

The role of native riparian tree species in decomposition of invasive tree of heaven (*Ailanthus altissima*) leaf litter in an urban stream¹

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Abstract: Increasingly, interactions between human and natural systems centre on the multi-scale restoration of ecosystems. Humans rely on ecosystem services provided by streams, yet human activities degrade water quality worldwide. Re-planting streamside vegetation is a common restoration practice, since trees reduce runoff and stabilize banks. But does riparian tree biodiversity matter? Detrital inputs from riparian vegetation impact in-stream processes, e.g., leaf decomposition. Since the increasing distribution of invasive plant species alters the structure of streamside forest communities, input of invasive litter to streams could alter such processes. We followed decomposition rates of the invasive tree of heaven (*Ailanthus altissima*, TOH) and 6 native leaf species in an urban stream and complemented this effort with laboratory feeding experiments employing the same treatments and 2 common aquatic detritivores. TOH breakdown was rapid, exceeding native leaf decay. Mixing TOH with native species reduced its decay compared to TOH alone; however, the feeding study demonstrated that detritivores preferred TOH over native species. Subsequent estimates of species-specific structural integrity revealed TOH poorly resisted breakage. The relatively tougher nature of native species may slow TOH breakdown by armouring the invasive litter against the highly variable flow regime characteristic of urban streams. The presence of native riparian tree species may mediate how invasive trees decompose in human-impacted streams.

Keywords: detritivore, invasive species, leaf decomposition, riparian forest diversity, stream restoration, urban streams.

Résumé : De plus en plus, les interactions entre les humains et la nature sont centrées sur la restauration à plusieurs échelles des écosystèmes. Les humains comptent sur les services fournis par les écosystèmes tels les ruisseaux malgré le fait que les activités humaines dégradent la qualité de l'eau partout sur la planète. Revégétaliser les rives des ruisseaux est une pratique de restauration commune puisque les arbres réduisent le ruissellement et stabilisent les berges. Mais est-ce que la biodiversité des arbres ripariens a de l'importance? Les apports détritiques de la végétation riparienne ont un impact sur les processus se déroulant dans le ruisseau, par exemple la décomposition des feuilles. Puisque la distribution croissante des espèces invasives de plantes modifie la structure des communautés forestières riveraines, l'apport de litière de ces plantes dans les ruisseaux pourrait en modifier les processus. Nous avons suivi les taux de décomposition de l'ailante glanduleux (*Ailanthus altissima*, AG), une espèce invasive et 6 espèces indigènes de feuillus dans un ruisseau en milieu urbain. Une expérience complémentaire a été réalisée en laboratoire en utilisant les mêmes traitements pour alimenter 2 détritivores aquatiques communs. La décomposition des feuilles de AG était plus rapide que celle des espèces indigènes. En mélangeant des feuilles de AG avec celles d'espèces indigènes, on réduisait la vitesse de décomposition par rapport aux feuilles de AG seules. L'expérience d'alimentation a démontré que les détritivores se nourrissaient plus rapidement de feuilles de AG que de celles d'espèces indigènes. Des estimés de l'intégrité structurale spécifique à l'espèce ont démontré subséquemment que les feuilles de AG étaient peu résistantes à la rupture. La nature relativement plus résistante des feuilles d'espèces indigènes pourrait réduire la vitesse de rupture des feuilles de AG en les protégeant des grandes variations du régime d'écoulement caractéristiques des ruisseaux urbains. La présence d'espèces indigènes riveraines pourrait tempérer la façon dont les espèces invasives d'arbres se décomposent dans les ruisseaux affectés par les activités humaines.

Mots-clés : décomposition des feuilles, détritivore, diversité forestière riparienne, espèce invasive, restauration de ruisseau, ruisseau urbain.

Nomenclature: USDA, 2008.

Introduction

Interactions between human and natural systems focus on restoration of ecosystems at various scales and across diverse spaces (Falk, Palmer & Zedler, 2006). Of paramount importance is the restoration of biodiversity to compensate for loss of native, pre-disturbed species assemblages (Falk, Palmer & Zedler, 2006). Critical habitats such as streams

and rivers are quite disproportionately subjected to human activities, leading to degradation of water quality worldwide and subsequent alterations of key ecosystem services (Paul & Meyer, 2001). Re-planting of streamside vegetation is a common restoration practice, since riparian vegetation can reduce nutrient run-off, stabilize banks, and moderate extremes in water temperature (Gregory *et al.*, 1991; Sweeney, 1993; USDA, 1996; Naiman & Décamps, 1997). Urban streams in particular are susceptible to extensive changes to riparian forest communities, either via complete

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deforestation or replacement by invasive species (Paul & Meyer, 2001; Zipperer, 2002; Groffman *et al.*, 2003; Hope *et al.*, 2003; Burton, Samuelson & Pan, 2005). Decay of senesced organic matter derived from riparian vegetation is a major ecosystem function performed by streams, critical to both energy flow to higher trophic levels and nutrient transport to downstream water bodies, and alterations in patterns of riparian species richness likely modify this process (Cummins *et al.*, 1989; Wallace *et al.*, 1997; Hall, Wallace & Eggert, 2000; Ponsard, Arditi & Jost, 2000). Therefore, restoration of riparian forests should not only improve habitat stability and attenuation of nutrient inputs to streams, but the tree species composition planted should have in-stream consequences for important ecosystem processes, specifically decomposition of organic matter (Swan & Palmer, 2004).

The rate at which senesced plant litter degrades is mediated by a number of abiotic and biotic factors and is related to tree species identity (Golladay, Webster & Benfield, 1983; Webster & Benfield, 1986; Chauvet, 1987; Cummins *et al.*, 1989; Ostrofsky, 1997; Haapala, Muotka & Markkola, 2001). Taxa-specific differences in litter nutritional quality for both microbial and invertebrate consumers exists in both terrestrial and aquatic ecosystems (Bärlocher & Kendrick, 1975; Webster & Benfield, 1986; Cornelissen, 1996; Ostrofsky, 1997; Charcosset & Gardes, 1999; Gartner & Cardon, 2004). Invertebrate detritivores generally exhibit significant preferences for labile litter, such as maples and dogwoods, over more refractory litter, such as oaks (Campbell & Fuchshuber, 1995; Findlay *et al.*, 1996; Swan & Palmer, 2006a). Therefore, approaches to stream restoration that include planting diverse riparian tree species should have implications for rates of decomposition and detritivore performance (Wallace *et al.*, 1997; Swan & Palmer, 2004; LeRoy & Marks, 2006; Swan & Palmer, 2006a).

Replacement of native species by non-natives, as is common in urban ecosystems (Zipperer, 2002; Burton, Samuelson & Pan, 2005), could present consumers with very different resources in terms of quality. For example, loss of an oak species would result in loss of a very refractory resource for consumers, while replacement with a labile invasive might induce faster feeding and overall higher rates of decomposition. However, loss of a native labile species and replacement with a refractory invasive should drive decay rates down. Assessment of such a situation is complicated by the fact that, in general, streamside communities do not become completely replaced with invasives (Zipperer, 2002; Burton, Samuelson & Pan, 2005; Walsh *et al.*, 2005). Therefore, in-stream consumers forage on mixtures of leaf species that can include the invasive species. Subsequent foraging decisions, *e.g.*, preferential *versus* compensatory feeding, could become altered by the presence of the invasive, changing any emergent effect of biodiversity on decomposition rates overall (Swan & Palmer, 2006b).

If invertebrate feeding contributes substantially to litter decay (Anderson & Sedell, 1979; Cuffney, Wallace & Luthgart, 1990; Luthgart & Wallace, 1992; Graça, 2001), feeding activity and preference can play a role in decay of speciose litter. For example, Swan and Palmer (2006b) demonstrated that preferential feeding by a leaf-chewing aquatic

detritivore (hereafter “shredders”, *sensu* Cummins & Klug, 1979) resulted in slower than predicted decay of speciose litter. The shredders, when given a choice, left refractory species alone and fed on more labile species in a mixture. However, shredders accelerated their feeding on refractory species when labile litter was not available. Consumers, then, can mediate how diversity invokes emergent effects on ecosystem processes. In the case of litter decomposition, this is related to interspecific variation in quality. When an invasive species establishes and contributes litter to the stream, the relative quality of litter resources changes for consumers. While studies examining litter decay of invasives alone do exist (Dangles, Jonsson & Malmqvist, 2002), no study to date has estimated how decay of invasive litter changes in the presence of native leaf species. In the context of riparian restoration efforts, the relative emphasis on planting and maintaining natural levels of forest biodiversity could have implications for decay of litter from invasive species that may colonize a location after restoration is said to be complete.

A gardener in Philadelphia introduced tree of heaven (*Ailanthus altissima*) to North America in 1740, and this species subsequently became widely available in nurseries by 1840 (Hu, 1979). This highly successful colonizer spreads clonally and produces large quantities of seeds, thus establishing quickly in newly opened forest patches and edge habitats, both typical in urban areas (Bazzaz, 1979; Hu, 1979; Feret, 1985; Heisey, 1990). Furthermore, tree of heaven inhibits colonization by native tree species by expressing allelopathic qualities (Heisey, 1990). Tree of heaven (hereafter, TOH) is quite common in Maryland, USA, where this study took place. Given its fast growth, we predicted litter from this species to be rather labile, as is typical of native, fast-growing taxa (Webster & Benfield, 1986). When mixed with more refractory native litter species (*e.g.*, red maple, white oak; also common to Maryland), we expected that in-stream consumers would accelerate their feeding on TOH relative to when TOH was alone. Native tree species, then, should mediate how this invasive decays in stream ecosystems.

Many stream restoration efforts embrace riparian replanting as a cost-effective means by which to stabilize stream banks, retain nutrients, and provide shade (Sweeney, 1993; USDA, 1996). Streamside forests in general provide for these needs, yet the choice of certain species over others can have implications for in-stream food webs given interspecific variation in leaf quality to consumers. The emergent effects of diverse leaf assemblages have been reported elsewhere for relatively pristine ecosystems (Swan & Palmer, 2004; LeRoy & Marks, 2006), highlighting the role riparian tree diversity plays in leaf decomposition in streams. Given our knowledge of how consumers respond to leaf quality and diversity (Swan & Palmer, 2006b), restoration of native biodiversity may also play a role in how invasive leaf species decay in streams. Our general goal here was to address this idea in an urban stream. Specifically, we asked: (1) How does TOH decay compare to that of native leaf species in an urban stream? (2) Does mixing TOH with native leaves change its decay rate? and (3) Is any such change mediated by aquatic detritivores? We addressed these questions by carrying out a field decomposition study of TOH

and litter of 6 native tree species and a complementary laboratory feeding study employing the same leaf species and focusing on 2 common aquatic detritivores.

Methods

We carried out the field component of this study in Herbert Run, in Baltimore County, Maryland, USA (39° 15.035' N, 76° 42.720' W; 50 m asl). This first-order Piedmont stream drains 0.78 km², of which 31.1% classifies as urban (36.0% impervious surface, estimated using GISHydro [http://www.gishydro.umd.edu]). Herbert Run resides within the Eastern Piedmont physiographic province of Maryland and exhibits a riffle–pool–run channel geomorphology. During the study, stream width varied from 1 to 2 m, depth at baseflow averaged 7.7 cm, dry weather water velocity averaged 46 cm·s⁻¹, and water temperature ranged from 2 to 11 °C, averaging 6.7 °C.

We estimated leaf decomposition rate using a standard litter bag technique (Benfield, 1996) for tree of heaven (*Ailanthus altissima*) and 6 common native species: blackgum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), and white oak (*Quercus alba*). We allocated ~2 g freshly fallen, senesced litter to individual leaf packs, composed of leaves collected from the forest adjacent to Herbert Run during leaf fall in 2003. Leaves were maintained in a coarse mesh bag (7 × 11 mm mesh; Swan & Palmer, 2004) and closed at both ends with a Zip-Tie®. We constructed $n = 12$ leaf packs per leaf species, enough to remove 3 packs on each of 4 sample dates.

Six additional leaf litter treatments were made to assess the role of native leaf litter in mediating decay of TOH. Leaf packs combined TOH in 3 different mixtures (2.0 g total) with red maple and 3 with white oak in 25:75, 50:50, and 75:25 ratios, by weight. Red maple and white oak were chosen as they are common to the forest community adjacent to the study stream and exhibit an appreciable range in decomposition rate (Ostrofsky, 1997). All leaf packs ([7 single-species treatments + 6 mixtures] × [$n = 3$] × 4 sample dates = 156 leaf packs total) were placed in Herbert Run on December 1, 2003. We anchored the packs to the riffle–run areas of the streambed with 20-cm metal stakes, spacing the packs 15–30 cm apart in the thalweg. A temperature logger recorded readings at 15-min intervals throughout the study.

Leaf packs were sampled on days 7, 21, and 37; a spate washed away the study after day 37. Sampling involved lifting the leaf pack into a 250-µm sieve and rinsing the bag and the contents into a Ziploc® bag. The samples were returned immediately to the laboratory for processing, where they were emptied into a 250-µm sieve and rinsed under tap water. The rinsed leaves were dried in the oven at 70 °C in pre-weighed tins, re-weighed, combusted at 550 °C for 45 min, then re-weighed to determine ash-free dry mass remaining at sampling (Benfield, 1996). We altered the processing procedure for the mixed-litter packs by first separating the litter by species into their own tins, then following the same procedure as above. All invertebrates were rinsed from the packs and preserved in 70% ethanol for enumeration of the shredder taxa.

To determine feeding rates on the 7 leaf litter taxa employed in the field study, we offered 2 detritivores, the freshwater isopod *Caecidotea communis* and the limnephilid caddisfly *Frenesia* sp., both numerically common in small Piedmont streams, two 2.54-cm leaf discs (~ 0.05 g dry mass) of each species separately. We collected the shredders from a nearby stream and maintained them in bins of aerated stream water in an environmental unit set to 15 °C until the start of the experiment. Individual shredders were fed 2 pre-weighed leaf discs and housed in a mesh tea infuser (Toby TeaBoy Ltd., Aldridge, England; 56- × 43-mm plastic chambers lined with 244-µm mesh; Benke & Jabobi, 1986; Rosemond *et al.*, 2001; Eggert & Wallace, 2003). We allocated 6 replicates to each leaf treatment × shredder combination (2 taxa, plus a no shredder control; 3 shredder treatments × 7 leaf species × 6 replicates = 126 chambers total). We submerged the chambers in bins of aerated, filtered stream water (43 µm), 40–50 per bin, in an environmental unit set to 15 °C and a 16:8 light–dark diurnal cycle. For all treatments, leaf litter was conditioned for 14 d before we added the invertebrates to the chambers. This allowed for soluble compounds to leach from the litter and for microbial conditioning to begin. We stopped the experiment 6 d after adding the shredders to each chamber given the intense feeding rates and to minimize food limitation.

At the end of the experiment, we separated the invertebrates from the litter in a 500 µm sieve, placed the litter into tins, and dried it at 70 °C for 24 h. We obtained individual caddisfly mass gravimetrically (after removing them from their cases) using the same method used to measure litter mass, but we used a published length–weight regression to estimate isopod dry mass (Swan & Palmer, 2006b). We weighed the litter and caddisflies to the nearest 0.001 g and estimated isopod mass to the nearest 0.0001 g. Caddisflies averaged 0.0052 g (SE = 0.0005, $n = 39$), and the isopods 0.0026 g (SE = 0.0002, $n = 41$). Feeding rate was calculated as

$$\text{Feeding Rate (d}^{-1}\text{)} = \frac{(DM_{+i} - DM_{+f}) - (DM_{-i} - DM_{-f})}{IM_f \cdot d} \quad [1]$$

where DM_{+i} and DM_{+f} define the initial and final leaf disc dry mass (g) for a chamber with a shredder, respectively, and DM_{-i} and DM_{-f} define the average initial and final leaf disc dry mass (g) in the corresponding leaf treatment lacking a shredder. Subtracting this value accounted for losses due to physical and microbial processes. IM_f is the individual shredder mass (g), and d is time in days.

Finally, as a relative test of structural integrity, we measured toughness of each leaf species using a simple penetrometer, similar to that of Feeny (1970). We recorded the mass of steel shot needed to drive a 4-mm bolt through the tissue of a single leaf. Five locations were measured on each of 5 leaves for each species used in the study, carefully avoiding the mid-vein. We averaged the values of each leaf, yielding $n = 5$ replicates per species.

We analyzed decomposition rates of all 7 species using an ANCOVA. Mass loss of litter in streams commonly follows an exponential decay function (Petersen & Cummins, 1974), where the slope of the natural logarithm of the frac-

tion of mass remaining at sampling regressed on time yields k , the exponential decay rate. An ANCOVA, when day is modeled as the covariate that interacts with leaf treatment, is a test of differences between slopes. Upon a significant F -test, we used the output of the ANCOVA to perform all pair-wise comparisons of the time \times treatment interaction (e.g., the slope of the line relating mass remaining *versus* time, or k) between the 7 species. We used the sequential Bonferroni procedure to preserve a Type I error rate of $\alpha = 0.05$ (Rice, 1989). To ascertain the effect of mixing TOH with native species on TOH decay, we performed another ANCOVA similarly, but only on the TOH mass in treatments of TOH alone, all mixtures of TOH with red maple, and all mixtures of TOH with white oak. No effect of the relative composition of each leaf species in mixtures was found, so we chose to create 2 “mixed” treatments, one for TOH mixed with red maple and the other for TOH mixed with white oak. We used the output of the ANCOVA to perform 2 planned comparisons: TOH *versus* the average decay of TOH mixed with red maple and TOH *versus* the average decay of TOH mixed with white oak.

We employed a similar approach to analyzing shredder abundance on the various litter species, with the exception that we made post-ANCOVA pairwise comparisons of shredder abundance for day 20, approximately half-way through the study when, in general, invertebrate abundance peaked on the leaf packs. Again, to preserve Type I error of $\alpha = 0.05$, we used a sequential Bonferroni procedure to evaluate the significance of each comparison. To test for differences in shredder abundance between TOH alone and TOH mixed with either red maple or white oak, we employed a simple 1-way ANOVA, since day explained no significant variation as a covariate. As with the decomposition study, we made 2 planned comparisons between average shredder abundance on TOH *versus* TOH mixed with either red maple or white oak.

Since we used 3 shredder treatments, *i.e.*, isopod, cadisfly, and none, crossed with each of the 7 leaf species treatments, we calculated a 3×7 two-way ANOVA to test for differences in feeding rate among leaf species for each taxa. To apply the correction for losses due to microbial and physical processes (Equation 1), we subtracted the no shredder effect for each leaf species using the ESTIMATE statement in SAS (version 9.1.3) to get true feeding rates. Given that shredders would prefer TOH because of its labile nature and that mixing TOH with less labile species should increase its decay because of preferential feeding, we compared feeding rates between TOH and red maple and TOH and white oak to complement the mixture component of the decay study.

We analyzed toughness using a simple 1-way ANOVA, followed the analysis with all pairwise comparisons, and determined statistical significance using the sequential Bonferroni procedure to maintain our Type I error rate. We performed all analyses using SAS version 9.1.3 (SAS Institute, Cary, North Carolina). We adhered to assumptions of normality using the Shapiro–Wilkes test and homogeneity of variance by inspecting residuals. For all analyses, we chose the Kenward–Roger adjustment to denominator degrees of freedom in SAS, based on calculations by Kenward and Roger (1997).

Results

We saw overall significant effects of leaf species on decomposition rates (ANCOVA, Day \times Leaf Species $F_{6, 16.9} = 116.7$, $P < 0.0001$; Figure 1a) and of TOH decay alone and in the presence of native litter species (ANCOVA, Day \times Leaf Species $F_{6, 37} = 9.7$, $P < 0.0001$; Figure 1b). TOH decay was $> 2\times$ that of the flowering dogwood, the next fastest species, and $> 18\times$ that of northern red oak, the slowest species used in the study. Of the native species, flowering dogwood, tulip poplar, and blackgum grouped into a category of the fastest decomposers, followed by red maple and the 2 oak species (Figure 1a). TOH decay was significantly slower when mixed with native species; TOH alone lost mass nearly $2\times$ faster than it did when mixed with

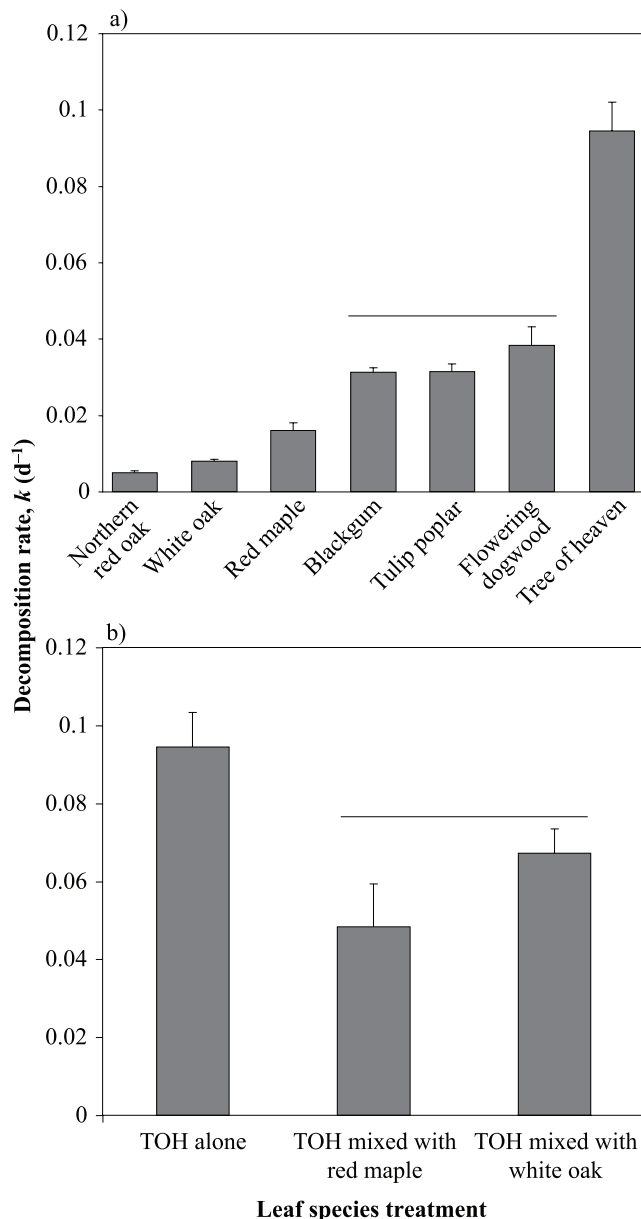


FIGURE 1. Decomposition rates of 7 species (a) and of tree of heaven alone and in mixtures (b). Bars are the mean decay rate + SE. Bars connected by a line are not significantly different.

red maple and ~1.4× faster than when mixed with white oak (Figure 1b).

Shredder abundance on leaf packs was dominated (> 90%) by stoneflies from the genus *Taeniopteryx* (Plecoptera: Taeniopterygidae) and varied significantly with leaf species (ANCOVA, Day × Leaf Species $F_{6, 19.8} = 2.8$, $P = 0.0396$; Figure 2a). TOH packs supported numbers of shredders per g > 5× those of northern red oak, white oak, and tulip poplar. However, abundances on flowering dogwood, blackgum, and red maple were statistically indistinguishable from those on TOH (Figure 2a). We observed significantly lower abundances on mixture leaf packs compared with TOH alone (ANOVA, $F_{6, 26.9} = 3.9$, $P = 0.0059$; Figure 2b). TOH leaf packs alone supported 2.7–3.8× greater numbers of shredders per g than either mixture treatment.

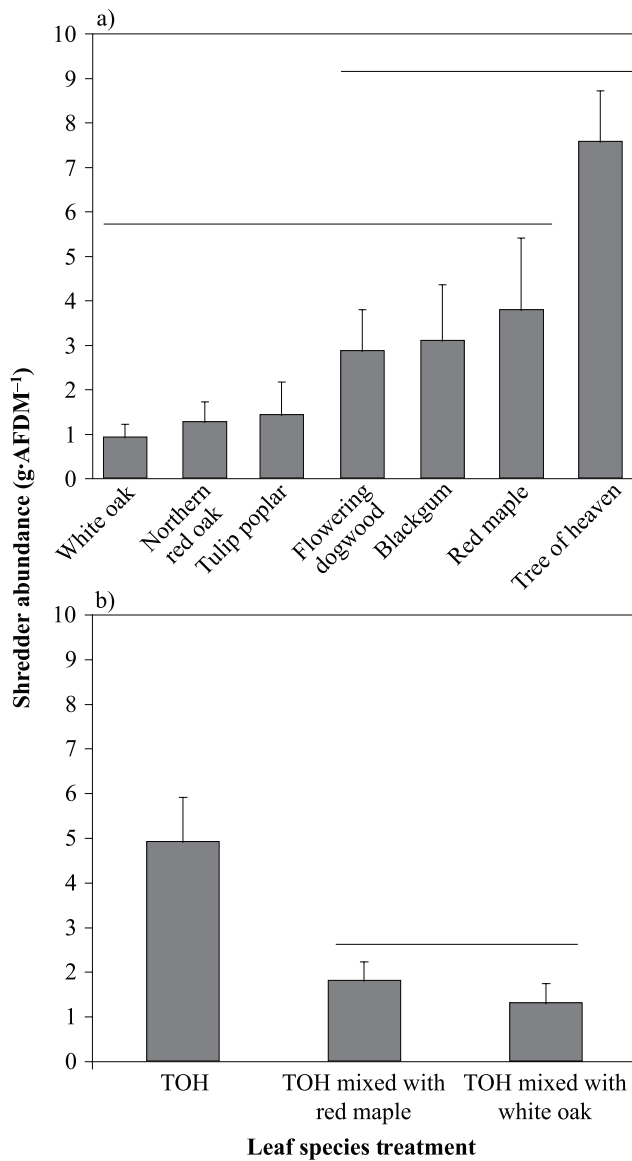


FIGURE 2. Shredder abundance on leaf packs estimated for the 7 leaf species 20 d after the start of the decomposition experiment (a), and abundance of shredders on tree of heaven alone and in mixtures for the entire study (b). Bars are the mean shredder abundance + SE. Bars connected by a line are not significantly different.

Both shredder taxa responded significantly to leaf species (ANCOVA, Leaf species × Shredder $F_{12, 94} = 3.5$, $P = 0.0003$; Figure 3), feeding the fastest on TOH in both cases. The isopod consumed TOH significantly faster than white oak ($P = 0.005$), but not red maple ($P = 0.291$). However, the caddisfly increased its feeding significantly on TOH compared to both native species used in the mixtures employed in the field (white oak $P = 0.0046$, red maple $P = 0.0243$).

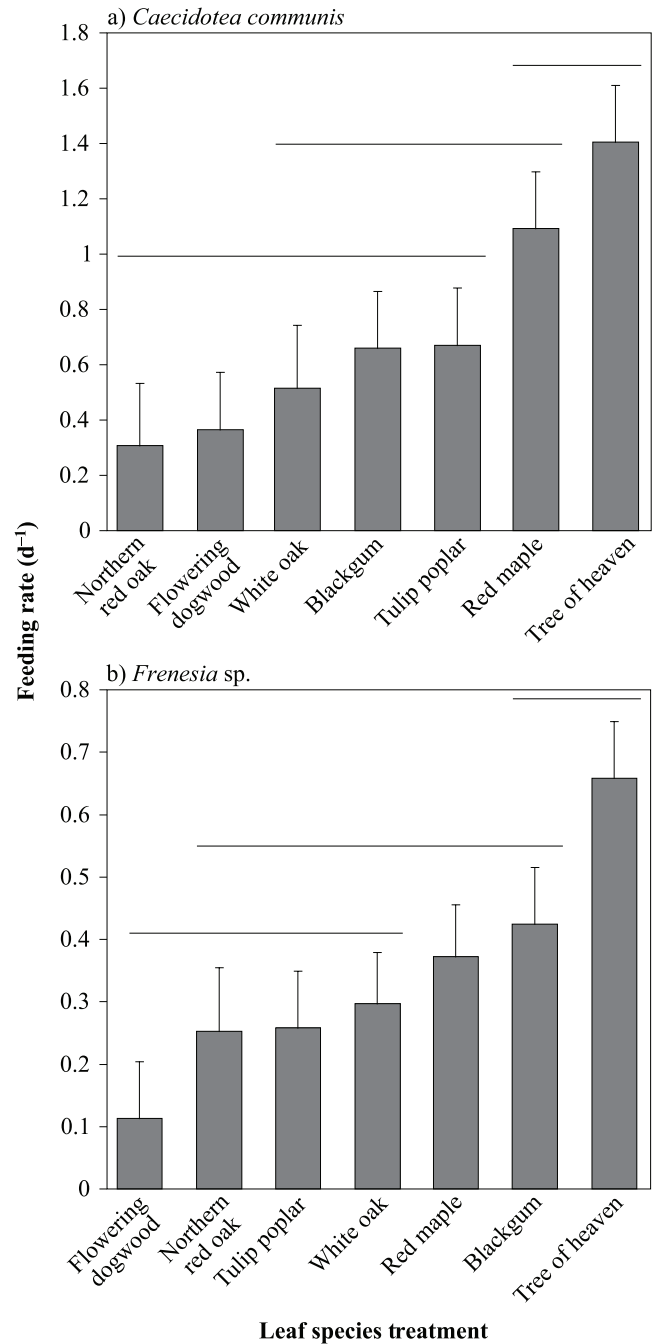


FIGURE 3. Feeding rates of the isopod *Caecidotea communis* (a) and the caddisfly *Frenesia* sp. (b). Bars are the mean feeding rate + SE. Note both the difference in scale of the y-axes and the difference in the order of leaf species treatments.

We detected significant interspecific variation in leaf toughness (ANOVA, $F_{6,13,1} = 30.8$, $P < 0.0001$; Table I) The oak species resisted breakage the most, followed by all other native species. TOH proved to be the weakest of them all, requiring less than 100 g to break through the leaf tissue.

Discussion

The purpose of this study was both to ascertain the litter decomposition rate of a common invasive species in urban areas, tree of heaven, compared to the litter of 6 native tree species in an urban stream and to determine the role such native species play in mediating decay of a non-native. We predicted that since (1) TOH exhibits very rapid colonization and growth, and such characteristics typify fairly labile litter for decomposers, and (2) detritivorous invertebrates in streams feed preferentially and can contribute substantially to litter decay rates, mixing TOH with native litter should accelerate its decomposition rate. The role of native litter biodiversity in this context should be to mediate the rate of decay of a non-native invader. The results from our field decomposition study, coupled with complementary laboratory feeding experiments with common shredder taxa, revealed that while shredders both colonize TOH in higher abundance and exhibit substantially higher feeding rates on TOH compared to native taxa, TOH decayed much more slowly when mixed with native species. Data on the structural integrity of the leaf litter suggest that the relatively weak nature of TOH compared to native taxa could have driven this result. Native leaf species may have “armoured” the fragile TOH against the extreme physical forces typical of urban streams, overwhelming the preferential feeding effect by shredders that we predicted should occur.

Decay of organic matter, particularly leaf litter, in stream ecosystems is a complex process involving water chemistry, flow, physical abrasion by sediments, invertebrate and microbial consumption, temperature, and litter chemistry (Webster & Benfield, 1986). Many studies, both in lab and the field, have focused on how invertebrates and microbes respond to leaf species identity via interspecific variation in litter chemistry (Golladay, Webster & Benfield, 1983; Campbell & Fuchshuber, 1995; Paul & Meyer, 1996; Haapala, Muotka & Markkola, 2001). Often, significant contributions by the biological community occur under benign environmental conditions, such as in small, first-order streams buffered against large hydrologic events (Cuffney, Wallace & Lugthart, 1990; Wallace *et al.*, 1997).

Research on the role of waterborne nutrients have highlighted the biological response, as bacteria and fungi thrive on nutrients from the water column, increasing litter resource quality for invertebrates and enhancing decomposition rates (Meyer & Johnson, 1983; Gratton & Suberkropp, 2001; Gulis, Ferreira & Graça, 2006). Indeed, this is a valuable mode of inquiry because the detritivore–litter relationship is precisely how such a tremendous energy source as senesced leaf litter becomes available to higher trophic levels (Wallace *et al.*, 1997). However, with widespread conversion of natural landscapes to a built environment, small streams become influenced by hydrologic fluctuations (Schueler, 1994), reducing the potential for strong biological control of litter decay in these systems. Indeed, research intensity is increasing on the role of the aforementioned variables important to litter decay in altered systems, and results are only now beginning to reveal the complex interactions involved (Paul & Meyer, 2001; Sponseller & Benfield, 2001; Paul, Meyer & Couch, 2006). Our study highlights not only the importance of altered environments as a context for inquiry into decomposition of native and invasive tree litter in general, but also how streamside biodiversity can persist in mediating the rate at which litter decays in this system.

As ecosystem function becomes increasingly embraced as a desirable endpoint for restoration efforts, the effect of restoring biodiversity on ecosystem processes such as litter decomposition in streams is important to understand. Results of investigations into how leaf litter diversity should alter in-stream decomposition rates overall are now emerging (Swan & Palmer, 2004; 2006a,b; LeRoy & Marks, 2006). While the theory underpinning how biodiversity should alter rates of various ecosystem processes can rely on facilitation and competitive interactions between species (Naeem *et al.*, 1994; 1995; 1996; Hooper & Vitousek, 1997; Tilman, Lehman & Thompson, 1997; Tilman *et al.*, 1997; Loreau *et al.*, 2001; Hooper & Dukes, 2004; and others), diverse leaf litter assemblages cannot exhibit such ecological phenomena. Therefore, for species richness of leaf litter to matter, consumer feeding has been targeted as critical to the mechanism (Swan & Palmer, 2006a,b). Litter mixtures present a heterogeneous set of resources for detritivores and, in general, can be predicted to respond to this heterogeneity in a number of meaningful ways. The resources derived from litter mixtures may contain complementary essential nutrients, therefore supporting a more complete diet (Simpson & Simpson, 1990; Pennings, Masatomo & Paul, 1993). Under such circumstances, consumers increase their feeding rates on litter mixtures compared to predicted feeding rates on each of the litter species alone. However, leaf litter can contain very refractory structural compounds (*e.g.*, lignin) or significant levels of secondary compounds (*e.g.*, tannins), which vary between species, influencing both consumption and decomposition. If a highly refractory species is present in a mixture, consumers may avoid it to exploit a more labile species (Swan & Palmer, 2006b). However, when offered alone, most refractory species are fed upon because the consumer has no choice. Under these circumstances, diverse litter mixtures degrade more slowly compared to predicted feeding rates on each leaf species alone (Swan & Palmer, 2006b).

TABLE I. Mean leaf toughness, measured as the mass (g) of steel shot required to force a 4-mm bolt through the leaf using a simple penetrometer. Standard errors are in parentheses. Values with the same letter are not significantly different.

Leaf species treatment	Mass to breakage (g)
Tree of heaven	86.9 ^a (7.73)
Red maple	221.3 ^b (21.74)
Flowering dogwood	235.7 ^b (44.10)
Tulip poplar	237.4 ^b (44.10)
Blackgum	251.3 ^b (44.10)
Northern red oak	461.5 ^c (44.10)
White oak	472.0 ^c (44.10)

We predicted that preferential feeding would reveal the effect of native species on TOH in the study presented here. TOH proved to be highly labile, decaying quickly, attracting the highest numbers of shredders in the study, and supporting the fastest feeding rates among all species we investigated. Given this, we predicted that in mixtures, shredders would reduce their feeding rate on red maple and white oak and increase their feeding on TOH (Swan & Palmer, 2006b). Under the assumption that shredder feeding is important to decay rate of leaf litter in Herbert Run, mass loss of TOH in mixtures should have been faster than when it was alone. This was not the case. Instead, decay of TOH was significantly slower in mixtures. The presence of native species in this study still seemed to regulate decay of TOH, but via a different mechanism. Subsequent estimates of structural integrity revealed substantial interspecific variation, with TOH the most fragile compared to the 6 native species. We hypothesize that since the native species we manipulated to mediate decay of TOH (*e.g.*, red maple and white oak) were tougher, they may have “armoured” TOH against high flows. We observed substantial bed movement in Herbert Run over the course of the study, suggesting this system experiences the harsh physical forces predicted to pervade urban streams. Lack of protection by tougher litter species may have resulted in very fast decay of TOH alone, exceeding some of the fastest decay rates reported in the literature (Paul & Meyer, 2006).

Human alteration of natural rates of ecosystem processes is increasing and can result from species loss, species replacement with invasive species, and transformation of natural landscapes to those with varying levels of impervious surface. Stream ecosystems are particularly sensitive given their topographic position in the landscape and as necessary conveyors of nutrients and energy downstream to larger water bodies. Restoration efforts in streams can often take the form of riparian replanting (Sweeney, 1993; USDA, 1996; Naiman & Décamps, 1997). Work in more pristine streams and complementary laboratory studies have revealed that the importance of native tree biodiversity to aquatic decay rates can depend on the foraging behaviour of the primary consumers in these systems (*e.g.*, shredders; Swan & Palmer, 2006a,b). This study revealed that while consumers do respond as predicted to the quality of a common invasive species, tree of heaven, the role of native species in mediating its decay may not depend on consumer foraging. The value of our results lies in the fact that we tested our predictions in a stream with conditions typically targeted for restoration efforts, and the very nature of this environmental context illuminated another mechanism by which native species can play a role in regulating ecosystem processes. Via interspecific variation in structural integrity, native leaf litter may mediate how invasive tree litter decomposes in human-impacted streams. We emphasize that further experimentation on the effectiveness of restoration should be done in damaged ecosystems, such as those found in urban areas.

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