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LEAF LITTER MASS LOSS RATES AND ASSOCIATED FAUNA OF TREE SPECIES COMMONLY USED IN NEOTROPICAL RIPARIAN REFORESTATION

Tasas de pérdida de masa de la hojarasca y fauna asociada en especies de árboles comúnmente utilizados en la reforestación de riberas neotropicales

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ABSTRACT

A signature of globalization is the prevalence of exotic trees along reforested urban and rural riparian zones in the Neotropics, but little is known about the instream processing of its leaf litter. In this study, leaf litter breakdown rates were measured during 35 days using mesh bags within a reference headwater stream for seven exotic and three native tree species commonly used in urban and rural reforestation. *Artocarpus altilis*, *Schefflera actinophylla* and *Terminalia catappa* scored the highest mass loss rates (>85 %; mean life: t_{50} <15 d), while *Cecropia* sp. and *Cespedesia macrophylla* (mass loss =36 and 15 %; t_{50} =58 and 172 d, respectively) scored the lowest rates. However, a broad range of rates was observed among the ten species studied. The carbon to phosphorus ratio (C:P) and toughness of the leaf litter were the best predictors of breakdown rates. However, these leaf properties were not correlated with the very low values of macroinvertebrates abundance and diversity, and the few morphs classified as shredders. Therefore physical rather than biological controls seem to best explain the observed variability of mass loss rates, and thus slow decomposing leaf litter species seems to provide a habitat rather than a food resource, particularly to collectors. This study suggests that riparian reforestation will propagate species-specific ecological influences on instream processes such as leaf litter processing depending on leaf quality properties, therefore ecosystem-wide influences should be considered for improving reforestation strategies. Future studies should test for differences in breakdown rates and colonization by macroinvertebrates relative for leaf litter species origin (native *vs.* exotic).

Keywords: leaf litter mass loss rates, leaf quality, macroinvertebrates, exotic trees, riparian reforestation.

RESUMEN

Una de las señales más evidentes de la globalización es la prevalencia de especies de árboles exóticos a lo largo de las zonas ribereñas urbanas y rurales del Neotrópico, pero poco se sabe sobre el procesamiento de su hojarasca dentro de las quebradas. En este estudio se midieron las tasas de pérdida de masa de la hojarasca usando bolsas de angeo en una quebrada de referencia durante 35 días, para siete especies exóticas y tres nativas comúnmente usadas en la reforestación urbana y rural. *Artocarpus altilis*, *Schefflera actinophylla* y *Terminalia catappa* obtuvieron las mayores tasas de pérdida de masa (>85 %; vida media: t_{50} <15 d), mientras que las menores tasas las obtuvieron *Cecropia* sp. y *Cespedesia macrophylla* (pérdida de masa =36 y 15 %; t_{50} =58 y 153 d, respectivamente). Sin embargo, se observó una amplia gama de tasas de pérdida de masa entre las diez especies estudiadas. La proporción carbono:fósforo (C:P) y la dureza de la hojarasca fueron los mejores predictores de las tasas de pérdida de masa. Sin embargo, estas características no se correlacionaron con los muy bajos valores de abundancia y diversidad de macroinvertebrados, y la escasez de morfotipos de insectos clasificados como fragmentadores. Por lo tanto, los controles físicos parecen ser más importantes que los biológicos para explicar la variabilidad de las tasas de pérdida de masa; y, las especies con tasas más bajas podrían estar proveyendo hábitat, más que alimento para las especies de insectos acuáticos, principalmente los recolectores. Este estudio sugiere que la reforestación ribereña propagará efectos específicos sobre los procesos dentro del cauce dependiendo de las especies de árbol plantadas, mediados por la calidad de la hojarasca, los cuales deberían ser considerados para mejorar las estrategias de reforestación. Estudios futuros deben someter a prueba si existen diferencias en las tasas de fragmentación y colonización de macroinvertebrados entre especies de hojarasca de diferente origen (nativa *vs.* exótica).

Palabras clave: tasas de pérdida de masa, calidad de hojarasca, macroinvertebrados, árboles exóticos, reforestación ribereña.

INTRODUCTION

Local floras in urban, suburban and rural settings have been homogenized worldwide due to reforestation (McKinney, 2006), but little attention has been paid to the consequences on ecosystem function in the Neotropics (Lugo, 2004). Homogenization of floras is a major issue in anthropogenic settings, promoted by the fact that a rich native flora is replaced by a few exotic (non-native) species (McKinney, 2006). In the case of the Tropics, riparian floras in urban and rural settings have been transformed into "novel ecosystems", homogenized by monoculture of non-native trees commonly used for restoring and managing degraded lands (Lugo, 2004; Lugo and Helmer, 2004). In addition, the "green" planning paradigm of cities and towns has populated parks, green belts and waterfronts with common exotic species, and a few widespread natives (McKinney, 2006). Awareness has just recently risen in tropical countries on the influence of riparian non-indigenous floras in stream processes in a changing climate (Boyero *et al.*, 2012a).

It is important to study the species-specific influences of riparian vegetation because its detritus is the major energy source in closed-canopy and narrow low order streams, and therefore, it is the most important linkage between the riparian zone and the instream function (Wantzen *et al.*, 2008). The leaf litter entering into a stream is decomposed throughout a process of various distinctive phases (Abelho, 2001). After leaf fall, the decomposition process is initiated with a leaching phase (abiotically removing soluble substances), followed by the microbial colonization phase and, subsequently, by a mechanical breakdown phase promoted by the shredder insect feeding, alongside with water flow (Wantzen *et al.*, 2008). While temperate-zone leaf species are classified according to the breakdown rate (k) as fast ($k > 0.01$), medium ($0.005 < k < 0.01$) and slow ($k < 0.005$) (Petersen and Cummins, 1974; Webster and Benfield, 1986), little is known about the spectrum of such rates in tropical vascular plants. However, recent reviews and experiments suggest that a similar range of breakdown rates is observed (Ardón and Pringle, 2008; Wantzen *et al.*, 2008). The velocity of the entire decomposition process depends on the climate and instream fauna, but if these two factors are set as constants in a reference stream, then the breakdown rates depends locally on the chemical and physical characteristics of the leaf litter, ultimately linked to the taxonomic identity of the tree species (Gessner *et al.*, 1999).

In the Tropics, while the important role of shredder macroinvertebrates has been recently highlighted in a global experiment (Boyero *et al.*, 2011a and b; 2012b), the role of leaf litter quality seems to be an overriding control of leaf litter breakdown at a local scale where the other factors controlling the decomposition process are constants, as demonstrated by the available studies comparing multiple species (e.g. O'Connor *et al.*, 2000; Mathuriau and Chauvet, 2002; Rincón and Martínez, 2006; Rueda-Delgado *et al.*, 2006; Chará *et al.*, 2007; Ardón and Pringle, 2008; Wantzen *et al.*, 2008). Leaf litter quality or palatability is defined as the pool of chemical and physical properties conferring a feeding value for shredding macroinvertebrates and microbes, and thus speed up the breakdown rates (Ardón and Pringle, 2008; Wantzen *et al.*, 2008). Shredder and microbial activities are strongly influenced by primary and secondary chemical compounds on leaves (Ardón and Pringle, 2008), despite the fact that most of these compounds have evolved as chemical defenses against terrestrial herbivores (Coley, 1983). Phenolic, tannin and lignin, among others account as chemicals negatively influencing the biotic controls of litter breakdown. Strong cuticles and fibers as a consequence of high lignin and cellulose content, in addition to prevent the leaching, increase leaf toughness, thus reducing terrestrial herbivory and instream detritivory (Wantzen *et al.*, 2008).

The growing awareness on the ecological consequences of plant species introductions in tropical riparian zones have urged stream ecologists and conservationists to ask: How different is the leaf litter processing between tree species commonly used in urban and rural reforestation (as a consequence of their differences in leaf quality) (e.g. Boyero *et al.*, 2012a)? Urban and rural streams in Colombia provide a good opportunity to test for the influence of species-specific and origin effects on leaf litter breakdown rates because a great number of exotic and native plant species have been used in riparian restoration and management (e.g. Varón *et al.*, 2002), and, at the same time, many pristine riparian zones exhibit a great diversity (Valencia *et al.*, 2009). Finally, the number of studies about leaf litter breakdown and insect shredders has rapidly grown during the last decade (e.g. Mathuriau and Chauvet, 2002; Rueda-Delgado *et al.*, 2006; Chará *et al.*, 2007; Chará-Serna *et al.*, 2010; 2012), and some sites have been included within the "Global Stream Decomposition Network" (Boyero *et al.*, 2011a and b; 2012b).

In this paper, we tested for species-specific effects by experimentally quantifying mass loss rates of leaf litter from ten tree species (three natives and seven exotics) commonly used in riparian reforestation. The objectives of this study were the following: 1) to compare mass loss rates among tree species, 2) to relate mass loss rates to leaf quality variables, and 3) to relate leaf litter species, mass loss rates and leaf quality with macroinvertebrates found in litter bags. We hypothesize that leaf toughness (inversely correlated with nitrogen and phosphorus content) will exert a negative effect on mass loss rates and associated macroinvertebrates, across the assessed spectrum of species.

METHODS

Study Site

The breakdown experiments were carried out at a reference first order headwater stream, Quebrada Piedras, a tributary of the Río Nus (a tributary of the Río Cauca) located in the San Roque Municipality of Antioquia State (Colombia) (Aguirre *et al.*, 2004). The Quebrada Piedras extends between 700 and 1000 m (6°29'14"N, 76°1'21"W). Mean annual precipitation is 2000 mm, and mean annual air temperature is 23 °C. The headwater of this stream is covered by mature tropical rainforest, while the lowlands are predominantly covered by secondary-growth forest, as a consequence of abandonment of livestock farming during the early nineties. The study stream is located close to the Estación Piscícola San José del Nus (Universidad de Antioquia).

The experiment was carried out between June and August 2009, corresponding to the dry period (monthly rainfall range: 150-220 mm) (Aguirre *et al.*, 2004). The leaf litter bags were installed into five pools with similar water physico-chemistry and geomorphology (summarized in Table 1). The study reach (100 m) at Quebrada Piedras consisted of a series of riffle-pool and step-and-pool sequences, underlain by granite cobbles, boulders, and megaboulders. The stream bed in experimental pools was interspersed with patches of sand and leaf litter.

Preparation, Collection and Procesing of Litterbags

Senescent leaves of ten tree-species (three natives and seven exotics) commonly used in urban and rural reforestation (Varón *et al.*, 2002) were collected according to their predominance in leaf fall of different places. Between June and December 2008, leaf litter samples were collected from riparia and parks in Medellín city, a mosaic of land uses in the Estación Piscícola and a private farm, and the rainforest in Gorgona Island National Natural Park of the Pacific Coast of Colombia (Table 2). Because litter fall phenology is unknown for many tropical species (Wantzen *et al.*, 2008), and due to limitations for simultaneous access to different collection places to obtain a broad range of leaf litter qualities, samples from all species were not collected synchronically. Therefore entire leaves were pressed, oven-dried (50 °C during 48 hours, as temperatures in the literature range between 40 and 60 °C; see Hirobe *et al.*, 2004), and stored in a dry room during several months to avoid microbial decomposition prior to the experimental trial. When all species were collected, leaf discs of a known weight (3.0 ± 0.01 g) of each species were separately placed in 15 x 20 cm, 10 mm mesh-size nylon bags to allow macroinvertebrates access (Bärlocher, 2005). Leaf litter bags were installed on July 26th and collected on August 30th, 2009. One bag for each leaf species was deployed in each of the five experimental pools (equaling five replicated bags for species) at Quebrada Piedras. A total of 50 bags were prepared, and each replicated pool contained ten species. Within each pool, leaf bags for each species were randomized and tethered to two fishing lines tied to wooden poles buried in the stream margin.

The leaf litter bags were collected by placing a plastic zip-lock bag underneath immediately before being lifted from the

Table 1. Physical and chemical punctual characteristics of the experimental pools in Quebrada Piedras, San José del Nus (Antioquia, Colombia). The slight differences among pools might reflect the influence of the time of day for the measurement, rather than pervasive differences due to location, elevation or any other hidden factor.

Pool	Conductivity(µs/cm)	Total dissolved solids (ppm)	pH	Water temperature (°C)	Dissolved oxygen (mg/L)
1	97	48	7.76	21.4	9.1
2	100	50	7.51	21.7	8.7
3	100	51	7.67	22.8	9.2
4	110	55	7.70	22.2	9.4
5	108	54	7.73	24.3	9.1
Mean	103	52	7.67	22.5	9.1
Std. deviation	5.7	2.9	0.1	1.2	0.3
C.V. (%)	5.5	5.6	1.3	5.1	2.8

Table 2. Tree species used in the two leaf litter breakdown experiments. Superscript letters indicated collection site. Mass loss as percentage, exponential decay coefficient (k) calculated using the equation $k = (\ln M_0 - \ln Mt)/t$ (Bärlocher, 2005), mean life time (time required for 50 % mass loss) (Bärlocher, 2005) and leaf quality characteristics are reported. E= Exotic, N= Native, N/A= Not Applicable

Scientific name (source)	Trial 1 % weight loss	Trial 1 $k(d^{-1})$	Trial 1 t_{50}(d)	Trial 2 $k(d^{-1})$	Trial 2 t_{50}(d)	Toughness (g)
[c]*Mangifera indica* (E)	22.05 ± 4.3	0.0075 ± 0.002	97.65 ± 19.5	N/A	N/A	350.95 ± 57.7
[a]*Schefflera actinophylla* (E)	73.75 ± 19.1	0.0395 ± 0.023	19.85 ± 13.3	0.1385 ± 0.052	6.35 ± 4.3	338.25 ± 92.8
[a]*Araucaria* sp. (E)	58.55 ± 36.2	0.0265 ± 0.015	78.65 ± 121.3	N/A	N/A	N/A
[a]*Terminalia catappa* (E)	31.15 ± 6.1	0.0115 ± 0.003	65.65 ± 15.6	0.0935 ± 0.005	14.25 ± 16.7	164.85 ± 35.7
[a]*Bauhinia picta* (E)	39.85 ± 13.4	0.015 5 ± 0.007	52.45 ± 23.1	N/A	N/A	313.75 ± 68.0
[a]*Hibiscus* sp. (E)	55.15 ± 31.6	0.0245 ± 0.019	47.65 ± 50.4	0.0245 ± 0.010	35.85 ± 20.1	277.95 ± 48.9
[a]*Artocarpus altilis* (E)	27.85 ± 22.8	0.0135 ± 0.013	51.05 ± 26.3	0.1225 ± 0.022	5.95 ± 1.1	191.15 ± 33.5
[a]*Ficus benjamina* (E)	19.75 ± 1.8	0.0065 ± 0.001	108.45 ± 10.8	N/A	N/A	343.25 ± 66.9
[a]*Ficus elastica* (E)	25.25 ± 6.9	0.0095 ± 0.003	86.05 ± 24.1	0.0175 ± 0.006	44.85 ± 13.6	915.75 ± 92.5
[a]*Ficus lyrata* (E)	15.55 ± 0.8	0.0055 ± 0.0003	140.25 ± 8.4	N/A	N/A	691.35 ± 119.7
[b]*Ficus* sp. (E)	35.15 ± 5.2	0.0135 ± 0.002	55.85 ± 12.0	N/A	N/A	N/A
[a]*Eucalyptus* sp. (E)	49.25 ± 29.3	0.0265 ± 0.026	47.95 ± 32.8	0.0205 ± 0.005	37.45 ± 13.5	391.75 ± 65.9
[a]*Eugenia malacensis* (E)	28.95 ± 19.3	0.0115 ± 0.010	89.85 ± 42.2	N/A	N/A	240.45 ± 74.0
[a]*Syzygium jambos* (E)	28.95 ± 14.6	0.0115 ± 0.007	81.15 ± 31.9	N/A	N/A	359.15 ± 56.8
[a]*Fraxinus chinensis* (E)	40.05 ± 12.6	0.0165 ± 0.007	49.75 ± 15.7	N/A	N/A	354.5 ± 55.2
[c]*Tectona grandis* (E)	34.05 ± 11.7	0.0125 ± 0.005	63.45 ± 25.5	0.0495 ± 0.018	15.85 ± 5.1	304.5 ± 76.8
[b]*Campnosperma panamensis* (N)	1.75 ± 0.5	0.0005 5 ± 0.0001	1479.85 ± 418.0	N/A	N/A	N/A
[a]*Pachira insignis* (N)	49.35 ± 20.5	0.0205 ± 0.016	40.65 ± 19.8	N/A	N/A	442.65 ± 59.0
[d]*Theobroma cacao* (N)	15.25 ± 2.0	0.005 5 ± 0.001	145.65 ± 23.1	N/A	N/A	349.85 ± 65.8
[b]*Sapium* sp. (N)	22.25 ± 27.9	0.0095 ± 0.014	231.75 ± 164.0	N/A	N/A	N/A
[a]*Inga* sp. (N)	13.25 ± 14.3	0.005 5 ± 0.005	273.05 ± 329.7	N/A	N/A	228.65 ± 49.1
[a]*Guadua angustifolia* (N)	50.85 ± 31.9	0.0295 ± 0.028	52.65 ± 47.5	N/A	N/A	221.25 ± 50.9
[a]*Persea americana* (N)	11.65 ± 8.1	0.0045 ± 0.003	1066.75 ± 1832.2	0.0255 ± 0.024	48.45 ± 31.8	255.15 ± 57.8
[d]*Cecropia* sp. (N)	9.45 ± 1.5	0.0035 ± 0.0005	244.35 ± 43.3	0.0135 ± 0.005	58.85 ± 22.6	364.25 ± 59.7
[d]*Ficus* sp. (N)	9.45 ± 1.9	0.0035 ± 0.001	244.65 ± 44.8	N/A	N/A	N/A
[a]*Psidium guajava* (N)	32.25 ± 12.3	0.0125 ± 0.005	70.65 ± 37.1	N/A	N/A	N/A
[b]*Cespedesia macrophylla* (N)	9.05 ± 0.8	0.0025 ± 0.002	1340.95 ± 1099.1	0.0055 ± 0.002	172.65 ± 77.4	459.45 ± 68.6

a: Medellín city; b: Gorgona island; c: dry forest (private farm); d: rain forest (Estación Piscícola).

stream to avoid macroinvertebrate loss. All bags were then packed in sealed plastic bags and transported to the laboratory for processing. In the laboratory, leaves and small fragments were removed and gently rinsed with tap water to eliminate sediment. They were packed in paper and oven-dried until constant weight (50 °C for 48 hours). Then these fragments were let to cool down and weighed using an analytical balance (Sartorius Basic, BA210S), following standard methods (Rincón *et al.*, 2005). Mass loss of each leaf disc was expressed as a percentage. Macroinvertebrates were transferred to vials with 70 % alcohol, and they were counted and sorted under stereomicroscope (Leika Zoom 2000, Model No. Z 45 V) to the family level using taxonomic keys (e.g. Roldán, 1996). Each taxa was assigned to a functional feeding group (FFGs) by using Cummins *et al.* (2005) and Tomanova *et al.* (2006) classification. A previous trial was carried out using 27 leaf species in June but because a flash flood disturbed the litter bags, these samples were not used for statistical analyzes, and only included in the Table 2 as a preliminary reference of mass loss rates because many species were not included during the second trial.

Leaf Quality Analysis

Leaf toughness (or critical mass, surrogate of physical attributes) was estimated for 21 leaf species (out of total 27) (Table 2 and Table 3), and it was defined as the force needed to penetrate a leaf sample using a penetrometer (Graça and Zimmer, 2005). Leaf discs were cut using a circular metal template, and each one was firmly clamped into the base of the penetrometer. The position of the leaf disc was checked to make sure that the punching piece fitting the central hole of the base did not touch any high-order vein of the leaf, as these parts are avoided by shredders. A glass beaker placed on top of the punching piece was filled with water to increase

Table 3 Mass loss and leaf quality characteristics of leaf litter of tree species commonly used in riparian reforestation. Species are ranked in decreasing order of mass loss. Species origin: E= Exotic, N= Native, N/A= Not Applicable. Means (± standard deviations) are based on five observations for mass loss, and 30 observations for leaf toughness. A single leaf chemistry value was obtained for a compound sample of leaves for each species. Different superscripts are significantly different using Bonferroni's pairwise comparisons test for a p <0.05 significance.

			Leaf quality		
Families	Scientific name (Origin)	Mass loss (%)	Chemical		Toughness (g)
			C:N	C:P	
Moraceae	*Artocarpus altilis* (E)	98.21 ± 1.33^{a}	29.1	340.2	191.1 ± 33.5
Araliaceae	*Schefflera actinophylla* (E)	95.52 ± 7.46^{a}	55.6	244.7	338.2 ± 92.8
Combretaceae	*Terminalia catappa* (E)	85.81 ± 24.46^{a}	17.96	227.5	164.8 ± 35.7
Verbenaceae	*Tectona grandis* (E)	78.99 ± 10.53^{a,b}	N/A	N/A	304 ± 76.8
Malvaceae	*Hibiscus* sp. (E)	53.93 ± 16.28^{b,c}	39.7	569.3	277.9 ± 48.9
Myrtaceae	*Eucalyptus* sp. (E)	52.80 ± 3.14^{b,c}	57.1	637.3	391.7 ± 65.9
Lauraceae	*Persea americana* (N)	48.35 ± 26.18^{b,c}	N/A	N/A	255.1 ± 57.8
Moraceae	*Ficus elastica* (E)	43.77 ± 11.38^{c,d}	58.1	564.7	915.7 ± 92.5
Moraceae	*Cecropia* sp. (N)	36.44 ± 11.19^{c,d}	40.1	526.9	364.2 ± 59.7
Ochnaceae	*Cespedesia macrophylla* (N)	14.63 ± 4.71^{d}	40.2	1025.5	459.4 ± 68.6

the mass until a critical value was reached and the punching piece pierced the leaf disc. The mass needed to cut the leaves was the critical mass and it is correlated with toughness (Graça and Zimmer, 2005).

Due to funding and logistic limitations, chemical analyses were conducted only on eight of the ten species used during the second and definitive experimental trial (Table 3). A sample of ground leaf litter of each tree species was sent to a commercial laboratory for quantifying initial concentrations (before incubation in the stream) of carbon (C), nitrogen (N), and phosphorus (P). Total N content on leaves was determined using the Kjeldahl method and potentiometric titration. Total P was determined by digestion of fresh plant tissue in a microwave. Total C was quantified using the Walkley Black method. All protocols used are described in IGAC (2006). The element concentrations were expressed as percentages. C:N and C:P ratios were computed for each species.

Data Analyses

Mass loss percentages were compared among tree-species after using a square root of arcsine transformation. Because the variances of mass loss percentages were unequal among tree-species, we ran a one way ANOVA with Welch's correction for comparing mean values. A pairwise t-test was performed for multiple comparisons with Holm adjust (R Core Team, 2009). Toughness, C:N and C:P ratios were correlated with mass loss percentage using Pearson correlation (Table 4) (PRISM, 2007). The macroinvertebrate community parameters (abundance and Shannon-Wiener [H'] diversity index) were calculated for each leaf litter species, and the differences between pairs of tree-species were compared with a t-test (PAST, 2012). These parameters were afterwards correlated with mass loss and physical and chemical properties of the leaves (Table 4) (PRISM, 2007).

The composition of macroinvertebrate families (with abundance >5 %) was compared among tree species using a cluster analysis, and also the occurrence on particular tree species was compared among macroinvertebrate families using the same analysis (R Core Team, 2009).

RESULTS

Leaf Litter Breakdown Rates

Leaf litter mass loss percentages for the ten tree species studied were shown in Table 3. The tree species showed a significant difference in mass loss (ANOVA; F (df) = 84.86 (9); p < 0.0001), and post-hoc analyzes identified four major groups: a high mass loss group (> 79 %) (*A. altilis*, *S. actinophylla*, *T. catappa* and *T. grandis*), a low mass loss group (< 36 %) (*C. macrophylla* and *Cecropia* sp.) and two intermediate mass loss groups (range: 44-54 %).

Controlling Factors of Leaf Litter Breakdown

F. elastica exhibited the highest toughness, followed by *Eucalyptus* sp., *C. macrophylla* and *Cecropia* sp.; while *P. americana*, *A. altilis* and *T. catappa* exhibited the lowest (Table 3). A negative and significant correlation between leaf toughness and mass loss was observed, despite of the great dispersion of the data (Table 4). No correlation was found between leaf toughness and chemical quality characteristics, or between leaf toughness and community parameters (Table 4).

The ratios C:N and C:P were not correlated (Table 4) and for that reason their effects on mass loss percentages were independently analyzed. While mass loss percentages were not correlated with C:N ratios ($r^2 = 0.08$; $p > 0.05$; Table 4), they were negatively correlated with C:P ratios ($r^2 = 0.68$; $p < 0.0001$; Table 4). No correlation was found between these chemical properties and macroinvertebrates community parameters (Table 4). Most species classified as fast decomposers

Table 4. Pearson correlation coefficient in the upper diagonal and *p*-values in the lower diagonal.

	C:N	C:P	Mass loss (%)	Toughness (g)	Abundance	H'
C:N		r = 0.27;	r = -0.28;	r = 0.65;	r = 0.57;	r = 0.45;
		r^2= 0.08	r^2 = 0.08	r^2 = 0.42	r^2 = 0.32	r^2 = 0.1
		n = 8	n = 40	n = 240	n = 8	n = 8
C:P	>0.05		r = 0.83;	r = 0.38;	r = 0.14;	r = 0.20;
			r^2 = 0.68	r^2 = 0.15	r^2 = 0.02	r^2 = 0.04
			n = 40	n = 240	n = 8	n = 8
Mass loss (%)	>0.05	<0.001		r = 0.46;	r = 0.18;	r = 0.08;
				r^2=0.21	r^2=0.03	r^2 = 0.01
				n = 300	n = 50	n = 50
Toughness (g)	>0.05	>0.05	<0.05		r = 0.17;	r = 0.53;
					r^2 = 0.03	r^2 = 0.28
					n = 300	n = 300
Abundance	>0.05	>0.05	>0.05	>0.05		-
H'	>0.05	>0.05	>0.05	>0.05	-	

exhibited low C:P ratios (< 500), while species classified as medium or slow decomposers scored higher ratios (being *C. macrophylla* the highest).

Leaf litter Associated Macroinvertebrates

A total of 428 individuals were found in the leaf litter bags at the end of the second trial, and they were classified into 28 taxa. The family diversity index (H') was significantly larger in *T. grandis* (H'=2.33) than in leaf species with intermediate (*F. elastica*, *T. catappa*, *Eucalyptus* sp.) (t-test; t = 2.1; $p < 0.05$) and some low (*C. macrophyll*a, *A. altilis*, *Hibiscus* sp.) (t-test; t = 2.3; $p < 0.05$) mass loss percentages. Both abundance and diversity were slightly correlated with some leaf quality properties (Table 4).

The insect families Lepthophlebiidae, Baetidae, Leptoceridae, Elmidae and Chironomidae were the most abundant taxa, and they were found in all leaf species. Tree clusters of macroinvertebrates were obtained based on their occurrence on the leaf species studied (Fig. 1A). Lepthophlebiidae was separated from other two groups because it was equally and highly abundant in all leaf species. In a second group, Baetidae, Leptoceridae, Elmidae and Chironomidae were separated from the remaining families with low abundance and frequency. No consistent clustering was observed among leaf litter species based on macroinvertebrate family composition (Fig. 1B). Representatives of native and non-native species were present in the two clusters observed, however, one cluster comprised the slow decomposing species and the other the fast decomposers. Fast decomposing leaf litter cluster (*Hibiscus*, *Artocarpus*, *Cecropia*, *Schefflera*) contained the less abundant macroinvertebrate groups. Most macroinvertebrates were collectors such as Baetidae, Elmidae and Chironomidae and some Lepthophlebidae. Some Lepthophlebidae are scrapers, while some Leptoceridae are shredders and others are predators (Fig. 1A). In general, filtering collectors and shredders were scarce. Baetidae (FFG: Collector) was an important attribute that defined the two clusters obtained in the analysis of leaf species in terms of composition of FFG. No difference was observed among leaf species identity and origin in terms of composition of FFG, however, collectors were abundantly found in slow decomposing leaf litter.

DISCUSSION

This study suggested that for a wide range of leaf litter from trees species commonly used in riparian reforestation in Colombia, was broken in streams depending on the leaf quality (expressed as selected physical and chemical properties). These results provide the arena to test for species-specific effects and the influence of riparian tree diversity on instream processes such as organic matter processing. Using the model of exponential decay described in Bärlocher (2005), we calculated the exponential decay coefficient (k) (Table 2) as a way to classify species according Petersen and Cummins (1974) categories. Despite of the broad rage observed, only *C. macrophyll*a was classified as slow decomposing species whereas the others were classified as fast decomposing species. The low percentages of mass loss observed in native species such as *Cecropia* sp. and *Cespedesia macrophylla* may reflect their character as pioneer trees commonly found in riparian zone canopy gaps of the tropical rainforest (Valencia *et al.*, 2009), and thus their frequent use as ornamental urban trees due to the resistance of their foliage (Varón *et al.*, 2002). Many of the exotic species included in the present study were introduced in the Tropics as fruit trees, thus explaining the low C:N and C:P ratios and fast breakdown rates (examples of fast decomposing species: *Artocarpus altilis*, *Terminalia catappa*). Other fast decomposing species such as *Schefflera actinophylla* and *Hibiscus* sp. were introduced as ornamental trees, while *Tectona grandis* and

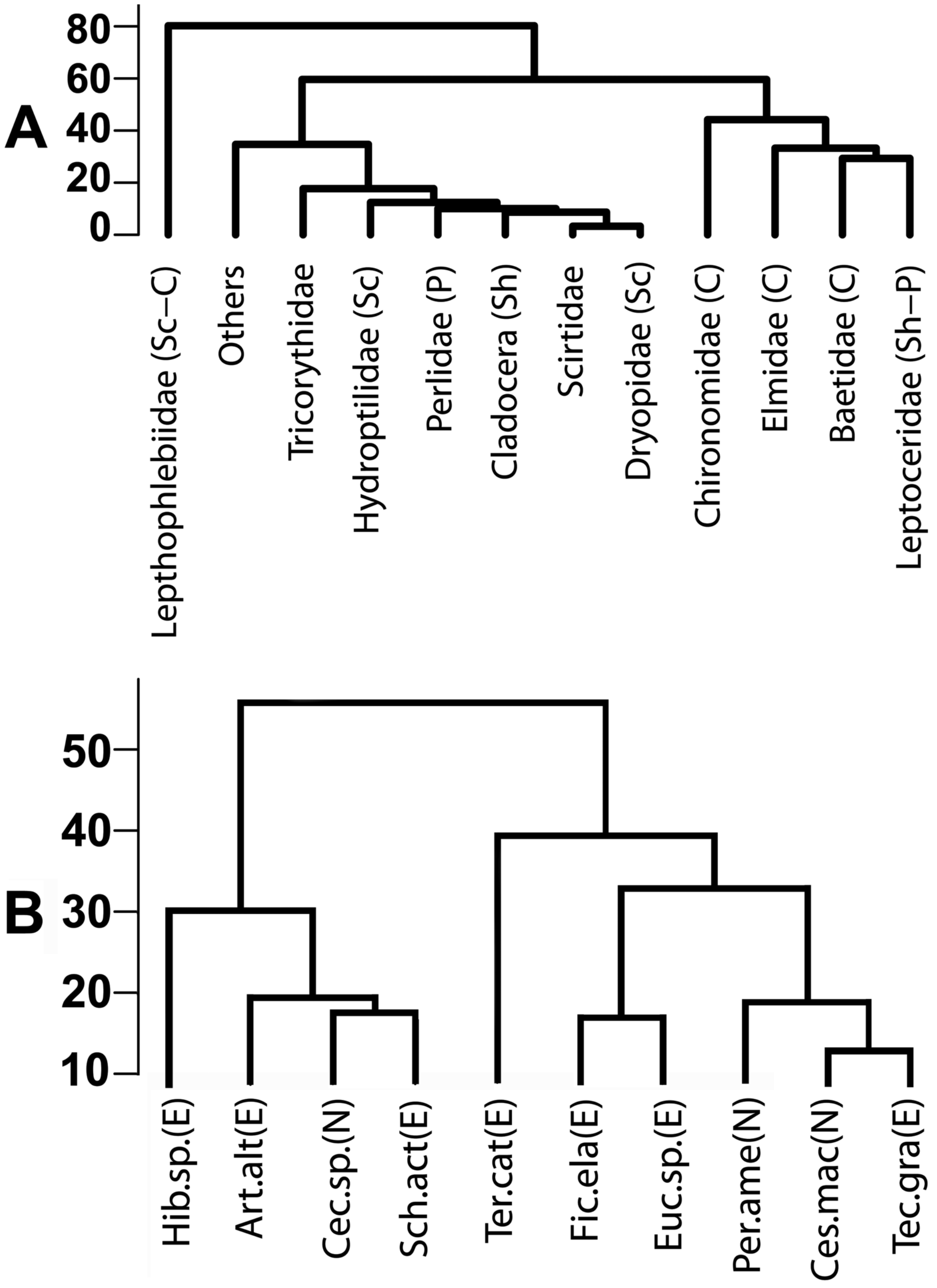

Figure 1. Cluster analysis: A. macroinvertebrate families and FFG based on their occurrence on leaf litter species (C: Collectors, Sc: Scrappers, Sh: Shredders, P: Predators); B. leaf litter species (N: Native, E: Exotic) compared based on the macroinvertebrate families present.

Eucaliptus sp. were introduced for wood (Varón *et al.*, 2002). The mass loss percentages of the native tree *Persea americana* probably reflected differences in leaf quality and thus in physiology relative to the other natives studied. We suggest to be cautious in interpreting these results until new laboratory and field trials be conducted. Future studies should include a broader range of native and exotic tree species dominant at the riparian zones to obtain more reliable results.

Leaf quality is an important control of the decomposition process (Gessner *et al.*, 1999; Wantzen *et al.*, 2008). The great dispersion of breakdown rates for low leaf toughness and C:P ratios suggest that these two variables are major constraints when they reach critical values (leaf toughness > 700 g and C:P > 700), characteristic of poor leaf quality thus conferring low palatability or resistance to mechanical damage. In addition, the lack of correlation between leaf toughness and C:N and C:P indicate that they represent different components of leaf quality. Toughness is more related to structural molecules such as lignin and cellulose with high C content, while N and P concen-trations are more influenced by non-structural and storage molecules such as proteins (Reich and Oleksyn, 2004). The poor quality in terms of C:N (> 20) makes leaf litter unattractive to aquatic consumers (Graça *et al.*, 2001; Rincón and Martínez, 2006). The low mass loss percentages observed with C:P > 700 may be mediated by a reduced microbial activity (Mathuriau and Chauvet, 2002; Abelho, 2001; Ardón and Pringle, 2008), in addition to the low palatability for macroinvertebrates.

Despite of the significant influence of physical and chemical properties of leaf litter on mass loss percentages, our results suggest that such correlation is not strongly mediated by macroinvertebrate consumers in the study stream. Firstly, abundance of shredder insect families was low in comparison to other sites in Colombia and the Neotropics (e.g. Chará-Serna *et al.*, 2010; 2012). However, the observed dominance of collector families in the litter bags has been also found in Andean and Amazonian streams (Rueda-Delgado *et al.*, 2006; Chará *et al.*, 2007). Thus, the discussion on the role of shredders across Colombian life zones might be as relevant as it was at a global scale during the past decade (e.g. Wantzen *et al.*, 2008). Secondly, the not significant correlation between macroinvertebrate parameters and leaf quality (toughness and C:N and C:P ratios), suggested that macroinvertebrates colonized the litter bags for reasons other than feeding. Some authors have suggested that macroinvertebrates colonize leaf packs in search of refuge (Dudgeon and Wu, 1999) or as resources for building their cases (e.g. Calamoceratidae: *Phylloicus*; Rincón and Martínez, 2006). At one end, tough leaf litter may provide a durable habitat, and, at the other, soft and more breakable litter (low C:N ratios) may provide a wide range of particle size to be used for building cases or to be collected. However, our results should be seen as preliminary as we did not study the succession process of macroinvertebrates community, and therefore a colonization approach might provide more reliable data. Moreover, to be certain about the paucity or low richness of shredders in a study site and their relationships with leaf litter and detritus, efforts should be done to determine the diet of insects in order to properly assign FFG (e.g. Chará-Serna *et al.*, 2010; 2012). Extrapolations from the literature, even from other tropical locations, should be avoided, and therefore, the allocation of FFG according to Cummins *et al.* (2005) and Tomanova *et al.* (2006) in our study might over estimate the incidence of omnivores, and hide the facultative shredding observed in some Elmidae, Chironomidae, Baetidae, Hydropsychidae, Tipulidae and Perlidae (Tomanova *et al.*, 2006).

This study concluded that a great range of leaf litter mass loss (14.6 -98.1 %) is observed in tree species commonly planted in tropical urban and rural riparian zones, as a consequence of reforestation practices with native and exotic species. Although intuitively differences in rates can be partially attributed to leaf origin, future studies need to include a larger and balanced data set (see preliminary data in Table 2). Differences in mass loss percentages were explained by leaf toughness and C:P ratio as elsewhere but surprisingly not by C:N ratio. No significant influence of leaf litter species was observed on the associated macroinvertebrates community, and probably species-specific relationships depending on the leaf quality are more likely. Due to the paucity of shredders in the study stream, the exposed leaf species probably provided refuge rather than food, but it remains to be tested across a wide range of life zones. This study warns that although differences in leaf quality in native and exotic species may have no strong influence in occurrence of stream macroinvertebrates, differential breakdown rates may have important ecosystem-level consequences in organic matter processing and carbon downstream exports. In our case, reforesting riparian zones with exotic trees with fast decomposing leaf litter may increase organic carbon exports and reduce retention in urban and rural watersheds. Although the results from the first trial cannot be quantitatively analyzed due to the uncertainty imposed by the flash flood disturbance on the litter bags (Table 2), they suggested that native Neotropical leaf litter may exhibit slower breakdown rates than exotic species, at least for the range of species covered in the study. Future studies should test the hypothesis that native (tropical) tree species exhibit a greater concentration of defensive compounds against terrestrial herbivores, thus indirectly influencing the effects of instream detritivores (Coley, 1983; Rincón and Martínez, 2006; Wantzen *et al.*, 2008; Boyero *et al.*, 2012a). An alternative hypothesis states that exotic plant species exhibited pre-adaptations (low palatability) that allowed them to survive to selective forces such as foliar herbivorism and leaching in the tropical climates, and for this reason they have become "naturalized" and dominant in many landscapes (Lugo and Helmer, 2004; Boyero *et al.*, 2012a).

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