ɪry Weight Loss and Chemical Changes in the detritus ꞙf three tropical aquatic macrophyte species (*Eleocharis nterstincta*, *Nymphaea ampla* and *Potamogeton ɪtenostachys*) during decomposition

BRUM, P. R. & ESTEVES, F. DE A.

ıboratório de Limnologia, Departamento de Ecologia, Universidade Federal do Rio de Janeiro - CS, Bloco A, sala A0-008.Cx. Postal 68.020, CEP 21941-590 - e-mail paulinho@biologia.ufrj.br

RESUMO: Perda de peso e alterações químicas no detrito de três espécies de macrófitas aquáticas 'opicais (*Eleocharis interstincta, Nymphaea ampla e Potamogeton stenostachys*) durante a ecomposição. Neste estudo descreveram-se as variações de peso seco e dos teores de , N e P dos detritos de três espécies de macrófitas aquáticas - *Eleocharis interstincta* /AHL) Roemer et Schults (emergente), *Potamogeton stenostachys* K. Schum. (submersa) *Nymphaea ampla* (Salisb.) DC. (folhas flutuantes) - e relacionou-se tais variações om o habitat ocupado pelas diferentes espécies. Os dados de perda de peso foram justados a um modelo exponencial de duplo decaimento, admitindo-se a existência e material particulado lábil e refratário. Os coeficientes de perda de massa das 'ações refratárias foram fortemente diferenciados, com valores de meia-vida entre dias (*N. ampla*) e 147 dias (*E. interstincta*), com *P. stenostachys* apresentando uma ıeia-vida de 29 dias. Os compostos químicos analisados apresentaram quedas .centuadas nos detritos após 1 (um) dia de experimento, devido à predominância los processos de lixiviação, à exceção do teor de nitrogênio em *P. stenostachys*, o ɪual exibiu um incremento. Após este período, os teores de carbono orgânico ıpresentaram quedas, enquanto que os teores de nitrogênio apresentaram ncrementos e os teores de fósforo permaneceram relativamente constantes. Estas ılterações se refletem em diferentes razões C:N:P no detrito de cada espécie, esultando assim em detritos de diferente qualidade nutricional, com implicações ıas taxas de perda de peso.

'alavras-chave: Decomposição, macrófitas aquáticas, C:N:P, perda de peso seco, lagoas :osteiras.

ABSTRACT: Dry weight loss and chemical variation in the detritus of three tropical aquatic macrophyte species (*Eleocharis interstincta, Nymphaea ampla and Potamogeton stenostachys*) during decomposition. In this study we described the changes in dry weight and in the contents of C, N and P in the detritus of three species of aquatic macrophytes - *Eleocharis interstincta* (VAHL) Roemer et Schults (emergent), *Potamogeton stenostachys* K. Schum. (submersed), and *Nymphaea ampla* (Salisb.) DC. (floating leaves) - and related these changes to the habitat occupied by the different species. The data of dry weight loss were adjusted to a double decay exponential model, assuming that there was labile and refractory particulate matter in detritus. The coefficient of dry weight loss found for each species had a marked difference among them, with half-life values ranging from 6 days (*N. ampla*) to 147 days (*E. interstincta*), with *P. stenostachys* having a half-life of 29 days. The analyzed compounds had significant drops in their contents after one day of incubation, due to the dominance of leaching processes, with the exception for the content of nitrogen in *P. stenostachys*, which increased. After this period, the contents of organic carbon dropped, while the contents of nitrogen increased and the contents of phosphorus remained constant. These changes are reflected in different C:N:P ratios in the detritus of each species, which leads to detritus with different nutritional qualities, with consequences in dry weight loss rates.

Key words: Decomposition, aquatic macrophytes, C:N:P, dry weight loss, coastal lagoons

Introduction

Coastal lagoons are among the most productive aquatic environments of the planet, with values of primary production close to those of estuaries, approximately $280gC.m^{-2}.year^{-1}$ (Knoppers, 1994). They are, by and large, shallow environments, parallel to the ocean shore and separated from it by a sandbar, with a predominance of deposition and small hydrological fluctuations in natural conditions (Kjerfve, 1994). Some of these morphometric characteristics (high perimeter/volume ratio, absence of pronounced fluctuations in the water level) favor the development of aquatic macrophyte communities, bestowing upon the littoral region an important role in the nutrient and carbon cycling within the aquatic environment (Wetzel, 1993).

The community of aquatic macrophytes is an active participant in several processes in aquatic environments. Some species are able to remobilize the nutrient stock of the sediments, otherwise inaccessible in the short run, since they have access to this stock through their roots (Pomeroy, 1970; Carpenter, 1980). They provide substrate for the growth of periphytic organisms and shelter for benthic and nektonic animals (Hutchinson, 1975), and some of these species are among the most productive yet studied (Wetzel, 1990; Piedade *et al.*, 1991; Enrich-Prast, 1998).

Most of the biomass produced by the community of aquatic macrophytes is not subjected to the effects of herbivory to a degree observed in other plant communities, probably due to their low nutritional quality (Polunin, 1984). Therefore, the biomass and accumulated nutrients, both in dissolved and particulate state, are returned to the ecosystem, mainly, by the detritus chain (Pieczynska, 1993).

The process of dry weight loss from the litter bags is a result of the sum of three distinct processes: leaching, catabolism and fragmentation (Swift *et al.*, 1979). Throughout the leaching process, soluble compounds are removed from the substrate by abiotic processes, as a result of the different contents of these compounds in the external medium and in the detritus. This process contributes, therefore, to the chemical alteration of the detritus as well as the dry weight loss. The catabolism is the transformation, by the decomposing organisms, of complex organic compounds into simpler molecules, through oxidation reactions. These reactions may be complete, oxidizing the material to the inorganic state or incomplete, resulting in the production of other organic compounds that may be incorporated in the biota or accumulated in the environment, as it happens to the so called humic compounds (Wetzel, 1993). The fragmentation is the reduction of the particle size. It is a physical process, but the activities of decomposing organisms enhance it, either through the ingestion (releasing particles of smaller size) or through the incomplete digestion (releasing particles of smaller size and chemically altered) of the particulate detritus (Swift *et al.*, 1979). These three processes occur simultaneously in nature, and therefore it is difficult to distinguish each one of them in a field experiment.

Regarding the quality of the detritus, important factors are the C:N ratio, the initial levels of nutrients, and the content of structural materials, such as lignin and cellulose (Godshalk & Wetzel, 1978; Morris & Lajtha, 1986). These factors vary among the several species of aquatic macrophytes and in the same species, according to the phenological state and the structure under analysis - leaves, roots, culms (Polunin, 1984). In another view, the habit of the species has an important role in the definition of these factors (Esteves, 1998). So, emergent macrophytes rooted to the sediment and exhibiting a significant portion of its biomass above the water level have a higher content of structural compounds when compared to those found in submersed macrophytes, which are supported by the water and have little or no wind stress (Wetzel, 1993).

In this research, three species of aquatic macrophytes found in the Cabiúnas Lagoon (Rio de Janeiro, Brazil) were selected - *Eleocharis interstincta* (VAHL) Roemer et Schults, *Potamogeton stenostachys* K. Schum., and *Nymphaea ampla* DC. The three species were rooted in the sediment but were chosen because they belong to different ecological groups, according to the classification proposed by Esteves (1998). *E. interstincta* is an emergent macrophyte, with photosynthetic structures above the water level. *N. ampla* is an aquatic macrophyte with floating leaves. *P. stenostachys* is a submersed macrophyte, with no structures above the water level. These differences in the habit of each species denote different chemical compositions due to their structural material, since the role of water in the support of the plants is different in each case (different stress among the ecological groups), according to Wetzel (1993) and Esteves (1998). These differences influence the rates of weight loss of the detritus in the course of the decomposition of the three species. The hypothesis guiding this research was that these differences would be reflected in different contents of C, N and P in the detritus in the course of time. Therefore, the aim of this research was to describe the decomposition of the detritus of three species of aquatic macrophytes, regarding the dry weight loss of detritus and changes in its contents of carbon, nitrogen and phosphorus.

Study area

This study was executed in Cabiúnas Lagoon, between the coordinates 22° and 22° 30' S and 41° 30' and 42° W, in the municipality of Macaé, inside National Park of the Restinga of Jurubatiba, in the north of the State of Rio de Janeiro, between November 1998 and January 1999 (Fig. 1). It is a shallow lagoon (maximum depth of 4m), with an area of 0,34 km² (Panosso *et al.*, 1998) and dendritic shape, which represents a greater perimeter/volume ratio and enhances the colonization by aquatic

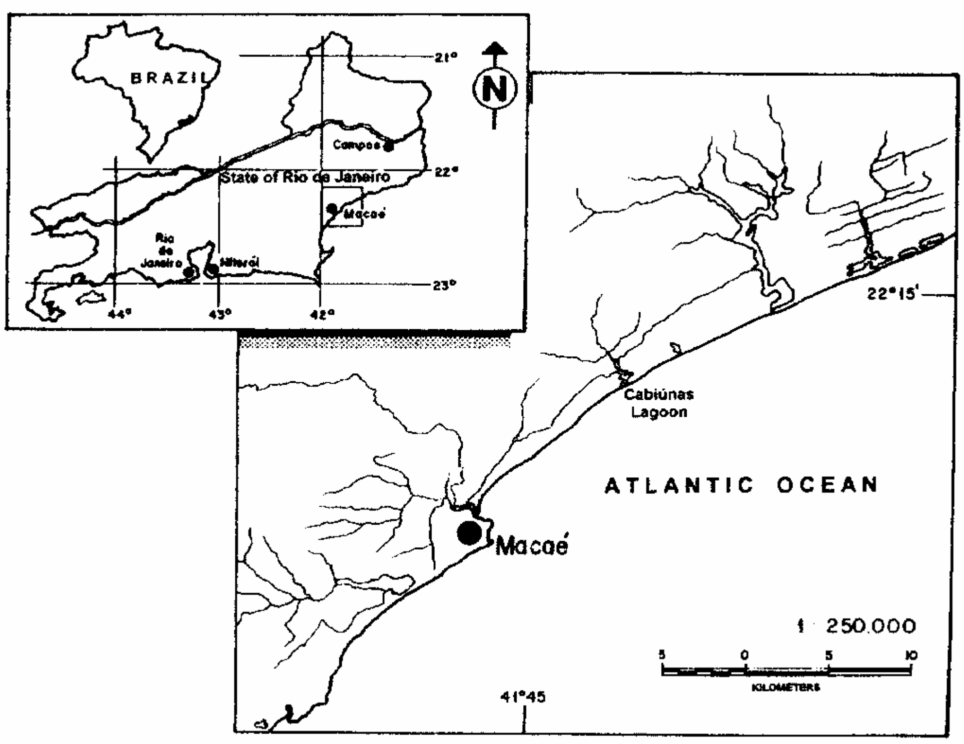

Figure 1: Map of the study site

macrophytes. It is the lagoon that has the greatest diversity of aquatic macrophytes in the region, showing 15 species identified (Henriques *et al.*, 1988). The climate of the region is hot and humid, with a yearly average temperature of 26.6 °C, and the yearly total precipitation reaches 1,164 mm, with a fairly pronounced dry season (Henriques *et al.*,1988).

According to Esteves *et al.* (1983), Cabiúnas Lagoon may be classified as a dark water lagoon due to the high contents of humic compounds which are a result of decomposition of the organic matter produced in great amounts by the marginal vegetation and in its draining area.

Materials and methods

The decomposition process of *E. interstincta*, *P. stenostachys* and *N. ampla* was studied by the method of litter bags. Green parts of the plants were collected and dried at 70°C, in the case of *E. interstincta* and *P. stenostachys*, and at 60°C in the case of *N. ampla*, a more fragile species, until constant weight was reached. Prior to the beginning of the experiment, some material was ground down with a mill, and its content of organic carbon (Embrapa, 1994), organic nitrogen (Allen *et al.*, 1974) and phosphorus (Fassbender, 1973) was determined, and these contents were considered as pertaining to the day 0 of the experiment. Approximately 5g of dry weight of the material were placed into each litter bag. Litter bags with 5mm mesh size allowed the passage of most organisms associated to the decomposition process (Gonçalves Jr., 1999). Litter bags were incubated in the littoral region of the lagoon, in an area colonized by the three species. With the great width of the mesh, some overestimation of the losses, due to the fragmentation of the material caused by the movements of the water, was expected. To minimize this effect, a site relatively sheltered from the wind action was chosen.

For each kind of detritus, bags were withdrawn from the lagoon after 1, 2, 4, 7, 11, 15, 30, 60, 81 and 95 days, with three replicates being collected for each species under study. The material was taken to the laboratory and placed over absorbing paper for two hours. After this, the samples were dried at 70°C until constant weight was reached.

At each sampling, the temperature (thermistor YSI 30/10 FT), pH (pHmeter Analion PM608) and content of dissolved oxygen (method of Winkler modified by Golterman *et al.*, 1978) were determined. Besides that, samples of water from the site were also taken for analyses of total nitrogen and reactive phosphorus (ortho-phosphate) (Mackereth, 1978).

After constant weight was reached, the material was weighed and ground down for the chemical analyses. The contents of organic nitrogen were obtained by the Kjeldahl method (Allen *et al.*, 1974), of phosphorus, by the method proposed by Fassbender (1973), and of organic carbon, by the method of oxidation with potassium dichromate, described in Embrapa (1994).

The data of dry weight loss from the detritus were adjusted to a first order double decay model (Bianchini Jr., 1997), assuming the existence of two kinds of particulate material (labile and refractory) in the beginning of the experiment, according to the equation:

$POM_t = POM_L * e^{-(k1t)} + POM_R * e^{-(k2t)}$ (equation 1)

where : POM_t = dry weight of the detritus at the time t; POM_L = labile fraction of the detritus in the beginning of the experiment; POM_R = refractory fraction of the detritus in the beginning of the experiment; k_1 = coefficient of decay of the labile fraction, day^{-1}; k_2 = coefficient of decay of the refractory fraction, day^{-1}.

According to Bianchini Jr. (pers. com.), the coefficients of decay of the labile fraction (k_1) were assumed to be 1,5 day^{-1} for the adjustment of the model, since it was impossible to estimate it with only one sample, and after the first day all of the labile fraction had already been lost from the litter bags.

The values of k, estimated as above, allow for the deduction of the half-life of each fraction, through the equation:

$T_{1/2} = \ln 2 / k$ (Equation 2)

where : $T_{1/2}$ = half-life of the fraction, in days; k = coefficient of decay of the fraction

The adjustment of the data of dry weight loss to the decay model was made with the transformation of the data to their logarithm and a linear regression. The detritus of the three species composed independent temporal series. Therefore, an ANOVA (significance level – 0,05) with repeated measures in each series was executed, beginning with the day 1, for the estimate of the variation of the contents of C, N and P and of the dry weight in relation to the length of time of the decomposition process. If a significant variation was registered, the data were compared with a Tukey-Kramer multiple comparisons test. This procedure was adopted for each chemical component analyzed, organic carbon, nitrogen and phosphorus. The C:N:P ratio was not analyzed since it was derived from variables previously tested. When only one pair of data was available, a non-paired t test was used. The GraphPad Instat 3.0 software was used in these statistical analyses.

Results

Dry weight loss

The changes in the percentage of detritus (% D.W.) are represented in Fig. 2. In the double decay exponential model used, the course of the leaching process is measured by the estimate of labile material in the detritus. As it can be observed, in the three models (Tab. I), the labile fraction of the detritus of all species presented high decay rates, and the process was for all practical purposes finished by the second day of experiment.

Organic Carbon

The detritus of *E. interstincta* and *P. stenostachys* exhibited significant reductions ($P<0,05$) in organic carbon contents during the decomposition process (Fig. 3). On the other hand, the detritus of *N. ampla* showed a significant reduction in organic carbon content only between the days 0 and 1.

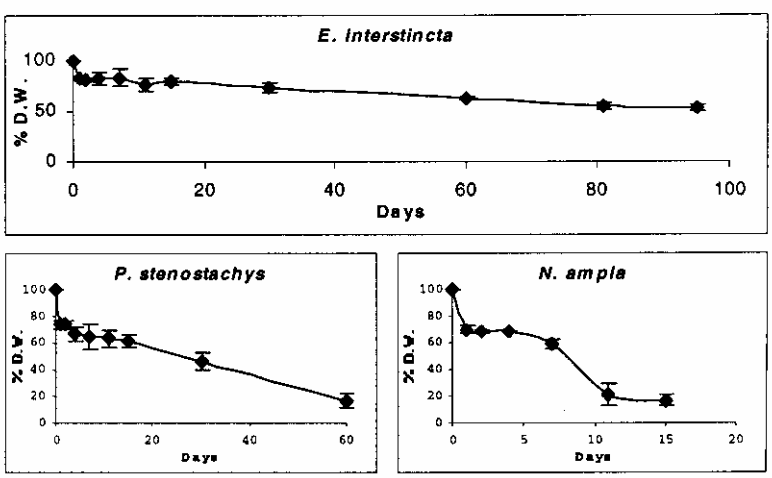

Figure 2: Dry weight loss, in % of dry weight, in the detritus of three species of aquatic macrophytes in the Cabiúnas Lagoon. The bars indicate the standard deviation.

Table I: Parameters of the double decay exponential models throughout the decomposition of three species of aquatic macrophytes in the Cabiúnas Lagoon (see Equation 1). The bracketed numbers indicate the adjustment of the model (r of Pearson).

	POM_L (%)	k_1	POM_R (%)	k_2	$T_{1/2}$ (days)
E. interstincta (0,95)	17.30	1.5	82.70	0.0047	147
P. stenostachys (0,96)	20.77	1.5	79.23	0.024	29
N. ampla (0,93)	27.20	1.5	72.80	0.1122	6

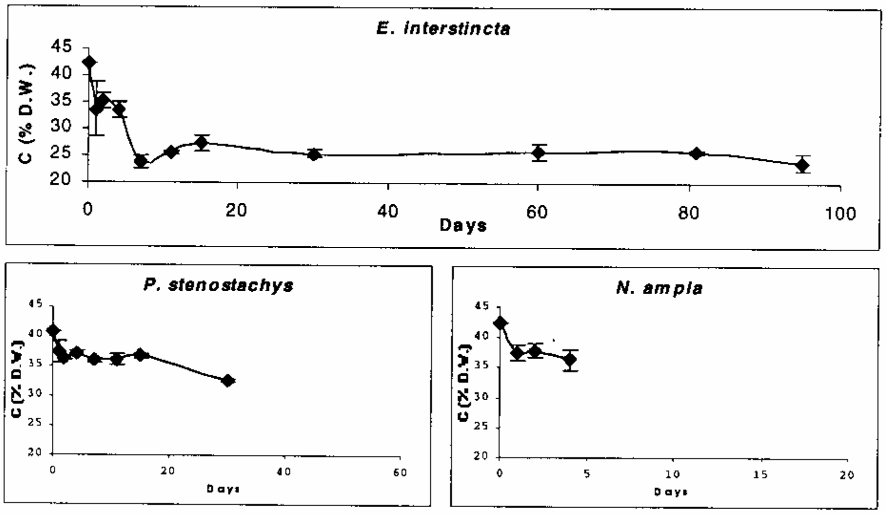

Figure 3: Fluctuation of the concentrations of organic carbon found in the detritus of three species of aquatic macrophytes at Cabiúnas Lagoon through time. Values in % of dry weight. The error bars indicate the standard deviation of the samples (n=3).

Nitrogen

Different patterns for the changes in nitrogen content of each species were observed (Fig. 4). All kinds of detritus had significant variations (P<0,05) between the days 0 and 1; *P. stenostachys* showed an increase in the content of this element, while *N. ampla* and *E. interstincta* presented a decrease in their values of nitrogen concentration. After this first phase, the nitrogen contents presented a reversed trend, decreasing in *P. stenostachys* and increasing in *N. ampla* and *E. interstincta*.

Phosphorus

There was an abrupt decrease in phosphorus content in the detritus of the three species between the days 0 and 1 (Fig. 5). Detritus of the three species behaved in the same way, differing only in the absolute values, without significant variation (P<0,05) after the first day of incubation.

C:N:P ratio

The C:N:P ratio of the three kinds of detritus was markedly different, as it can be seen in Tab. III. The highest ratios were observed for the detritus of *E. interstincta* during the experiment. *P. stenostachys* exhibited the lowest ratios, which were actually very close to the ideal values for bacterial growth (Goldman *et al.*, 1987) in the beginning of the experiment. *N. ampla* showed intermediate values, depicted in Tab. III, but in the course of decomposition it reached the highest values of C:N ratio (Fig. 6). At the day 7, it reached values of C:N ratio close to those of *P. stenostachys*.

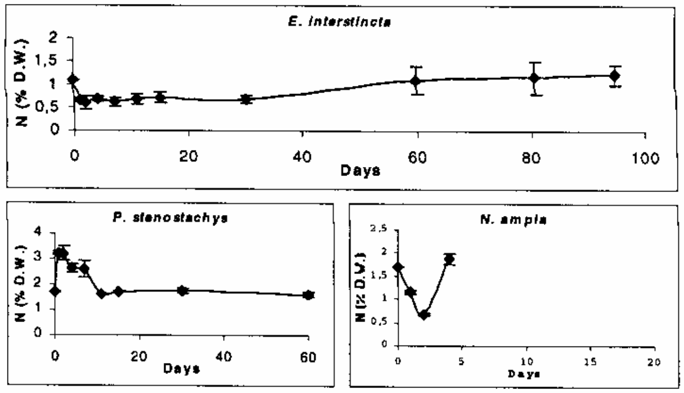

Figure 4: Fluctuation of the concentrations of nitrogen found in the detritus of three species of aquatic macrophytes at Cabiúnas Lagoon through time. Values in % of dry weight. The error bars indicate the standard deviation of the samples (n=3).

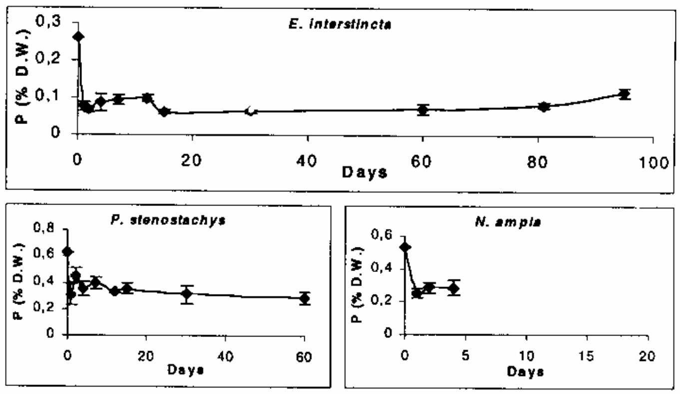

Figure 5: Fluctuation of the concentrations of phosphorus found in the detritus of three species of aquatic macrophytes at Cabiúnas Lagoon through time. Values in % of dry weight. The error bars indicate the standard deviation of the samples (n=3).

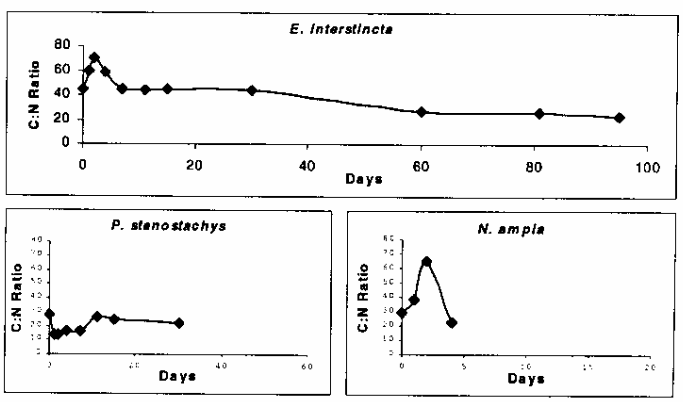

Figure 6: Fluctuation of the C:N ratios found in the detritus of three species of aquatic macrophytes at Cabiúnas Lagoon through time.

Table II: Average values of temperature, dissolved oxygen, pH, total nitrogen and available phosphorus in the site of the experiment. Bracketed values represent the range of the data (n=12).

Temperature (°C)	Dissolved Oxygen (mg l^{-1})	pH	Total-N (mg l^{-1})	Available P (mg l^{-1})
26.19 (23.2 – 29.0)	7.75 (6.6 – 8.7)	6.57 (6.2 – 6.8)	0.407 (0.37 – 0.46)	N.D. (<0.093)

Table III: C:N:P ratio in the detritus of three species of aquatic macrophytes at Cabiúnas Lagoon throughout its decomposition.

Days	*E. interstincta*	*P. stenostachys*	*N. ampla*
0	418:9:1	168:6:1	205:7:1
1	1,143:19:1	313:23:1	377:10:1
2	1,345:19:1	207:16:1	340:5:1
4	991:17:1	270:16:1	330:15:1
7	660:15:1	236:15:1	
11	678:15:1	280:11:1	
15	1,148:26:1	269:11:1	
19	1,063:26:1		
30	1,043:24:1		
60	962:35:1		

Discussion

Dry weight loss

Leaching is controlled by abiotic factors, such as the temperature of the environment and the water flowing, and biotic factors, such as the structure of the detritus, and the treatment to which the material was subjected prior to the experiment (drying at 60 and 70 °C) enhances this process (Godshalk & Wetzel, 1978). These processes allow for the possibility that the high rates observed are in part due to an experimental artifact. Almost all the fluctuation in detritus C, N and P contents between the days 0 and 1 are a result therefore of the leaching of the labile fraction, a process quantitatively more important than the biological oxidation in this period. The difference between the species was basically due to the amount of labile/soluble material, and they may be classified in a decreasing order of labile material as: *N. ampla* > *P. stenostachys* > *E. interstincta*.

This pattern is also observed for the refractory material decay coefficients. Therefore, the detritus with the greatest dry weight loss, even after the end of the leaching process, is that of *N. ampla*, and *E. interstincta* shows the most refractory kind of detritus. The dry weight loss by *N. ampla* was very quick, and after the day 15 of the experiment only little amounts of detritus were found in the litter bags. After the day 7 the material was already insufficient for the chemical analysis. On the other hand, *E. interstincta* still exhibited 79.7% of its initial dry weight in the litter bags in the day 15.

Dry weight loss from the refractory fraction is a result of the combined effects of fragmentation and catabolism. Based in the results of the model, we may assume that the effect of the fragmentation process was not an important factor in the experiment, in spite of the 5 mm mesh size of the litter bags, which may be considered large, since there were no water currents in the site and small numbers of detritivore macroinvertebrates were observed. The main detritivore macroinvertebrate observed in the litter bags was the gastropod *Heleobia australis*, and even this species was found in small densities, never superior to 5 individuals in one litter bag.

Catabolism of the particulate detritus is a microbial process, controlled by characteristics such as the oxygen condition of the medium, temperature, available organisms for the decomposition, amount and quality of the detritus, pH, and available nutrients (Bianchini Jr., 1997). The concentration of dissolved oxygen never reached values limiting the activity of aerobic organisms during the experiment (Tab.II), indicating the dominance of the aerobic community, more efficient to process the detritus (Bianchini Jr., *op. cit.*). Furthermore, the temperature was kept at relatively high levels during the experiment (Tab. II). These factors accounted for the great rates of dry weight loss.

Comparison of the dry weight loss data observed in this work with those found by other authors is beset with problems, since not only the environmental characteristics are different in each study, but there are also important methodological differences such as the mesh size, which may exclude (or not) the detritivore macroinvertebrates that facilitate the process of decomposition. Howard-Williams & Junk (1976), in one of the first papers that compare the weight loss rates in several locations, mention values of $T_{1/2}$ between 200 and 426 days in England, 100 days in Africa, and only 30 days in the Amazonian Region, for species of emergent aquatic macrophytes. More recently Emery & Perry (1996), studying the decomposition of *Typha* spp. at 14 wetlands, registered a variation of the coefficient of decay between 0.00018 and 0.0024 day^{-1} (half-life between 294 and 3851 days). Lemos & Bianchini Jr. (1998), using the oxygen consumption in a closed system to measure the catabolism under several nutrient regimes, mention a maximum coefficient of decay of 0.034 day^{-1} (half-life of 20 days) for *Scirpus cubensis*, another emergent aquatic macrophyte. This value is very close to the theoretical maximum, since the conditions of the experiment are near the ideal (closed system, constant oxygenation, plants previously ground, constant temperature of about 25 °C).

The rates of dry weight loss obtained by these authors are related to a simple decay model, without the conceptual separation in labile and refractory fractions. Therefore, values of the decay rates obtained in this research, related exclusively to the refractory fraction, have a tendency to be smaller, and so the values of $T_{1/2}$ should be greater. Nevertheless, this effect is clearly secondary to the differences in the quality of detritus and in environmental conditions of each study, especially the temperature. *E. interstincta*, the emergent species of this study, exhibited a $T_{1/2}$ of 147 days, which is in the range found in the literature for emergent aquatic macrophytes of tropical regions (Howard-Williams & Junk, 1976; Nogueira, 1993; Lemos & Bianchini Jr., 1998).

When we compare the decay rates of these three species, we can observe that the detritus of *P. stenostachys* (submersed) presented a coefficient 5 times greater than the one presented by *E. interstincta* (emergent). *N. ampla* (floating leaves), on the other hand, exhibited a coefficient 5 times greater than the one presented by *P. stenostachys*. Lopes-Ferreira & Esteves (1992), studying the decomposition of *P. stenostachys* in Cabiúnas Lagoon but without constructing a model for the description of detritus decay, found the loss of half of the detritus weight at day 20, a result slightly smaller than the $T_{1/2}$ found in the present study (29 days). Esteves & Barbieri (1983), describing the decomposition of an aquatic macrophyte with floating leaves (*Nymphoides indica*) in litter bags, found a half-life of 15 days. Roland *et al.* (1990), in an research with *Eichhornia azurea* (floating) in litter bags, observed a half-life of 45 days. On the other hand, Bianchini Jr. & Toledo (1998), studying the decomposition of *Nymphoides indica* in controlled conditions, observed a decay coefficient of 0.0079 day^{-1} (half-life of 88 days), with material previously ground. Therefore, the rates of decomposition observed for *P. stenostachys* and especially *N. ampla* may be considered as high, and they are among the highest ever observed in field experiments with litter bags. These high rates are probably due to the favorable conditions found in the site of the experiment (high temperature, probably constant oxygenation, and intrinsic characteristics of the substrates).

Organic Carbon

Considering the leaching process completed after one day, the effect in the organic carbon content of *E. interstincta* and *P. stenostachys* is probably the result of the microbial activity on the detritus, assimilating the particulate fraction or transforming through enzymes the refractory particulate fraction into soluble components, which are then lost through solubilization or assimilation. Belova (1993), observing several species of aquatic macrophytes, concluded that approximately 33% of their biomass are converted to microbial biomass after the first month of decomposition. However, the role of the microbial community is not restricted to the assimilation of carbon, since the enzymes produced by this community act on the detritus, solubilizing it even when there is no assimilation (Peduzzi & Herndl, 1991).

Nitrogen

The changes in nitrogen content between days 0 and 1 are mainly due to leaching, the most important process on a quantitative basis during this period. The different patterns of variation observed in the three species between days 0 and 1 indicate the leaching process in each kind of detritus presents different chemical characteristics (Fig. 4). Indeed, while *E. interstincta* and *N. ampla* showed reductions in this period, hinting at a loss of a nitrogen-rich leachate, *P. stenostachys*, with an increase in nitrogen content, is an example of a leachate with relatively smaller nitrogen content and therefore keeps more nitrogen in the particulate fraction. Nitrogen content is one of the regulating factors of decomposition rate (Godshalk & Wetzel, 1978), and high contents of this nutrient are considered to favor the consumption by decomposers. Therefore, examining solely the nitrogen content, the particulate detritus of *P. stenostachys* would be the one with better nutritional quality. This would certainly have an influence on its high dry weight loss coefficient.

The detritus of *E. interstincta* exhibited an enrichment in nitrogen after the leaching loss. This pattern was observed for several kinds of detritus in temperate and tropical aquatic environments (de La Cruz & Gabriel, 1974; Howard-Williams & Davies, 1979; Polunin, 1982; Morris & Lajtha, 1986; Hietz, 1992) and it is a sign that the processes of nitrogen immobilization prevail over the processes of mineralization during decomposition. As the decomposition process unfolds, plant material is converted by the decomposing organisms (mainly fungi and bacteria) into microbial biomass, richer in nitrogen (Polunin, 1984). This community obtains the nitrogen necessary for its growth directly from the water, or possibly through the fixation of atmospheric nitrogen (Enrich-Prast *et al.*,1999).

Detritus of *N. ampla* showed a similar pattern to that of *E. interstincta*, compressed in 4 days of observation. The decrease in nitrogen content due to leaching indicates that this process releases compounds rich in nitrogen in this species. Increasing in nitrogen content between the days 2 and 4 is large enough to result in values near those found in the original material (day 0). The main factor which is influencing the detritus chemical composition in this stage of decomposition is the microbial activity, and so we may suggest that, in the same way as with *E. interstincta*, but with a much greater speed (between the days 2 and 4), the plant biomass was converted in bacterial biomass.

Phosphorus

Observing Fig. 5, the detritus of *P. stenostachys* seems to have the best nutritional quality regarding the phosphorus content, with values significantly higher ($P<0.05$) than those of other species, as it was observed in the case of nitrogen content. The stability of the values of phosphorus, without a significant change during decomposition, suggests a balance between the processes of immobilization and mineralization of this element. Possibly this is an evidence that the microbial community found adequate amounts of this element in the detritus.

C:N:P ratio

The C:N:P ratio is one of the most important factors that explain the rates of detritus decomposition. Enriquez *et al.* (1993), examining detritus from several sources, from macroalgae to trees, were able to explain 89% of the data variation with the analysis of differences in the C:N:P ratio. As decomposers usually exhibit high nitrogen and phosphorus contents, i.e., low C:N and C:P ratios, they require a substrate with high content of these elements (Swift *et al.*, 1979). Therefore, balanced bacterial growth requires substrates with an atomic C:N:P ratio close to 106:12:1 (Goldman *et al.*, 1987).

C:N:P ratios near to these values result in fast microbial growth, while ratios higher than this, i.e., with an excess of carbon, give as consequence a microbial activity limited by the lack of nutrients. In this context, the data indicate that there was limitation of the microbial activity by lack of nutrients in the detritus of the three species (Tab. III).

Observing the results from a nutritional point of view, it is possible to consider the detritus of *E. interstincta* as the least favorable (Fig. 6). Microbial activity was possibly limited by a lack of nitrogen and phosphorus in this substrate, and a great amount of detritus must be assimilated when the contents of these nutrients are reached, reducing therefore the decomposers' efficiency. Values of the C:N ratio got closer to those found in the other studied species of aquatic macrophytes only at the end of the experiment.

The C:N ratios of *N. ampla* and *P. stenostachys* fluctuated according to the detritus nitrogen content, since the change in organic carbon content is much smaller than the change in the nitrogen content. These two variables, C:N ratio and nitrogen content, exhibited a strong negative correlation for the two species (R^2 = 0.93 and 0.95, respectively). Comparing the two kinds of detritus, it may be observed that *P. stenostachys* showed the smaller C:N and C:P ratios. Therefore, it would be expected that the detritus of *P. stenostachys* would be the easiest to decompose, since it had the highest coefficient of decay. According to Twilley *et al.* (1986), there is a correlation between the starting C:N ratio of the detritus and the decay rate (k). However, this correlation was not observed in this study. Differences in the quality of the carbon (structural differences) between the detritus of the two plants may explain this phenomenon. These differences could influence the microbial activity (Swift *et al.*, 1979), or simply enhance the fragmentation of *N. ampla*, which would result in a greater dry weight loss (transfer of material to the outside of the litter bags).

The C:N:P ratio fell in the course of decomposition in the detritus of the three species. This pattern was observed by several authors (Twilley *et al.*, 1986, Peduzzi & Herndl, 1991, Buchsbaum *et al.*, 1991) and it is explained by the increase of microbial biomass (compared to plant biomass) richer in nitrogen and phosphorus in the detritus. Despite this fall in the C:N:P ratios, they never reached values considered ideal to the animal nutrition (Russell-Hunter, 1970), allowing the conclusion that the detritus is metabolized mainly by the microbial community, which is able to use less favorable detritus (with higher C:N:P ratios).

The detritus of each species studied had distinct patterns of dry weight loss and change in C, N and P contents, both in absolute values and regarding trends in the course of decomposition, confirming the initial hypothesis. *E. interstincta* presented the detritus with the lowest decomposition rates, while the detritus of *N. ampla* was the fastest one. These differences are attributed to their different structural characteristics, which are related to the habitat occupied by each species. So, while the detritus of *E. interstincta* is refractory to decomposition, that one of *P. stenostachys* and *N. ampla* presented favorable characteristics to microbial colonization and therefore high rates of dry weight loss.

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