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Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem

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Abstract

Plant species can differ in the quantity and quality of leaf litter they produce, and many studies have examined whether plant species diversity affects leaf-litter decomposition and nutrient release. A growing number of studies have indicated that intra-specific variation within plant species can also affect key ecosystem processes. However, the relative importance of intra- versus inter-specific variation for the functioning of ecosystems remains poorly known. Here, we investigate the effects of intra-specific variation in a dominant old-field plant species, tall goldenrod (*Solidago altissima*), and inter-specific variation among goldenrod species on litter quality, decomposition, and nitrogen (N) release. We found that the nutrient concentration of leaf litter varied among genotypes, which translated into ~50% difference in decomposition rates. Variation among other goldenrod species in decomposition rate was more than twice that of genetic variation within *S. altissima*. Furthermore, by manipulating litterbags to contain 1, 3, 6, or 9 genotypes, we found that *S. altissima* genotype identity had much stronger effects than did genotypic diversity on leaf-litter quality, decomposition, and N release. Taken together, these results suggest that the order of ecological importance for controlling leaf-litter decomposition and N release dynamics is plant species identity $\gg$ genotype identity $>$ genotypic diversity.

Zusammenfassung

Pflanzenarten können sich in der Quantität und Qualität der Laubstreu, die sie produzieren, unterscheiden und viele Studien haben untersucht, ob die Diversität der Pflanzenarten die Zersetzung der Laubstreu und die Freisetzung der Nährstoffe beeinflusst. Eine zunehmende Anzahl von Studien wies darauf hin, dass die intraspezifische Variation innerhalb einer Pflanzenart ebenso Schlüsselprozesse in einem Ökosystem beeinflussen kann. Die relative Bedeutung der intraspezischen im Vergleich zur interspezifischen Variation bleibt wenig verstanden. Hier untersuchen wir die Auswirkungen der intraspezifischen Variation einer dominanten Pflanze auf Brachen, der Kanadischen Goldrute (*Solidago altissima*), und die interspezifische Variation zwischen Goldrutenarten auf die Streuqualität, die Zersetzung und die Stickstoff-(N)-Freisetzung. Wir fanden, dass die Nährstoffkonzentration der Laubstreu zwischen den Genotypen variierte, was sich in einem ~50%igen Unterschied in der Zersetzungsrate fortsetzte. Die Variation zwischen den Zersetzungsraten der Goldrutenarten war mehr als doppelt so groß wie die genetische Variation innerhalb von *S. altissima*. Durch die Manipulation von litterbags, die 1, 3, 6, oder 9 Genotypen enthielten, fanden wir

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darüber hinaus, dass die Identität des Genotyps von *S. altissima* eine viel größere Auswirkung auf die Streuqualität, die Zersetzung und die Stickstoff-(N)-Freisetzung hatte als die genotypische Variation. Zusammengefasst lassen diese Ergebnisse vermuten, dass die Reihenfolge in der Bedeutung für die Kontrolle der Laubstreuzersetzung und N-Freisetzungsdynamik wie folgt ist: Identität der Pflanzenart ≫ Identität des Genotyps > Genotypendiversität.

Keywords: Biodiversity; Community genetics; Decomposition; Ecosystem functioning; Genotypic diversity; Nutrient cycling; *Solidago altissima*

Introduction

Inputs of senesced plant leaf litter link above- and below-ground subsystems of terrestrial ecosystems (Coleman & Crossley 1996). Plant species vary considerably in litter production, nutrients, and secondary chemistry, all of which can lead to species-specific differences in rates of litter decomposition and nutrient release (Aber & Melillo 1982; Gartner & Cardon 2004; Wardle, Nilsson, Zackrisson, & Gallet 2003). Moreover, plant species rarely exist in pure monocultures and numerous studies have found that interactions among co-occurring species in litter mixtures often result in decomposition dynamics that differ (either accelerated or decelerated) from the predictions of component plant species decomposing in monocultures (Gartner & Cardon 2004; Hättenschwiler, Tiunov, & Scheu 2005).

Recent research has found that intra-specific variation can influence ecosystem structure and function, including primary productivity (Crutsinger et al. 2006; Zhu et al. 2000), ecosystem stability (Hughes & Stachowicz 2004; Reusch, Ehlers, Hammerli, & Worm 2005), and invasion resistance (Crutsinger, Souza, & Sanders 2008). Like plant species, plant genotypes can vary considerably in the quantity and quality of leaf litter produced, creating genotype-specific differences in rates of decomposition and nutrient release (Madritch & Hunter 2002, 2004; Madritch, Donaldson, & Lindroth 2006; Schweitzer, Bailey, Hart, & Whitham 2005; Silfver, Mikola, Rousi, Roininen, & Oksanen 2007). Furthermore, the number of genotypes (i.e. genotypic diversity) within a plant population could be important for litter dynamics if co-occurring genotypes in litter mixtures interact in ways similar to co-occurring plant species (Schweitzer et al. 2005). Yet, many biodiversity studies confound diversity effects with the identity and/or abundance of a particular genotype/species (Hooper, Chapin III, Ewel, Hector, & Inchausti 2005). In fact, genotype/species identity effects might be more important than diversity effects for litter decomposition and nutrient release (Wardle et al. 2003). Only a handful of studies to date have examined the relative importance of plant genotype identity versus genotypic diversity for litter decay and the relative importance of intra- versus inter-specific variation for leaf-litter decomposition and nutrient release remains unclear (Madritch & Hunter 2003).

In this study, we investigate the relative effects of intra-specific variation of a dominant old-field perennial plant, tall goldenrod (*Solidago altissima*), and inter-specific variation among congener goldenrods, on leaf-litter decomposition and nitrogen (N) release. Specifically, we ask: (1) Does genetic variation alter leaf-litter nutrient concentrations, decomposition, and N release? (2) What are the relative effects of intra- versus inter-specific variation on leaf-litter decomposition and N release? (3) What are the relative effects of genotype identity versus genotypic diversity on litter decomposition and N release?

Materials and methods

Study system

S. altissima is a rhizomatous, out-crossing, perennial species that dominates old fields throughout eastern North America (Semple & Cook 2006). Local populations of *S. altissima* can contain a few to thousands of ramets, and densities of genotypes can vary from 1 to more than 12 genotypes m^{-2}, creating a natural mosaic of single-genotype and mixed-genotype patches of plants (Maddox, Cook, Wimberger, & Gardescu 1989). Clones exhibit considerable inter-clonal genetic variation in many plant traits, including biomass production, leaf length and width, and green leaf N concentration (Abrahamson & Weis 1997; Crutsinger et al. 2006; Wise, Abrahamson, & Landis 2006). In east Tennessee, *S. altissima* makes up, on average, 20% (range = 5–47%) of the aboveground biomass in old-field ecosystems (L. Souza, unpublished data). We also examine inter-specific variation in three other goldenrod species that commonly co-occur with *S. altissima* in old-field ecosystems and have similar natural histories: *S. gigantea* (giant goldenrod), *S. speciosa* (showy goldenrod), and *Euthamia* (formally *Solidago*) *graminifolia* (lance-leaf goldenrod).

Leaf-litter decomposition experiment

In spring 2006, we initiated a litter decomposition experiment using senesced leaf litter from 12 *S. altissima* genotypes and three goldenrod species grown in a common garden on the Oak Ridge National Laboratory National Ecological Research Park (35°58′N 84°17′W). The soil at the study site is classified as a Typic Hapludult and has a silty clay loam texture. Precipitation is generally evenly distributed throughout the year with an annual mean of 1322 mm; the average July maximum temperature is ~31 °C and the average January minimum temperature is ~3 °C.

In April 2005, we planted 21 *S. altissima* genotypes that were collected from local patches growing in old fields adjacent to the common garden. We identified each ramet as a unique genotype by means of amplified fragment length polymorphisms (AFLPs) using four selective primer pairs. When we examined genetic similarity, we found little or no genetic structure among the 21 ramets indicating that all genotypes were approximately equally related (Crutsinger et al. 2006). We established 42 1-m^2 experimental plots with genotypes randomly assigned to each of two replicate plots. For further details on the study site, common garden establishment, or AFLP analyses see Crutsinger et al. (2006). The three goldenrod species were started from seeds and so represented multiple genotypes planted within the common garden (1–2 replicate plots per species). We pooled species litter from their replicate plots to minimize intra-specific variation in the species-level litter treatment.

In autumn of 2005, we randomly chose 12 genotypes from the common garden. We hand collected litter from all replicate plots after plants senesced and it was taken to the laboratory and air dried. To obtain enough litter for each genotype, we pool the litter from replicate plots. This may have increased environmental effects on leaf litter if variation existed among plots within the common garden. However, these effects are likely negligible, as genotypes were grown in a small area of old field (15 m × 20 m) and randomly assigned to plots within the garden. Four grams of air-dried leaf litter was placed into litterbags constructed of polyester mesh for each treatment (see below for treatments). Four grams approximates the amount of goldenrod leaf litter from a 0.0225-m^2 area in natural fields (G. Crutsinger, unpublished data). Mesh sizes were 3 mm on the top of each litterbag and 0.5 mm on the soil surface to allow entry by decomposer fauna while minimizing loss of litter from fragmentation. The litterbags were sealed with an impulse heat sealer (United Plastics Corp., Lima, OH). An initial set of litterbags was transported out to the field and returned to the laboratory to establish loss in transit. We used the litter from this set of litterbags to examine initial nutrient concentration for treatments. This litter was removed from litterbags, oven dried at 65 °C for 3 days and weighed. Samples were ground to a fine powder using a ball mill grinder (Cianflone 2601, Pittsburgh, PA). Subsamples were analyzed for total carbon (C) and nitrogen (N) using a Carlo-Erba Model 2500 CHN analyzer (Milan, Italy). Another set of subsamples were ashed at 550 °C for 6 h. All data are shown on an ash-free oven-dry basis.

Litterbags were placed randomly in an old field adjoining the established common garden and were fixed to the soil surface using stainless steel nails. Bags were collected after 3, 6, 12, and 24 weeks of incubation in the field. At each collection date, decomposition bags were returned to the laboratory in individual paper bags, air dried, and sorted to remove materials, such as soil, plants, or roots that had fallen onto or grown into the bags. Bags were processed for mass loss and nutrient concentration (as described above). We estimated decomposition rate constants (k) for mass loss based on the negative slope from the exponential regression of the natural logarithm of the fractional ash-free dry mass remaining or fractional N remaining at each collection date (Hart, Firestone, & Paul 1992; Schlesinger & Hasey 1981). Decomposition rate constants (k) were estimated for each of the treatments (genotypes, levels of genotypic diversity, and species).

In total, the experiment consisted of 450 litterbags: 180 bags for genotypes (12 genotypes × 3 reps × 5 dates), 45 for species (3 species × 3 replicates × 5 dates), and 225 for genotypic diversity (3 levels of mixed genotypes × 5 random combinations × 3 replicates × 5 dates).

Does genetic variation alter leaf-litter nutrient concentration, decomposition, and N release?

To address whether differences among genotypes of *S. altissima* affect leaf-litter quality and decomposition, we placed 4 g of each of the 12 different *S. altissima* genotypes in monoculture litterbags with 3 replicates per genotype.

What are the relative effects of intra- versus inter-specific variation on decomposition and N release?

To compare the relative importance of intra-specific versus inter-specific variation, we placed 4 g of each goldenrod species (*S. gigantea*, S. *speciose*, and *E. graminifolia*) leaf litter in individual monoculture litterbags. We placed the bags randomly with the *S. altissima* genotypes in the field.

What are the relative effects of genotype identity versus genotypic diversity on litter decomposition and N release?

To compare the relative effects of S. *altissima* genotype identity and genotypic diversity on decomposition and N release, we created treatments of 1, 3, 6, or 9 genotypes. The 1-genotype treatment data were

taken from the 12 different *S. altissima* genotypes in monoculture. Mixtures were created by randomly sampling from the pool of 12 genotypes with the constraint that no two mixtures could have identical composition (5 random mixtures per level of diversity × 3 replicates per random mixture). All mixtures contained of 4 g of litter with equal ratios of litter among treatments (1.33 g of each genotype for the 3-genotype, 0.66 g each for the 6-genotype, and 0.44 g each for the 9-genotype mixture).

Statistical analyses

This experiment consisted of three separate treatments: genotype identity, species identity, and genotypic diversity. We examined whether initial nutrient concentrations (%C, %N, and C:N ratios) of leaf litter differed among treatments using separate univariate ANOVAs. To examine if litter mass loss or N release (% of initial at each collection date) varied among treatments, we used separate full-factorial, fixed effects ANOVAs with treatment and time as main effects. We also used separate one-way ANOVAs within each collection date to examine when treatment effects may have occurred. Proportional mass and N loss data were arcsine square-root transformed to improve normality. Non-transformed mean values are shown in all graphs. To examine whether decomposition rates differed among treatments, we used separate Kruskal–Wallis tests, a non-parametric equivalent to an ANOVA, because these data failed assumptions of normality. We used Pearson correlation coefficients to examine the relationships among initial nutrient concentrations (%N, %C, and C:N ratio) and decomposition rates (k). For these correlations, we pooled genotype and species identity data together.

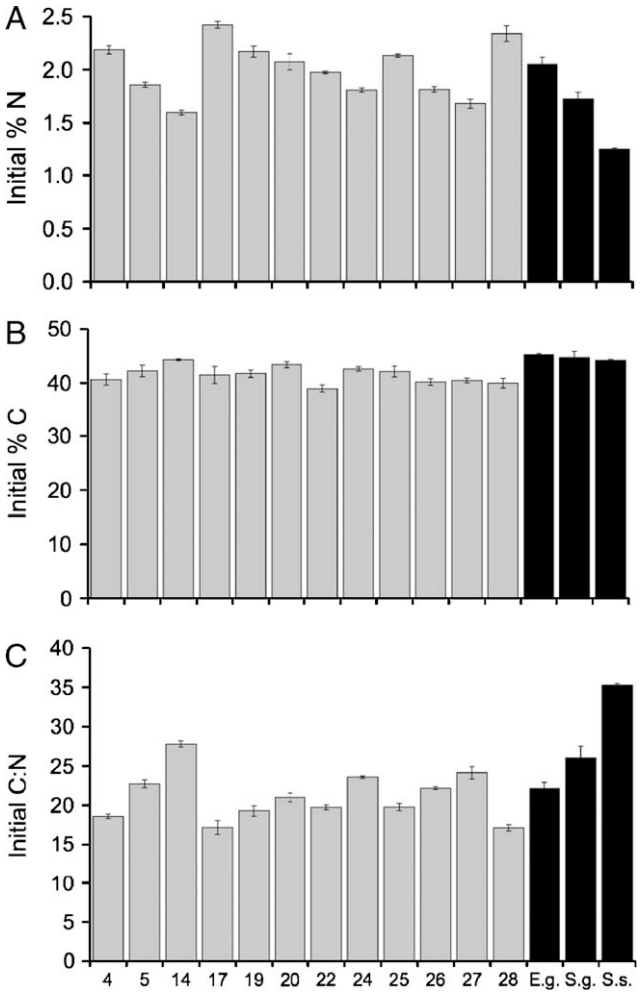

Fig. 1. Mean (±1 SE) initial percent nitrogen (N) (A), carbon (C) (B), and C:N ratio (C) for 12 genotypes of *Solidago altissima* (gray bars), along with three closely related species (black bars), *Solidago gigantea*, *Solidago speciosa*, and *Euthamia* (formally *Solidago*) *graminifolia*.

Results and discussion

Genetic variation altered leaf-litter nutrient concentration, decomposition, and N release

We found that variation among genotypes of a dominant herbaceous plant species, *S. altissima*, affected the quality of leaf litter produced. Among genotypes, initial N concentration varied by 47% ($df = 11, 24$, $F = 38.949$, $P < 0.001$), initial C by 14% ($df = 11, 24$, $F = 3.303$, $P < 0.01$), and C:N ratios by 62% ($df = 11, 24$, $F = 37.071$, $P < 0.001$) (Fig. 1). Variation in initial litter quality translated into variation in mass loss and N release among genotypes. Genotypes differed 34% in percent mass remaining after 24 weeks in the field (Tables 1 and 2, Fig. 2A). There was a 30% difference in %N remaining among genotypes at 12 weeks (Table 1, Fig. 2B), but these differences disappeared by 24 weeks. We found a significant genotype × time interaction for both mass loss and N loss. These interactions resulted from stronger genotypic effects early relative to late in the experiment (Table 1, Fig. 2). The overall rate of decomposition (k) also varied among genotypes; there was a 49% difference in the decomposition rate between the fastest and slowest decomposing genotypes ($df = 11$, $H = 21.0937$, $P = 0.032$; Fig. 3). Decomposition rates (k) were negatively related to initial %N concentration ($r = -0.37$, $P = 0.045$), but not initial %C or C:N.

Similar differences in decomposition and nutrient release among plant genotypes have been observed in other studies (e.g., Madritch et al. 2006; Schweitzer et al. 2005; Silfver et al. 2007). For example, Schweitzer et al. (2005) found a 41% difference among cottonwood genotypes in decomposition rates after 2 years. Madritch et al. (2006) observed a 15% difference in

Table 1. Full model summaries of separate full-factorial, fixed effects ANOVAs using genotype identity, species identity, and genotypic diversity and time as main effects and mass and N loss as response variables.

Effect	df	MS	*F*	*P*-value
Mass loss				
Genotype	11, 96	0.006	4.563	**<0.0001**
Time	3, 96	0.963	655.906	**<0.0001**
Genotype × time	33, 96	0.004	2.891	**<0.0001**
N loss				
Genotype	11, 96	0.039	14.844	**<0.0001**
Time	3, 96	0.596	224.788	**<0.0001**
Genotype × time	33, 96	0.005	1.918	**0.0076**
Mass loss				
Species	2, 24	939.508	45.736	**<0.001**
Time	3, 24	2753.558	134.048	**<0.001**
Species × time	6, 24	52.716	2.566	**0.046**
N loss				
Species	2, 23	1308.578	19.022	**<0.001**
Time	3, 23	2476.467	36.000	**<0.001**
Species × time	6, 23	86.783	1.261	0.3131
Mass loss				
Genotypic diversity	3, 306	0.018	8.448	**<0.0001**
Time	3, 306	1.684	778.675	**<0.0001**
Gen div × time	9, 306	0.002	1.088	0.3758
N loss				
Genotypic diversity	3, 307	0.013	2.721	**0.0447**
Time	3, 307	1.007	205.600	**<0.0001**
Gen div × time	9, 307	0.004	0.764	0.6491

Statistically significant *P*-values shown in bold.

Table 2. ANOVA summary of *S. altissima* genotype identity, goldenrod species, and genotypic diversity effects on litter mass loss and N release at each collection date (for full models see Appendix A).

	3 weeks	6 weeks	12 weeks	24 weeks
Genotype identity				
Mass loss	**4.541****	**2.833***	**4.868*****	**2.444***
	11, 23	11, 24	11, 24	11, 25
N loss	**7.312*****	**7.370*****	**9.267*****	1.911
	11, 23	11, 24	11, 24	11, 25
Species identity				
Mass loss	**21.028****	**9.825***	**10.644****	**15.703*****
	2, 6	2, 6	2, 6	2, 6
N loss	2.94	2.34	**7.32***	**11.673****
	2, 6	2, 6	2, 6	2, 6
Genotypic diversity				
Mass loss	**3.963***	1.240	**5.411****	1.452
	3, 74	3, 77	3, 77	3, 80
N loss	1.159	1.115	0.749	2.1746
	3, 74	3, 77	3, 76	3, 80

F-values are given with degrees of freedom immediately below. Significant values are given in bold type (*$P<0.05$, **$P<0.01$, ***$P<0.001$).

mass loss and 1.6-fold difference in N released among aspen genotypes after 1 year. Silfver et al. (2007) observed a 28% differences in litter mass loss among genotypes of birch after 3 months in incubation. In a study using a congeneric goldenrod species, Güsewell, Jakobs, and Weber (2006) examined differences in litter decomposition rates among 22 populations of *S. gigantea* in the native range (United States) and 20 goldenrod populations from its non-native range Europe all grown in a common garden. They found much greater variation in litter nutrient concentration and rates of litter decomposition among their populations than we found among our genotypes of *S. altissima*. Since we collected genotypes from within a single population of *S. altissima*, it is not surprising that Güsewell, Jakobs, and Weber (2006) found more variation in litter among populations than we did. In fact, the genotypes we collected may represent a conservative estimate of intra-specific variation within *S. altissima* for litter nutrients and decomposition rates, as other studies have found high levels of genetic variation due to polyploid events in local *S. altissima* populations in North America (Halverson, Heard, Nason, & Stireman 2008). We found that the decomposition rate of *S. altissima* genotypes and congener species was related to initial litter quality, in our case weakly negatively related to initial N concentration. The negative relationship is rather unusual. For example, Güsewell, Jakobs, and Weber (2006) found that mass loss of *S. gigantea* litter was weakly negatively correlated with the litter C:N. More research is needed to tease apart the precise chemical mechanisms that mediate *Solidago* leaf-litter decomposition both within and among species. Taken together, these results indicate genetic variation within a local population of *S. altissima* affects litter traits and can subsequently affect litter decomposition and nutrient release in old-field ecosystems.

Plant species effects were greater than genotype effects on decomposition and N release

We found that among-species variation in three other goldenrods (*S. gigantea*, S. *speciosa* and *E. graminifolia*) in litter quality was comparable to within species variation in *S. altissima,* with the exception of initial %C concentration. There was a 64% difference in initial %N concentration ($df = 2,6$, $F = 59.202$, $P<0.001$), and a 60% difference in initial C:N among species ($df = 2,6$, $F = 48.732$, $P<0.001$). *E. graminifolia* maintained the highest N concentration (2.05% of total) and *S. speciosa* was the lowest (1.25% of total). The three

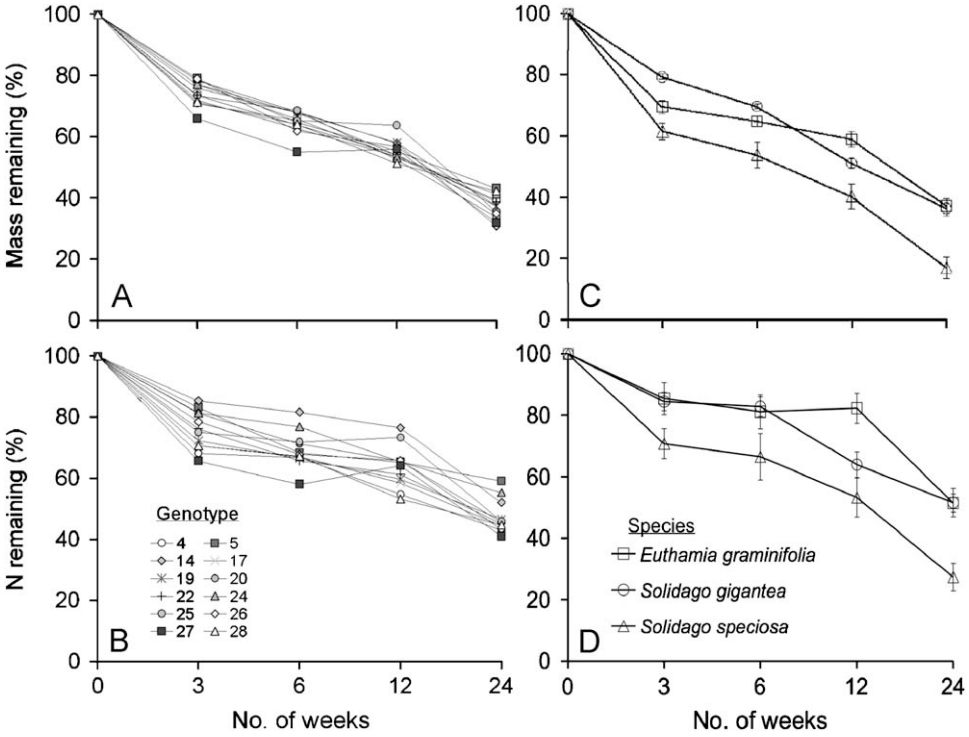

Fig. 2. Mean percent mass remaining (A) and nitrogen (N) remaining (B) in litterbags containing 12 *Solidago altissima* genotypes in monoculture over 24 weeks in the field. Each genotype is represented by a unique shape and a line connects each genotype across collection dates (for a colour version of the graph see Appendix B). For clarity, we do not present SE bars for the different genotypes. In addition, mean (±1 SE) mass remaining (C) and N remaining (D) for three closely related species, *Solidago gigantea*, *Solidago speciosa*, and *Euthamia* (formally *Solidago*) *graminifolia* are shown, represented by different shapes only.

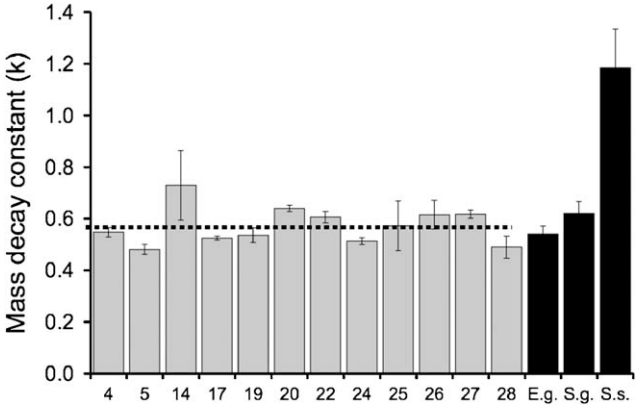

Fig. 3. Mean (±1 SE) decomposition rates (*k*) for 12 genotypes of *Solidago altissima* (gray bars), and three closely related species (black bars), *Solidago gigantea*, *Solidago speciosa*, and *Euthamia graminifolia* over 24 weeks in the field. Dashed line shows mean *k* for *S. altissima* genotypes.

species did not differ in initial %C (df = 2,6, $F = 0.546$, $P = 0.605$) (Fig. 1). As with plant genotypes, variation in initial litter quality translated into variation in mass loss and N loss among species (Tables 1 and 2). There was a 117% difference in percent mass remaining among species by the final collection date, with *E. graminifolia* decomposing the slowest and *S. speciosa* the fastest (37% versus 17% mass remaining at 24 weeks) (Fig. 2C). There was a 47% difference in N remaining among species by the final collection date, with *E. graminifolia* and *S. gigantea* having more N remaining compared to *S. speciosa* (51% versus 27% of initial N remaining at 24 weeks) (Fig. 2D). We found a significant species × time interaction for mass loss, but not for N remaining (Table 1). Plant species differed in overall decomposition rate (*k*), with a 119% difference between the fastest and slowest decomposing species (df = 2, $H = 5.955$, $P = 0.050$) (Fig. 3).

Despite having comparable variation in initial nutrient concentrations, goldenrod species always maintained stronger effects on litter decomposition and nutrient release than did genotypes within *S. altissima.* Species were more than twice as variable in decomposition rate (*k*) and differences in N concentration remaining among species through the final collection date, while differences in initial N concentration among *S. altissima* genotypes were not detectable after 12 weeks in the field. Stronger differences in litter dynamics among species than among genotypes are not surprising, given that differences in traits such as leaf size, shape, and toughness are much more apparent among species than among genotypes (Madritch & Hunter 2003).

Though *S. altissima* genotypes may not be as variable as congener species are, variation among genotypes in decomposition rates should not be overlooked as a key influence on ecosystem processes. *S. altissima* is a dominant species in old fields throughout eastern North America and is the most abundant goldenrod in old fields in east Tennessee. Therefore, genetic variation within *S. altissima* could have a substantially greater influence on old-field nutrient cycling at our study site than other goldenrod species. Our estimates of among-species variation in litter decomposition are conservative as we only examined three other goldenrod species and most of the variation was driven by a single species, *S. speciosa*. Adding more goldenrod species to the study, along with numerous other old-field plant species would clearly increase the amount of inter-specific variation in litter decomposing rates. In sum, our results demonstrate that when litter quantity is kept constant between plant species and genotypes, species effects are much stronger and longer lasting than genotypic effects on decomposition and nutrient release. An experiment that crossed plant genotypes and species in a single manipulation would further clarify the relative importance of the two levels of variation for litter decomposition.

Genotypic diversity had minimal impacts on litter decomposition and N release

While the identity of *S. altissima* genotypes had substantial effects on decomposition and N release, genotypic diversity had weak and idiosyncratic effects. There was no difference in the initial nutrient concentrations (%N, %C, or C:N ratio) of litter in genotype mixtures ($P > 0.25$ for all), and only minimal differences in mass or N remaining over time. Single-genotype monocultures had 5% more mass remaining compared to the 9-genotype mixtures at 3 weeks and 9% more mass remaining at 12 weeks (Tables 1 and 2, Fig. 4A). There was no effect of genotypic diversity at 6 or 24 weeks, nor was there an effect of genotypic diversity on overall decomposition rate (k) ($df = 3$, $H = 5.408$, $P = 0.144$). For leaf litter N remaining, we found a significant overall effect of genotypic diversity, but only marginal effects at 24 weeks (~10% increase in N remaining in 3-genotype mixtures compared to monocultures, $P = 0.09$) (Table 1, Fig. 4B).

To date, only a few studies have manipulated genotypic diversity in leaf litter, and most have observed similarly weak or idiosyncratic effects on litter dynamics (Madritch & Hunter 2002, 2005; Madritch et al. 2006). One exception is Schweitzer et al. (2005), who found that the mean decomposition rate of mixtures containing 5 genotypes was 12% higher and rate of nutrient release was 57% higher than expected based on the individual component genotypes of cottonwood. We did not compare observed decomposition results in mixtures to predictions from component genotypes (i.e. test for non-additive effects), because the overall responses of decomposition or nutrient release to genotypic diversity were minimal.

The magnitudes of the effects of genotypes and genotypic diversity on ecosystem functions differ between the above- and below-ground subsystems. ANPP varied 1.75-fold among genotypes (Crutsinger et al. 2006), but decomposition varied only 0.5-fold among genotypes here. Similarly, ANPP was 36% greater in genotypically diverse plots than their monoculture plots, but here we found only limited effects of genotypic diversity on decomposition rate and N dynamics. In *S. altissima*, positive interactions among genotypes likely

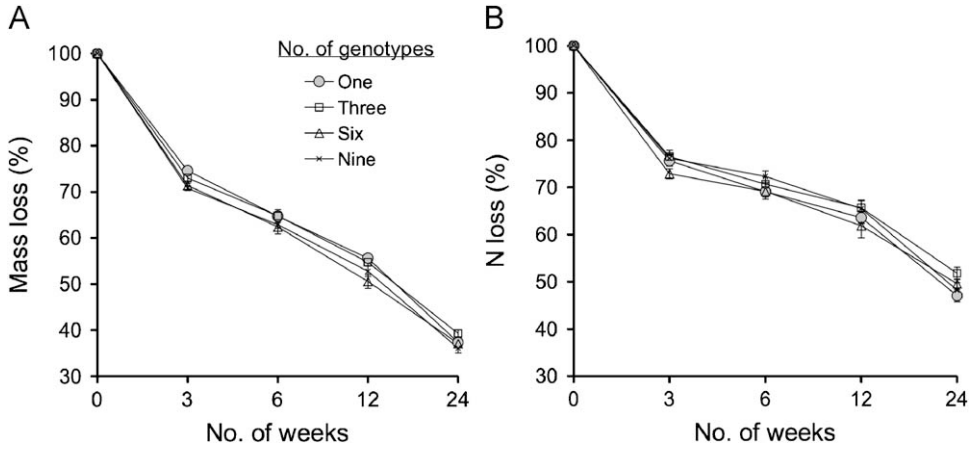

Fig. 4. Mean (±1 SE) percent of starting mass remaining (A) and nitrogen (N) remaining (B) in litterbags containing 1, 3, 6, or 9 genotypes over 24 weeks in the field. Each level of genotypic diversity is represented by a unique shape and a line connects each level across collection dates.

explained increased biomass production in genotypically diverse plots (Crutsinger et al. 2006). While senesced leaf litter in mixtures can also positively interact to affect decomposition (Gartner & Cardon 2004; Hättenschwiler, Tiunov, & Scheu 2005), such interactions did not appear to have measurable effects on leaf-litter decomposition in our experiment. One caveat of our study is that we examined variation in litter C:N ratios among our different treatments, but there are numerous other traits (e.g. phosphorus, lignin, secondary defenses, etc.) that likely vary among goldenrod genotypes and species. Further chemical analyses might reveal the precise traits that contribute to litter dynamics in this ecosystem, but these analyses were beyond the main goals of this study, which were to examine within- and among-species variation in overall litter decomposition and N dynamics. Another caveat is that our leaf-litter mixtures started with the same amount of initial material in each litterbag. Increasing genotypic diversity can lead to higher aboveground net primary productivity (ANPP) in patches of *S. altissima* (Crutsinger et al. 2006). Therefore, plant genotypic diversity may influence decomposition and nutrient dynamics via the amount of litter being produced.

Conclusions

Recent studies have illustrated the importance of intra-specific diversity for ecosystem functioning (Crutsinger et al. 2006; Hughes & Stachowicz 2004; Reusch et al. 2005; Whitham, Young, Martinsen, Gehring, Schweitzer, et al. 2003; Whitham, Bailey, Schweitzer, Shuster, Bangert et al. 2006), and our study contributes to the ongoing debate about the extent to which plant diversity is related to ecosystem function. Like many biodiversity studies at the species level (Hooper, Chapin III, Ewel, Hector, & Inchausti 2005), we observed that plant genotype identity had larger effects on leaf-litter decomposition rates and N dynamics than did genotypic diversity. Furthermore, variation among several closely related goldenrod species yielded much stronger effects on leaf-litter decomposition rates and N dynamics than did variation among genotypes within a species. Together, these results suggest that the order of ecological importance for influencing litter dynamics is *plant species identity* $\gg$ *genotype identity* $>$ *genotypic diversity*.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2008.10.011.

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