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Genetic Identity of *Populus tremuloides* Litter Influences Decomposition and Nutrient Release in a Mixed Forest Stand

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Abstract

Recent research has shown that genetic variation can directly impact community and ecosystem level processes. *Populus tremuloides* (trembling aspen) is an extremely widespread and genetically diverse tree species important to many North American forest ecosystems. Using leaf litter from five genotypes grown in a common garden under two nutrient treatments, we tracked litter decomposition in a natural aspen stand for 1 year. Here we show that aspen leaf litter decomposes and releases carbon, nitrogen, and sulfur in relation to its genetic identity. In a secondary experiment, we show that the genetic diversity of aspen litter mixtures can influence decomposition, however weakly so. Overall, nutrient treatments influenced leaf litter decomposition the most, followed by genetic identity, and then by genetic diversity (if at all in some cases). In this widespread, genetically diverse, and dominant species, genetic variation within a single species is important to ecosystem functioning. The relatively weak effect of genetic diversity on the processes measured here does not preclude its importance to ecosystem functioning, but does suggest that genetic identity and composition are more important than genetic diversity per se.

Key words: genotype; tannin; intraspecific genetic variation.

Introduction

The influence of genetic variation on the structure and function of communities and ecosystems is an emerging frontier in ecology (Whitham and others 2003). Genetic variation has long been known to influence population level processes, but recent evidence also supports direct genetic effects on community and ecosystem level processes. For instance, the genetic diversity of individual species can affect the loss of species from grassland communities (Booth and Grime 2003) and the genetic identity of two cottonwood species and their hybrids can influence canopy insect communities (Wimp and others 2004; Martinsen and others 2000; McIntyre and Whitham 2003) and beaver feeding preferences (Bailey and others 2004), as well as decomposition and belowground nitrogen cycling (Schweitzer and others 2004). The influence of genetic variation on ecosystem level processes is particularly important in light of the widespread reductions in forest genetic diversity caused by anthropogenic forces (Ledig 1992; Vitousek and others 1997).

Most primary production enters the detrital pathway, and leaf litter represents an important source of carbon and nutrients to soil organisms (Coleman and Crossley 1996; Moore and others 2004). Recent studies have suggested that

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intraspecific genetic variation in leaf litter quality can influence decomposition. Madritch and Hunter (2002) showed that genetically-mediated phenotypic variation in litter chemistries (polyphenolics) resulted in significant variation in litter decomposition and subsequent nutrient cycling in underlying soils. They did not, however, differentiate between genotypic variation and phenotypic variation. Similarly, Treseder and Vitousek (2001) found that genetically distinct populations of *Metrosideros polymorpha* trees exhibited considerable variation in litter nitrogen and lignin content. Although these chemistries are both important to decomposition and nitrogen cycling, actual decomposition was not measured. Thus, despite recent advances, the importance of *genetic* identity and diversity within a *single species* to decomposition and nutrient cycling remains unclear.

Belowground responses to litter diversity treatments are extremely variable and are frequently non-additive (see Gartner and Cardon 2004 for a review). Often it is the species composition that influences belowground processes because species identity is generally more important than species diversity to leaf litter decomposition (Chapman and others 1998; Wardle and others 1997; Nilsson and others 1999). Specific litter qualities may explain non-additive behavior. For instance, Hoorens and others (2002) suggest that individuals with high tannin contents may disproportionately decrease decomposition rates in species mixtures, whereas individuals with high nitrogen contents may increase decomposition rates in a non-additive manner. Although our understanding of species identity and diversity interactions is rudimentary at best, even less is known about the relative importance of identity and diversity for intraspecific genetic variation.

Trembling aspen (*Populus tremuloides*) is the most widely distributed native tree species in North America, and among the most genetically variable plant species known to science (Perala and Alm 1990; Mitton and Grant 1996). This genetic variation, combined with widespread distribution and adaptation to a variety of habitats, produces striking variation in expressed phenotype, including leaf litter chemistry (Lindroth and others 2002). It is possible that phenotypic variation within a species can have extended consequences on ecosystem functioning and community dynamics (Whitham and others 2003). Because extended phenotypes (sensu Dawkins 1982) are likely to be expressed in dominant species (Whitham and others 2003), and because the community genetics approach is warranted particularly for species with large amounts of genetic variation (Chase and Knight 2003), we hypothesize that intraspecific genetic variation in trembling aspen has important consequences for nutrient dynamics during litter decomposition.

Here we build upon previous work (Lindroth and others 2002) addressing genetic variation in litter chemistry to determine: (1) if the genetic identity of aspen influences leaf litter decomposition, and (2) whether the expression of such variation is influenced by soil nutrient availability. Although our primary goal was to assess the importance of genotypic identity, we also explored the ecosystem level effects of genotypic diversity within a single species.

Methods

In the fall of 2002, we collected senesced leaf litter from five *P. tremuloides* genotypes grown under two nutrient conditions in a common garden. Aspen genotypes were originally established via micropropagation techniques (Sellmer and others 1989; Donaldson and Lindroth 2004) and transferred to outside pots (4 L) in the spring of 2001. Trees were transferred in spring 2002 to 40 L pots filled with 60% sand and 40% silt loam from southern Wisconsin. At the time of litter collection, aspen trees ranged from approximately 1 to 2 m tall, with at least 300 leaves each (depending upon genotype and nutrient treatment). Half of the trees were subjected to a high nutrient treatment (Osmocote 18:6:12 NPK 8–9 month slow release fertilizer, 4.5 g/L soil) in May 2001 and 2002. The remaining trees (low nutrient treatment) received no fertilizer. At the time of leaf litter collection, aspen genotypes had completed two summer seasons of growth. Individual trees were loosely wrapped with 1×1 cm mesh and senesced leaves were collected periodically until the end of leaf drop in 2002. The five aspen genotypes were originally collected from southern Wisconsin: Dan1 and Dan2 (Dane County, WI), Sau3 (Sauk County, WI), Wau1 (Waushara County, WI), and PI3 (Pine Island Wildlife Area, WI). All five have been identified as distinct genotypes by microsatellite markers. Of 16 loci evaluated, each genotype contained at least 4, and up to 8, unique alleles (C.T. Cole and R.L. Lindroth, unpublished data).

We tracked decomposition in litterbags over a 1-year period. Our primary objective was to determine whether different aspen genotypes grown under two nutrient regimes decomposed at different rates. Fiberglass litterbags (15×15 cm) were filled with approximately 4 g of senesced litter and placed on a common forest floor (described below). Litterbags had a mesh size of 1 mm^2, which allowed coloni-

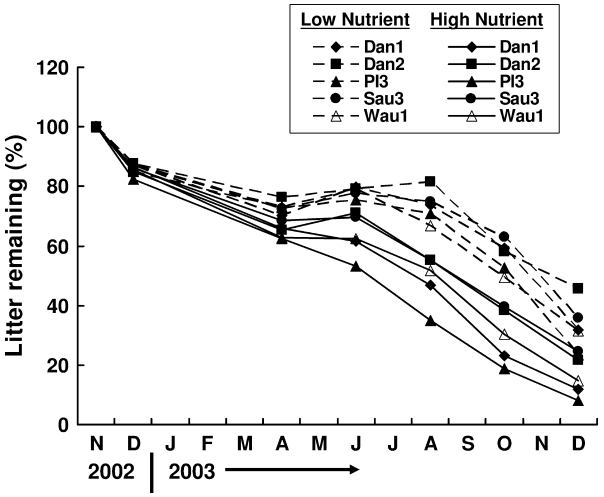

Figure 1. Effects of aspen genotype and soil nutrient availability on litter mass remaining over time. Single-genotype litters lost mass at different rates over time with marked differences within and across nutrient treatments ($P < 0.05$, see Table 1).

zation by microbes, microfauna, and some mesofauna, but excluded macrofauna. For our single-genotype experiment we used 5 genotypes × 2 nutrient regimes × 5 replicates × 6 collections over time (300 litterbags). Each replicate consisted of litter obtained from a unique set of two trees of the same genotype and nutrient treatment (individual trees did not produce sufficient amounts of litter).

As a secondary experiment, we also varied the diversity of aspen genotypes contained in litterbags. In addition to the single-genotype design described above, we created three- and five-genotype mixtures within each nutrient treatment. Our medium diversity treatment consisted of 3 three-genotype mixtures × 2 nutrient regimes × 5 replicates × 6 collections (180 litterbags). Genotype mixtures were novel random mixtures of the five available genotypes: Dan1, PI3, Sau3 (mix 1); Dan1, Sau3, Wau1 (mix 2); and Dan2, PI3, Wau1 (mix 3). Our high diversity, five-genotype litter treatment was simply a combination of all five available genotypes: 1 five-genotype mix × 2 nutrient regimes × 5 replicate × 6 collections (60 litterbags).

Litterbags were randomly deployed in November 2002 over a 50 m × 50 m section of contiguous mixed forest in the University of Wisconsin-Madison Arboretum. Forest cover consisted primarily of *P. tremuloides*, *Quercus rubra*, and *Pinus resinosa*. Litterbags were collected at six dates: December 2002, and April, June, August, October, and December 2003. Bag contents were immediately freeze-dried, then weighed and ground for chemical analysis. Five replicates of each litter treatment were collected at each of the six collection dates, allowing for five independent estimates of decomposition rates (k-values) for each litter treatment. k-values were calculated as $y = e^{-kt}$, where y is the proportion remaining and t time in years. Condensed tannins were quantified with the n-butanol method of Porter and others (1986) using a purified aspen tannin standard (Hagerman and Butler 1989). Lignin fractions were estimated with an Ankom 200 Fiber Analyzer. Carbon, sulfur, and nitrogen concentrations were determined by combustion analysis with a LECO CNS 2000 analyzer.

Statistics

All data were tested to fit the assumptions of normality using a Shapiro–Wilk's W-test, and non-normal data were log transformed. We analyzed data in two complementary fashions using SAS v8 software. We first used repeated measures ANOVA procedures to test for differences over time among single-genotype litter treatments as well as among litter diversity treatments. We then performed simple ANOVAs on nutrient concentrations averaged over time and on decomposition constants (k-values). Simple and stepwise regressions were employed to correlate variation in decomposition rates with variation in litter chemistries.

To test for non-additive effects of mixing litter genotypes, we used ANOVAs to compare the observed k-values of genotype mixtures (those measured in the field) with the averaged k-values of the constituent single genotype litters (the expected response). This is similar to the analysis suggested for decomposition experiments by Loreau (1998) and demonstrated by Wardle and others (1997). Although all statistical analyses were performed on normal or normalized data, data presented in figures are untransformed.

Results

In general, the genetic identity of litter influenced decomposition and nutrient fluxes. We first describe the effects of genotype identity (single-genotype treatments), and then describe the effects of litter genotype mixtures.

Both genotype identity and nutrient availability treatments influenced mass loss over time and decomposition constants (Figures 1, 2, Table 1). As expected, low nutrient litters decomposed lower, losing approximately 60% of litter mass after 1 year compared with approximately 80% loss for high nutrient litters (Figure 1). The amount of decom-

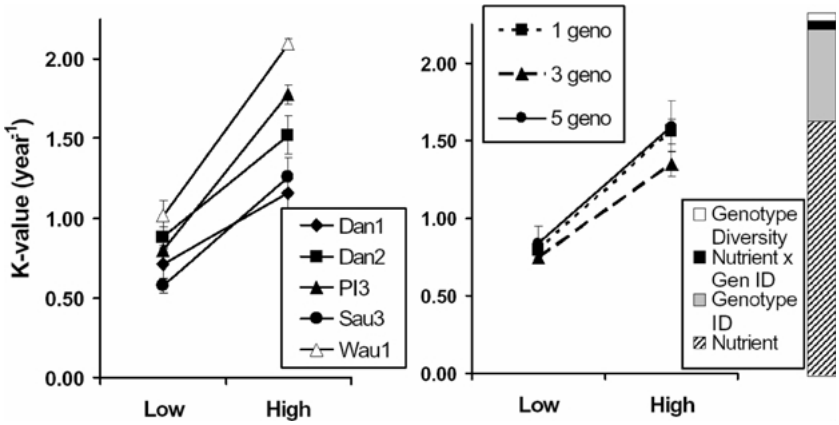

Figure 2. Norm of reaction plots showing the effects of genotype identity and diversity on decomposition rates across two levels of nutrient availability. The *bar to the right* shows the proportion of variation in decomposition rates (*k*-values) explained by treatments, as calculated from ANOVA results. An ANOVA summary for these data is given in Table 2.

Table 1. Repeated Measures ANOVA Results Showing the Effects of Genotype, Nutrient Treatment, and their Interaction on Mass Remaining and Litter Chemistries for Single-genotype Litter Treatments

	D.F.	Mass Remaining	Carbon	Nitrogen	Sulfur	Condensed Tannin	Litter C:N
Genotype	4	17.79	3.16	26.35	15.98	16.08	27.57
		<0.001	*0.026*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Nutrient	1	307.02		1215.0	440.11	93.51	1099.2
		<0.001	n.s.	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Geno*Nutr	4	2.84	4.49	13.21	13.33	2.82	7.60
		0.038	*0.005*	*<0.001*	*<0.001*	*0.038*	*<0.001*
Geno*Time	24	1.91		1.79	5.41	6.51	1.90
		0.014	n.s.	*0.0401*	*<0.001*	*<0.001*	*0.033*
Nutr*Time	6	31.92	5.48	9.16	30.94	6.51	13.17
		<0.001	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Geno*Nutr*Time	24	n.s.	n.s.	n.s.	2.00	n.s.	1.68
					0.013		*0.069*

D.F.—degrees of freedom.
F-values are given with P-values immediately below in italics.
n.s. indicates non-significant relationship ($\alpha = 0.05$).

position among genotypes within nutrient treatments varied markedly (Figure 1). *k*-values also varied widely among and within nutrient treatments, according to genotype identity (Figure 2, Table 2).

Initial litter chemistries important to decomposition varied across genotype and nutrient treatments (Table 3). For instance, initial condensed tannin concentrations varied several fold among genotypes within both nutrient treatments. Litter carbon, nitrogen, sulfur, condensed tannin, and C:N ratio all varied significantly by genotype, nutrient treatment, and their interaction over time (Table 1). Variation in litter C:N (Figure 3), condensed tannin, and lignin content were of particular interest because large genetic variation in these indices is likely to correlate with decomposition and nutrient fluxes (Madritch and Hunter 2002; Schweitzer and others 2004). Although variation in lignin content existed, we observed no treatment effects.

For both low and high nutrient treatments, litter C:N ratio and condensed tannin concentration averaged over time explained 74% of the variation in single-genotype decomposition constants (Table 4). Over both nutrient treatments, decomposition decreased with increasing C:N ratios and condensed tannin concentration (Figure 4). In the high nutrient treatment, variation in litter C:N ratios was more important than tannin concentrations to decomposition rates, as indicated by simple regressions and stepwise regression values (Figure 4, Table 4). Conversely, under low nutrient conditions, variation in condensed tannins was more important to decomposition (Figure 4, Table 4). However, within the low nutrient treatment, we unexpectedly found a significant, albeit weak, positive relationship between decomposition rate and condensed tannin

Table 2. ANOVA Summary of Genotype Identity, Nutrient Availability, and Genotype Diversity Effects on Decomposition Rates and Nutrient Release

	D.F.	*k*-value (y^{-1})	Carbon release (g kg^{-1} y^{-1})	Nitrogen release (g kg^{-1} y^{-1})	Sulfur release (g kg^{-1} y^{-1})
Genotype	4	18.3	5.17	13.01	13.64
		<0.001	*0.002*	*<0.001*	*<0.001*
Nutrient	1	19.1	44.73	314.7	6.97
		<0.001	*<0.001*	*<0.001*	*0.012*
Geno*Nutrient	4	4.39			8.55
		0.005	n.s.	n.s.	*<0.001*
Diversity	2	3.3	4.36		
		0.039	*0.016*	n.s.	n.s.

The effects of genotype identity, nutrient availability, and the interaction of the two factors on decomposition were calculated using single genotype treatments only, whereas the effect of genetic diversity on decomposition rates was calculated using all three diversity treatments.
D.F.—degrees of freedom.
F-values are given with P-values immediately below in italics.
n.s. indicates non-significant relationship ($\alpha = 0.05$).

Table 3. Initial Leaf Litter Chemistry Ranges (% dry weight), Averaged across Genotypes

	Low Nutrient	High Nutrient
Carbon	49.17–52.14	46.80–49.43
Sulfur	0.14–0.26	0.18–0.25
Nitrogen	0.54–0.69	1.13–1.95
Condensed Tannin	3.31–10.57	1.61–8.90
Lignin	8.85–11.89	7.43–8.90

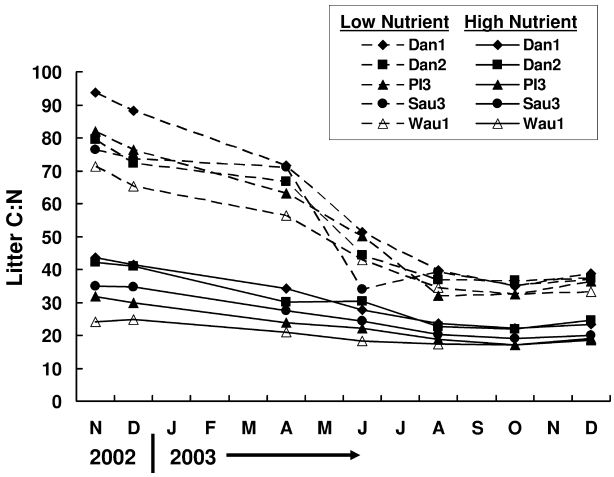

Figure 3. C:N ratios of leaf litter during decomposition. Litter C:N ratios generally decline over time, with significant variation in the rate of decline among single-genotype and nutrient treatments ($P < 0.05$, see Table 1).

content (Figure 4). Decomposition rate was not significantly correlated with condensed tannin content when considered only within the high nutrient treatment (no regression shown).

Leaf litter provides about half of the organic carbon and nitrogen inputs to deciduous forest floors (belowground root turnover providing the other half, Coleman and Crossley 1996). Consequently, the flux of nutrients to and from litter is an important component of terrestrial nutrient cycling. We calculated the total grams of carbon, nitrogen, and sulfur released from aspen leaf litter per kilogram of initial litter during 1 year of decomposition (Figure 5). All nutrient fluxes varied with genotype and nutrient treatments (Table 2). When averaged across both nutrient treatments, genotypes varied considerably in the amount of carbon (360–413 g kg^{-1} y^{-1}) and nitrogen (4.1–10.7 g kg^{-1} y^{-1}) released (Figure 5).

While genotype identity strongly influenced decomposition and nutrient fluxes, we observed few effects of genotype diversity on these processes. However, two effects are worth noting. First, overall decomposition varied significantly with genotype diversity (Figure 2, Table 2), although not in a linear fashion. Our three-genotype mixture decomposed the slowest, whereas the five-genotype mixture decomposed quickly and the single-genotype treatments were intermediate. We also compared the observed *k*-values to *k*-values calculated from the individual genotype litter treatments. Of our three replicates of three-genotype mixtures, the calculated *k*-value was significantly higher than the observed in one case, and marginally so in another (Figure 6). Although the three-genotype mixtures tended to decompose more slowly than expected, there was no difference between the observed and calculated *k*-values for the five-genotype mixture treatment (Figure 6).

Table 4. Stepwise Regression Results of Litter Chemistries and Decomposition Rates for Single Genotype Litter Treatments

	Average C:N	Average Condensed Tannin	Total Model R^2
High and low nutrient combined	0.695	0.048	0.743
	<0.001	*0.005*	*<0.001*
High nutrient alone	0.418	0.097	0.515
	0.005	*0.048*	*<0.001*
Low nutrient alone		0.157	0.157
	n.s.	*0.050*	*0.050*

Lignin content was included in the model statement, but failed to enter any regression at P = 0.15, and was therefore excluded from the table.
R^2 values are reported with P values given directly below in italics.

Discussion

This research demonstrates that leaf litter decomposition of a dominant and genetically diverse tree species is strongly influenced by genetic identity, environment, and gene by environment interactions. Genetic diversity also appears to affect decomposition processes. For the genotypes and soil conditions used in this study, the relative influence of genetic identity, genetic diversity, and nutrient availability on leaf litter decomposition was: nutrient availability > genotype identity > genetic diversity (Figure 2).

Genetic effects can be moderated by the environment (G × E interactions), as demonstrated by several genotype by nutrient interactions in this study. Decomposition rates as well as carbon, nitrogen, sulfur, and condensed tannin concentrations all showed significant G × E interactions with nutrient treatment (Table 1). Although nutrient availability is just one aspect of environmental variation, it is an important determinant of expressed plant phenotype. Previous work has also shown G × E interactions with aspen genotypes and nutrient treatments for relative growth rate, leaf mass, and foliar nitrogen and tannin concentrations (Lindroth and others 2001). G × E interactions are important for maintaining genetic variation in quantitative traits in natural populations because such variation—upon which selection acts—is expressed differently in different environments. The common G × E interactions of aspen genotypes and their environment may, in part, explain the wide genetic variation found in natural *P. tremuloides* populations.

Environmental effects on leaf litter decomposition and nutrient release have been studied for decades as an important aspect of ecosystem ecology. Increased nutrient availability during plant growth is typically thought to increase leaf litter quality, and hence, decomposition rates. Although common in other species, increased nutrient availability does not necessarily increase decomposition rates of aspen litter (Prescott and others 1999; King and others 2001). Here, high nutrient availability significantly increased decomposition and accounted for a large amount of variation in litter decomposition constants (Figure 2, Table 2). Other environmental factors known to influence aspen decomposition may also elicit G × E effects on leaf litter decomposition. For instance, atmospheric CO_2 and O_3 enrichment retard aspen litter decomposition (W.F.J. Parsons and R.L. Lindroth, unpublished), but the interactive effect of atmospheric change and genotype identity remain unknown.

In general, we found few effects of genetic diversity on leaf litter decomposition. Although the intermediate diversity level (three genotypes) did decompose significantly slower than the low and high diversity mixes (single and five genotypes respectively), the effect was not large. When testing for non-additive effects among our mixed litter treatments, the observed decomposition constant (*k*-value) of the three-genotype mixtures was always lower than the expected *k*-value (Figure 6). Although only one of the three-genotype mixture replicates was significantly lower than expected (Figure 6), this general trend may account for the lower decomposition rates of the mid-level diversity treatments shown in Figure 2. Non-additive effects were stronger in our high nutrient treatments (Figure 6). This result agrees with past work which showed that phenotypic diversity was more important to soil respiration under simulated nitrogen deposition (Madritch and Hunter 2003).

Litter species diversity experiments typically yield very mixed results. For instance, litter species diversity can increase (Salamanca and others 1998); decrease (Nilsson and others 1999); or randomly influence (Wardle and others 1997) leaf litter decomposition. Specific species identities

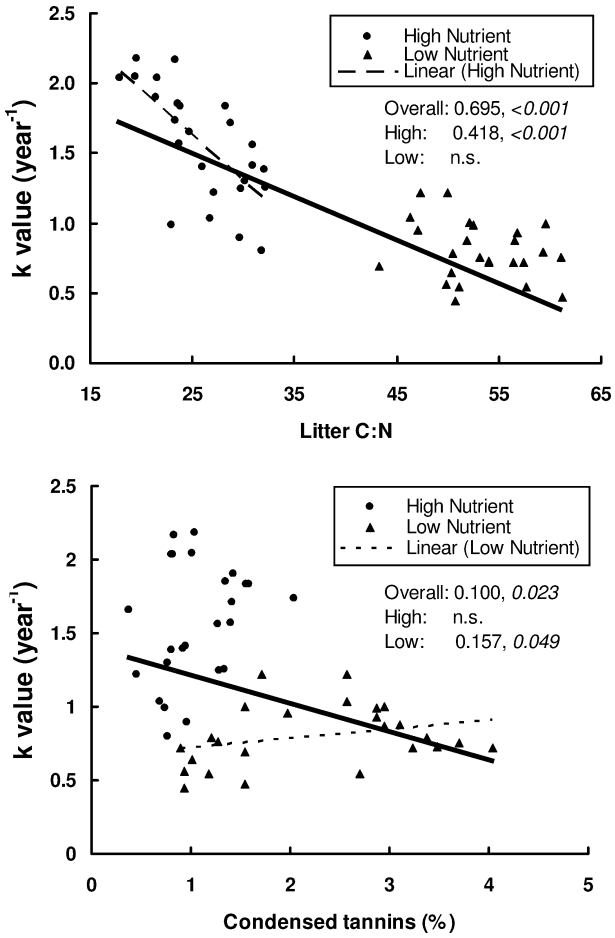

Figure 4. Regressions of litter chemistries and decomposition constants (*k*-values). Litter C:N ratio and condensed tannin concentration explained most of the variation in litter *k*-values. C:N and condensed tannin contents were averaged over time before regression analyses. *Solid regression lines* indicate the relationship across both high and low nutrient treatments. *Dashed and dotted lines* refer to high and low nutrient treatments, respectively. Each *point* represents the *k*-value calculated from six collection dates (six litter bags) for each replicate (five total) of each genotype × nutrient treatment combination. Simple regression results are given below legends for all data shown (R^2, p-value) as well as high and low nutrient treatments analyzed separately.

within mixtures are most likely responsible for variation in decomposition rates among diversity treatments (Chapman and others 1988; Wardle and others 1997; Nilsson and others 1999). Prescott and others (2000) found either no effect, or a slight negative effect, of species diversity on leaf litter decomposition when aspen was present. Gartner and Cardon (2004) reviewed the leaf litter diversity and decomposition literature and concluded that non-additive effects are common and that mixtures rarely decompose according to their single-species constituents. Here we show the potential for *intraspecific* genetic diversity to influence decomposition in a non-additive manner.

Litter nitrogen and polyphenolic (specifically tannin) content have long been known to influence decomposition (Melillo and others 1982; Aber and others 1990; Hättenschwiler and Vitousek 2000). We hypothesized that genetically mediated variation in leaf chemistries would drive variation in decomposition rates. Litter C:N ratios were strongly negatively correlated to decomposition constants, whereas litter condensed tannin concentrations were relatively weakly correlated to decomposition rates (Figure 4). C:N variation was more important to decomposition in the high nutrient treatments, whereas condensed tannin concentration was more important in the low nutrient treatments (Table 4). However, the positive relationship between condensed tannin concentration and litter decomposition constants in the low nutrient treatments (Figure 4) was unexpected. Tannins are typically considered to retard, not enhance, leaf litter decomposition (Hättenschwiler and Vitousek 2000). Schimel and others (1996) showed that low molecular weight phenolics increased respiration, presumably by acting as a carbon substrate, but that high molecular weight tannins inhibited soil respiration. Others, however, have found that soil respiration increases with increasing amounts of tannin (Hernes and Hedges 2004; Kraus and others 2004), presumably enhancing decomposition. Condensed tannins may also correlate with other, stronger, drivers of decomposition that were not measured here.

In addition to other, unknown chemical drivers of decomposition, our chosen litterbag mesh size may have influenced litter decomposition rates. The 1 mm^2 mesh size allowed microbial and mesofauna colonization of litter, but excluded larger macrofauna. Mesh sizes that allow colonization by meso- and macrofauna increase decomposition rates, despite indirectly inhibiting microbial decomposition (Bradford and others 2002). Although our results are limited to evaluation of the microbial and mesofauna influences on decomposition, we feel these relationships would persist in the presence of larger meso- and macrofauna. Schädler and Brandl (2005) demonstrated that allowing macrofauna to colonize litterbags increased the strength of decomposition and litter chemistry correlations. In addition, the nonadditive effects of species mixtures on decomposition increased with macrofauna presence (Schädler and

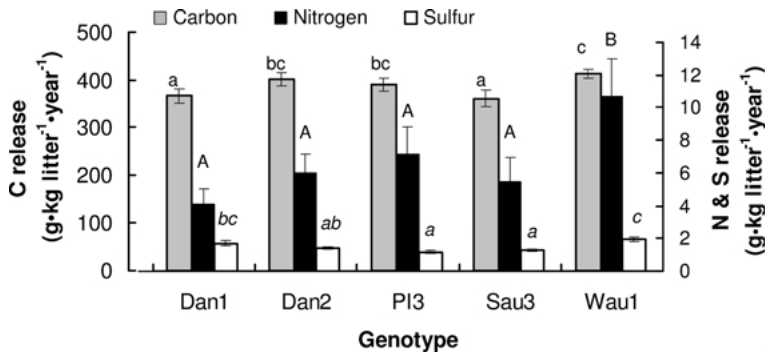

Figure 5. Effect of aspen genotype on the amount of carbon, nitrogen, and sulfur released during leaf litter decomposition. Single-genotype litter treatments displayed significant differences in the amount of carbon, sulfur, and nitrogen lost. Changes in nutrients were calculated as the total amount of nutrient lost per kilogram of initial litter per year of decomposition averaged across both high and low nutrient treatments for each genotype. *Different letters* indicate significant differences ($P < 0.05$) within each nutrient category (*lower case* for carbon, *upper case* for nitrogen, *lower case italics* for sulfur).

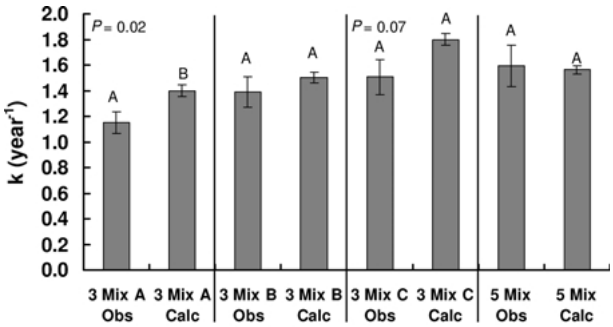

Figure 6. Additive and non-additive effects of aspen genotype diversity on decomposition rates. The observed (obs.) and expected (calc.) *k*-values of the three genotype mixtures differed significantly in one repetition, marginally in another, and not in the third. The observed and expected *k*-values did not differ in the five genotype mixtures. Data shown are from high nutrient treatments only; low fertility treatments showed no differences between observed and expected decomposition rates. *Letters* represent differences ($P < 0.05$) between the observed and expected *k*-values.

Brandl 2005). Thus, the exclusion of macrofauna may have dampened the effects of litter identity and diversity on decomposition rates that we found here.

Genetic variation is often overlooked when considering ecosystem level effects of species composition. Whitham and others (2003) stressed the importance of exploring the extent to which extended phenotypes (sensu Dawkins 1982) exist in natural ecosystems. Chase and Knight (2003), however, warned of being unnecessarily fine-scaled in approach and questioned the usefulness of investigating ''genes to ecosystem function'' relationships. In a widespread, genetically diverse species such as *P. tremuloides*, extended effects of specific genotypes may influence large tracts of land over long periods of time: monogenotypic aspen clones can cover upwards of 40 hectares and may live for thousands of years (Mitton and Grant 1996). Using data reported here in conjunction with previously reported litterfall values for aspen in Wisconsin (1,100 kg aspen litter ha^{-1} y^{-1} for mixed forests with 50% aspen NPP, Pastor and Bockheim 1984), we estimate the range of nutrient losses from leaf litter in mixed aspen stands at 397–455 kg ha^{-1} y^{-1} for carbon, and 4.6–12.2 kg ha^{-1} y^{-1} for nitrogen (values would double for pure aspen stands). Because aspen genotypes can span large distances in time and space, genotypic variation in nutrient release rates such as these are likely to influence community composition.

Strong genotype effects also highlight the importance of G × E interactions. Large scale effects of specific *P. tremuloides* genotypes could be commonplace in expansive, genetically distinct aspen clones found in the western U.S.A. Alternatively, smaller clones common in the eastern U.S.A. may create genetically mediated spatial mosaics of ecosystem functioning. When natural selection acts upon these genotypes, a corresponding chunk of ecosystem is also influenced, whether it be a relatively small piece in a spatial mosaic, or a large piece covering many hectares. The influence of genotype and of G × E interactions likely plays a large role in existing aspen forests. For instance, forest herbivores influence soil processes through a number of mechanisms (Hunter 2001), all of which can be influenced by the host plant genotype.

In addition to G × E interactions, factors (such as population size) that influence genetic variation within a single species may effect variation in ecosystem processes. For instance, forces that reduce intraspecific genetic variation lead to bottlenecks in genetic diversity, and may similarly result in a bottleneck of variation in ecosystem processes. Conversely, forces that increase intraspecific genetic variation could lead to an increase in the variation of associated ecosystem processes (in our case, decomposition and the release of nutrients from leaf litter). Both cases demonstrate the importance of considering genetic effects on ecosystem processes.

We conclude that genetic variation within a single tree species can influence leaf litter decomposition, and therefore potentially affect long-term soil nutrient dynamics. Although environmental variation can overshadow genetic effects on decomposition, the persistence of genetic effects across, and interactions with, nutrient treatments (as shown here) highlights the significance of genetic variation to ecosystem processes. The genetic diversity of our litter treatments also significantly influenced decomposition rates, but overall, genetic identity was much more important to decomposition than was genetic diversity. Although former work has stressed the importance of genetic variation in general to leaf litter decomposition (Madritch and Hunter 2002; Schweitzer and others 2004), this research demonstrates that *genetic* variation *within a single species* can influence decomposition dynamics.

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