Oecologia (2006) 149: 107–114
DOI 10.1007/s00442-006-0436-x

Christopher M. Swan · Margaret A. Palmer

Preferential feeding by an aquatic consumer mediates non-additive decomposition of speciose leaf litter

Received: 25 June 2005 / Accepted: 3 April 2006 / Published online: 5 May 2006

Abstract Forest soils and streams receive substantial inputs of detritus from deciduous vegetation. Decay of this material is a critical ecosystem process, recycling nutrients and supporting detrital-based food webs, and has been attributed, in part, to leaf litter species composition. However, research on why speciose leaf litter should degrade differently has relied on a bottom-up approach, embracing interspecific variation in litter chemistry. We hypothesized that preferential feeding by an aquatic detritivore interacts with species-specific leaf palatability and slows decay of speciose leaf litter. We addressed this by offering four single- and mixed-species leaf resources to field densities of a leaf-shredding consumer. Mixing leaf species resulted in slower total leaf decomposition. Decreases in mixed-species decomposition was partly explained by preferential feeding by the consumers in one case, but the lack of preferential feeding in other mixtures suggested an interactive effect of feeding and microbial degradation. Loss of riparian tree biodiversity may have implications for in-stream consumer-resource interactions.

Keywords Consumers · Decomposition · Preferential feeding · Riparian · Species richness

Introduction

Plant species richness can profoundly influence the rate of primary production, nutrient cycling, and, once senesced, decay of organic matter (Tilman et al. 1996; Hooper and Vitousek 1997; Gartner and Cardon 2004; Swan and Palmer 2004). Since the majority of primary production from deciduous vegetation is delivered to the detrital pool (McNaughton et al. 1989; Cebrian 1999), loss of plant species from natural communities may have important implications for how this material becomes available to detritivores and adjacent trophic levels. The effect of litter quality on rates of decomposition can depend on the contribution of the component leaf species, and these rates have been reported to deviate considerably from predictions based on single-species decay estimates (Wardle et al. 1997; Swan and Palmer 2004; Hättenschwiler and Gasser 2005; Swan and Palmer 2006). Given continued interest in how loss of biodiversity can alter rates of ecosystem processes and services, understanding the mechanisms explaining such departures is the focus of much ecological inquiry.

Research on why decay of speciose litter proceeds non-additively has progressed much faster in terrestrial versus aquatic ecosystems (as reviewed by Gartner and Cardon 2004; but see Swan and Palmer 2004, 2006). This is despite knowledge that aquatic food webs in shaded temperate streams rely almost exclusively on riparian-derived leaf litter for energy (Wallace et al. 1997; Wallace et al. 1999; Hall et al. 2001). The majority of research has approached assessing non-additive decay of speciose litter from the bottom-up by looking at whether interspecific variation in leaf litter quality interacts synergistically/antagonistically to change decay rate (Wardle et al. 1997; Hoorens et al. 2003; Gartner and Cardon 2004; Swan and Palmer 2004; but see Swan and Palmer 2006). However, both terrestrial and aquatic ecologists know that detritivorous consumers can contribute substantially to leaf litter decay (Wallace et al. 1982; Sponseller and Benfield 2001; Hieber and Gessner 2002), and exhibit striking changes in feeding behavior and colonization dynamics in response to leaf litter nutrient content and secondary compounds (Herbst 1982; Golladay et al. 1983; Irons et al. 1988; Cuffney et al. 1990; Sweeney 1993; Swan and Palmer 2005).

Communicated by Steven Kohler

C. M. Swan (✉)
Department of Geography & Environmental Systems,
University of Maryland, Baltimore County,
Baltimore, MD 21250, USA
E-mail: Chris.Swan@umbc.edu
Tel.: +1-410-4553957
Fax: +1-410-4551056

M. A. Palmer
Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA

Evidence from terrestrial ecosystems suggests that these consumers may mediate how speciose leaf litter degrades via preferential and/or compensatory feeding, but this mechanism has not been tested in aquatic ecosystems (Hättenschwiler and Gasser 2005).

Detritivores inhabiting shaded streams rely on inputs of leaf litter to meet their energy demands (Fisher and Likens 1973; Cummins et al. 1989; Hall et al. 2001). To a large extent, the amount and species distribution of leaf litter on the streambed available to leaf-chewing consumers (shredders; sensu Cummins and Klug 1979) reflect the input rates and species composition of the deciduous tree species in the riparian zone (Johnson and Covich 1997; Swan and Palmer 2004). Known differences in leaf litter chemistry exist between leaf species (Webster and Benfield 1986; Ostrofsky 1997), allowing ecologists to relate the quality of leaf litter as a resource for detritivores to leaf species identity (Golladay et al. 1983). In general, leaf species with lower levels of essential nutrients (e.g., N) and higher concentrations of secondary and structural compounds (e.g., tannins, phenolics, lignin), such as oaks, alter shredder growth/feeding and slow overall decomposition rate (Campbell and Fuchshuber 1995; Tuchman et al. 2002; Swan and Palmer 2004). Conversely, leaf species with higher nutrient levels and lower concentrations of secondary compounds, such as maples and alders, can support higher growth rates of shredders and have been shown to exhibit faster decomposition rates in the field (Iversen 1974; Herbst 1982; Irons et al. 1988; Smock and MacGregor 1988; Swan and Palmer 2004). Given the reported high variability in resource quality that is related to leaf species identity, loss of riparian tree species could impact how in-stream shredders perform, as well as how leaf litter degrades overall (Swan and Palmer 2004, 2006).

Generalist consumers often forego subsisting on a single resource to exploit mixed resources. The advantage of a mixed diet can be to reduce or dilute the intake of toxic substances or to acquire essential nutrients from complementary resources (Freeland and Janzen 1974; Pulliam 1975; Rapport 1980; Bernays et al. 1994). Work on the relationship between consumer performance and resource heterogeneity has focused mostly on herbivores (e.g., Hagele and Rowell-Rahier 1999), omnivores (e.g., Bjorndal 1991), and predators (e.g., Evans et al. 1999), and less on detritivores (but see Swan and Palmer 2006). Leaf litter comprises the food base of many detritivores in both aquatic and terrestrial ecosystems where the majority of primary production enters the detrital pool (McNaughton et al. 1989; Cebrian 1999). Thus, leaf litter can be an inherently heterogeneous resource, requiring detritivores to exploit a mixed diet.

We have previously shown that decomposition rates of mixed-litter assemblages in the field cannot always be predicted by averaging the decomposition rates of each species individually (Swan and Palmer 2004) and, furthermore, that mixed-litter can substantially alter patterns in detritivore growth and feeding (Swan and Palmer 2006). We hypothesized that this non-additive effect was due to preferential feeding by shredders fed mixtures containing low quality detritus. For example, if a consumer is offered two resources, A and B, where A is more palatable than B, the consumer should exhibit higher feeding rate on A. However, when the consumer has no choice, its feeding rate on B may increase in order to compensate for poor resource quality. Therefore, the total mass loss rate of the mixture of A and B should be *slower* compared with the *average* of A and B, individually. This shift in feeding rate on a mixed-diet could therefore explain why decay rate of speciose litter can be slow compared to what would be predicted based on single species diets alone (Swan and Palmer 2006). To address this experimentally, we asked: (1) do shredders exhibit preferential feeding on high quality resources when alternative resources are available, and (2) if preferential feeding occurs, is this consistent with non-additive patterns of leaf decomposition of litter mixtures?

Materials and methods

The isopod crustacean *Caecidotea communis* is a common leaf-shredding detritivore that inhabits small streams across the eastern half of North America (Williams 1972). In early January 2003, gravid female isopods were collected from a spring-fed tributary of the Middle Patuxent River, a 3rd-order Piedmont stream located west of the Chesapeake Bay in Howard County, Maryland, USA (39°15′N, 76°55′E; elevation 100 m). These individuals were kept in the laboratory in aerated stream water and allowed to feed on leaf material collected at the time of sampling. Shortly after hatching, juveniles were collected and the adult isopods separated until enough juveniles had been collected for the experiment (a period of ~10 days).

Invertebrates and leaf treatments were housed in 500-ml plastic chambers (75 mm in height × 112 mm in diameter). Chamber lids were perforated with two holes (6 mm in diameter), one to accommodate air supply via standard aquarium airline and the other to relieve air pressure. Each chamber was filled to ~1 cm depth (capacity 100 ml) with air-dried stream sediment (size-distribution, by volume: 4.5% <0.25 mm, 30.6% 0.25–0.50 mm, 39.4% 0.50–1.0 mm, 20.6% 1.0–2.0 mm, 4.8% >2.0 mm) collected from the Middle Patuxent at the time the isopods were sampled.

The study began on 15 January 2003. The design was a two-way factorial design [3 shredder treatments (0, 3, 6 isopods), 8 litter treatments (Table 1)] with a total of $n=10$ chambers per litter × shredder combination. Isopod density was chosen to approximate the range in isopod densities occurring in the field (975 m^{-2}, SE = 675, $n=4$). Leaf litter of the common riparian trees boxelder (*Acer negundo* L., C:N = 21.1), American sycamore (*Platanus occidentalis* L., C:N = 47.5), black willow (*Salix nigra* Marsh,

Table 1 Summary of leaf litter treatments

Litter composition	Species	Species AFDM (mg)	Total initial AFDM (mg)
Boxelder			195.2 (0.77)
Slippery elm			216.5 (1.15)
American sycamore			246.1 (1.00)
Black willow			235.3 (1.07)
B + E + S	B	66.2 (0.41)	223.0 (1.45)
	E	72.4 (0.84)	
	S	84.4 (1.02)	
B + E + W	B	67.1 (0.63)	219.5 (1.91)
	E	72.1 (1.02)	
	W	80.3 (0.95)	
B + S + W	B	66.8 (0.42)	228.8 (1.34)
	S	82.7 (1.31)	
	W	79.3 (0.89)	
E + S + W	E	74.1 (0.62)	238.9 (1.81)
	S	83.5 (1.04)	
	W	81.2 (1.17)	

Estimates for the average initial mass of each species in each mixture treatment (species AFDM) and total initial AFDM are given, with SE in parentheses. Units are in mg. $n = 30$ for all estimates

B Boxelder, *E* Slippery elm, *S* American sycamore, *W* Black willow

C:N = 47.2) and slippery elm (*Ulmus rubra* Muhl., C:N = 41.1) were collected during the autumn of 2002 (just after leaf abscission) from the riparian zone of the Middle Patuxent River, and kept in plastic bins in the laboratory until needed the following January. These species represent the dominant species in local riparian habitats and exhibit a realistic range in C:N content, a commonly used index of palatability (analyzed with an automated CHN analyzer, University of Maryland Soils Testing Laboratory, College Park, Maryland, USA). Eight litter treatments were established: four single-species treatments and four three-species treatments (hereafter, "mixed" treatments; Table 1). Each chamber received approximately 300 mg of leaf material (fresh weight) as coarsely broken fragments (Table 1). We attempted to hold mass of the leaf treatments constant; thus, mixed-species treatments were comprised of ~100 mg of each species.

The chambers were randomly assigned locations on a laboratory workbench, leaf litter was added and then the chambers were filled with ~300 ml of deionized water. Each chamber was inoculated with 5 ml of stream water that had been collected from the Middle Patuxent, aerated since the time of sampling, and filtered twice at 45 µm to remove invertebrates, while still adding microbes. Chambers were arranged in 10 groups of 24 chambers, with each group constituting a sample date. Each group of 24 chambers was supplied with air from a standard aquarium air pump, with air-flow controlled by a separate air valve for each chamber. Water temperature for the duration of the experiment averaged 23.2°C (SD = 0.6°C, $n = 7$; range = 6.6°C). Light regime was set to a long day cycle of 16 h:8 h light:dark with standard fluorescent lighting. Water was added throughout the study to correct for evaporation.

After 8 days of pre-conditioning and leaching, a complete water change was made and newly hatched isopods (0, 3, or 6) were added to chambers designated for shredders using a pipette (23 January 2003 = day 0). Isopod juveniles averaged 0.039 mg dry mass $\{\mathrm{SE} = 0.0020,\ n = 70;\ \ln(\text{mg dry mass}) = -4.241 + 2.424\,[\ln(\text{length, mm})],\ r^2 = 0.97,\ n = 22\}$. Estimates of leaf ash-free dry mass (AFDM) available at day 0, after leaching, were made by conducting a companion study. Each leaf treatment (Table 1) was allocated to containers ($n = 5$ per treatment, 40 containers total) in the same manner as the main study. After 8 days of leaching/conditioning, the leaf litter was removed, dried to a constant weight at 60°C, combusted for 90 min at 550°C then re-weighed to determine AFDM. The fraction of AFDM estimated from this parallel study was used to estimate leaf AFDM available on day 0 when the shredders were added.

Samples were taken on days 4, 10, 15, 22, 29, 36, 43, 51, 59 and 75. Sampling involved first removing the isopods and preserving them in 70% ethanol, including any newly hatched individuals due to reproduction during the study. Individual isopod dry mass was estimated for each sample using the allometric equation above; length measurements were made with a stereomicroscope fitted with an ocular micrometer. If a chamber assigned to an isopod treatment was found to have none at sampling, that replicate was dropped from the study (this was the case in 22 of the 240 chambers). Leaf litter remaining was removed and sorted by leaf species into separate, pre-weighed tins. The leaves were then dried at 60°C, combusted for 90 min at 550°C, and re-weighed to determine AFDM remaining (Benfield 1996).

Data analysis

Leaf decomposition rate

Due to reproduction during the experiment, the distinction between the three and six individual isopod treatments was no longer clear, and thus all treatments with isopods were combined into a "shredder present" treatment, making the final analysis a two-way factorial [(2 shredder treatments (present, absent), 8 litter treatments]. Decomposition rate was assessed by estimating k in the exponential decay model $W_t = W_o\, e^{-kt}$, where W_o is initial mass and W_t is the mass of the litter at time t (Petersen and Cummins 1974). Mass at day t (ln AFDM_t; g) was analyzed as a function of day, shredder treatment, litter treatment and all interactions. The estimate of the interaction term (day × leaf treatment × shredder treatment) was taken as the k-value for each shredder × leaf treatment combination.

Output from the ANCOVA was used to make three sets of comparisons within each shredder treatment: (1) comparisons between single- and mixed-species treatments, (2) comparisons among single-species treatments, and (3) comparisons between observed decay rate of each mixed-treatment and the predicted decay rate of each mixture (i.e., the average of the decay rates of each leaf species separately). Significance for comparisons among single-species leaf treatments were adjusted using Hommel's correction for multiple-comparisons (Westfall et al. 1999). For the third set of comparisons, a linear contrast was used to test for differences between the average decay rate across single-species litter treatments and that of the corresponding mixed treatment. For example, a significant difference between the mean of the decay rates estimated for boxelder (B), slippery elm (E), and black willow (W) treatments and that of the mixed treatment of these three species (i.e., B + E + W) would indicate that decay rate on the mixed treatment was non-additive. To maintain Type I error rate and orthogonality, a multiple-linear contrast procedure was first conducted for all four mixed-treatments and, upon obtaining a significant *F*-test, individual contrasts were then calculated (Sokal and Rohlf 1981).

Shredder feeding rate

Feeding rate was calculated as:

$$\text{Feeding Rate} = \frac{\text{Leaf Mass Consumed}}{\text{Shredder Mass Gained} \cdot \text{days}},$$

where leaf mass consumed is the difference in leaf AFDM at sampling and initial leaf AFDM in the treatments containing the isopods. Shredder mass gained is the difference between total isopod dry mass at sampling and initial isopod dry mass, and days are the number of days since the study began. To ascertain the presence of preferential feeding, analysis of feeding rates of each leaf species—alone, and in mixture—were carried out. To account for the altered availability of leaf species between single and mixed-species diets (i.e., each leaf species was ~3 times more available in the single-species diet versus any of the three mixed diets), feeding rates in single-species treatments were corrected. On each sample date, the average AFDM of a particular leaf species *in mixture* across all three shredder treatments (i.e., 0, 3, 6 isopods) was divided by the average AFDM of that same litter species alone. For each species, this correction factor averaged: boxelder: 0.3392, slippery elm: 0.3321, sycamore: 0.3437, and Willow: 0.3452. For example, 33.92% of boxelder AFDM present in the single-species treatment was available initially in each of the three mixtures in which boxelder was present. Then, for each species, a single ANOVA was performed, and comparisons done between feeding rate on the single-species treatment and that species within each of the three mixtures. If the feeding rate was higher in the mixed-species treatment compared to feeding on that species individually, this was taken as evidence for preferential feeding.

All analyses were performed using SAS version 9.1 and evaluated at $\alpha = 0.05$. Denominator degrees of freedom were adjusted using the Satterthwaite approximation.

Results

Leaf decomposition rate

Strong interactions between leaf treatment and the presence of the isopod were evident with respect to total leaf decomposition rate (significant day × leaf × shredder treatment effect; Table 2). Comparing single- and mixed-litter treatments, no difference was evident in the absence of the shredder, but decomposition rate of mix-litter treatments was significantly slower than single-species litter (Fig. 1a). Mixtures of three leaf species were on average 60% slower to lose mass than single-species treatments. This was accentuated by the strong differences seen between single-species leaf treatments in the presence of the isopod. In the presence of the shredder, boxelder was the fastest decomposer, degrading nearly 3.7 × faster than elm, sycamore and willow combined (Fig. 1b). This was not the case in single-species treatments lacking the isopod where decomposition rates quite similar (Fig. 1c).

Three of the four mixed-treatments decomposed significantly slower than predicted when the isopod was present ($F_{4,120} = 4.45$, $P = 0.0022$), but were completely additive in the absence of the shredder ($F_{4,115} = 0.39$, $P = 0.8170$). Focusing on the mixtures containing the shredder (Fig. 1b), the B + E + S, B + E + W and B + S + W mixtures were significantly slower than predicted, whereas decomposition of the mixture that lacked the *fastest* decomposer, E + S + W, was found to be additive. The magnitude of the reduction in decomposition rate due to mixing averaged $k = 0.0099$, which is greater than the decomposition rate of willow alone ($k = 0.0092$), suggesting that the effect of mixing on slowing decomposition rate was substantial.

Feeding rate

With respect to whether this shredder exhibits preferential feeding, analysis of species-specific feeding rates revealed that *Caecidotea communis* fed equally among

Table 2 Statistical results for leaf decomposition and feeding rate

Effect	NDF	DDF	*F*	*P*
Leaf decomposition rate				
Day	1	79.8	157.71	< 0.0001
Leaf treatment	7	101.0	1.60	0.1446
Shredder treatment	1	81.4	1.18	0.2811
Leaf × shredder treatment	7	101.0	0.50	0.8311
Day × leaf treatment	7	100.0	3.43	0.0025
Day × shredder treatment	1	79.8	46.00	< 0.0001
Day × leaf × shredder treatment	7	100.0	2.70	0.0134
Feeding rate				
Day	1	103.0	51.39	< 0.0001
Leaf treatment	7	103.0	2.97	0.0071

Sample day was found to be a significant covariate in the final analysis of feeding rate

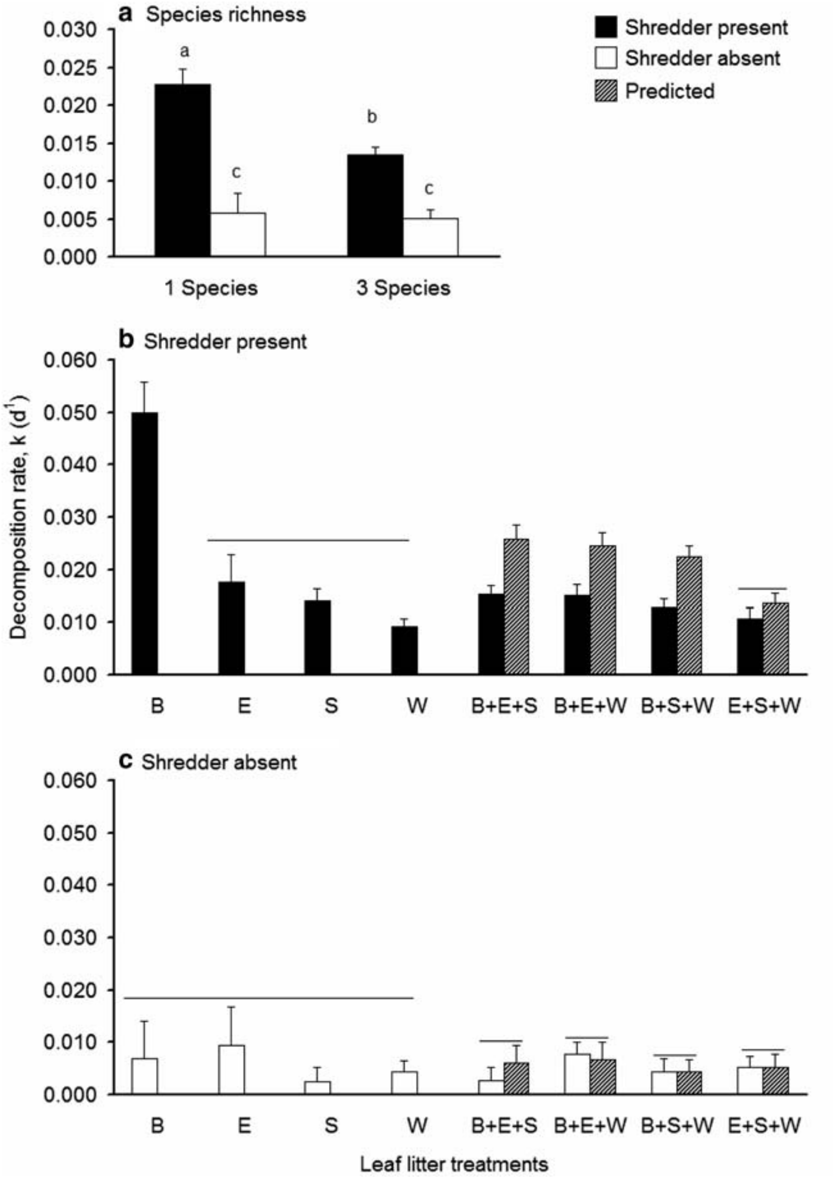

Fig. 1 Total leaf decomposition rate as a function of **a** number of leaf species, **b** leaf treatments with shredders present, and **c** leaf treatments with shredders absent. For the *top panel*, *bars* with the same letter are not significantly different. Predicted means (*hatched bars*) are the average of the single-species estimates for each mixture. All *bars* are the mean + 1SE. *Connected bars* for single-species leaf treatments indicate no significant difference, otherwise observed decomposition rate differs ($P < 0.05$). For mixtures, comparisons are limited to observed and predicted for each mixture; *connected bars* indicate no non-additive mixing effect ($P > 0.05$). Species abbreviations are as follows: *B* boxelder, *E* slippery elm, *S* American sycamore and *W* black willow

three of the four leaf species used in this study. Feeding rates on boxelder (ANOVA $F_{3,61} = 0.19$), elm (ANOVA $F_{3,57} = 0.96$) and willow (ANOVA $F_{3,52} = 2.11$) were not significantly different when comparing feeding on the leaf species alone, or when it was in mixture (all P values > 0.05; Fig. 2). However, feeding rate on sycamore alone was significantly faster than on this same species in mixture with boxelder and willow (ANOVA $F_{3,51} = 3.93$, $P < 0.05$; shaded bars Fig. 2c). Isopods consumed sycamore 1.88 times faster when it had no other leaf species to feed upon compared to the B + S + W treatment. However, this was the only mixture demonstrating a significant pattern; feeding rates on sycamore alone compared to sycamore in either the B + E + S or E + S + W treatment did not differ.

Discussion

Plant species richness can alter ecosystem processes in many ways, including decay of senesced leaf tissue (Gartner and Cardon 2004; Swan and Palmer 2004, 2006). In temperate terrestrial and aquatic ecosystems, leaf litter enters the detrital pool in a large pulse during

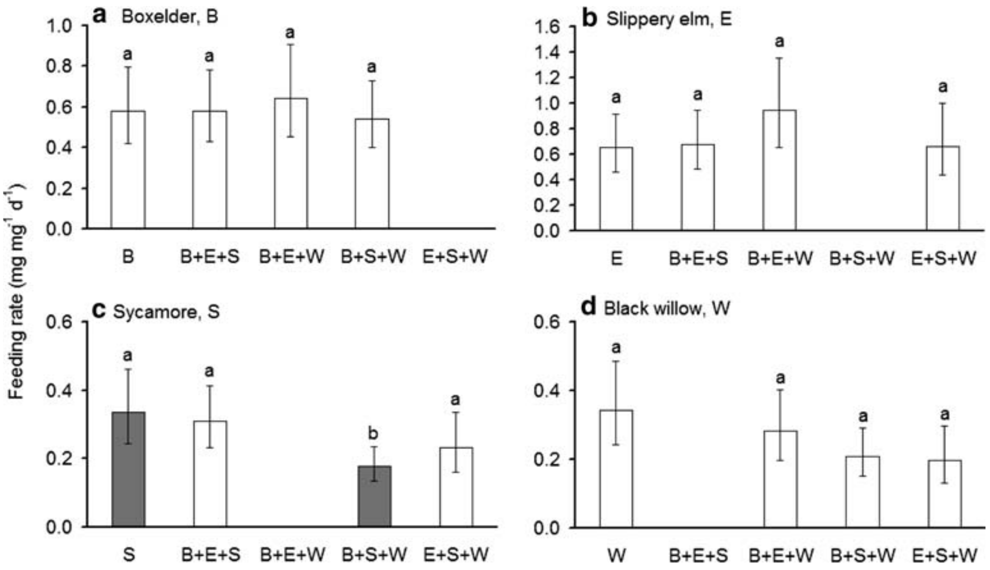

Fig. 2 Shredder feeding rate (mg per mg per day) on each leaf species individually and for that species in mixture, **a** boxelder, **b** slippery elm, **c** sycamore, **d** black willow. *Shaded bars* in (**c**) highlight the significant difference between feeding rate of sycamore alone versus the mixture treatment B + S + W. *Bars* are the back-transformed means and *error bars* are the back-transformed 95% confidence interval. All mixtures are indicated in each plot for clarity. *Bars* with the same letter are not significantly different ($P > 0.05$); comparisons are made for each species separately. Note differences in scale of Y-axes. Species abbreviations are as in Fig. 1

autumnal leaf fall and then decomposes, both releasing energy to the food web and recycling nutrients back into the soil or downstream. Extensive work in terrestrial ecosystems and, to a lesser extent, aquatic ecosystems has demonstrated that interspecific variation in leaf litter chemistry can lead to non-additivity in the decay of speciose leaf litter (Gartner and Cardon 2004; Swan and Palmer 2004, 2006). Here, we tested an alternative mechanism for how multi-species leaf litter should degrade by incorporating foraging behavior of detritivorous consumers. We found that preferential feeding by an aquatic detritivore, the isopod *Caecidotea communis*, can change the decomposition of litter mixtures when compared to the average decay rate of leaf species in the mixture estimated alone.

Shaded stream ecosystems harbor a diverse assemblage of detritivores that rely on terrestrially-borne detritus (Wallace et al. 1997, 1999). Leaf-shredding invertebrates occupy a critical link between terrestrial energy sources (i.e., leaf litter) and adjacent trophic levels by transforming this detritus into biomass thereby creating food for predators and producing particles as a by-product of feeding for downstream filter-feeding consumers (Shepard and Minshall 1984; Cuffney et al. 1990; Dieterich et al. 1997). Given the extent to which quality of leaf litter can alter both shredder growth and feeding rates (Smock and MacGregor 1988; Sweeney 1993; Swan and Palmer 2006), the goal of this study was to determine if shredders alter feeding rates when provided mixed-species leaf litter, and if any such effects explain patterns in mixed-species decomposition rate. Our results revealed that feeding rate by the consumer was elevated on American sycamore, a lesser quality resource, when the animal was not given a choice. When the consumer was given the choice to feed on more palatable leaf species (e.g., boxelder), feeding rate on American sycamore slowed, thus slowing the rate of multi-species litter as a whole. However, this phenomenon was not revealed for all mixtures studied, suggesting other factors need to be considered in future studies. Taken together, this work suggests that consumer foraging may be critical to understanding how diverse leaf litter decomposes in aquatic ecosystems.

What then could be causing the strong, non-additive slowing of total decomposition rates of mixtures in cases where preferential feeding was not evident (i.e., mixtures B + E + S, B + E + W)? Effects of mixing resources, in addition to any interaction with the presence of the shredder, were not assessed with respect to the microbial community. If we chose to correct for microbial degradation, however, we assume that there is no interaction between shredder feeding activity and the degradative ability of the microbes. This may or may not be the case. A recent paper by Ribblet et al. (2005) demonstrates that bacterivory by protists can alter decay rate of leaf litter in aquatic microcosms. Shredders, when consuming leaf material, consume both leaf and microbial biomass. In doing so, they both reduce microbial biomass (via direct consumption) on the substrate and open up fresh leaf material to be colonized by bacteria and fungi. Both activities could alter the fraction of decay rate contributed by the microbial community, but not predictably. Complicating this assumption is the fact that leaf quality varies, and thus feeding activity could induce both positive and negative (or no) changes in activity by the microbial community.

Bacteria and, to a larger extent, fungal communities can contribute to leaf decomposition, but this contribution is estimated to be small compared to loss due to invertebrates and the physical environment (Webster and Benfield 1986; Hieber and Gessner 2002). This occurs via direct digestion of leaf tissue with exo-enzymes, which soften the leaf tissue for shredder consumption (Bärlocher 1985; Webster and Benfield 1986). In the present study, however, differences between single-species treatments and between observed and predicted decomposition rates of mixtures without the shredder did not mirror the pattern seen when the isopod was present. Lack of such consistency suggests that, among mixtures lacking evidence of preferential feeding, there may have been an interaction between shredder presence and microbial degradative ability. While we know of no study to date documenting any such interaction between arthropods and microbes, evidence does exist that bacteria-feeding protists alter the degradative ability of the bacteria, enhancing decomposition rate (Ribblet et al. 2005). Therefore, exploring the interaction between resource quality, shredder presence and microbial activity (e.g., production, enzyme activity) could be vital to completely understanding the complex role mixing leaf species can have on total leaf decomposition rate.

We acknowledge the evidence we present here is from a laboratory study, and necessarily so given the difficulty in isolating detritivore impact on decay in the field (but see Wallace et al. 1982). Leaf decomposition in streams is a function of a number of factors besides detritivore feeding; indeed, leaves do decompose in aquatic systems where shredders are rare or absent (Sponseller and Benfield 2001). Mechanical forces such as substrate abrasion and flow are responsible for a substantial fraction of mass loss (Paul and Meyer 2001; Hieber and Gessner 2002). Also, burial can slow decay by creating anoxic conditions that are less hospitable to invertebrate consumers (Tillman et al. 2003). These factors, combined with water chemistry variables like nutrient concentration and pH, may be quite important to how multi-species litter decays (Grattan and Suberkropp 2001; Dangles and Chauvet 2003). However, in shaded headwater streams where detritivores are abundant, we expect a substantial contribution of feeding to mass loss, even in the context of the aforementioned environmental conditions (Hieber and Gessner 2002). More work under these circumstances is required, and will be essential to completely understanding the mechanisms by which speciose leaf litter decays in aquatic ecosystems.

One impetus for this work was the growing realization that the loss of deciduous riparian tree species is a real phenomenon (Smock and MacGregor 1988; Sweeney 1993; Snyder et al. 2002; Ellison et al. 2005). Since stream ecosystems rely on the delivery of leaf material to the stream during annual leaf-fall, such losses could impact in-stream detritivores (Wallace et al. 1997, 1999; Swan and Palmer 2004, 2005, 2006). The strong, non-additive effects of mixing leaf species suggests that consumer-resource interactions are complicated, and can change if riparian tree species richness is reduced (Swan and Palmer 2006). Evidence from this study supports previous findings that detritivore feeding rates will change, and the subsequent effects on both organic matter dynamics (i.e., leaf decomposition) and detritivore growth can be substantial (Swan and Palmer 2006). Further work is required to broaden these results to other consumers from streams comprised of different deciduous riparian communities.

Decomposition of organic matter is a key ecosystem process, defining the rate at which detritus becomes available to consumers, and is recycled into nutrient pools. The results from this study suggest that the loss of species richness of deciduous vegetation can lead to alterations in the magnitude of leaf decomposition in aquatic ecosystems. The role leaf shredders play in the decomposition process can be further extended to how they mediate the role played by species diversity of leaf litter. By showing that *Caecidotea communi*s exhibits preferential feeding when a diverse diet is present, this work suggests loss of particularly refractory species (e.g., American sycamore) could impact how natural assemblages of leaves degrade in the stream. At elevated levels of leaf species richness, if refractory leaf material is present, it may decompose *slower* than if alone, increasing the retentiveness of that material in the system. Therefore, preferential feeding by detritivores could be a critical ecological mechanism mediating how species richness of riparian deciduous vegetation can alter in-stream ecosystem processes.

Acknowledgements We thank Robert Denno, Laura Craig, Holly Menninger, Aaron Moore, Dave Richardson, John Richardson, Bob Smith and Gina Wimp for their comments and editing. Comments from Steve Kohler and two anonymous reviewers greatly improved the text. This research was supported by grants awarded to C.M.S. from the Chesapeake Bay Fund (University of Maryland) and to M.A.P. from the National Science Foundation (DEB-9981376).

References

Bärlocher F (1985) The role of fungi in the nutrition of stream invertebrates. Bot J Linn Soc 91:83–94

Benfield EF (1996) Leaf breakdown in stream ecosystems. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic, San Diego, pp 579–589

Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. Ecology 75:1997–2006

Bjorndal KA (1991) Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. Ecology 72:1234–1241

Campbell IC, Fuchshuber L (1995) Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. J N Am Benthol Soc 14:174–182

Cebrian J (1999) Patterns and the fate of production in plant communities. Am Nat 154:449–468

Cuffney TF, Wallace JB, Lugthart GJ (1990) Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. Freshwater Biol 23:281–299

Cummins KW, Klug MJ (1979) Feeding ecology of stream invertebrates. Annu Rev Ecol Syst 10:147–172

Cummins KW, Wilzbach MA, Gates DM, Perry JB, Taliaferro WB (1989) Shredders and riparian vegetation. BioScience 39:24–30

Dangles O, Chauvet E (2003) Effects of stream acidification on fungal biomass in decaying beech leaves and leaf palatability. Water Res 37:533–538

Dieterich M, Anderson NH, Anderson TM (1997) Shredder-collector interactions in temporary streams of western Oregon. Freshwater Biol 38:387–393

Ellison AM, Bank MS, Barker-Plotkin AA, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Jefts S, Kloeppel BD, Knoepp JD, Lovett GM, Malloway J, Mathewson B, McDonald R, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Snow P, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486

Evans EW, Stevenson AT, Richards DR (1999) Essential versus alternative foods of insect predators: benefits of a mixed diet. Oecologia 121:107–112

Fisher SG, Likens GE (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol Monogr 43:421–439

Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. Am Nat 108:269–289

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246

Golladay SW , Webster JR, Benfield EF (1983) Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecol 6:157–162

Grattan RM, Suberkropp K (2001) Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. J N Am Benthol Soc 20:33–43

Hagele B, Rowell-Rahier M (1999) Dietary mixing in three generalist herbivores: nutrient complementation or toxin dilution. Oecologia 119:521–533

Hall RO Jr, Likens GE, Malcom HM (2001) Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. J N Am Benthol Soc 20:432–447

Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects on decomposition. Proc Natl Acad Sci USA 102:1519–1524

Herbst GN (1982) Effects of leaf type on the consumption rates of aquatic detritivores. Hydrobiologia 89:77–87

Hieber M, Gessner MO (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Hoorens B, Aerts R, Stroetenga M (2003) Does initial litter chemistry explain litter mixture effects on decomposition? Oecologia 137:578–586

Irons JG III, Oswood MW, Bryant JP (1988) Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. Hydrobiologia 160:53–61

Iversen TM (1974) Ingestion and growth in *Sericosoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. Oikos 25:278–282

Johnson SL, Covich AP (1997) Scales of observation of riparian forests and distributions of suspended detritus is a prairie river. Freshwater Biol 37:163–175

McNaughton SJ, Osterfield M, Frank DA, Williams KJ (1989) Ecosystem level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341:142–144

Ostrofsky ML (1997) Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. J N Am Benthol Soc 16:750–759

Paul MJ, Meyer JL (2001) Streams in the urban landscape. Annu Rev Ecol Syst 32:333–365

Petersen RC, Cummins KW (1974) Leaf processing in a woodland stream. Freshwater Biol 4:343–368

Pulliam HR (1975) Diet optimization with nutrient constraints. Am Nat 109:765–768

Rapport DJ (1980) Optimal foraging for complimentary resources. Am Nat 116:324–346

Ribblet SG, Palmer MA, Coats DW (2005) The importance of bacterivorous protists in the decomposition of stream leaf litter. Freshwater Biol 50:516–526

Shepard RB, Minshall GW (1984) Role of benthic insect feces in a rocky mountain stream: fecal production and support of consumer growth. Holarctic Ecol 7:119–127

Smock LA, MacGregor CM (1988) Impact of the American chestnut blight on aquatic shredding macroinvertebrates. J N Am Benthol Soc 7:212–221

Snyder CD, Young JA, Lemarié DP, Smith DR (2002) Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Can J Fish Aquat Sci 59:232–275

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. W.H. Freeman, New York

Sponseller RA, Benfield EF (2001) Influences of land-use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis. J N Am Benthol Soc 20:44–59

Swan CM, Palmer MA (2004) Leaf diversity alters litter breakdown in a Piedmont stream. J N Am Benthol Soc 23:15–28

Swan CM, Palmer MA (2005) Leaf litter diversity leads to non-additivity in stream detritivore colonization dynamics. Oceanol Hydrobiol Stud 34:19–38

Swan CM, Palmer MA (2006) Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia 147:469–478

Sweeney BW (1993) Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. Proc Acad Natl Sci Philadelphia 144:291–340

Tillman DC, Moerke AH, Ziehl CL, Lamberti GA (2003) Subsurface hydrology and degree of burial affect mass loss and invertebrate colonisation of leaves in a woodland stream. Freshwater Biol 48:98–107

Tilman D, Knops D, Wedin J (1996) Productivity and sustainability influenced by biodiversity in grassland systems. Nature 379:718–720

Tuchman NC, Wetzel RC, Rier ST, Wahtera KA, Teeri JA (2002) Elevated atmospheric CO_2 lowers leaf litter nutritional quality for stream ecosystem food webs. Glob Change Biol 8:163–170

Wallace JB, Webster JR, Cuffney TF (1982) Stream detritus dynamics: regulation by invertebrate consumers. Oecologia 53:197–200

Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104

Wallace JB, Eggert SL, Meyer JL, Webster JR (1999) Effects of resource limitation on a detrital-based ecosystem. Ecol Monogr 69:409–442

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258

Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. Annu Rev Ecol Syst 17:567–594

Westfall PH, Tobias RD, Rom D, Wolfinger RD, Hochberg Y (1999) Concepts and basic methods for multiple comparisons and tests. In: Multiple comparisons and multiple tests using the SAS system. SAS Institute, pp 13–40

Williams WD (1972) Freshwater isopods (Assellidae) of North America. Biota of freshwater ecosystems identification manual no. 7. U.S.E.P.A