

## Leaf litter of *Erythrina crista-galli* L. (ceibo): trophic and substratum resources for benthic invertebrates in a secondary channel of the Middle Paraná River

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### ABSTRACT

#### Leaf litter of *Erythrina crista-galli* L. (ceibo): trophic and substratum resources for benthic invertebrates in a secondary channel of the Middle Paraná River

The decomposition of *Erythrina crista-galli* L. (Leguminosa) leaf litter and its colonization by invertebrates were studied in a secondary channel of the Middle Paraná River. This species is native to and very abundant in South America in riverside areas and in Argentina it is known as 'ceibo'. The objectives were to estimate the *E. crista-galli* leaves' decomposition rate, to determine the proportion of functional feeding groups of invertebrates throughout the process of decomposition, and to evaluate the use of leaf detritus by the benthic invertebrates. The leaves were collected at abscission and 6 g dry weight were placed in 5 mm mesh nylon bags. The samplings were carried out between May and September 2002 and six replicates were collected after 7, 14, 28, 56 and 112 days. The decomposition rate ( $k$ ) calculated over 112 days of decomposition was  $0.0129 \text{ d}^{-1}$ . Invertebrate densities increased with the progressive decomposition of the leaves, reaching the maximum at 14 days ( $306 \text{ ind g}^{-1} \text{ dw leaf}^{-1}$ ) and 112 days ( $298 \text{ ind g}^{-1} \text{ dw leaf}^{-1}$ ). The highest species richness (18.5) was found at 7 days of leaf decomposition. Colonization of decomposing leaves was dominated by Diptera Chironomidae (*Polypedilum* spp., *Phanopsectra* sp.), Crustacea (Cladocera, Ostracoda), Oligochaeta Naididae (*Pristina americana*, *Slavina evelinae*, and *S. isochaeta*), and Mollusca (*Limnoperna fortunei*).

The shredders were dominant at the beginning of the decomposition process and the collector-filterers increasing at the end of the period because of the highest density of *Limnoperna fortunei* which used the leaf litter as substratum.

**Key words:** Decomposition rate, feeding functional groups, colonization.

### RESUMEN

#### Hojarasca de *Erythrina crista-galli* L. (ceibo): recurso trófico y sustrato para invertebrados bentónicos en un cauce secundario del río Paraná Medio

Se estudió la descomposición de hojas de *Erythrina crista-galli* L. (Leguminosa) y su colonización por invertebrados en un cauce secundario del río Paraná Medio. Esta especie es nativa y muy abundante en América del Sur, principalmente en los bosques riparios en las márgenes de los ríos y en Argentina se conoce como 'ceibo'. Los objetivos fueron estimar la tasa de descomposición de las hojas de *E. crista-galli*, determinar la proporción de grupos funcionales a lo largo del proceso de descomposición y evaluar el uso que realizan los invertebrados bentónicos del detritus vegetal que colonizan. Las hojas fueron colectadas de los árboles y 6 g de peso seco de hojas fueron colocadas en bolsas de 5 mm de abertura de malla. La experiencia fue llevada a cabo entre Mayo y Setiembre de 2002 y se recolectaron seis réplicas a los 7, 14, 28, 56 y 112 días. La tasa de descomposición ( $k$ ) a los 112 días fue de  $0.0129 \text{ d}^{-1}$ . La densidad de los invertebrados aumentó con la progresiva descomposición de las hojas, alcanzando la máxima densidad a los 14 días ( $306 \text{ ind g}^{-1} \text{ ps}^{-1}$ ) y 112 días ( $298 \text{ ind g}^{-1} \text{ ps}^{-1}$ ) y la riqueza de especies fue mayor a los 7 días (18.5). Los grupos colonizadores fueron principalmente, Diptera Chironomidae, (*Polypedilum* spp., *Phanopsectra* sp.) Crustacea (Cladocera, Ostracoda), Oligochaeta Naididae (*Pristina americana*, *Slavina evelinae* and *S. isochaeta*) and Mollusca (*Limnoperna fortunei*).

*Los trituradores fueron dominantes durante las primeras etapas de descomposición y los colectores-filtradores aumentaron hacia el final de la experiencia debido a la gran densidad de *Limnoperna fortunei* que utilizó a las hojas como sustrato.*

**Palabras clave:** Tasa de descomposición, grupos funcionales, colonización.

## INTRODUCTION

Freshwater and terrestrial ecosystems are linked by pathways of organic matter exchange. These exchanges are particularly important in the low order streams with dense riparian forests, where the leaves of the trees are the most abundant organic matter inputs and constitute the most important source of energy to heterotrophic organisms (Sponseller & Benfield, 2001; Hoffmann, 2005; Graça & Canhoto, 2006). Many studies have analyzed the importance of the allochthonous inputs, demonstrating that the temporary and spatial contributions depend on the surrounding riparian vegetation (Pozo *et al.*, 1997). In temperate deciduous forests, most of the litter falls in a relatively short period (Pozo, *et al.*, 1997), in contrast to other forested systems where the leaf litter input is rather constant throughout the whole year (Stewart, 1992). Other studies have demonstrated the important influence of the riparian zone in the structure and ecological functioning of the streams due to their intrinsic ecosystem characteristics, acting often like a load of nutrients for the rivers (Sabater *et al.*, 2000). The leaf litter decomposition of the riparian forest and the aquatic macrophytes is a key to ecosystem processes in running waters such as carbon cycle, spiraling of nutrients and energy transfer (Wallace *et al.*, 1999). In many studies it was determined that the leaf quality, the nutrients concentration, dissolved oxygen and the physical conditions are factors that affect the leaf breakdown in streams (Gamage & Asaeda, 2005; Rueda Delgado *et al.*, 2006; Ardón *et al.* 2006; Poi de Neiff *et al.*, 2006). Nevertheless, the role of invertebrates in this process is not very well known, especially in tropical and subtropical regions (Mathuriau & Chauvet, 2002, Wantzen & Wagner, 2006; Gonçalves *et al.*, 2006).

Leaf breakdown in running waters proceeds in three phases that, rather than work separately, act simultaneously: leaching, conditioning, and fragmentation (Gessner, 1999). Leaching is a rapid phase, releasing the soluble organic compounds in a few hours; therefore the majority of soluble constituents may leach within 48 h after the immersion of the leaves. Then, a leaf colonization by fungi and bacteria occurs conditioning the litter, the fungi being dominant and more active than the bacteria at the beginning of this breakdown stage. The principal function of the fungi in this stage is the degradation of the vegetation (Irons *et al.*, 1994, Graça & Canhoto, 2006) by the digestion of the cellulose and especially the lignin (Magee, 1993). Through its action they increase the palatability of the leaf litter and make it more acceptable for the consumption by invertebrates (Irons *et al.*, 1994). Initially, the fungi exhibit the most rapid accumulation of biomass and dense sporulation and bacteria biomass increase when fungal biomass starts to decline (Baldy *et al.*, 1995, Sridhar & Bärlocher, 2000). The decomposition rate is influenced by the structure and the initial chemistry of the leaves (Mathuriau & Chauvet, 2002). Stewart (1992) suggests that leaves rich in nutrients breakdown faster than those with lower concentrations. Furthermore, Ostrosfky (1997) pointed that the rate of decomposition is positively related to the nutrients' concentrations (C:N ratio) and negatively to the concentration of lignin and total phenols, because tannins are considered to be defensive against microbial colonization (Mathuriau & Chauvet, 2002). In the third and last phase, the physical and biotic fragmentation of decomposing leaf litter in running waters is carried out by invertebrates, such as shredders, herbivores, and detritivores, and by physical fragmentation (action of the current velocity). Many studies ha-

ve shown the importance of the shredders and scrapers in the decomposition, owing to their action and the passage through their digestive tract which modifies the particle size (Varga, 2003). According to Mathuriau & Chauvet (2002), the leaves in the tropical rivers have a triple function, depending on the invertebrates and on the decomposition degree of the leaves, they can act like substrate, offer a trap for fine particulate organic matter (FPOM) and sediments and can be a direct source of C and nutrients. Thus, a high diversity of invertebrates is able to colonize the litter, but many of them use it as a temporary substrate rather than a food resource. Not all the organic matter input is decomposed in the river, part of it will be transported downstream; and a great amount of litter is deposited in sand banks of the floodplain rivers or lakes without significant processing (Nessimian *et al.*, 1998). The rate of decomposition and the colonization by invertebrates in different trees species for several types of systems have been documented by numerous studies (e.g.: Casas & Gessner, 1999; Graça, 2001; Mathuriau & Chauvet, 2002; Maynard, 2002; Hieber & Gessner, 2002; Gonçalves *et al.*, 2006; Wantzen & Wagner, 2006; Callisto *et al.*, 2007). On the other hand, in environments from the Middle Paraná River floodplain, there is information on the colonization and rate of decomposition of macrophytes such as *Typha latifolia* (Bruquetas de Zozaya & Neiff, 1991), *Eichhornia crassipes*, *Panicum prionites*, *Paspalum repens* (Poi de Neiff & Neiff, 1988; Hammerly *et al.*, 1989; Poi de Neiff, 1991) and trees such as *Tessaria integrifolia* (Neiff & Poi de Neiff, 1990; Poi de Neiff *et al.*, 2006; Galizzi & Marchese, 2007), *Copernicia alba* (Poi de Neiff & Casco, 2001) and *Salix humboldtiana* (Capello *et al.*, 2004). One of the unanswered questions is the reason for the paucity of shredders in some tropical and subtropical regions (Irons *et al.*, 1994; Dudgeon & Wu, 1999; Dobson *et al.*, 2002; Rueda Delgado *et al.*, 2006). Therefore, it is important to know the dominant functional feeding groups and to determine the use by invertebrates of the decayed and accumulated leaves in the freshwater environments' bottom. The objectives of this study were to estimate the *Erythrina crista-galli* leaves' decomposition

rate, to determine the proportion of functional feeding groups of invertebrates throughout the decomposition process to characterize their participation in the degradation of the organic matter and to evaluate the use of leaf litter by the invertebrates. This study is the first contribution on the rate of decomposition and colonization of this very important tree species in the forest gallery of the Paraná River system. It is a native species in Argentina and Uruguay that also is distributed in the south of Brazil, Paraguay and Bolivia.

## MATERIALS AND METHODS

### Experimental design

Fresh leaves were collected at abscission from the trees (ceibo) growing in the banks of the Tiradero Viejo River (secondary channel of the Middle Paraná River). The leaves were air-dried and placed in an oven at 60 °C for 24 h to obtain dry weight before their immersion in the river. Six g dry mass samples were placed in polypropylene litterbags, which were 10 cm wide × 30 cm length with a 5 mm mesh sieve (according to Wantzen & Wagner, 2006). The litterbags were placed in the right bank of the Tiradero Viejo River (31°40'S and 60°33'W), and fixed to a 30 cm nylon rope that was anchored to the riverbed using metal stakes. Six litterbags were collected during a low water period (may 16- September 9, 2002) in separated plastic bags at 7, 14, 28, 56 and 112 days exposure and transported on ice to the laboratory for further analysis. Water velocity (with floating), pH (Hellige pH-meter), dissolved oxygen (YSI oxymeter), water temperature (standard thermometer), and conductivity (Beckman conductivity meter) were measured *in situ* and grain size of bottom sediments (Wentworth scale) was determined in the laboratory. In the laboratory, the leaves were rinsed over a 200 µm mesh sieve and all the invertebrates were hand picked from samples at 10× magnification using a dissection microscope and were preserved in 70 % alcohol for subsequent counting and identification to a species or morphospecies. The leaves were dried at 60 °C to constant mass and weighed

with a Mettler electrobalance (0.1 mg accuracy). The abundance of the invertebrates' taxa (ind  $g^{-1} dw^{-1}$  remaining leaves) was determined in each replicate and the mean and standard error were obtained. The breakdown rate coefficient ( $k$ ) was determined using the exponential decay model given by Petersen & Cummins (1974),  $W_t = W_0 e^{-kt}$ , where  $W_t$  is the final mass of leaf material,  $W_0$  is the initial mass and  $k$  is the exponential decay coefficient expressed in mass loss per day and  $t$  is the elapsed time in days.

Sampling dates were grouped by cluster analysis using abundance data of all the invertebrates' taxa matrix (unweighted pair group average linkage based on the Bray-Curtis dissimilarity). All taxa were categorized into functional feeding groups based on available information (Merritt & Cummins, 1994; Cummins *et al.*, 2005). A Kruskal-Wallis analysis was used to test for differences in density and taxa richness between the days of exposure. Pearson correlation index was calculated to analyze significant relationships among the density, taxa richness, and coarse particulate organic matter (CPOM).

## RESULTS

### Environmental variables

The depth of the right bank of the Tiradero Viejo River where the litterbags were placed varied between 1.4 m and 0.65 m in relation to the water level of the Paraná River in Santa Fe, Argentina. The average discharge was 500  $m^3/s$  with a channel width of 130 m, and the river flows through a gallery forest with dense canopy mainly in the left bank. The right bank is dominated by riparian trees typical of a first successional stage, such as *Tesaria integrifolia*, *Salix humboldtiana*, and *Erythrina crista galli* and a high density of shrubs, such as *Sesbania virgata* y *Panicum prionites*.

The water temperature ranged from 12 to 20 °C, the water transparency between 23 and 53 cm; the lower value coincided with a maximum water level of the Paraná River, and the resuspended fine sediments and higher transport of suspended solids. The conductivity varied

**Table 1.** Average values of environmental variables in the sampling sites. *Valores promedio de las variables ambientales registradas en el sitio de muestreo.*

Variables	Mean $\pm$ Standard deviation
Depth (m)	1.2 $\pm$ 0.4
Transparency (cm)	35.2 $\pm$ 13.7
Temperature (°C)	17 $\pm$ 2.9
Conductivity ( $\mu S/cm$ )	85 $\pm$ 14.1
O <sub>2</sub> (mg/l)	6.3 $\pm$ 2.6

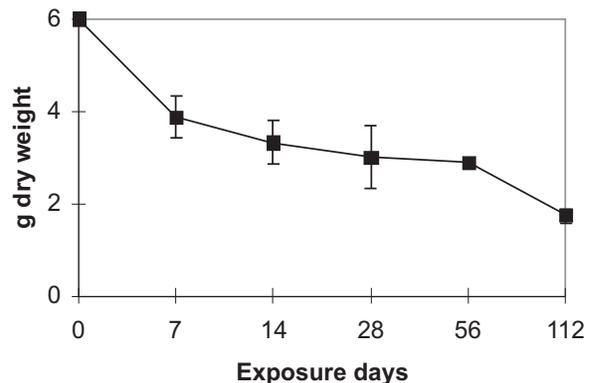
between 70  $\mu S/cm$  and 100  $\mu S/cm$ , the water dissolved oxygen between 3.7 mg/l and 10.9 mg/l (Table 1), the average value of the current velocity in the site sampled was 0.61 m/s ( $\pm 0.2$ ). The bottom sediment granulometry was composed by 38 % of sand, 44 % of mud and 27 % of clay.

### Leaf mass loss

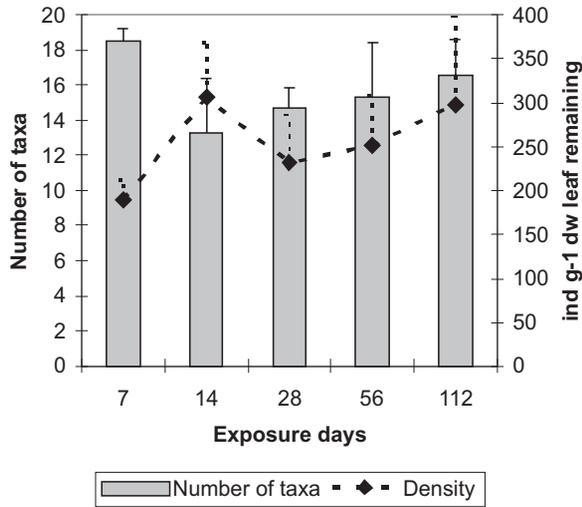
Mass loss of *E. crista-galli* leaves was high during the first 7 days of the experience (36 % of the initial mass was lost), it stabilized between days 14 and 56, and 72 % of the initial mass was lost after 112 days (Fig. 1). The  $k$  (breakdown rate) calculated over 112 days decomposition was  $-0.0129 d$ ; and the estimated time for a 50 % decomposition was 53 days.

### Invertebrates colonization

Colonization of leaves of *E. crista galli* by invertebrates was fast, and reached an average density of 189 invertebrates/dry weight remaining leaves

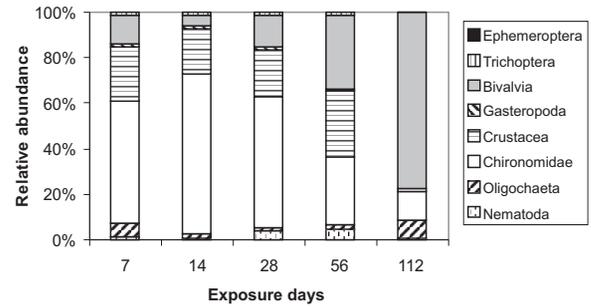


**Figure 1.** Dry weight remaining during decomposition of *Erythrina crista galli* leaves. The bars are standard error. *Peso seco remanente de las hojas de Erythrina crista galli en el periodo de descomposición. Las barras indican error estándar.*



**Figure 2.** Density of invertebrates and taxa number during decomposition of *Erythrina crista galli* leaves. The bars are standard error. *Densidad de invertebrados y número de taxa en hojas de Erythrina crista galli en descomposición. Las barras indican el error estándar.*

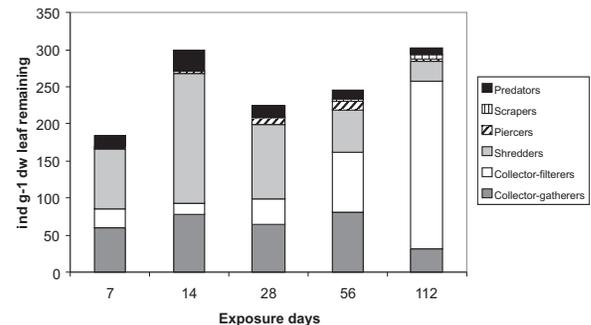
at 7 days of immersion. The density did not differ significantly between dates (Kruskal-Wallis) and the highest mean values of 306 ind g<sup>-1</sup> dw and 298 ind g<sup>-1</sup> dw<sup>-1</sup> were reached at days 14 and 112, respectively (Fig. 2). The litter bags were colonized by 18 taxa after 7 days, but decreased afterwards without significant differences between time periods (Kruskal-Wallis) (Fig. 2). The total number of taxa collected from litter bags throughout the experience was 41 (Table 2), but only 11 taxa were recorded in all the samplings: (Nematoda, *Chironomus gr decorus*, *Ablabesmyia* (*Karelia*) sp., *Polypedilum* spp., *Phaenopsectra* sp., *Caenis* sp., Trichoptera, Cyclopida, Harpacticoida, Ostracoda and *Limnoperna fortunei*. Oligochaeta Tubificinae was only recorded at the end of the experiment while the Chironomidae (54 %) and Crustacea (24 %) were dominant at the initial phase of decomposition (Fig. 3). The abundance of Crustacea (19 %) declined at 14 days and Chironomidae had a considerable increase (71 %) but decreased afterwards and reached a low percentage (3 %) at 112 days where Bivalvia had a high abundance (76 %). Trichoptera, Ephemeroptera, Gasteropoda, Nematoda, and Oligochaeta Naididae were collected throughout the study in low percentages (Fig. 3). *Polypedilum* spp. was the dominant chironomid and



**Figure 3.** Relative abundance (%) of invertebrates colonizing *Erythrina crista galli* leaves during decomposition. *Abundancia relativa (%) de taxa invertebrados que colonizaron las hojas de Erythrina crista galli en descomposición*

*Phaenopsectra* sp., *Endotribelos* sp., *Ablabesmyia* spp. and *C. gr decorus* were subdominant. The mollusk *Heleobia parchappei* was collected in lower abundance and *L. fortunei*, an invasive mussel which colonized the litterbags from the beginning of the experiment, ranged from 12 % to 76 % at 112 days (Fig. 3). The more representative oligochaetes were *Pristina americana*, *Slavina evelinae* y *S. isochoeta* (Table 2). With the Bray-Curtis classification, the samples were divided according to the temporal gradient indicating a high similarity between the initial colonization phase and a very low one with the results obtained at the end of the experiment, suggesting a period of degradative ecological succession.

The functional feeding group's proportion was shifted in relation to the leaves' decomposition (Fig. 4). Throughout the decomposition of *E. crista galli*, collector-gatherers, collector-filterers and shredders were the dominant groups, with a progressive replacement during the 112 days of



**Figure 4.** Number of individuals by feeding functional groups during the experience. *Densidad de individuos por grupos funcionales encontrados durante la experiencia.*

**Table 2.** List of taxa recorded during the experience and the feeding functional groups adjudicated to each taxa. P: predator, M: pierces, C-G: collector-gatherers, C-F: collector-filterers, S: shredders, Sc: scrapers. *Lista de taxa registrados durante la experiencia y los grupos funcionales adjudicados a cada taxa.* (x): presencia. P: depredador, M: minador, C-G: colector-recolector, C-F: colector-filtrador, S: triturador, Sc: raspador

List of Taxa	Functional feeding groups	Exposure days				
		7	14	28	56	112
Turbellaria	P					x
Nematoda	M	x	x	x	x	x
Oligochaeta						
Naididae						
<i>Dero</i> sp.	C-G	x			x	
<i>Dero furcatus</i>	C-G	x	x	x		x
<i>Dero botrytis</i>	C-G		x		x	
<i>Dero multibranchiata</i>	C-G	x	x	x		x
<i>Dero nivea</i>	C-G	x	x			
<i>Dero obtusa</i>	C-G	x			x	
<i>Dero pectinata</i>	C-G		x			
<i>Dero sawyai</i>	C-G				x	x
<i>Slavina evelinae</i>	C-G					x
<i>Slavina isochaeta</i>	C-G				x	x
<i>Pristina aequiseta</i>	C-G	x				
<i>Pristina leidyi</i>	C-G		x	x	x	
<i>Pristina americana</i>	C-G					x
<i>Nais variabilis</i>	C-G					x
Tubificinae						
<i>Aulodrilus pigueti</i>	C-G					x
<i>Limnodrilus</i> immature	C-G					x
<i>Limnodrilus hoffmeisteri</i>	C-G					x
<i>Limnodrilus udekemianus</i>	C-G					x
Rhyacodrilinae						
<i>Bothrioneurum americana</i>	C-G					x
Opistocystidae						
<i>Opistocysta funiculus</i>	C-G				x	
Diptera Chironomidae						
<i>Chironomus</i> gr. <i>decorus</i>	C-G	x	x	x	x	x
<i>Cryptochironomus</i> sp.	P		x			
<i>Tanytarsus</i> genus F	C-F			x		
<i>Ablabesmyia karelia</i>	P	x	x	x	x	x
<i>Polypedilum</i> spp.	S	x	x	x	x	x
<i>Phaenopsectra</i> sp.	S	x	x	x	x	x
<i>Endotribelos</i> sp.	S	x	x	x	x	
Ephemeroptera						
<i>Caenis</i> sp.	C-G	x	x	x	x	x
Trichoptera	C-G	x	x	x	x	x
Decapoda Trychodactilidae						
<i>Zilchiopsis</i> sp.	S		x	x	x	
Cladocera	C-F	x				
Calanoidea	C-G	x				
Cyclopida	C-G	x	x	x	x	x
Harpacticoida	C-G	x	x	x	x	x
Ostracoda	C-G	x	x	x	x	x
Mollusca						
<i>Limnoperna fortunei</i>	C-F	x	x	x	x	x
<i>Heleobia parchappei</i>	Sc		x	x	x	x
<i>Heleobia guaranitica</i>	Sc	x				x
Planorbidae	Sc	x			x	x

the experiment. The miners, scrapers and predators were always present in low densities. Neither the number of taxa nor the invertebrate density was explained by the remaining organic matter of the leaves (Pearson correlation).

## DISCUSSION

The rates of decomposition of leaves of different tree species can be affected by diverse factors, such as temperature, pH, concentration of nutrients, the addition of sediments (Webster & Benfield, 1986; Stewart, 1992), type of habitat (stream, lake, rivers, etc.) and the experimental protocol (size of the leaf packs and the mesh net of the bags) (Ostrofsky, 1997). These reasons may explain the great variability of rates obtained in the same vegetal species and between different species. The leaf breakdown rate of *E. crista galli* was fast according to the classification of three processing categories: slow ( $< 0.005 \text{ day}^{-1}$ ), medium ( $0.005\text{-}0.010 \text{ day}^{-1}$ ) and fast ( $> 0.010 \text{ day}^{-1}$ , Petersen & Cummins, 1974). These results coincide with the rates obtained by Neiff & Poi de Neiff (1990); Poi de Neiff (1991); Poi de Neiff & Casco (2001); Capello *et al.* (2004); Poi de Neiff *et al.* (2006) and Galizzi & Marchese (2007) for typical trees species in the Paraná River wetlands (*T. integrifolia*, *S. humboldtiana*, *C. alba*) as well as in studies carried out in tropical environments (Dudgeon & Wu, 1999; Mathuriau & Chauvet, 2002; Ardón *et al.* 2006; Rueda-Delgado, *et al.*, 2006). The estimated time for the 50 % decomposition of *E. crista galli* leaves was 53 days and similar results were obtained for tree species associated to the ceibo in the floodplain of the Middle Paraná River, such as *T. integrifolia* (48 days, Galizzi & Marchese, 2007) and *S. humboldtiana* (56 days, Capello *et al.*, 2004).

Four taxa considered shredders in this study (*Polypedilum* spp. *Phaenopsectra* sp. *Endotribelos* spp., and *Zilchiopsis* sp.) were dominant in the initial phase of the experiment (59 %) which were replacements for collector-filterers at advanced stages of the degradative succession (76 %). The amount of shredders collected was high compared

to the data obtained for *S. humboldtiana* (0.82 %) by Capello *et al.*, (2004), where miners and piercers were very abundant. The Chironomidae *Polypedilum* spp., *Phaenopsectra* sp., and *Endotribelos* spp., were categorized as shredders because they were observed burrowing the leaf tissue from the inside, between the abaxial and adaxial epidermis, and may therefore also be considered facultative shredders that are able to use well conditioned leaves as food resources as was also reported by Callisto *et al.* (2007).

Many studies have suggested a low abundance of shredders in tropical running waters and that the leaf litter breakdown appeared to be related to higher microbial communities (Maltby, 1992; Irons *et al.*, 1994; Wantzen *et al.*, 2002; Gonçalves *et al.*, 2004; Wantzen & Wagner, 2006), whereas others have suggested that shredder activity is important to leaf processing in some tropical streams (Crowl *et al.*, 2002; Rincón & Martínez, 2006). However, there are differences in the literature about the functional feeding groups classification of different taxa and more studies are necessary on invertebrates' diets to determine their food preferences and what they consume.

According to Richardson (1992), many organisms can live on the organic matter or use it as food, thus the organic substrate offers two types of resources. The leafpacks in the rivers provide food resources for many species of aquatic invertebrates, either directly or by fine particle accumulation; and the invertebrates' densities are related to their nutritive quality. Nevertheless, many do not consume this material, but they are associated because leaf material can also provide habitat and refuge to avoid predators.

The high density of *L. fortunei* obtained at the end of the experiment is similar to the values reported by Capello, *et al.* (2004) and by Galizzi & Marchese (2007) for *S. humboldtiana* and *T. integrifolia*, respectively. *L. fortunei* (Dunker, 1857), or golden mussel, is an Asiatic species that was first recorded in America in 1991 in the Río de la Plata coast. Introduction into South America is probably due to the thousands of tons of ballast water discharged from ships coming from Asia with high bivalve larvae concentrations (Brugnoli & Clemente, 2006). This species has a fast dis-

persion rate due to its biological characteristics, such as rapid growth, early maturation, high fecundity rate, short life span, and great adaptive strategies that allow this mussel to occupy a wide geographic distribution with dense populations, causing several water quality and macrofouling problems (García & Montalto, 2006; Ezcurra de Drago *et al.*, 2006). *L. fortunei* has a life cycle with a planktonic (veliger) larva instar and an epifaunal stage young-adult with a bivalve attachment to solid substrata. Many studies have demonstrated that the geomorphological characteristics of the Middle Parana River allow *L. fortunei* a constant repopulation of larvae from the floodplain channels. In this experience, *L. fortunei* colonized the litter bags with the bivalve attachments to the leaves of *E. crista-galli*, protecting themselves from their possible predators, mainly fish, using the litter bags as substrate and not as a food resource. Other invertebrates (included in the functional groups as shredders and scrapers) used the leaves of *E. crista-galli* as a food resource in relation to the degree of decomposition and the type of feeding. The oligochaetes tubificids were found only at the end of the experience because with the dense colonization of *L. fortunei* a microhabitat was generated with the increase in detritus retention. These organisms used also the leaves in decomposition mainly as substrate. On the other hand, the predator invertebrates colonized the leaves in decomposition because of the food supply offered by the first invertebrate colonizers.

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#### REFERENCES

- ARDÓN, M., L. A. STALLCUP & C. PRINGLE. 2006. Does leaf quality mediate the simulation of leaf breakdown by phosporous in Neotropical stream. *Freshwat. Biol.*, 51: 618-633.
- BRUGNOLI, E. & J. M. CLEMENTE. 2006. Los moluscos exóticos en la Cuenca del Plata: Su potencial impacto ambiental y económico. Sección Limnología, Facultad de Ciencias, Universidad de la República Oriental del Uruguay. *Ambios*, 3: 27-30.
- BRUQUETAS DE ZOZAYA, I. & J. J. NEIFF. 1991. Decomposition and colonization by invertebrates of *Typha latifolia* L. litter in Chaco cattail swamp (Argentina). *Aquat. Bot.*, 40: 185-193.
- CALLISTO, M., J. F. CONÇALVES Jr & M. A. S. GRAÇA. 2007. Leaf litter as a possible food source for chironomids (Diptera) in Brazilian and Portuguese headwater streams. *Rev. Bras. Zool.*, 24: 442-448.
- CAPELLO, S., M. MARCHESE & I. EZCURRA de DRAGO. 2004. Descomposición y colonización por invertebrados de hojas de *Salix humboldtiana* en la llanura aluvial del río Paraná Medio. *Amazoniana*, 18: 125-143.
- CASAS, J. J. & M. O. GESSNER. 1999. Leaf litter breakdown in a Mediterranean stream characterized by travertine precipitation. *Freshwat. Biol.*, 41: 781-793.
- CUMMINS K. W., R. W. MERRITT & P. C. N. ANDRADE. 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected stream and rivers in south Brazil. *Stud. Neotrop. Fauna and Environ.*, 40: 69-89.
- DOBSON, M., A. MAGANA, J. M. MATHOOKO & F. K. NDEGWA. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshwat. Biol.*, 47: 909-919.
- DUDGEON, D. & K. K. WU. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? *Arch. Hydrobiol.*, 146: 65-82.
- EZCURRA de DRAGO, I., L. MONTALTO & O. B. OLIVEROS. 2006. Desarrollo y ecología larval de *Limnoperna fortunei*. En: *Bio-invasión del mejillón dorado en el continente americano*. G. Darrigran y C. Damborena (eds.): 83-91. Edulp, La Plata, Argentina.
- GAMAGE, N. P. D. & T. ASAEDA. 2005. Decomposition and mineralization of *Eichhornia crass-*

- pes litter under aerobic conditions with and without bacteria. *Hydrobiologia*, 541: 13-27.
- GALIZZI, M. C. & M. MARCHESE. 2007. Colonización de hojas en descomposición de *Tessaria integrifolia* (Asteraceae) por invertebrados en un cauce secundario del río Paraná medio. *Inter ciencia*, 32: 535-540.
- GARCÍA, M. & L. MONTALTO. 2006. Los peces depredadores de *Limnoperna fortunei* en los ambientes colonizados. En: *Bio-invasión del mejillón dorado en el continente americano* G. Darrigran y C. Damborena (eds.): 111-127. Edulp, La Plata, Argentina.
- GONÇALVES Jr, J. F., J. S. FRANÇA, A. O. MEDEIROS, C. A. ROSA & M. CALLISTO. 2006. Leaf breakdown in a tropical stream. *Internat. Rev. Hydrobiol.*, 91: 164-177.
- GRAÇA, M. A. S. 2001. The role of invertebrates on leaf litter decomposition in streams—a review. *Internat. Rev. Hydrobiol.*, 86: 383-393.
- GRAÇA, M. A. S. & C. CANHOTO. 2006. Leaf litter processing in low order stream. *Limnetica*, 25: 1-10.
- HAMMERLY, J., M. LEGUIZAMÓN, M. A. MAINE, D. SCHIVER & M. J. PIZARRO. 1989. Decomposition rate of plant material in the Paraná Medio River. *Hydrobiologia*, 183: 179-184.
- HIEBER, M. & GESSNER, M. O. 2002. Contribution of stream detritivores, fungi and bacteria to leaf breakdown based on biomass estimates. *Ecology*, 83: 1026-1038.
- HOFFMANN, A. 2005. Dynamics of fine particulate organic matter (FPOM) and macroinvertebrates in natural and artificial leaf packs. *Hydrobiologia*, 549: 167-178.
- IRONS, J. G., M. W. OSWOOD, R. J. STOUT & C. M. PRINGLE. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important?. *Freshwat. Biol.*, 32: 401-411.
- MAGEE, P. A. 1993. Detrital accumulation and processing in wetlands. *Fish and Wildlife Leaflet*, 13: 3-14.
- MATHURIAU, C. & E. CHAUVET. 2002. Breakdown of leaf litter in a neotropical stream. *J. N. Am. Benthol. Soc.*, 21: 384-396.
- MAYNARD, K. 2002. Leaf quality and the strength of top-down control in a detritus-based food web. In: *Organization for Tropical Studies*. E. Notman (ed.): 82-93. Yale University, New Haven, CT.
- MERRITT, R. W. & K. W. CUMMINS. 1994. *An introduction to the Aquatics Insects of North America*. Kendal-Hunt Publishing Company Iowa. 862 pp.
- NEIFF, J. J. & A. POI DE NEIFF. 1990. Litterfall, leaf decomposition and litter colonization of *Tessaria integrifolia* (Compositae) in the Paraná River floodplain. *Hydrobiologia*, 203: 45-52.
- NESSIMIAN, J. L., L. F. M. DORVILLE, A. M. SANSEVERINO & D. F. BAPTISTA. 1998. Relation between flood pulse and functional composition of the macroinvertebrate benthic fauna in the Lower Rio Negro, Amazonas, Brazil. *Amazoniana*, 15: 35-50.
- OSTROFSKY, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *J. N. Am. Benthol. Soc.*, 16: 750-759.
- PETERSEN, R. C. & K. W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwat. Biol.*, 4: 343-368.
- POI DE NEIFF, A. 1991. Descomposición y colonización del detrito de distintas especies de plantas en ambientes inundables del río Paraná. *Biología Acuática*, 15: 158-159.
- POI DE NEIFF, A. & S. L. CASCO. 2001. Caída de hojas, descomposición y colonización por invertebrados en palmares de la planicie de inundación del río Paraná (Chaco, Argentina). *Inter ciencia*, 26: 567-571.
- POI DE NEIFF, A. & J. J. NEIFF. 1988. Decomposition of *Eichhornia crassipes* in a pond of Paraná River valley and colonization by invertebrates. *Tropical Ecology*, 29: 79-85.
- POI DE NEIFF, A., J. J. NEIFF & S. L. CASCO. 2006. Leaf litter decomposition in three wetland types of the Paraná River floodplain. *Wetlands*, 26: 558-566.
- POZO, J., E. GONZALEZ, J. R. DIEZ, J. MOLINERO & A. ELOSEGUI. 1997. Inputs of particulate organic matter to streams with different riparian vegetation. *J. N. Am. Benthol. Soc.*, 16: 602-611.
- RICHARDSON, J. S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwat. Biol.*, 27: 169-176.
- RUEDA-DELGADO, G., K. M. WANTZEN & M. BELTRÁN TOLOSA. 2006. Leaf-litter decomposition in an Amazonian floodplain stream: effects of seasonal hydrological changes. *J. N. Am. Benthol. Soc.*, 25: 233-249.
- SABATER, F., A. BUTTURIN, E. MARTI, I. MUÑOZ, A. ROMANI, J. WRAY & S. SABATER.

2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *J. N. Am. Benthol. Soc.*, 19: 609-620.
- SPONSELLER, R. A. & E. F. BENFIELD. 2001. Influences of land use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis. *J. N. Am. Benthol. Soc.*, 20: 44-59.
- SRIDHAR, K. & F. BÄRLOCHER. 2000. Initial colonization, nutrient supply and fungal activity on leaves decaying in streams. *Appl. Environ. Microbiol.*, 66: 1114-1119.
- STEWART, B. A. 1992. The effect of invertebrates on leaf decomposition rates in two small woodland streams in southern Africa. *Arch. Hydrobiol.*, 124: 19-33.
- VARGA, I. 2003. Structure and changes of macroinvertebrate community colonizing decomposing rhizome litter of common reed at Lake Fertő/Neusiedler See (Hungary). *Hydrobiologia*, 403: 1-8.
- WALLACE, J. B., J. L. MEYER & J. R. WEBSTER. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs*, 69: 409-442.
- WANTZEN, K. M. & R. WAGNER. 2006. Detritus processing by invertebrate shredders: a neotropical-temperate comparison. *J. N. Am. Benthol. Soc.*, 25: 216-232.
- WEBSTER, J. R. & E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. *Ann. Rev. Ecol. and Syst.*, 17: 567-594.