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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Disparate effects of plant genotypic diversity on foliage and litter arthropod communities

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Abstract Intraspecific diversity can influence the structure of associated communities, though whether litter-based and foliage-based arthropod communities respond to intraspecific diversity in similar ways remains unclear. In this study, we compared the effects of host-plant genotype and genotypic diversity of the perennial plant, *Solidago altissima,* on the arthropod community associated with living plant tissue (foliage-based community) and microarthropods associated with leaf litter (litter-based community). We found that variation among host-plant genotypes had strong effects on the diversity and composition of foliage-based arthropods, but only weak effects on litter-based microarthropods. Furthermore, host-plant genotypic diversity was positively related to the abundance and diversity of foliage-based arthropods, and within the herbivore and predator trophic levels. In contrast, there were minimal effects of plant genotypic diversity on litter-based microarthropods in any trophic level. Our study illustrates that incorporating communities associated with living foliage and senesced litter into studies of community genetics can lead to very different conclusions about the importance of intraspecific diversity than when only foliage-based community responses are considered in isolation.

Keywords Community genetics · Herbivores · Leaf litter · Microarthropods · *Solidago altissima*

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Introduction

The diversity of primary producers has been positively linked to the diversity of associated animals through the provision of different types of food and habitat resources (Hutchinson 1959; Southwood et al. 1979). For example, it is well established that plant species diversity positively affects the diversity of aboveground arthropods through increased primary production and the presence of preferred host plants (Siemann et al. 1998; Haddad et al. 2001). Yet, most plant biomass is not consumed by herbivores and returns to the environment as litter resources (Cyr and Pace 1993; Hairston and Hairston 1993). Litter is an important interface between plants and the soil and supports a diverse detrital community (Moore et al. 2004). While a few studies have shown that plant species diversity can positively influence the diversity of litter animals by determining the quality, amount, and structural complexity of leaf litter inputs (Hansen 2000; Armbrecht et al. 2004), few general conclusions have been made. By examining foliage- and litter-based communities simultaneously, we can enhance our understanding of how diversity at lower trophic levels

affects diversity at higher trophic levels and whether the responses of two community types are coupled (De Deyn and Van der Putten 2005; Wardle 2006).

Like diversity among species, intraspecific diversity is increasingly recognized as having an important influence on the structure of associated communities and the function of ecosystems (Whitham et al. 2003, 2006). For example, foliage-based arthropods have been shown to respond to genetically variable host-plant traits, such as plant biomass, leaf nutrients, and leaf secondary chemistry, resulting in unique suites of species on different host-plant genotypes (Maddox and Root 1987; Johnson and Agrawal 2005; Wimp et al. 2005; Crutsinger et al. 2006). Consequently, as the number of genotypes (i.e., genotypic diversity) within a host-plant patch increases, so does the number of arthropod species (Wimp et al. 2005; Johnson et al. 2006; Crutsinger et al. 2006, 2008). Different plant genotypes can also vary considerably in the quantity and quality of litter they produce, resulting in genotype specific rates of decomposition and nutrient release (Madritch and Hunter 2002; Schweitzer et al. 2005; Silfver et al. 2007). However, little is known about the responses of litter-based communities to intraspecific diversity (Madritch and Hunter 2005; Schweitzer et al. 2007), and no study to date has asked whether there are congruent responses of the foliage- and litter-based arthropods to plant genotypic diversity.

In this study, we examine the arthropod communities associated with living plant tissue (hereafter the "foliage-based community") of tall goldenrod (*Solidago altissima*) along with microarthropods associated with *S. altissima* leaf litter (hereafter the "litter-based community"). Microarthropods are important members of the litter-based community in many ecosystems because they often feed on the microflora that are directly responsible for litter breakdown (Maraun and Scheu 2000). While feeding, microarthropods fragment leaf litter, thereby creating a new surface area for microbial or fungal colonization and altering litter decomposition and nutrient mineralization rates (Hansen 1999; Heneghan et al. 1999; Gonzalez and Seastedt 2001). Previous results from this study system revealed substantial variation in foliage-based arthropod community composition among genotypes (Maddox and Root 1987; Crutsinger et al. 2006) and positive, non-additive responses of arthropod species richness to *S. altissima* genotypic diversity during the first year of a common garden experiment (Crutsinger et al. 2006, 2008). We also found that the quality of leaf litter varied among *S. altissima* genotypes: C:N ratios varied by up to 62%, resulting in ~50% difference among genotypes in decomposition rate after 24 weeks in the field. More than 60% of the original N and 50% of the original mass was lost by the end of the experiment (Crutsinger et al., in review). These differences in litter quality suggest that litter-based microarthropod communities should show strong responses to intraspecific variation in *S. altissima.* Here, we examine the effects of *S. altissima* genotype identity and genotypic diversity on the diversity and trophic structure of foliage-based and litter-based arthropods. Foliage-based arthropod responses are from the second year of a common garden experiment, with the results from the first year presented elsewhere (Crutsinger et al. 2006, 2008). In addition, this paper focuses explicitly on comparing the responses of the foliage-based and litter-based communities, whereas previous work in this system has focused entirely on the foliage-based community. Because previous work in this system indicated that substantial variation exists among *S. altissima* genotypes in the characteristics of foliage and senesced leaf litter, we predicted that: (1) species diversity and composition of the two community types will vary among plant genotypes; (2) foliage- and litter-based arthropod diversity will be correlated with one another if they are responding to intraspecific variation in a similar manner (i.e., cueing in on the same genetically variable host-plant traits); and (3) if both community types vary among plant genotypes, then both foliage- and litter-based diversity will increase with the number of plant genotypes in a patch.

Materials and methods

Study system

Solidago altissima is a dominant and well-studied perennial plant species found throughout eastern North America (Semple and Cook 2006) and is host to a diverse foliage-based arthropod community (Root 1996). Local populations of *S. altissima* vary greatly in size from just a few to thousands of ramets, and genotypic diversity within natural patches can range from 1 to more than 12 genotypes m^{-2} (Maddox et al. 1989). Clones exhibit considerable interclonal genetic variation in many plant traits that could have substantial implications for both the foliage- and litter-based communities, including aboveground biomass production and green leaf and litter nutrient content (Maddox and Root 1987; Abrahamson and Weis 1997; Crutsinger et al. 2006, 2008). In east Tennessee, *S. altissima* makes up, on average, 20% (range = 5–47%) of the aboveground biomass in old-field plant communities (L. Souza, unpublished data).

This research was conducted from 2005 to 2006 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory National Environmental Research Park near Oak Ridge, Tennessee (35°58′N, 84°12′W). The study area is made up of at least 21 separate old fields that contain a variety of plant species that are common in the southeastern United States. Dominant species at the study site include

S. altissima, Verbesina occidentalis, *Verbesina virginica*, and *Rubus* spp.; sub-dominants include about 60 other herbaceous and woody species (L. Souza, unpublished data).

Intraspecific plant diversity and foliage-based communities

In May 2005, we manipulated plot-level genotypic diversity (the number of genotypes per plot) of *S. altissima*. We collected 21 *S. altissima* ramets from local *S. altissima* patches growing in fields surrounding the study site, and identified each ramet as a unique genotype by means of amplified fragment length polymorphisms (AFLPs). All 21 genotypes were approximately equally related (Crutsinger et al. 2006). We propagated clones of each genotype from rhizome cuttings in a common greenhouse environment for 6 weeks prior to planting in the field in 2005. We established sixty-three 1-m^2 experimental plots spaced 1 m apart in a 15-m × 20-m grid, with each plot randomly assigned to contain 12 individuals and 1, 3, 6, or 12 genotypes. The one-genotype treatment consisted of all 21 genotypes planted individually in two replicate monoculture plots. Genotype mixtures (seven replicates each) were created by randomly sampling from the pool of 21 genotypes with the constraint that no two plots could have the same composition. The treatments were comparable to natural levels of genotypic diversity (Maddox et al. 1989). All treatments were randomly placed within the common garden, and using a small field area ensured that all plots were equally susceptible to colonization by the local arthropod species pool. Each experimental plot was lined with 12-ml heavy plastic 30 cm deep to prevent rhizomes from spreading into neighboring plots between years. A 3-m-tall fence made of 2.54-cm poultry wire encircled the entire common garden to exclude deer. For further details on the study site, common garden establishment, or AFLP analyses see Crutsinger et al. (2006).

In July 2006 (second year of the study), we used a combination of techniques to sample the foliage-based arthropod community. First, we visually surveyed each plot for all sessile arthropod species, including galls, spittlebugs, aphids, and leaf miners. Patches were then vacuum-sampled for 5 min, followed by 15 person-min of hand collection for larger arthropods. Vacuum and hand-collected samples were taken back to the laboratory and identified to species or morphospecies, counted, and assigned to trophic level based on feeding morphology, observations in the field (Crutsinger et al. 2006, 2008) and the literature (Fontes et al. 1994). We compared these results to arthropod responses in the first year of the study (July of 2005), where we visually surveyed every single ramet in the common garden (Crutsinger et al. 2006, 2008). Both methods yielded similar numbers of arthropod species (94 species and 8,617 individuals in July 2005 versus 104 species and 13,224 individuals in 2006). Species accumulation curves based on Chao1 richness estimator (Chao 1984) plateaued in both years (Supplemental 1), indicating that the communities were adequately sampled and are comparable. We also estimated aboveground net primary productivity (ANPP) in each plot to ask whether ANPP was associated with the responses of arthropods to the treatments. In August 2006, we harvested aboveground biomass from each plot, which was oven-dried at 60°C and weighed.

We used two separate multivariate ANOVAs to examine the effects of host-plant genotype or genotypic diversity on foliage-based total, herbivore, and predator richness and abundance together. We followed these analyses with individual one-way ANOVAs with genotype identity or the number of genotypes in a plot (fixed factor) as the main effects in the models for each variable separately. We used a separate analysis of similarity (ANOSIM) test based on the Bray-Curtis similarity index (Bray and Curtis 1957) to examine if overall foliage-based community composition, as well as herbivore and predator composition, shifted between survey years or varied among *S. altissima* genotypes in 2006. ANOSIM is analogous to an ANOVA on community similarity values. The generated *R*-statistic is a relative measure of separation of defined groups. A value of 0 indicates there is complete overlap in the community composition between groups, while a value of 1 indicates that there is no overlap (Clarke and Gorley 2001). We present between-year differences graphically using non-metric multidimensional scaling. ANOSIM and ordination procedures were run using Primer statistical package (version 6; 21 Primer-E, Plymouth Marine Laboratory, Plymouth, UK). We used separate one-way ANOVAs to examine whether *S. altissima* genotype and genotypic diversity affected ANPP in 2006. For all analyses, variables were log-transformed prior to analysis as necessary to improve normality and homogeneity of variance.

Intraspecific plant diversity and litter-based communities

In autumn of 2005, we collected senesced leaf litter from 12 *S. altissima* genotypes from the common garden (see description above). Litter was air dried, homogenized between replicate plots of each genotype, and put into decomposition bags (15 × 15 cm) constructed of polyester mesh. Mesh sizes were 3 mm on the top of each litterbag and 0.5 mm on the soil surface to allow microarthropods entry, but minimize loss of litter from fragmentation. Bags were sealed on three edges using an impulse heat sealer (United Plastics, Lima, Ohio), filled with 4 g of air-dried litter, and sealed on the fourth edge. Four grams represents the natural input of leaf litter produced in a 0.0225-m^2 area in the field (G. M. Crutsinger, unpublished data).

In spring 2006, we created mixtures of one, three, six, or nine genotypes in litterbags. The one-genotype treatment

consisted of 12 different *S. altissima* genotypes in monoculture with three replicates each. Mixtures were created by randomly sampling from the pool of 12 genotypes with the constraint that no two mixtures could have an identical composition (5 random mixtures per level of diversity × 3 replicates per random mixture). All mixtures contained equal ratios of litter among treatments (1.33 g of each genotype for the three-genotype, 0.66 g each for the six-genotype, and 0.44 g each for the nine-genotype mixture). Litterbags were randomized among treatments and placed 10 cm apart in a 10-m × 20-m area of an old field immediately adjacent to the established common garden. We did not place litterbags in the experimental plots because we were interested in microarthropod responses to the litter itself, rather than potential plot-level differences among plant genotypes in factors such as soil nutrients or microclimate. Treatments were randomized in their location and litterbags were fixed to the soil surface using stainless steel nails. We collected bags after 3, 6, 12, and 24 weeks in the field. An initial set of litterbags was transported out to the field and returned to the laboratory to establish litter lost in transit. In total, the experiment consisted of 405 litterbags.

At each collection date, we put litterbags inside individual paper bags and immediately returned them to the lab. We extracted litter microarthropods from each litterbag for 72 h using modified Berlese-Tullgren funnels (Merchant and Crossley 1970) made from 25-cm-diameter plastic funnels with 0.5-cm-diameter hardware cloth in the bottom on which litterbags were placed. A 25-W light bulb was hung 10 cm above the litterbags and microarthropods were collected in plastic cups filled with 70% ethanol. Microarthropods were counted, assigned individually to a trophic level, and identified to species or morphospecies. In total, we extracted 10,730 individuals of ~140 morphospecies from 14 orders.

To examine the effects of leaf litter genotype and genotypic diversity on total litter-based richness and abundance, we used separate repeated-measures ANOVAs with either genotype identity or genotypic diversity as main effects and total, predator, herbivore, and detritivore richness and abundance as response variables, as well as collembolan and mite richness and abundance. For significant repeated-measures analyses, we followed up with separate univariate ANOVAs for each response variable within each collection date to determine when genotype or genotypic diversity effects occurred. We did not use Bonferroni corrections for any of the analyses because this can inflate the probability of committing type II errors (Gotelli and Ellison 2004). We examined whether litter-based community composition varied among plant genotypes using separate ANOSIMs based on the Bray-Curtis similarity index for each collection date. We correlated the litter-based community with mass loss and C and N content in the litter [see Crutsinger et al. (in review) for the effects of genotypic diversity on litter decomposition and nutrient release]. Lastly, we asked whether diversity within foliage-based communities correlated with that of litter-based communities. To do this, we correlated foliage-based richness and abundance with litter-based richness and abundance associated with the 12 genotypes used in both experiments.

Results

Intraspecific diversity and foliage-based communities

There was a shift in composition of the foliage-based community between 2005 and 2006 (global $R = 0.975$, $P = 0.001$). Herbivore composition (global $R = 0.971$, $P = 0.001$; Fig. 1a) and predator composition also differed between years (global $R = 0.483$, $P = 0.01$; Fig. 1b). Shifts in composition might have been caused by new host-plant ramet production within the plots. At the initiation of the experiment, there were 12 ramets planted into each plot but there were, on average, ~123 (range 63–166) ramets per plot the following year.

In 2006, S. *altissima* genotype identity had strong impacts on total foliage-based arthropod richness and abundance. We found the overall model including all variables to be significant (Wilks' $\lambda = 0.0017$, $P = 0.004$). Total richness varied by approximately twofold (range: 20–38 species) and abundance by threefold (range 97–304 individuals) among genotypes (Table 1). Genotype effects occurred across trophic levels: herbivore richness varied by 50% (Fig. 2a), herbivore abundance by 2.9-fold (Fig. 2b), predator richness by 4.6-fold (Fig. 2c), and predator abundance by ninefold (Fig. 2d) among genotypes. Overall community composition (global $R = 0.435$, $P = 0.001$, as well as herbivore (global $R = 0.44$, $P = 0.01$) and predator composition (global $R = 0.227$, $P = 0.013$) also varied among *S. altissima* genotypes.

In 2006, host-plant genotypic diversity was positively related to total foliage-based arthropod richness and abundance. We found the overall model including all variables to be significant (Wilks' $\lambda = 0.543$, $P = 0.01$). Total richness was 22% higher (Fig. 4) and abundance was 34% higher in genotypically diverse plots relative to monoculture plots, though diversity effects saturated quickly at approximately three genotypes. Similar to genotype identity effects, genotypic diversity effects occurred across trophic levels. Herbivore richness (Fig. 5a) was 16% higher and abundance (Fig. 5b) was 34% higher in genotypically diverse plots. Predator richness (Fig. 5c) was 36% higher in genotypically diverse plots, but predator abundance (Fig. 5d) showed no significant response (Table 1).

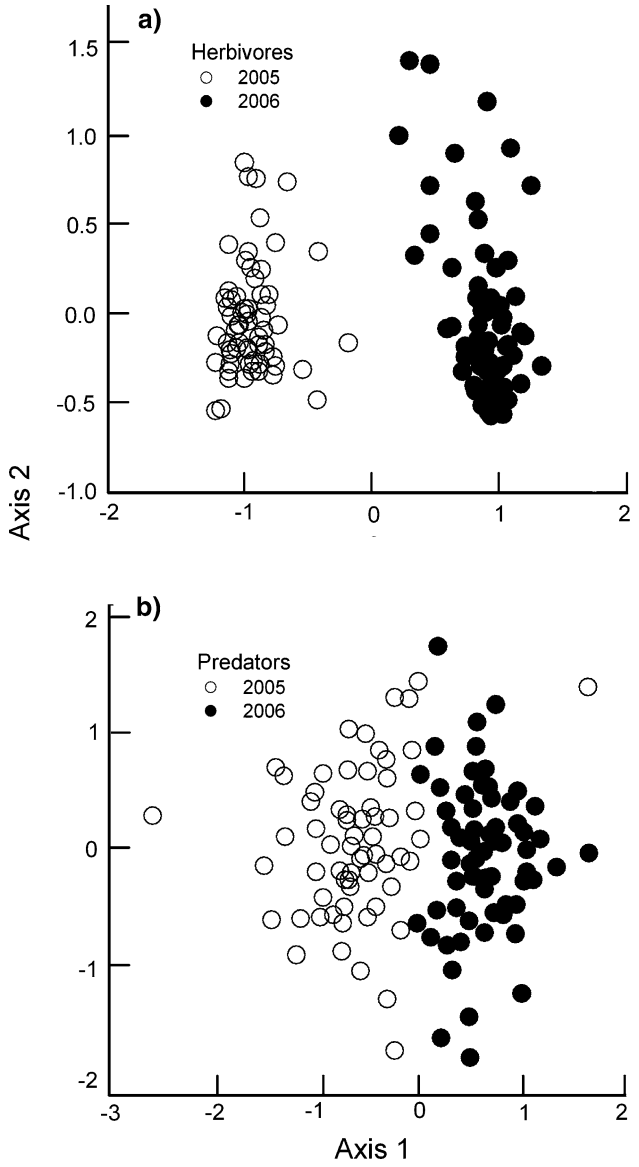

Fig. 1 Non-metric multidimensional scaling ordination based on Bray-Curtis similarities of **a** foliage-based herbivore and **b** predator communities in 63 experimental plots of *Solidago altissima* plants in 2005 (*open circles*) and 2006 (*filled circles*). Each circle indicates a community within an individual plot. Two-dimensional ordinations are presented for simplicity, but three-dimensional representations maintained the lowest stress for both herbivores (stress = 0.07) and predators (stress = 0.19)

S. altissima genotypes varied by approximately fivefold in ANPP, but ANPP showed no response to genotypic diversity during the second year of this study (Table 1). Total foliage-based arthropod richness ($r = 0.62$, $P < 0.0001$) and abundance ($r = 0.64$, $P < 0.0001$) were positively correlated with plot-level ANPP, but only in monoculture plots. Richness and abundance were not related to ANPP in genotype mixtures ($P > 0.33$ for both), indicating that plant biomass did not drive observed increases in arthropod diversity in mixture plots in 2006.

Table 1 ANOVA summary of *Solidago altissima* genotype identity and genotypic diversity effects on arthropods associated with living plant tissue and aboveground net primary productivity. *ANPP* Aboveground net primary productivity

	df	MS	*F*	*P*-value
Genotype				
Total richness	20, 21	50.16	3.73	**0.002**
Total abundance	20, 21	6,568.20	5.24	**0.0002**
Herbivore richness	20, 21	11.07	2.16	**0.043**
Herbivore abundance	20, 21	5,031.05	4.81	**0.0004**
Predator richness	20, 21	15.32	4.56	**0.0005**
Predator abundance	20, 21	73.41	3.75	**0.002**
ANPP	20, 21	2,514,924.00	5.82	**<0.0001**
Genotypic diversity				
Total richness	3, 59	125.37	5.07	**0.003**
Total abundance	3, 59	11,960.40	3.53	**0.020**
Herbivore richness	3, 59	9,985.88	3.60	**0.018**
Herbivore abundance	3, 59	28.88	3.93	**0.012**
Predator richness	3, 59	30.41	3.88	**0.013**
Predator abundance	3, 59	65.83	1.71	0.173
ANPP	3, 59	78,810.00	0.66	0.575

Significant *P*-values are shown in *bold*

Intraspecific diversity and litter-based communities

As with the effects of genotype identity, *S. altissima* genotypic diversity had weak effects on the litter-based community. Initially, there was an approximately fourfold difference among genotypes in collembolan abundance at 3 weeks (Table 2; Fig. 3), and an approximately twofold difference in collembolan richness at 12 weeks (Table 2; Fig. 3). However, neither total microarthropod (Fig. 2) or mite richness and abundance were affected by leaf litter genotype at any time (Table 2; Supplemental 2). Host-plant genotype also had minimal effects on the richness and abundance of predators, herbivores, or detritivores (Supplemental 3). Microarthropod community composition varied among genotypes (global $R = 0.146$, $P = 0.05$), but only at the 3-week collection date and likely due to initial collembolan responses.

As with genotype effects, *S. altissima* genotypic diversity also had weak effects on the litter-based community. At 3 weeks, there were 90% more collembolan species and fivefold more collembolan individuals in three-genotype mixtures compared to monocultures. At 12 weeks, there were 1.2-fold more mite individuals in three-genotype mixtures. During the final collection at 24 weeks, there were 36% fewer total species in nine-genotype mixtures, but 30% more individuals in three-genotype mixtures compared to

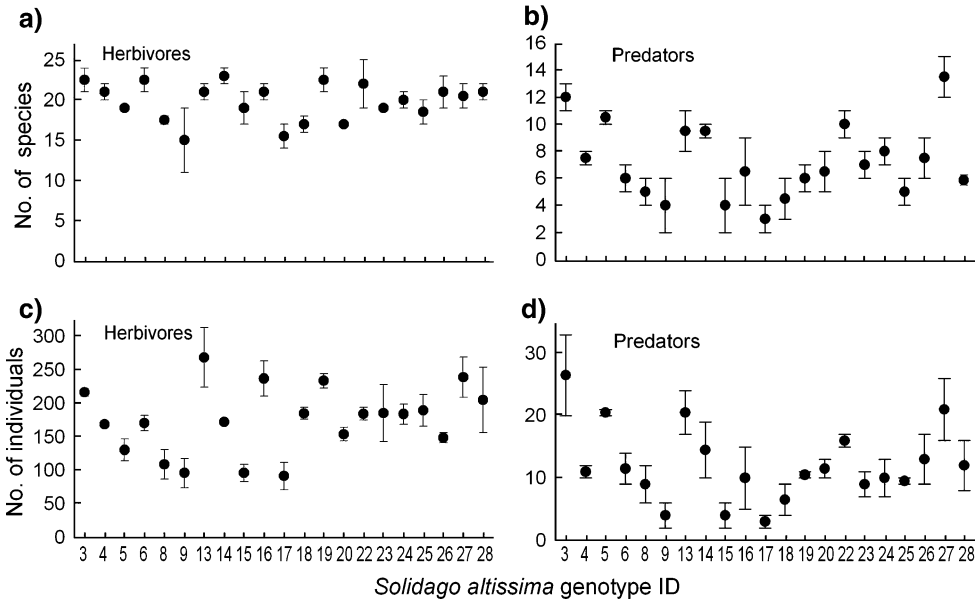

Fig. 2 The relationship between **a** herbivore richness, **b** predator richness, **c** herbivore abundance and **d** predator abundance and genotype identity of *S. altissima* in 2006. *Bars* represent mean (±SEM) number of species and individuals in 1-m^2 experimental plots

Table 2 Summary of full model repeated-measure ANOVAs examining the effects of *S. altissima* genotype identity on total microarthropod, collembolan, and mite richness and abundance over time

	df	*F*	*P*-value
Total richness			
Genotype	11	1.11	0.36
Time	3	23.26	**<0.0001**
Genotype × time	33	1.69	**0.02**
Total abundance			
Genotype	11	1.23	0.27
Time	3	30.73	**<0.0001**
Genotype × time	33	1.17	0.26
Collembola richness			
Genotype	11	0.63	0.79
Time	3	11.79	**<0.0001**
Genotype × time	33	1.33	0.14
Collembola abundance			
Genotype	11	0.66	0.76
Time	3	6.87	**0.0003**
Genotype × time	33	1.53	**0.05**
Mite richness			
Genotype	11	1.26	0.25
Time	3	22.10	**<0.0001**
Genotype × time	33	1.10	0.35
Mite abundance			
Genotype	11	2.39	**0.01**
Time	3	10.32	**<0.0001**
Genotype × time	33	1.15	0.29

Significant *P*-values are shown in *bold*

monocultures (Table 3; Supplemental 2). There was no response of the different trophic groups to genotypic diversity (Supplemental 4).

Leaf litter decomposition and N release were correlated with several of the litter-based community variables, but only weakly and not after 6 weeks in the field. At 3 weeks, percent N remaining in litterbags was positively correlated with mite richness ($r = 0.25$, $P = 0.026$) and total abundance ($r = 0.29$, $P = 0.009$). Total abundance ($r = 0.37$, $P = 0.0008$) and mite abundance ($r = 0.32$, $P = 0.004$) were also positively correlated with percent mass remaining during this time. At 6 weeks, total richness and collembolan richness were positively correlated with percent N remaining ($r = 0.22$, $P = 0.04$ for both).

When we examined the relationship between foliage- and litter-based communities, we found no relationship between species richness or abundance of the two communities ($P > 0.35$ for all correlations) (Fig. 6), indicating that the two communities varied independently of one another in their responses to host-plant intraspecific variation.

Discussion

This study revealed that variation among host-plant genotypes affected species diversity and composition of arthropods associated with living plant tissue, but only weakly affected litter microarthropod communities. Foliage-based species richness and abundance were positively related to host-plant genotypic diversity, whereas genotypic diversity had minimal effects on the litter-based community. Similarly, both foliage-based herbivore and predator diversity and composition responded to plant genetic variation and genotypic diversity, but litter-based trophic levels (herbivores, predators, and detritivores) did not. There was no relationship between foliage- and litter-based richness or abundance, which suggests a decoupling in the biotic factors

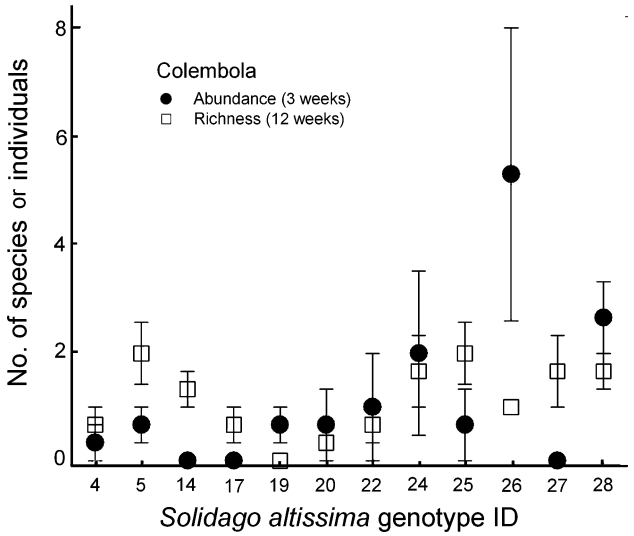

Fig. 3 The relationship between collembolan abundance at 3 weeks (*open squares*) and collembolan species richness at 12 weeks into the experiment (*closed circles*) and genotype identity of *S. altissima*. *Bars* represent mean (±SEM) number of collembolan individuals or species in litterbags. Other time steps during the 24 week experiment were not significant and are not presented for clarity

that structure communities associated with living plant material versus detritus within old-field ecosystems.

Intraspecific diversity and foliage-based communities

The responses of the foliage-based community, including herbivore and predator trophic levels, to variation among genotypes and genotypic diversity were strong between study years, despite substantial shifts in community composition. Total richness was 37% greater and total abundance was 56% greater in genotypically diverse plots in 2005 (Crutsinger et al. 2008) and total richness was 22% higher and abundance was 34% higher in 2006. The ability of foliage-based arthropod species to discriminate genetic variation within host plants has been established in numerous other plant species, including cottonwoods (Wimp et al. 2005), eucalyptus (Dungey et al. 2000), willows (Hochwender and Fritz 2004), oaks (Tovar-Sánchez and Oyama 2006), and primrose (Johnson and Agrawal 2005). Likewise, observed increases in arthropod richness and abundance with plant genotypic diversity in this study are mostly consistent with other studies (Wimp et al. 2005; Johnson et al. 2006), though few studies have sampled arthropod communities for longer than one season (Wimp et al. 2007). Taken together, there is broad support for the notion that the identity and number of host-plant genotypes within local patches are important drivers of foliage-based arthropod diversity and community structure, particularly within dominant or foundation plant species (Ellison et al. 2005; Whitham et al. 2003; 2006).

Table 3 Summary of full model repeated-measure ANOVAs examining the effects of *S. altissima* genotypic diversity on litter microarthropods over time. *Gen div* Genotypic diversity

	df	*F*	*P*-value
Total richness			
Gen div	3	0.45	0.71
Time	3	36.05	**<0.0001**
Gen div × time	9	1.36	0.20
Total abundance			
Gen div	3	0.55	0.64
Time	3	48.37	**<0.0001**
Gen div × time	9	0.93	0.49
Collembola richness			
Gen div	3	1.44	0.22
Time	3	15.16	**<0.0001**
Gen div × time	9	2.52	**0.008**
Collembola abundance			
Gen div	3	2.82	**0.03**
Time	3	1.36	0.25
Gen div × time	9	2.70	**0.004**
Mite richness			
Gen div	3	0.48	0.69
Time	3	35.58	**<0.0001**
Gen div × time	9	1.20	0.29
Mite abundance			
Gen div	3	1.72	0.16
Time	3	20.14	**<0.0001**
Gen div × time	9	1.61	0.11

Significant *P*-values are shown in *bold*

While the responses of arthropods to plant genotypic diversity were consistent between years, the underlying mechanisms were not. For example, increased ANPP explained most of the positive arthropod responses to genotypic diversity during the first year of the study (Crutsinger et al. 2006, 2008), but we did not observe an increase in ANPP during the second year. This was because several highly productive genotypes growing in monocultures swamped genotypic diversity effects on ANPP. Despite no increase in ANPP, there were still more arthropod species in genotypically diverse plots. One possible explanation is that arthropods still cue in on many of the other qualitative traits that vary among *S. altissima* genotypes, such as leaf nutrients or stem thickness (Abrahamson and Weis 1997; Crutsinger et al. 2006, 2008). Previous results in this and other studies (Johnson and Agrawal 2007) have indicated that the cues arthropods use to discriminate between host plants may change with the phenology of either the arthropod species or host plants during a growing season (Crutsinger et al. 2008). Therefore, the genetically based mechanisms driving foliage-based community responses to

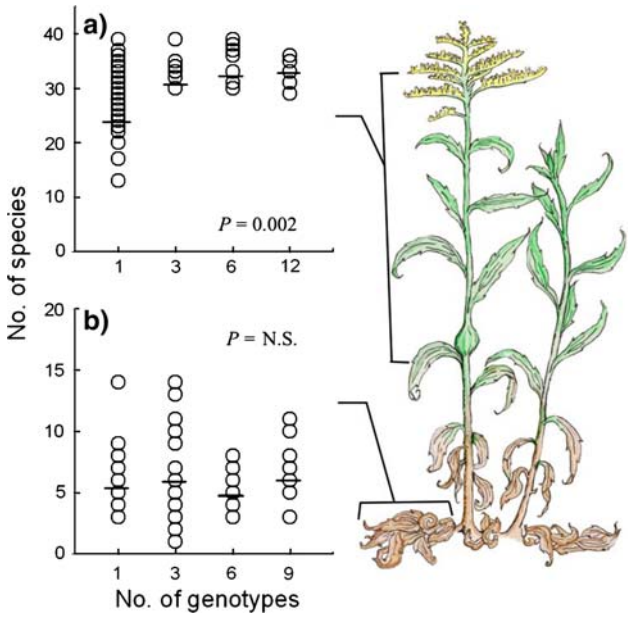

Fig. 4 Relationship between population-level genotypic diversity of *S. altissima* and total species richness in **a** foliage- and **b** litter-based arthropod communities. *Circles* indicate plot-level observations and *horizontal lines* indicate treatment means. Note that the litter community had fewer species. *Brackets* connect the graphs to their corresponding resource (living plant material or leaf litter)

intraspecific diversity likely change both within and among years depending on which community members are present and which plant traits they are responding to. Such temporal shifts add complexity to predictions of associated community composition based on host-plant genotypes (Shuster et al. 2006; Whitham et al. 2006).

Intraspecific diversity and litter-based communities

While foliage-based arthropods demonstrated strong responses to variation among *S. altissima* genotypes and genotypic diversity, litter-based microarthropods showed few responses, aside from some initial differences in collembolan richness and abundance. These results are contrary to our initial predictions that litter-based communities would respond to observed qualitative differences in litter produced by the different plant genotypes. Initial litter qualitative differences may have driven the observed collembolan responses. For example, initial N content varied by 47% among genotypes (Crutsinger et al., in review), and collembolan richness was weakly related to percent N remaining in litterbags at the beginning of the experiment. But litterbags had not been established in the field for very long and contained few individuals. So no major conclusions can be drawn from initial community differences among genotypes. Also during the 3-week collection period, higher collembolan richness occurred in three-genotype mixtures. There were no differences in initial leaf chemistry among genotypic diversity treatments that might explain this pattern (Crutsinger et al., in review). Another potential mechanism might be that collembolans responded positively to increased structural heterogeneity from different leaf sizes or shapes among genotypes in mixtures (Armbrecht et al. 2004; Hättenschwiler et al. 2005; Wardle 2006), though we did not explicitly test this hypothesis.

Our findings are consistent with the only other study, to our knowledge, that has examined the effects of genotype mixing on microarthropods. Madritch and Hunter (2005) manipulated different phenotypes of turkey oak (*Quercus laevis*) in monoculture treatments, and included one treatment that contained equal proportions of each phenotype in a mixture. They found no effect of plant phenotype or litter mixing on microarthropod communities. Perhaps relatively weak (or nonexistent) responses of the leaf litter communities to plant genotypic diversity are not surprising, given that litter-based communities show mixed responses to plant *species* diversity manipulations in other systems (Kaneko and Salamanca 1999; Hansen 2000; Armbrecht et al. 2004; Wardle et al. 2006).

So why are there such discrepancies in foliage- and litter-based species responses to plant genetic variation and genotypic diversity? After all, both communities rely on tissue from the same individual plants. One explanation is that foliage-based arthropods are more adept at distinguishing host-plant qualitative differences than microarthropods. For example, most aboveground herbivores show some degree of specificity on particular host-plant species or families, as well as feeding specialization on particular plant parts (e.g., stems, leaves, flowers) (Bernays and Chapman 1994; Bernays 1998). Aboveground arthropods are also much more able to disperse to preferred hosts, compared to species that occur in the litter or soil (Hooper et al. 2000). In contrast, microarthropod species are typically thought to be generalists in feeding and habitat preferences (Maraun et al. 1998; De Deyn and Van der Putten 2005), though there is some evidence for trophic niche differentiation (Schneider et al. 2004). Also, many microarthropods are not necessarily feeding on the leaf litter directly, but rather on bacterial or fungal decomposers or other microarthropods (Maraun et al. 1998; Schneider et al. 2004). Yet, foliage-based predators do not feed directly on host plants, and they responded strongly to host-plant genetic variation and genotypic diversity. It is possible that microarthropod communities are not affected by the levels of variation in litter quality among *S. altissima* genotypes and are structured by numerous other biotic and abiotic factors unrelated to host-plant genetics (Maraun and Scheu 2000; De Deyn and Van der Putten 2005; Wardle 2006). Bacterial or fungal communities that feed directly on leaves might be more sensitive to intraspecific diversity. For example, Schweitzer

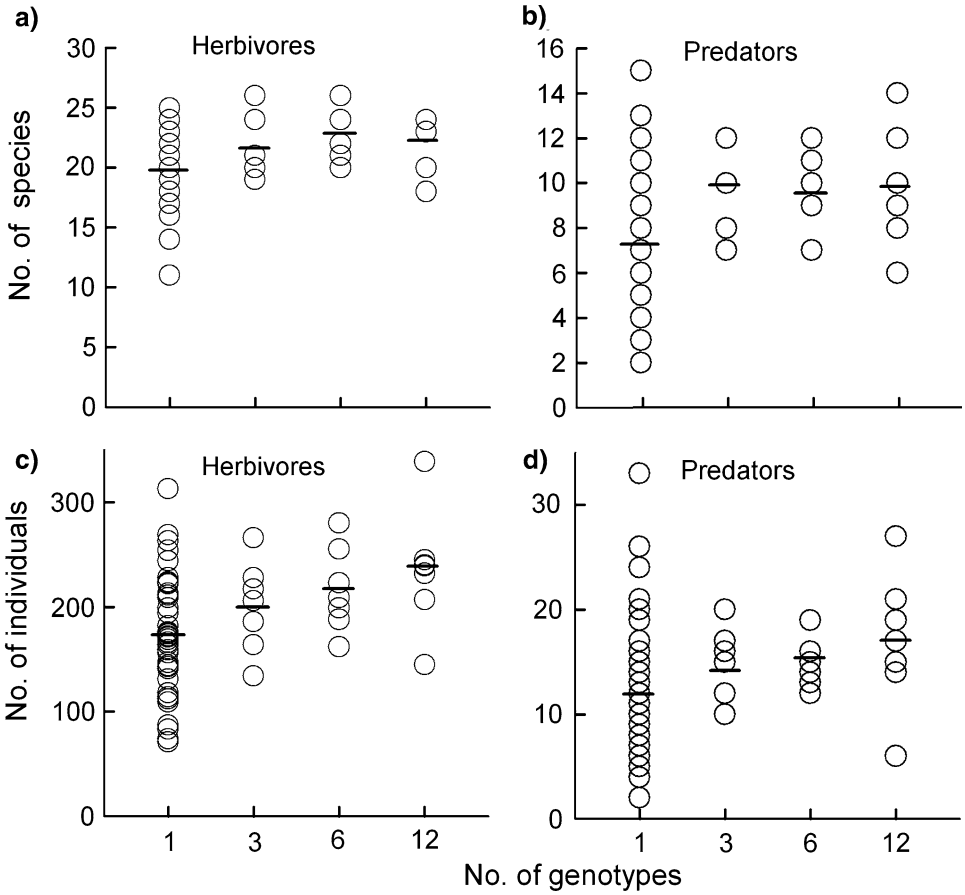

Fig. 5 Relationship between population-level genotypic diversity of *S. altissima* and **a** herbivore richness, **b** predator richness, **c** herbivore abundance and **d** predator abundance. *Circles* indicate plot-level observations and *horizontal lines* indicate treatment means

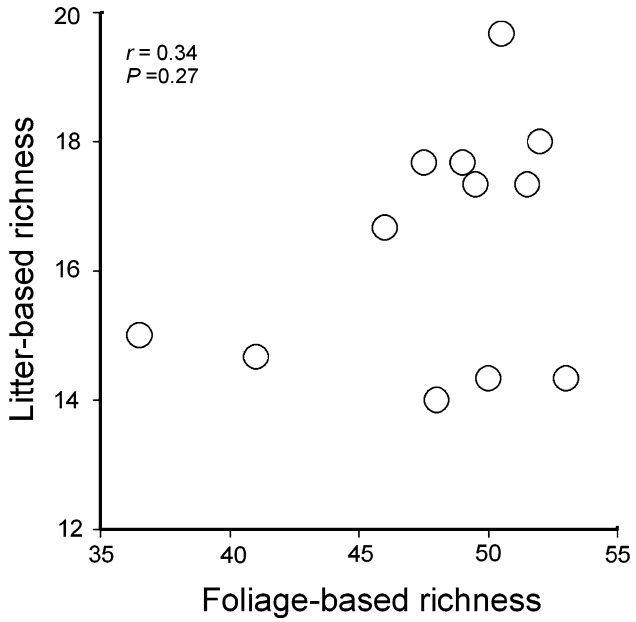

Fig. 6 Relationship between foliage-based richness and litter-based richness for 12 *S. altissima* genotypes used in both the common garden and litterbag manipulations. Lack of a correlation indicates a decoupling in the responses of the two communities to variation among host-plant genotypes

et al. (2007) examined soils under different genotypes of cottonwood (*Populus angustifolia*) and found that genetic factors explained 70% of the variation in soil microbial communities.

A caveat of our study is that all litterbags started with the same amount of initial material in each litterbag. *S. altissima* genotypes varied by several fold in ANPP and so genetic variation may affect microarthropods by determining the amount of litter available for colonization (Wardle 2006). Also, the relative density of arthropod species in litterbags was much lower than in the common garden plots, which may have made it more difficult to detect genotypic effects at the community level. Finally, we focused on how microarthropods responded to characteristics of the litter produced by different plant genotypes. We did not examine root herbivores, rhizosphere communities, or "bulk soil communities" (e.g., fungi or nematodes) directly under host-plant genotypes in our experimental plots. Another approach would have been to collect senesced litter from a plot, place it in a decomposition bag, and put the bag back into the plot from which it came. However, such an approach would not have allowed us to disentangle the effects of litter quality from the indirect effects of the treat-

ment in the plot. By placing the bags in a common environment, we were able to focus solely on whether differences among genotypes led to differences in litter-based community structure.

Conclusion

In the past decade, two major foci of ecological research have been on the role of biodiversity in ecosystem structure and function (Hooper et al. 2005), and understanding the links between the foliage-based and litter-based or belowground components of ecosystems (Wardle et al. 2004). Our work, and that of others (Whitham et al. 2003, 2006; Hughes and Stachowicz 2004; Johnson et al. 2006), has highlighted the role of within-species diversity in structuring communities and ecosystems. This study highlights that the responses of foliage-based and litter-based arthropods to intraspecific host-plant diversity are decoupled. Our results illustrate that comparing trophic interactions among community types associated with the same plant genotypes can lead to very different conclusions about the extent to which intraspecific diversity structures associated communities.

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References

Abrahamson WG, Weis AE (1997) Evolutionary ecology across three trophic levels. Princeton University Press, Princeton

Armbrecht I, Perfecto I, Vandermeer J (2004) Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science 304:284–286

Bernays EA (1998) The value of being a resource specialist: behavioral support for a neural hypothesis. Am Nat 151:451–464

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman & Hall, New York

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:326–349

Chao A (1984) Non-parametric estimation of the number of classes in a population. Scand J Stat 11:265–270

Clarke KR, Gorley RN (2001) Primer v5: user manual/tutorial. Primer-E, Plymouth

Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968

Crutsinger GM, Collins MD, Fordyce JA, Sanders NJ (2008) Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. Oikos 117:255–264

Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial Ecosystems. Nature 361:148–150

De Deyn GB, Van der Putten WH (2005) Linking aboveground and belowground diversity. Trends Ecol Evol 20:625–633

Dungey HS, Potts BM, Whitham TG, Li HF (2000) Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. Evolution 54:1938–1946

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers Ecol Environ 3:479–486

Fontes EMG, Habeck DH, Slansky F Jr (1994) Phytophagous insects associated with goldenrods (*Solidago* spp.) in Gainesville, Florida. Fla Entomol 77:209–221

Gonzalez G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82:955–964

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Sunderland

Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. Am Nat 158:17–35

Hairston NG Jr, Hairston NG Sr (1993) Cause–effect relationships in energy-flow, trophic structure, and interspecific interactions. Am Nat 142:379–411

Hansen RA (1999) Red oak litter promotes a microarthropod functional group that accelerates its decomposition. Plant Soil 209:37–45

Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81:1120–1132

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36:191–218

Heneghan L, Coleman DC, Zou X, Crossley DA, Haines BL (1999) Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. Ecology 80:1873–1882

Hochwender CG, Fritz RS (2004) Plant genetic differences influence herbivore community structure: evidence from a hybrid willow system. Oecologia 138:547–557

Hooper DU, Bignell DE, Brown VK, Brussaard L, Dangerfield JM, Wall DH, Wardle DA, Coleman DC, Giller KE, Lavelle P, Van der Putten WH, de Ruiter PC, Rusek J, Silver WL, Tiedge JM, Wolters V (2000) Interaction between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. Bioscience 50:1049–1061

Hooper DU, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge D, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc Natl Acad Sci USA 101:8998–9002

Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159

Johnson MTJ, Agrawal AA (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86:874–885

Johnson MTJ, Agrawal AA (2007) Covariation and composition of arthropod species across plant genotypes of evening primrose (*Oenothera biennis*). Oikos 116:941–956

Johnson MTJ, Lajeunesse MJ, Agrawal AA (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. Ecol Lett 9:24–34

Kaneko N, Salamanca EF (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. Ecol Res 14:131–138

Maddox GD, Root RB (1987) Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*—genetic variation and heritability. Oecologia 72:8–14

Maddox GD, Cook RE, Wimberger PH, Gardescu S (1989) Clone structure in 4 *Solidago altissima* (Asteraceae) populations—rhizome connections within genotypes. Am J Bot 76:318–326

Madritch MD, Hunter MD (2002) Phenotypic diversity influences ecosystem functioning in an oak sandhills community. Ecology 83:2084–2090

Madritch MD, Hunter MD (2005) Phenotypic variation in oak litter influences short- and long-term nutrient cycling through litter chemistry. Soil Biol Biochem 37:319–327

Maraun M, Migge S, Schaefer M, Scheu S (1998) Selection of microfungal food by six oribatid mite species (Oribatida, Acari) from two different beech forests. Pedobiologia 42:232–240

Maraun M, Scheu S (2000) The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research. Ecography 23:374–383

Merchant VA, Crossley DA Jr (1970) An inexpensive high-efficiency Tullgren extractor for soil microarthropods. J Ga Entomol Soc 5:83–87

Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, NadelhoVer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7:584–600

Root RB (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77:1074–1087

Schneider K, Migge S, Norton RA, Scheu S, Langel R, Reineking A, Maraun M (2004) Trophic niche differentiation in soil microarthopods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biol Biochem 36:1769–1774

Schweitzer JA, Bailey JK, Hart SC, Whitham TG (2005) Non-additive effects of mixing cottonwood genotypes on litter decomposition and nutrient dynamics. Ecology 86:2834–2840

Schweitzer JA, Bailey JK, Bangert RK, Hart SC, Whitham TG (2007) The role of plant genetic variation in determining above- and belowground microbial communities. In: Bailey MJ, Lilley AK, Timms-Wilson TM, Spencer-Phillips PTN (eds) Microbial ecology of aerial plant surfaces. CABI

Semple JC, Cook RE (2006) Solidago. In: Flora of North America. Oxford University Press, Oxford

Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. Evolution 60:991–1003

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750

Silfver T, Mikola J, Rousi M, Roininen H, Oksanen E (2007) Leaf litter decomposition differs among genotypes in a local *Betula pendula* population. Oecologia 152:707–714

Southwood TRE, Brown VK, Reader PM (1979) Relationships of plant and insect diversities in succession. Biol J Linn Soc 12:327–348

Tovar-Sánchez E, Oyama K (2006) Effect of hybridization of the *Quercus crassifolia* x *Quercus crassipes* complex on the community structure of endophagous insects. Oecologia 147:702–713

Wardle DA (2006) The influence of biotic interactions on soil biodiversity. Ecol Lett 9:870–886

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633

Wardle DA, Yeates GW, Barker GM, Bonner KI (2006) The influence of plant litter diversity on decomposer abundance and diversity. Soil Biol Biochem 38:1052–1062

Whitham TG, Martinsen GD, Young W, Gehring CA, Schweitzer JA, Wimp GM, Bailey JK, Fischer DG, Lindroth R, Keim P (2003) Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84:559–573

Whitham TG, Bailey JK, Schweitzer JA, LeRoy CJ, Fischer DG, Lonsdorf E, Shuster SM, Lindroth RL, Hart SC, Allan GJ, Gehring CA, Keim P, Potts BM, Woolbright S (2006) A framework for community and ecosystem genetics: from genes to ecosystems. Nat Rev Genet 7:510–523

Wimp GM, Martinsen GD, Floate KD, Bangert RK, Whitham TG (2005) Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69

Wimp GM, Wooley S, Bangert RK, Young WP, Martinsen GD, Keim P, Rehill B, Lindroth RL, Whitham TG (2007) Plant genetics predicts intra-annual variation in phytochemistry and arthropod community structure. Mol Ecol 16:5057–5069