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Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river

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Abstract. Leaf-litter inputs provide substrate and energy to stream systems. These contributions vary based on species-specific differences in litter quality, but little is known about how differences in litter quality within a species can affect ecosystem processes. Genetic variation within tree species, such as oaks and cottonwoods, affects ecosystem processes including decomposition and nutrient cycling in forest ecosystems and has the potential to do the same in streams. We collected litter from 5 genotypes of each of 4 different cottonwood cross types (*Populus fremontii*, *Populus angustifolia*, and natural F_1 and backcross hybrids), grown in a common garden, and measured their decomposition rates using litter bags in the Weber River, Utah. The proportion of 35 species-specific *P. fremontii* restriction-fragment length polymorphism markers in the genotype explained 46% and genetically controlled phytochemical mechanisms (e.g., % soluble condensed tannin in litter) explained >72% of the variation in leaf-litter decomposition rate, respectively. Understanding how natural genetic variation in plants can affect ecosystem processes will provide baseline information with which to address the loss of genetic variation (through habitat fragmentation and global change) and altered genetic variation through hybridization with cultivars and transgenic manipulations in the wild.

Key words: aquatic terrestrial interaction, *Populus*, hybrids, intraspecific variation, riparian restoration, fungal biomass.

Conservation biologists recognize the importance of diversity at multiple levels, including genetic, species, and functional diversity, and that diversity at all levels is threatened in many habitats across the globe (Noss 1990, Purvis and Hector 2000). Much of the debate on the effect of diversity on ecosystem processes has focused on species diversity, but intraspecific diversity also may be important, particularly in systems where species diversity is relatively low (McGraw 1995). Genetic studies in conservation biology have focused primarily on rare species with far less attention to the consequences of reduced genetic diversity in dominant or foundation species. However, the loss of genetic diversity in dominant species could have consequences for biodiversity conservation and ecosystem function, particularly if genetic effects cascade through multiple trophic levels (Whitham et al. 2003, 2006). Human activities are dramatically reducing the genetic diversity in forests (Ledig 1992) through logging, development, recreational use, and global climate

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change. We address the effects of genetic variation on ecosystem function in a model system dominated by 2 cottonwood species, *Populus fremontii* S. Wats (Fremont cottonwood) and *Populus angustifolia* James (narrowleaf cottonwood), and their natural hybrids in a riparian forest where species diversity, consisting mostly of several species of *Populus* and *Salix*, is relatively low.

A recent surge in research on the effects of biodiversity on ecosystem function has shown that functional group diversity and species diversity are important for maintaining ecosystem processes such as productivity or nutrient cycling (e.g., Naeem et al. 1994, Tilman et al. 1997, Loreau et al. 2001, 2002, Kinzig et al. 2002). A much smaller set of studies has shown that genetic variation within tree species or hybrids also can influence decomposition and nutrient cycling in oaks (Madritch and Hunter 2002, 2003, 2004), aspen (Madritch et al. 2006), cottonwoods (Driebe and Whitham 2000, Schweitzer et al. 2004, 2005a, b, Fischer et al. 2006), and 'Ohia lehua (*Metrosideros polymorpha*; Treseder and Vitousek 2001).

Genetic variation in trees may be most important for ecosystem function when it is correlated with variation in leaf-litter quality or productivity. For example, leaves of different genotypes of *Leucaena trichandra* displayed a 30-fold difference in condensed tannin concentration (Dalzell and Shelton 2002). Similarly, condensed tannin concentration varied 10- to 30-fold among different cross types in this hybridizing *Populus* complex where tannin concentrations among parental and hybrid cross types depressed decomposition rates in terrestrial systems (Driebe and Whitham 2000, Schweitzer et al. 2004).

Terrestrial inputs to streams can provide as much as 90% of the energy used by streams (Petersen and Cummins 1974, Webster and Benfield 1986), making it important to consider how both tree species diversity (e.g., Swan and Palmer 2004, LeRoy and Marks 2006) and genetic variation within these species might affect stream function. To date, only 2 aquatic studies have manipulated litter quality within a hybridizing species complex. These studies have shown differences in decomposition rate and macroinvertebrate community composition between 2 parental species, *P. fremontii* and *P. angustifolia*, and 2 classes of their naturally occurring hybrids (Driebe and Whitham 2000, LeRoy et al. 2006).

We expand on recent studies by manipulating fine-scale intraspecific genetic variation. We made 3 major predictions: 1) leaf litter from trees with different genotypes will differ in initial leaf-litter quality, aquatic decomposition rates, fungal biomass accumulation, and macroinvertebrate colonization; 2) elevated condensed tannin and lignin concentrations will significantly affect rates of decomposition, fungal biomass on leaf surfaces, and macroinvertebrate community structure; and 3) differences in phytochemistry and decomposition rates among these genotypes will be comparable to the differences among common plant families. To the best of our knowledge, our study is the first to examine fine-scale genetic differences in decomposition of leaf litter in an aquatic ecosystem. The cottonwood system is an ideal model with which to test our predictions because genotypic variation in this system already has been shown to affect terrestrial decomposition and N cycling (Schweitzer et al. 2004, 2005a, b), fine root production (Fischer et al. 2006), beaver browsing (Bailey et al. 2004), and terrestrial arthropod communities (Wimp et al. 2004, 2005, Bangert et al. 2005). Conservation biologists recognize the importance of genetic diversity for rare and endangered organisms. However, the issues addressed in our study are important because genetic diversity within common, dominant organisms also may significantly affect community structure and ecosystem function (Whitham et al. 2003, 2006).

Methods

Common garden

A common garden of cottonwood genotypes was planted from wild cuttings in spring 1991 (Ogden, Utah; lat 41°14′48″N, long 112°00′00″W). Cuttings for this garden were taken from isolated individuals along a 105-km transect along the Weber River. Based on our knowledge of their life-history and reproductive strategies, we know that these individuals represent different genotypes because of their geographic isolation. Up to 20 clones from each individual were propagated and planted in a random grid of 1.5 ha. The garden consists of replicated individuals of many genotypes of 4 cottonwood cross types: 2 parental types, *P. fremontii* and *P. angustifolia*, and 2 classes of hybrids, F_1 hybrids between the 2 parental species (*P. fremontii* × *P. angustifolia*), and backcross hybrids to *P. angustifolia*. Previous research using restriction-fragment length polymorphisms (RFLPs) showed unidirectional introgression in backcross to the narrowleaf parent and between 1 and 13 of 35 species-specific *P. fremontii* markers (Keim et al. 1989, Martinsen et al. 2001). The variation observed among litter types was assumed to be a result of genetic effects because a common garden standardizes environmental effects. In autumn 2002, naturally abscised leaf litter was collected from 5 genotypes per cross type in the common garden using whole-tree mesh bags. Whole-tree mesh bags enabled the collection of both mature

and juvenile foliage from an entire tree and enabled us to address all of the genetic variation, including ontogenetic variation, within a tree (Kearsley and Whitham 1997). Whole-tree collections are important because collecting leaf litter from single-branch bags might have resulted in underestimation of the level of variability within a genotype, showing false differences among genotypes. Litter was collected at weekly intervals and air dried before being placed in litter bags.

Site description

Mesh litter bags were incubated in pools along a 4.5-km reach of the Weber River (Utah) to determine litter decomposition rates. The Weber River is a 4th-order stream at the location used in our study (lat 41°08′13″N, long 111°55′43″W), and its riparian vegetation is dominated by the 4 cottonwood cross types (*P. fremontii*, *P. angustifolia*, and both F_1 and backcross hybrids) and multiple willow species (*Salix* spp.). Water-quality variables were measured throughout the study period using a Hydrolab Minisonde (Hydrolab–Hach Corporation, Loveland, Colorado). Temperature, dissolved O_2, pH, total dissolved solids, specific conductance, and salinity were measured on each harvest date. On harvest dates in January and March, 3 replicate water samples for nutrient and ionic composition were collected in 250-mL polyethylene bottles, filtered through 0.4-μm glass-microfiber filters, and acidified to a pH <2.0 with H_2SO_4. Water analyses (PO_4^{3-}, NO_3^-, NH_4^+) were conducted using a Technicon Auto Analyzer II (Technicon Instruments Corporation, Tarrytown, New York). See Table 1 for mean values of water-chemistry variables and site descriptors.

Initial litter chemistry

Naturally abscised leaf litter was air-dried, and 2 replicate litter bags from each treatment were used to determine initial litter-quality measures such as N, P, soluble condensed tannins, and lignin. In all cases, analytical replicates were used for each of the 2 replicates used for litter chemistry. We determined total litter N and P concentrations by modified micro-Kjeldahl digestion (Parkinson and Allen 1975) followed by analysis on a Lachat AE Flow Injection Analyzer (Lachat Instruments, Loveland, Colorado), using the salicylate and molybdate–ascorbic acid methods, respectively (Lachat Instruments 1992). Depending on the cross type, 25-mg (back cross or *P. angustifolia*) or 50-mg (*P. fremontii* or F_1) subsamples of ground material were extracted for soluble condensed tannins with 70% acetone and 10 mM ascorbic acid.

Table 1. Mean (±1 SE) values for site descriptors and water-quality variables in the Weber River, Utah, averaged across all blocks and harvest dates ($n = 32$) in winter 2002/2003.

Variable	Mean (±1 SE)
Elevation (m asl)	4450 ± 10
Water temperature (°C)	2.4 ± 1.5
pH	8.1 ± 0.12
Dissolved O_2 (% saturation)	111.6 ± 5.9
Total dissolved solids (mg/L)	0.37 ± 0.07
Specific conductance (μS/cm)	573 ± 126
Salinity (mg/L)	0.29 ± 0.07
NH_4^+ (mg/L)[a]	0.08 ± 0.04
NO_3^- (mg / L)[a]	0.07 ± 0.20
PO_4^{3-} (mg/L)[a]	0.21 ± 0.10
Mg^{2+} (mg/L)[b]	20.6 ± 1.5
Ca^{2+} (mg/L)[b]	69.8 ± 3.5
Na^+ (mg/L)[b]	32.9 ± 5.4
Cl^- (mg/L)[b]	55.1 ± 5.4
SO_4^{2-} (mg/L)[b]	34.5 ± 0.9

[a] Measured on 5 January 2003 and 15 March 2003, $n = 6$
[b] Measured on 5 January 2003, $n = 3$

We used the butanol–HCl method to determine soluble condensed tannin concentrations (Porter et al. 1986), with standards purified from narrowleaf cottonwood following the methods of Hagerman and Butler (1989). We measured absorbance on a spectrophotometer (Spectramax-Plus 384; Molecular Devices, Sunnyvale, California). Litter % lignin was determined using an ANKOM 200 Fiber Analyzer (AOAC 2000; ANKOM Technologies, Macedon, New York).

Litter decomposition

Leaves were air-dried, weighed into 4-g quantities, and placed in 6.4-mm-mesh litter bags (Trical netting, diamond-shaped; Aquatic Eco-Systems, Apopka, Florida). The 20 genotype-level leaf-litter treatments consisted of litter from 5 genotypes of each of the 4 cottonwood cross types: *P. fremontii*, *P. angustifolia*, F_1 hybrids, and backcross hybrids. Five additional treatments consisted of genotype and cross type mixtures (Table 2). Eight replicate litterbags ($n = 8$) were used for each treatment on each harvest date for a total of 1000 litter bags. An additional 250 litter bags were created from 1-mm mesh to exclude large shredders (1.5 g leaf litter/bag, 25 treatments, $n = 5$ for harvest dates 7 and 28). All litter bags were randomly assigned a harvest date and a block along the 4.5-km reach. Bags were anchored along 2-m lengths of steel rebar wedged in active depositional areas near the shore. Litter bags were color-coded by harvest date to assist harvesting and prevent disturbance of neighboring bags. Litter bags were harvested

TABLE 2. Mean ±1 SE ($n = 2$) initial % soluble condensed tannins (SCT), % lignin, % N, % P, and C : N ratios for leaf litter from 20 individual cottonwood genotypes and 5 genotype mixtures. Decomposition rate constants (k) were calculated as mean (±1 SE) slopes of the exponential regression lines for mass loss as a function of time for each genotype and genotype mixture. F-ratios and R^2_{adj} statistics are associated with regression lines ($n = 40$ per regression line). All regression equations are significant at $p < 0.0001$. Means with the same lower-case superscript are not significantly different among genotypes or genotype mixtures (Tukey's honestly significant difference, $p > 0.05$).

Genotype	Cross type	% SCT	% lignin	% N	% P	C : N	k (/d)	F-ratio	R^2_{adj}
KSCR-1	Fremont	0.043 ± 0.008^{a}	6.38 ± 0.762^{a}	0.533 ± 0.007^{b}	0.067 ± 0.002^{b}	75.63 ± 3.093^{b}	0.0107 ± 0.0005^{a}	16.38	0.748
0031	Fremont	0.294 ± 0.024^{b}	4.38 ± 0.085^{a}	0.307 ± 0.003^{a}	0.144 ± 0.001^{c}	135.41 ± 1.998^{a}	0.0109 ± 0.0004^{a}	16.76	0.823
H-14	Fremont	0.142 ± 0.035^{ab}	4.86 ± 0.061^{a}	0.525 ± 0.023^{b}	0.027 ± 0.001^{a}	84.13 ± 7.9^{b}	0.0099 ± 0.0005^{a}	15.1	0.765
17	Fremont	0.067 ± 0.028^{a}	4.72 ± 0.582^{a}	0.443 ± 0.009^{ab}	0.029 ± 0.001^{a}	95.47 ± 4.712^{b}	0.0111 ± 0.0005^{a}	16.84	0.825
KH-8	Fremont	0.221 ± 0.004^{ab}	5.40 ± 0.775^{a}	0.481 ± 0.001^{ab}	0.029 ± 0.001^{a}	89.49 ± 0.247^{b}	0.0096 ± 0.0004^{a}	14.59	0.864
MH-2	F_1 hybrid	1.283 ± 0.243^{a}	11.63 ± 0.137^{bc}	0.469 ± 0.002^{bc}	0.084 ± 0.003^{c}	92.35 ± 1.109^{b}	0.0103 ± 0.0005^{a}	15.66	0.792
WH-2	F_1 hybrid	4.765 ± 0.093^{a}	19.66 ± 1.699^{ab}	0.478 ± 0.001^{bc}	0.072 ± 0.001^{bc}	91.01 ± 0.013^{b}	0.0089 ± 0.0005^{ab}	13.67	0.816
989	F_1 hybrid	3.579 ± 0.337^{a}	9.23 ± 0.027^{bc}	0.472 ± 0.016^{bc}	0046 ± 0.002^{ab}	95.09 ± 6.705^{b}	0.0102 ± 0.0004^{a}	15.54	0.852
1935	F_1 hybrid	4.295 ± 1.612^{a}	13.91 ± 0.557^{b}	0.385 ± 0.003^{ab}	0.028 ± 0.001^{a}	118.04 ± 2.106^{ab}	0.0078 ± 0.0004^{b}	11.84	0.708
H-1	F_1 hybrid	2.589 ± 0.202^{a}	9.03 ± 0.485^{bc}	0.325 ± 0.001^{a}	0.161 ± 0.002^{d}	131.97± 0.844^{a}	0.0092 ± 0.0005^{ab}	14.08	0.695
999	Backcross	8.454 ± 2.075^{a}	21.06 ± 0.894^{bc}	0.567 ± 0.012^{c}	0.092 ± 0.003^{b}	78.64 ± 3.329^{c}	0.0089 ± 0.0005^{a}	13.54	0.774
3200	Backcross	24.674 ± 0.098^{c}	30.89 ± 1.989^{ab}	0.362 ± 0.001^{a}	0.132 ± 0.004^{cd}	126.27 ± 0.622^{a}	0.0063 ± 0.0003^{b}	9.65	0.646
1017	Backcross	17.086 ± 0.094^{bc}	23.53 ± 0.996^{b}	0.343 ± 0.001^{a}	0.149 ± 0.001^{cd}	132.54 ± 0.629^{a}	0.0071 ± 0.0005^{ab}	10.89	0.679
WH-3	Backcross	10.758 ± 0.139^{ab}	20.11 ± 0.029^{bc}	0.455 ± 0.001^{b}	0.054 ± 0.001^{a}	96.51 ± 0.158^{b}	0.0078 ± 0.0005^{ab}	11.84	0.670
11	Backcross	7.593 ± 0.884^{a}	18.1 ± 0.206^{bc}	0.553 ± 0.003^{c}	0.118 ± 0.001^{bc}	79.94 ± 0.354^{c}	0.0077 ± 0.0003^{ab}	11.69	0.815
XSU-1	Narrowleaf	5.342 ± 0.377^{a}	21.55 ± 0.422^{bc}	0.538 ± 0.005^{bc}	0.178 ± 0.004^{b}	84.79 ± 1.573^{bc}	0.0103 ± 0.0005^{b}	15.7	0.843
1008	Narrowleaf	6.187 ± 0.132^{a}	17.70 ± 0.448^{a}	0.538 ± 0.005^{bc}	0.037 ± 0.004^{a}	83.99 ± 1.413^{bc}	0.0089 ± 0.0006^{ab}	13.69	0.723
1000	Narrowleaf	15.46 ± 0.951^{b}	23.64 ± 0.029^{c}	0.489 ± 0.001^{b}	0.035 ± 0.001^{a}	91.67 ± 0.314^{b}	0.0071 ± 0.0004^{a}	10.9	0.702
T-21	Narrowleaf	8.318 ± 0.182^{a}	19.33 ± 0.566^{ab}	0.566 ± 0.005^{c}	0.257 ± 0.001^{c}	77.53 ± 1.327^{c}	0.0087 ± 0.0004^{ab}	13.34	0.831
1019	Narrowleaf	13.794 ± 0.378^{b}	21.34 ± 0.388^{bc}	0.408 ± 0.004^{a}	0.220 ± 0.004^{bc}	109.99 ± 2.138^{a}	0.0087 ± 0.0006^{ab}	13.31	0.699
Mixture	Fremont	0.209 ± 0.071^{d}	5.46 ± 0.122^{c}	0.501 ± 0.009^{a}	0.069 ± 0.001^{b}	83.65 ± 4.689^{a}	0.0101± 0.0007^{a}	15.42	0.759
Mixture	F_1 hybrid	4.021 ± 1.22^{cd}	11.25 ± 0.418^{b}	0.469 ± 0.004^{a}	0.077 ± 0.001^{b}	94.79 ± 2.677^{a}	0.0094 ± 0.0007^{a}	14.29	0.794
Mixture	Backcross	13.023 ± 0.288^{a}	19.29 ± 1.086^{a}	0.482 ± 0.005^{a}	0.117 ± 0.001^{a}	92.64 ± 2.817^{a}	0.0088 ± 0.0007^{a}	13.43	0.793
Mixture	Narrowleaf	8.732 ± 0.213^{ab}	18.40 ± 0.342^{a}	0.529 ± 0.001^{a}	0.139 ± 0.002^{a}	84.66 ± 0.135^{a}	0.0090 ± 0.0007^{a}	13.76	0.788
Mixture (all)	0031, 989, 999, T-21	5.321 ± 0.095^{bc}	11.015 ± 0.424^{b}	0.456 ± 0.005^{a}	0.128 ± 0.005^{a}	94.76 ± 2.740^{a}	0.0098 ± 0.0007^{a}	15.08	0.861

from the stream 7, 28, 56, and 125 d after deployment in November 2002. An additional complete set of litter bags was created to permit determination of losses caused by handling and transport on harvest date 0 and to determine initial litter-quality measures. Upon harvest, litter bags were placed in individual polyethylene zipper bags and transported on ice to the laboratory.

Litter bags were processed within 12 h of harvesting. Leaf material was rinsed with stream water and processed for ergosterol extraction (see *Fungal biomass*). Sediment and invertebrates were sieved through 250-μm nets and preserved in 70% ethanol. Remaining leaf material was oven-dried at 60°C for 72 h. Dry leaf material was weighed and ground in a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey) to 425-μm particles. A subsample of ground material was combusted for 1 h at 500°C in a muffle furnace (Barnstead International, Dubuque, Iowa) and % organic material and ash-free dry mass (AFDM) were determined.

Fungal biomass

Aquatic fungal biomass was estimated using an ergosterol assay by high-performance liquid chromatography (HPLC; Suberkropp 2001). Ten 11-mm leaf discs were punched from 5 randomly selected leaf laminae in each coarse- and fine-mesh litter bag ($n = 5$) on harvest dates 7 and 28. Five of these leaf discs were oven-dried at 50°C for 72 h to determine the dry mass of the leaf discs. The other 5 leaf discs were preserved in 5 mL of HPLC-grade (99.99%) methanol for ergosterol extraction. Leaf discs and methanol were refluxed at 80°C for 30 min in a mixture of methanol (25 mL) and alcoholic KOH (5 mL). The leaf particles were removed and discarded, and the extractant was partitioned into 20 mL of pentane. The pentane was evaporated, and the residue was redissolved into 1 mL of HPLC-grade methanol and filtered through HPLC-certified, 13-mm syringe filters with 0.2-μm polytetrafluoroethylene membranes. Samples were passed through a C-18 column with methanol as the mobile phase and a 1.0 mL/min flow rate, which yielded a mean ergosterol standard retention time of 6.35 min. Ergosterol concentration was converted to fungal biomass (mg/g leaf litter) using a 5.5-μg ergosterol/mg fungal biomass conversion factor (Gessner and Chauvet 1993).

Aquatic invertebrates

Preserved invertebrate samples were sieved through 1-mm mesh to separate the macroinvertebrates. Macroinvertebrate samples from harvest date 28 were sorted under 2× magnification and counted and identified under a dissecting scope to the lowest taxonomic level practical. Enumeration and identification of macroinvertebrates were feasible only for samples from 1 harvest date because of the large number of treatments and replicates in our study. Harvest date 28 was chosen to correspond to the predicted highest fungal biomass on leaf surfaces after 4 wk of incubation (Mille-Lindblom and Tranvik 2003). Reference specimens are maintained in the LeRoy Aquatic Ecology Lab at The Evergreen State College. Twenty-five taxa were identified from 22 families and 10 orders.

Statistical analyses

Analysis of leaf-litter decomposition rate constants required ln(x) transformation of AFDM to meet assumptions of normality and equal variances and to permit determination of the daily exponential decay rate constant (k; Jenny et al. 1949). Litter from bags used to estimate handling loss (harvest date 0) was ashed to determine initial AFDM for k determination. Values of k were compared using an equality of slopes test (SAS version 8.01; SAS Institute, Cary, North Carolina). Expected ks for the 3- and 5-species mixtures (calculated as the mean k of each species in isolation) were compared with the observed ks for the mixtures using linear contrasts (at Hommel's corrected α levels) to test whether litter breakdown of mixtures was nonadditive (Swan and Palmer 2004).

Fungal biomass, leaf chemistry, and macroinvertebrate community measurements were compared using 1-way (to test for differences among cross types) and nested (to test for differences among genotypes nested in cross types) analysis of variance (ANOVA) and post-hoc comparisons (Tukey's honestly significant difference). Each genotype also could be classified as belonging to a cross type, so genotypes were nested in cross types in all nested ANOVAs. All ANOVA factors were considered fixed effects. Species abundance, species richness, species evenness, and Shannon's diversity index (H') of the macroinvertebrate community were calculated for the litter bags harvested after 28 d to correspond with fungal biomass measurements. Nonmetric multidimensional scaling ordination was used to visualize community-wide responses to leaf-litter treatments, and multiresponse permutation procedures (MRPP) were used to test for differences among cross types and genotypes (PC-ORD version 4.02; MjM Software, Gleneden Beach, Oregon). Species abundances were normalized relative to the species maximum before ordination. MRPP analyses were used to compare differences in macroinvertebrate

community structure among cross types, among genotypes, and among mixtures. A Mantel test was used to compare macroinvertebrate community similarity to genetic similarity among genotypes, and Indicator Species Analysis was used to determine if any macroinvertebrate species showed high fidelity to the leaf litter from individual genotypes or cross types (PC-ORD 4.02).

Results

Leaf chemistry and decomposition

Initial litter mean % soluble condensed tannin, % lignin, % N, % P, and C:N differed significantly among genotypes within cross types (within species and hybrid types; Table 2). Our hypothesis that these differences in initial litter quality would lead to significant differences in decomposition rates among cross types and genotypes was supported. The variation in k was most pronounced among genotypes of the *P. angustifolia* (narrowleaf) species, but variation among *P. fremontii*, F_1 hybrid, and backcross hybrid genotypes also was considerable (Table 2).

Percent soluble condensed tannin, % lignin, and % P content differed significantly among cross types when litter from all 5 genotypes per cross type was mixed in equal parts into a cross type mixture (Table 2). However, among-genotype variability appeared to mask differences in % N, C:N, and k among cross type mixtures. Backcross and *P. angustifolia* genotypes consistently had higher % soluble condensed tannin, % lignin, and % P compared to *P. fremontii*, and F_1 hybrids had intermediate concentrations for all variables. Despite significant differences in initial litter quality among cross types, k did not differ among cross type mixtures. Moreover, observed values of k for each mixture did not deviate from expected values of k-based means for each genotype in isolation ($p > 0.05$ in all cases; Fig. 1).

The proportion of 35 species-specific *P. fremontii* RFLP markers (proportion Fremont RFLP markers) in the genotype explained ~80% of the variation in % lignin (Fig. 2A), ~52% of the variation in % soluble condensed tannin (Fig. 2B), and ~43% of the variation in k (Fig. 2C). Percent soluble condensed tannin explained ~72% of the variation in k (Fig. 3A), whereas % lignin explained ~53% of the variation in k (Fig. 3B), and C:N was a very poor predictor of k ($R^2 = 0.01$, $p = 0.67$; Fig. 3C).

Differences in mass loss were detected as early as harvest date 7 when mass loss at each harvest date was compared using a nested ANOVA with genotypes nested within cross types (Fig. 4A–E). These differences remained strong through harvest dates 28 and 56, but were weaker by harvest date 125. Similar patterns among genotypes and mixtures were seen in the 1-mm-mesh litter bags, which excluded macroinvertebrates (data not shown). The effects of genetic variation on mass loss persisted throughout the decomposition process, from the initial leaching stages until the final, highly recalcitrant stages.

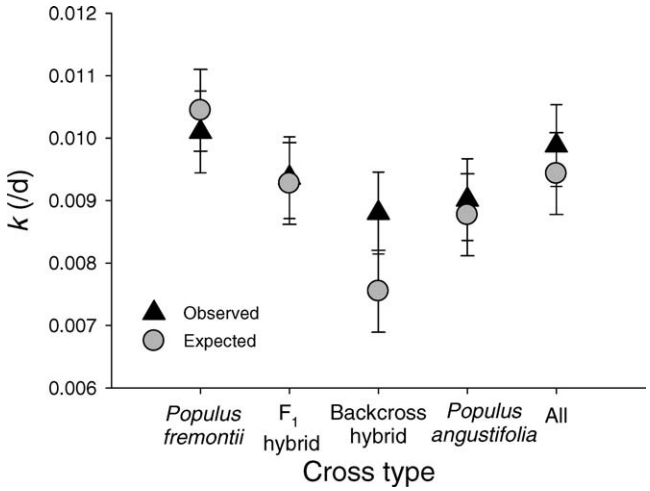

FIG. 1. Decomposition rate constants (k) for leaf-litter mixtures of 5 genotypes per cross type and 1 mixture of all 4 cross types. Expected values are based on mean values of k for each genotype in isolation. Observed and expected ks did not differ, and observed ks did not differ among mixtures ($p > 0.05$).

Differences in decomposition among genotypes and among cross types are ecologically meaningful. A comparison of genotype-specific k to a large data set of k values from many plant families shows that the variation among genotypes of *P. fremontii*, *P. angustifolia*, and their hybrids spans the range of average values of k for the plant families Ericaceae, Fabaceae, Pinaceae, Platanaceae, and Fagaceae (Fig. 5; CJLR, D. G. Fischer, Evergreen State College, and J. A. Schweitzer, University of Tennessee, unpublished data).

Fungal biomass and macroinvertebrate communities

Accumulated fungal biomass on leaf litter varied significantly among genotypes on harvest dates 7 and 28 (Fig. 6A, B). However, this variation was not linearly related to initial % soluble condensed tannin ($R^2 = 0.08$, $F_{1,18} = 1.56$, $p = 0.23$), initial % lignin ($R^2 = 0.05$, $F_{1,18} = 0.86$, $p = 0.37$), k ($R^2 = 0.12$, $F_{1,18} = 2.46$, $p = 0.13$), or proportion *P. fremontii* RFLP markers ($R^2 = 0.03$, $F_{1,18} = 0.61$, $p = 0.44$).

Aquatic macroinvertebrate communities showed weak differences among cottonwood genotypes. We found no siginificant differences in species richness,

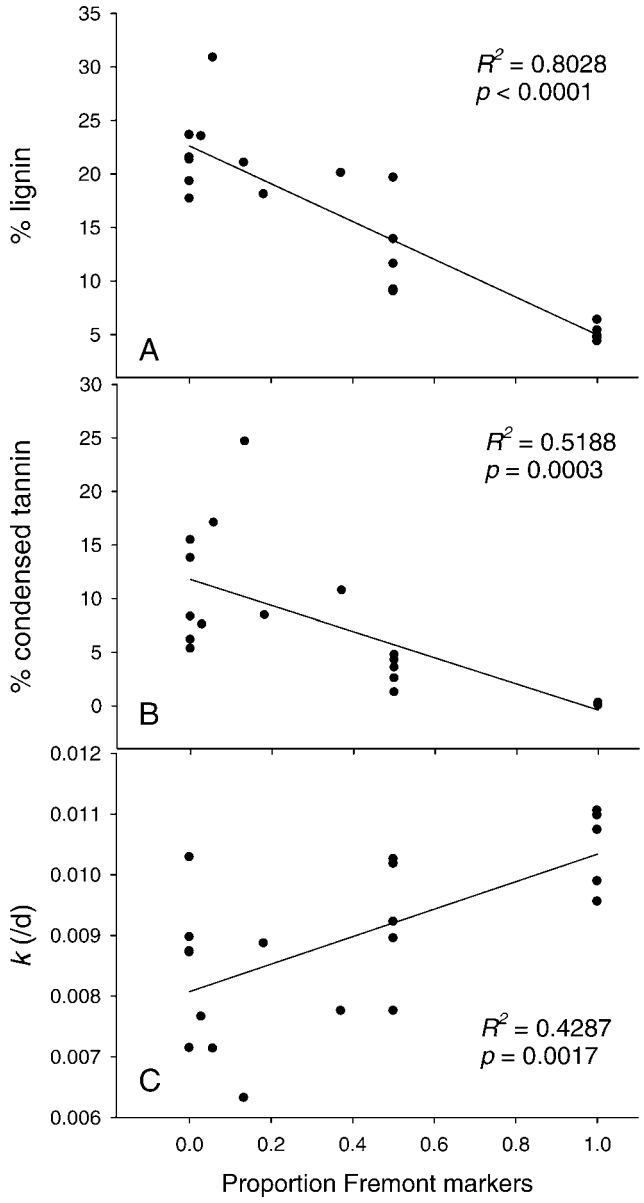

FIG. 2. Linear regressions between the proportion of 35 species-specific *Populus fremontii* restriction-fragment length polymorphism (RFLP) markers (proportion Fremont markers) in the genotype and initial % soluble condensed tannin (A), initial % lignin (B), and daily decomposition rate constants (k) (C) of leaf litter from 20 genotypes of 4 cottonwood cross types (data from 6.4-mm-mesh litter bags only).

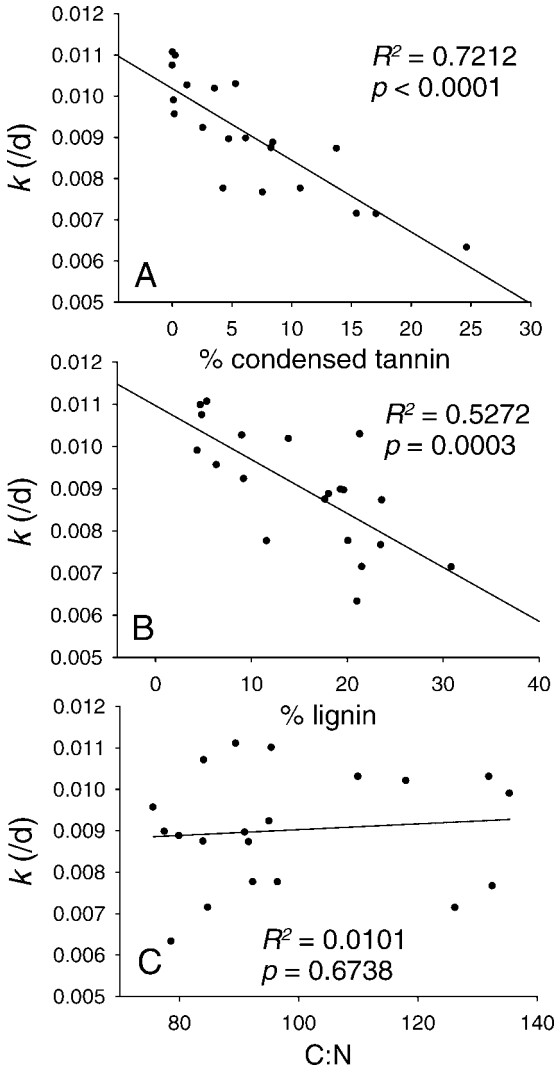

FIG. 3. Linear regressions between daily decomposition rate constants (k) and initial % soluble condensed tannin (A), initial % lignin (B), and initial C : N (C) of leaf litter from 20 genotypes of 4 cottonwood cross types (data from 6.4-mm-mesh litter bags only).

evenness, Shannon's H', or Simpson's D among cross types or genotypes. Moreover, we found no significant differences in community structure (Fig. 7) and no significant Indicator Species ($p > 0.05$) when data from all litter bags were analyzed for differences among cottonwood cross types or genotypes. A Mantel test showed no significant correlation between a matrix of aquatic invertebrate abundances and the matrix of *P. fremontii* RFLP markers for all genotypes ($r = 0.02$, $p = 0.17$).

Discussion

Tree genotype influences litter decomposition

Our study is the first to demonstrate that fine-scale genetic differences in plant leaf litter can affect aquatic ecosystem function. Overall, our results suggest genetic control of decomposition, mediated through tannin and lignin concentrations, where tannin and lignin concentrations increase as the proportion of *P. fremontii* markers decreases, thereby decelerating

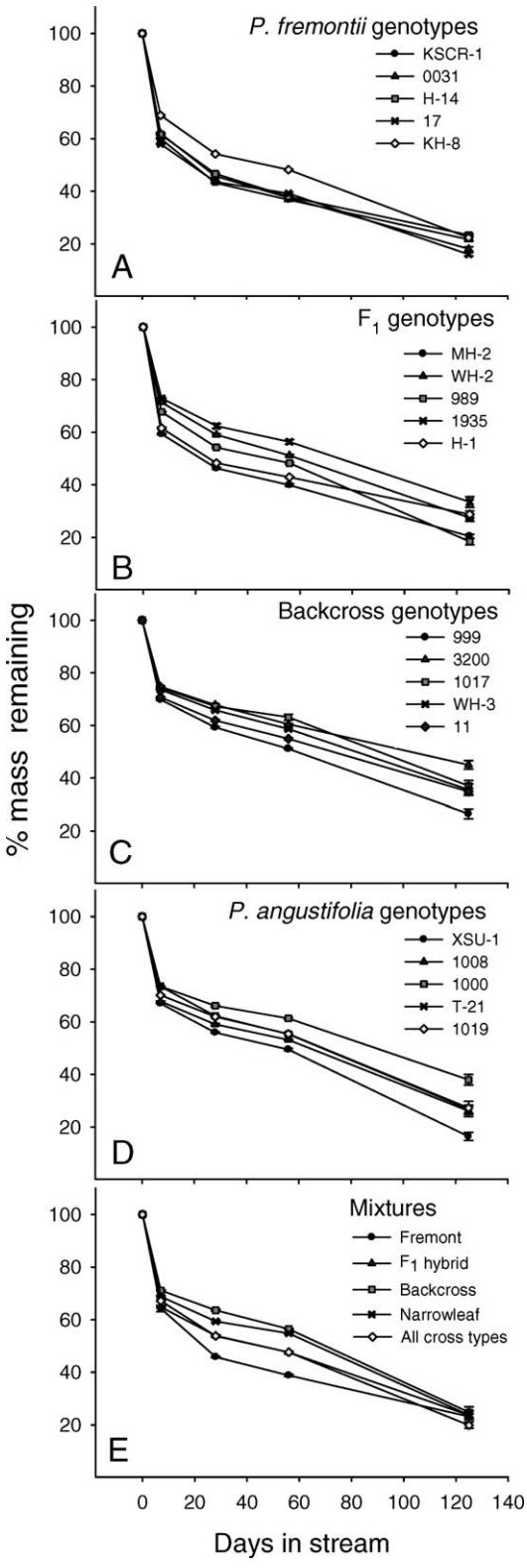

FIG. 4. Mean (±1 SE, $n = 8$) % mass (as ash-free dry mass) remaining on each harvest date of leaf litter from 20 cottonwood genotypes of *Populus fremontii* (A), F_1 hybrid (B), backcross (C), and *Populus angustifolia* (D) cross types, cross type mixtures, and a mixture that included all 4 cross types (E).

decomposition. These patterns persist through time even though soluble condensed tannins are thought to leach rapidly from litter and are not thought to control decomposition directly (Ostrofsky 1997). Several nonexclusive explanations for our results are possible: 1) differences in initial soluble condensed tannins are correlated with persistent differences in bound condensed tannins (SCW and R. L. Lindroth, University of Wisconsin–Madison, unpublished data), 2) the early influence of condensed tannins is amplified by the correlated, but lesser, influence of lignin on decomposition, or 3) differences in initial soluble condensed tannin are correlated with some other phenotypic trait that was not measured during our study. Our results are similar to those of other recent studies in terrestrial systems that have also found phenotypic-, genotypic-, or cross type-level differences in both phytochemistry and leaf-litter decomposition on land (Madritch and Hunter 2002, 2004, Schweitzer et al. 2004, 2005a, b, Madritch et al. 2006).

We saw no evidence for nonadditive decomposition when 5 genotypes of the same species or 1 genotype from each cross type were combined in mixture in 1 litter bag. These results contradict other recent research comparing species-level mixtures (Swan and Palmer 2004, LeRoy and Marks 2006), and a terrestrial study using similar cottonwood genotypes (Schweitzer et al. 2005a). A likely explanation for this observation is the paucity of shredding invertebrates in the Weber River (see *Fungal biomass and macroinvertebrate communities*). Swan and Palmer (2006) argue that the mechanism behind nonadditive decomposition in aquatic systems is probably mediated by consumer preference.

Fungal biomass and macroinvertebrate communities

Aquatic fungi colonized the litter of particular cottonwood genotypes preferentially over other genotypes of the same species or hybrid cross type. Other research has shown that aquatic fungi will differentially colonize leaf litter of different species (Bärlocher and Kendrick 1974, Bärlocher and Graça 2002), but no study has compared fungal colonization among genotypes of the same species or among different cross types within a hybridizing complex (i.e., *P. fremontii*, *P. angustifolia*, and F_1 and backcross hybrids). We were unable to determine the mechanism for this discrimination. Differences in fungal biomass across genotypes might have been caused by a number of factors. For example, aquatic fungi might respond to phenotypic differences in leaf toughness, cuticle thickness, leaf surface roughness, or other unmeasured phenotypic differences.

Other research in the adjacent riparian forest using

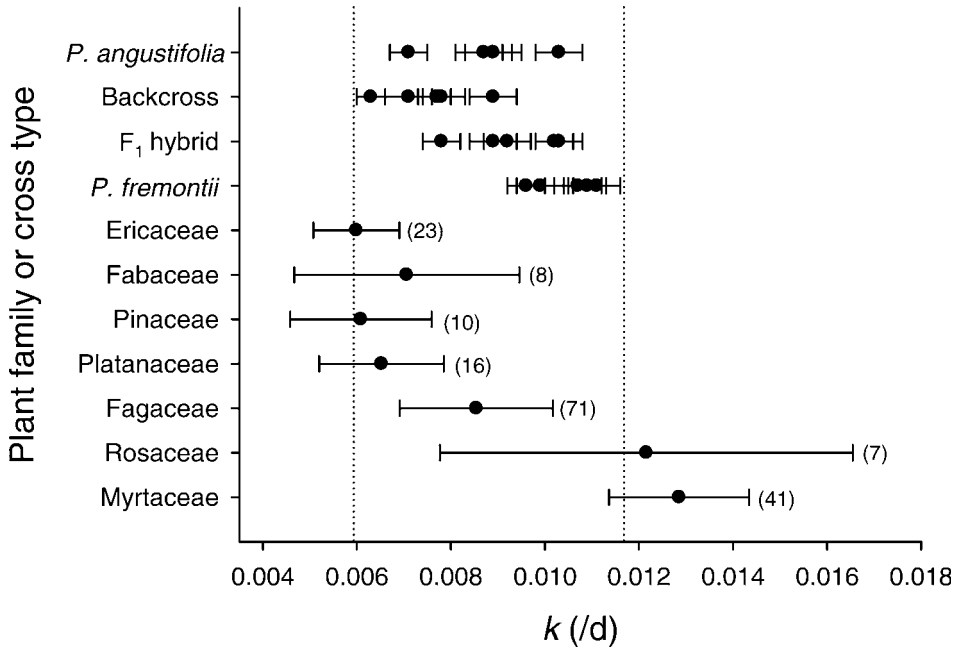

FIG. 5. Mean (±1 SE) values of daily decomposition rate constants (k) from our study of *Populus fremontii*, *Populus angustifolia*, F_1 hybrids, and backcross hybrid genotypes ($n = 8$ per genotype) and from ln(x)-transformed regressions of data collected in >50 studies and 300 observations of k values across plant families in aquatic ecosystems (values in parentheses denote sample size). The vertical dotted lines indicate the range of k values observed in our study.

the same common-garden trees showed that terrestrial arthropods have high fidelity to trees of one parental or hybrid type over others (Wimp et al. 2004, 2005, Bangert et al. 2005). However, we did not observe corresponding fidelity of aquatic macroinvertebrates to litter of one cross type as compared to others in the stream (but see LeRoy et al. 2006). We conducted an earlier cross-type-mixture study in Oak Creek (Arizona) using leaf litter from the same common-garden trees, and we found distinctly different communities on *P. fremontii* as compared to the other 3 cross types (LeRoy et al. 2006). However, we found no evidence that aquatic macroinvertebrate communities in the Weber River were discriminating among cross types or genotypes in our present study. These results contradict numerous studies showing the influence of plant genetics on arthropod communities (Preszler and Boecklen 1994, Johnson and Agrawal 2005, Bangert et al. 2006, Crutsinger et al. 2006).

Macroinvertebrate communities showed no relationship to plant genes in our study for 3 possible reasons. First, plant genes might have limited influence in aquatic ecosystems, and their effects might become more diffuse through multiple trophic levels (genetic diffusion hypothesis; LeRoy et al. 2006). Second, sample sizes might not have been large enough to detect differences given the heterogeneous habitats found in the Weber River. Third, we might have been unable to detect the influence of plant genes at higher trophic levels because of the paucity of specialist organisms making up the shredder guild in the Weber River at this location. In general, macroinvertebrate shredders include some families of stoneflies, tipulids, isopods, amphipods, and caddisflies, but the only true shredders present in the Weber River are the isopod *Asellus* sp., which is not common, and the facultatively shredding leptocerid caddisflies *Nectopsyche* sp. and *Oecetis* sp. (Table 3). In contrast, the shredder community in Oak Creek included the amphipod *Gammarus* sp.; the caddisflies *Phylloicus* sp., *Limnephilus* sp., *Mystacides* sp., *Nectopsyche* sp., and *Oecetis* sp.; the crayfish *Orconectes* sp.; and the lepidopteran *Petrophila* sp. (LeRoy et al. 2006). We would expect leaf shredders to have the highest fidelity to different cross types of leaf litter, and the paucity of these organisms in the Weber River may explain the discrepancy in pattern between the 2 studies.

Litter bags themselves affect decomposition rates by restricting dissolved O_2 and fungal growth (Cummins et al. 1980), and we realize that litter bags could have affected the true leaf-litter decomposition rates, aquatic fungal biomass, and invertebrate assemblages through a variety of physical mechanisms (Boulton and Boon 1991). However, our findings reflect real differences among genotypes because we standardized methods across treatments.

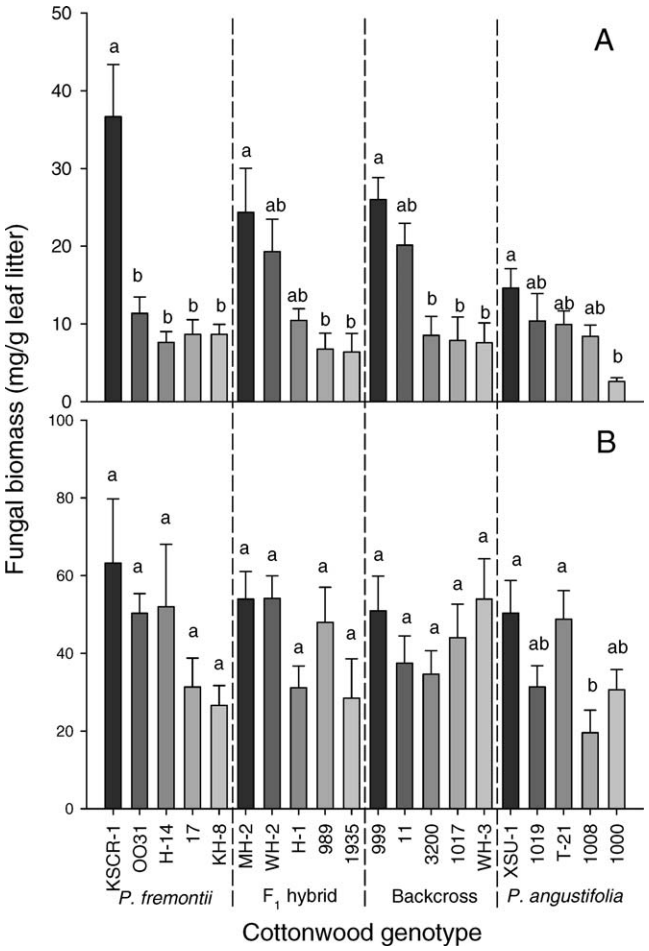

FIG. 6. Mean (±1 SE) aquatic fungal biomass accumulation on leaf litter of 20 cottonwood genotypes (*Populus fremontii*, *Populus angustifolia*, F_1 hybrids, and backcross hybrids) on harvest dates 7 (A) and 28 (B). Bars with the same lower-case letters are not significantly different (Tukey's honestly significant difference, $p > 0.05$). Vertical dashed lines separate genotypes within different cross types.

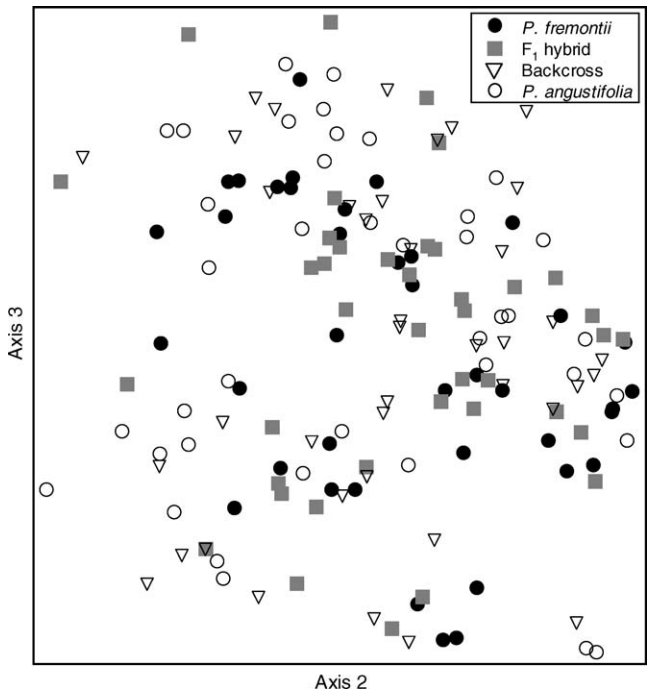

FIG. 7. Nonmetric multidimensional scaling ordination plot of leaf-associated macroinvertebrate community similarity across 4 cottonwood cross types (*Populus fremontii*, *Populus angustifolia*, F_1 hybrids, and backcross hybrid genotypes). No significant grouping was demonstrated (multiresponse permutation procedures, $p > 0.05$).

Implications of a genotype perspective

Overall, we have shown a genetic component to variation in instream decomposition that is associated with significant differences in foliar chemistry. Our experiments also show significant variation in aquatic fungal biomass among genotypes within a cross type and among cross types, but the differences were not associated with a known phytochemical mechanism. Our research suggests that the genetic makeup of riparian species could substantially affect stream function and that changes in genetic diversity and the genes themselves (e.g., transgenic manipulations) could affect stream community composition and ecosystem function.

This work is important to the fields of stream ecology and ecological genetics. Understanding natural genetic variation in these and other species will enable us to contextualize alterations to genetic variation caused by habitat loss, riparian vegetation restoration projects (Winfield and Hughes 2002), and transgenic manipulations of riparian tree species (Wang et al. 1996, Rishi et al. 2001, Meilan et al. 2002). The ecosystem consequences of these various practices are unknown, making it imperative to understand the effects of genetic variation on ecosystem function. A report by the Ecological Society of America (Snow et al. 2005) stresses the importance of understanding the effects of genetically modified organisms on ecosystems, specifically in comparison to baseline conditions. In addition, establishing that genetic variation in *Populus* can influence stream ecosystem function could lead to important collaborations between ecosystem ecologists and researchers who have finished the *Populus* Genome project (Tuskan et al. 2006) to investigate finer-scale genetic differentiation and ecosystem function. For these reasons, our study informs conservation science and might make significant contributions to restoration ecology.

Table 3. Macroinvertebrate taxa found in association with leaf litter throughout the decomposition process in the Weber River, Utah.

Collector-gatherer	Collector-filterer	Scraper	Shredder	Predator
Baetis sp.	*Brachycentrus* sp.	*Asellus* sp.	*Asellus* sp.	Ceratopogonidae
Ceratopogonidae	*Hydropsyche* sp.	*Baetis* sp.	*Nectopsyche* sp.	*Chelifera* sp.
Chironomidae	Simuliidae	*Brachycentrus* sp.	*Oecetis* sp.	*Nectopsyche* sp.
Nematoda		*Fossaria* sp.		*Enallagma* sp.
Oligochaeta		*Helicopsyche* sp.		Hirudinea
Ostracoda		*Hydroptila* sp.		Hydracarina
Seratella sp.		*Potamopyrgus antipodarum*		*Oecetis* sp.
Tricorythodes sp.		*Physella* sp.		Turbellaria
		Valvata sp.		

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