Growth of an invertebrate shredder on native (*Populus*) and non-native (*Tamarix, Elaeagnus*) leaf litter

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SUMMARY

1. Large-scale invasions of riparian trees can alter the quantity and quality of allochthonous inputs of leaf litter to streams and thus have the potential to alter stream organic matter dynamics. Non-native saltcedar (*Tamarix* sp.) and Russian olive (*Elaeagnus angustifolia*) are now among the most common trees in riparian zones in western North America, yet their impacts on energy flow in streams are virtually unknown.

2. We conducted a laboratory feeding experiment to compare the growth of the aquatic crane fly *Tipula* (Diptera: Tipulidae) on leaf litter from native cottonwood (*Populus*) and non-native *Tamarix* and *Elaeagnus*. *Tipula* showed positive growth on leaf litter of all three species; however, after 7 weeks, larvae fed *Tamarix* leaves averaged 1.7 and 2.5 times the mass of those fed *Elaeagnus* and *Populus*, respectively. *Tipula* survival was highest on *Populus*, intermediate on *Tamarix* and lowest on *Elaeagnus*.

3. High *Tipula* growth on *Tamarix* probably reflects a combination of leaf chemistry and morphology. Conditioned *Tamarix* leaf litter had intermediate carbon : nitrogen values (33 : 1) compared to *Populus* (40 : 1) and *Elaeagnus* (26 : 1), and it had intermediate proportions of structural carbon (42%) compared to *Elaeagnus* (57%) and *Populus* (35%). *Tamarix* leaves are also relatively small and possibly more easily ingested by *Tipula* than either *Elaeagnus* or *Populus*.

4. Field surveys of streams in the western U.S.A. revealed that *Tamarix* and *Elaeagnus* leaf packs were rare compared to native *Populus*, probably due to the elongate shape and small size of the non-native leaves. Thus we conclude that, in general, the impact of non-native riparian invasion on aquatic shredders will depend not only on leaf decomposition rate and palatability but also on rates of leaf litter input to the stream coupled with streambed retention and subsequent availability to consumers.

Keywords: detritivore, exotic species, leaf chemistry, leaf morphology, *Tipula* (*Sinotipula*)

Introduction

Invasions by non-native species threaten native species and alter ecosystem processes (Wilcove *et al.*, 1998) and are a major component of anthropogenic global change (Lodge & Shrader-Frechette, 2003). Stream and river floodplains are particularly susceptible because they are subject to natural disturbances and anthropogenic alteration of natural disturbance regimes, both of which provide opportunities for invasion (Hood & Naiman, 2000). Non-native trees are replacing native riparian forests along streams and rivers around the world (Rood & Mahoney, 1990; Pysek & Prach, 1994; Friedman *et al.*, 2005). Many non-native tree species have been deliberately introduced as plantation species (Abelho & Graça, 1996; Valdovinos, 2001; Thompson & Townsend, 2003), others have escaped cultivation (Schulze & Walker, 1997; O'Connor *et al.*, 2000; Decruyenaere & Holt, 2005) and some have

spread after intentional introduction for the purposes of environmental management, such as erosion control (Shafroth *et al.*, 2005).

Introduced non-native riparian tree species have the potential to modify stream ecosystem structure and function through input of allochthonous leaf litter to the stream. Because leaf litter can provide an important habitat for many invertebrates (Mackay & Kalff, 1969), it has been suggested that non-native vegetation can modify habitat structure and thus influence benthic community composition (Thompson & Townsend, 2003). For example, in Australian streams, litter from native *Eucalyptus* trees supports higher invertebrate densities than does litter from non-native willow (*Salix*) (Pidgeon & Cairns, 1981), perhaps because the native species decomposes more slowly and thus provides more enduring habitat (Schulze & Walker, 1997).

A potentially more important mechanism by which non-native species can modify stream ecosystems is by altering energy flow through the aquatic detrital food web. The importance of allochthonous material to stream energy budgets is well established (Vannote *et al.*, 1980; Cummins *et al.*, 1989), and riparian invasion can alter organic matter dynamics if allochthonous inputs from non-native species differ in food quality from native species (Schulze & Walker, 1997; O'Connor *et al.*, 2000; McKie & Cranston, 2001; Kennedy & Hobbie, 2004; Reinhart & VandeVoort, 2006). For example, in Australian streams invertebrates grew faster on non-native *Salix* litter compared to native *Eucalyptus* (Yeates & Barmuta, 1999). In Portugal, a tipulid shredder in streams dominated by non-native *Eucalyptus* had slower growth and lower survival compared to streams with native vegetation (Canhoto & Graça, 1995). Reduced shredder growth on *Eucalyptus* probably reflects not only the relatively thick cuticle and high proportion of refractory compounds in this species' leaves (Canhoto & Graça, 1999), but also its relatively slow decomposition rate (Basaguren & Pozo, 1994).

In general, the potential for modification of stream ecosystems by non-native riparian trees is expected to vary among species, depending on several morphological and chemical characteristics of the leaves that influence their suitability as habitat and food for benthic invertebrates. Among these important characteristics are the extent to which leaves may be retained on the streambed (Rounick & Winterbourn, 1983), the decomposition rate of the leaves which influences their availability over time (Pidgeon & Cairns, 1981; Basaguren & Pozo, 1994; Sampaio, Cortes & Leao, 2001; Valdovinos, 2001), and the chemical composition of the leaves which influences their palatability to invertebrate shredders (Canhoto & Graça, 1995; Albarino & Balseiro, 2002).

In the arid and semi-arid western United States, non-native saltcedar (*Tamarix* sp., L.) and Russian olive (*Elaeagnus angustifolia*, L.) are the third and fourth most frequently occurring trees in stream and river riparian zones (Friedman *et al.*, 2005). Introduced from Eurasia in the mid-1800s, *Tamarix* now occurs mainly in the warmer, drier south, whereas *Elaeagnus* dominates in the cooler, wetter north (Friedman *et al.*, 2005). The effect of the *Tamarix* invasion (Shafroth *et al.*, 2005) on stream-riparian communities has received considerably more attention than the *Elaeagnus* invasion (Katz & Shafroth, 2003), although previous investigations have focused primarily on terrestrial species and food webs (e.g. Ellis, 1995; Ellis, Crawford & Molles, 1997; Yard *et al.*, 2004; Wiesenborn, 2005).

Limited research suggests that leaf litter from *Tamarix* and *Elaeagnus* provides either poorer habitat or lower quality food for invertebrates than native *Populus* litter, but the evidence is equivocal. Bailey, Schweitzer & Whitham (2001) found that *Tamarix* leaf packs supported significantly lower invertebrate abundance than *Populus* leaf packs after 3 weeks in a northern Arizona, U.S.A. stream. These authors suggested that the difference was the consequence of rapid decomposition rate of *Tamarix* leaves. Similarly, Royer, Monaghan & Minshall (1999) found invertebrate abundance to be lower in *Elaeagnus* leaf packs than in *Populus* leaf packs after 30 days in an Idaho, U.S.A. stream. Both Bailey *et al.* (2001) and Royer *et al.* (1999) concluded that the native *Populus* litter provided both better habitat and higher food quality for aquatic invertebrates than the non-native species. Importantly, however, neither of these studies examined the relative value of native and non-native leaf litter as food nor did they determine the dietary preference of consumers. Interestingly, in a study comparing the signatures of stable isotopes of invertebrates inhabiting *Tamarix* and *Populus* leaf litter, Pomeroy, Shannon & Blinn (2000) found that invertebrates were apparently not consuming the litter of either leaf species in the Colorado River. The two leaf

types had distinctive stable isotope signatures, but the isotopic signatures of invertebrates inhabiting *Tamarix* and *Populus* leaf packs were similar and did not match either leaf species.

Given the spatial extent of riparian invasion in the western U.S.A. by *Tamarix* and *Elaeagnus*, coupled with the general poor understanding of how these species may be influencing food resources in invaded streams, we designed an experiment to test whether a common invertebrate shredder grows faster on native or non-native leaf litter. Over a 7-week period we compared the growth rates of crane fly larvae (Diptera: Tipulidae) on pre-conditioned *Populus*, *Tamarix* and *Elaeagnus* leaf litter in a controlled laboratory setting.

Methods

Invertebrate growth

We compared the relative growth of crane fly larvae (*Tipula* sp.) on *Populus deltoides* subsp. *monilifera* (Aiton) Eckenwalder, *Elaeagnus angustifolia* and *Tamarix* sp. In autumn 2004, senescent leaf litter was collected from trees, air-dried and stored at ambient temperature in the laboratory until needed. *Populus* and *Elaeagnus* leaf litter was collected from the Cache la Poudre River in Fort Collins, CO, U.S.A. (105.03°N, 40.54°W) and *Tamarix*, which is uncommon along the Poudre River, was collected from the Dolores River near Egnar, CO, U.S.A. (108.89°N, 38.44°W).The carbon : nitrogen values of the unconditioned leaf litter used for the experiment fell within the range observed for *Populus*, *Tamarix* and *Elaeagnus* in riparian forests in southern UT, U.S.A. (Moline, 2007). To minimize potential differences in the biofilm colonizing the three leaf species, the leaves were conditioned in a common aquarium of aerated Poudre River streamwater for 2 weeks prior to the start of the experiment.

We used the crane fly larva *Tipula* (*Sinotipula*) sp. (*commisicibilis* group), hereafter *Tipula*, for this experiment. We collected larvae from the Poudre River in February 2006 and allowed them to acclimate in the laboratory for 3–5 days prior to the experiment. *Tipula* is a large insect shredder commonly found in western streams, where it can constitute the greatest biomass of all stream invertebrates in some locations (Gelhaus, 1986).We chose *Tipula* for this experiment because members of the genus are commonly used as model shredders (Sinsabaugh, Linkins & Benfield, 1985;

Findlay, Meyer & Smith, 1986; Canhoto & Graça, 1995; Rong, Sridhar & Baerlocher, 1995), are easy to collect from the field and survive well in the laboratory.

Tipula larvae were maintained in separate mini-aquaria (500 mL) and fed *ad libitum* on a diet of a single species of pre-conditioned leaves. There were 20 replicates per leaf species for a total of 60 *Tipula* larvae in 60 separate containers. The experiment was carried out in an incubator at a constant temperature (12.5 °C) and under a 12L : 12D photoperiod. The aquaria contained sterilized sand, aerated water from the Poudre River and leaf litter. Every 2 weeks streamwater was replaced, the sand was thoroughly rinsed to remove faecal matter and detritus, and new leaves were added from the incubation tank. At weekly intervals, each larva was blotted dry and weighed to the nearest 0.001 g on a Sargent-Welch SWT-104 balance (Buffalo, NY, U.S.A.). At the end of the 7-week experiment, larvae were also dried at 60 °C and weighed.

Leaf chemistry

Lignin analysis, also called carbon fraction analysis (Ryan, Melillo & Ricca, 1990), was conducted on unconditioned leaves at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth, MN, U.S.A.). Structural components analysed were lignin and the acid-soluble fraction, which includes cellulose and hemicellulose (Ryan *et al.*, 1990). A few other standard chemical components were also reported (see Table 1).

Carbon and nitrogen analyses were conducted on unconditioned and conditioned *Populus*, *Elaeagnus* and *Tamarix* leaf samples that had been air-dried and ground in a coffee grinder. Samples were analysed for carbon and nitrogen content on a LECO CHN1000 auto-analyser (LECO Corporation, St. Joseph, MI, U.S.A.). All leaf chemistry samples (lignin analysis and carbon/nitrogen content) were run in duplicate and the values averaged. Carbon to nitrogen (C : N) ratios were calculated from dry mass by dividing the carbon fraction (%C) by the nitrogen fraction (%N).

Statistical methods

All statistical analyses were conducted using wet larval mass of *Tipula*. Prior to analysing the data we

Table 1 Summary of leaf chemistry values for *Populus*, *Tamarix* and *Elaeagnus*

Litter chemistry	*Populus*	*Tamarix*	*Elaeagnus*
Unconditioned leaf litter*			
Ash (%)	16.7	17.8	9.3
Non-polar extractable (%)	10.5	13.3	16.2
Water soluble (%)	54.1	44.3	26.6
WS polyphenols as tannin (%)	5.9	8.9	3.5
WS polysaccharides as glucose equivalents (%)	7.1	13.4	7.0
Acid soluble (%)	33.6	37.3	49.2
AS polysaccharides as glucose equivalents (%)	16.9	18.7	25.6
Lignin (%)	1.8	5.1	8.0
Carbon (%)	41.0	35.7	44.4
Nitrogen (%)	0.6	1.2	1.5
Carbon : nitrogen	70.3	30.1	30.2
Conditioned leaf litter[†]			
Carbon (%)	44.5	45.8	45.0
Nitrogen (%)	1.1	1.4	1.7
Carbon : nitrogen	40 : 1	33 : 1	26 : 1
Unconditioned field-collected leaf litter[‡]			
Carbon : nitrogen (min, max)	46 : 1, 152 : 1	31 : 1, 83 : 1	15 : 1, 30 : 1

*Chemistry of the unconditioned leaf litter used in the *Tipula* growth experiment.
[†]Carbon and nitrogen chemistry of conditioned leaf litter, which were soaked in aerated streamwater for 2 weeks prior to the experiment.
[‡]Minimum and maximum carbon : nitrogen values of leaf litter collected in autumn from trees on 14 streams on the Colorado Plateau. The leaf litter used for the *Tipula* feeding experiment falls near the midpoint of this range. Water soluble (WS) includes amino acids, simple sugars and soluble phenolics. Acid soluble (AS) includes cellulose, hemicellulose, starch, polypeptides and nucleic acids.

tested weekly *Tipula* mass for each leaf species for normality and homogeneity of variance and untransformed data were used (Shapiro–Wilk, $P > 0.1$; Levene, $P > 0.1$). In order to test for differences in mean larval mass among leaf species at the start of the experiment, we used a one-way ANOVA with leaf species as the independent variable and initial larval mass as the dependent variable.

We analysed differences in *Tipula* wet mass over time and leaf species with a repeated-measures analysis of covariance (RMANCOVA) using SAS 9.1 (SAS Institute, 2007). The RMANCOVA tested for significant differences in larval mass over time, among treatments (leaf species) and in the time × species interaction. The RMANCOVA model included initial larval wet mass as a covariate; leaf species treatment error was not included in the RMANCOVA. Tukey's HSD *post hoc* test was used to test for significance of the time × leaf species term among the treatments. We conducted the RMANCOVA with all individuals that started the experiment ($n = 60$). Individuals that died during the experiment were dropped from the analysis in the weeks after their death.

We estimated larval growth rates for each leaf species with linear regression, which provided a better fit to the data than exponential regression. We used average *Tipula* wet weight (grams) as the independent variable and time (days) as the dependent variable ($n = 8$). At the end of the experiment, we constructed a regression of *Tipula* wet mass to dry mass to facilitate comparison of our data with that in the literature. All statistical analyses were conducted with Statistica software (StatSoft, Inc., Tulsa, OK, U.S.A.).

Results

The initial wet mass of *Tipula* was not significantly different among leaf species ($F = 0.54$; d.f. = 2; $P = 0.58$, Fig. 1). There was a significant change in *Tipula* mass over time (RMANCOVA; $F = 64.0$, d.f. = 7, $P < 0.001$), leaf species ($F = 196.2$, d.f. = 2, $P < 0.001$) and in the time × treatment (leaf species) interaction
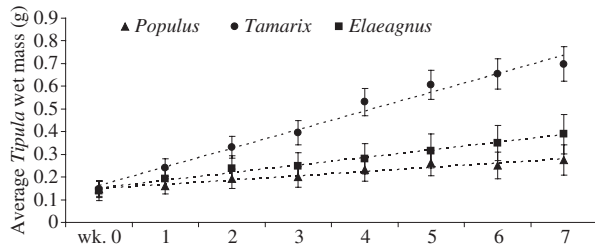
Fig. 1 Change in *Tipula* mass throughout the 7-week experiment. There was no difference in *Tipula* mass among treatments at week 1. Linear regression equations were fitted to each of the leaf species to express mean *Tipula* wet mass (grams) in terms of time (days): *Populus* ($y = 0.14 + 0.003x$, $r = 0.97$, $P < 0.001$), *Tamarix* ($y = 0.16 + 0.012x$, $r = 0.99$, $P < 0.001$) and *Elaeagnus* ($y = 0.14 + 0.005x$, $r = 0.99$, $P < 0.001$). Error bars represent 95% confidence intervals.

term ($F = 10.6$, d.f. $= 14$, $P < 0.001$). Mean larval wet mass in the *Tamarix* treatment was significantly greater than that in *Populus* by week 2 (Tukey HSD; $P = 0.012$) and *Elaeagnus* by week 3 (Tukey HSD; $P < 0.01$). The *Populus* and *Elaeagnus* treatments had approximately the same mean larval weight until week 5, when larvae feeding on *Elaeagnus* were significantly heavier than larvae fed *Populus* (Tukey HSD; $P = 0.024$). By the end of the experiment (week 7), crane fly larvae feeding on *Tamarix* were 1.7 and 2.5 times the average wet weight of larvae fed *Elaeagnus* and *Populus* respectively. Larval wet mass (x) was a good predictor of dry mass (y) for the *Tipula* used in this study: $y = 0.0644x - 0.00078$ ($r^2 = 0.895$, $P < 0.01$).

Twenty-eight per cent of the 60 *Tipula* larvae that started the experiment died over the course of the 7-week experiment. Most of the mortality (88%) occurred within the first 2 weeks. At the end of the experiment, *Tipula* survival was highest in the *Populus* treatment (90% surviving), intermediate in the *Tamarix* treatment (70%) and lowest in the *Elaeagnus* treatment (55%).

Leaf chemistry

Populus, *Tamarix* and *Elaeagnus* leaf litter differed in their chemical composition (Table 1). Lignin analysis revealed that unconditioned *Populus* contained the lowest amount of structural carbon (35%) of the three species, as indicated by the combined lignin and acid-soluble fractions. *Elaeagnus* contained the most structural carbon (57%) and *Tamarix* was intermediate (42%). Unconditioned *Populus* leaf litter had approx-

imately half the nitrogen content of *Tamarix* and *Elaeagnus* litter, which were similar (Table 1). The C : N ratio for unconditioned *Populus* leaf litter was the highest C : N (70 : 1), followed by similar values for *Tamarix* (30 : 1) and *Elaeagnus* (30 : 1).

All three leaf species increased in percent nitrogen and carbon during the conditioning process (Table 1), presumably due to loss of non-carbon chemical components and to microbial colonization. *Populus* leaf litter gained proportionately more nitrogen than *Tamarix* or *Elaeagnus* during conditioning, which greatly reduced the difference in C : N values among the three species, but conditioned *Populus* leaf litter still had the highest C : N value (40 : 1) of the three species. Conditioned *Elaeagnus* had the lowest C : N ratio (26 : 1) and *Tamarix* was intermediate (33 : 1).

Discussion

Tipula larvae were able to grow and survive on *Tamarix*, *Populus* and *Elaeagnus* leaf litter. In previous research, *Tipula* was unable to survive and grow, even when fed *ad libitum,* on some non-native species. For example, Canhoto & Graça (1995) observed 100% *Tipula* mortality on diets of non-native *Eucalyptus globulus*, Labill and native *Quercus faginea*, Lam. For *Lepidostoma* sp. caddisflies, Going & Dudley (in press) observed 80% mortality when larvae were fed litter from the non-native giant reed *Arundo donax* L. Both of these studies suggested that leaf structure was partially responsible for poor growth; specifically, the thick cuticles of *Eucalyptus* and *Quercus* and the tough, silicaceous *Arundo* leaves made consumption difficult for invertebrates.

In our experiment, and contrary to expectations, crane fly larvae had higher growth rates on non-native leaf litter. *Tipula* larvae grew twice as fast on *Tamarix* as on *Elaeagnus* and almost three times faster on *Tamarix* than on *Populus*. Other researchers have found mixed results when investigating insect growth rates on *Tamarix* relative to other types of leaf litter. For example, Going & Dudley (in press) found that the growth rate of Trichoptera larvae on conditioned alder (*Alnus*), *Tamarix* and *Salix* leaf litter varied among genera. One caddisfly, *Gumaga* sp., grew faster on *Alnus* and slower on *Salix* than on *Tamarix*. A second caddisfly, *Lepidostoma* sp., however, showed a similar growth rate on all three leaf species.

We have two hypotheses for why *Tipula* grew faster on *Tamarix* than on *Elaeagnus* or *Populus*. First, *Tamarix* leaves may be relatively easy for *Tipula* to ingest because of their morphology. *Tamarix* is commonly known as salt cedar because of its scaly, overlapping leaves that resemble the leaves of a cedar tree (unlike cedar, *Tamarix* is an angiosperm). In contrast, *Elaeagnus* and *Populus* have typical deciduous leaves with long petioles and a single expanded blade rather than overlapping scales. Although we did not measure leaf consumption, it is possible that *Tipula* grew better on *Tamarix* because the long, thin *Tamarix* leaves were simply easier to consume than the broad, flat *Elaeagnus* and *Populus* leaves.

Second, *Tamarix* leaves may be more palatable or more easily assimilated because of leaf nutrient and/or structural chemistry. Aquatic insects are known preferentially to consume leaves that are relatively high in nitrogen and have low amounts of structural carbon (Canhoto & Graça, 1993; Rincon & Martinez, 2006). Nitrogen is generally considered a limiting nutrient for primary consumers (Cross *et al.*, 2005); therefore, leaves with low C : N values are considered high-quality food (Chapin, Matson & Mooney, 2002). Shredding caddisflies exhibit higher growth and survivorship rates on leaf litter that is high in nitrogen (Anderson & Cummins, 1979; Canhoto & Graça, 1995), and tipulid larvae can convert as much as 61% of ingested nitrogen into larval biomass (Martin *et al.*, 1980). The C : N of the *Populus* leaf litter used for this experiment (70 : 1) is similar to values observed in the field (46 : 1 to 152 : 1; Moline, 2007) and values published in the literature (*c.* 35 : 1 to 181 : 1; Royer *et al.*, 1999; Tibbets & Molles, 2005). However, *Populus* had the highest C : N value of the three species used for this experiment (Table 1). The low nitrogen content of the *Populus* litter used in the experiment may partially explain the relatively poor growth on *Populus*.

Poor insect growth on oak and eucalyptus leaves has been attributed to leaf structural chemistry, including cellulose and lignin (Canhoto & Graça, 1995). In our study *Elaeagnus* had a relatively high nitrogen content; however, it also contained the most combined structural carbon (acid soluble + lignin fractions) of the three species (Table 1). *Tipula* is generally thought to be a poor processor of cellulose, as Sinsabaugh *et al.* (1985) showed cellulytic activity in *T. abdominalis* to be very low in natural popula-

tions. In a ^{14}C-label study, *T. abdominalis* assimilated only about 18% of the carbon in cellulose (Sinsabaugh *et al.*, 1985). *Tamarix* leaf chemistry appears to be the best balance between high nitrogen and low structural carbon of the three leaf species we examined.

Although our laboratory results suggest that non-native tree species support higher (*Tamarix*) or similar (*Elaeagnus*) growth by shredders than native *Populus* trees, the broader ecological implications of riparian invasion by these species in natural streams of the western U.S.A. will depend not only on leaf chemistry and invertebrate assimilation but also on the availability of leaf litter in streams. The retention of leaves on the streambed, and thus their availability to consumers, is expected to vary considerably among these species because leaf morphology can interact with high flows to influence retention (Scarsbrook & Townsend, 1994). For example, Moline (2007) collected and identified leaf litter from stream transects at each of 21 small, unregulated streams on the Colorado Plateau and observed *Populus* leaf litter to frequently form leaf packs on the streambed, whereas *Elaeagnus* and *Tamarix* leaf litter did not. In particular, *Tamarix* leaves were never observed to aggregate in the stream, and she rarely found more than single leaves. The relative scarcity of *Tamarix* in these streams is probably also due, in part, to its rapid decomposition rate (Bailey *et al.*, 2001). Moline (2007) found approximately five times more *Populus* litter in the stream channel than *Elaeagnus* litter and approximately 80 times more *Populus* than *Tamarix* litter. The relative scarcity of *Tamarix* and *Elaeagnus* litter in these 21 streams may also reflect the relatively low levels of riparian invasion in small, free-flowing streams (Moline, 2007) compared to large, regulated rivers (Friedman *et al.*, 2005). Further, even where *Tamarix* leaf inputs are high, retention in the western U.S.A. streams may be low because these systems tend to be flashy (Poff *et al.*, 2006), which can both accelerate rates of leaf breakdown and reduce the residence time of stream organic matter (Rounick & Winterbourn, 1983; Schade & Fisher, 1997).

Current understanding of the role of leaf litter in stream ecosystems is based mostly on the contribution of allochthonous material to stream energy budgets (Wallace *et al.*, 1997), leaf litter decomposition rates (Irons *et al.*, 1994) and invertebrate nutrition (Cummins *et al.*, 1989) in heavily forested

headwater streams. An increased understanding of the ecological consequences of non-native riparian leaf litter on stream invertebrate communities and organic matter budgets in more open-canopied and hydrologically flashy streams, such as those in the western U.S.A., will require quantification of both leaf litter availability in the field and relative palatability and nutrition of non-native species to macroinvertebrates.

Acknowledgments

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