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FUNCTIONAL CONTRIBUTION OF INVERTEBRATES, BACTERIA AND FUNGI TO LEAF DECOMPOSITION IN A BLACK WATER TROPICAL RIVER

CONTRIBUCIÓN FUNCIONAL DE INVERTEBRADOS, BACTERIAS Y HONGOS A LA DESCOMPOSICIÓN DE HOJAS EN UN RÍO TROPICAL DE AGUAS NEGRAS

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ABSTRACT

A functional analysis on leaf breakdown under flooded conditions of four common tree species of the Leguminosae family: *Bauhinia* sp. (PV), *Pithecellobium pedicellare* (HP), *Albizia glabripetala* (SC) and *Centrolobium paraense* (C) and leaf litter (LL) from the floor of the dry forests around Caruachi Reservoir was conducted in the lower Caroní River basin, Venezuelan Guiana. Leaf bags technique (5 mm Ø mesh) was used over a 4-week period. Rate of leaf weight lost (k) was determined by the Olson model (1963). Decay of leaves by bacteria, fungi and macroinvertebrates was photographed along with the decomposition period. Soft leaved species (SL) coming from SC and C decomposed more rapidly (k = 0.0373 and k = 0.0285 respectively) than Hard leaved species (HL) coming from HP and PV and LL (k = 0.0188 and k = 0.0143 k = 0.0229 respectively at 28 days); SL (C and SC) had a greater lost (54% - 64%) of its initial mass within 4 week compared to HL (PV and HP) (33 - 44 %) and litter (47%). The former high rates (SL) were probably related to a softer texture favoring strong biological activity. Up to 1087 and 950 invertebrates per leaf bag were found on SL and HL, respectively and 480 on LL after 21 days. Shredders accounted for <1% or the absence of the total numbers and biomass, meanwhile, Recolectors/Scrapers reached to >90%. Fungal density reached at 60 (CFU)/mg of the detrital mass and bacterial abundance 476.7 and 395.0 on HL and SL and 398.3 (CFU)/mg on LL, suggesting that bacteria and fungi contributed considerably to leaf mass loss. The difference in breakdown rates between leaf species was consistent with the faster colonization of SL (SC and C) by macroinvertebrates. The rapid breakdown of tropical leaves combined with a low influence by shredders in this study seems to present similar patterns as previous findings (Covich *et al.*, 1999 and Benstead, 1996). In this experiment, we found a strong influence by Recolectors/Scrapers, evidenced by photographs. The high bacterial, double role of macroinvertebrates and fungal activities associated with rapid leaf breakdown appear to be important on leaf processing in this tropical stream.

RESUMEN

Se estudió el proceso de descomposición de cuatro especies de hojas de plantas (familia leguminosae): *Bahuinia* sp. (*PV*), *Pithelcellobium pedicellare* (HP), *Albizia glabripetala* (SC), *Centrolobium paraense* (C) y hojarasca (LL) del suelo del bosque seco en los alrededores del Embalse Caruachi en el río Caroni (Venezuela). Para determinar la tasa semanal de pérdida de peso mediante el modelo de Olson (1963) se usó la técnica de las bolsas de descomposición por un período de 4 semanas. Se fotografió el material sujeto a descomposición por bacterias, hongos e invertebrados durante el período de estudio. Las especies de hojas blandas (SL) SC y C tuvieron una descomposición más rápida (k = 0.0373 y k = 0.0285 respectivamente) que las especies de hojas duras (HL) de HP y PV, y LL (k = 0.0188 y k = 0.0143 k = 0.0229, a los 28 días, respectivamente). Al inicio del experimento, el material de C y SC mostró una mayor pérdida de peso (54% - 64%) que el material HL (PV y HP) (33 - 44 %) y hojarasca (47%). Las altas tasas de descomposición de SC y C están probablemente relacionadas con la textura más suave, la cual favorece una fuerte actividad biológica. Después de 21 días, las densidades de invertebrados alcanzaron 1.087 org./bolsa y 480 org./bolsa en hojarasca. Los organismos partidores se encontraron en <1% o totalmente ausentes tanto en densidad como en biomasa, mientras que los Recolectores/Raspadores alcanzaron >90%. La densidad de los hongos alcanzó 60 CFU/mg de la masa del detrito y la abundancia bacteriana 476.7 y 395.0 para HL y SL mientras que 398.3 CFU/mg en LL, lo cual sugiere que las bacterias y hongos contribuyeron considerablemente con la pérdida de masa de las hojas. Las diferencias en las tasas de descomposición (k= 0.0143 (PV), k =0.0188 (HP), k =0.0285 (C), k =0.0373 (SC), k =0.0229 (H)) estarían asociadas con una mayor colonización de las bacterias y una doble función de los macroinvertebrados (Raspadores/Recolectores).

Key words: Leaf breakdown, invertebrates, bacteria, fungi, Caroní River.
Palabras clave: Descomposición, invertebrados, bacterias, hongos, Río Caroní.

INTRODUCTION

Ciudad Guayana an industrial city in Southeastern Venezuela, is surrounded by two important rivers, Orinoco and Caroní, the latter being the main source of hydropower electricity and drinking water. Currently, biochemical changes were identified in a drinking water source at the Macagua Reservoir due to the construction of the new Caruachi Dam located some 23 km upstream the Caroní River.

Deforestation has many consequences for stream ecosystems, including increased silting, higher insolation, enhanced nutrient loads, and changes in the relative availability of basal food resources. Long-term consequences for the taxonomic structure of stream communities lag far behind its ecosystem-scale effects, particularly in the tropics (Benstead *et al.*, 2003).

Decomposition of logs, leaves, sticks, fruits, and, other components, release to the soil an important quantity of nutrients and colloidal materials. On the other hand, leaf litter breakdown is the result of physical and biological mineralization and transformation processes resulting in the generation of CO_2 and other inorganic compounds, dissolved organic matter (DOM), fine-particulate organic matter (FPOM), and decomposed biomass (Gessner, 1999). Breakdown appears to occur more rapidly in hard-water streams than in softwater ones, which is probably due to higher levels of dissolved macro and micronutrients in the former systems (Suberkropp & Chauvet, 1995).

The organisms driving these processes include invertebrates, bacteria and filamentous fungi, and there is evidence that all three groups play significant roles in the process of litter breakdown (Anderson and Sedell, 1979; Gessner, 1999). The assessment of the functional contribution of different organisms to the process of decomposition requires elucidating physiologic aspects of growth and feeding (Weyers and Suberkropp, 1996; Jonsson and Malmqvist, 2000; Hieber and Gessner 2002). Another approach would be to quantify the roles of individual species or functional groups (Hieber and Gessner, 2002).

In South America, there are very well known studies about decomposition rates of macrophytes in lentic and lotic systems (Bruquetas de Zozaya and Neiff, 1991; Bruquetas de Zozaya and Poi de Neiff, 1993; Poi de Neiff and Casco, 2001), but few reports exists for Venezuela. Salazar and Weibezahn (1983) reported decomposition values for *Inga edulis* in a Venezuelan white water river, Bastardo (1979; 1993), Bastardo and Rivera (1991) and Bastardo et al. (1982) reported rates of decomposition of several tropical grasses of Venezuelan plains. Furthermore, Dezzeo et al. (1998) studied the rates of decomposition of tree leaves in a flooding forest of the Mapire and lower Caura black water rivers, and Rincón et al. (2005) examined some factors influencing leaf litter breakdown of *Anacardium exelsum* in a second-order intermittent river of Northwestern Venezuela.

The purpose of this study was to determine the functional variation of macroinvertebrates, bacteria and fungus during the decomposition process of four predominant species of scrubs during the first stage of flooding of a dry forest in a Venezuelan black water river under dam regulation.

METHODS

The study was carried out in Caruachi Dam, a 95.000 km^2 water reservoir built on the lower Caroní River, a blackwater river located in the northern part of Bolivar State, Venezuela (8° 40' N, 64° 10' W, see Fig. 1). The Caroní River drains a 238 km^2 catchment area and it is mostly underlain with Precambrian bedrock. Caruachi Dam is located between the Guri Dam (by far the largest, southernmost and most upstream) and Macagua Dam (the northernmost and built very close to the mouth of Caroní River on the Orinoco River). Local climate at Caruachi reservoir is warm year round, with a mean annual temperature of 27 °C and rainfall of 2.800 mm and a mean relative humidity of 76%. Dominant vegetation types are tropical dry forests, savannas, gallery forests and successional scrubs. Table 1 summarizes selected physical and chemical characteristics of the Caroní River water during the study period.

Field methods. Mature leaves of the four dominant species were chosen randomly. Leaves from *Bauhinia* sp. (PV), *Pithecellobium*

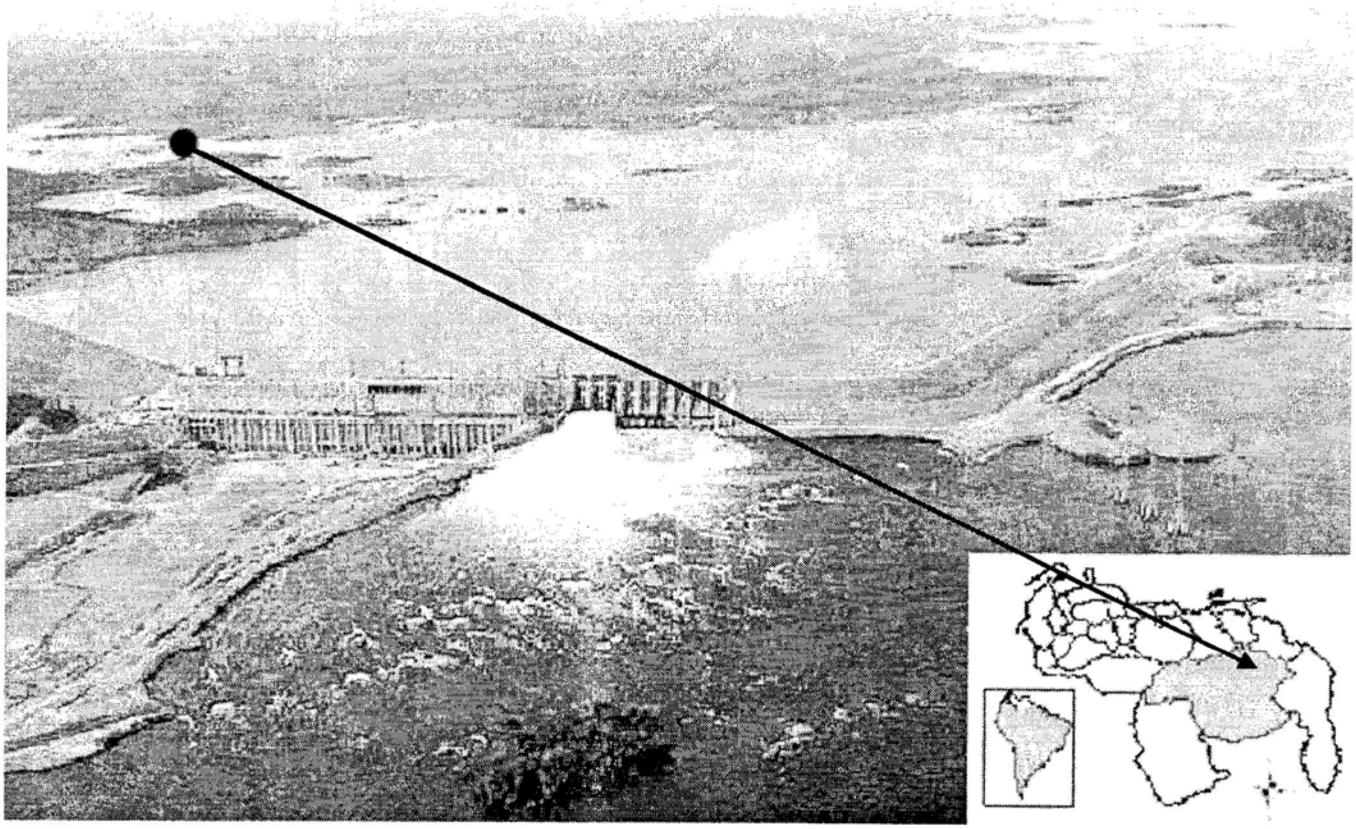

Figure 1. View of the dam of Caruachi reservoir at Caroní River (Source: CVG Electrificación del Caroní C.A). The black circle on the photo shows the approximate location of the experimental station.

Tabla 1. Localidad de origen y número de ejemplares de estudio

Variable	N	Mean	Range
Water Temperature (°C)	12	28.54	28.9-29.2
Water conductivity (μS/cm^{-1}; at 27°C)	12	9.66	8.72-11.0
pH	12	6.41	6.1-6.67
O_2 (mg/L)	9	6.65	6.4 - 6.8

N= Number of measurements; Mean: Average value of Nitrogen content

pedicellare (HP), *Albizia glabripetala* (SC) and *Centrolobium paraense* (C) and leaf litter (LL) of Leguminosae plants were collected in March 2003. Llitter bags (10 x 20 cm, 0.5 cm mesh) were incubated at a field experimental station in the right margin of the reservoir. Each litter bag contained 2.5 g ± 0.05 (mean ± SD) of leaf material (dry weight). The bags were distributed in three rigid structures (2 cm mesh) hanging from floating empty barrels, in turn anchored to land. Each structure was vertically aligned by 3 kg iron weights. After 7, 14, 21 and 28 days of submersion, respectively, 3 bags representing replicates for each species were randomly retrieved, placed in polyethylene sealed bags and returned to the laboratory in portable coolers and immediately processed. At every collection of samples water temperature, pH, conductivity and dissolved oxygen were measured in situ at 27 °C, with a multi-parametric probe (Hatch Mod. 2511).

Laboratory methods. At the laboratory, the leaves were carefully removed from the bags and two portions of 0.1 g were cut from each pack and placed in a sterile test-tube containing peptone broth and were shaked for one minute. One ml of this homogenized product was inoculated in Petri dishes containing plate count agar and Saboraud medium (Mariñelarena y Mariazzi, 1995). After incubation at 28 ± 1 °C for 96 hours, bacterial and fungal density were determined by counting the number of colony forming units (CFU/mg leaf tissue). The remaining leaf material was removed from the mesh bags and freed of invertebrates by rinsing with tap water through a 0.25 mm mesh sieve. Macroinvertebrates were counted and assigned to the lowest possible taxonomic level under a dissecting microscope, and preserved in 70% alcohol. Macroinvertebrates were assigned to different feeding categories following Merritt & Cummins (1996). Some stomachs of *Cyclestheria hislopi* collected the first week were analyzed and placed in a sterile test-tube containing 3 ml of sterilized water to observe bacterial growth on a plate. Macroinvertebrate biomass was estimated for *Cyclestheria hislopi* (Table 2) by means of the body-length fresh-weight relationship following Benke *et al.,* (1999).

The remaining leaves were oven-dried at 60 °C until constant dry weight. The decomposition rate (k) was determined with the equation k=- [ln(W/Wo)]/t (Olson, 1963), where: t is time (in days); W_o is the initial weight of the leaf pack; W_1 is the weight of the leaf pack after t days; k is the leaf processing rate (in day-1). The period for

Table 2. Width–weight relation for *Cyclestheria hislopi.* N: Number of individuals; X: range-mean: S: standard deviation.

		Weight (mg)	
Width range (mm)	N	X	S
< 1	1000	1.5×10^{-5}	0.007
1 – 1.9	500	2.3×10^{-4}	0.007
2 – 2.9	500	8.0×10^{-4}	0.026
> 3	150	1.3×10^{-3}	0.003

decomposition of 50% of the initial biomass (2,5 g) was estimated. Biochemical assays (carbohydrates, cellulose and pectin utilization as carbon resource) were carried out in isolated bacterial colonies from plate count agar to determine functional groups (FG) and were expressed as percentage of FG presence (Bastardo, 1979). An analysis of Anova (F-test) were used to compare the weight loss for each species through time.

RESULTS

Leaf dry weight loss. There were no significant differences between *Albizia glabri-petala* (SC) and *Centrolobium paraense* (C) (F-value= 0.4273 P>0,05) nor between *Bauhinia* sp. (PV) and *Pithecellobium pedicellare* (HP) (F-value= 1.42123 P>0.05) in decomposition rate (k), bacterial, fungi or macroinvertebrate density in 28 days. Hereafter, decomposition rates from SC and C are given as soft-leaved (SL), and rates from HP and VP are given as hard-leaved (HL) species. Results shows that leaf breakdown was faster in SL (k C = 0.037 and k SC = 0.0285) than in HL (k HP = 0.0188 and k PV = 0.0143) and Leaf litter (k LL = 0.0229) at 28 days. SL (C and SC) had a greater dry weight loss (54-64%) compared to HL (PV and HP) (33-40 %) or litter (47%) at 28 days. (Figure 2, Table 3).

Bacteria. Bacterial density was highest in the first week of the experiment in SL (X=506.7 CFU/mg), while HL reached its maximum at the second week (X=394 CFU/mg) (Table 3). Sugar-reducer and pectinolytic groups were found at higher ratios (75% y 35%) respectively in SL at one week. Cellulolytic groups increased progressively in the experiment time (18% 30% and 45%). No significant variation in SL and HL were found in sugar-reducer and pectinolytic groups by the fourth week. However, an increase of the cellulolytic group (20%) was observed at the end of the experiment (Figure 3).

Fungi. Fungal density was highest 4 weeks after leaf submersion (X=50 CFU/ mg) in SL and in HL (X=32.5 CFU/ mg). No significant variation in fungal density on SL and HL was found at 21 days of the experiment, but a significant difference ($p<0.05$) was evident by the fourth week between SL and HL. However, LL didn't show significant variations (Table 4).

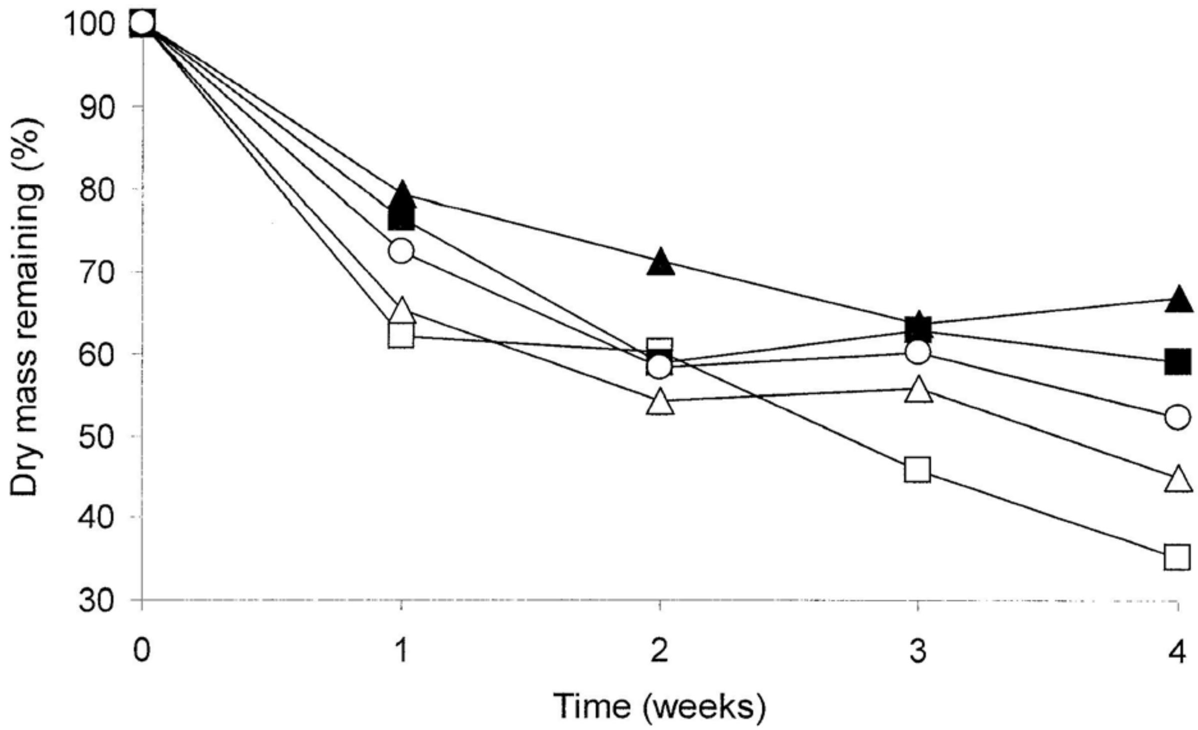

Figure 2. Dry mass remaining of SC (open squares), C (open triangles), LL (open circles), HP (solid squares), and PV (solid triangles) leaf packs decomposing in Caruachi Dam.

Table 3. Variation of the bacterial density (CFU/mg) in the four species of leaves and leaf litter during 28 days of decomposition: *Bauhinia* sp. (PV), *Pithecellobium pedicellare* (HP), *Albizia glabripetala* (SC) and *Centrolobium paraense* (C) and leaf litter (LL).

Time (days)	C	SC	PV	HP	LL
7	446.7	506.7	370.7	405.0	398.3
14	394.0	390.7	343.3	446.7	356.7
21	341.3	393.3	393.3	328.3	375.0
28	348.3	323.7	282.0	313.7	371.0

Table 4. Variation of percentage (presence %) of the fungal density (CFU/mg) in four species of leaves and leaf litter during 28 days of decomposition: *Bauhinia* sp. (PV), *Pithecellobium pedicellare* (HP), *Albizia glabripetala* (SC) and *Centrolobium paraense* (C) and leaf litter (LL).

Time (days)	C	SC	PV	HP	LL
7	5	10	3	13	20
14	9	20	10	22	25
21	17	36	20	30	32
28	40	60	30	35	40

Macroinvertebrates. Leaf bags were rapidly colonized by macroinvertebrates. Maximum densities were observed at 2 weeks of the experiment, with an average of 716 (SL) and 505 (HL) org/2,5 g leaf pack (Fig. 4), corresponding to a biomass of 302 (SL) and 260 (HL) mg/bag respectively (Fig. 3). Collectors-gatherers was the predominant functional feeding group found in bags of all leaf species, accounting for an average of 88% of total invertebrate numbers and 90% of total biomass (Fig. 4). Three weeks after leaf submersion, Collectors-gatherers declined in importance to 64% of total macroinvertebrate biomass in both groups of leaves. The collectors-gatherers, branchiopod *Cyclestheria hislopi,* accounted for 95% of total density and 98% of biomass of macroinvertebrates found. Collector-filterers and predators were minor components of the macroinvertebrate assemblage.

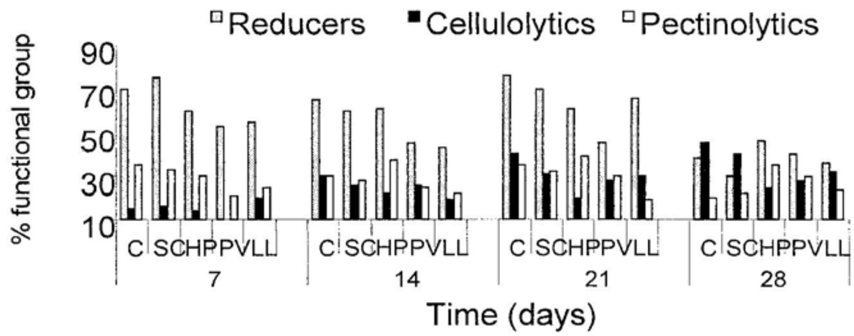

Figure 3. Functional dynamics of the bacterial community (% composition by functional group) during the decomposition of leaves of *Bauhinia* sp. (PV), *Pithecellobium pedicellare* (HP), *Albizia glabripetala* (SC) and *Centrolobium paraense* (C), and leaf litter (LL).

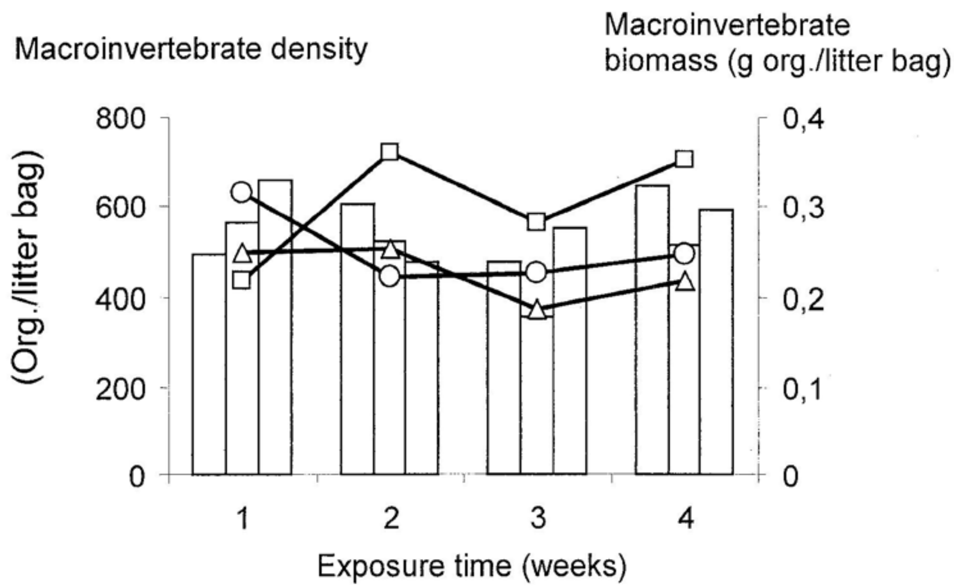

Figure 4. Macroinvertebrate densities (lines) and biomass (bars) on decaying SL (open squares, open bars), LL (open circles, striped bar), and HL (open triangles, solid bar) in Caruachi Dam. Data are averages of 3 replicates.

DISCUSSION

Petersen and Cummins, (1974) presented half-life values <46, 46-138 and >138 days for "fast", "medium" and "slow" species respectively. In the Caruachi Dam experiment, the half-life for SL was 14 days and for HL and LL 21 days. Thus, examined groups of leaves qualify as "fast" decomposing species. Actually, plant material decomposed very fast, with a dry weight loss of 33% (HL) to 50% (SL) in four weeks. The time needed for 50% of the initial plant material to be lost provides an alternative to k-values when comparing breakdown rates between different studies. The rate of weight loss obtained in this study is far higher than those reported for other studies in Venezuela (Rincón *et al.*, 2005; Salazar and Weibezahn, 1983; Dezzeo *et al.*, 1998), but it is close to the values of Benstead (1996) and Fellerhoff *et al.*, (2003) for small whitewater streams in Costa Rica and

Pantanal (Brazil). Dudgeon (1982) concluded that the rapid breakdown rate in a subtropical stream in Hong Kong was largely due to high temperatures. In this study, temperature and oxygen concentration are important factors controlling organic matter decomposition. Naturally occurring high water temperatures (27 °C) and high concentrations of dissolved oxygen (>7 mg/l) in our study site contributed to the rapid decay by enhancing microbial activity. In the tropics, high temperatures and precipitation also enhance chemical weathering of phosphorus (Lewis, 1996). Castillo *et al.,* (2003) found that phosphorus rather than carbon is the primary limiting nutrient; carbon is an important secondary constraint to bacterial production in Venezuelan blackwater rivers.

Sridhar and Bärlocher (2000), found that the initial fungal colonization of leaves in tropical streams was typical after an initial lag phase. The enzymes used by aquatic hyphomycetes to degrade pectin, lignin and cellulose appear, on the basis of limited research, to have pH optima of about 8.0 and operate most efficiently under alkaline conditions (Suberkropp & Klug, 1980). Since Caruachi reservoir presented slightly acid pH values (Table 1), we believe this could be one reason for the low densities of fungi observed in this experiment (Table 4).

In this study, sugar-reducers and pectinolytic bacterial groups were found at higher ratios in SL and HL (75% y 35%, respectively) at one week, but they decreased when the cellulolytic group increased progressively (18%, 30% y 45%). In humic rivers of North America, Meyer *et al.,* (1987) and Tranvik & Höfle (1987) reported that bacteria decomposed 54% of dissolved organic carbon (DOC) of low molecular weight and 21% of high molecular weight DOC. The efficiency of microorganisms to convert DOC into particulate organic carbon (POC) ranged from 20 to 30%, while the used DOC was considered to be of refractory nature (Cunha-Santino & Bianchini Júnior, 2002). Although DOC is abundant in other Venezuelan blackwaters, like Autana and Cataniapo rivers (Castillo *et al.*, 2003), humic compounds comprise a high proportion of the DOC (Villaró, 1997), which suggests that the bulk of this organic carbon might be refractory. The results of this study indicate that some fraction of DOC is readily available to bacteria, and no obvious factor is co-limiting the bacterial growth. In essays at Venezuelan rivers, Castillo *et al.*, (2003) found that bacterial production responded to glucose addition in systems where the availability of DOC is low and nutrient concentrations are high.

Golterman, (1975) and Swift *et al.*, (1979) claim that the trend of accentuated consumption of tannic acid carbon at the beginning of the decomposition processes followed by stabilization is the result of the microbial biosynthesis (particulate form), and probably from the humification processes. The prevalence of the aerobic decay processes in Caruachi´s reservoir, as observed by Cunha-Santino *et al.,* (2002) in the reservoir of Monjolinho (Brazil), probably help the tannic acid and other polyphenols to be quickly metabolized. It is known that phenolic concentrations are 80 times greater in the vegetation of blackwater rivers than in that of clearwater rivers (St. John & Anderson, 1982). Plants grown in nitrogen or phosphorous deficient soils produce higher quantities of phenolic compounds than those grown in non-deficient soils (Davies *et al.*, 1964). These phenolic compounds and condensed tannins are potential inhibitors of biotic litter processing (Benstead, 1996). This could explain the low density of fungi and insects in the first weeks of the experiment at Caruachi reservoir.

After an initial peak of colonization by invertebrates within the first 7 to 14 days, abundances of *C. hislopi* in SL, LL and HL decreased after 28 days. The high predominance of C. *hislopi* in all leaf bags can be related to deforestation of the lands dammed by Caruachi. Benstead *et al.*, (2003) found that deforestation in Madagascar is asso-ciated to several changes in the structure of stream insect communities. Community simplification shifts the relative importance of functional feeding groups and also reduces the species richness. Wardle *et al.,* (1997) found that removing all plants in perennial grassland vegetation often affected negatively three further trophic levels of the decomposer functional food web: microflora, microbe-feeding nematodes, and predaceous nematodes. Other studies in the Caura river, with the same chemical characteristics as the Caroní River, suggest high richness and diversity of invertebrates in this region (García and Pereira, 2003; Blanco-Belmonte, 2005).

Dominance of Branchiopoda in leaf bags is possibly related to a higher incidence and concentration of defensive compounds in leaves from tropical trees; they are generally less palatable to herbivores (insects) than those from species from temperate forests (Stout, 1989; Graça *et al.*, 2001). Leaf quality is an important factor determining the feeding behavior of organisms (Graça *et al.*, 2001). We observed circles of scrapings on SL (*Albizia glabripetala* and *Centrolobium paraense*) in the first week of the experiment (Fig. 5). These scrapings were somewhat puzzling in our study because *Cyclestheria hislopi* is often described as a filter feeder, but recently Martin and Boyce (2004) reported a large amount of scraping and tearing of food by this species. The samples of stomach contents of C. *hislopi* obtained during the first week were analyzed under the microscope to elucidate whether the clearings on the leaves were a product of mechanical abrasion or a direct scraping of *C. hislopi*, and we observed vegetal tissue in the stomachs. The cultivation of *C. hislopi* stomach contents in plates to analyze bacterial presence and growth showed very similar results to those found with leaves. We hypothesized an initial "protocooperation" (Bastardo, 1993) between *Cyclestheria* and bacteria, consisting of an initial scraping by *C. hislopi* followed by bacterial colonization. The subsequent harvesting of bacteria by Branchiopoda enhanced bacterial growth.

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