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Mass and nutrient loss of fresh plant biomass in a small black-water tributary of Caura river, Venezuelan Guayana

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Abstract. Decomposition rates and nutrient dynamic (N, P, K, Ca and Mg) were determined for green leaves and fine branches immersed in the water of a small tributary of Caura river (SE-Venezuela). 16% of the original dry weight of leaves and 11% of branches were lost at the end of the first sampling period: first month for leaves and second month for branches. This dry weight reduction was probably due to leaching of soluble material. After a 9-month period, the mass loss was 60% for leaves and 20% for fine branches. The pattern of dry weight and nutrient losses are in general agreement with previous studies of decomposition of leaf litter in both terrestrial and aquatic ecosystems. Potassium and magnesium are the elements most rapidly lost, showing the dominance of leaching processes; at the end of the first month 7% of the initial amount of K and 18% of the initial amount of Mg remained in leaves. The loss of calcium and phosphorus was much slower: 61% of Ca and 47% of P remained in the leaf material after the first sampling period. In contrast to K, Mg, Ca and P, the initial amount of nitrogen in leaves remained relatively unchanged during the first month of decomposition; in the subsequent sampling period, the amount of N decreased. The elements K and Mg in branches behaved similar to leaves: 4% of K and 22% of Mg were left at the end of the first sampling period. The initial amount of Ca and P in branches decreased slightly: 88% of Ca and 83% of P remained in branches at the end of this first sampling. Nitrogen behaved differently in branches than that in leaves. In branches the amount of N remained relatively unchanged during the first 5 months of decomposition; afterwards, N showed gradual increases, probably due to immobilization. At the end of the experiment the amount of N in branches was 16% higher than the initial amount.

Key words: aquatic condition, decomposition of leaves and branches, South America, tropical forest, weight and nutrient loss

Introduction

In the last years hydroelectric development has increased in the tropics. This requires a constant water supply. Because the flow rate of large rivers fluctuate seasonally, a dam must be constructed in order to store rainy season excess of water and use it during the dry season (Castro & Gorzula 1986). The building of such dams severely impacts the environment, both in the formation of a reservoir upstream of the site of the dam and in the modification of the hydrological regimen downstream.

In Venezuela, the rivers with the greatest hydroelectric potential are located in the Venezuelan Guayana. The Caroní river, a tributary of Orinoco, has the largest river basin in this region. Between 1963 and 1986 the Guri dam was built in the lower course of Caroní river, with a surface area of 4,300 km^2 and an elevation of 270 m above sea level (Alvarez et al. 1986). The second largest river basin in the Venezuelan Guayana is the Caura river basin (Huber 1995), which has been considered as one of the last major tropical watersheds still under virtually pristine conditions (Rosales & Huber 1996). Due to its dense forest cover, this river basin produces 0.079 $m^3/s/km^2$, twice as much water per area as the Caroní river, and more than any other the river in the Venezuelan Guayana (Vargas & Rangel 1996). Part of the Caura river (Middle Caura) has been identified by CVG-EDELCA, the Venezuelan Hydroelectric Company, as a potential site for expansion of hydroelectric development.

One of the most significant environmental impacts of the hydroelectric development in the Caura region will be the loss of large densely forested areas. In the Middle Caura about 95% of the total surface that would be affected by the creation of the reservoir is covered by non- flooded terra firme forest (Dezzeo & Briceño 1997). Although there is no doubt that the consequences during the conversion from an upland forest to a flooding forest are considerable, there is still very little quantitative information on the biological effects of this anthropogenic conversion. Goldman (1979), Henningsgaard (1980), Fearnside (1989) and Lemos de Sá (1992) have pointed out that submerging a tropical forest produces severe environmental effects; for example, the decomposition of large quantities of organic material in the water would totally consume the available oxygen in the reservoir and this would result in anaerobic decomposition with the subsequent formation of hydrogen sulfide. This gas would be detrimental to all life forms downstream and would also affect the structures and equipment of the dam. Moreover, shallow reservoirs with a large forest area which are alternately flooded and exposed, may generate methane, a greenhouse gas which contributes to the warming global climate.

On the other hand, plant nutrient may be released by the decomposition of flooded standing biomass, and it may lead to changes in the water quality. Furch et al. (1989) and Furch & Junk (1997) showed that during decomposition under the aquatic phase, leaf litter of the floodplain forest in Amazonas releases a large portion of its nutrient stock into the water. However, there are no data available about decomposition and nutrient input of standing biomass of trees under flooded conditions; therefore, the potential effects of these nutrients into the water remained unclear.

In order to identify and assess the environmental impacts of the hydroelectric development in the study region in an early phase of the project planning and design, researchers of EDELCA and also scientists of other institutions, are conducting detailed studies in the Middle Caura. In the light of the importance of leaf decomposition in the drastic changes in water chemistry (Furch et al. 1989), and considering the uncertainty in the contribution of fresh biomass to these changes, particularly during a first phase after flooding, the primary objective of the present study was to provide information in order to quantify the nutrient input of the submerged standing biomass into the water of the future reservoir. The specific objectives were to measure dry weight and nutrient loss of terrestrial green leaves and of small branches under constant waterlogging.

Study site

The study site is located in the middle drainage of Caura river, in southeastern Venezuela, about 5°10′N and 64°10′W, at 280 m asl. Applying the criteria of Holdridge's life zone system, Martínez (1996) has classified the bioclimate of the region as humid tropical rainforest. The closest metereological station to the site is that of Ceiato, about 30 km south of the study area; in this station (25 years of precipitation records) the annual precipitation averages 2,594 mm (Vargas & Rangel 1996). The wettest months are June and July and the driest months January and February.

Geologicaly, the region belongs to the Proterozoic Cuchivero Province of the Guayana Shield, and includes acid volcanic, granitic and metasedimentary rocks (Rincón & Estanga 1996). The soils are old, deeply weathered, acid and of low natural fertility, and have been classified according to the USDA classification system as Ultisols (Fuentes & Madero 1996). About 90% of the surface of the Caura river Basin is covered by non-flooded terra firme forest (Marín & Chaviel 1996); in our study area, these authors have classified the forests as evergreen humid tropical forest. These forests are characterized by a closed to relatively open canopy of 20–25 m tall, high basal area, and high species diversity (Dezzeo & Briceño 1997).

The Caura river is the last remaining main tributary of the Orinoco river that has not yet experienced major human impacts in its watershed (Vargas & Rangel 1996). This river has been classified as a black water river due to its brown color and due to its low status of nutrients and suspended materials (García 1996). The present research was conducted in a low-order tributary of Caura river (Caño Maní), approximately 200 m upstream from the confluence of this Caño into the Caura river. Caño Maní is a small black-water stream that flows through the forest, and its water depth in the experimental site ranged from 2.5 m in the wettest months of the rainy season to 50 cm in the driest months of the dry season. The experimental site also chosen to simulate the conditions of a reservoir with regards to the low water velocity.

Methods

Decomposition was studied by the litter bag technique (Bocock & Gilbert 1957; Crossley & Hoglund 1962). The material was collected at the beginning of May by cutting green leaves and small branches (< 2 cm diameter) from standing living trees of the following dominant species in the forest of the region (Dezzeo & Briceño 1997): *Alexa imperatricis, A. canarecunensis and Eperua grandiflora* (Leguminosae), *Oenocarpus bataua* (Palmae), *Protium sp*. (Burseraceae), *Eschweilera sp*. (Lecythidaceae), *Mabea sp*. (Euphorbiaceae), *Chrysophyllum sp.* (Sapotaceae), *Iryanthera sp*. (Myristicaceae) and *Catostemma sp*. (Bombacaceae). Separate samples of fresh leaves of each species were taken to the laboratory to determine the initial nutrients status.

Litter bags (22 × 35 cm) were prepared from nylon material with a 3 mm mesh. Eighty litter bags were filled each with 50 g of mixed-species fresh leaves; forty litter bags were filled with 80 g of mixed-species fresh branches. Subsamples of the fresh leaves and branches were taken to determine moisture and initial chemical constituents. The bags were placed in the stream (Caño Maní), into the first 50 cm of the water column. To prevent floating and to maintain the bags on the first 50 cm of the water column, floats were placed on the water surface, and approximately 250 g of small quartzitic stones was introduced as ballast into each bag. The stones were collected in the bank of Caura river.

The bags were placed in the water column on 10 May 1995. From June 1995 to February 1996 eight bags of leaves were collected at monthly intervals, and eight bags of branches were collected every 2 months. The collected bags were air dried and placed in individual envelopes and transported to the laboratory for analysis. The final collection was on February due to fact that the depth of the water in the stream was very low, approximately 50 cm, because of little rainfall. On each date, the dry mass of the material in the bags was determined after it being dried at 70 °C to constant mass. In some cases the litter in the bags were covered with sediment. Before the dry mass was weighed, the sediment was carefully removed with a fine bristle brush.

Dry samples of the original plant material and of the material from each collected bag were kept for chemical analysis. The ovendried material was milled and digested. Total nitrogen was determined after distillation by the

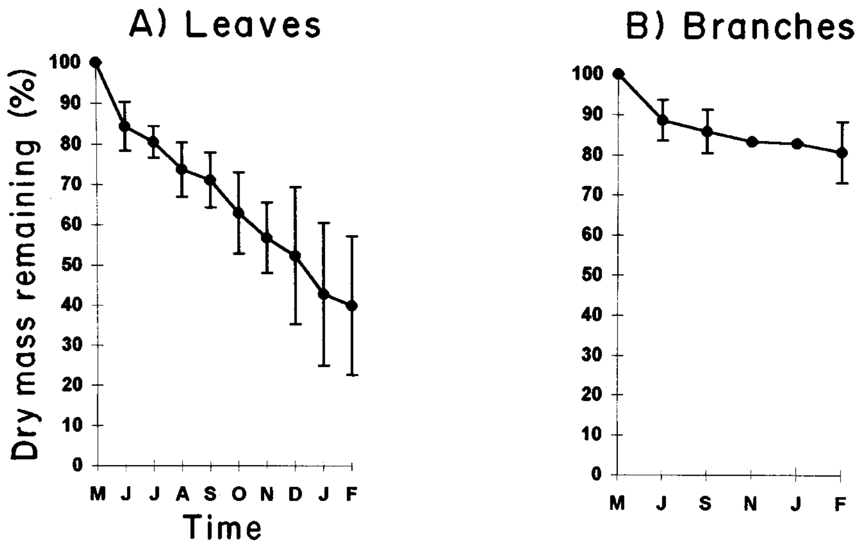

Figure 1. Dry mass loss of leaves and branches during the 9-month period of the decomposition experiment, expressed as percentage of the initial dry weight.

micro-Kjeldahl method (Jackson 1976). Total phosphorus was measured colorimetrically (Murphy & Riley 1962) in samples digested with 4:1 H_2SO_4-$HClO_4$ mixture, with vanadium pentoxide as catalyzer. Concentrations of magnesium, potassium and calcium were determined in the same extract by atomic-absorption spectrophotometry.

Results and discussion

Mass loss of leaves and branches

Losses in dry weight of the samples of leaves and fine branches over the 9-month period are shown as percent of the original remaining dry weight in Figure 1. The mean values of dry weight loss and its respective standard deviations are indicated in Table 2. At the end of 9 months, the mass remaining was 40% for leaves and 80% for branches. A more detailed look at the rate of mass loss over the study period indicate that 16% of the initial dry weight of leaves was lost during the first month, while during the subsequent months the loss fluctuated between 3–9%. In the case of the branches, loss was only 11% of its original dry weight during the two first months, and in the following sampling periods the loss fluctuated between 0.5–3% per two month.

The marked dry weight reduction observed at the end of the first month for leaves and at the end of the second month for fine branches is consistent with the general pattern observed in decomposition studies, and was probably mainly due to leaching of soluble material. It is in general accepted that important changes in the physical and chemical characteristics of the leaves take place in the first few days to weeks of decomposition (Findlay & Arsuffi 1989). In this period the plant detritus rapidly begins to lose soluble organic and inorganic materials (Webster & Benfield 1986) mobilized either by passive physical processes or by decomposer activity (Singh & Gupta 1977; Brinson et al. 1981). The leaching loss would be enhanced by the fact that plant material was kept in running water.

In this study the relatively gradual decline after the rapid initial loss of dry weight is also in agreement with the general pattern of decomposition in terrestrial and aquatic ecosystems. This gradual decline has been associated with changes in the composition of the detritus during the decay process (Swift et al. 1979; Webster & Benfield 1986). Likewise Singh & Gupta (1977) suggested that after initial loss, the organic matter becomes more resistant to decay mainly caused by the relative accumulation of condensed or polymerised polyphenols with very slow rates of decomposition.

As it was expected, the branches were more resistant to decay or have less leachable material than the leaves. The significant differences in the rate of weight loss between leaves and branches are probably related to the differences in the quality of the detritus as well as in the types of tissues between both materials. The decomposition rates according to Olson (1963), were after 9 months K = 0.10 for leaves and K = 0.02 for branches ($X/X_0 = e^{kt}$; X = weight remaining at time t, X_0 original weight, K = decomposition constant). Comparable investigation of green leaves and branches decomposition in flowing black water in the tropics have not yet been published. For fresh leaf litter, however, Irmler & Furch (1980) obtained similar decomposition rates (in months) in the emersion phase of Igapó (K = 0.04) and Várzea (K = 0.09) in Central-Amazonian inundation forest. These authors attributed this extremely low loss rate to the nutrient poor soils, and particularly to the effects of seasonal inundation.

Nutrient loss from leaves and branches during decomposition

The initial nutrient mass per unit weight (nutrient concentration) of the freshly green leaves from the single species as well as from the mixed species of leaves and fine branches which were placed in the litter bag, are shown in Table 1. There is a great chemical variability between the leaves of the different species, particularly of nitrogen and calcium. The phosphorus and nitrogen concentrations of the mixed species of leaves are over three times higher than that of the mixed species of branches. The potassium, magnesium and calcium concentrations, however, were relatively similar between leaves and branches.

Changes in leaves and fine branches chemistry during the 9-month period of decomposition are shown in Table 2 (mean concentration ± standard deviation). The amount of nutrients lost during decomposition is calculated as the ratio of the nutrient concentration at sampling period corrected for dry weight loss over the original nutrient concentration and expressed as a percentage (Figure 2). The pattern of element loss was relatively similar to that reported in the literature. Looking at the values from leaves (Figure 2), potassium is the element which was most rapidly lost, followed by magnesium. After the first month less than 10% of K remained in leaves. This element is a highly mobile, readily-leached ion, usually occurring in amounts in excess of decomposer demand (Gosz et al. 1973). The rapid rate of K loss shows the dominance of the leaching process (Swift et al. 1981). Due to the fact that magnesium is relatively leachable (Attiwill 1967; Gosz et al. 1973), its initial loss also occurred rapidly, and at the end of the first month the original amount of Mg was reduced to 18%.

In contrast to the rapid loss of potassium and magnesium, the loss of calcium during the first month was relatively slow: 61% of the initial amount of Ca remained in leaves at the end of this month. Until the five month, the pattern of Ca loss was similar to the pattern of dry weight loss; afterwards the amount of Ca shows slightly increase and decrease. Ca is little susceptible to leaching (Attiwill 1967) and shows patterns of increase and decrease with the time (Gosz et al. 1973). The latter author suggested also that the similarity between the pattern of Ca loss and dry weight loss indicates that decomposition was responsible for Ca release to the ecosystem. On the other hand, Swift et al. (1979) have reported that increase in absolute amounts of mineral element is relatively common and is probably due to import from external sources.

With respect to phosphorus, 47% of its original amount remained in leaves after the first month, presumably due to leaching; in the following 3 months the amount of this element remained practically unchanged, and afterwards decreased gradually to 29% at the end of the 9-months period.

The pattern of nitrogen loss showed a relatively different tendency than that of the other elements. The initial amount of N decreased only 2% during the first month; in the subsequent sampling period the rest of this element was lost gradually, and at the end of the 9 months the remained amount of N was 40%.

Although in the forest ecosystem the branches represent large quantities of organic matter and nutrients, its decomposition has received little attention. This is probably due to the fact that long-term experiments are necessary to obtain results of the decay of these materials, which have tissues resistant

Table 1. Initial nutrient concentration of the individual green leaves per species, of the mixed species leaves and of the mixed species branches which were used for the decomposition experiments.

	P	N	K	Mg	Ca
			(mg g^{-1})		
Leaves per specie					
Catostemma sp. (Bombacaceae)	0.42	9.38	4.49	1.21	5.76
Protium sp. (Burseraceae)	0.59	13.10	5.62	1.03	4.12
Mabea sp. (Euphorbiaceae)	0.76	16.66	6.88	1.24	7.51
Eschweilera sp. (Lecythidaceae)	0.56	16.10	5.86	1.03	4.04
Alexa canaracunensis (Leguminosae)	0.75	22.00	6.37	0.64	1.85
Alexa imperatricis (Leguminosae)	0.99	19.04	6.62	1.48	4.23
Eperua grandiflora (Leguminosae)	0.62	12.32	5.19	1.46	4.85
Iryanthera sp. (Myristicaceae)	0.51	13.80	6.75	1.59	5.91
Oenocarpus bataua (Palmae)	0.79	13.30	5.49	1.16	1.92
Chrysophyllum sp. (Sapotaceae)	0.33	16.20	5.52	0.95	3.50
Mixed-species leaves					
Mean ± SD	0.56 ± 0.05	14.42 ± 0.91	6.00 ± 0.60	1.16 ± 0.10	4.32 ± 0.53
Mixed- species branches					
Mean ± SD	0.15 ± 0.04	4.20 ± 0.63	4.29 ± 0.56	0.57 ± 0.27	3.19 ± 1.32

Table 2. Changes (mean ± SD) of the dry weight and nutrient concentration of the green leaves and fine branches during the 9 months of the decomposition experiment.

Month	Dry weight (g)	P	N	K	Mg	Ca
				(mg g^{-1})		
Leaves						
May	22.28 ± 0.52	0.56 ± 0.05	14.42 ± 0.91	6.00 ± 0.60	1.16 ± 0.10	4.32 ± 0.53
June	18.79 ± 1.13	0.31 ± 0.06	16.76 ± 1.00	0.49 ± 0.09	0.24 ± 0.03	3.14 ± 0.45
July	17.94 ± 0.70	0.34 ± 0.08	16.10 ± 1.19	0.57 ± 0.16	0.17 ± 0.01	2.77 ± 0.25
August	16.43 ± 1.10	0.35 ± 0.11	15.40 ± 0.81	0.66 ± 0.18	0.15 ± 0.03	2.60 ± 0.86
September	15.88 ± 1.08	0.37 ± 0.04	15.26 ± 0.83	0.51 ± 0.16	0.12 ± 0.01	2.35 ± 0.32
October	14.03 ± 1.41	0.37 ± 0.04	14.49 ± 0.80	0.50 ± 0.05	0.11 ± 0.01	2.10 ± 0.28
November	12.67 ± 1.11	0.43 ± 0.09	14.70 ± 1.72	0.57 ± 0.10	0.15 ± 0.01	2.81 ± 0.21
December	11.66 ± 1.19	0.40 ± 0.09	14.60 ± 0.57	0.73 ± 0.13	0.19 ± 0.03	3.28 ± 0.42
January	9.54 ± 1.70	0.33 ± 0.06	14.60 ± 1.00	0.68 ± 0.14	0.19 ± 0.02	3.17 ± 0.34
February	8.91 ± 1.54	0.40 ± 0.07	14.32 ± 1.10	0.69 ± 0.09	0.29 ± 0.40	3.86 ± 0.61
Branches						
May	33.85 ± 0.99	0.15 ± 0.04	4.20 ± 0.63	4.29 ± 0.56	0.57 ± 0.27	3.19 ± 1.32
July	30.08 ± 1.54	0.14 ± 0.04	4.36 ± 0.60	0.19 ± 0.03	0.14 ± 0.05	3.15 ± 0.56
September	29.06 ± 1.57	0.11 ± 0.03	4.16 ± 0.67	0.20 ± 0.05	0.09 ± 0.05	2.41 ± 0.90
November	28.18 ± 0.05	0.11 ± 0.07	4.81 ± 1.04	0.31 ± 0.07	0.09 ± 0.02	2.62 ± 0.66
January	28.05 ± 0.06	0.15 ± 0.06	5.32 ± 0.97	0.41 ± 0.11	0.09 ± 0.03	2.45 ± 0.54
February	27.30 ± 2.08	0.12 ± 0.04	6.02 ± 0.58	0.41 ± 0.15	0.13 ± 0.02	2.67 ± 0.37

to decomposition. In our case (Figure 2), the elements potassium and magnesium in fine branches behaved similar to leaves. 4% of the initial amount of K and 22% of the initial amount of Mg were left at the end of the first sampling period. The initial loss of calcium and phosphorus was, however, much less: 88% of the initial amount of Ca and 83% of the initial amount of P remained in branches at the end of this first sampling. The pattern of nitrogen in the branches was different than in the leaves and showed gradual increases during the last five months of the decomposition experiment. At the end of the sampling period, the N amount in the branches was 16% higher than the initial amount. The increase of N during initial stage of decomposition has been reported in terrestrial as well as in aquatic ecosystems (Bocock 1963; Gosz et al. 1973; Swift et al. 1979; Day 1982; Melillo et al. 1982; Webster & Benfield 1986; Garden & David 1988). Tentative mechanisms that appear to explain this N-increase include additions of N by fixation, fungal translo-

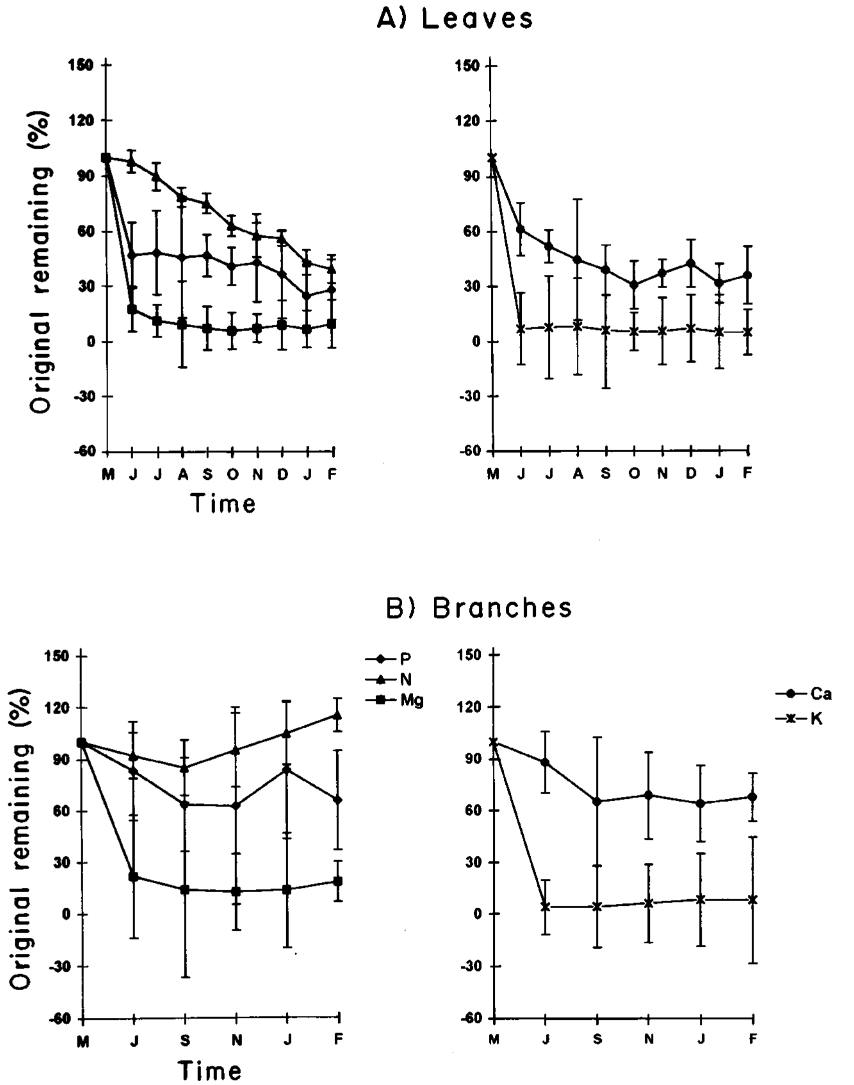

Figure 2. Pattern of change in nutrient amount in leaves and branches during the 9-month period of the decomposition experiment, expressed as percentages of the original amount of nutrients.

cation and or immobilization (Melillo et al. 1982). The N immobilization is usually attributed to accumulation of microbial protein (Suberkropp et al. 1976; Triska & Sedell 1976). Regarding this subject Brinson et al. (1981) suggested that in decomposition experiment in freshwater accumulation of a nutrient may be dependent on both the nutrient composition of the water and the heterotrophic demand of the nutrient.

Conclusions

Decomposition is a complex interaction of processes influenced by a number a factors including activity and nutrient demand of heterotrophs, environmental conditions regulating activity, species differences in tissue palatability and nutrient content, and differences in nutrient mobility (Gosz et al. 1973). This phenomena cannot be quantified by short-term experiment such as these presented here. Our results, however, provide a basis to the understanding of some of these processes, which are essential for evaluating effects of anthropogenic disturbance on the trophic dynamics of terrestrial and aquatic ecosystems.

Eijsackers & Zehnder (1990) have pointed out that there are only small differences in the structure or general scheme of the decomposition processes between terrestrial and aquatic soils. There are, however, considerable differences in the dynamics of this process on land and in water, which can be attributed in part to different leaching rates in both ecosystems (Furch & Junk 1997). Our decomposition data are in general agreement with previous studies of decomposition of leaf litter on land and in water. We found that the patterns of dry weight and nutrient losses were relatively consistent with patterns and rates reported previously (e.g. Gosz et al. 1973; Suberkropp et al. 1976; Triska et al. 1976; Brinson 1977; Day 1982; Killingbeck et al. 1982; Anderson et al. 1983; Furch et al. 1989; Furch & Junk 1997). Detailed comparisons with results from the other sites cannot be made, however, because here the experiments were carried out with green material obtained directly from standing living trees and from different species. The use of this material rather than those that had fallen from the tree introduces a bias into the experiments because it ignores the changes in chemical composition that may occur prior to abscission (Swift et al. 1981). The present investigation, however, adds a new type of material to complement the existing studies of decomposition in tropical forest, namely green leaves and small branches, which are an important component of the forest biomass, and can be easily exposed to decomposition processes when forests are flooded after dam construction.

Decomposition under aquatic conditions is accompanied by drastic changes in the chemical composition of the water (Furch et al. 1989). According to the results of this study, large quantities of potassium and magnesium are lost during the decomposition experiment. The lost quantities of calcium and phosphorus were also relatively large in leaves, but their loss rates were far lower than those of K and Mg. Incorporation of plant nutrients in the water may lead to an increase in the populations of aquatic macrophytes. Alvarez et al. (1986) reported that since 1983 the Guri reservoir has been colonized by aquatic plants, which have followed a successional sequence; these authors suggested also that the nutrients leached from the flooded soil and released by the decay of flooded vegetation has contributed in the development of these plant communities.

Finally it is important to emphasize that the present results are a contribution to the technical group of EDELCA in order to estimate the impact of biomass decomposing on a future reservoir in the Caura region. In addition to the present result it should also, however, be considered that in a forested region, a reservoir can be characterized by low water velocities and throughflow with little erosive power; likewise it is important to have information on the quantity of biomass in the area of the future reservoir, as well as on the chemistry of water, the water retention time in the reservoir, the reservoir depth and the water level fluctuations.

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