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Colonisation of low- and high-quality detritus by benthic macroinvertebrates during leaf breakdown in a subtropical stream

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ABSTRACT

Leaf litter in streams is exploited by benthic macroinvertebrates, and leaf traits may influence colonisation by this group. This study aimed to compare the leaf decomposition rates, structure, and composition of the macroinvertebrate fauna colonising the litter of plant species with contrasting leaf traits. Litter bags from two native plant species (*Sebastiania brasiliensis* and *Campomanesia xanthocarpa*) and two non-natives (*Hovenia dulcis* and *Platanus* × *acerifolia*) were incubated in a subtropical stream. After 7, 14, 21, and 28 days, four leaf bags for each species were removed, and the leaf decomposition rates, density of organisms and trophic guilds, taxonomic richness, and functional composition of the macroinvertebrates were compared. The decomposition rates and densities of organisms, shredders, and collector–gatherers were higher for the leaves considered to be better quality, with lower C:N and Lignin:N ratios (from *S. brasiliensis* and *H. dulcis*). Additionally, the taxonomic and functional compositions of the macroinvertebrates were different for these leaves. In contrast, the species richness and density of the other guilds showed no significant difference between species. This study shows that detritivorous groups prefer leaves of better quality, and most results may be influenced by the high nutritional content and low amount of compounds that complicate fragmentation, such as tannins, lignin, and cellulose. Therefore, the effects of the replacement of riparian plant species on the local macrofauna depend of the traits of the introduced and replaced plant, regardless of their origin.

Introduction

The benthic macroinvertebrate fauna include several groups important for metabolism in aquatic systems and may influence nutrient cycling, detritus decomposition, energy flow, and sediment mixing (Wallace and Webster, 1996). Among the components of the substrate, leaves are usually the dominant energy source for the communities of low-order streams (Vannote et al., 1980). Upon entering the aquatic environment, this organic material is subjected to physical fragmentation (by the flow), microbiological action (particularly fungal action), and being used and processed by detritivorous benthic macroinvertebrates (Hieber and Gessner, 2002).

Studies have suggested that macroinvertebrates prefer leaf detritus of certain plant species over others (Friberg and Jacobsen, 1994; Graça, 2001; Moretti et al., 2007). This preference is mainly due to structural and chemical leaf traits, which can vary significantly among different plant species, increasing or decreasing the palatability and quality of the resources (Webster and Benfield, 1986; Moretti et al., 2007). Generally, decay rates increase with a high essential nutrient content of the leaves and decrease with a high degree of chemical and physical plant defences (Canhoto and Graça, 1996). A greater amount of nitrogen may also indirectly affect decomposition by increasing the utilisation by macroinvertebrates and, consequently, secondary production (Leroy and Marks, 2006), also stimulating the action of the heterotrophic microorganisms associated with the leaves (Gulis and Suberkropp, 2003). A high fibre content composed of cellulose and lignin, which increase the hardness of the leaf, can hinder the action of invertebrates (Gessner, 2005), as can the presence of chemical inhibitors, such as tannins (Gessner and Chauvet, 1994).

The replacement of species in riparian zones can affect the quality of the available detritus and the colonisation by detritivores (Swan et al., 2008). If the introduced species are nitrogen-fixers, it is expected that decomposition will be accelerated, whereas degradation rates will be slow for chemically or physically protected species (Graça and Canhoto, 2006). Thus, the introduction of plant species with characteristics that are different from the species

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being replaced can affect nutrient cycling, the community structure of invertebrates and microorganisms (Hieber and Gessner, 2002; Alonso et al., 2010), and food webs (Cummins et al., 1989).

Studies investigating the influence of leaf quality on macroinvertebrate communities have been performed with different approaches. Some show that there are differences in colonisation and assemblage compositions (Abelho and Graça, 1996; Pozo et al., 1998) and rates of decomposition (Canhoto and Graça, 1996; Pozo et al., 1998), whereas others argue if the leaf preferences of macroinvertebrates are related to the origin of the detritus (Pereira et al., 1998; Royer et al., 1999). The present study aimed to compare, in a subtropical stream, the decay rates of leaves and the structure and composition of the macroinvertebrate community using plant species with contrasting leaf traits. The hypotheses of the study were as follows: (i) decay rates are determined by the chemical composition of the detritus, and leaves considered more labile decompose more rapidly; (ii) macroinvertebrates, particularly shredders, have a preference for more nutritious plants; and (iii) the macrofaunal structure (taxonomic richness, total density, and density of the functional feeding groups) and composition are determined by leaf traits. Therefore, this work aimed to contribute to the understanding of macroinvertebrate community ecology, exploring the influence of the chemical differences of leaf litter and generating data for the discussion of the factors that generate these differences, such as the replacement of plant species in riparian environments.

Materials and methods

Study area

The study was conducted in a second-order stream (27°42′58.7″ S; 52°14′43.8″ W, 660 m a.s.l) named Rio Cravo, located in southern Brazil. The draining area is 668.3 ha, the riparian zone is 50 m wide, and the slope is approximately 16.5%. The land use is 40% agriculture and 15% native vegetation. The annual mean temperature is 18 °C, and the annual rainfall is 1800 mm. The riparian vegetation is an extension of the Atlantic Forest (Oliveira-Filho et al., 2006) and exhibits a transition between Seasonal Semidecidual Forest and Araucaria Forest (Budke et al., 2010). Among the native trees in the surrounding area of the stream are: *Araucaria angustifolia* (Bertol.) Kuntze, *Ocotea puberula* (Rich.) Nees, *Cabralea canjerana* (Vell.) Mart., *Nectandra megapotamica* (Spreng) Mez., *Sebastiania brasiliensis* Spreng., and *Campomanesia xanthocarpa* O. Berg. Some exotic species are also present, such as *Eucalyptus grandis* Hill, *Hovenia dulcis* Thunb., and *Platanus* × *acerifolia* (Aiton) Willd.

The stream has well-developed surrounding vegetation and scarce land use. The benthic area of the water body is composed of a rocky and sandy substrate, and some areas have plant material from the surroundings. During the experiment, several abiotic variables were measured (three replicates) in each sampling day. These abiotic variables were as follows (mean ± standard error) based on three measures in each sampling day were as follows: width (2.1 ± 0.2 m); depth (0.3 ± 0.0 m); current velocity (0.7 ± 0.1 m s^{-1}); temperature (14.2 ± 0.1 °C); pH (6.4 ± 0.1); dissolved oxygen (7.9 ± 0.7 mg L^{-1}); total nitrogen (7.2 ± 0.6 mg L^{-1}); total dissolved solids (0.03 ± 0.0 mg L^{-1}); conductivity (51.5 ± 0.5 μS cm^{-1}); and alkalinity (1.8 ± 0.1 mg L^{-1}).

Plant species

Leaves of four tree species were selected for the field experiment by considering the leaf chemical properties and the presence of the species at the study site. All species selected are abundant near the streams of the studied region. The qualitative aspects of the leaves were used to group the plants to high- and low-quality species; an exotic species and a native species were chosen for each of these two treatments. The leaf quality of the four tree species was mainly determined by (i) the ratio of the carbon and nitrogen contents (C:N ratio), which is regarded as an indication of nutritional quality (Greenwood et al., 2007); (ii) the lignin, cellulose, and tannin content, which are compounds that hinder biological decomposition, and (iii) the ratio of the lignin and nitrogen contents. For all of the leaf properties, higher values suggest lower quality.

The total nitrogen was determined by the Kjeldahl method (Flindt and Lillebo, 2005), and the tannin content was determined by the Folin–Ciocalteu method (Bärlocher and Graça, 2005). The cellulose and lignin content was measured by the determination of the acid detergent fibre (Gessner, 2005). The total carbon of the leaves was based on the amount of organic matter (OM) (C = 0.47 × OM), which was determined by the ash-free method, with ignition at 550 °C for 3 h (Hauer and Lamberti, 2007).

Based on the chemical analyses, the species with high-quality leaves were as follows: *S. brasiliensis*, a native tree that frequently occurs along the water bodies of the study area, and *H. dulcis*, a species originating in Japan and China and that is cultivated to provide fruit and shade but became problematic due to its aggressive expansion in native forests. The low-quality leaf species were as follows: *C. xanthocarpa*, a native tree that has a wide distribution, mainly occurring in the wet and compact soils of plains and wetlands and in the soils of gentle slopes, and *P. acerifolia*, a native to Eurasia and North America that is readily found in subtropical and temperate climates, resulting in a considerable abundance in the study area.

Field experiment and laboratory procedures

In July 2010, litter bags that were 20 × 15 cm with 10 mm mesh and contained 2.5 ± 0.1 g of air-dried leaves were immersed along a 150 m stretch of the stream. The bags were arranged in four blocks with a similar water velocity. Four litter bags (one from each block) for each plant species were removed after 7, 14, 21, and 28 days of incubation in the stream. These days were defined and limited to the number of days in which there was 80% mass loss in the two species with the faster decomposition. The time required for this mass loss was estimated during the experiment. Thus, the curve with the initial days was modelled to define the final day. The value of 80% was chosen to obtain a balance between sufficient mass loss for the occurrence of some existing standard and very advanced mass loss, because the variance between replicas increases with time of incubation. During each sampling occasion, leaves were washed in the laboratory to remove any sediment and associated macroinvertebrates. The remaining leaf detritus were subsequently dried (35 °C for 72 h) to calculate the dry mass loss during the experiment and to obtain the decay rates for the four plant species. The associated macroinvertebrates were fixed in 70% alcohol and identified to the lowest possible taxonomic level. The identification keys of Merritt and Cummins (1996), Salles et al. (2004), Pes et al. (2005), and Mugnai et al. (2010) were used.

Data analysis

Using data of leaf samples at the beginning of the experiment, a variance analysis (one-way ANOVA with an *a posteriori* Tukey test) was applied to compare each one of the variables used in determining the initial detritus quality (lignin + cellulose, tannins, and C:N and lignin:N ratios).

For each species, the decay coefficient (k) was determined by adjusting the values of the remaining dry mass to a negative exponential model: $W_t = W_0 \cdot e^{-kt}$, where W_t is the remaining mass at time t (in days) and W_0 is the initial mass (Webster and Benfield,