition. Potassium accounts for the largest portion of the nutrients dissolved in the

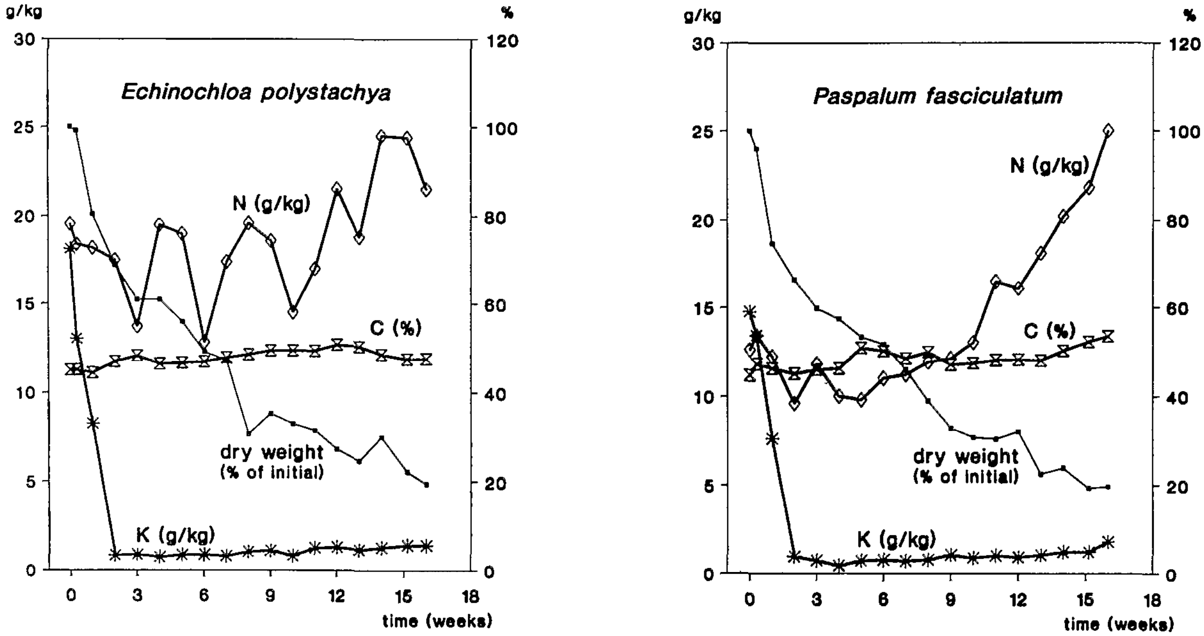

FIG. 4. - Dry weight loss (% of initial) and changes in the content of the bio-elements N, K (g kg^{-1}) and C (%) in the plant biomass from *Echinochloa polystachya* and *Paspalum fasciculatum* during decomposition in water.
Poids sec perdu, en pourcentage du poids initial, et changements de teneur en bio-éléments N, K (g kg^{-1}) et C (%) dans la biomasse des plantes Echinochloa polystachya *et* Paspalum fasciculatum *pendant la décomposition dans l'eau.*

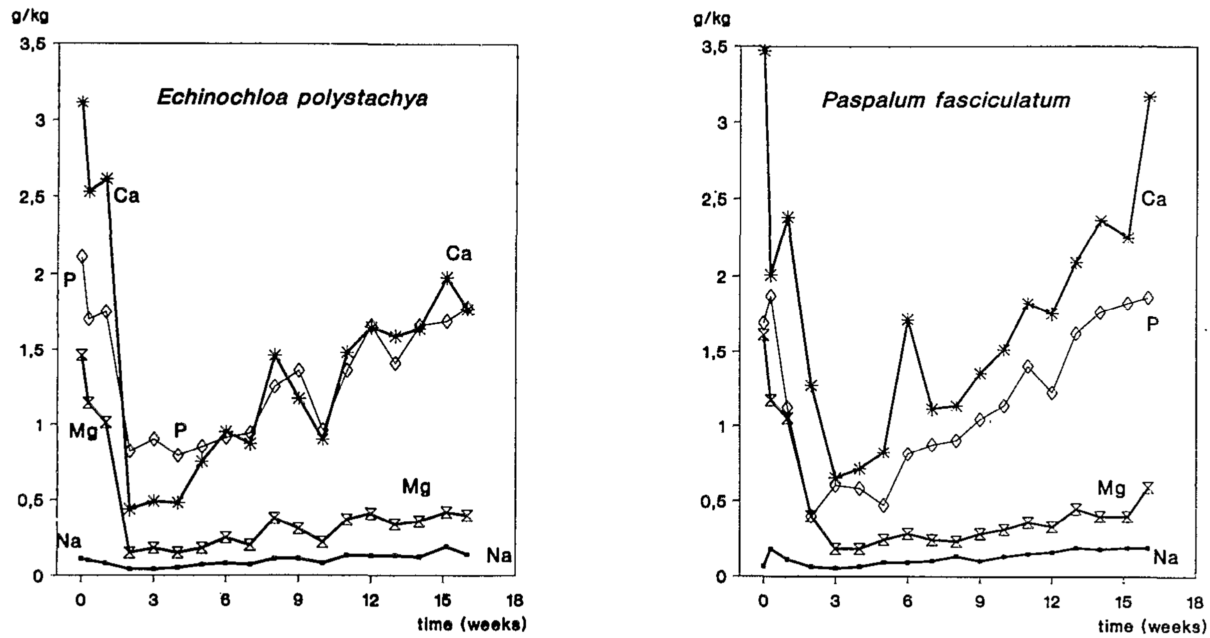

FIG. 5. - Changes in the content of the bio-elements Na, Mg, Ca, and P (g kg^{-1}) in the plant biomass from *Echinochloa polystachya* and *Paspalum fasciculatum* during decomposition in water.
Évolution des teneurs en bio-éléments Na, Mg, Ca et P (g kg^{-1}) de la biomasse des plantes Echinochloa polystachya *et* Paspalum fasciculatum *pendant la décomposition dans l'eau.*

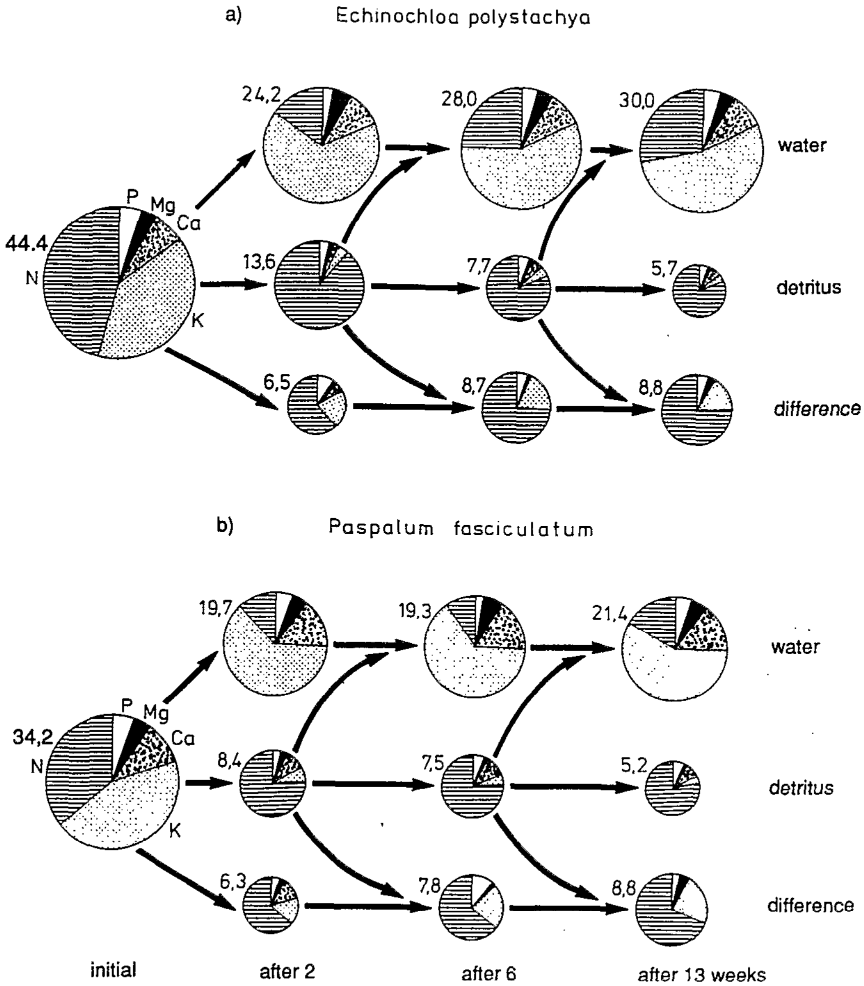

FIG. 6. — Distribution of the plant nutrients K, Mg, Ca, N and P at different stages of decomposition of 1 kg dry weight of *Echinochloa polystachya* (a) and *Paspalum fasciculatum* (b) in water. The circle area is proportional to the sum of the five nutrients, given in g as numbers to the left of the circles. Upper row : nutrients released into the water; middle row : nutrients stored in the plant biomass; bottom row : nutrients distributed elsewhere, calculated as the difference between the initial amount and the amount of nutrients released plus nutrients stored in the detritus.

Distribution des éléments nutritifs K, Mg, Ca, N et P à différents niveaux de décomposition d'un kg de poids sec de Echinochloa polystachya *et* Paspalum fasciculatum *dans l'eau. La surface des cercles est proportionelle à la somme des 5 éléments nutritifs présentée en g à gauche des cercles. Rangée supérieure : éléments nutritifs libérés dans l'eau; rangée du milieu : éléments nutritifs retenus par les plantes; rangée inférieure : éléments nutritifs distribués ailleurs, calculés à partir de la différence entre le taux initial et le taux d'éléments nutritifs libérés, additionné des éléments nutritifs retenus par les plantes.*

water. Later on, the nitrogen portion increases slightly, while portions of phosphorus, magnesium and calcium remain relatively constant. Thus the chemical composition of the water, as a result of released solutes from plant material, doesn't show marked changes during the further course of decomposition. Among the nutrients, which remained in the residual plant material, nitrogen is the most abundant, corresponding to 76-78 % of total nutrients *(Paspalum fasciculatum)* and 81-89 % *(Echinochloa polystachya)*.

Portions of the other four elements are accordingly very low, especially those of potassium, although it represents the most dominant nutrient in fresh plant material. After six weeks of decomposition a remarkable conformity occurs between the two species regarding both chemical composition and amount of total nutrients in the residual plant material.

A comparison between nutrients detected in the water and those lost from the remaining detritus shows that there are considerable discrepancies (fig. 6, bottom rows), which are explained by loss of fine detritus particles from the litter bags, fixation by consumer organisms (such as bacteria and fungi) not fixed on the substrate, dissolution of organic N and P compounds and losses of N and C to the atmosphere, which were not analyzed. The identities and amounts of those missing nutrients are very similar for both species.

DISCUSSION

Decomposition patterns

The weight loss of decomposing plant material in the experimental tanks was very quick, reaching more than 30 % in the first two weeks due to leaching processes and about 80 % after 16 weeks at the end of the experiment. However, it was somewhat slower than in the *in situ* experiments, performed by Howard-Williams & Junk (1976) and Junk & Furch (1991). This indicates that there are even greater dynamics under natural conditions, which are probably due to better oxygen supply in the surface water layers of the floodplain lakes, a more diverse consumer population and a more intensive leaching due to a permanent water exchange (Cuffney & Wallace 1987).

Patterns of nutrient losses were similar in the tank experiments in comparison with the *in situ* experiments. The exposed plant material suffered a strong and quick impoverishment of potassium, calcium, phosphorus, magnesium and, to a lesser extent, nitrogen. As well as the loss of nutrients from the exposed plant material, increasing amounts of electrolytes, mainly K, Ca, Mg, NH_4 and PO_4, were found in the water. As a result values of both specific conductance and pH showed a remarkable increase.

Thus, due to plant decomposition, acidic, oxygen-rich and electrolyte-poor water had changed to an oxygen-free, electrolyte-rich and well buffered water. These findings agree with results from decomposition experiments made with other herbaceous plant species and with leaves of floodplain forest trees (Furch & Junk 1985, Furch *et al.* 1988, 1989).

After 2-3 weeks, nutrient contents of the residual plant material started to increase (strongly in respect of nitrogen, calcium and phosphorus and slightly in respect of magnesium), while potassium content remained very low during the whole decomposition period. Such an increase has been reported by various authors (Suberkropp *et al.* 1976, Gopal 1984, Mattingly 1986, Webster & Benfield 1986, Twilley *et al.* 1986, James *et al.* 1988, Murty & Seshavatharam 1989, and others) and is explained partly 1) by the increasing number of consumer organisms attached to the organic material, 2) by ion exchange processes and 3) by a higher loss of C compounds in comparison with the other elements.

A tentative budget of nutrients

A detailed evaluation of the impact of the released nutrients from decomposing macrophytes on the nutrient budget of the Várzea is still difficult, because all nutrient sources can not be quantified. However, an estimate of the contribution of the various terrestrial plant communities in comparison with the input of dissolved nutrients by inflowing river water can be made. The following calculation considers a hypothetical floodplain lake during the flood-period under the following assumptions, which correspond to many floodplain lakes near Manaus.

— At low water level, the lake area is covered by 30 % floodplain forest, 30 % annual terrestrial plants, 10 % perennial herbaceous plants (5 % *Paspalum fasciculatum*, 5 % *Echinochloa polystachya*), 30 % free water surface.

—With rising water level, 6 t ha^{-1} annual terrestrial plants decompose (Junk *et al.* 1989). The perennial *Paspalum fasciculatum* (60 t ha^{-1}) becomes inundated and 50 % of its biomass decompose (Junk & Howard-Willimas 1984). *Echinochloa polystachya* continues to grow during the flood periode. It contributes bioelements to the water mainly from decomposing stems, low in element content, only at the end of the flood period (Piedade *et al.* 1991). Therefore decomposition data of *Echinochloa polystachya* will not be considered in the calculations. The floodplain forest adds about 50 % of its annual leaffall of 10.6 t ha^{-1} directly into the water (Furch & Klinge 1989, Furch *et al.* 1989). Due to the slow decomposition, 100 % of annual coarse woody litter production of about 6 t ha^{-1} is assumed to contribute nutrients directly to the water (Martius 1989).

— For herbaceous terrestrial plants chemical data of *Paspalum fasciculatum* of this study are used.

— The nutrient input from consumers, sediments, the atmosphere and litter, which decomposes during the terrestrial phase is not taken into account.

— A mean water depth of 4 m is assumed at high water level and annual average of chemical composition of the Amazon water is used for calculation (Furch *et al.* 1989).

TABLE II

Chemical composition of the various sources of bio-elements. In parentheses : maximum amounts of bio-elements released to the water from 1 kg dry weight of fresh plant material during decomposition within a four month period

Composition chimique de diverses sources de bio-éléments. Entre parenthèses : valeurs maximales de bio-éléments libérés dans l'eau à partir d'un kg de poids sec de matériel végétal frais pendant la décomposition durant une période de quatre mois

Bio-elements	Na	K	Mg	Ca	N	P
Amazon water* (mg kg^{-1})	2.99	0.87	1.35	9.72	0.16[a]	0.03[b]
fresh leaf litter* (g kg^{-1})	0.18 (0.12)	4.33 (3.41)	3.02 (1.93)	18.58 (10.65)	13.50 (3.73)[a]	1.02 (0.62)[b]
fresh wood** (g kg^{-1})	0.11 (0.06)	6.59 (4.00)	1.45 (0.68)	3.25 (0.73)	4.75 (0.85)[a]	0.82 (0.30)[b]
fresh herbs*** (g kg^{-1})	0.07 (0.06)	14.76 (12.48)	1.61 (1.23)	3.47 (3.25)	12.60 (4.04)[a]	1.69 (1.10)[b]

* FURCH *et al.* (1989)
** FURCH & KLINGE (1989) and unpublished data
*** This paper. a : dissolved inorganic nitrogen (sum of NH_4-N, NO_3-N, NO_2-N), b : PO_4-P

* *FURCH et al. (1989)*
** *FURCH & KLINGE (1989) et résultats non publiés*
*** *Le présent travail. a : azote minéral dissous (somme NH_4-N, NO_3-N, NO_2-N), b : PO_4-P*

TABLE III

Amounts of dissolved bio-elements contributed from various sources to a hypothetical floodplain lake in kg ha^{-1} during one flood period in an annual cycle. The amount of bio-elements from plant material is calculated according to the maximum quantities delivered to the water during an experimantal decomposition period of 4 months, according to tab. II. N_{tot} = sum of NO_2-N, NO_3-N, NH_4-N). For further explanations, see text

Quantités de bio-éléments dissous issus de diverses sources et fournies à un lac hypothétique de plaine inondée, en kg ha^{-1}, pendant une période d'inondation année. Le montant en bio-éléments issus du matériel végétal à partir de la quantité maximale libérée dans l'eau pendant une expérience de décomposition de 4 mois, suivant le tableau II. N_{tot} = somme de NH_4-N, NO_3-N, NO_2-N. Pour plus d'explications se reporter au texte

Bio-elements kg ha^{-1} y^{-1}	Na	K	Mg	Ca	N_{tot}	PO_4-P
Inflowing river water (%)	119.6 (99.5)	34.8 (39.3)	54.0 (86.5)	388.8 (93.0)	6.2 (22.8)	1.04 (16.8)
Leaf litter (%)	0.2 (0.2)	5.4 (6.1)	3.1 (5.0)	17.0 (4.1)	6.0 (22.1)	0.99 (16.0)
Woody litter (%)	0.1 (0.1)	7.2 (8.1)	1.2 (1.9)	1.3 (0.3)	1.6 (5.9)	0.54 (8.7)
Terrestrial annual plants (%)	0.1 (0.1)	22.4 (25.3)	2.2 (3.5)	5.8 (1.4)	7.3 (26.8)	1.98 (31.9)
Perennial herbs (%)	0.9 (0.1)	18.7 (21.1)	1.9 (3.1)	4.9 (1.2)	6.1 (22.4)	1.65 (26.6)
Total (%)	120.1 (100)	88.5 (100)	62.4 (100)	417.8 (100)	27.2 (100)	6.20 (100)

The amounts of nutrients in Amazon water, fresh leaf litter, fresh wood and fresh terrestrial herbaceous plants as well as the maximum amounts of nutrients released to the water from 1 kg dry weight of the different categories of plant material during a four month decomposition period in water are given in tab. II.

The values given in tab. III for the hypothetical floodplain lake show that river water is the main source for Na, Ca, and Mg, contributing 99.5 %, 93 %, and 86.5 % respectively to the system. However, herbaceous plants and the floodplain forest, which grow during the terrestrial phase, are the main sources for the important plant nutrients nitrogen, phosphorous and potassium. Together, they contribute 77.2 % N, 83.2 % P and 60.7 % K of the total input into the hypothetical lake. Herbaceous plants contribute 49.2 % N, 58.5 % P and 46,4 % K into the system.

Terrestrial herbs and trees of the floodplain forest take up their nutrients during the terrestrial phase mostly from the sediments (the impact of nitrogen-fixation is still unknown). Therefore, the terrestrial vegetation growing in the floodplain has to be considered a very important pump of nutrients from the sediment into the water. Its contribution to the budget of N, P, and K is by far greater than the input by the inflowing river water.

During the aquatic phase, abundantly growing aquatic macrophytes, and to a much smaller extent, algae consume these nutrients and store them in their tissue (HOWARD-WILLIAMS & JUNK 1976 and FURCH 1984b). When the water level drops, part of the aquatic vegetation is transported into the river channel, but major amounts are stranded on the dry lake bottom. There they decompose and partially replenish the sediments with nutrients. According to the flood pulse concept (JUNK *et al.* 1989) such a nutrient transfer mechanism is required to explain the great productivity of floodplain-systems.

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