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ORIGINAL ARTICLE

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Comparison of leaf decomposition and macroinvertebrate colonization between exotic and native trees in a freshwater ecosystem

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Abstract One of the most important sources of energy in aquatic ecosystems is the allochthonous input of detritus. Replacement of native tree species by exotic ones affects the quality of detritus entering freshwater ecosystems. This replacement can alter nutrient cycles and community structure in aquatic ecosystems. The aims of our study were (1) to compare leaf litter decomposition of two widely distributed exotic species (*Ailanthus altissima* and *Robinia pseudoacacia*) with the native species they coexist with (*Ulmus minor* and *Fraxinus angustifolia*), and (2) to compare macroinvertebrate colonization among litters of the invasive and native species. Litter bags of the four tree species were placed in the water and collected every 2, 25, 39, 71, and 95 days in a lentic ecosystem. Additionally, the macroinvertebrate community on litter bags was monitored after 25, 39, and 95 days. Several leaf chemistry traits were measured at the beginning (% lignin; lignin:N, C:N, LMA) and during the study (leaf total nitrogen). We detected variable rates of decomposition among species (*k* values of 0.009, 0.008, 0.008, and 0.005 for *F. angustifolia*, *U. minor*, *A. altissima* and *R. pseudoacacia*, respectively), but we did not detect an effect of litter source (from native/exotic). In spite of its low decay, the highest leaf nitrogen was found in *R. pseudoacacia* litter. Macroinvertebrate communities colonizing litter bags were similar across species. Most of them were collectors (i.e., they feed on fine particulate organic matter), suggesting that leaf material of either invasive or native trees was used as substrate both for the animals and for the organic matter they feed on. Our results suggest that the replacement of the native *Fraxinus* by *Robinia* would imply a reduction in the rate of leaf processing and also a slower release of leaf nitrogen to water.

Keywords Invasive species · Leaf litter decay · Community · Nitrogen · Lignin

Introduction

One of the most important sources of energy in aquatic ecosystems is the allochthonous input of dead particulate organic matter (e.g., detritus), especially in oligotrophic systems and headwater streams in temperate regions (Cummins 1974; Allan and Castillo 2007). Therefore, replacements of native by exotic tree species in riparian ecosystems can affect the quality and quantity of detrital inputs (Reinhart and VandeVoort 2006; Swan et al. 2008). Such changes can modify detritus processing through changes in microbial communities or macrodetritivorous colonization (Bärlocher and Graça 2002; Reinhart and VandeVoort 2006). All these changes finally alter nutrient cycling and community structure of the aquatic ecosystems. Most previous research on processing of native and non-native leaf litter has focused on streams and rivers, while lentic ecosystems have received less attention.

Macrodetritivorous invertebrates play a key role in the breakdown process of the allochthonous material in aquatic ecosystems because they fragment coarse particulate organic matter (CPOM, diameter > 1 mm) into fine particulate organic matter (FPOM, diameter between 1 and 0.0005 mm) (Cummins 1974) accessible to microorganisms, therefore contributing to recycling of nutrients. Several studies have shown that macroinvertebrates prefer leaf litter of some species over others (Friberg and Jacobsen 1994; Graça 2001). These preferences are related to different leaf properties, such us leaf toughness, nitrogen content, microorganism preconditioning of leaves, and presence of secondary metabolites, all of which determine leaf palatability (Webster and Benfield 1986; Graça 2001). Therefore a

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change in the quality of detritus inputs can modify the contribution of macrodetritivores to the whole breakdown process in the aquatic ecosystems.

During the last decades, native riparian vegetation has been modified by human activities, promoting major changes in species composition and allowing the colonization by exotic tree species (Naiman and Décamps 1997; Richardson et al. 2007). Exotic species can cause alterations on nutrient cycles and community structures (Royer et al. 1999; Ehrenfeld 2003; Harner et al. 2009). River corridors, lowland areas, and irrigated lands are among the most susceptible habitats to plant invasions in Europe (Chytry et al. 2009), especially in Mediterranean regions, where summer aridity prevents many exotics from establishing. Our study focuses on two widely distributed exotic species: the tree of heaven *Ailanthus altissima* (Mill.) (Simabouracea) and the black locust *Robinia pseudoacacia* (L.) (Fabaceae) (Sanz Elorza et al. 2004; Swan et al. 2008; DAISIE 2009). *A. altissima* is native to China, and it was introduced in Europe and America during the 18th century (Kowarik and Saumel 2007; Swan et al. 2008). It has colonized different areas, such us urban habitats, transportation corridors, borders of agricultural fields, riparian forests, and mesic and xeric woodlands (Kowarik and Saumel 2007; Swan et al. 2008). *R. pseudoacacia* is native to North America (Boring and Swank 1984), and it is found in semi-arid environments, gardens, recreational areas, and disturbed riparian forests. Unlike *A. altissima, R. pseudoacacia* can fix atmospheric N, which can increase the rate of N input to soils and/or continental waters, altering litter decomposition processes (Royer et al. 1999; Ehrenfeld 2003). *R. pseudoacacia* is one of the most widely planted American trees in Europe, and *A. altissima* is also spreading in North America and Europe, especially around terrestrial and aquatic ecosystems near urban areas (Swan et al. 2008; DAISIE 2009). *A. altissima* litter has shown a faster decay than that of coexisting native riparian tree species in lotic ecosystems (Swan et al. 2008). However, little is known about the ecological consequences of litter inputs from these invasive species in lentic ecosystems.

To understand the effects of these common tree invasions on freshwater ecosystems, we focus on two aims: (1) comparing the leaf litter decomposition rates and dynamics of both exotic species with the native species growing in the same habitat [*Ulmus minor* (Mill.) (Ulmaceae) and *Fraxinus angustifolia* (Vahl.) (Oleaceae)], and (2) comparing the macroinvertebrate colonization between the litters of the invasive and native tree species. In a previous study we found contrasting decay rates between those species in terrestrial ecosystems, *A. altissima* decomposing faster than *U. minor*, and *R. pseudoacacia* slower than *F. angustifolia* (Castro-Díez et al. 2009). Additionally, these exotic species release more nitrogen into the invaded soils (Castro-Díez et al. 2009). We hypothesized that leaf litter decomposition of these species in a freshwater ecosystem will have a similar trend than that found in terrestrial ecosystems, and that macroinvertebrates will prefer native over exotic litter. The results of this study can contribute to understanding the ecological consequences of the replacement of native by exotic tree species on lentic ecosystems.

Materials and methods

Study area and selected species

The experiment was conducted in a man-made lake at the Botanical Garden of Alcalá University (40°30′N, 3°20′W, altitude 596 m a.s.l.) (Province of Madrid, central Spain) from December 2006 to March 2007. Water depth in the study area averaged 92.3 ± 24 cm ($n = 6$) (mean ± SD). Physical–chemical properties ($n = 3$–6) of the lake water during the experiment were as follows: temperature: 9.7 ± 4.4°C, dissolved oxygen: 10.8 ± 0.4 mg O_2/l, conductivity: 844 ± 18 µS/cm, pH: 8.5 ± 0.37, nitrate: 2.4 ± 1 mg NO_3-N/l, ammonia: $<$0.05 mg NH_4-N/l, dissolved phosphorus: $<$0.05 mg PO_4-P/l, and hardness: 307.7 ± 12.6 mg $CaCO_3$/l. The shore was dominated by pebbles and the benthic area by fine sediment (particles $<$ 1 mm diameter). The aquatic vegetation was dominated by *Typha* sp.

The two exotic tree species (*Ailanthus altissima* and *Robinia pseudoacacia*) were selected because they frequently grow on the river banks of central Spain, and they are included in the catalogue of invasive species of Spain (Sanz Elorza et al. 2004). The native tree species, *Ulmus minor* and *Fraxinus angustifolia*, were selected because they naturally occur in habitats where *A. altissima* and *R. pseudoacacia* can be found (henceforth all species will be mentioned by their genus).

Leaf litter decomposition and macroinvertebrate community

Senesced leaves of the four species were collected in autumn. All leaves from each species were pooled and dried at laboratory temperature. For each species, ca. 3 g of air-dried leaves were aggregated into mesh bags (12 × 12 cm). Three additional air-dried grams per species were oven-dried (60°C for 96 h) to correct for water content, and ground for subsequent chemical analysis (see below). The upper side of the litter bag was made with a mesh size of 0.5 × 0.5 cm to allow macroinvertebrate colonization. The other side was constructed with a mesh size of 0.1 × 0.1 cm to reduce sediment entry from the benthic area. A total of 20 bags were constructed for each species. Five randomized groups with four bags of each species were attached to a brick with strings and situated on the benthic area of the lake. After 2, 25, 39, 71, and 95 days, one randomly chosen brick was collected (16 bags collected per date and four bags per species). This approach minimized disturbances to other litter bags during the sampling. Given than benthic conditions were homogeneous, and that bag distances were similar within and across bricks, each bag was considered as a replicate. Litter bags were placed into plastic bags and stored in a plastic cooler until taken to the laboratory. For the samplings of days 25, 39, and 96, macroinvertebrates were rinsed from the leaves over a 250-µm sieve, and placed in plastic bottles with 4% formalin. The remaining litter in the bags was gently washed, placed in paper bags, and dried at 60°C for 96 h. The number of macroinvertebrates in each sample was counted, and they were identified at family level under a stereomicroscope.

Leaf litter traits

Initial samples used for litter water content corrections were ground with a Culatti mill (< 1-mm particle size) and analyzed for total nitrogen content (Kjeldahl method), mass-based C/N ratio (Elementar varioMAX N/CN, Hanau, Germany), and lignin content (Van Soest method, Febertec, Ankom Fiber analyzer) and mass-based lignin/nitrogen ratio. Samples collected after 2, 25, 39, 71, and 95 days of experiment were also ground to analyze total nitrogen content (Kjeldahl automatic analyzer, Vapodest 50). Additionally, eight green leaves were collected for each species, and the fresh leaf area was measured with a Delta-T leaf area meter device (Delta-T, Cambridge). Green leaves were subsequently oven-dried (> 48 h at 60°C) and weighed. The ratio of leaf dry mass to fresh area (LMA) was determined for each species. This ratio was considered a proxy for leaf toughness (Choong et al. 1992).

Statistical analyses

The effects of time and leaf litter species on the percentage of remaining mass, total nitrogen content, and total number of macroinvertebrates per litter mass unit were assessed with a two-way ANOVA. A Tukey post-hoc test was conducted to compare species after the two-way ANOVA. Rough data were used for remaining mass and total nitrogen, while the number of invertebrates was square-root transformed to improve normality. Additionally, a linear regression between percentage of remaining material (ln transformation) and time (days) was conducted for each tree species to estimate the decay coefficient k (equal to slope) and number of days to reach 50% of mass loss (T50) (Bärlocher 2005). For both parameters, the 95% confidence intervals were estimated. Differences in k or T50 values between tree species were considered significant when their 95% confidence limits did not overlap. To analyze the macroinvertebrate community, a principal component analysis (PCA) was performed on the average number ($n = 4$) of macroinvertebrate for each family, each sampling period (25, 39, and 95 days), as well as each tree species. This ordination provided an overall view of the temporal changes on communities along the study period for each species, and revealed the most influential families in that ordination (scores of each family in each axis). Data were log-transformed prior to analysis. Results were interpreted on the basis of the scores obtained for the two-first components. Differences in green leaves LMA and freshly fallen content of lignin, nitrogen, lignin:N and C:N among tree species were assessed using a one-way ANOVA test (for data with equal variances, Levene test) or a Kruskal–Wallis test (for unequal variances). When the species effect was significant ($p < 0.05$), a post-hoc test (Tukey test) or a Mann–Whitney U test was conducted to check for differences between pairs of species. Univariate tests were conducted using SPSS 15.0 software (Landau and Everitt 2004) and PCA was conducted using CANOCO 4.5 software (Leps and Smilauer 2003).

Results

At the beginning of the experiment, *Robinia* had higher contents of nitrogen and lignin, higher lignin:N ratio and lower C:N than other species ($p < 0.05$; ANOVA or Kruskal–Wallis test) (Table 1). *Ulmus* had higher leaf mass per area (LMA) than other species (Table 1).

Over the course of the experiment, *Fraxinus* tended to have the lowest and *Robinia* the highest remaining leaf mass (Fig. 1a) and *Ailanthus* and *Ulmus* showed similar proportions of remaining mass (two-way ANOVA, Tukey test; $p < 0.05$) (Fig. 1a; Table 2). Time, species and their interaction were significant for remaining litter mass and litter N ($p < 0.05$, two-way ANOVA) (Table 2). Therefore, dynamics of mass and N loss were different between species (Fig. 1a, b). *Robinia* showed the highest litter nitrogen content through the study period (Table 2; Fig. 1b).

The decay rates (k) and days to reach the 50% of leaf mass loss (T50) differed across species, with the strongest difference between *Fraxinus* (highest decay rate and lowest T50) and *Robinia* (lowest decay rate and highest T50) (Table 3).

The total number of macroinvertebrates per gram of remaining leaf material increased with time, but was not affected by litter type ($p = 0.156$, two-way ANOVA) (Fig. 1c; Table 2). Only five families of macroinvertebrates were found in the leaf litter (Fig. 2), four of which were insects (Caenidae, Baetidae, Chironomidae, and Cordulegastridae) and the other was a mollusc (Physidae). None of them were shredders (i.e., animals that eat CPOM, Cummins 1974; Cummins et al. 1989). The PCA analysis reduced the five families to two main factors that explained 88% of variance (Axis 1–73% and Axis 2–15%) (Fig. 2). Invertebrates found in the litter of *Robinia*, *Ulmus*, and *Ailanthus* exhibited similar temporal trends, moving from a dominance of Baetidae at the beginning of the experiment, to a higher diversity of

Table 1 Mean values (±SD) for percentage of lignin, lignin/nitrogen, carbon/nitrogen, leaf mass area, and mg nitrogen per gram of leaf or freshly fallen litter for each species

	Ailanthus	*Ulmus*	*Robinia*	*Fraxinus*
% Lignin	5.23 ± 0.25^{a}	4.78 ± 0.77^{a}	14.5 ± 0.84^{b}	6.02 ± 0.46^{a}
Lignin:N	10.0 ± 1.11^{a}	10.3 ± 1.12^{a}	21.1 ± 2.30^{b}	12.2 ± 1.76^{a}
C:N	$47.2 \pm 2.9^{a,b}$	42.0 ± 4.1^{a}	29.4 ± 0.9^{c}	52.6 ± 2.1^{b}
LMA (mg/cm^2)	7.9 ± 0.6^{a}	11.8 ± 1.2^{b}	7.3 ± 1.3^{a}	8.7 ± 1.6^{a}
mg N/g leaf	$9.4 \pm 0.9^{a,b}$	10.2 ± 1.2^{b}	13.3 ± 0.4^{c}	8.2 ± 0.6^{a}

Different letters within a row indicate significant differences among species for each parameter (ANOVA test with Tukey test for % Lignin, Lignin:N, C:N and LMA (mg/cm^2), and Kruskal–Wallis test followed by Mann–Whitney *U* test for mg N/g leaf, $p < 0.05$)

families, and higher relevance of Caenidae and Chironomidae at the end (Fig. 2). By contrast, invertebrates found in *Fraxinus* litter showed a more constant family composition through the time, as the three sampling times (after 25, 39, and 95 days of incubation) were closer each other than for the other types of litter (Fig. 2).

Discussion

The present study has shown a contrasting decay dynamics between the litter of two native and two coexisting exotic tree species. Similar to our decomposition study in soils, we found that *Robinia* litter decomposed slower than *Fraxinus* litter (Castro-Díez et al. 2009). However, contrary to our findings in soils, where *Ailanthus* litter lost mass and N faster than *Ulmus* litter, both species exhibited similar decay dynamics in water. Several authors have found that leaf nitrogen has a positive association with leaf decay (see Enriquez et al. 1993; Zhang et al. 2008 for reviews). However, in our study, the species with the highest leaf nitrogen content, *Robina*, had the lowest litter decay. In aquatic ecosystems, microbes can take up nitrogen from both the leaf litter and the water column (Suberkropp and Chauvet 1995; Suberkropp 1998; Driebe and Whitham 2000): therefore, the initial amount of nitrogen in the leaf litter may not limit microbial activity if enough nutrients are available in water. Other studies have shown that leaf nitrogen content is not a good predictor of leaf decay in freshwater ecosystems (Gessner and Chauvet 1994; Royer et al. 1999; Driebe and Whitham 2000). Royer et al. (1999) showed that leaf litter decay of the exotic tree *Eleagnus angustifolia* depended more on the water hardness than on the initial leaf nitrogen content. Therefore differences in leaf decomposition across species may be explained by differences in other physical–chemical traits, such us lignin, cellulose, or/and tannin content (Webster and Benfield 1986; Gessner and Chauvet 1994), which also affect palatability of leaves for macroinvertebrates (Cummins 1974; Cummins et al. 1989). Particularly, lignin has been shown to slow down leaf litter decay in freshwater ecosystems (Webster and Benfield 1986; Gessner and Chauvet 1994) because it binds to cellulose or hemicellulose forming lignocellulose, which is less accessible to enzymatic processing (Webster and Benfield 1986). This may explain the low decay of *Robinia* litter, which had the highest lignin content and lignin:N ratio.

The total density of macroinvertebrates per mass of remaining litter was similar across species. However, the temporal analysis of the community revealed that macroinvertebrates colonized *Fraxinus* litter faster than the litter of the other species, likely due to the more rapid leaf decay, which may have produced a higher amount of FPOM on leaf litters. FPOM is the main food resource for collectors (as Chironomidae) and it probably remains on the litter bags because of the lack of flow in the aquatic system. Collectors also have the ability to process leaves (at least under laboratory conditions) (Bird and Kaushik 1985), probably by consuming the microbes that grow in leaves. The aggregation of collectors in litter bags suggests that leaf material of either invasive or native species was mainly used as an indirect source of food. In contrast, macroinvertebrate colonization in the litter of *Robinia*, *Ailanthus*, and *Ulmus* was slower, reaching the highest density at day 95. In these species, the dominant families at the end of study were Caenidae and Chironomidae. The density of Chironomidae has been found to be high in the litter of both native and non-native trees in lotic ecosystems (Harner et al. 2009). Our experiment was conducted in a lentic ecosystems without shredders (e.g., invertebrates that feed directly on CPOM), and therefore most of the decomposition process is caused by the microbial activity (and maybe by collectors). However, with lotic aquatic ecosystems, such as headwater streams, the results of this experiment might have been different: Firstly, lotic systems are dominated by shredders, which probably results in faster litter-decay rates for all species (Cummins 1974; Cummins et al. 1989). Secondly, shedders have a high plasticity to exploit different sources of leaf food (Graça et al. 2001), which would lead to less differences across species in decay rates. Thirdly, the energy of the flowing water also helps to fragment the litter, facilitating macro and micro-organism colonization and speeding up breakdown processes, regardless of the origin (native or exotic) of the litter.

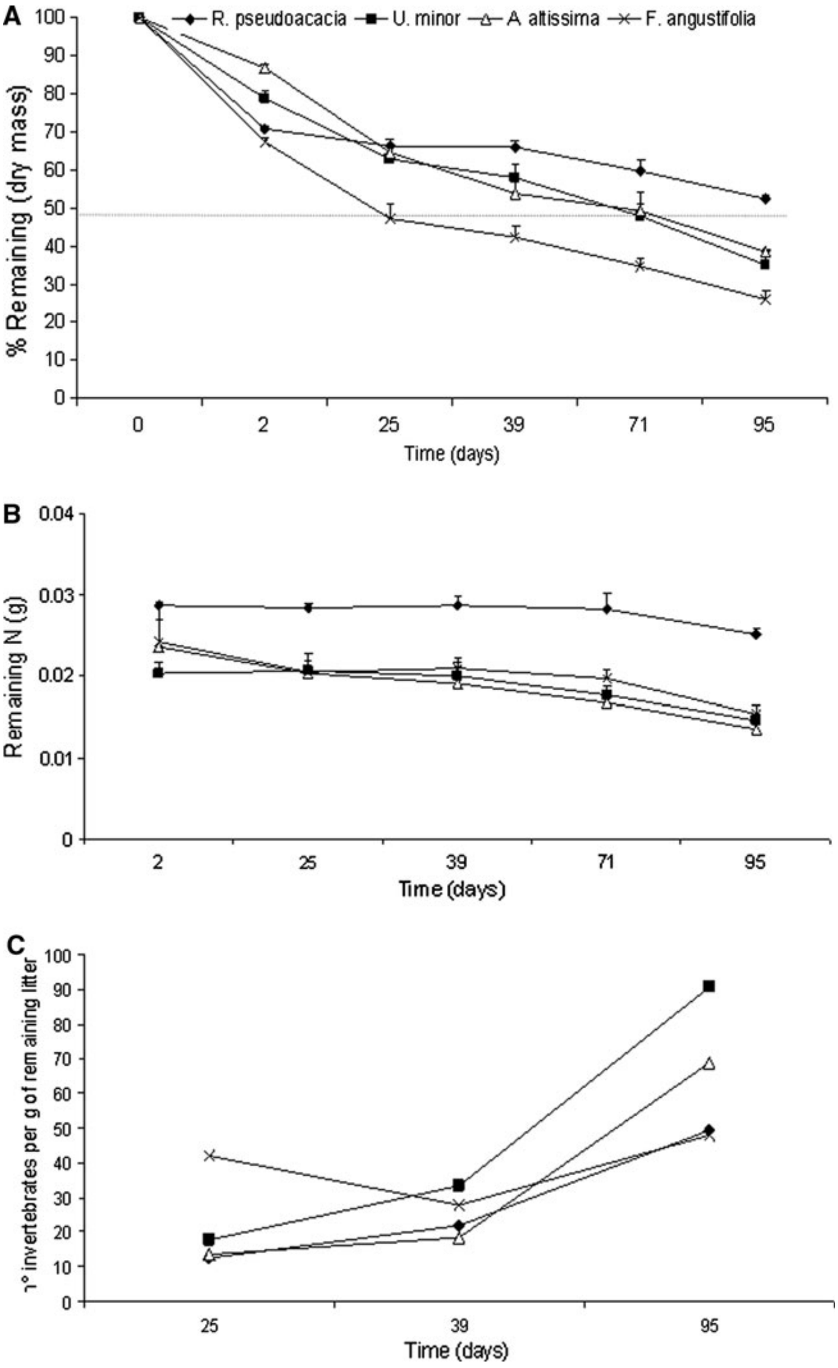


Fig. 1 Percentage of remaining leaf litter for each tree species after 0, 2, 25, 39, 71, and 95 days of sampling collection (**a**). Total nitrogen (g N) in the remaining litter for each tree species, after 2, 25, 39, 71, and 95 days of incubation (**b**). Total number of macroinvertebrates per gram of remaining material in leaf litter for each tree species after 25, 39, and 95 days of incubation (**c**). **a**, **b** Mean (± SD) is shown and **c** SD is not shown for clarity ($n = 4$)

The effects of the replacement of native riparian-forest species by exotic ones in terrestrial and aquatic ecosystems are context-dependent (Bärlocher and Graça 2002; Harner et al. 2009). For example, studies comparing litter decomposition between the exotic *Eleagnus angustifolia* and the native *Populus deltoides*, found faster decay in the nitrogen-rich litter of *Eleagnus* in a lotic aquatic ecosystem, but found the reverse trend in a terrestrial ecosystem (Harner et al. 2009). Similarly, *Ailanthus altissima* litter decomposed faster than *Ulmus minor* in a terrestrial ecosystem (Castro-Díez et al. 2009), but in our lentic system, both species decomposed at a similar rate. By contrast, *Robinia pseudoacacia* litter decomposed slower than *Fraxinus angustifolia* both in the terrestrial (Castro-Díez el al. 2009) and in the lentic ecosystems. Therefore, the replacement of the native *Fraxinus* by the exotic *Robinia* would slow down leaf processing and leaf nitrogen release in lentic ecosystems, causing an increase of the long-term reservoir of nitrogen. This can have drastic consequences in oligotrophic systems where leaves are the main source of food, as primary production is limited by light and nutrients. Our

Table 2 Results of the two-way analysis of variance assessing the effects of incubation time and leaf litter species on the proportion of remaining mass, amount of remaining nitrogen, and number of macroinvertebrates per gram of remaining leaf material

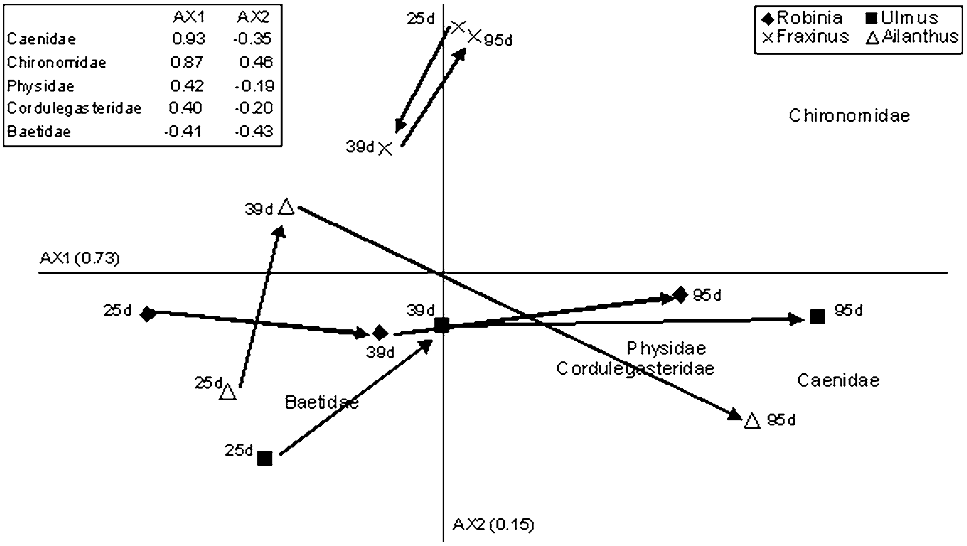
	ANOVA two-way			Tukey test			
	df	*F*	*p*	*Robinia*	*Ailanthus*	*Ulmus*	*Fraxinus*
% Remaining							
Time	4	442.7	0.000				
Species	3	195.0	0.000	c	b	b	a
Time × species	12	16.8	0.000				
Nitrogen							
Time	4	35.1	0.000				
Species	3	119.4	0.000	b	a	a	a
Time × species	12	2.04	0.036				
Invertebrates/leaf							
Time	2	20.3	0.000				
Species	3	1.84	0.156	a	a	a	a
Time × species	6	1.09	0.387				

A post-hoc Tukey test was conducted for species. Different letters between species indicate significant differences for each variable

Table 3 Decomposition rates (k, day^{-1}) with 95% confidence intervals and number of days to lose 50% of initial litter mass (T50) for each species

Species	k (lower and upper intervals)	T50
Fraxinus angustifolia	0.009 (0.008–0.010)^{b}	26.8 (17.2–38.3)^{a}
Ulmus minor	0.008 (0.007–0.009)^{b}	57.3 (44.6–73.6)^{b}
Ailanthus altissima	0.008 (0.007–0.009)^{b}	60.3 (45.7–79.0)^{b}
Robinia pseudoacacia	0.005 (0.003–0.006)^{a}	96.6 (68.7–184.7)^{b}

R^2 values exceeded 0.70 and $p < 0.001$ for all linear regression models. Different letters indicate significant differences among species for k or T50 values ($p < 0.05$; overlap test)



	AX1	AX2
Caenidae	0.93	-0.35
Chironomidae	0.87	0.46
Physidae	0.42	-0.19
Cordulegasteridae	0.40	-0.20
Baetidae	-0.41	-0.43

Fig. 2 Ordination of the macroinvertebrate communities in the leaf litter bags based on a principal component analysis (PCA) of the densities (as number of individuals of each family per dry weight of remaining leaf material) found in the litter of every tree species and sampling period (25, 39, and 95 days). For each *axis* the eigenvalue is shown in *parenthesis*. The relative weight of each family on the main components is shown by the position of each family in the ordination

results show that the effects of litter on decomposition are species-dependent rather than species origin (native/exotic)-dependent. The higher leaf nitrogen content of *Robinia* did not speed up the litter decay in this freshwater ecosystem. By contrast, the litter of this species showed the slowest rates of mass and nitrogen loss among the studied species, probably due to its high lignin content. The macroinvertebrate community colonizing litter bags was similar across tree species, being mostly composed of collectors. Therefore, leaf material of either invasive or native species was used mainly as substrate and indirect source of food for macroinvertebrates. We can conclude that the replacement of the native *Fraxinus* by *Robinia* would slow down leaf decay and release of leaf nitrogen to water, while the replacement of *Ulmus* by *Ailanthus* would have less consequences for the nutrient cycle in lentic ecosystem.

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