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Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates

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SUMMARY

1. We examined the relative importance of litter quality and stream characteristics in determining decomposition rate and the macroinvertebrate assemblage living on autumn-shed leaves.
2. We compared the decomposition rates of five native riparian tree species (*Populus fremontii*, *Alnus oblongifolia*, *Platanus wrightii*, *Fraxinus velutina* and *Quercus gambelii*) across three south-western streams in the Verde River catchment (Arizona, U.S.A.). We also compared the decomposition of three- and five-species mixtures to that of single species to test whether plant species diversity affects rate.
3. Decomposition rate was affected by both litter quality and stream. However, litter quality accounted for most of the variation in decomposition rates. The relative importance of litter quality decreased through time, explaining 97% of the variation in the first week but only 45% by week 8. We also found that leaf mixtures decomposed more quickly than expected, when all the species included were highly labile or when the stream environment led to relatively fast decomposition.
4. In contrast to decomposition rate, differences in the invertebrate assemblage were more pronounced across streams than across leaf litter species within a stream. We also found significant differences between the invertebrate assemblage colonising leaf mixtures compared with that colonising pure species litter, indicating non-additive properties of litter diversity on stream invertebrates.
5. This study shows that leaf litter diversity has the capacity to affect in-stream decomposition rates and stream invertebrates, but that these effects depend on both litter quality and stream characteristics.

Keywords: leaf decomposition, litter diversity, litter mixtures, macroinvertebrate assemblages, stream comparison

Introduction

Leaf litter subsidies to aquatic ecosystems provide large quantities of energy to headwater streams that typically exhibit low levels of primary productivity (Petersen & Cummins, 1974; Vannote *et al.*, 1980). Leaf breakdown in streams is controlled mainly by two factors, litter inputs (litter quality, quantity and timing) and biotic or abiotic differences among streams (Webster & Benfield, 1986). The species composition of riparian forests can alter the quality, quantity and temporal dynamics of leaf litter resources. For example, litter from different tree species decomposes at significantly different rates in streams (Webster & Benfield, 1986; Ostrofsky, 1997; Webster *et al.*, 1999) and supports different microbial (Baldy, Gessner & Chauvet, 1995; Wallace *et al.*, 1997; Hieber & Gessner, 2002) and invertebrate assemblages (Wallace, Webster & Cuffney, 1982; Cummins *et al.*, 1989; Graça, 2001).

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Catchment characteristics and water quality can also affect leaf litter decomposition rates (Chergui & Pattee, 1988; Maamri *et al.*, 2001; Sponseller & Benfield, 2001). Commonly, decomposition experiments show that, within a stream, upstream reaches have a greater capacity to break down litter than downstream reaches (Minshall *et al.*, 1983; Fleituch, 2001) and that breakdown in high-velocity microhabitats, such as riffles, is faster than in pools (Stout & Coburn, 1989). Leaf litter breaks down faster in streams that are hard (Jenkins & Suberkropp, 1995; Suberkropp & Chauvet, 1995), alkaline (Jenkins & Suberkropp, 1995), warm (Dangles & Guérold, 2001) or have high nutrient concentrations (Meyer & Johnson, 1983; Suberkropp & Chauvet, 1995).

Understanding the relative contribution of these two sources of variability (litter quality and stream characteristics) and their interactions will elucidate the main factors affecting variability in the process of decomposition and associated macroinvertebrate composition on leaf litter. Other studies that have examined the interaction between litter quality and stream characteristics in determining decomposition have shown mixed results. Some studies show interactions between leaf species and site, where decomposition rate of the same species differs among streams (Carpenter, Odum & Mills, 1983; Minshall *et al.*, 1983; Benfield *et al.*, 1991), whereas others show no such interaction (Francis *et al.*, 1983; Cortes, Graça & Monzón, 1994; Whiles & Wallace, 1997; Pozo *et al.*, 1998; Benfield *et al.*, 2001).

Plant species diversity may produce non-additive patterns of decomposition that would not be predicted by patterns of decomposition of single species. The few studies that have directly tested for effects of litter diversity in aquatic ecosystems have found inconsistent results. Some studies show no difference between the decomposition rate of species in mixture when compared with the rates for single species (Leff & McArthur, 1989; Ashton, Hogarth & Ormond, 1999), whereas others show that decomposition is slower (Jonsson & Malmqvist, 2003; Swan & Palmer, 2004), suggesting that any diversity effect is simply a function of the species present. The effects of diversity on decomposition may also be context-dependent, change seasonally or be a function of detritivore preference (Swan & Palmer, 2004). Research in terrestrial ecosystems is more extensive but also shows idiosyncratic patterns in which effects of diversity depend on both species and environment (Briones & Ineson, 1996; Finzi & Canham, 1998; Hansen, 1999; Kaneko & Salamanca, 1999; Zimmer, 2002; Dalias, Mprezetou & Troumbis, 2003; Hoorens, Aerts & Stroetenga, 2003).

We tested for the relative importance of litter quality versus stream characteristics on decomposition and the macroinvertebrate assemblage and whether the effects of leaf diversity on ecosystem function are dependent on the stream environment. In three south-western U.S. streams within 71 km of each other, we compared decomposition rates and macroinvertebrate assemblages for five native litter species and a mixture of all five litter species. The five litter species are the dominant trees found in headwater streams of the Colorado Plateau and the streams represent the range of perennial headwater streams in the area. We predicted that (i) different species of leaves would decompose at different rates and harbour different invertebrate assemblages because of differences in initial litter quality, (ii) breakdown of these leaf species would differ between streams because of contrasting water quality and macroinvertebrate assemblages, (iii) mixtures of litter species would decompose in all three streams at rates not predicted by the rate of decomposition of the individual species and would be colonised by different invertebrate assemblages than expected from single leaf species and (iv) litter species would account for a higher proportion of the variance in decomposition than differences among streams.

Methods

Site descriptions

The three streams included in this project, Fossil Creek, Oak Creek and Wet Beaver Creek, are in the upper Verde River catchment (14 100 km^2) and flow off the south-western edge of the Colorado Plateau in north central Arizona, U.S.A. (Fig. 1). Specific sites include Oak Creek's confluence with Pumphouse Wash (35°02′N, 111°43′W), Wet Beaver Creek 1.5 km above Arizona state road 179 (34°41′N, 111°41′W) and 1 km above the bridge connecting the Tonto and Coconino National Forests at Fossil Creek (34°24′N, 111°38′W).

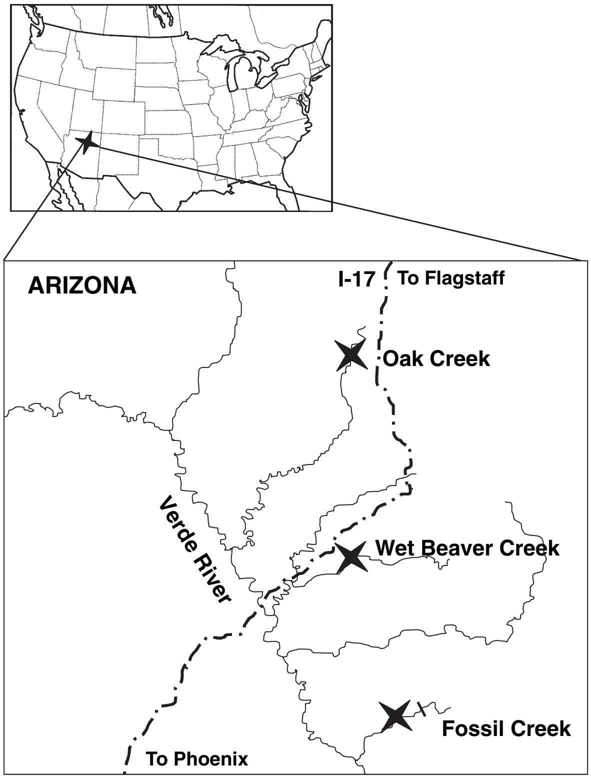

Fig. 1 Map of study area showing the northern section of the Verde River catchment (Arizona, U.S.A.) and the three study streams, Oak Creek, Wet Beaver Creek and Fossil Creek. Map courtesy of Brett Dickson, Colorado State University.

Riparian vegetation is similar at all three locations and includes Fremont cottonwood (*Populus fremontii* S. Wats.), narrowleaf cottonwood (*Populus angustifolia* James), Arizona alder (*Alnus oblongifolia* Torr.), box elder (*Acer negundo* L.), Gambel oak (*Quercus gambelii* Nutt.), Arizona sycamore (*Platanus wrightii* S. Wats), velvet ash (*Fraxinus velutina* Torr.), coyote willow (*Salix exigua* Nutt.) and Goodding's willow (*Salix gooddingii* Ball).

The three streams are representative of the variation in perennial headwater streams in northern Arizona and demonstrate an altitudinal gradient from 2333 to 866 m a.s.l. The highest altitude stream, Oak Creek, has an average annual flow of 368 L s^{-1}. Wet Beaver Creek's average annual flow is 340 L s^{-1} and, although base flow at Fossil Creek is 1218 L s^{-1}, a 10-m diversion dam reduced its average annual flow to approximately 56 L s^{-1} at the location used in this study. Geomorphology of all three streams is similar, consisting of Palaeozoic sandstones and Tertiary igneous formations, giving all three streams high alkalinity. Only Fossil Creek, however, exhibits active travertine deposition at the study location, as well as geothermally regulated temperature from its spring source. Water quality parameters were measured four times during the study period using a Hydrolab minisonde (Hydrolab-Hach Corporation, Loveland, CO, U.S.A.). Temperature, pH, total dissolved solids, specific conductivity and salinity were measured at each harvest date in each stream (Table 1), while dissolved oxygen measurements at the same time unfortunately were unreliable. Three replicate water samples were collected from the study locations in 250-mL plastic bottles for nutrient and ionic analyses,

Table 1 Physical and water chemistry characteristics for Fossil Creek, Oak Creek and Wet Beaver Creek (Arizona, U.S.A.) from 20 January 2002 to 12 April 2002. All measurements were taken between 9:00 AM and 2:00 PM on each harvest day ($n = 5$).

Parameter	Fossil Creek	Wet Beaver Creek	Oak Creek
Altitude (m a.s.l.)	1133	1400	1945
Average annual flow (L s^{-1})	56	340	368
Mean temperature (°C)	12.63 ± 0.18*	8.04 ± 0.31	7.86 ± 0.22
Minimum temperature (°C)	11.92	6.41	6.46
Maximum temperature (°C)	14.62	17.1	13.45
Salinity (ppt)	0.33 ± 0.001*	0.12 ± 0.000	0.13 ± 0.0008
pH	8.26 ± 0.02	8.12 ± 0.04	8.12 ± 0.04
Total dissolved solids (g L^{-1})	0.414 ± 0.0005*	0.164 ± 0.0002	0.167 ± 0.0004
Specific conductivity (μS cm^{-1})	646 ± 0.71*	255 ± 0.32	259 ± 0.84
Ammonium (mg NH_4^+ L^{-1})	$<0.02^{\dagger}$	$<0.02^{\dagger}$	0.1240 ± $0.01^{*,\dagger}$
Nitrate (mg NO_3^- L^{-1})	0.1126 ± $0.002^{\dagger}$	$<0.02^{\dagger}$	0.2780 ± $0.01^{*,\dagger}$
Phosphate (mg PO_4^{-3} L^{-1})	0.0441 ± $0.01^{\dagger}$	0.0566 ± $0.02^{\dagger}$	0.1692 ± $0.02^{*,\dagger}$

Values represent mean ± 1 SE except for altitude, flow and minimum/maximum temperatures.

*Mean values that differed significantly from the two other values (ANOVA, Tukey's HSD) for that parameter $P < 0.001$.

†Average annual water chemistry measures taken following the study period, in the autumn/winter of 2003–04.

filtered through a 0.4-μm-glass microfibre filter and acidified to a pH < 2.0 with sulphuric acid. Water analyses were conducted in the laboratory using a Technicon Auto Analyser II (Technicon Instruments Corporation, Tarrytown, NY, U.S.A.).

Litter collection and chemistry

Five riparian species that were common and dominant in the three drainages and that would provide a gradient of predicted decomposition rates were selected. The predicted order of decomposition rates was based on reported differences at the family level and was as follows: velvet ash > Arizona alder > Fremont cottonwood > Arizona sycamore > Gambel oak (Webster & Benfield, 1986). Leaves were collected just after abscission through natural leaf fall into hanging perforated tarpaulines strung among trees at Wet Beaver Creek in the autumn of 2001 ($n = 5$). Multiple tarpaulines were hung under the canopies of these five species to ensure the collection of leaves from several individual trees. This leaf litter was used at all three sites to compare leaf decomposition rates of the same litter among streams.

Leaf litter for initial chemical analyses was air-dried and ground in a Wiley Mill (Thomas Scientific, Swedesboro, NJ, U.S.A.) to 425 μm. Subsamples (25–50 mg) were extracted for condensed tannins with 70% acetone and 10 mM ascorbic acid. We used the butanol-HCl method to determine condensed tannin concentrations (Porter, Hrstich & Chan, 1986), with standards purified from narrowleaf cottonwood following the methods of Hagerman & Butler (1989). We quantified absorbance on a Spectramax-Plus 384 spectrophotometer (Molecular Devices, Sunnyvale, CA, U.S.A.). We also determined total litter per cent nitrogen and per cent phosphorus by modified micro-Kjeldahl digestion (Parkinson & Allen, 1975) followed by analysis on a Lachat AE Flow Injection Analyser (Lachat Instruments, Inc., Loveland, CO, U.S.A.), using the salicylate and molybdate-ascorbic acid methods, respectively (Lachat Instruments, Inc., 1992).

Litter decomposition

Air-dried leaves were weighed into 4-g quantities and placed in 6.4-mm-mesh litterbags (Trical netting, Edo. Aragua., Venezuela: available through Aquatic Ecosystems, Apopka, FL, U.S.A.). Six leaf litter treatments were included in each of three streams (Fossil Creek, Oak Creek and Wet Beaver Creek): one treatment of each species in isolation and one treatment of an equal mixture of all five species (0.8 g each). Three additional treatments were used to compare three, three-species mixtures (1.33 g each) in just Wet Beaver Creek: three fast-decomposing species (ABC mixture: ash + alder + cottonwood), three slow-decomposing species (CDE mixture: cottonwood + sycamore + oak) and a mixture (ACE mixture) of the fastest (alder), slowest (oak) and the mid-rate species (cottonwood). Eight replicate bags ($n = 8$) were created for each treatment in each stream at each harvest date for a total of 720 litterbags (plus an additional 120 three-species mixture litterbags at Wet Beaver Creek). Litterbags were randomly assigned a harvest date, stream and a location (block) within the stream. Bags were anchored in the stream along 2-m lengths of steel rebar and wedged into place in active depositional areas. Litterbags were colour-coded by harvest date to assist harvesting and avoid disturbing neighbouring bags. Litterbags were harvested from the stream after 7, 14, 28, 56 and 83 days, placed into individual polyethylene zipper bags and transported on ice to the laboratory.

Litterbags were processed within 16 h of harvesting. Sediment and invertebrates were sieved through 250-μm nets for preservation in 70% ethanol. Remaining leaf material was rinsed with tap water and dried at 70 °C for 72 h. Dry leaf material was weighed and ground in a Wiley Mill to 425 μm. Ground material was combusted at 500 °C in a muffle furnace (Barnstead International, Dubuque, Iowa, U.S.A.) for 1 h to determine ash-free dry mass (AFDM).

Aquatic invertebrates

Preserved invertebrate samples were sieved through 1-mm-mesh to separate micro- from macroinvertebrates. Macroinvertebrate samples from harvest dates 7, 28 and 83 days were sorted under 2× magnification and aquatic insects (except some members of Diptera) were identified to genus using Merritt & Cummins (1996) and Wiggins (1996). Other invertebrates were identified to the lowest taxonomic level possible using Thorpe & Covich (2001). Reference specimens are maintained in the LeRoy Aquatic Ecology Laboratory at The Evergreen State College.

We identified 72 genera from a total of 49 families and 12 orders.

Statistical analyses

Data on water chemistry and physical parameters for each stream were analysed using analysis of variance (ANOVA) and *post hoc* comparisons (Tukey's honest significant difference, HSD) in JMP-IN 4.0.4 (Academic version; SAS Institute, Inc. 1989–2001, Cary, NC, U.S.A.). An alpha (type I error rate) of 0.05 was selected for all analyses.

Analysis of leaf litter decomposition required a natural log-transformation of AFDM remaining for two reasons, (i) to meet normality and equal variance assumptions and (ii) to determine the exponential decomposition rate constant (k) (Jenny, Gessel & Bingham, 1949; Olson, 1963; Benfield, 1996). Decomposition rate constants were compared using an equality of slopes test in SAS 8.01 (SAS Institute, Inc. 1999–2000). Expected decomposition rates for the three- and five-species mixtures (an average of each species in isolation) were compared with the observed decomposition rates for the mixtures using linear contrasts (at Hommel's corrected alpha levels) to test if litter breakdown of mixtures was non-additive (Swan & Palmer, 2004).

Invertebrate data were analysed using a variety of community analysis techniques. Species abundances, species richness, species evenness and Shannon's diversity index (H') were calculated for each litterbag at harvest dates 7, 28 and 83 days. Values were compared using ANOVA and *post hoc* comparisons (Tukey's HSD). To visualise assemblage-wide responses to leaf litter treatments, we used a relativised (to species maximum) non-metric multidimensional scaling (NMDS) ordination method with a Bray-Curtis distance measure in PC-ORD (Version 4.02, MJM Software, Gleneden Beach, OR, U.S.A.) and to test for differences among treatments we used a multi-response permutation procedure (MRPP) in the same program.

The invertebrate assemblages on mixed litter treatments were compared with assemblages we would expect to find in mixture based on the assemblages on species in isolation. We compared a matrix of invertebrate abundances on mixed litter to a matrix of the average abundance for each litter species in isolation in the same stream block using MRPP and NMDS ordination.

Results

Chemical parameters

Oak Creek and Wet Beaver Creek had similar water chemistries, despite differences in altitude (Table 1) and flow. All three streams had similar pH ($F = 1.09$, $P = 0.345$), although, the travertine chemistry of Fossil Creek resulted in significantly higher specific conductivity ($F = 52989.55$, $P < 0.0001$), total dissolved solids ($F = 65474.42$, $P < 0.0001$) and salinity ($F = 7513.52$, $P < 0.0001$). Because of its low altitude and geothermal source, Fossil Creek was also the warmest ($F = 8.57$, $P = 0.001$). Nutrient concentrations differed among the three streams, including significantly higher nitrate, ammonium and phosphate at Oak Creek than either Wet Beaver Creek or Fossil Creek (NO_3^-: $F = 181.12$, $P < 0.0001$; NH_4^+: $F = 42.53$, $P < 0.0001$; PO_4^{-3}: $F = 30.57$, $P < 0.0001$; Doucett *et al.*, unpublished data).

Litter decomposition

Initial litter chemistry differed among the species, with oak and alder having a higher N content, ash and oak having more P, and sycamore and oak having the highest condensed tannin concentrations (Table 2). These chemical differences could help explain why the trends in decomposition rate among the five leaf species were similar among all three streams, but showed overall different rates of decomposition (Fig. 2). In all three streams we found that cottonwood, alder and ash decomposed faster than oak and sycamore litter.

Comparing decomposition rates among streams, all species and the five species mixture showed slowest decomposition rates in Fossil Creek, fastest rates in Oak Creek and intermediate rates in Wet Beaver Creek (Table 2). When all five litter species were combined in equal proportions, the five-species mixture decomposed faster than expected compared with the five species alone in Oak Creek, although there was no difference in the other two streams (Fig. 3).

When the five species were mixed in three different three-species mixtures in just Wet Beaver Creek, we found that only the mixture including the three fastest

Table 2 Initial litter chemistry (N, nitrogen; P, phosphorus; CT, condensed tannin) and decomposition rates for each species incubated in each stream

Species	Stream	% N	% P	% CT	Decomposition rate (day^{-1})
Alnus oblongifolia	OC	1.31 ± 0.03^{c}	0.05 ± 0.01^{a}	0.61 ± 0.07^{a}	0.0199 ± 0.0011^{a}
	WBC				0.0173 ± 0.0006^{b}
	FC				0.0149 ± 0.0009^{b}
Fraxinus velutina	OC	0.68 ± 0.09^{a}	0.22 ± 0.00^{c}	0.01 ± 0.01^{a}	0.0172 ± 0.0011^{a}
	WBC				0.0151 ± 0.0006^{ab}
	FC				0.0138 ± 0.0008^{b}
Platanus wrightii	OC	0.60 ± 0.01^{a}	0.13 ± 0.01^{b}	4.72 ± 0.12^{c}	0.0121 ± 0.0011^{a}
	WBC				0.0081 ± 0.0006^{b}
	FC				0.0069 ± 0.0008^{b}
Populus fremontii	OC	0.42 ± 0.00^{a}	0.04 ± 0.01^{a}	0.06 ± 0.05^{a}	0.0206 ± 0.0012^{a}
	WBC				0.0186 ± 0.0006^{a}
	FC				0.0176 ± 0.0008^{a}
Quercus gambelii	OC	0.85 ± 0.01^{b}	0.25 ± 0.02^{c}	2.13 ± 0.18^{b}	0.0138 ± 0.0011^{a}
	WBC				0.0076 ± 0.0006^{b}
	FC				0.0073 ± 0.0009^{b}
5 species mixture	OC	n/a	n/a	n/a	0.0200 ± 0.0011^{a}
	WBC				0.0133 ± 0.0006^{b}
	FC				0.0119 ± 0.0008^{b}

Values represent mean ± 1 SE for litter chemistry data and regression slopes ±1 SE for the natural log-transformed linear regression model of decomposition rates (day^{-1}). Significant differences among initial leaf chemical measurements (Tukey's HSD) and in decomposition rates among streams for each species (Hommel's multiple comparison test) denoted with different lower-case letters.

FC: Fossil Creek, Arizona; OC: Oak Creek, Arizona; WBC: Wet Beaver Creek, Arizona; n/a: not applicable.

decomposing species showed non-additive decomposition in mixture. The mixture including alder + ash + cottonwood decomposed faster than expected (Fig. 4). The mid-rate mixture (alder + cottonwood + oak) and the slow decomposing mixture (cottonwood + sycamore + oak) decomposed as expected.

Litter species explained a larger proportion of the total variance in decomposition than either stream or the stream-species interaction. The per cent variance explained by stream and the interaction term were relatively constant ranging between 0% and 22% over the entire study period (Fig. 5), whereas the per cent variance explained by leaf species decreased through time. At harvest day 7 almost 97% of the variance in decomposition rate was due to leaf species differences, but by day 83 the variance explained by species had dropped to about 45%, which was still considerably higher than the variance explained by either stream or the interaction term.

Macroinvertebrate assemblages

Aquatic invertebrate richness, evenness and diversity were affected by harvest date and differences among streams. Throughout the study, macroinvertebrate species diversity increased with harvest date in all three streams and also increased within each stream for each leaf litter species, with the exception of alder leaves in Oak Creek (Table 3). In general, invertebrate diversity measures did not differ among leaf litter species with three exceptions. In Fossil Creek at harvest day 28, cottonwood litter had fewer invertebrate species than sycamore. In Wet Beaver Creek at day 7 cottonwood litter had fewer species than alder and at day 28 cottonwood and ash hosted assemblages with lower species evenness values than oak. Of 27 comparisons only these three were significant at Bonferroni-corrected alpha levels, indicating that plant species explained little of the variation in invertebrate species richness, evenness or diversity.

The MRPP procedure with NMDS visualisation revealed that aquatic invertebrate assemblages differed among the three streams (MRPP $A = 0.09$, $P < 0.0001$; Fig. 6), the three harvests (MRPP $A = 0.04$, $P < 0.0001$) and among the five species (MRPP $A = 0.01$, $P < 0.0001$). The A statistic provides an estimate of the effect size of a treatment on assemblage structure. An A of 0.09 for stream shows a

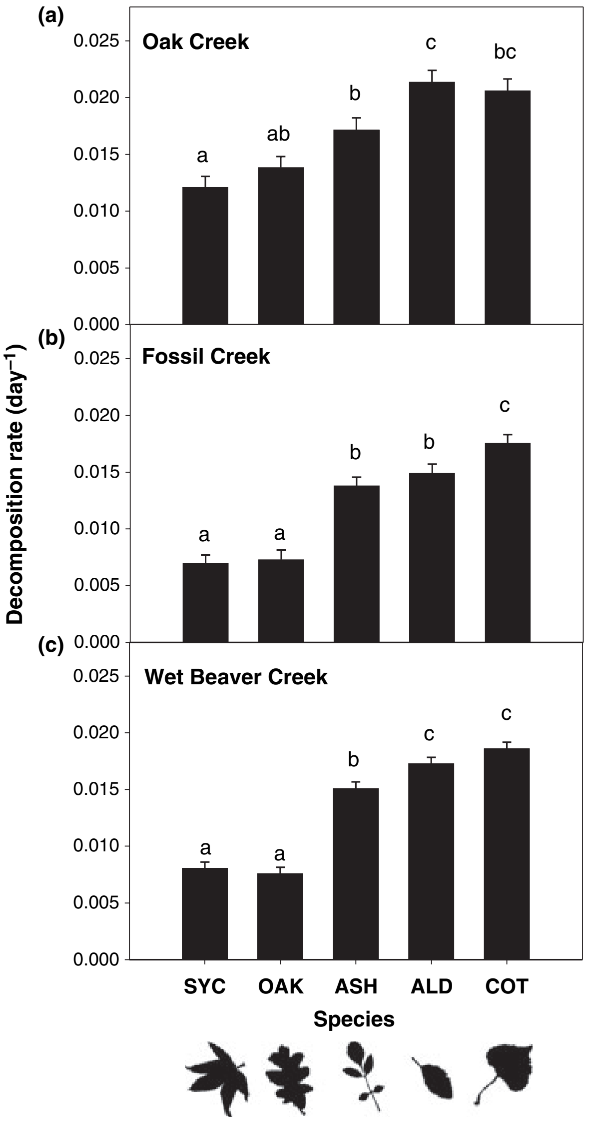

Fig. 2 Leaf litter decomposition rates for five species in three streams (SYC = *Platanus wrightii*, OAK = *Quercus gambelii*, ASH = *Fraxinus velutina*, ALD = *Alnus oblongifolia*, COT = *Populus fremontii*). Values represent regression slopes ±1 SE for the ln-transformed regression model of decomposition rate (day^{-1}). Lower case letters denote pairwise slope differences at a Hommel's corrected alpha-level.

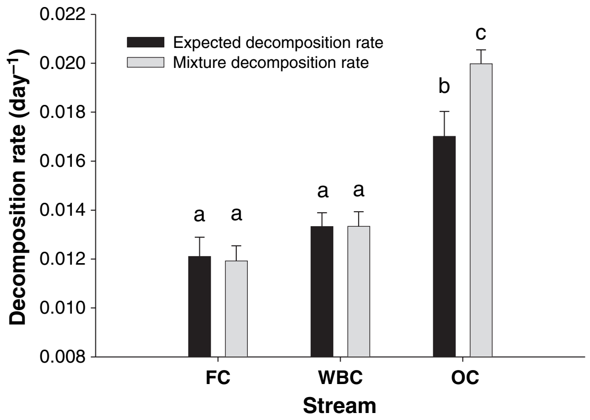

Fig. 3 Decomposition rates of the five-species mixed litter treatments (▨) compared with the expected decomposition rates (■) based on each of the five species in isolation (five-species mixture = alder + ash + cottonwood + sycamore + oak; FC = Fossil Creek; OC = Oak Creek and WBC = Wet Beaver Creek). Values represent regression slopes ±1 SE for the ln-transformed regression model of decomposition rate (day^{-1}). Lower case letters denote pairwise slope differences at a Hommel's corrected alpha-level.

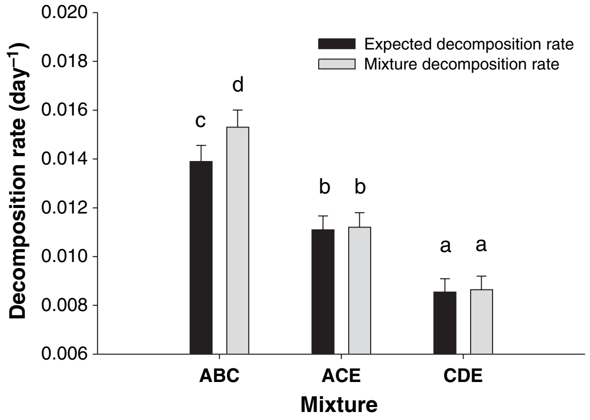

Fig. 4 Decomposition rates of the three-species mixed litter treatments (▨) compared with the expected decomposition rates (■) based on each of the three species in isolation (ABC = ash + alder + cottonwood; ACE = ash + cottonwood + oak; CDE = cottonwood + sycamore + oak). Values represent regression slopes ±1 SE for the ln-transformed regression model of decomposition rate (day^{-1}). Lower case letters denote pairwise slope differences at a Hommel's corrected alpha-level.

relatively strong effect according to McCune & Grace (2002), whereas the leaf litter species treatment only shows an *A* of 0.01, a relatively weak effect. Of the three sources of variation, stream was the strongest factor structuring invertebrate assemblages and it was driven mostly by differences in invertebrate abundances overall (Pearson's $r = 0.502$, $r^2 = 0.252$). A list of indicator species shows that over 40 species were unique to a particular stream environment, whereas no species was unique to a particular litter species or mixture (Table 4).

Differences among streams can be attributed to a number of genera being found in only one of the streams, as well as to differences in the abundance of widespread taxa. In general, the invertebrate assem-

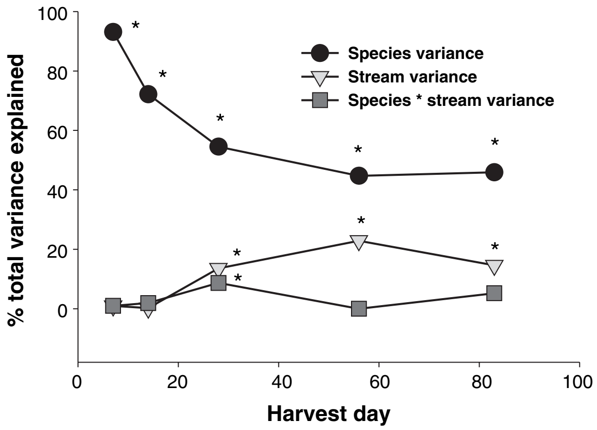

Fig. 5 Per cent variance explained by litter species (●), stream characteristics (▽) and species × stream interaction (▨) through time in stream. Asterisks (*) denote factors that describe a significant fraction of the variability ($P < 0.05$).

Table 3 Macroinvertebrate species richness as a function of harvest day for each leaf litter species in each stream

Species	Stream	Slope	r^2	P-value
Platanus wrightii	FC	0.09174	0.4610	0.0004*
	OC	0.06881	0.3396	0.0028*
	WBC	0.21031	0.8352	<0.0001*
Quercus gambelii	FC	0.15232	0.4848	0.0005*
	OC	0.04952	0.2468	0.0135*
	WBC	0.24350	0.8886	<0.0001*
Populus fremontii	FC	0.10337	0.5230	<0.0001*
	OC	0.05615	0.3765	0.0018*
	WBC	0.18828	0.8060	<0.0001*
Fraxinus velutina	FC	0.11454	0.4308	0.0007*
	OC	0.09646	0.5307	<0.0001*
	WBC	0.20687	0.8124	<0.0001*
Alnus oblongifolia	FC	0.12141	0.5048	0.0001*
	OC	0.02879	0.1063	0.1289
	WBC	0.17813	0.6848	<0.0001*

Values represent slopes, r^2 and P-values for linear regression (asterisks denote significance above an alpha 0.05 level).
FC: Fossil Creek, Arizona; OC: Oak Creek, Arizona; WBC: Wet Beaver Creek, Arizona.

blages among streams differed in terms of species richness, species abundances, species evenness and Shannon's diversity index (*H′*). Fossil Creek and Wet Beaver Creek had significantly higher overall species richness than Oak Creek ($F = 26.62$, $P < 0.0001$). Wet Beaver Creek had significantly more invertebrates per litterbag than either Fossil Creek or Oak Creek ($F = 29.91$, $P < 0.0001$), but significantly lower species diversity than either other creek according to Shannon's diversity index ($F = 34.15$, $P < 0.0001$). Oak Creek showed the highest species evenness and was significantly different from both other streams, but Fossil Creek also showed significantly higher species evenness than Wet Beaver Creek ($F = 99.33$, $P < 0.0001$). All three streams also showed significantly different macroinvertebrate assemblages colonising the five-species litter mixture at each of the three harvest dates (day 7: $A = 0.11$, $P < 0.0001$; day 28: $A = 0.13$, $P < 0.0001$; day 83: $A = 0.14$, $P < 0.0001$). Similar differences in taxa among streams resulted in this pattern.

There were 40 genera unique to one of the three streams, although many of these genera may not be directly involved in shredding leaf litter. Taxa that were likely involved in decomposition include the leaf shredding caddisfly larvae, *Hesperophylax designatus* Walk. and *Limnephilus* sp. (Limnephilidae), which were abundant at the highest altitude site (Oak Creek) and *Phylloicus* sp. (Calamoceratidae), which was abundant in Wet Beaver Creek. A shredding beetle larva, *Peltodytes* sp. (Haliplidae), was common in Fossil Creek and a shredding stonefly larva, *Zealeuctra* sp. (Leuctridae), was only found in Oak Creek.

Species diversity of litter also affected the invertebrate species colonising leaf packs. In all three streams, the invertebrate assemblage colonising mixed litter treatments differed from the expected assemblage based on all species in isolation for both five-species and three-species mixtures (Table 5). Specifically, in Fossil Creek, the invertebrate assemblage colonising the five-species litter mixture differed from the expected invertebrate assemblage for the five-species in isolation on harvest date 28. In Oak Creek, the invertebrate assemblage colonising the five-species litter mixture differed from the expected invertebrate assemblage on harvest dates 7 and 28. And in Wet Beaver Creek, the invertebrate assemblage colonising the five-species litter mixtures differed from the expected invertebrate assemblage on all three harvest dates (Table 5).

In Wet Beaver Creek, the invertebrate assemblage colonising the three three-species litter mixtures differed from the expected assemblage based on the three species in isolation for all species mixtures (Table 5). The fast decomposing mixture (ABC: alder + ash + cottonwood) invertebrate assemblage differed from the expected assemblage on all three harvest dates. The mid-rate mixture (ACE: alder + cottonwood + oak) invertebrate assemblage differed

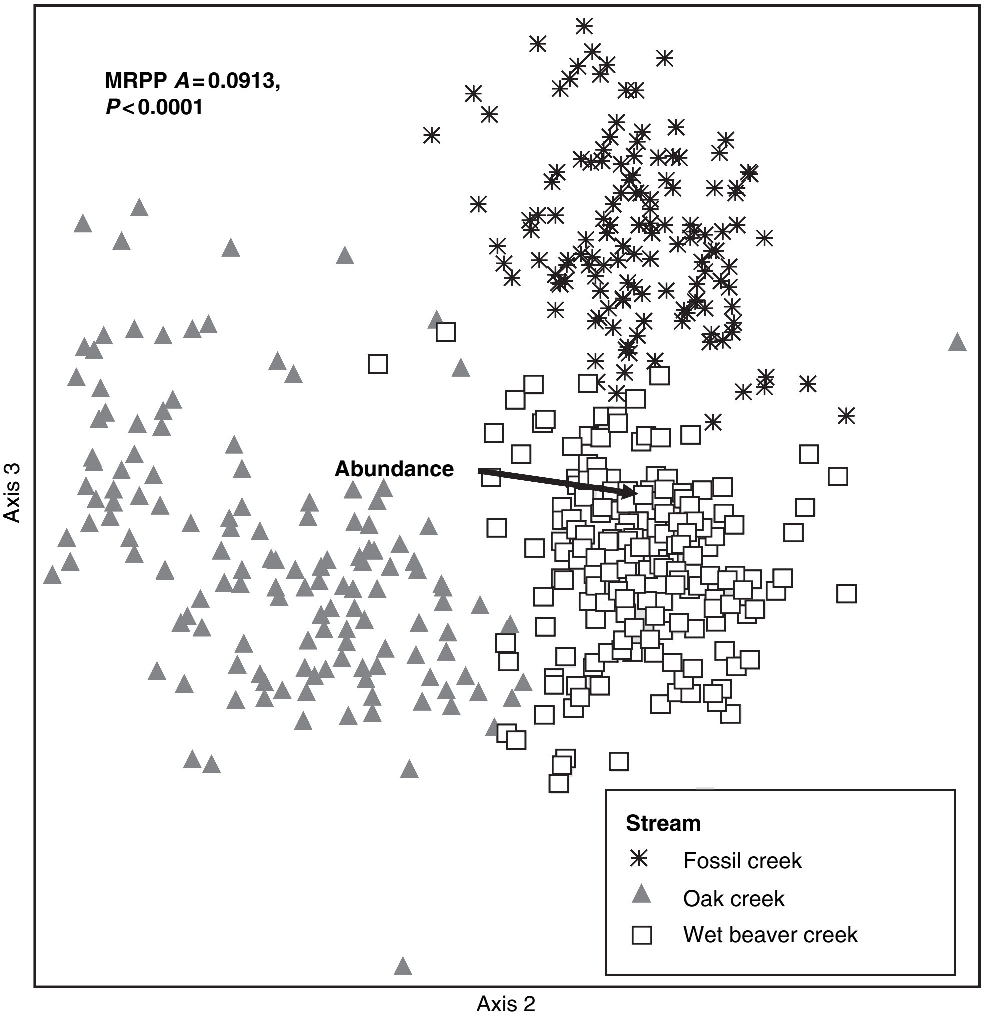

Fig. 6 NMDS ordination of macroinvertebrate composition for Fossil Creek (✳), Oak Creek (▲) and Wet Beaver Creek (□), MRPP $A = 0.09$, $P < 0.0001$. Bi-plot vector shows a correlation of the matrix with invertebrate abundance (Pearson's $r = 0.502$, $r^2 = 0.252$).

from the expected assemblage on harvest dates 28 and 83. And the slow decomposing mixture (CDE: cottonwood + sycamore + oak) invertebrate assemblage differed from expected on harvest dates 7 and 28.

Discussion

Our results show that leaf quality was more important than stream differences in determining decomposition rate, among the measured streams, at least in this restricted range of streams. Leaf quality affected decomposition in predictable ways based on leaf toughness, leaf chemistry and generalisable patterns based on taxonomic family (Webster & Benfield, 1986). Although there were not significant differences in decomposition among all five species as we predicted, we did find consistent differences in all three streams where ash, alder and cottonwood decomposed more rapidly than sycamore and oak.

Although species differences explain the majority of the variation in decomposition rates, differences among streams are also important sources of variation. Of course, the streams chosen here are relatively similar and the choice of a more heterogeneous range of sites may have shown stronger differences among them, relative to differences among species. Nevertheless, these results confirmed our prediction that streams would differ in litter breakdown, because of differences in water quality and macroinvertebrate assemblages, despite their geographic proximity. Because of the correlative nature of this study, we

Table 4 Indicator species analysis results for species (or taxa) unique to different streams

Indicator species or taxon (Family)	Indicator value	*P*-value	Stream
Hydracarina	7.8	0.027	Fossil Creek
Huleechius sp. (Elmidae)	34	0.001	Fossil Creek
Peltodytes sp. (Haliplidae)*	5.2	0.001	Fossil Creek
Ceratopogonidae	43.9	0.001	Fossil Creek
Caloparyphus sp. (Stratiomyidae)	29.6	0.001	Fossil Creek
Fossaria sp. (Lymnaeidae)	34.1	0.001	Fossil Creek
Physella sp. (Physidae)	97.1	0.001	Fossil Creek
Gyraulus sp. (Planorbidae)	32.5	0.001	Fossil Creek
Nematoda	24.5	0.001	Fossil Creek
Hetaerina sp. (Calopterygidae)	16.7	0.001	Fossil Creek
Argia sp. (Coenagrionidae)	57.1	0.001	Fossil Creek
Ostracoda	21.8	0.001	Fossil Creek
Hydroptila sp. (Hydroptilidae)	29.8	0.001	Fossil Creek
Mayatrichia sp. (Hydroptilidae)	3.7	0.003	Fossil Creek
Oxyethira sp. (Hydroptilidae)	3	0.008	Fossil Creek
Pisidium sp. (Sphaeriidae)	26.3	0.001	Oak Creek
Copepoda	27.4	0.001	Oak Creek
Callibaetis sp. (Baetidae)	24.8	0.001	Oak Creek
Cinygmula sp. (Heptageniidae)	6.4	0.001	Oak Creek
Zealeuctra sp. (Leuctridae)*	13.8	0.001	Oak Creek
Lepidostoma sp. (Lepidostomatidae)	3.5	0.006	Oak Creek
Hesperophylax sp. (Limnephilidae)*	80.9	0.001	Oak Creek
Limnephilus sp. (Limnephilidae)*	22.3	0.001	Oak Creek
Polycentropus sp. (Polycentropodidae)	71.9	0.001	Oak Creek
Gumaga sp. (Sericostomatidae)	17	0.001	Oak Creek
Psephenus sp. (Psephenidae)	16.4	0.001	Wet Beaver Creek
Chironomidae	59.2	0.001	Wet Beaver Creek
Baetis sp. (Baetidae)	40.4	0.001	Wet Beaver Creek
Caenis sp. (Caenidae)	35.5	0.001	Wet Beaver Creek
Choroterpes sp. (Leptophlebiidae)	12.4	0.001	Wet Beaver Creek
Paraleptophlebia sp. (Leptophlebiidae)	43.6	0.001	Wet Beaver Creek
Tricorythodes sp. (Tricorythidae)	60.1	0.001	Wet Beaver Creek
Leptohyphes sp. (Tricorythidae)	5.5	0.003	Wet Beaver Creek
Ferrissia sp. (Ancylidae)	6.5	0.001	Wet Beaver Creek
Hirudinea	6.3	0.004	Wet Beaver Creek
Brachycentrus sp. (Brachycentridae)	4	0.003	Wet Beaver Creek
Phylloicus sp. (Calamoceratidae)*	11.6	0.001	Wet Beaver Creek
Helicopsyche sp. (Helicopsychidae)	47	0.001	Wet Beaver Creek
Hydropsyche sp. (Hydropsychidae)	11.8	0.001	Wet Beaver Creek
Cheumatopsyche sp. (Hydropsychidae)	5	0.002	Wet Beaver Creek
Mystacides sp. (Leptoceridae)	14.4	0.001	Wet Beaver Creek
Nectopsyche sp. (Leptoceridae)	50.8	0.001	Wet Beaver Creek
Oecetis sp. (Leptoceridae)	5.5	0.015	Wet Beaver Creek

Values represent indicator values, Monte Carlo *P*-values and the stream indicated. Asterisks denote potential shredding taxa.

were unable to determine the mechanisms for these differences, although we suggest that decomposition was fastest in Oak Creek because of high nitrogen concentration and high abundance of the shredding caddisfly *H. designatus*. The location we chose in Oak Creek was 0.5 km downstream from a fish hatchery, which is has been shown to cause high nutrient concentrations in a related monitoring project (Doucett *et al.*, unpublished data). High nitrate is generally correlated with faster decomposition (Meyer & Johnson, 1983; Suberkropp & Chauvet, 1995) and may also indirectly affect decomposition through an increase in invertebrate secondary production.

Although invertebrate species richness was low in Oak Creek, invertebrate biomass was high. Specifically, the large (2-cm average length) leaf shredding caddisfly *H. designatus* was abundant, occasionally reaching over 90 individuals per litterbag. The site

Table 5 NMDS ordination results comparing the invertebrate assemblages on each litter mixture to the average invertebrate assemblage on each litter species in isolation (5-mix = alder + ash + cottonwood + sycamore + oak; ABC mix = alder + ash + cottonwood; ACE mix = alder + cottonwood + oak; CDE = cottonwood + sycamore + oak)

Mixture	Harvest 1 (7 days)	Harvest 3 (28 days)	Harvest 5 (83 days)
5-mix FC	$A = 0.0171$, $P = 0.1038$	$A = 0.0214$, $P = 0.0261$*	$A = 0.0138$, $P = 0.0815$
5-mix OC	$A = 0.0413$, $P = 0.0072$*	$A = 0.0261$, $P = 0.0342$*	$A = 0.0221$, $P = 0.0532$
5-mix WBC	$A = 0.0413$, $P = 0.0005$*	$A = 0.0394$, $P = 0.0054$*	$A = 0.0369$, $P = 0.0129$*
ABC mix WBC	$A = 0.0286$, $P = 0.0244$*	$A = 0.0296$, $P = 0.0145$*	$A = 0.0453$, $P = 0.0108$*
ACE mix WBC	$A = 0.0120$, $P = 0.0956$	$A = 0.0506$, $P = 0.0002$*	$A = 0.0468$, $P = 0.0036$*
CDE mix WBC	$A = 0.0282$, $P = 0.0228$*	$A = 0.0545$, $P < 0.0001$*	$A = 0.0263$, $P = 0.0588$

Values represent MRPP *A* values and *P*-values for each comparison. Asterisks denote significant differences at an alpha of 0.05. FC: Fossil Creek, Arizona; OC: Oak Creek, Arizona; WBC: Wet Beaver Creek, Arizona.

chosen within Oak Creek was also the highest in altitude of the three stream sites and, because of its relatively closed canopy, potentially the most dependent on leaf litter inputs. This could also have led to faster decomposition (Vannote *et al.*, 1980). In contrast, the lower decomposition rates in Fossil Creek were probably because of travertine deposition on leaf surfaces, which can impede microbial conditioning and physical fragmentation (Casas & Gessner, 1999). Travertine deposition can also affect leaf surface interactions with detritivores and may have led to a reduction in leaf shredding in Fossil Creek.

In contrast to leaf litter decomposition, the main source of variation in macroinvertebrate assemblages was the difference among streams. We found distinct assemblages of invertebrates among the three streams and over 40 indicator species for a specific stream. We also found differences in invertebrate assemblages across the three harvest dates and among the five leaf species and mixtures, although these differences were more subtle than the differences among streams. Although invertebrate assemblages differed dramatically among streams, leaf decomposition was most affected by substrate quality, not stream-to-stream differences in the shredder assemblage.

We predicted that mixtures of litter would breakdown in all three streams at rates different from those expected from the rate of each species alone, although we did not predict the direction of this difference. Such effects were modest overall. We found the five-species mixture showed accelerated decomposition rates in one of the three streams (Oak Creek). We also showed some acceleration of decomposition when three relatively labile litter species are mixed (alder + ash + cottonwood), but not for three recalcitrant species (cottonwood + sycamore + oak) or for a mixture of labile and recalcitrant species (alder + cottonwood + oak). These results provide evidence for the potential effects of riparian tree species diversity on stream ecosystem function, especially under conditions of rapid decomposition. Interestingly, these results contradict recent research showing depressed rates of decomposition for mixed litters (Jonsson & Malmqvist, 2003; Swan & Palmer, 2004), arguing that diversity effects on stream ecosystems might be species-specific or location-specific.

We also predicted that the litter mixtures would show differences in aquatic macroinvertebrate assemblages compared with the five species in isolation. Although decomposition rates in mixture only differed from expected in one stream, macroinvertebrate assemblages differed from expected in all three streams showing that invertebrate assemblages colonising leaf litter mixtures differ from the assemblages colonising single species. The three-species mixtures showed non-additive effects on aquatic macroinvertebrate assemblages, regardless of which three species were present. These results provide strong evidence for the importance of species diversity (riparian tree diversity in this case) for invertebrate diversity.

This research provides evidence that diverse litter inputs may be important in maintaining aquatic diversity and should be considered during the formulation of riparian restoration strategies (Knopf *et al.*, 1988). Riparian restoration projects often involve the re-vegetation of slopes adjacent to rivers with single species or single clones of species (Winfield & Hughes, 2002). Additionally, many stream ecosystems are being overrun by invasive species, dramatically reducing tree biodiversity [e.g. *Tamarix* sp., *Elaeagnus angustifolia* L., *Ailanthus altissima* (P. Mill.) Swingle]. The continued neglect of systems affected by invasive species and the continued use of single-species restoration practices in riparian forestry could lead to the loss of aquatic species diversity and possibly to the alteration of aquatic ecosystem processes.

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