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Leaf degradation of *Salix humboldtiana* Willd. (Salicaceae) and invertebrate colonization in a subtropical lake (Brazil)

Degradação foliar de *Salix humboldtiana* Willd. (Salicaceae) e colonização por invertebrados em um lago subtropical (Brasil)

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Abstract: Aim: To evaluate leaf degradation and invertebrate colonization of *Salix humboldtiana* Willd. in a subtropical shallow lake on the coastal plain of Rio Grande do Sul, Brazil; **Methods:** Litter bags containing 6.85 g of leaves were incubated in the superficial layer of sediment in the littoral region for 1, 4, 7, 14, 32, 47 and 71 days; **Results:** After 71 days, a loss of 51% of the initial leaf weight was observed ($k = 0.0100\ d^{-1}$). We estimated that it would take 300 days to lose 95% of the initial weight. A total of 16040 organisms and 35 taxa were identified. Caenidae (25.9%), Oligochaeta (19%), Ostracoda (13.8%), Hydracarina (9.8%), Tanypodinae (9.7%) and Coenagrionidae (7.7%) were the most highly represented taxa. We observed increases in density, richness and diversity of taxa over time, with a stabilizing trend noted in the taxa diversity. Regarding the functional trophic groups (FTGs), gathering-collectors accounted for 57.6% of the community, while predators (25%), scrapers (15.8%), filtering-collectors (0.88%) and shredders (0.73%) were also represented. The diversity and evenness of the FTGs had stabilized by day 14; **Conclusions:** *S. humboldtiana* detritus provides a favorable habitat for a sufficient duration to support a high density and diversity of aquatic invertebrates. The small percentage of shredders indicates the minor influence of the invertebrate community on the rate of detrital degradation. The main contribution of invertebrates to detrital processing comes from the consumption of fine particulate organic matter by gathering-collectors.

Keywords: leaf decay coefficients, decomposition, functional trophic groups, sandy coastal plain.

Resumo: Objetivos: Avaliar a degradação foliar de *Salix humboldtiana* Willd. e a colonização pela comunidade de invertebrados aquáticos em um lago raso subtropical, planície costeira do Rio Grande do Sul, Brasil; **Métodos:** Bolsas de decomposição contendo 6,85 g de folhas foram incubadas na região litorânea, na superfície do sedimento, e retiradas após 1, 4, 7, 14, 32, 47 e 71 dias de decomposição; **Resultados:** Aos 71 dias foi registrada a degradação de 51% do peso inicial ($k = 0{,}0100\ d^{-1}$). O tempo estimado para a degradação de 95% do peso inicial dos detritos foi 300 dias. Foram identificados 16.040 organismos, distribuídos em 35 táxons. Caenidae (25,9%), Oligochaeta (19%), Ostracoda (13,8%), Hydracarina (9,8%), Tanypodinae (9,7%) e Coenagrionidae (7,7%) foram os táxons mais representativos. Foi observado incremento na riqueza, densidade e diversidade dos táxons ao longo do tempo, com tendência à estabilização dos valores de diversidade. Em relação aos grupos tróficos funcionais (GTFs), coletores-catadores representaram 57,6% da comunidade, enquanto predadores (25%), raspadores (15,8%), coletores-filtradores (0,88%) e fragmentadores (0,73%) também foram representados. A diversidade e homogeneidade dos GTFs apresentaram estabilização a partir do 14º dia; **Conclusões:** Os detritos de *S. humboldtiana* fornecem um habitat favorável por tempo suficiente para suportar alta densidade e diversidade de invertebrados aquáticos. A baixa abundância de fragmentadores indica pouca influência da comunidade de invertebrados na velocidade de degradação dos detritos. A principal contribuição desta comunidade no processamento dos detritos ocorre por meio do consumo de matéria orgânica particulada fina por coletores-catadores.

Palavras-chave: coeficientes de degradação foliar, decomposição, grupos tróficos funcionais, planície costeira arenosa.

1. Introduction

The organic detritus of aquatic systems derives from the autochthonous production and input of allochthonous organic matter (Webster and Benfield, 1986). The latter is less important as an energy resource for most lentic systems; however, it can significantly influence the food chains in lakes associated with developed riparian forests (Pieczynska, 1986).

The decomposition of detritus in aquatic environments involves a series of events, e.g., leaching of soluble compounds, colonization and conditioning of detritus by microbial action, fragmentation by physical abrasion and colonization and processing by aquatic invertebrates (Webster and Benfield, 1986; Bianchini Jr, 1999; Pope et al., 1999; Abelho, 2001). This complex process involves both abiotic and biotic factors and is frequently used to assess the functional and structural integrity of ecosystems (Pascoal et al., 2003; Lecerf et al., 2006).

An ecological succession process takes place on the detritus, involving microorganisms, invertebrates and vertebrates (Begon et al., 1996; Gonçalves et al., 2003), until the detritus are completely decomposed. According to Janke and Trivinho-Strixino (2007), the association between aquatic invertebrates and detrital decomposition is not completely clear, but detritus is known to provide food and shelter to these organisms (Dudgeon and Wu, 1999; Graça, 2001). This community can present a great diversity of species, which may result in the redundancy of individual functions (Lawton, 1991; Wallace and Webster, 1996). Species diversity and functional redundancy are crucial to the integrity and stability of ecosystems (Odum and Barrett, 2007). Therefore, freshwater ecology studies of detritivorous invertebrates have traditionally focused on the roles of these organisms in the processing of organic matter. Different taxa have been classified into functional trophic groups (FTGs) as shredders, gathering-collectors, filtering-collectors, predators or scrapers (Begon et al., 1996; Callisto et al., 2001; Cummins et al., 2005; Merritt et al., 2008).

In shallow lakes, the detrital food chain can consume half of the net primary production (Odum and Barrett, 2007). Most studies on decomposition in lentic systems refer to macrophytes (e.g., Cunha and Bianchini Jr, 1998, 1999; Asaeda et al., 2000; Gonçalves et al., 2000, 2003, 2004; Kim and Rejmánková, 2004; Kufel et al., 2004; Shilla et al., 2006). There is little information about the decomposition of allochthonous detritus originating from trees or its colonization by invertebrates in lakes (Webster and Benfield, 1986; Pope et al., 1999; Sampaio et al., 2008).

The pioneer tree species, *Salix humboldtiana* Willd., grows on the banks of streams, lakes, ponds or in environments with abundant groundwater in South and Central America (Backes and Irgang, 2002; Carvalho, 2003). This species is common and abundant in the study area (Trindade et al., 2009, 2010), and Aceñolaza et al. (2010) showed that *S. humboldtiana* produces a large quantity of leaf litter in the flood plain forest of the Paraná River (Argentina). Studies on the leaf decomposition of *S. humboldtiana* are scarce, with the exception of Leguizamon et al. (1992), Capello et al. (2004) and Poi de Neiff et al. (2006), which were all performed in the hydrological system of the Paraná River, Argentina.

Considering the abundance of *S. humboldtiana* in the riparian forests of the study region, its significant contribution to the detritus of aquatic environments and the participation of detritivorous invertebrates in the processing of organic matter, this study aimed to analyze the community of aquatic invertebrates colonizing *S. humboldtiana* leaf detritus in a subtropical lake and to estimate the leaf degradation coefficients (*k*) in this environment. We hypothesized that (i) allochthonous detritus from *S. humboldtiana* provides shelter for aquatic invertebrates and that (ii) the invertebrate community influences the rate of detrital degradation.

2. Material and Methods

2.1. Study area

The aquatic ecosystems of the sandy coastal plain of Rio Grande do Sul (Southern Brazil) mainly comprise wetlands and shallow lakes (Vieira and Rangel, 1988). The climate of this region is characterized as Cfa (humid subtropical) by the Köppen classification. The average annual temperature varies between 13 °C (winter) and 24 °C (summer), and total annual rainfall is between 1200 and 1500 mm (Klein, 1998).

The study was conducted at Polegar Lake (32° 01’ 40” S and 52° 05’ 40” W), located at the Campus Carreiros of the Federal University of Rio Grande, municipality of Rio Grande, Rio Grande do Sul State, Brazil. The lake area is approximately 1 ha, with an average depth of 1.5 m that varies by rainfall. It is characterized as an oligotrophic lake, with low primary production and nutrient concentrations (Albertoni et al., 2007; Furlanetto et al., 2008; Trindade et al., 2008; Marinho et al., 2009). The sediment is sandy and contains low concentrations of nutrients and organic matter (Leonardo Marques Furlanetto, personal communication). During the study period, the mean water temperature was 23.95 °C (± 1.64); the pH was 7.4 (± 0.96); and the concentrations of dissolved oxygen, chlorophyll-*a*, total nitrogen and total phosphorus were 6.73 $mg.L^{-1}$ (± 1.28), 8.34 $\mu g.L^{-1}$ (± 8.86), 0.5719 $mg.L^{-1}$ (± 1.339) and 0.0153 $mg.L^{-1}$ (± 0.008), respectively.

2.2. Methodology

Between March and May 2009, 21 litter bags containing 6.85 g of *S. humboldtiana* leaves, collected directly from adult trees and air-dried, were incubated in the littoral region of Polegar Lake. The bags were 20 × 30 cm in size, with a mesh size of 0.1 cm on the side facing the sediment and 1.0 cm on the side facing the water column (adapted from Bedford, 2004). Three litter bags were collected after 1, 4, 7, 14, 32, 47 and 71 days of incubation. In the laboratory, the remaining leaves were washed over a sieve (mesh size 250 µm), and the invertebrates were sorted, fixed in 80% alcohol and identified using a stereomicroscope (30x magnification) following specific taxonomic keys (Thorp and Covich, 1991; Elmoor-Loureiro, 1997; Buckup and Bond-Buckup, 1999; Merritt et al., 2008; Mugnai et al., 2010). The remaining leaves were dried at 60 °C for 48 hours to determine the dry weight. Linear regression was performed following Bärlocher (2005) to calibrate the air-dried weight against the oven-dried weight.

The density of invertebrates was expressed as the number of individuals per 100 g of detritus dry weight ($ind.100\ g.DW^{-1}$). The abundance (%) of each taxa was calculated. The succession of the most representative taxa (abundance > 7.68) was analyzed. Aquatic invertebrate composition and structure were evaluated according to Magurran (2004), using richness (taxa number), diversity (Shannon-Wiener Index) and evenness (Pielou Index).

To determine the pattern of succession of organisms in relation to their use of detrital resources, invertebrates were classified according to their FTGs as shredders, gathering-collectors, filtering-collectors, predators or scrapers (Callisto et al., 2001; Cummins et al., 2005; Merritt et al., 2008). Diversity (Shannon-Wiener Index) and evenness (Pielou Index) were calculated in relation to the FTGs. This analysis omitted chironomid pupae. Invertebrates were deposited in the Subtropical Limnic Invertebrate Collection (Limnology Laboratory, Biological Science Institute, Federal University of Rio Grande, Brazil).

Using the model proposed by Petersen and Cummins (1974), for each sampling, the percentage of remaining leaves and the leaf decay coefficient (*k*) were calculated using the equations $\%\ R = (W_t/W_0)*100$ and $k = -(1/t)*\ln(W_t/W_0)$, respectively, where W_t is the dry weight at time t and W_0 is the initial dry weight. We estimated the number of days needed for the degradation of 95% of the original leaf material with the equation $t = -\ln(\%R/100)/k$, using the *k* value estimated for the last sampling period.

All data on leaf degradation and aquatic invertebrates were log(x+1)-transformed. The averages were tested using analysis of variance (ANOVA – *one way*) followed by the Tukey test, using $p < 0.05$ and 6 degrees of freedom for all tests. A presence-absence matrix was constructed to compare the similarity (Jaccard) of samples and to order all samples during the decomposition process.

3. Results

After 24 hours of incubation, leaf mass loss was 30% ($k = 0.3520\ d^{-1} \pm 0.0443$) (Figure 1). The decay velocity then diminished until day 32. Subsequent variation in this coefficient exhibited a stabilizing trend. After 71 days of incubation, we measured a 51% loss of the initial dry weight ($k = 0.0100\ d^{-1} \pm 0.0002$). The length of the period that would result in a loss of 95% of the initial dry weight was estimated at 300 days. The analysis of variance showed significant differences between decay coefficients over time (F = 210.1) (Figure 1). The percentage of remaining leaf detritus also showed significant differences over time (F = 82.50).

A total of 16040 organisms and 35 taxa were identified (Table 1). Caenidae (25.9%), Oligochaeta (19%), Ostracoda (13.8%), Hydracarina (9.8%), Tanypodinae (9.7%) and Coenagrionidae (7.7%) were the most highly represented taxa. These groups represented 85% of the community. The richness index increased from 15 (24 hours) to 34 at day 71 and exhibited significant differences over time (F = 10.84) (Table 1). The density also significantly increased during the decomposition period (F = 33.36), from 2315.03 $ind.100\ g.DW^{-1}$ (± 861.38) on the first day to 58881.58 $ind.100\ g.DW^{-1}$ (± 2761.01) on

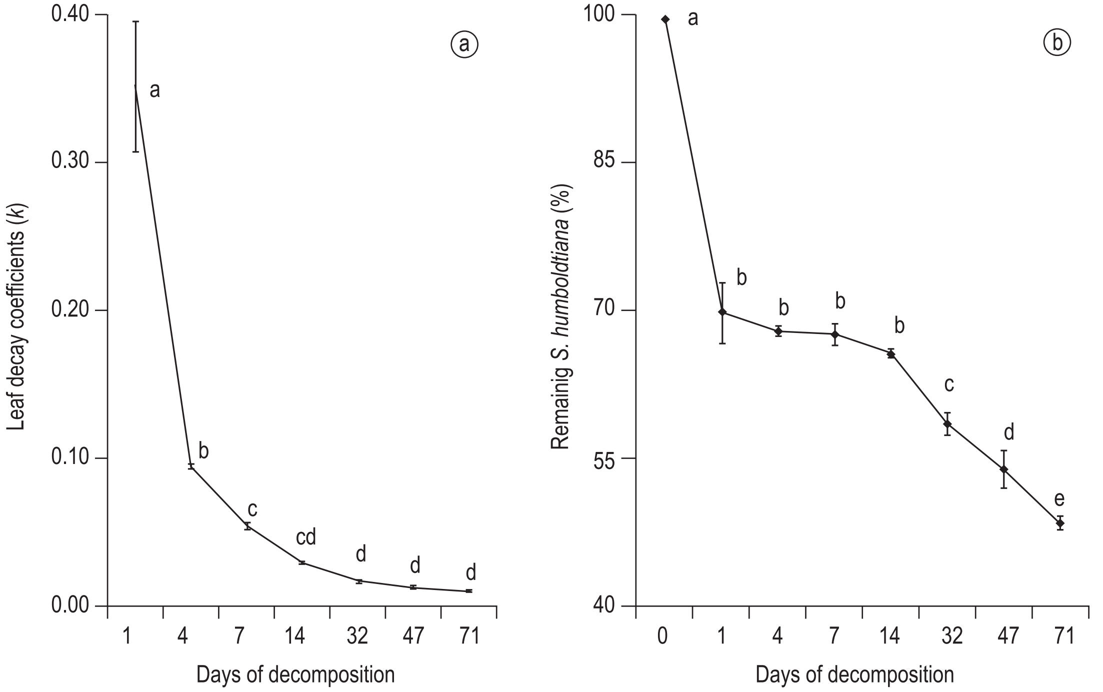

Figure 1. a) Leaf decay coefficients (*k*); and b) leaf remaining (%R) at each sampling day, obtained for *Salix humboldtiana* in an oligotrophic shallow lake on sand coastal plain of Rio Grande do Sul, Brazil. Different letters represent statistical significant differences (a-e) ($p < 0.05$). The bars represent standard deviation.

day 71 (Table 1). This measure showed a linear tendency ($R^2 = 0.91$).

The Shannon diversity index also exhibited an increase over time (Table 1). It presented significant differences (F = 6.58) throughout the experiment, ranging from 1.173 (± 0.404) on the first day to 2.051 (± 0.070) on day 71. Evenness ranged between 0.515 (± 0.113) on the first day and 0.701 (± 0.024) on day 14, with significant differences (F = 3.394). These indexes exhibited stabilizing trends by the end of the experiment.

Community similarity analysis revealed two distinct groups, one corresponding to the initial decomposition phase (from day 1 to day 14) and the second representing the final phase (from day 32 to day 71) (Figure 2). These phases corresponded to the significant differences found in the percentage of remaining leaves and decay coefficients (Figure 1).

The abundance variations of the most highly represented taxa were individually analyzed (Figure 3). Caenidae, Oligochaeta, Hydracarina and Tanypodinae exhibited low abundances during the first day of decomposition. Caenidae increased gradually and represented 39% of the community by day 32. Oligochaeta accounted for only 4% of the community on the first day but increased to 25% by day 4. Hydracarina and Tanypodinae each represented 14% of the total by the last day of the experiment. An analysis of the densities of these groups revealed significant differences (Table 2).

In contrast to those taxa cited above, Ostracoda and Coenagronidae showed inverse patterns of abundance. Ostracoda represented 61% of the total number of organisms on the first day but decreased to 5% on day 71. Coenagrionidae represented 10% of the total on the first day, increased to 19% on days 7-14, and then decreased to less than 2% at the end of the experiment. Coenagrionidae showed significant differences in density over time (Table 2).

The analysis of FTGs revealed that 57.6% of the invertebrates were gathering-collectors, 25% were predators, 15.8% were scrapers, 0.88% were filtering-collectors and 0.73% were shredders. During the first 24 hours of decomposition, gathering-collectors represented 83% of the total invertebrate abundance (Figure 4). The abundance of this group subsequently decreased but always exceeded 50% of the total.

The other FTGs generally presented low abundances in the early days of the experiment. Scrapers showed an increase in abundance over time. On day 32, they represented 22.4% of the community. Predators showed expressive abundance throughout the experiment. This group increased in abundance up to day 14 (33.2%) and then displayed a stabilizing trend. The lowest abundance

Table 1. Community of aquatic invertebrates colonizing *Salix humboldtiana* leaf detritus in a subtropical lake on sand coastal plain of Rio Grande do Sul, Brazil. Mean densities (ind.100 g.DW^{-1}) and abundance (%) per taxa at each period of sample (days of decomposition).

Taxa		FTGs	Mean densities (ind.100 g.DW^{-1})							%
			1	4	7	14	32	47	71	
Nemertea		Pr	0	7.15	63.29	7.29	0	0	39.68	0.09
Gastropoda										
	Ampullaridae	Ga-Co / Sc	0	7.15	7.25	14.78	16.57	17.36	357.04	0.27
	Ancylidae	Ga-Co / Sc	0	0	0	0	16.57	253.80	341.13	0.41
	Lymnaeidae	Ga-Co / Sc	0	0	0	0	8.40	0	58.48	0.04
Annelida										
	Hirudinea	Pr	0	0	7.03	14.64	8.09	123.13	486.00	0.42
	Oligochaeta	Ga-Co	86.04	2388.80	2410.81	2220.38	1739.06	5041.34	12651.33	19.00
Tardigrada		Pr	0	0	0	0	0	8.80	286.31	0.19
Hydracarina		Pr	19.76	534.54	412.73	897.52	1598.93	2809.33	7994.01	9.82
Copepoda										
	Calanoida	Ga-Co / Pr	6.99	92.35	42.84	14.78	98.03	131.81	167.67	0.41
	Cyclopoida	Ga-Co / Pr	0	0	0	0	8.09	70.25	127.87	0.14
	Harpacticoida	Ga-Co / Pr	0	0	7.03	0	0	104.97	1134.19	0.80
Cladocera										
	Chydoridae	Ga-Co	303.63	1241.27	1459.79	73.33	24.27	220.40	831.63	3.41
	Daphniidae	Fi-Co	0	63.95	77.78	95.16	49.01	0	19.79	0.26
	Ilyocryptidae	Ga-Co	0	0	0	0	16.18	79.16	98.87	0.13
	Macrothrycidae	Ga-Co	19.76	63.59	35.80	73.18	73.29	635.87	664.53	1.09
	Sididae	Fi-Co	0	0	7.03	0	0	176.88	59.24	0.17
Ostracoda		Ga-Co	1415.38	3502.55	4034.47	1482.92	1588.83	2409.26	2746.83	13.75
Coleoptera										
	Elmidae	Ga-Co / Sc	0	0	0	7.34	0	0	9.75	0.01
	Gyrinidae	Pr	0	0	0	0	0	0	19.49	0.01
	Staphylinidae	Pr	0	0	0	7.39	0	0	9.75	0.01
Collembola										
	Entomobryidae	Ga-Co	6.59	7.06	0	7.29	0	0	19.84	0.03

The richness, diversity and evenness were calculated for each day of decomposition using data from all taxa and for the functional trophic groups (FTGs). Sh: shredders, Ga-Co: gathering-collectors, Fi–Co: filtering-collectors, Pr: predators, Sc: scrapers. Different letters represent statistical significant differences (a-c).

Table 1. Continued...

Taxa		FTGs	Mean densities (ind.100 g.DW^{-1})							%
			1	4	7	14	32	47	71	
Chironomidae										
	Chironominae	Ga-Co / Fi-Co / Sh / Pr / Sc	27.55	99.66	134.19	154.68	510.60	577.20	1665.85	2.20
	Orthocladiinae	Ga-Co / Sh / Pr / Sc	13.77	7.15	0	7.39	65.35	18.57	426.69	0.36
	Tanypodinae	Ga-Co / Pr	82.64	255.36	375.98	507.20	2041.88	2837.86	8042.16	9.66
	Pupa Chironomidae		0	28.37	0	14.68	57.40	34.95	119.12	0.18
Ceratopogonidae		Ga-Co / Pr / Sc	0	0	0	0	0	8.80	9.92	0.01
Ephemeroptera										
	Baetidae	Ga-Co / Sc	13.18	14.12	21.31	29.42	196.96	488.08	238.31	0.70
	Caenidae	Ga-Co / Sc	48.11	198.89	461.72	1766.16	6515.35	10455.17	18282.71	25.86
Lepidoptera										
	Pyralidae	Sh	0	0	0	0	0	17.59	0	0.01
Odonata										
	Coenagrionidae	Pr	236.71	1107.22	2245.92	1877.75	1155.03	1993.98	1082.64	7.68
	Libellulidae	Pr	21.16	28.40	105.77	102.60	106.79	99.23	147.84	0.47
Trichoptera										
	Hydroptilidae	Ga-Co / Sc	13.77	7.09	70.75	255.87	402.59	1265.19	493.39	1.78
	Leptoceridae	Ga-Co / Sh / Pr	0	35.70	21.46	59.13	254.42	175.28	49.55	0.45
	Polycentropodidae	Fi-Co / Sh / Pr	0	0	7.25	0	0	18.08	49.96	0.05
	Hydropsychidae	Fi-Co	0	0	0	0	8.40	9.29	0	0.01
Nematoda		Ga-Co	0	0	0	0	0	8.80	150.00	0.10
Total density (ind.100 g.DW^{-1})			2315.03^{a}	9690.38^{b}	12010.21^{b}	9690.89^{b}	16560.08^{b}	30090.38^{c}	58881.58^{c}	
Richness			15^{a}	20^{ab}	21^{ab}	23^{ab}	24^{bc}	29^{bc}	34^{c}	
Diversity (*H'*)			1.173^{a}	1.733^{ab}	1.764^{b}	1.928^{b}	1.957^{b}	2.045^{b}	2.051^{b}	
Evenness (*E*)			0.515^{a}	0.641^{ab}	0.662^{ab}	0.701^{b}	0.665^{ab}	0.677^{b}	0.623^{ab}	
Diversity (*H'*) – FTGs			0.557^{a}	0.635^{ac}	0.743^{c}	1.011^{b}	1.122^{b}	1.066^{b}	1.054^{b}	
Evenness (*E*) – FTGs			0.365^{a}	0.394^{a}	0.462^{a}	0.628^{b}	0.697^{b}	0.662^{b}	0.655^{b}	

The richness, diversity and evenness were calculated for each day of decomposition using data from all taxa and for the functional trophic groups (FTGs). Sh: shredders, Ga-Co: gathering-collectors, Fi–Co: filtering-collectors, Pr: predators, Sc: scrapers. Different letters represent statistical significant differences (a-c).

of shredders was observed on day 7 (0.3%) and the highest on day 32 (1.23%). Filtering-collectors presented their lowest abundance (0.24%) during the first days of the experiment and their highest (1.3%) on day 14. Significant differences between means were observed for all FTGs (Table 2).

The Shannon diversity index, calculated with respect to FTGs, showed a significant, gradual increase (F = 44.13) from the first (0.557 ± 0.075) to the last day of the experiment (1.054 ± 0.014) (Table 1). The evenness index also significantly increased (F = 36.04) from the beginning to the end of the experiment (day 1 = 0.365 ± 0.060; day 71 = 0.655 ± 0.009). These indexes exhibited stabilizing trends by the end of the experiment.

4. Discussion

We found that leaf decay coefficients (*k*) differed between the beginning and the end of the experiment. According to Webster and Benfield (1986), breakdown rates change over time because of the complex nature of plant material. Weight loss is rapid during the first few weeks because of the loss of soluble and labile materials through leaching and microbial metabolism. The remaining material is more resistant to decay, and subsequent weight loss proceeds more slowly. This pattern was observed in the present study.

According to Abelho (2001), various factors can influence the rate of decomposition. In lotic environments, the physical abrasion caused by moving water influences the rate of leaf decay, especially during flood periods (Carvalho and Uieda, 2009a). In lakes, fragmentation by physical abrasion probably has a minimal influence on decomposition. However, waves and water circulation may be important for the processing of detritus (Pabst et al., 2008).

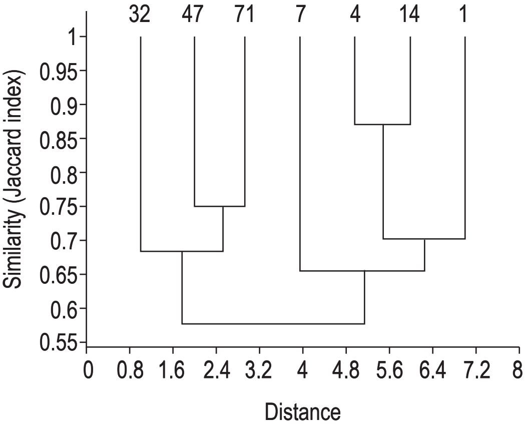

Figure 2. Analysis of community similarity (Jaccard index) constructed with data of presence-absence of invertebrates colonizing *Salix humboldtiana* leaf detritus, sampled after 1, 4, 7, 14, 32, 47, 71 days of decomposition in a subtropical lake on sand coastal plain of Rio Grande do Sul, Brazil.

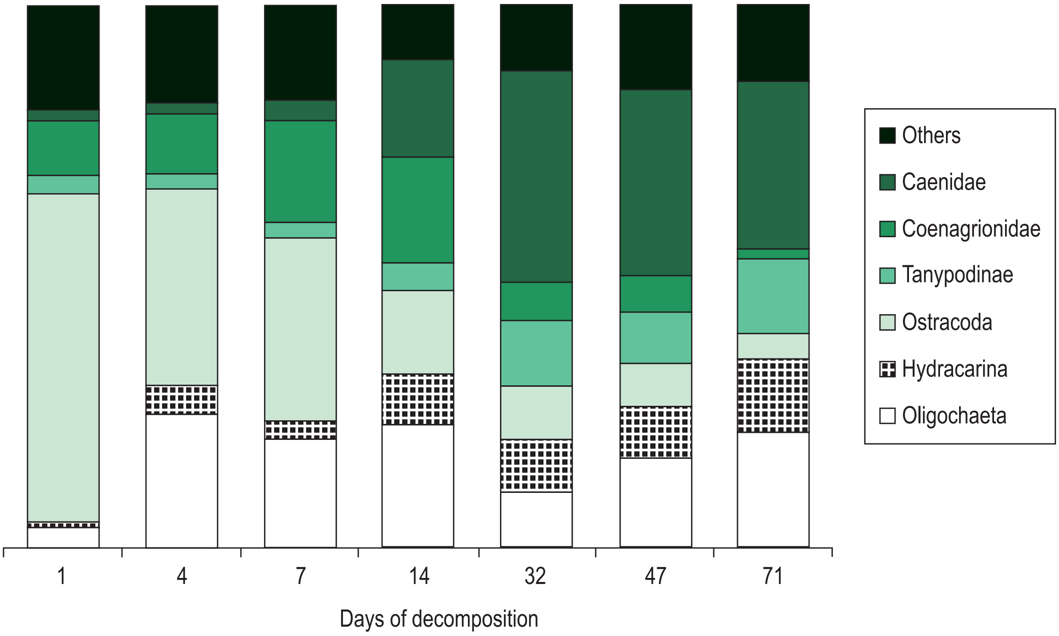

Figure 3. Succession of the most representative taxa (abundance > 7.68%) of invertebrates colonizing *Salix humboldtiana* leaf detritus in a subtropical lake on sand coastal plain of Rio Grande do Sul, Brazil.

Table 2. Results of ANOVA comparing the means densities of the most representative taxa (abundance > 7.68%) and functional trophic groups (FTGs) of invertebrates colonizing *Salix humboldtiana* leaf detritus in a subtropical lake on sand coastal plain of Rio Grande do Sul, Brazil.

Taxa / FTG	Days of decomposition							F
	1	4	7	14	32	47	71	
Oligochaeta	a	ab	ab	ab	a	b	c	41.51
Hydracarina	a	b	b	bc	bc	bc	c	17.35
Tanypodinae	a	b	b	b	c	c	d	89.80
Coenagrionidae	a	ab	b	ab	ab	ab	ab	3.34
Caenidae	a	b	b	c	d	de	e	160.07
Gathering-collectors	a	ab	b	ab	b	c	d	59.37
Predators	a	b	bc	bcd	cd	d	e	55.21
Scrapers	a	b	b	c	d	de	e	96.44
Filtering-collectors	a	ab	ab	b	b	b	b	6.15
Shredders	a	a	a	ab	b	b	c	26.27

Different letters represent statistical significant differences (a-e) ($p < 0.05$; F = test results).

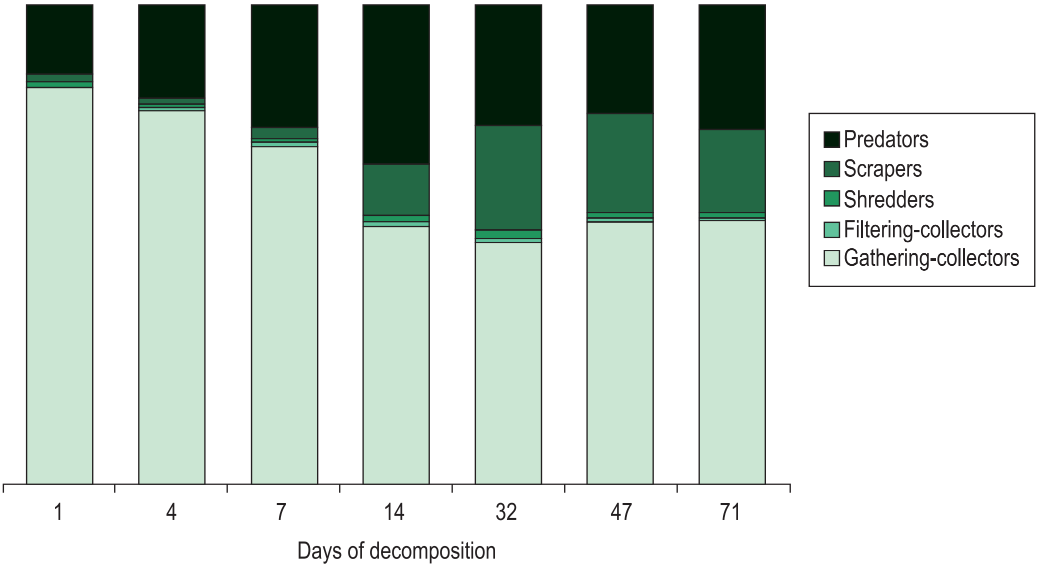

Figure 4. Participation of each functional trophic groups (relative abundance) of invertebrates colonizing *Salix humboldtiana* leaf detritus in a subtropical lake on sand coastal plain of Rio Grande do Sul, Brazil.

The shallow lakes of the coastal plain of Rio Grande do Sul have a large surface area relative to depth and, due to their location, are strongly influenced by the wind (Furlanetto et al., 2008; Trindade et al. 2009). These characteristics allow such systems to undergo daily circulation of the whole water column, which, in turn, identifies them as holomitic-polimitic lakes (Esteves, 1998). These factors may influence the rate of leaf degradation in shallow lakes of the coastal plain of Rio Grande do Sul.

Considering that *k* showed a stabilizing trend after day 32, the coefficient estimated for the last day of decomposition can be used to represent the process of mass loss. According to Petersen and Cummins' (1974) classification, the coefficient found at day 71 in this study (k = 0.0100 d^{-1}) represents the threshold between medium and fast degradation velocities. However, all other values obtained in our study are characterized as fast velocities.

The leaf decay coefficient found at the end of the experiment is similar to those found by Leguizamon et al. (1992), Capello et al. (2004) and Poi de Neiff et al. (2006); these authors evaluated the decomposition of *S. humboldtiana* in a new dam (k = 0.0101 d^{-1}; 50% loss = 69 days; 90% loss = 228 days), a river (k = 0.0119 d^{-1}; 50% loss = 58 days; 95% loss = 252 days) and a marsh (k = 0.019 d^{-1}; 50% loss = 36 days), respectively. All studies were performed in the hydrological system of the Paraná River, Argentina.

In our study, the highest rates of weight loss were observed in the initial phase, with a stabilizing trend extending from day 32 to the end of experiment. This behavior was reflected by the composition of the invertebrates colonizing the detritus. As emphasized by the results of similarity analysis, the invertebrates were separated into two groups based on their presence-absence patterns over time. Considering that the mass loss coefficients can probably serve as indirect measures of the potential use of detritus as food resources (Dobson et al., 2003), these two groups may represent the community's overall response to the availability of litter. These results indicate that the availability of detritus may influence the occurrence of different taxa.

The rapid increase in evenness at the beginning of the experiment reflects the decreased dominance of Ostracoda. Though they were present in great abundance at the beginning of the experiment, predation pressure may have contributed to the reduction in their numbers. The subsequent stabilizing trend in evenness resulted from a more balanced distribution of taxa.

We estimated that 95% of the initial dry weight would be lost after 300 days of decomposition. Combined with the increases in richness, Shannon diversity and total density as well as the achievement of a more balanced distribution of taxa over time, we suggest that *S. humboldtiana* detritus provides a favorable habitat over a sufficient duration to support a high density and diversity of aquatic invertebrates.

In contrast to the findings of the present study, Capello et al. (2004) observed significant decreases in diversity and richness of invertebrates associated with decomposing *S. humboldtiana* in a lotic system. Nevertheless, these authors observed a continual increase in the density of organisms. According to Capello et al. (2004), this increase would be expected in advanced stages of decomposition because of the increase in fine particulate organic matter (FPOM).

We observed a low density of shredders in the present experiment (less than 1% of the total community). The contribution of this group to the fragmentation of detritus is very significant in temperate zones (Vannote et al., 1980; Graça et al., 2001). In tropical and subtropical regions, however, shredders have low representation in the invertebrate assemblages that colonize detritus (Benstead, 1996; Dudgeon and Wu, 1999; Dobson et al., 2002; Capello et al., 2004; Gonçalves et al., 2007; Carvalho and Uieda, 2009b). According to Irons et al. (1994), the importance of invertebrate shredders for the decomposition of detritus is lower at low latitudes where the contribution of decomposing microorganisms is greater.

Gathering-collectors were a dominant part of the invertebrate assemblage in the detritus from the first to the last day of our experiment. These organisms are adapted to feed on FPOM (Wallace and Webster, 1996). In lotic environments, they are usually the most abundant group (Lugthart and Wallace, 1992; Callisto et al., 2001, 2004; Carvalho and Uieda, 2009b). According to Richardson (1992) and Grubbs et al. (1995), the dominance of this group is associated with the accumulation of FPOM from its own detritus or from organic particles arising from the seston on the detrital surface. The high abundance of this group observed within the first 24 hours of our experiment indicates that the leaves of *S. humboldtiana* are used primarily as habitat, because FPOM had not yet produced.

The increase in scrapers observed in the present study is probably related to the development of biofilm on the surface of the detritus. Lester et al. (1994) evaluated the development of biofilm on leaves of *Salix fragilis* L. in a New Zealand river and observed gradual increases in the concentrations of total nitrogen and chlorophyll-*a* that were related to colonization by microorganisms and periphyton.

Our results suggest that the leaf detritus of *S. humboldtiana* provides a favorable habitat for a sufficient duration to support a high density and diversity of aquatic invertebrates in Polegar Lake. This community uses the detritus primarily as habitat and secondarily as food (e.g., FPOM). In addition, the detritus provides surface area for the development of biofilms, which are crucial for the recruitment of scrapers. The small percentage of shredders reflects the minor influence of the invertebrate community on the rate of detrital degradation. The main contribution of invertebrates to detrital processing comes from the consumption of FPOM by gathering-collectors.

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