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Leaf diversity alters litter breakdown in a Piedmont stream

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Abstract. Work in terrestrial ecosystems has suggested that the breakdown rate of leaf litter may not change predictably with increasing plant species richness. Indeed, it may be that certain combinations of leaf species demonstrate significant non-additive effects on breakdown rates, mediated by the presence of a single key species. Such effects have not been explored in running-water ecosystems despite the strong interest in the conservation and restoration of riparian systems. We documented the magnitude and species composition of leaf litter inputs, the species richness and composition of leaf litter on the streambed, and estimated the breakdown rate of mixed litter in both the summer and autumn in a warmwater stream. We found that leaf species richness of litter packs on the streambed varied from 1 to 11 species, and leaf species composition reflected the composition of litter inputs from May through November. We did not find a general relationship between breakdown rate and leaf litter *species richness.* However, we did find a strong effect of species *composition* of leaf packs on the breakdown rate during the summer. Overall, breakdown rates of mixed-species leaf packs were non-additive during the summer, but very predictable in the autumn. In particular, leaf mixtures containing American sycamore always exhibited slower breakdown rates than predicted in summer. One explanation for the discrepancy between summer and autumn results may be decreased temperature in autumn; reduced temperature may have slowed breakdown rates across treatments to the extent that any non-additive effects found in summer were masked by the effect of temperature. Given the importance of detritus to stream food webs, the simplification of plant assemblages along intact or restored streams may have important implications for stream ecosystems.

Key words: mixed litter, leaf species richness, leaf breakdown rate, ecosystem processes, riparian, streams, leaf litter.

The relationship between species richness and the rates of key ecosystem processes has received considerable attention given the dramatic loss of biodiversity across the landscape (see reviews in Chapin et al. 2000, Loreau et al. 2001). In contrast to work in terrestrial ecosystems (e.g., Taylor et al. 1989, Blair et al. 1990, Kaneko and Salamanca 1999), little work has been done on the relationship between leaf breakdown rate, a vital ecosystem process, and leaf litter species richness in streams (Boulton and Boon 1991; but see Leff and McArthur 1989, McArthur et al. 1994). Leaf litter from deciduous vegetation in temperate climates is an integral component of terrestrial and aquatic ecosystems. Breakdown of this material is a critical ecological process determining the availability of food resources for large and complex food webs (Cummins et al. 1989, Wallace et al. 1997, Ponsard et al. 2000, Hall et al. 2001) .

An increase or decrease of breakdown rates in streams as a function of leaf litter composition, as has been reported in terrestrial systems (e.g., Wardle et al. 1997), could have far-reaching implications for aquatic ecosystem management. Maintaining vegetated cover along stream margins is a well-accepted practice among natural-resource managers (Gregory et al. 1991, Naiman and Décamps 1997); however, the spe-

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cies richness of trees and shrubs within this zone may also be critical if it influences the detrital food web. Riparian vegetation is the focus of many conservation and restoration efforts in freshwater ecosystems (Sweeney 1993, USDA 1996), so the decisions made about what type of vegetation to protect or plant may have consequences for stream ecosystems that go beyond issues related to riparian habitat.

The structural and chemical attributes of leaves can vary dramatically among species (Webster and Benfield 1986, Chauvet 1987, Ostrofsky 1997), so breakdown may be related to the number and type of chemically unique species present in the detrital matrix. The chemical and structural nature of particulate detritus interacts with the biotic (i.e., bacteria, fungi, invertebrates; Harrison 1971, Bärlocher and Kendrick 1975, Cummins et al. 1989) and abiotic (i.e., temperature, water flow, soil/water chemistry; Allard and Moreau 1986, Webster and Benfield 1986) components of ecosystems to regulate the rate of breakdown. In terrestrial systems, leaf species containing low C:N content tend to stimulate breakdown rate, whereas leaves with certain refractory compounds (e.g., phenolics, tannins) tend to slow breakdown rate (Harrison 1971, Chapman et al. 1988, Taylor et al. 1989) in mixed-litter assemblages. However, a comprehensive study examining the decay dynamics of single vs mixed species, using 32 species of deciduous and herbaceous leaves, failed to find any general relationship between breakdown, C mineralization, and the number of leaf species present (Wardle et al. 1997).

A general relationship between breakdown rate and plant species richness has not been found for terrestrial ecosystems, but non-additive effects of litter mixing on breakdown rates have been documented. Nutrient-rich pine needles generated greater than expected N and P availability in a spruce/pine mixture, and resulted in higher than expected microbial respiration compared to spruce alone (Chapman et al. 1988). Oak served a similar function in mixtures with pine and a shrub species; breakdown was faster and there were higher numbers of soil microarthropods than expected based on estimates of pine or shrubs alone (Kaneko and Salamanca 1999). Mixed-species composition does not necessarily lead to higher breakdown rates because inhibitory compounds in some leaves (e.g., tannins) can slow breakdown rates in mixed litter (e.g., spruce/oak and spruce/alder mixtures; Chapman et al. 1988). In sum, breakdown rates may not change predictably or monotonically with increasing plant species richness, but certain leaf litter combinations may lead to strong non-additive effects on ecosystem-level processes (e.g., breakdown, respiration, nutrient availability) and community-level properties (e.g., invertebrate species composition; Hansen 2000). Furthermore, these effects may be mediated by the presence of a single species that exerts strong positive or negative control.

We present work designed to answer the following questions: 1) What is the species composition and magnitude of leaf litter inputs to a 3rd-order Piedmont stream? 2) What is the species composition of leaf litter on the streambed? 3) Does the breakdown rate of leaf litter change in a predictable way when more leaf species are present? 4) If not, is the breakdown rate of heterogeneous leaf litter ($\geq$ 2 leaf species) non-additive (i.e., can the breakdown rate of multispecies detritus be predicted from the average of single-species estimates)? and 5) Are the magnitudes of any such non-additive effects biologically significant?

Methods

Study site

Our work was conducted in the Middle Patuxent River, a stream west of the Chesapeake Bay in Howard County, Maryland, USA (lat 39° 15′ N, long 76° 55′ E; elevation 100 m asl). The channel is ~6 m wide, has an average water depth of 29 cm and baseflow discharge of 0.17 m^3/s, with water temperatures averaging 22 °C during summer and 4.5 °C in autumn. The streambed is dominated by small cobble and gravel, and is characterized by a typical run–riffle–pool geomorphology. The riparian zone is dominated by American sycamore (*Platanus occidentalis* L.) and boxelder (*Acer negundo* L.), and inhabited to a lesser extent by slippery elm (*Ulmus rubra* Muhl.), black willow (*Salix nigra* Marsh.), silver maple (*Acer saccharinum* L.), and black walnut (*Juglans nigra* L.).

Leaf litter input rates

Surveys of leaf litter input rates were completed over a 3-y period (June–November 1999,

August–November 2000, May–November 2001). Litter traps were commercially available plastic storage bins (0.40 m W x 0.55 m L x 0.45 cm H) staked streamside as close to the shoreline as possible on gravel and sand bars. Each trap had 5 holes drilled in the bottom to facilitate water drainage during rainfall events. Traps were placed every 100 to 200 m on alternate banks in an effort to capture spatial variability in litter inputs. The traps (n = 12) were put in the field at the beginning of each sample period and emptied every 6 to 14 d through November. Traps that had been disturbed were excluded from the survey; thus, the number of traps varied among dates. All of the detritus in each trap was placed in a separate Ziploc© bag in 1999, whereas samples from all traps were pooled on each sample date in 2000 and 2001. For the 1999 and 2000 season, the leaf litter was removed, dried at 60 °C to a constant mass, combusted at 550 °C for 45 min, and then reweighed to determine ash-free dry mass (AFDM, g). For the 2001 season, leaf litter from each sample date was first sorted by leaf species, and then AFDM was estimated for each species separately. AFDM of leaf litter per trap was divided by the trap area and then by the number of days that had elapsed since the last sampling to determine leaf litter input rates (g AFDM m^{-2} d^{-1}).

Streambed leaf litter composition

Samples were collected in early December 2000 after leaf fall had occurred to determine the composition of leaf litter on the streambed. Three riffle areas were chosen along a 200 m section of stream and 4 transects were placed randomly across each riffle, perpendicular to the flow. All leaf accumulations (hereafter ''packs'') on the streambed within 1 m of each transect were collected by gently lifting the leaf material into a Ziploc© bag. Leaf packs were defined as any leaf material retained on the streambed by cobble substrate and, therefore, included single-leaf accumulations. A total of 50 leaf packs was collected. Samples were placed on ice and immediately returned to the laboratory for processing. Leaves were removed from each bag, rinsed free of invertebrates, and sorted by leaf species, herbaceous material, twigs, and seeds. Each fraction was dried at 60 °C to a constant mass, combusted at 550 °C for 45 min, and reweighed to determine AFDM.

Breakdown experiment

Breakdown experiments were carried out during summer and autumn 2000. Freshly fallen leaves were collected in the autumn of 1999. Six species were chosen that were dominant at the site. Leaves were stored in well-aerated plastic bins in the laboratory until needed. Breakdown rates were estimated by the traditional method of placing mesh litter bags with a known mass of leaves into the stream and collecting replicate bags over time to estimate the rate of mass loss (Petersen and Cummins 1974).

Our study focused on breakdown dynamics of leaf packs ranging in species richness (S) from S = 1–5 species for summer (Table 1) and S = 1–4 species for autumn (Table 2), in a fast-flowing (summer: near-bed velocity 20.9 cm/s, SD = 5.8, n = 25; autumn: near-bed velocity 20.6 cm/s, SD = 6.3, n = 5), riffle–run area of the stream. Black walnut was only included in the summer study because of its limited availability. Studies for each season were carried out in the same section of the stream. Breakdown rates of packs were determined for each species separately for the single-species treatments (S = 1). Multispecies treatments were randomly chosen from all possible combinations of 2–5 species to yield j = 4 species combinations per level of species richness for the summer (Table 1), and j = 5 per level of species richness for the autumn (Table 2).

Leaf packs for both single and mixed species consisted of 3.0 g total dry leaf mass enclosed in 2 coarse-mesh bags (8 mm x 3 mm effective mesh size, Fiber Products Inc., Baltimore, Maryland; 2 bags were needed to hold the very narrow black willow leaves). Leaf packs were secured to a 20 cm metal stake with a Zip-Tie©, and anchored to the bottom of the stream. Packs to be sampled on similar days were placed in blocks in the stream. Packs were randomly positioned within a block, placing blocks of early samples downstream to minimize disturbance during sampling. Spacing between packs was kept between 0.5 and 1.0 m. Summer leaf packs were deployed on 3 June 2000 (day 0) and autumn leaf packs were deployed on 30 October 2000. Sampling involved gently lifting a pack into a large Ziploc © bag underwater, sealing the bag, and placing it on ice for transport to the laboratory. Each pack was rinsed into a 500-μm sieve, the entire contents were oven-dried

TABLE 1. Composition of leaf packs used in summer 2000. S is the number of leaf species present; j is the number of species combinations used within each level of S. Mass/Sp is the dry mass of each component species within the leaf pack. The number of days sampled for each leaf pack combination is the sample size (*n*) for that combination. Leaf species abbreviations are: M = silver maple, B = boxelder, S = American sycamore, Wa = black walnut, E = slippery elm, Wi = black willow.

S	j	Leaf pack composition	Mass/Sp (g)	Days sampled	*n*
1	1	S	3.00	3, 14, 35, 59, 84	5
1	2	E	3.00	3, 14, 35, 59	4
1	3	B	3.00	3, 14, 35, 59, 84	5
1	4	Wi	3.00	3, 14, 35, 59, 84	5
1	5	M	3.00	3, 14, 35	3
1	6	Wa	3.00	3, 14, 35, 59	5
2	1	S + E	1.50	3, 14, 35, 59, 84	5
2	2	M + S	1.50	3, 14, 35, 59, 84	5
2	3	B + Wi	1.50	3, 14, 35, 59, 84	5
2	4	Wa + E	1.50	3, 14, 35, 59, 84	5
3	1	Wa + Wi + S	1.00	3, 14, 35, 59, 84	5
3	2	M + E + S	1.00	3, 14, 35, 59, 84	5
3	3	B + Wi + M	1.00	3, 14, 35, 59, 84	5
3	4	B + Wa + E	1.00	3, 14, 35, 59, 84	5
4	1	Wa + M + Wi + S	0.75	3, 14, 35, 59, 84	5
4	2	B + S + E + M	0.75	3, 14, 35, 59, 84	5
4	3	B + S + E + Wa	0.75	3, 14, 35, 59, 84	5
4	4	B + Wa + M + Wi	0.75	3, 14, 35, 59, 84	5
5	1	S + E + Wi + M + Wa	0.60	3, 14, 35, 59, 84	5
5	2	B + S + Wi + M + Wa	0.60	3, 14, 35, 59, 84	5
5	3	B + S + E + Wi + Wa	0.60	3, 14, 35, 59, 84	5
5	4	B + E + Wi + M + Wa	0.60	3, 14, 35, 59, 84	5

for 24 to 48 h at 60°C to a constant mass, then combusted at 550 °C for 45 min to determine AFDM remaining (Benfield 1996).

Data analysis

Breakdown rate (k) was determined using the exponential decay model $W_t/W_o = e^{-kt}$, where W_o is the initial mass, W_t is the mass remaining on day t, and k is the rate of breakdown (Petersen and Cummins 1974, Webster and Benfield 1986). To estimate breakdown rates for individual species combinations, an ANCOVA was used to analyze $\ln(W_t/W_o)$ as a function of day and the interaction between day and the particular combination of species present (a categorical variable) separately for each breakdown study. No intercept was fitted for any of the decay models because initial dry mass was fixed for each leaf pack. Breakdown rate of each seasonal leaf litter combination (Tables 1, 2) was regressed on S to determine the relationship between litter breakdown and the number of leaf species present. In addition, pair-wise comparisons of breakdown rates were made between single-species litter, adjusting the *p*-values using Hommel's correction for multiple comparisons (Westfall et al. 1999).

Linear contrasts were done on the output of the ANCOVA to test if litter breakdown of mixtures was non-additive. Specifically, we tested the hypothesis that the actual breakdown of leaf litter species in combination was different from that predicted by the *average* of the breakdown rates estimated for each of the component species independently (H_o: $k_{\text{COMBINATION}} - [(\Sigma\ k_i)/n] = 0$, where i = particular leaf species in the multi-species combination treatment). If the difference in breakdown (actual − predicted) differed significantly from 0, there was evidence for non-additive effects of litter mixing. To control Type I error, a multiple -contrast procedure was first done on all hypotheses (a single contrast for the treatments with ≥ 2 litter species present). In-

TABLE 2. Composition of leaf packs used in autumn 2000. Details as in Table 1.

S	j	Leaf pack composition	Mass/Sp (g)	Days sampled	*n*
1	1	S	3.00	4, 13, 30, 87	4
1	2	E	3.00	4, 13, 30, 51, 87	5
1	3	B	3.00	4, 13, 30, 51, 87	5
1	4	Wi	3.00	4, 13, 30, 51	4
1	5	M	3.00	4, 13, 30, 51, 87	5
2	1	E + M	1.50	4, 13, 30, 51, 87	5
2	2	B + Wi	1.50	4, 13, 30, 51, 87	5
2	3	M + Wi	1.50	4, 13, 30, 87	4
2	4	B + E	1.50	4, 13, 30, 51	4
2	5	S + E	1.50	4, 13, 30, 51, 87	5
3	1	B + S + E	1.00	4, 13, 30, 87	4
3	2	E + Wi + M	1.00	4, 13, 30, 51, 87	5
3	3	B + S + Wi	1.00	4, 13, 30, 87	4
3	4	S + Wi + M	1.00	4, 13, 30, 51, 87	5
3	5	S + E + Wi	1.00	4, 13, 30, 51, 87	5
4	1	S + E + Wi + M	0.75	4, 13, 30, 51, 87	5
4	2	B + E + Wi + M	0.75	4, 13, 30, 51, 87	5
4	3	B + S + Wi + M	0.75	4, 13, 30, 51, 87	5
4	4	B + S + E + M	0.75	4, 13, 30, 51, 87	5
4	5	B + S + E + Wi	0.75	4, 13, 30, 51, 87	5

dividual contrasts were done if the *F*-test was significant (Sokal and Rohlf 1981). Data were examined to ensure the assumptions of homogeneity and normality (Shapiro–Wilks test) of residuals were met. All statistical tests were performed using SAS (version 8.0, SAS Institute Inc., Cary, North Carolina).

Results

Leaf species composition of litter inputs and benthic standing stock

Leaf litter inputs to the Middle Patuxent occurred throughout summer and autumn, peaking in late October for all 3 years of the survey (Fig. 1). Maximum input rates (g AFDM m^{-2} d^{-1}) in late October were 7.02 in 1999, 10.11 in 2000, and 8.93 in 2001. Total leaf input to the Middle Patuxent in 2001 was dominated by American sycamore (1.09 g AFDM m^{-2} d^{-1}) , followed by boxelder (0.42 g AFDM m^{-2} d^{-1}) (Fig. 2).

Richness of leaf accumulations on the streambed in late autumn 2000 averaged 3.2 species per leaf pack (SD = 2.41, n = 50; Fig. 3A). The distribution was highly skewed because >46% of the leaf packs sampled were composed of only 1 leaf species. Summarizing across all samples, the species composition of leaf material collected from the streambed paralleled the pattern of leaf species inputs the following year (Fig. 2). American sycamore AFDM dominated on the streambed, composing > 50%, followed by boxelder (12%), and silver maple (11%) (Fig. 3B).

Summer leaf breakdown

The exponential decay model described the breakdown dynamics well. Of the 22 breakdown curves fitted, 13 had r^2 values $\geq$ 0.90 (range = 0.70–0.99), and all were highly significant ($p \leq 0.0001$). There was a strong interactive effect of leaf species combination on breakdown rate (ANCOVA, Day x Leaf combination, $F_{21,84}$ = 22.42, $p < 0.0001$). Differences between the single-species treatments were strongest in sycamore and black walnut, with these species having breakdown rates most different from other species (Fig. 4). The test of the hypothesis that breakdown rate changes as leaf species richness increased was not supported (Fig. 5).

Most multispecies litter treatments decomposed differently than predicted based on averaging single-species breakdown estimates

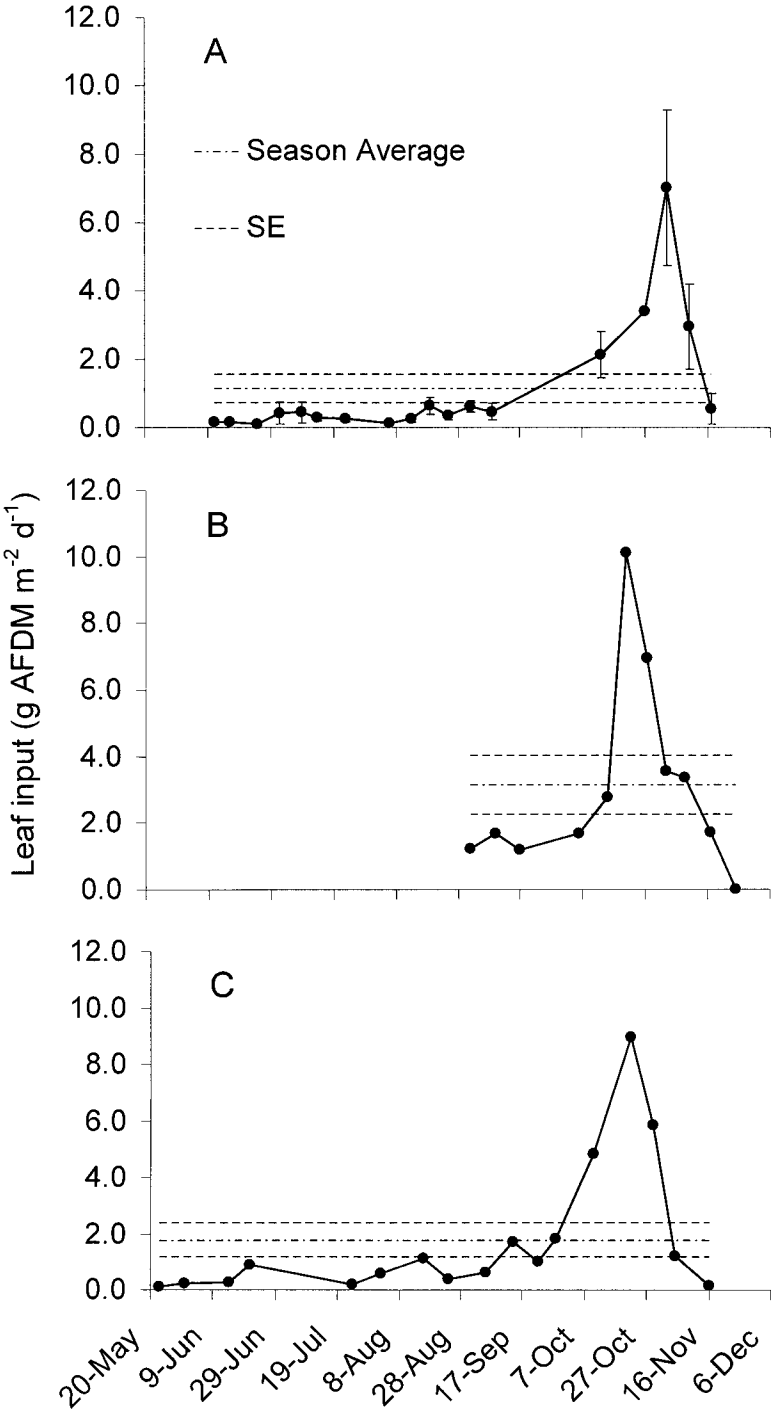

FIG. 1. Leaf litter input rates to the Middle Patuxent River in 1999 (A), 2000 (B), and 2001 (C). Date-specific means (±1 SE) are provided for 1999, and means only for 2000 and 2001. Average and SE for each survey are also indicated.

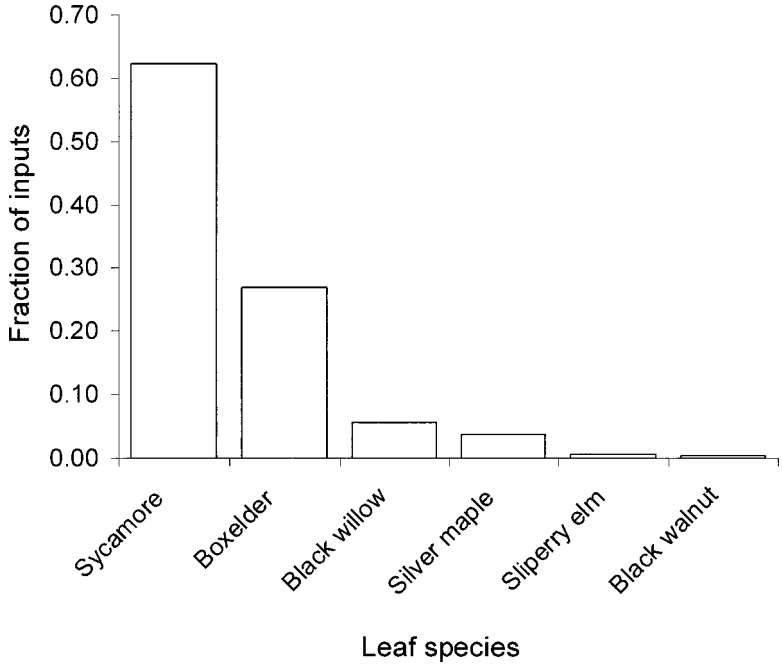

FIG. 2. Relative species composition of leaf litter inputs to the Middle Patuxent from May through November 2001. Data are the fraction of total inputs summed across all sample dates.

(overall $F = 9.48$, df = 16, $p < 0.0001$; black versus white bars, Fig. 4). In 13 of the 16 treatments that contained >1 leaf species, breakdown was slower than predicted assuming additivity. The only 3 cases in which breakdown rates could be predicted based on the additive effects of single species were: B Wi, B Wi M, and B E Wi M Wa (Fig. 4).

Autumn leaf breakdown

The exponential decay model explained variance in mass loss adequately in autumn, similar to the summer study. Across all 20 treatments, 16 had r^2 values ≥ 0.90 (range = 0.73–0.99), and all were highly significant ($p \leq 0.0124$). Further, there was a significant effect of leaf species combination on breakdown rate (ANCOVA, Day x Leaf combination, $F_{19,74} = 6.18$, $p < 0.0001$). Sycamore decomposed significantly slower than all other single-species treatments (Fig. 6). Slippery elm, boxelder, and black willow decomposed at similar rates, whereas silver maple was fastest, being different from all species except black willow (Fig. 6). The slope relating breakdown rate to leaf pack species richness was not as strong as in the summer study, nor was it different from 0 (Fig. 7).

Unlike the strong non-additive effects observed across multispecies leaf treatments in summer, none of the multispecies litter treatments decomposed differently than predicted based on averaging single-species breakdown estimates (overall $F = 0.82$, df = 15, $p = 0.6510$; black versus white bars, Fig. 6). Breakdown of leaf litter mixtures could be predicted by averaging the breakdown rates of the single species in each treatment.

Discussion

Few studies have explored the importance of leaf litter species richness to organic matter breakdown in stream ecosystems (but see Leff and McArthur 1989, McArthur et al. 1994), despite the recognition that many riparian corridors are losing plant species and/or becoming highly managed because of disease or invasive herbivores (Smock and MacGregor 1988, Sweeney 1993, Snyder et al. 2002). We showed that inputs of leaf litter into a warmwater temperate stream occurred continuously through the sum-

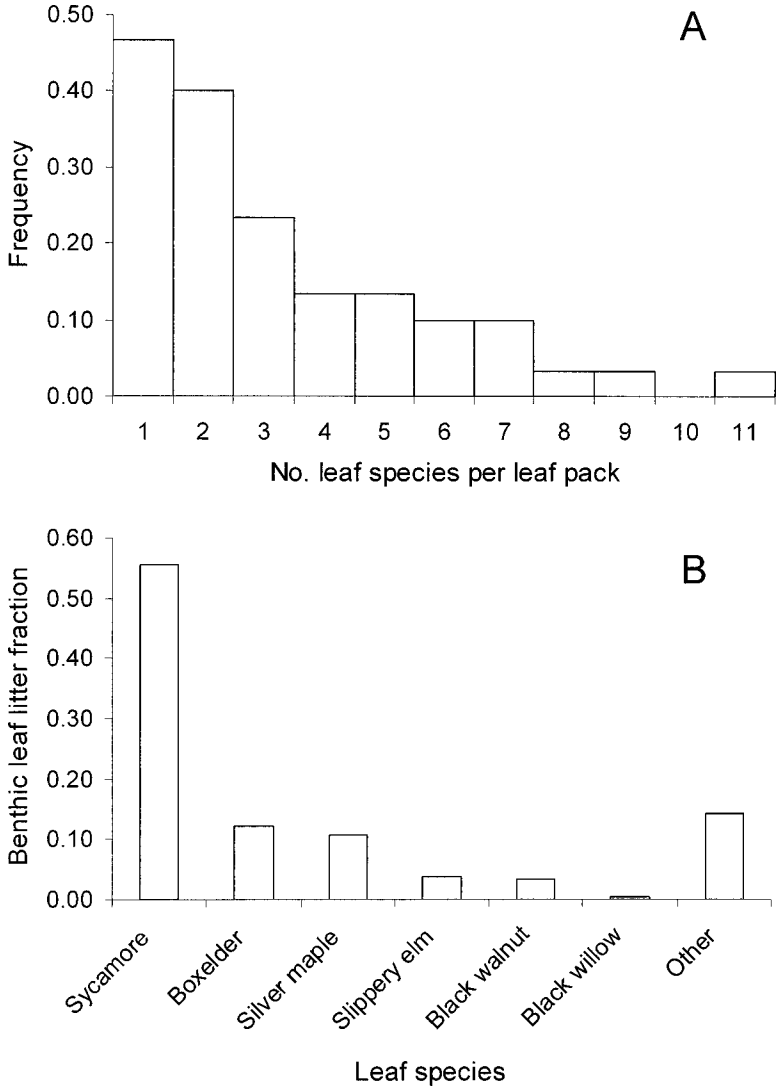

FIG. 3. Frequency distribution of leaf species richness per leaf patch (A) and relative biomass of each leaf species (B) encountered in Middle Patuxent riffles, December 2000.

mer months, peaking during late October. Species richness of leaf litter on the streambed in late autumn varied substantially, with the relative biomass of leaf species largely reflecting the composition of leaf litter inputs. Studies of mixed-litter breakdown resulted in very different patterns between summer and autumn. Breakdown rates in summer not only failed to change in a predictable way as leaf species richness increased but most multispecies litter packs decomposed differently than predicted based on average single-species breakdown rates. However, breakdown rates of mixed detritus in the autumn were predictable (i.e., additive) such that breakdown of mixed litter could be estimated based on knowledge of single-species breakdown rates. Thus, breakdown of heterogeneous detritus ($\geq$ 2 leaf species) was non-additive only during summer.

Leaf litter inputs and benthic standing stock

The source of leaf litter captured in our study was more from direct litter fall than from lateral

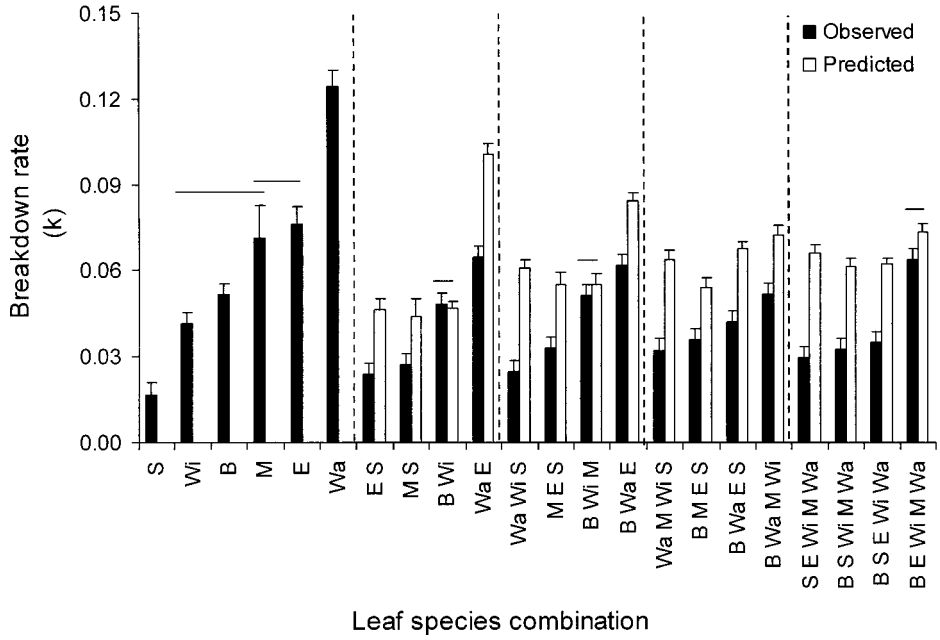

FIG. 4. Estimates of breakdown rate (k, +1 SE) for each litter treatment for summer 2000. Dashed lines separate treatments by leaf species richness. Connected bars are not significantly different within the single-species treatments. For treatments with ≥ 2 leaf species, black bars are observed breakdown rates from the field, and white bars are the average of the single-species estimates for each species within the corresponding mixtures. For each mixture, connected black and white bars indicate no difference between observed and predicted breakdown rates. Litter species abbreviations: M = silver maple, B = boxelder, S = American sycamore, Wa = black walnut, E = slippery elm, Wi = black willow.

blow-in given the design of the litter traps used (i.e., tall plastic bins). Therefore, estimates of inputs during the summer may be conservative because blow-in during these months is likely substantial compared to direct litter fall (Benfield 1997). Nevertheless, inputs were present and speciose, underscoring the potential role that leaf litter may play in stream ecosystems during summer (e.g., Short and Smith 1989, Maloney and Lamberti 1995). Further, patterns in species richness of leaf litter on the streambed reflected that observed in the input data; American sycamore and boxelder dominated.

Summer vs autumn leaf breakdown

The interesting discrepancy in the results between summer and autumn studies suggests that species richness of leaf litter matters little to breakdown of organic matter during the autumn when inputs to streams reach their maximum. One explanation may be the substantial change in temperature observed during autumn. Lower temperatures decrease breakdown rates by reducing microbial and detritivore activity (Webster and Benfield 1986) and may have been a factor in our study, despite the presence of a substantial shredder community during the autumn in the Middle Patuxent (e.g., stoneflies: *Shipsa* sp., *Taeniopteryx* sp.; crayfish: *Orconectes limosus*; CMS, personal observation). There may not have been enough of a difference in breakdown rates among leaf mixtures relative to any accelerating/inhibitory effect of mixing that was present during the summer months. Such cases of environmental context (e.g., temperature, flow, disturbance regime) can explain how species richness alters ecosystem processes such as organic matter breakdown (Cardinale et al. 2000, Cardinale and Palmer 2002). Further work on how temperature may be altering the microbial and/or shredder interactions within mixed-species leaf litter will help explain the substantial differences observed between summer and autumn studies.

Different suites of shredder species occur

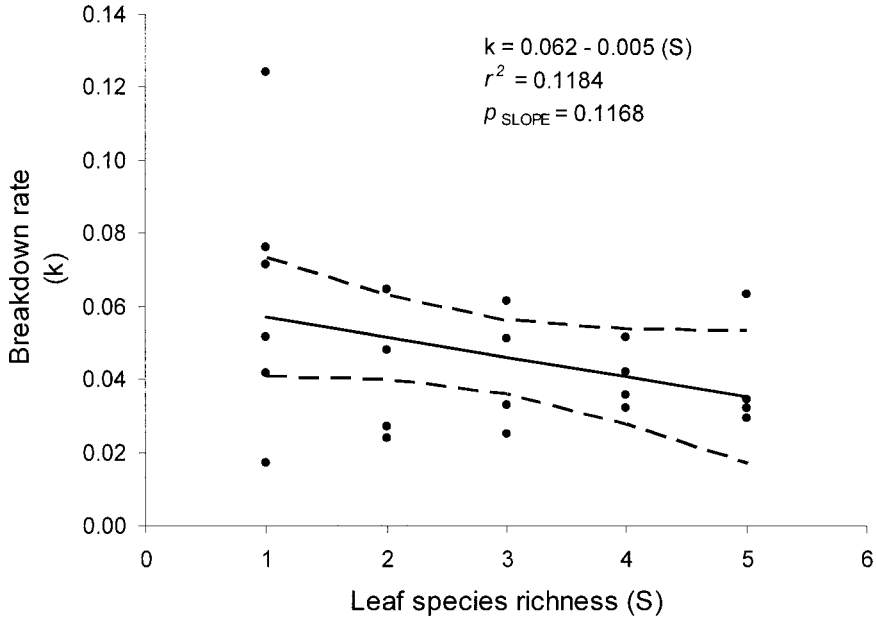

FIG. 5. Relationship between breakdown rate (k) and the number of species within a leaf pack for summer 2000. Dashed lines represent the 95% confidence interval.

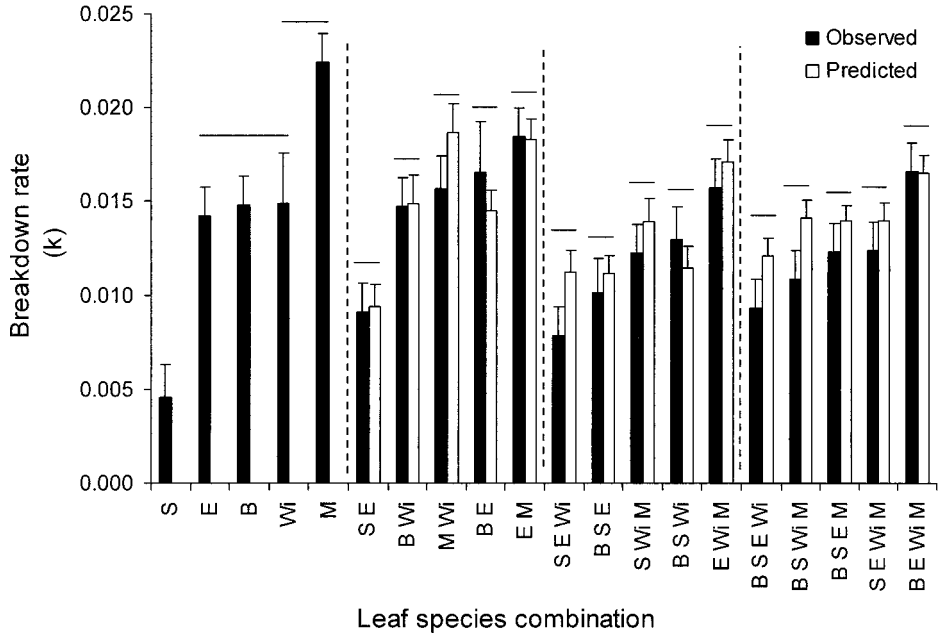

FIG. 6. Estimates of breakdown rate (k, +1 SE) for each litter treatment for autumn 2000. Details as in Fig. 4.

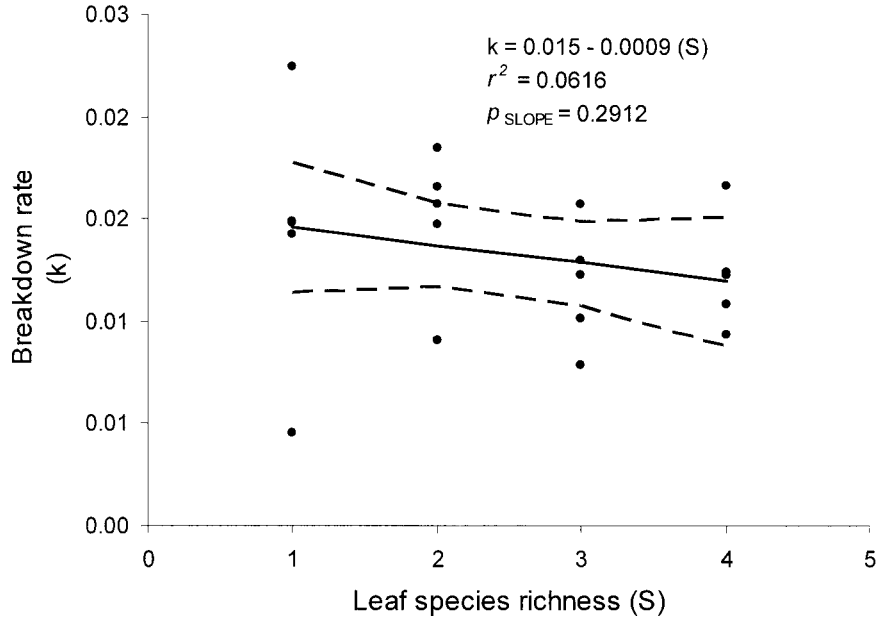

FIG. 7. Relationship between breakdown rate (k) and the number of species within a leaf pack for autumn 2000. Dashed lines represent the 95% confidence interval.

throughout the year, using leaf litter in both the summer and autumn months (Cummins et al. 1989, Short and Smith 1989, Maloney and Lamberti 1995). Thus, any non-additive effect of mixing leaf species on breakdown rate revealed in our study will only alter the availability of particulate detritus to shredders of the Middle Patuxent during the summer months (e.g., caddisflies: *Lepidostoma* sp., *Frenesia* sp.; isopod: *Caecidotea communis*; crayfish *O. limosus*; CMS, personal observation). Of particular interest is the role American sycamore appears to be playing. We manipulated species richness per se by holding initial leaf mass constant and varying composition, despite our later findings that leaf inputs were dominated substantially by American sycamore and boxelder. Nevertheless, American sycamore appeared to be important in the overall slowing of breakdown rates in summer. This reduction in mass loss because of mixing may influence the feeding pattern of shredders. Further work on the interaction between litter mixing and shredder feeding behavior will undoubtedly shed more light on the implications for altered species richness of leaf inputs to stream ecosystems.

Non-additive effects on leaf breakdown

Failure to find a general relationship between leaf species richness and breakdown rate prompted exploration into whether species composition may play a role. The non-additive effects during the summer were very common, occurring in 13 out of 16 of the mixture treatments, and the magnitude of this effect was substantial. In fact, the mixture that was the *least statistically significant* different from the predicted breakdown rate (M S, k_{DIFF} = 0.0170; Fig. 4) was similar to the estimate for the slowest decomposing single species (S, k = 0.0169; Fig. 4). The magnitude of the effect of mixing species in this study was at least >1x the rate of breakdown estimated for the slowest single-species treatment.

Leaf species composition

Wagener et al. (1998) suggested that the process of leaf litter breakdown proceeds similarly between aquatic and terrestrial systems, with the only major difference being the magnitude of decay rates (i.e., generally slower in terrestrial ecosystems). However, our results indicate that

the differences between systems may be more complex. The presence of very labile litter species in terrestrial systems, such as alder and aspen, can accelerate overall breakdown of mixed species litter (Chapman et al. 1988, Taylor et al. 1989, Briones and Ineson 1996) . However, Wardle et al. (1997) emphasized that mixing can also have negative effects on breakdown rates, depending on what species of litter are present in the mixture. Studies of mixed litter breakdown in streams either showed no effect of mixing (Leff and McArthur 1989), or that the presence of a slower, more refractory species such as oak decreased overall breakdown rate (McArthur et al. 1994). These findings, in combination with our results, present no evidence that litter mixing increases the overall rate of breakdown in stream ecosystems, as has been shown for some terrestrial ecosystems (e.g., Taylor et al. 1989, Kaneko and Salamanca 1999).

Wardle et al. (1997) suggested that breakdown of detritus may not necessarily be a strict function of the number of plant litter species present, but whether certain key leaf species are present or absent. Based on our results, we hypothesize that American sycamore, the slowest decomposing leaf species used, may be such a key species. Ostrofsky (1993, 1997) estimated the breakdown rates of leaves of riparian tree species common in the northeastern USA, and analyzed the major chemical and structural attributes generally thought to control the rate at which leaves decompose in aquatic systems. His work described all of the species used in our study (but reported genus level information for slippery elm). Ostrofsky (1993, 1997) reported American sycamore to be the slowest decomposer, with the lowest P content, and the highest C:N ratio, lignin content, and tannin activity. Thus, the chemical nature of American sycamore may have led to a slow breakdown rate, and may have slowed the breakdown rate of multispecies packs.

Three leaf mixtures that showed strong non-additive breakdown rates lacked American sycamore (Wa E, B Wa E, B Wa M Wi), suggesting that other factors contributed to non-additivity (Fig. 4). These mixtures all contained black walnut, the fastest decomposing single-species treatment, but the patterns of non-additivity resulted in slower breakdown rates. Conclusions about why mixed-litter assemblages ought to decompose differently than what is predicted, assuming additivity, are often based on the complex interactions between the biological community and leaf litter chemistry (Chapman et al. 1988, Wardle et al. 1997). In lotic systems, however, the physical force of flow and its differential effects on leaf species may alter breakdown rates in unexpected ways (Webster and Benfield 1986, Silver et al. 2004) . We observed that black walnut leaves were extremely brittle, and thus could have suffered disproportionately from flow abrasion. Brittleness would elevate its breakdown rate regardless of its palatability to bacteria, fungi or invertebrates. However, when placed in a mixed-litter pack, the other, more structurally stable species could have protected black walnut from quickly degrading.

In conclusion, our work focused only on tree species common along the study stream, but patterns of species composition vary across the landscape (Fleming et al. 2001). Species exist that degrade much more slowly than American sycamore (e.g., oaks; Webster and Benfield 1986), and perhaps faster than black walnut did in our study. Furthermore, other environmental conditions that influence litter breakdown in streams (e.g., temperature, pH, flow regime; Webster and Benfield 1986) may interact with different species in leaf mixtures. Elucidation of these factors will require work in streams with different riparian assemblages, varying environmental conditions, and across different seasons within the same system.

Our work suggests that breakdown of diverse leaf litter may change seasonally, possibly affecting detritivore community dynamics. The presence of slow-decomposing species such as American sycamore in summer may impart stability to other more labile litter resources by exerting strong, non-additive effects on the length of time high-quality litter is retained in streams (Palmer et al. 2000). Many stream invertebrates rely heavily on leaf litter for food (Cummins et al. 1989, Richardson 1991), so the amount of time that litter is available for consumption may be critical for detritivores. Confirmation by other studies of slower breakdown rates when litter species are mixed should have implications for the management and restoration of streams and rivers. Our work suggests that if riparian restoration is undertaken with the whole stream community in mind, focusing on tree species composition, and not merely the presence of deciduous riparian vegetation, could be important.

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