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Linking genotypic diversity within Solidago altissima to communities and ecosystems

Gregory M. Crutsinger
University of Tennessee

To the Graduate Council:

I am submitting herewith a dissertation written by Gregory M. Crutsinger entitled "Linking genotypic diversity within Solidago altissima to communities and ecosystems." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Nathan Sanders, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Nathan Sanders, Major Professor

We have read this thesis
and recommend its acceptance:

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Aimee Classen

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Daniel Simberloff

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James Fordyce

Accepted for the Council:

_____
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Linking genotypic diversity within *Solidago altissima* to communities and ecosystems.

A Dissertation presented for the Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Gregory M. Crutsinger

May 2009

DEDICATION

This dissertation is dedicated to the memories of Timothy Barhite and Caleb Clark.

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There are many great people who deserve the credit for my graduate education. First and foremost, my doctoral advisor, Nathan Sanders, has been an excellent mentor. Nate was incredibly supportive and generous with him time and patience throughout my dissertation. I can't imagine a better advisor for me and I look forward to having him as my friend and collaborator throughout my ecological career. I was also very fortunate to have great people on my committee. Aimée Classen provided solid advice at the ecosystem scale, where boxes and arrows prevail over species nomenclature. Aimée has also become a close friend to turn to for both personal and professional advice. Jim Fordyce was fantastic for bouncing ideas off of and for encouragement to push the boundaries of the field. I feel very privileged to have Dan Simberloff as a committee member. Dan provided a wealth of wisdom about ecology, old-time music, and surströmming. If there is ever someone who deserved a National Academy membership over the likes of Jared Diamond, it is Dan. Warren "Abe" Abrahamson was an unofficial member of my committee, but is an ecological legend in the field of plant-insect interactions. I couldn't have done my work on goldenrod without his vast knowledge of the goldenrod system.

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Funding for my dissertation work was graciously provided by the EPA STAR fellowship, the NSF Graduate Research Fellowship, the University of Tennessee Hilton Smith Fellowship, the Department of Energy, and the UTK Department of Ecology and Evolutionary Biology.

My family believes that, just like with raising a child, when it comes to education, it takes a village to get it done right. I thank my family for their emotional, logistical, and financial support for my education.

ABSTRACT

For almost two decades, ecological studies have addressed the importance of plant species diversity for associated animal diversity and the functioning of ecosystems. Recently, a burgeoning focus of research in ecology is on how population-level diversity scales up to affect patterns and processes at the community- and ecosystem-level. In this dissertation, I present results from a series of common garden experiments in which I manipulated genotypic diversity of tall goldenrod (*Solidago altissima*) to address a suite of questions about how intraspecific variation in a dominant old-field plant species shapes communities of associated arthropods and ecosystem processes. In these studies, I found that host-plant genotypic diversity had non-additive effects on insect herbivore and predator diversity and that incorporating temporal dynamics into community genetics studies is essential for predicting how different community members perceive and respond to genetically variable host-plant traits. I 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. Additionally, I found strong effects of instraspecific genetic variation in goldenrod functional traits on primary productivity, litter quality, decomposition rate, nitrogen release, and community invasibility. Together, my results indicate that within-species variation is an important, but all to often overlooked, influence on the structure and dynamics of communities and ecosystems.

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CHAPTER I. Introduction

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Introduction

In the past decade, there have been great strides in the advancement of molecular genetic techniques. These advancements have opened up the genetic toolbox for the application to many other scientific fields both rapidly and relatively inexpensively. In ecology, many subdisciplines have begun to apply molecular genetics to research questions. My dissertation focuses specifically on an area of community ecology being termed "community genetics" (Antonovics 1992, Whitham et al. 2003, 2006). Community genetics examines the role of intraspecific genetic variation in affecting community organization and ecosystem dynamics (Whitham et al. 2003, 2006). To remain consistent with recent papers, I will define a community as "an association of interacting species living in a particular area" (Whitham et al. 2003, 2006). Therefore, community genetics examines how genetic variation within one species influences the distribution, abundance, and interactions with other species. To date, most researchers in this field have addressed their questions in terms of genetic variation in host-plant traits and the influence variation in these traits has on associated communities. In many cases, these studies focus on arthropods associated with host plants. Since most temperate vegetation types are typically characterized by a few plant species that dominate in biomass, genetic variation within dominant species (e.g. oaks, willows, cottonwoods, eucalyptus, goldenrods) is likely to have some of the strongest impacts on communities (Maddox and Root 1987, Whitham et al. 2003, 2006, Reusch et al. 2005, Madricth et al. 2006). Many dominant plant species maintain high levels of genetic variation and have made ideal systems in which test the importance of genetic variation at the community and

ecosystem level (Hochwender and Fritz 2004, Whitham et al. 2003, 2006, Crutsinger et al. 2006, 2008).

In my dissertation, I use experimental and observational approaches to ask specific questions about how communities and ecosystem processes respond to different plant genotypes and levels of genotypic diversity (no. of genotypes per m^2). In Chapter 2, I report results from an experimental common garden study manipulating plots of tall goldenrod (*Solidago altissima*) to vary in their levels of genotypic diversity. I examine the cumulative responses of herbivorous and predatory arthropods over the course of an entire growing season, as well as goldenrod productivity responses to plant genotypic diversity. These results were reported in a paper in the journal Science in 2006.

Over the course of a growing season, there are many phenological shifts in both host plants and in arthropod community composition. Chapter 3 examines temporal dynamics in the relationship between host-plant genotypic diversity and arthropod species diversity from the beginning of the growing season until goldenrod flowering in the common garden. The results from this study are reported in the journal Oikos in 2008.

While the second and third chapters reveal how intraspecific diversity can influence the structure of foliage-based arthropod communities, it is unclear whether litter-based arthropods respond to intraspecific diversity in similar ways. In Chapter 4, I use litterbag experiments to examine the effects of goldenrod genotype and genotypic diversity on litter

microarthropods. The results from this study are reported in a paper in the journal Oecologia in 2008.

Finally, numerous studies have asked whether species-rich communities deter biological invasions more so than do species-poor communities. There has also been considerable research examining the role of dominant species in affecting invasion resistance in native communities. In Chapter 5, I switch from arthropod to plant communities. I address whether high intraspecific diversity within a dominant plant species can deter biological invasions or whether genotypes vary in their effectiveness at resisting other plant species colonizing the common garden. The results from this study are reported in a paper in the journal Ecology Letters in 2008.

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CHAPTER II. Plant genotypic diversity predicts community structure and governs an ecosystem process.

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The following section is a slightly modified version of a paper published in the journal Science:

Crutsinger G.M., Collins M.D., Fordyce J.A., Gompert Z., Nice C.C. & Sanders N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313: 966-968

The use of "we" in this part refers to my co-authors and me. As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the design of the experiment, data collection and statistical analysis. I also wrote most of the paper.

Abstract

Theory predicts, and recent empirical studies have shown, that the diversity of plant species determines the diversity of associated herbivores and mediates ecosystem processes, such as aboveground net primary productivity (ANPP). However, an often-overlooked component of plant diversity, namely population genotypic diversity, may also have wide-ranging effects on community structure and ecosystem processes. We showed experimentally that increasing population genotypic diversity in a dominant old-field plant species, *Solidago altissima*, determined arthropod diversity and community structure and increased ANPP. The effects of genotypic diversity on arthropod diversity and ANPP were comparable to the effects of plant species diversity measured in other studies.

Introduction

Ecological theory (Hutchinson 1959, MacArthur 1972) and field experiments (Siemann et al. 1998, Haddad et al. 2001) have revealed a positive relationship between plant species diversity and the diversity of associated consumers. At least two mechanisms might explain this pattern. First, because approximately 90% of herbivorous insects exhibit some degree of host specialization (Bernays and Graham 1988), as plant species richness increases, so should the number of associated herbivore species. This Resource Specialization Hypothesis has some theoretical support *(*Hutchinson 1959, MacArthur 1972, Price 1983). Second, if aboveground net primary productivity (ANPP) increases as plant species richness increases (Hooper et al. 2005), then more herbivore individuals, and therefore more species, will be

supported by increases in available energy (this has been called the 'More Individuals Hypothesis') (Srivastava and Lawton 1998). An increase in the number of herbivore species by either of these mechanisms should support more predator species (Hunter and Price 1992). Recent studies have shown that population genotypic diversity, like plant species diversity, can also have extended consequences for communities and ecosystems (Zhu et al. 2000, Hughes and Stachowicz 2004, Schweitzer et al. 2005, Reusch et al. 2005, Johnson et al. 2006). However, no studies to date have explicitly linked intraspecific genotypic diversity, the structure of associated communities, and the potential mechanisms driving these patterns, such as energy availability. This paucity of studies exists despite numerous calls for such research within the biodiversity-ecosystem function literature (Hooper et al. 2005, Loreau et al. 2002). Here, we test whether host-plant genotypic diversity determines the structure of associated arthropod communities and governs an ecosystem process, ANPP, which influences arthropod species richness.

Materials and Methods

Study Site

We initiated this research in Spring of 2005 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park (NERP) near Oak Ridge, Tennessee (35º58' N, 84º17'W). The site was abandoned from agricultural use in 1943, and has been extensively managed for open-space and wildlife habitat by ORNL and the Tennessee Wildlife Resource Agency (TWRA). The soil, classified as a Typic Hapludult,

has a silty clay loam texture and is moderately well drained and slightly acidic. Precipitation is generally evenly distributed throughout the year with an annual mean of 1322 mm; the mean annual temperature at the site is 13.9°C. The fields surrounding the experimental area are typical of other old fields in eastern Tennessee in terms of plant community composition. Besides *Solidago altissima*, dominant plant species include *Verbesina occidentalis* L. (yellow crownbeard), *V. virginica* L. (white crownbeard), and *Rubus* spp. (blackberry); sub-dominants include about 60 other herbaceous and woody species.

Plant Propagation

We manipulated plot-level genotypic diversity (the number of genotypes per plot) of *Solidago altissima*, tall goldenrod, a common perennial plant throughout eastern North America. We collected rhizomes from 21 *S. altissima* ramets in natural patches growing 50-150 m apart in several old fields surrounding the study site. Rhizomes were excavated with a hand trowel and only rhizomes directly attached to one another and to the stem from the previous year's growth were considered to be part of the same genet. Experimental ramets were propagated directly after excavation by cutting rhizomes into 3-cm sections and planting sections from each genotype in separate flats of sterilized potting soil (Pro-Mix BX, Premier Brands, New Rochelle, NY). Ramets were established in a common greenhouse environment set at 25° C for 9 weeks, watered as needed, and fertilized monthly using water-soluble fertilizer (15:20:25, N:P:K, Scotts Sierra Horticultural Co. Marysville, OH). Ramets were initially given a root stimulator (Roots 2, Roots inc. OSIA Independence, MO, 1 tsp per gal). Using small rhizome fragments and an extended greenhouse time period minimized any

maternal effects carried over from growing in previous local environments (Weis et al. 1987). One week prior to planting in the field, all genotypes were transferred to benches outside the greenhouse to adapt to natural light conditions and to minimize transplant shock.

We created treatments of 1, 3, 6, or 12 genotypes in May 2005, which are directly comparable to natural levels of genotypic diversity (Maddox et al. 1989). All 21 genotypes were planted in two replicate monocultures. Mixtures were created by randomly sampling from the pool of 21 genotypes with the constraint that no two patches in a treatment could have identical composition (7 replicates each). Each plot contained 12 ramets arranged in a 75-cm diameter circle in 1-m^2 plots spaced 1 m apart and randomized in a grid. A circular planting pattern ensured equal chance of colonization of any given plant in a plot (Johnson, and Agrawal 2005). Patches were spaced 1 m apart and arranged in a 15 m X 20 m grid. Trenches were cut around each plot (6 cm wide x 30 cm) using an EZ9000 Groundsaw trencher (E-Z Trench, Loris, SC.). Each plot was staked at the corners with 30 cm wooden stakes and lined with 12 mil heavy plastic (K-501R greenhouse film, Klerk's Plastic Inc., Richburg, S.C.) 30 cm deep to prevent rhizomes from spreading into neighboring plots. Three weeks prior to planting, all plots were sprayed with a broad-spectrum, post-emergent, systemic herbicide (Round-Up Pro, Monsanto Co., St. Louis, MO, 5 % solution) to eliminate any vegetation previously established in the plot. Plots were weeded by hand biweekly for the remainder of the growing season. Ramets were watered for the first 3 weeks as needed (2 gal per plot) from collected rainwater. Seven plants died during the first week and were replaced with the same genotypes. After this, mortality was noted (though minimal, 0.5% or

4 ramets). A 3-m tall fence made of 1-in poultry wire was built around the experiment to exclude deer (Fig. II-3).

Arthropod Surveys

We visually surveyed every ramet 5 times from May-October 2005. Although more time-consuming than destructive sampling methods, visual sampling allows for repeated measurements with minimal impact on the arthropod community. We identified and counted all herbivorous, omnivorous, and predatory arthropods down to morphospecies by looking over the entire genet, including all new ramets that were produced throughout the growing season. One individual of each morphospecies was taken back to the lab for further identification to the lowest taxonomic level possible. Arthropods were assigned to trophic levels and feeding guilds based on field guides and relevant literature. Because of logistical difficulties in field surveying, we lumped parasitoids and bees other than honeybees (*Apis mellifera)* or bumblebees (*Bombus sp.*) into size classes. Flowering obscured many arthropods during the last survey in October. To avoid under sampling, after visually surveying the entire stem, we shook each flower head three times onto white paper and counted all arthropods that fell off. In total, we counted 36,997 individuals of ~136 species. We used linear regression to determine overall effects of genotypic diversity on total arthropod, herbivore, and predator plot-level cumulative richness and abundance. We also used linear regression to determine the relationships of these variables with plot-level Aboveground Net Primary Productivity (ANPP). We used individual-based rarefaction to obtain rarefied total richness, herbivore richness, and predator richness (Ecosim 7.0) (Gotelli,

and Entsminger 2006). Rarefied richness was log-transformed to achieve normality. We used linear regression to determine overall effects of genotypic diversity on rarefied total, herbivore, and predator richness. To assess the relative effects of ANPP and genotypic diversity on rarefied herbivore richness, we used stepwise regression. We also used stepwise regression to test the relative effects of ANPP, genotypic diversity, and rarefied herbivore richness on rarefied predator richness.

Non-additive Effects

To test for non-additive effects of genotypic diversity on arthropod diversity, we used Monte Carlo simulations using data from genotype monoculture plots to construct null genotype mixtures and their associated arthropod communities. We compared the observed arthropod communities to these null communities. Each null mixture consisted of 3, 6, or 12 genotypes sampled to match the exact identities corresponding to a particular plot combination (e.g., for a 3-genotype plot containing G3, G13, and G19, we sampled only from monoculture plots containing these three genotypes) (Johnson et al. 2006). For each sampled genotype, the appropriate number of individual plants (4, 2, or 1) was randomly sampled without replacement from a randomly selected replicate monoculture plot. This process was repeated 5,000 times for every mixed genotype plot. To calculate statistical differences between arthropod diversity in observed versus null mixtures, we used a bootstrap approach. For each of 10,000 iterations, we sampled seven null mixtures and calculated mean number of arthropod species at the plot-level. We measured *P* values as the fraction of iterations in which the null mean arthropod richness was equal to or exceeded the observed mean

richness. We calculated 95% confidence intervals using the percentile method (2.5^{th} and 97.5^{th} percentiles). If the effects of genetic diversity on arthropod richness were additive, we would expect no difference between observed and predicted means ($P > 0.05$). All Monte Carlo simulations were coded in Microsoft Visual C++ 6.0 (Microsoft, Redmond, WA, USA).

For the expected values, we did not use the average of the monocultures, but instead constructed null mixtures based on individual plants drawn repeatedly. This test is more robust than simply taking the average as it takes into account the species turnover due to variation in susceptibility among genotypes. By doing so, this method is a more conservative test for non-additive effects of arthropods in response to genotypic diversity than simply taking plot averages. Our findings suggest that the bulk of our pattern in driven by differences in species composition among genotypes.

Plant Productivity

We estimated ANPP as plant biomass at the peak of the growing season (late July) using an allometric equation developed specifically for *Solidago altissima*, but averaged across haphazardly selected genotypes. Thirty individual ramets from patches growing near the study site were measured to the nearest mm, harvested, oven-dried at 60° C for 48 hours, and weighed to the nearest 0.1 g. This equation accurately predicts aboveground biomass (r = 0.77). Allometric methods allowed repeated arthropod sampling throughout the year. We used linear regression to determine overall effects of genotypic diversity on plot-level ANPP.

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Partitioning Selection and Complementarity

Using standard methods to partition effects in biodiversity experiments (Loreau and Hector 2001), a positive complementarity effect occurs if genotype yields in a mixture are on average higher than the weighted average monoculture yield of component genotypes. Selection effect is measured by the covariance between the monoculture yield of genotypes and the deviation from expected relative yield in a mixture. We used ANOVA to determine if complementarity and selection effects differed from zero. We used linear regression to determine the relationship of these effects with genotypic diversity.

AFLP Genotyping and Data Analysis

Each *S. altissima* ramet was identified as a unique genotype using Amplified Fragment Length Polymorphisms (AFLP). From The AFLP technique generates large numbers of genetic markers throughout the genome providing data on overall genetic similarity and diversity (Mueller and Wolfenbarger 1999) AFLP markers were generated by use of four selective primer pairs*: EcoRI*-ACA and *MseI*-CTC, *EcoRI*-AGT and *MseI*-CTT, *EcoRI*-AGT and *MseI*-CTC, and *EcoRI*-AGT and *MseI*-CTA. Amplicons were separated and visualized on 6% denaturing polyacrylamide gels, using an ABI PRISM 377 DNA sequencer (Applied Biosystems Inc). GeneScan was used to visualize AFLP bands, which were sized by comparison to a size standard ladder (ROX standard, Applied Biosystems Inc) added to each lane. Bands < 100 bp in length and bands with peak heights < 250 relative fluorescent units were not scored. We scored the presence and absence of 206 AFLP amplicons for all 21

ramets (Table S1). Mean dissimilarity between genotypes was 25.1% (range: 14.1-32.5%). AFLP data were analyzed using non-metric multidimensional scaling and Bayesian clustering. Genotypic similarity was measured as Cavalli-Sforza and Edwards distances (Cavalli-Sforza and Edwards 1967) using PHYLIP (Felsenstein 1993) and NMDS was performed to illustrate patterns of similarity among ramets using the NCSS 97 statistical software package. The results of this analysis reveal little or no genetic structure among the 21 ramets (Fig. II-9). The program STRUCTURE (Felsenstein 1993) was used to cluster individuals based on their AFLP banding profiles. STRUCTURE employs a model-based Bayesian clustering algorithm to assign individuals probabilistically to clusters to minimize deviations from linkage equilibrium. The admixture model was run for 500,000 generations with an initial burnin of 50,000 generations. Bayesian clustering using STRUCTURE with number of clusters (*k*) set to 2 found no evidence of genetic structure among the 21 ramets (Fig II-10), supporting the results of the non-metric multidimensional scaling ordination.

Herbivore Assemblages Among Genotypes

To examine how variation among plant genotypes influenced the structure of herbivore assemblages, we examined seperately the distribution of herbivore feeding guilds across the 21 unique *Solidago* genotypes using ANOVA. We found significant variation in abundance of four of six herbivore feeding guilds (Fig. II-7). To determine whether overall herbivore assemblage composition varied among genotypes, we used nonmetric multidimensional scaling (NMDS), a nonparametric analytical technique that is applied to the dissimilarity matrix calculated among genotypes using the Bray-Curtis dissimilarity coefficient (Faith et

al. 1987, Haskins and Gehring 2004). Comparisons between genotypes were made using an analysis of similarity (ANOSIM) statistical test (Primer version 5, Primer-E Ltd., Plymouth Marine Laboratory, Plymouth, UK). This analysis indicated that herbivore community composition differed among host-plant genotypes (ANOSIM: $R = 0.348$, $P = 0.01$) (Fig. II-6).

To examine herbivore performance on particular genotypes, we initiated a bioassay using *Spodoptera exigua* caterpillars (a generalist herbivore) of similar size and mass. In early August, we excised one leaf from 10 randomly chosen ramets from each genotype across the two replicate plots. We chose full-sized leaves undamaged by herbivores. We placed the leaf on moist filter paper in plastic containers in the lab and allowed a randomly selected neonate caterpillar to feed for 5 days. We then recorded the weight of surviving caterpillars. We analyzed these data using an ANOVA. We found significant differences in caterpillar performance among genotypes (Fig. II-8A).

Host Plant Quality

We examined variation among plant genotypes in the ratio of carbon:nitrogen of green leaf tissue. In July, we excised five full-sized leaves from 6 randomly chosen ramets of each genotype. Leaves were air-dried, run through a ball grinder, and then oven dried at 60°C for 72 hours. We calculated C:N ratios using a Carlo-Erba Model 2500 CHN analyzer (Milan, Italy). We analyzed these data using ANOVA. We found significant differences among genotypes in C:N ratios (Fig. II-8B**)**

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Results

Total cumulative arthropod species richness increased with genotypic diversity. The number of arthropod species was, on average, 27% greater in 12-genotype plots than in single-genotype plots (Fig. II-1) indicating that plant genotypic diversity was an important determinant of arthropod diversity. When we examined the effects of genotypic diversity on community structure we found that herbivore species richness (Fig. II-2A) and predator richness (Fig. II-2B) also increased with increasing genotypic diversity. The effects of genotypic diversity on arthropod communities were non-additive (Fig. II-1). That is, total arthropod richness, and herbivore and predator richness, were all greater in the 6- and 12-genotype plots than predicted by summing the number of arthropod species associated with the corresponding genotypes grown in monoculture ($P < 0.01$).

ANPP also increased with genotypic diversity and was 36% greater in 12-genotype plots than in single-genotype plots (Fig. II-2C). The effect of genotypic diversity on ANPP could be due to increased niche complementarity (mixed genotypes used available resources more completely or mixed genotypes facilitated one another, thereby increasing ANPP in mixtures) (Hooper et al. 2005, Loreau et al. 2002) or to sampling or selection effects (increased ANPP is caused by randomly assembled mixtures having a higher probability of containing highly productive genotypes) (Huston 1997). Using standard techniques (Loreau and Hector 2001) we found selection effects were highly variable and were not significantly

different from zero ($P > 0.60$ for all treatments), indicating that highly productive genotypes do not dominate in mixtures and drive observed increases in ANPP. Selection effects were not related to genotypic diversity (Fig. II-4A). We also found complementarity effects to be highly variable, generally positive, but not significantly different from zero ($P > 0.20$ for all treatments). We found a marginally significant increase in complementarity with increasing genotypic diversity (Fig. II-4B) indicating positive interactions among genotypes in mixtures may lead to increases in ANPP with increasing genotypic diversity.

We found that arthropod abundances were positively related to genotypic diversity (total: r2 = 0.27, P < 0.001; herbivores: r2 = 0.29, P < 0.001; predators: r2 = 0.07, P = 0.03). There was a positive relationship between ANPP and arthropod richness (total: r2 = 0.24, P < 0.001; herbivores: r2 = 0.17, P < 0.001; predators: r2 = 0.15, P = 0.001) and total abundance (r2 = 0.19, P < 0.001) and herbivore abundance (r2 = 0.23, P < 0.001). Arthropod richness and abundance were correlated (r = 0.74, P < 0.001; herbivores: r = 0.70, P < 0.001; predators: r = 0.29, P = 0.02).

Discussion

Arthropod richness might respond to genotypic diversity either because of increased productivity in plots with higher genotypic diversity, as the More Individuals Hypothesis predicts (Srivastava and Lawton 1998), or because genotypes vary in susceptibility to particular herbivores, as the Resource Specialization Hypothesis predicts (Price 1983). Like

species richness, arthropod abundances increased with genotypic diversity. In addition, there was a positive relationship between ANPP and both arthropod richness and abundance. Arthropod richness and abundance were positively correlated with one another. To test whether the effects of ANPP and genotypic diversity on arthropod species richness resulted from species-rich plots having more arthropod individuals, as the More Individuals Hypothesis predicts (Srivastava and Lawton 1998), we used rarefaction to examine the response of rarefied arthropod species richness to genotypic diversity. Rarefaction corrects for differences in the number of individuals among plots (Gotelli and Graves 1996). There was no relationship between rarefied total arthropod richness and ANPP, or between rarefied herbivore and predator richness and ANPP ($P > 0.10$ in all cases) indicating that ANPP controls richness by affecting the number of individual arthropods. Rarefied total richness and rarefied herbivore richness instead increased as plot-level genotypic diversity increased, but rarefied predator richness did not (Fig. II-5). However, rarefied predator richness did depend on rarefied herbivore richness suggesting an indirect effect of host-plant genotypic diversity on predator diversity mediated by herbivore diversity (Fig. II-5). These results indicate that increasing genotypic diversity increases the amount of resources (i.e., ANPP) available to herbivores. As ANPP increased, so did arthropod abundance, resulting in increases in the number of species, as the More Individuals Hypothesis predicts (Srivastava and Lawton 1998). When we controlled for variation in arthropod abundance using rarefaction, genotypic diversity explained an additional 12% of the variation in rarefied total and rarefied herbivore richness, indicating a second mechanism by which genotypic diversity affects arthropod communities - by increasing the diversity of resources available, as

predicted by the Resource Specialization Hypothesis (Price 1983). Moreover, the abundance and composition of herbivore assemblages was more similar within *Solidago* genotypes than among genotypes, and particular genotypes were more susceptible to herbivory than were others (Fig. II-6, Fig. II-7). Taken together, these results suggest that particular herbivores are associated with particular host-plant genotypes.

To compare our results to studies that have examined how plant species diversity affects arthropod diversity and ANPP, we calculated the standardized effect sizes (SES) (Scheiner and Gurevitch 1993) of genotypic diversity using our data and the SES of plant species diversity using data from the Cedar Creek LTER Biodiversity II experiment (Siemann et al. 1998). A SES measures the number of standard deviations that the most diverse plots (12 genotypes in our case, 16 species from Cedar Creek) is above or below the single-genotype or single-species plots. Surprisingly, the SES of plant genotypic diversity on arthropod diversity in our study (SES = 1.80) was nearly two times the SES of plant species diversity on arthropod diversity from Cedar Creek (SES = 0.93). The SES of plant genotypic diversity (SES = 1.33) on ANPP in our study was similar to SES of plant species diversity on ANPP at Cedar Creek (SES = 1.35). Our results indicate that the effect of genotypic diversity within a host-plant population is directly comparable to the effect of species diversity within a plant community on associated arthropod communities and ANPP (Siemann et al. 1998, Haddad et al. 2001). A field experiment that orthogonally manipulates genotypic diversity and species diversity in concert could further elucidate the relative contributions of intra- and interspecific diversity on community- and ecosystem-level processes.

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In conclusion, our work provides two mechanisms underlying the relationships among intraspecific genotypic diversity, the diversity of associated consumers, and ecosystem processes. We explicitly show that the effect of genotypic diversity on arthropods does not occur simply because of increased ANPP in diverse plots. It also arises because of an increase in diversity of resources available to herbivores. These effects are non-additive and cascade across trophic levels to structure associated communities. Our results demonstrate the need to incorporate intraspecific variation into current ecological theory that has emphasized the importance of interspecific variation (Siemann et al. 1998, Haddad et al. 2001, Hooper et al. 2005, Loreau et al. 2002, Huston 1997, Loreau and Hector 2001) or theory that ignores differences among species (Hubble 2001). Given the focus of conservation efforts on how the loss of species from communities affects ecosystem processes, our work suggests that loss of genotypes from populations can no longer be overlooked (Johnston et al. 2006, Whitham et al. 2003, Luck et al. 2003, Wimp et al. 2005).

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Appendix II: Figures and Tables

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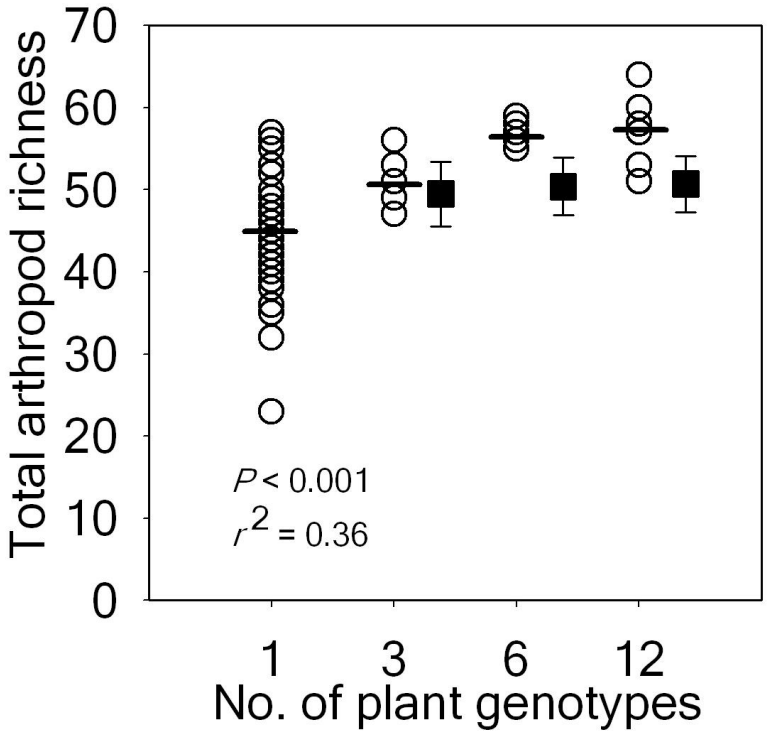

Figure II-1. Relationship between population-level genotypic diversity of *Solidago altissima* and total arthropod species richness. Open circles indicate plot-level observations, and horizontal lines indicate treatment means. Filled boxes indicate the number (± 95% confidence interval) of arthropod species predicted by simple additive models.

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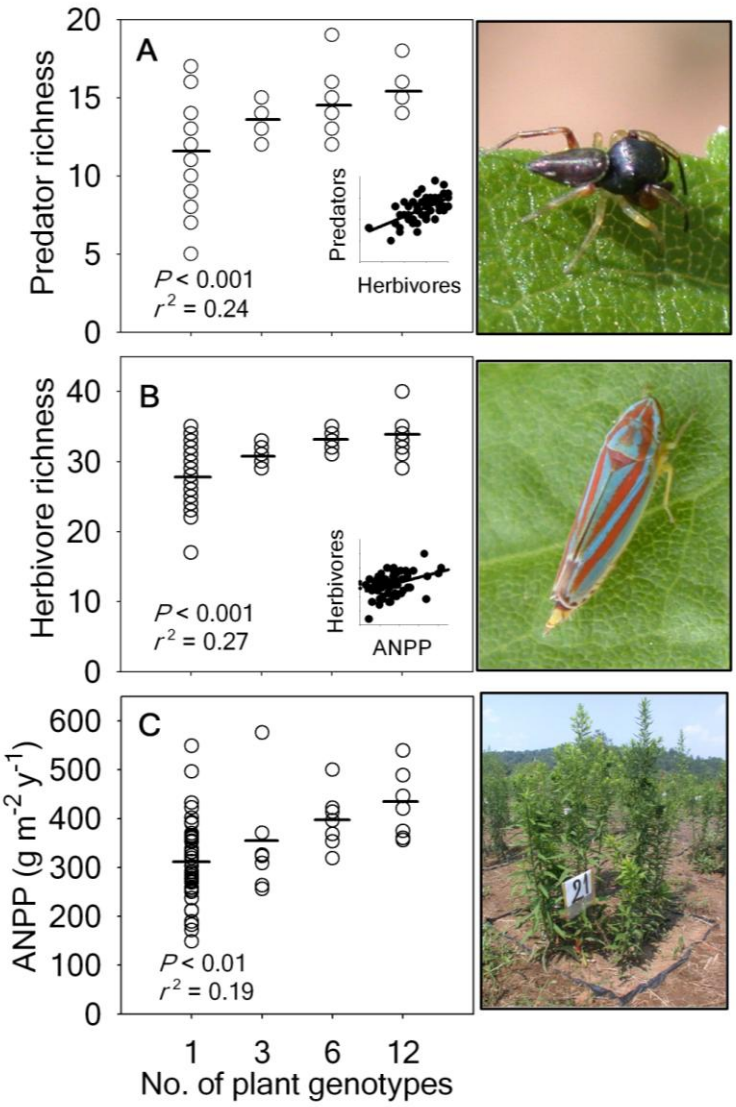
A
Predator richness
20
15
10
5
0
P < 0.001
r² = 0.24
Predators
Herbivores
B
Herbivore richness
40
30
20
10
0
P < 0.001
r² = 0.27
Herbivores
ANPP
C
ANPP (g m⁻² y⁻¹)
600
500
400
300
200
100
0
P < 0.01
r² = 0.19
21
1
3
6
12
No. of plant genotypes

.

Figure II-2 Relationship between population-level genotypic diversity and predator species richness (**A**), herbivore species richness (**B**), and aboveground net primary productivity (ANPP) of *Solidago altissima* (**C**). Open circles indicate plot-level observations, and horizontal lines indicate treatment means. Inset figure in (**A)** shows the relationship between herbivore species richness and predator species richness ($r^2 = 0.36$, $P < 0.001$), and inset in (**B**) shows the relationship between ANPP and herbivore richness ($r^2 = 0.17$, $P < 0.001$).

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Figure II-3. Photograph shows experiment in late July at the peak of the growing season

(Photo credit: G

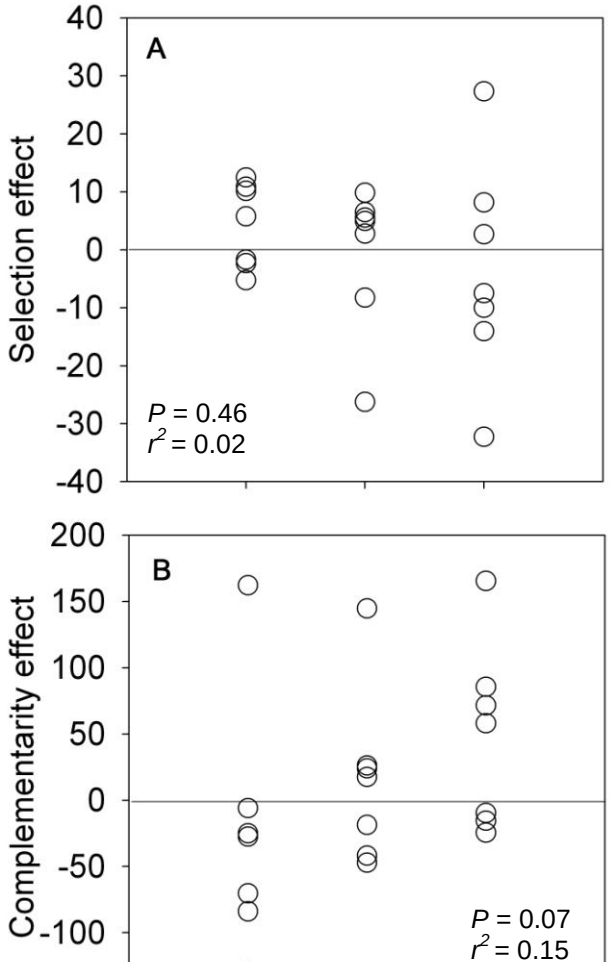

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Figure II-4. Relationship between selection effects (**A**) and complementarity effects (**B**) and *Solidago altissima* genotypic diversity.

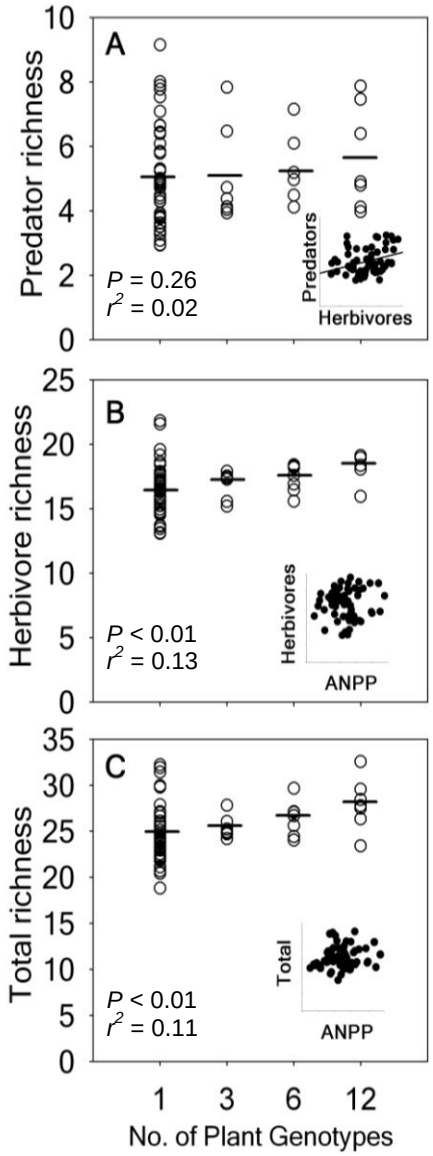

Figure II-5. Relationship between population-level genotypic diversity and rarefied predator species richness (**A**), rarefied herbivore species richness (**B**), and rarefied total species richness (**C**). Open circles indicate plot-level observations, and the horizontal lines indicate treatment means. The inset figure in (**A)** shows the relationship between rarefied herbivore species richness and rarefied predator species richness (r^2 = 0.10, P = 0.009). The inset in (**B**) shows the relationship between ANPP and rarefied herbivore richness (r^2 =0.0002, P = 0.95). The inset in (**C**) shows the relationship between ANPP and rarefied total richness (r^2 = 0.01, P = 0.28).

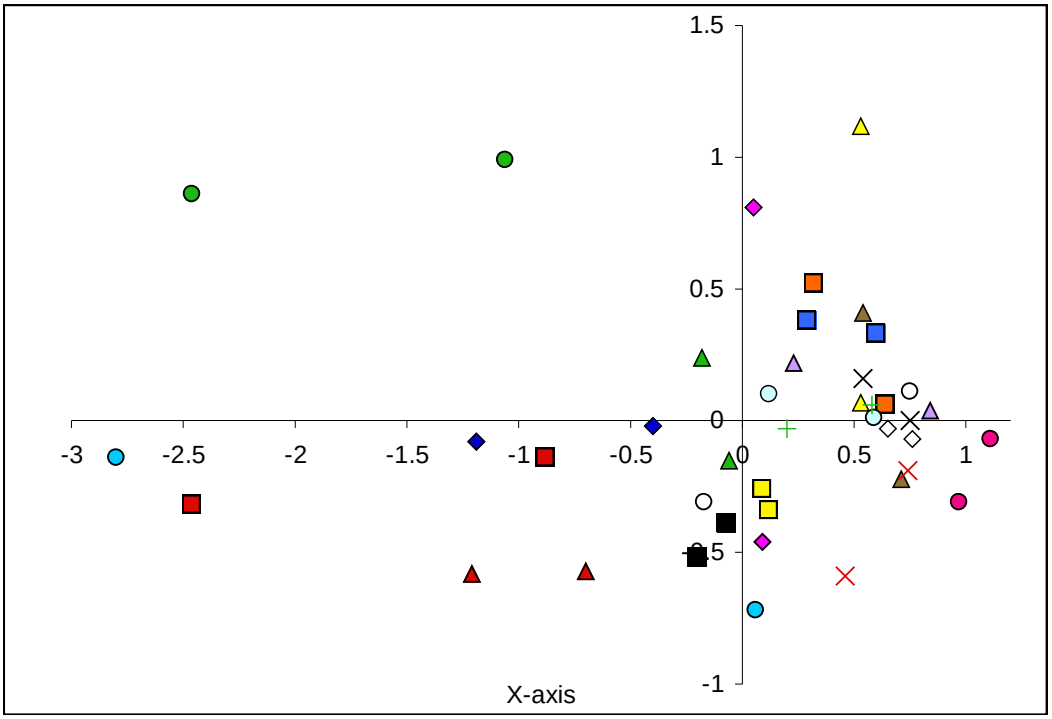

Figure II-6. NMDS (nonmetric multidimensional scaling) ordination demonstrates that the composition of herbivore assemblages on particular *Solidago altissima* genotypes differed significantly from one another (ANOSIM: $R = 0.348$, $P = 0.01$). Each point represents an herbivore assemblage for a given plot ($n = 2$ plots per genotype, matching in color and shape).

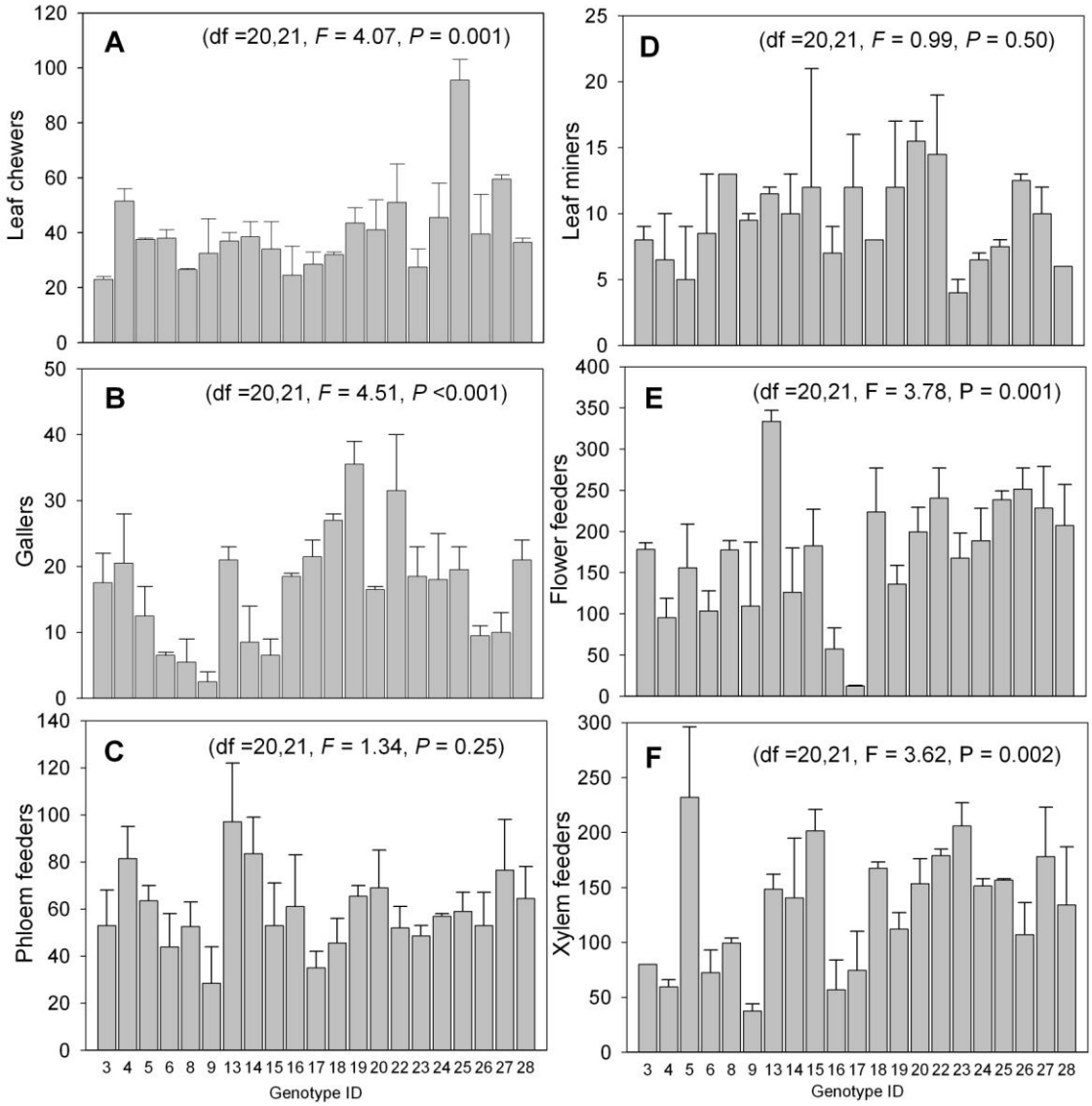

Figure II-7. Plot-level mean cumulative abundance (± SE) of six herbivore feeding guilds across 21 *Solidago altissima* genotypes, including leaf chewers (**A**), gallers (**B**), phloem feeders (**C**), leaf miners (**D**), flower feeders (**E**), and xylem feeders (**F**).

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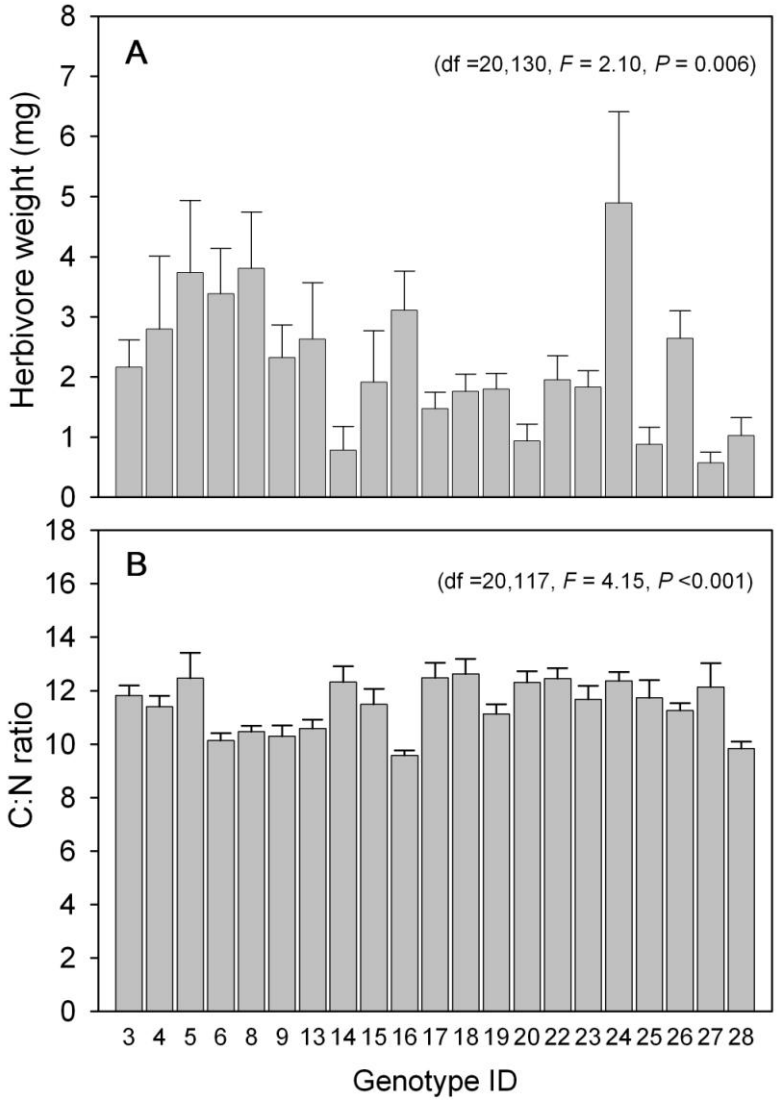

Figure II-8. Herbivore performance measured as mean final weight (± SE) of *Spodoptera* caterpillars during feeding trials (**A**) and mean C:N ratio (± SE) for green leaf tissue (**B**) for 21 *Solidago altissima* genotypes.

.

Fig.

Figure II-9. Results of AFLP genotyping analysis using Non-Metric Multidimensional Scaling. Individual *Solidago altissima* ramet genotypes are illustrated in this ordination based on overall genetic similarity measured as Cavalli-Sforza and Edwards distances.

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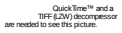

Figure II-10. Bayesian assignment probabilities for number of clusters, *k*=2. Each vertical bar corresponds to one individual *Solidago altissima* ramet. The proportion of each bar that is green represents an individual ramet's assignment probability to cluster 1, the proportion of each bar that is red represents an individual ramet's assignment probability to cluster 2. These results indicate that all ramets have approximately the same assignment probabilities and there is no significant structure among the 21 genotypes.

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Figure II-11. Presence (1) and absence (0) data from 206 AFLP amplicons for 21 *S. altissima* ramets labeled g3-g28.

g3
01110111111010100010101000010000111101111110111100011000010000010101110101000010110100100000011000000010011000000001000110010100011111100001111001100010110000100000000110100101010011001101000000000010000000001

g4
01010111111010100010101000010000111101110111011110101100111000000011111010100011010010001100010100110110011000010100001100101000110110000011100001000101100001000000001110001100100101011010000100000100100001

g5
01110111111010100010101010110000110101110110011100010001010000000110010001010010100010101000100010000001100110000101100001000000000110100000010001110001011001010000000010110010101001011110100000000000110100001

g6
01011111111010110010011000010010111101110110011100011001100100000111110101001010000100111000100011000010011100010110000000101000000100001000111000101100101000000010010101000000111000101110110011110100000000000000101001

g8
01010111111010100010110000010001110101111110111101110001010000010110010100010010100100100000010000000110011000010111000100001000110010001011000011000101001111000000000111111010110001110110100010000010110100001

g9
01110111111111010101010000001000000010111011001110001000111010001010101000101001001010011000010110000011011010010110000100001001010010001001101111100101100101100000000111110101010110001111000000000010100000001

g13
01010111111010100010100000010010011101110110011101010001100000010101110011000110100000101000010001001100110000101000011001010000100000100001011101100011000010001110001000100100001100000100000010010100101

g14
01010011111010100010011000010000111101110110011101010011010001000101100011000010000001010000100011000110111000010111000100001000000010101010111011011110000100000000101001001

g15
11110111111111010001110000101100011111111101101111000100010100000101111000110000100001001000000101000110011100010100000000000000001110000110110010100110011011100000000011100110101001011110000100100001001

g16
01011111111010100011101000011000011111111110111100010001100000010101011111000110000001101000010001000011101000000111000101110010101001000010010000100001

Figure II-11, continued. Presence (1) and absence (0) data from 206 AFLP amplicons for 21 *S. altissima* ramets labeled g3-g28.

g17
011101111111101000101010000100000101011101101011000100110100000101110100110000100000101100
000100010000100110001001100001000010001110100011110000111010001101010001000011100010101001
011110100110000000101111111
g18
010101111110101000101100000100001101011101100111100000100100010101111101010000101110001000
000110100000100111010101010001001100100100000000111000100010011000111000000011110011011111
0001110000000000000100100001
g19
011011111111101010101001000100011101011111100111000110111000001001110100010110101011001000
1001000100111011100001010000000011100101011000101110000000001011001011010000111100010011001
11011000010010001100001001
g20
001110111110110000101110000100011111011101100011000100110101000100111000010100111000010000
0001100100011001100001010000000000010001101100010111000100001111001111000000110100011001011
00111000010000000100100001
g22
011111111110101000101000010100010111111101100111000000010100000001010100000000100001010100
0001010000011001101001011000000100101001011000000110000000001011001110000010011001011000001
00111000010000010110101001
g23
011101111111101000101010000101001111011101101111010000011100010001111100010000100001011010
0001010101011011100001010000000000000000111001100010000010001011000110000000111100010111011
01111110010111110000101000
g24
011010111110101001101011000110101101011101111111000100010100000001010101010100101001001010
0001000000001001100001011100011001010001110000000111100000001001000011000001011100010011001
01011000010010000110101001
g25
0111011111101010001001010001010011011111101100110110100011100010001010100010000101000001000
010100000001100110000101100000000010001100100000110000010001011001010000000010110010101001
01110000100010000100100000
g26
001101111110101000101010100100000101111110101111010101110100111101011111010101101001001000
010101011000101100000101010001000000000101101000011001010001010010010000000111101010111011
110100000000000000000100001
g27
011011111110101000101000000100001100011101100111001010010101000101010101010010101001001010
00010001000010011110010101110100001000010110000001110010100010110010100000010010100011111011
01010110000000000000000001

g28
010010111110101000101010010110001100011101100111000110110110000111011101011000100001011110
01010011000010011100011100011000000100001011000000011000100001001001110000000011110110111001
001110100010100100011000000

Chapter III. Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity

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The following section is a slightly modified version of a paper published in the journal Oikos.

Crutsinger G.M., Collins M.D., Fordyce J.A. & Sanders N.J. (2008) Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. Oikos 117: 255-264

The use of "we" in this part refers to my co-authors and me. As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the design of the experiment, data collection and statistical analyses. I also wrote most of the paper.

Abstract

Genotypic diversity within host-plant populations has been linked to the diversity of associated arthropod communities, but the temporal dynamics of this relationship, along with the underlying mechanisms, are not well understood. In this study, we employed a common garden experiment that manipulated the number of genotypes within patches of *Solidago altissima*, tall goldenrod, to contain 1, 3, 6, or 12 genotypes m^{-2} and measured both host-plant and arthropod responses to genotypic diversity throughout an entire growing season. Despite substantial phenological changes in host plants and in the composition of the arthropod community, we detected consistent positive responses of arthropod diversity to host-plant genotypic diversity throughout all but the end of the growing season. Arthropod richness and abundance increased with genotypic diversity by up to ~ 65%. Furthermore, arthropod responses were non-additive for most of the growing season, with up to 52% more species occurring in mixtures than the number predicted by summing the number of arthropods associated with component genotypes in monoculture. Non-additive arthropod responses were likely driven by concurrent non-additive increases in host-plant aboveground biomass. Qualitative differences among host-plant genotypes were also important early in the season, when specialist herbivores dominated the arthropod community. Neither arthropod diversity nor flower number was associated with genotypic diversity at the end of the growing season, when generalist floral–associated herbivores dominated. Taken together, these results show that focusing on the temporal dynamics in the quantity and quality of co-occurring host-plant

genotypes and associated community composition can help uncover the mechanisms that link intraspecific host-plant diversity to the structure of arthropod communities. Furthermore, consistent non-additive effects in genotypically diverse plots may limit the predictability of the arthropod community based solely on genetic make-up of a host-plant patch.

Introduction

Recent work has shown that intraspecific genotypic diversity within host-plant populations is a key determinant of the diversity of associated communities (Hughes and Stachowicz 2004, Reusch et al. 2005, Wimp et al. 2005, Johnson et al. 2006, Crutsinger et al. 2006). For example, in a correlative study, Wimp et al. (2005) found that plant genotypic diversity explained almost 60% of the variation in arthropod diversity in natural stands of cottonwood trees. Using an experimental approach, Johnson et al. (2006) and Crutsinger et al. (2006) found that the number of species in the associated arthropod community increased as the number of host-plant genotypes in experimental plots increased. However, most studies that have examined the effects of host-plant genotypic diversity have taken only snapshot approaches, either examining the response of communities at a single point in time (Hughes and Stachowitcz 2004, Reusch et al. 2005) or combining repeated sampling events over a growing season (Wimp et al. 2005, Crutsinger et al. 2006). Incorporating temporal dynamics, however, can be important for understanding the consistency of the positive relationship between arthropod diversity

and host-plant genotypic diversity over time. For example, the extent to which arthropod communities respond to host-plant genotypic diversity might change because of temporal shifts in the arthropod species pool. Early season herbivores, such as galling insects, may differentiate between host-plant patches more readily than generalist herbivores (Bernays and Funk 1999), such as those that feed on flowers later in the season. Therefore, as arthropod community composition changes over the course of the growing season, the response of arthropods to host-plant genotypic diversity may also change. In addition, phenological shifts in the host plants themselves, from bolting in the spring, biomass production in the summer, and flowering in the fall, could mediate interactions among host-plant genotypes. Such interactions might include competition or facilitation among genotypes, or how host plants are selected by arthropods, such as plant susceptibility to herbivory. Therefore, host-plant phenology could shape the relationship between host-plant genotypic diversity and arthropod diversity. Distinguishing between these possibilities – whether the relationship between host plants and arthropods changes because of faunal shifts or floral shifts – requires incorporating a temporal perspective.

Examining temporal dynamics can also help distinguish among several competing mechanisms that might drive the positive relationship between arthropod and plant genotypic diversity, such as whether the effects of genotypic diversity are additive or non-additive. For example, different host-plant genotypes support unique arthropod assemblages in a variety of study systems (Maddox and Root 1987, Fritz and Simms 1992, Whitham et al. 2006), and as the number of genotypes in a host-plant population

increases, so should the number of corresponding arthropod species (Wimp et al. 2005, Bangert et al. 2005, Johnson et al. 2006, Crutsinger et al. 2006). Such additive effects of genotypic diversity on arthropod communities may occur because patches with more plant genotypes are more likely to contain genotypes that have strong effects on the arthropod community than do patches with fewer genotypes (i.e. sampling effects; Huston 1997, Loreau and Hector 2001, Hooper et al. 2005). By contrast, numerous direct and indirect interactions among host-plant genotypes or among arthropods within a patch can occur throughout a growing season resulting in more, or fewer, arthropod species in genotypically diverse plots than predicted by additive genotypic effects (Johnson et al. 2006). Such non-additive effects of genotypic diversity may be common, as the few other studies that have examined the effects of genotypic diversity have all found some degree of non-additivity in responses of associated communities and/or ecosystem processes (Schweitzer et al. 2005, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Crawford et al. 2007).

Whether arthropods respond additively or non-additively to host-plant genotypic diversity may vary over the course of the growing season. For example, interactions among plant genotypes early in the season, such as resource competition or facilitation, could lead to non-additive responses of host-plant biomass (Reusch et al. 2005, Crutsinger et al. 2006), which, in turn, could result in more or fewer arthropod species later in the season than predicted. Moreover, interactions among arthropods themselves, such as predators that directly feed on species trying to colonize plants or early-season

herbivores that affect plant quality or architecture for late-season species (Van Zandt and Agrawal 2004), might lead to more or fewer arthropod species than predicted. By examining temporal variation in whether arthropods respond additively or non-additively to host-plant genotypic diversity, we can determine whether particular genotypes shape the relationship between arthropod diversity and host-plant genotypic diversity over time, or whether interactions among co-occurring genotypes are also important.

Here, we examine the effects of host-plant genotypic diversity in the perennial plant, *Solidago altissima*, on the associated arthropod community throughout the course of an entire growing season. Previous results from this system revealed a positive, non-additive relationship between cumulative arthropod richness (summed over the entire season) and *S. altissima* genotypic diversity (Crutsinger et al. 2006). In this study, we ask three separate questions aimed at revealing the temporal dynamics of the effects of host-plant genotypic diversity on the diversity of associated arthropod communities and the mechanisms that might link host-plant genotypic diversity to arthropod diversity. Specifically, we ask: (1) Do phenological shifts in host plants or in arthropod community composition affect the relationship between arthropod diversity and plant genotypic diversity? (2) Are the responses of arthropods to genotypic diversity driven by particular genotypes (additive effects) versus interactions among genotypes (non-additive effects) over time? (3) Do host-plant quantitative traits (biomass and flower number) explain arthropod responses to genotypic diversity throughout the growing season?

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Materials and methods

Study site and system

This research was initiated during Spring of 2005 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park near Oak Ridge, Tennessee (35º58'N, 84º12'W). The site was abandoned from agricultural use in 1943 and has been managed for open-space and wildlife habitat by ORNL and the Tennessee Wildlife Resource Agency. The fields surrounding the experimental area are typical of other old fields in east Tennessee in plant community composition. Besides *Solidago altissima*, dominant plant species include *Verbesina occidentalis* L. (yellow crownbeard), *V. virginica* L. (white crownbeard), and *Rubus* spp. (blackberry); sub-dominants include about 60 other herbaceous and woody species (L. Souza et al. unpublished data).

Solidago altissima, or tall goldenrod, is a well-studied perennial that dominates old-field ecosystems throughout eastern North America (Werner 1980) and maintains a diverse community of arthropod species (Maddox and Root 1987, 1990; Root and Cappuccino 1992; Crutsinger et al. 2006, Crawford et al. 2007). Local populations of goldenrod contain clones that exhibit considerable inter-clonal genetic variation in many plant traits, including those that influence resistance to arthropod communities, such as leaf tissue quality, biomass production, or stem thickness (Abrahamson and Weis 1997, Crutsinger et al. 2006). As a result, individual genotypes of *S. altissima* can vary considerably in

their overall arthropod community composition (Maddox and Root 1987, 1990, Crutsinger et al. 2006), and resistance or susceptibility of genotypes to herbivore species can remained relatively constant over several years (Maddox and Root 1987). Genotypic diversity in natural goldenrod patches can vary from 1 to 12 genotypes m^{-2} creating a natural mosaic of single-genotype and mixed-genotype patches of plants (Maddox and Root 1989). At the study site, *S. altissima* plants bolt in mid-April with leaf senescence and peak flowering occurring in early October (Crutsinger *unpublished data*).

Common garden experiment

In May 2005, we manipulated plot-level genotypic diversity (the number of genotypes per plot) of *S. altissima*. Twenty-one *S. altissima* ramets were collected from local *S. altissima* patches growing in fields surrounding the study site, and each ramet was identified as a unique genotype by means of amplified fragment length polymorphisms (AFLPs). All 21 genotypes were approximately equally related (Crutsinger *et al*. 2006). From these 21 genotypes, we established 63 1 m^2 experimental plots in a 15 m x 20 m grid, with each plot randomly assigned to contain 12 individuals and 1, 3, 6, or 12 genotypes. Genotype mixtures were created by randomly sampling from the pool of 21 genotypes with the constraint that no two patches in a treatment could have identical composition (seven replicates each). The one-genotype treatment consisted of all 21 genotypes planted individually in two replicate monoculture plots. A 3 m tall fence made of 2.54 cm poultry wire encircled the experiment to exclude deer. For further details on

the study site, common garden establishment, or AFLP analyses see Crutsinger et al. (2006).

To examine responses of arthropod richness, abundance, and community composition to genotypic diversity within *S. altissima* plots, we visually censused arthropods on each ramet within each plot five times over the course of the growing season. Arthropod surveys were conducted on sunny, relatively wind-free days beginning on May 22nd, June 15th, July 23rd, Sept. 3rd, and Oct 3rd of 2005, and surveys lasted from one to four days. Between 0900 to 1600 hrs, we counted all arthropods by scanning the entire plant, which included all new ramets that sprouted from the original ramet during the course the growing season. Therefore, surveys took longer as genets produced more ramets throughout the season. All arthropods were identified to feeding guild and morphospecies. One or two individuals of each morphospecies were taken back to the lab for further identification (See Table III-8 for the most common species). Flowering by *S. altissima* in October obscured many floral-associated species, so after visually surveying the entire plant and any obvious species on flowers (e.g. bees, wasps), we shook each flower head three times onto a laminated piece of white paper and quantified all arthropods that fell onto the paper.

Statistical analyses

To examine whether the response of arthropod richness and abundance to host-plant genotypic diversity varied temporally, we used separate repeated-measures ANOVAs,

with richness and abundance as response variables and the number of genotypes as a treatment variable. We also used separate one-way ANOVAs to examine the effect of genotypic diversity treatments on arthropod species richness and abundance within each of the five survey periods. For both analyses, arthropod richness and abundances were log-transformed prior to analysis to improve normality and homogenize variances. However, for clarity, we show the untransformed values in all figures.

We examined whether arthropod community composition differed among treatments and sample periods because composition takes into account both the identity and relative abundance of species, not just the total number of species or individuals. We examined four aspects of temporal variation in arthropod community composition. First, we examined how the total arthropod community changed among survey periods for all plots for all time periods using the Bray-Curtis similarity index (Bray and Curtis 1957). We used analysis of similarity (ANOSIM), followed by separate pairwise comparisons, to examine whether arthropod community composition differed among survey periods. In ANOSIM, the generated *R* statistic is a relative measure of separation of defined groups. A value of 0 indicates that similarities between and within a survey period are the same on average (i.e. little or no between-survey differences). A value of 1 indicates that all replicates within a survey period are more similar to each other than any replicates from different surveys (i.e. high between-survey differences) (Clarke and Gorley 2001). We present these results graphically using non-metric multidimensional scaling (NMDS), which is an ordination procedure using Bray-Curtis similarity values (Clarke and Gorley

2001). Second, we examined whether arthropod community composition differed among genotypic diversity treatments within each survey period using separate ANOSIMs. ANOSIM and ordination procedures were run using Primer statistical package (Version 6, 21 Primer-E Ltd., Plymouth Marine Laboratory, Plymouth, UK). Third, we examined the proportion of total arthropod abundance that each feeding guild made up in each survey period. Guilds included herbivores (leaf/stem feeders), predators, omnivores, florivores (includes both pollen/flower feeders), and other (transients, detritivores, and unknowns). Species were assigned to guilds based on field observations or by consulting relevant primary literature (Fontes et al. 1994). Fourth, within the herbivore guild, we examined the relative abundances of generalists and specialists across the growing season.

To examine further the relationship between arthropod richness and host-plant genotypic diversity across the growing season, we performed Monte Carlo simulations to test whether the effects of genotypic diversity on arthropod communities varied from additive to non-additive. We used data from genotype monoculture plots to construct null genotype mixtures (termed "additive mixtures" hereafter), along with their associated "additive" arthropod communities. Each additive mixture consisted of 3, 6, or 12 genotypes sampled to match the exact identities corresponding to a particular plot combination (e.g., for a 3-genotype plot containing G3, G13, and G19, we sampled only from monoculture plots of these genotypes) (Johnson et al. 2006, Crutsinger et al. 2006). For each sampled genotype, the appropriate number of individual ramets for a given

diversity level (four, two, or one) was randomly sampled without replacement from a randomly selected replicate monoculture plot. This process was repeated 5,000 times for each mixed-genotype plot and within each of the five sampling periods (25,000 total randomization for each of the 21 mixed genotype plots). Here, we examined only arthropod richness, but arthropod abundance was highly correlated with richness throughout the growing season (May $r = 0.59$, $P < 0.001$; June $r = 0.83$, $P < 0.001$; July $r = 0.62$, $P < 0.001$; September $r = 0.74$, $P < 0.001$; October $r = 0.53$, $P < 0.001$).

To determine whether arthropod richness in observed mixtures differed from predicted richness in additive mixtures within each sampling period, we used a bootstrapping approach. For each of 10,000 iterations, we sampled seven additive mixtures and calculated the mean number of arthropod species at the plot-level. We calculated *P*-values as the fraction of iterations in which the additive mean arthropod richness was equal to or greater/less than the observed mean richness. 95% confidence intervals were calculated using the percentile method (2.5^{th} and 97.5^{th} percentiles). If the effects of genotypic diversity on arthropod richness were additive, we would expect no difference between observed and predicted means ($P > 0.05$). All Monte Carlo simulations were coded in Microsoft Visual C++ 6.0 (Microsoft, Redmond, WA, USA).

To examine whether host-plant biomass responded to genotypic diversity over the growing season, we estimated plot-level aboveground plant biomass throughout the growing season using an allometric equation developed specifically for *S. altissima* based

on plant height (for details see Crutsinger et al. 2006), which allowed for repeated estimates of biomass without affecting the arthropod community. To estimate flower number, we counted the number of blooming capitula on the inflorescences of every ramet during the October survey, the peak flowering time of *S. altissima* at our site. We then harvested all inflorescences after seeds had set at the end of the field season, oven-dried them for 48 hrs, and weighed them. There was a strong correlation between our visual estimates of flower number and inflorescence mass ($r = 0.64$, $P < 0.001$), indicating that our visual methods provide an adequate estimate of the potential floral resources and sexual reproductive output by host plants.

We used repeated-measures ANOVA to test for the effects of genotypic diversity on plant biomass from May to September. We used a one-way ANOVA to test for the effects of genotypic diversity on flower number in October. We then used a Monte Carlo simulation similar to that used for arthropods to test for non-additive responses of plant biomass to genotypic diversity from May-September, and non-additive responses of flower number to genotypic diversity in October.

In this paper, we focus mainly on whether the quantity of resources (biomass and flower abundance) provided by host plants links arthropod community structure to plant genotypic diversity throughout the growing season. It is possible that arthropods respond to numerous qualitative differences in host-plant genotypes in this system (Abrahamson et al. 1991, Root and Cappuccino 1992, Abrahamson and Weis 1997, Crutsinger et al.

2006), and identifying all the potential traits that arthropods respond to is beyond of the scope of this study. However, we can correct for qualitative differences among experimental plots, which would indicate when during the growing season qualitative differences among genotypic diversity treatments might be important. We corrected for the effects of resource quantity on arthropod richness using rarefaction. Rarefaction is a randomization-based procedure that corrects for biases in species richness that arise from differences in the number of individuals between two communities (Gotelli and Colwell 2001). In our case, rarefaction corrects for the influence of host-plant biomass/flower number by rarifying species abundances in all plots down to the abundance in the plot that has the fewest individuals. We rarefied arthropod richness within each survey period using EcoSim 7 (Version 7, Gotelli and Entsminger 2006). We compared rarefied richness to genotypic diversity within each month using separate single-factor ANOVAs. We did not use Bonferroni corrections for any of the analyses because such corrections inflate the probability of committing Type II errors (Gotelli and Ellison 2004).

Results

In each survey period except October, arthropod richness was greater in plots with high host-plant genotypic diversity than in plots with low genotypic diversity (Fig. III-1A, Table III-1 and III-2): richness in 12-genotye plots was 35% greater than richness in monoculture plots in May, 65% greater in June, 37% greater in July, and 43% greater in September. Similarly, arthropod abundance increased with host-plant genotypic diversity,

except in the May or October survey periods (Fig. III-1B, Table III-3 and III-4): arthropod abundance was 63% greater in 12-genotype plots than in monoculture plots in June, 56% greater in July, and 53% greater in September. No significant time × genotypic diversity interactions were detected for either arthropod richness or abundance (Table III-1 and III-3).

Though the effect of host-plant genotypic diversity on arthropod community composition varied at the end of the growing season, community composition of arthropods differed dramatically among survey periods. This indicates that there was substantial phenological turnover in arthropod communities on *S. altissima* plants from May to October (Fig. III-2, Table III-5), but that the effect of genotypic diversity on arthropod richness was mostly consistent among survey periods. All survey periods differed from one another in terms of arthropod community composition (Fig. III-2, Table III-5), but community composition did not vary among genotypic diversity treatments within any survey period ($P > 0.20$ for all survey periods). Herbivores associated with leaves and stems made up the largest proportion of total arthropod abundances within all survey periods, except in October when flower-associated species (floral/pollen feeders) were most common (Appendix C). Furthermore, early season herbivores consisted mainly of specialists (60% of total herbivore abundance), such as stem and leaf gallers and leaf miners. But by the end of the season, generalist herbivores, such as pollinators and *Lygus* bugs, comprised most of the herbivore community (94% of total herbivore abundance) (Fig. III-3).

For all survey periods except October, the response of arthropod species richness to genotypic diversity was non-additive. That is, there were more arthropod species present in at least one of the genotypic diversity treatments than the number predicted by additive models (Fig. III-5A). The magnitude of non-additive responses of arthropod species to genotypic diversity varied temporally. There were, on average, 22% more arthropod species in genotypically diverse plots than predicted in May, 52% more than predicted in June, 26% more than predicted in July, and 29% more than predicted in September (Fig. III-5A). In May, only the 12-genotype plots showed non-additive responses of arthropods; both 6- and 12-genotype treatments were non-additive in June; and all treatment levels showed non-additive responses in July and September (Fig. III-5A). In October, there was no difference in the number of observed species compared to the number predicted by the additive mixtures; that is, diversity of arthropod species on *S. altissima* was an additive function of genotypic diversity in October.

Aboveground plant biomass increased with host-plant genotypic diversity in each survey period, except May (Fig. III-4, Table III-6 and III-7). Biomass in June was on average 16% greater, biomass in July was 36% greater, and biomass in September was 28% greater when comparing 12-genotype treatments to monocultures. There was also a significant interaction between genotypic diversity and time, likely reflecting the higher plant biomass in genotypically diverse plots later in the season compared to early in the season (Appendix III-6).

For all survey periods, the response of aboveground plant biomass to genotypic diversity was non-additive. That is, there was more biomass in genotypically diverse plots than the biomass predicted by additive mixtures (Fig. III-5B). The magnitude of non-additive effects was consistent from the May-July with up to ~43% more biomass, and up to 29% more biomass than predicted by additive mixtures in September (Fig. III-5B).

We detected no effect of genotypic diversity on the total number of flowers per plot in October (Fig. III-4, Table III-7). However, when we compared the observed number of flowers present in mixtures to the number predicted by additive mixtures, there were 20% more flowers in 6-genotype mixtures ($P = 0.06$) and 103% more flowers in 12-genotype mixtures ($P < 0.001$) than the number of flowers predicted by additive mixtures (Fig. III-5B), suggesting that individual genotypes produced more flowers when grown in mixtures than in monocultures.

Arthropod species richness was positively correlated with host-plant biomass in each sample period from June through September, but not in May (May $r = -0.09$, $P = 0.47$; June $r = 0.51$, $P < 0.001$; July $r = 0.35$, $P = 0.004$; Sept. $r = 0.32$, $P = 0.009$). There was also a positive correlation between arthropod richness and flower number in October ($r = 0.74$, $P < 0.001$).

Rarified arthropod richness increased with genotypic diversity only in June (df = 3, 59, $F = 3.651$, $P = 0.017$; $P > 0.35$ for other survey periods). Thus, when correcting arthropod

richness for the effects of increased biomass with genotypic diversity, there was still an increase in arthropod diversity in June, indicating other qualitative traits were likely important at this time.

Discussion

This experiment showed that intraspecific genotypic diversity in experimental patches of *Solidago altissima* was consistently and positively related to arthropod diversity throughout most of a growing season, despite substantial phenological changes in both host plants and arthropod community composition. The strength of the relationship between genotypic diversity and arthropod diversity was dampened at the end of the growing season and the potential mechanisms driving the positive relationship varied temporally.

Both arthropod species richness and abundance were up to ~65% greater in genotypically diverse plots than in monoculture plots during early and middle parts of the season (Fig. III-1). These results are similar to those found by other studies investigating the effects of genotypic diversity on associated arthropod communities. For example, Johnson et al. (2006) experimentally examined the response of arthropod communities to genotypic diversity of common evening primrose (*Oenothera biennis*). They found that total arthropod richness, but not abundance, increased with genotypic diversity as the growing season progressed. Reusch et al. (2005) surveyed the aquatic invertebrate fauna on experimental plots of one to six genotypes of seagrass (*Zostera marina*), but only during

a final survey in September. They found higher total abundance, but not richness, of associated invertebrates with increased seagrass genotypic diversity.

We did not detect responses in arthropod abundance to genotypic diversity in May (Fig. III-1B), perhaps because few arthropod species had emerged to colonize host plants (i.e. small arthropod species pool), and there was not yet a strong plant biomass response to genotypic diversity (Fig. III-4). An alternative explanation is that resistance of plants to arthropods decreases as the season progresses, but this is probably not the case because resistance in *S. altissima* is known to increase with plant maturity (Abrahamson et al. 1991).

We did not detect a response of arthropods to genotypic diversity at the end of the season (Fig. III-1). During this time, the arthropod community consisted mostly of generalist, floral-associated species (Fig. III-3, Fig. III-6). Both richness and abundance of these species were strongly correlated with the number of open flowers in October. Because the average number of flowers did not increase with host-plant genotypic diversity (Fig. III-4), we did not observe an increase in arthropod richness with host-plant genotypic diversity during this survey. Contrary to our results, Johnson et al. (2006) found that total arthropod richness increased with host-plant genotypic diversity at the end of their growing season (mid-August). They hypothesize that genotypically diverse plots in their system flower earlier and longer, thus maintaining a longer period of resource availability and accumulating arthropod species for a longer period (Johnson et al. 2006). Though we

did not examine variation in flowering phenology in our study, flowering time is highly genotype dependent in *Solidago* (Pors and Werner 1989), and genotypic diversity appeared to be positively associated with longer patch-level flowering periods due to staggered flowering times among genotypes (GM Crutsinger, *personal observation*). While genotypically diverse plots may possess open flowers for an extended time, floral-associated arthropods in the *S. altissima* system probably do not appear to accumulate on patches with earlier and longer flowering periods. Goldburg (1987) manipulated the timing and duration of flowering in *Solidago* patches using multiple sequentially-flowering *Solidago* species, with *S. altissima* being the last to flower. Goldburg (1987) did not observe higher abundances (i.e. no accumulation) of experimentally-released florivorous beetles on *S. altissima* plants in patches with longer flowering times. Our results suggest that the number of open flowers in a patch rather than length of flowering time, shapes arthropod diversity during peak *S. altissima* flowering.

There were strong phenological shifts in arthropod community composition on *S. altissima* plants over the course of the growing season (Fig. III-2 and III-3).). Despite high compositional shifts, the effects of genotypic diversity on arthropod richness and abundance were consistent for all survey periods except at the end of the growing season. The July and September surveys had the most similar arthropod communities because the communities were comprised of similar mid- to late summer species. However, there were large compositional shifts between the September and October surveys, once flowering initiated (Fig. III-3). The composition of the arthropod community in the

genotypically diverse treatments never differed from the composition in the one-genotype treatment within any survey period. The similarity of the arthropod communities across treatments might be a consequence of the mixtures consisting of a subset of the same genotypes that made up the one-genotype treatment. Therefore, the arthropod species pool across genotypic diversity treatments was not different.

For most of the growing season, there were more arthropod species in genotypically diverse plots than the number predicted by summing the independent contributions of individual genotypes grown in monocultures (Fig. III-5A). That is, arthropod species richness consistently responded to genotypic diversity in a non-additive fashion from May through September, but not in October. Crutsinger et al. (2006) found 17% more arthropod species in genotypically diverse plots for the entire season than predicted by simple additive effects. Reusch et al. (2005) also tested for non-additive effects of genotypic diversity in *Z. marina* patches on invertebrate abundances and found 22% more individuals in 6-genotype plots compared to additive predictions. By contrast, Johnson et al. (2006) found that increases in arthropod richness with increasing genotypic diversity in evening primrose were almost entirely explained by additive effects, but did find non-additive responses when partitioning the arthropod community into various trophic levels, with cumulative omnivore abundances being 73% higher in plant genotype mixtures than predicted. But the question remains: why is species richness of associated arthropods a non-additive function of host-plant genotypic diversity?

As the growing season progressed, aboveground plant biomass was positively associated with the number of plant genotypes in a plot. Increased plant biomass could be due to sampling or selection effects, where randomly assembled mixtures have a higher probability of containing and becoming dominated by highly productive genotypes (Huston 1997, Loreau and Hector 2001, Hooper et al. 2005). We accounted for sampling effects by growing all genotypes in monocultures with replication to compare to how well the same genotypes grew in mixtures. Our Monte Carlo methods of additive partitioning produced qualitatively similar results to standard methods used in biodiversity experiments to test for overyielding (Trenbath 1974, Hector and Loreau 2001, Crutsinger et al. 2006), and indicate that highly productive genotypes are not entirely responsible for observed increases in aboveground plant biomass with genotypic diversity in any sampling period from June to September (Fig. III-5B). We did not detect a significant effect of genotypic diversity on flower number in October at the treatment level, but we did see an effect at the individual genotype level (see below). Our failure to detect a response in flowers was likely because of high variation in flower number in the one-genotype treatment. When some genotypes were in full bloom, others had finished flowering or were still in bud. Conversely, mixtures had staggered flowering times and always had a high likelihood of containing genotypes that had finished flowering or were still in bud. Therefore, while variation in the number of open flowers among plots was reduced in mixtures, the average number of open flowers was not different across diversity treatments.

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In our study, individual genotypes performed better (up to 46% more biomass than predicted, and 103% more flowers than predicted) when grown in mixtures than when grown in monocultures (Fig. III-5B). These non-additive plant performance results are consistent with other studies. For example, Johnson et al. (2006) found that genotypes of evening primrose growing in mixtures had 27% higher fruit production than when the same genotypes were reared in monocultures. Reusch et al. (2005) found that genotypically diverse plots of seagrass had 26% more biomass than predicted from monocultures because mixture plots suffered less from heat-related mortality. Zhu et al. (2000) found that rice yields increased with genotypic diversity because of reduced disease infection in diverse mixtures compared to monocultures. We have not yet explicitly examined potential mechanisms underlying increases in host-plant performance with increasing genotypic diversity, but we suspect that positive interactions such as niche complementarity or facilitation among genotypes play a role (Hooper et al. 2005).

Since arthropod species richness was positively correlated with plant biomass, observed increases in arthropod richness with host-plant genotypic diversity were probably due to concurrent increases in the amount of host-plant biomass available. Furthermore, because plant biomass responded non-additively to genotypic diversity (i.e. more biomass than predicted), the response of arthropod species richness to host-plant genotypic diversity was also non-additive. This explanation is consistent with the mechanisms proposed to explain why arthropod species richness increases with plant species richness (Siemann et al. 1998, Haddad et al. 2001). We fully recognize that numerous other plant traits that we

did not measure in this study, either correlated or uncorrelated with the quantity of host plants (biomass or flower abundance), might affect the arthropod community associated with *Solidago* (Abrahamson and Weiss 1997). However, biomass and flower abundance explained much of the observed responses of arthropods over the growing season. When we corrected for the influence of resource quantity on arthropod richness through the use of rarefaction, we found a significant increase in rarefied richness with host-plant genotypic diversity in June. This was the survey period with the highest non-additive responses of arthropod richness (~ 9 more species than predicted), and when the herbivore community was dominated by species that specialize on *Solidago*. Specialists may show more discrimination for qualitative differences among host-plant patches, compared to generalist herbivores that dominate later in the season (Bernays and Funk 1999). Therefore, while the positive relationship between genotypic diversity and arthropod diversity remained mostly consistent, the host-plant cues driving arthropod responses to host-plant genotypic diversity (qualitative versus quantitative) likely varied over the course of the growing season, depending on the arthropod species colonizing patches.

Numerous indirect effects of host-plant genotypic diversity, such as effects on keystone herbivores within the community (Whitham et al. 2003, Bailey et al. 2004, Crawford et al. 2007) can occur and might also positively and non-additively affect the diversity of associated species. For example, Crawford et al. (2007) found that the bunch-galling midge, *Rhopalomyia solidaginis*, that creates rosettes of leaves at the tips of *S. altissima*

plants provides a microhabitat for a unique suite of arthropod species that secondarily use the galls, thereby increasing species diversity on galled stems. Crawford et al. (2007) found a positive and non-additive relationship between gall abundance and *S. altissima* genotypic diversity. Since galling is initiated early in the season, more galls in genotypically diverse plots may have contributed to observed non-additive increases in arthropod diversity later in the season.

Conclusions

By taking a temporal approach to understand how and why arthropod diversity is related to host-plant genotypic diversity, we were able to disentangle several aspects of this relationship. First, particular host-plant genotypes do not drive positive arthropod responses to genotypic diversity; instead interactions among genotypes result in consistent non-additive effects for most of the season. Second, arthropod species during particular survey periods do not account for positive relationship between host-plant genotypic diversity and arthropod diversity. The arthropod community changed dramatically over the course of the season and yet we still observed consistent, positive responses of arthropod diversity over time. Third, our findings are not simply a host-plant biomass effect, where more arthropod species occur in more productive genotype mixtures. When we accounted for plant biomass effects on arthropods using rarefaction, arthropod richness still increased with host-plant genotypic diversity early in the season when specialist herbivores dominated. Finally, since arthropods were tightly linked to floral resources at the end of the growing season and there were not more flowers in

genotypically diverse plots compared to monocultures, this explained why arthropod diversity did not respond to host-plant genotypic diversity at the end of the season.

While many studies have examined the consequences of host-plant genotype identity on associated arthropods, our results stress that non-additive responses of communities to genotypic diversity might be the norm, rather than the exception. Non-additivity may limit the predictability of the arthropod community based solely on host-plant genotype identity. Finally, we suggest that focusing on temporal dynamics can help uncover the causal mechanisms linking intraspecific diversity to communities and ecosystems.

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Appendix III: Tables and figures

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Table III-1. Results of repeated-measures ANOVA examining arthropod richness responses to the manipulations of *Solidago altissima* genotypic diversity.

Variable	Effect	DF	*F*	*P*
Richness	Genotypic diversity	3, 59	14.750	< 0.001
	Time	4, 56	90.251	< 0.001
	Diversity x time	12, 148	1.356	0.202

.

Table III-2. Separate one-way ANOVA results examining the effect of *S. altissima* genotypic diversity treatments on arthropod species richness within each of the five survey periods.

Variable	Effect	DF	MS	*F*	*P*
Richness	May	3, 59	0.3716	2.766	0.049
	June	3, 59	0.1136	12.410	< 0.001
	July	3, 59	0.0730	11.688	< 0.001
	September	3, 59	0.1648	6.571	< 0.001
	October	3, 59	0.0378	1.573	0.205

.

Table III-3. Results of repeated-measures ANOVA examining arthropod abundance responses to the manipulations of *Solidago altissima* genotypic diversity.

Variable	Effect	DF	*F*	*P*
Abundance	Genotypic diversity	3, 59	8.825	< 0.001
	Time	4, 56	183.216	< 0.001
	Diversity x time	12, 148	1.159	0.325

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Table III-4. Separate one-way ANOVA results examining the effect of *S. altissima* genotypic diversity treatments on arthropod species abundance within each of the five survey periods.

Variable	Effect	DF	MS	*F*	*P*
Abundance	May	3, 59	0.0573	0.887	0.452
	June	3, 59	0.0258	11.460	<0.001
	July	3, 59	0.1967	8.178	<0.001
	September	3, 59	0.1951	4.028	0.011
	October	3, 59	0.1157	2.233	0.093

.

Table III-5. Results of Analysis of Similarity examining the overall effects of time on plot-level arthropod community composition, along with pairwise comparisons of each time period.

Variable	*R*	*P*
All months	0.845	< 0.001
May, June	0.879	<0.01
May, July	0.974	<0.01
May, Sept.	0.878	<0.01
May, Oct.	0.981	<0.01
June, July	0.895	<0.01
June, Sept.	0.878	<0.01
June, Oct.	0.991	<0.01
July, Sept.	0.235	<0.01
July, Oct.	0.966	<0.01
Sept, Oct.	0.940	<0.01

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Table III-6. Repeated-measures ANOVA results examining plot-level aboveground biomass of *Solidago altissima* plants responses to genotypic diversity.

Variable	Effect	DF	*F*	*P*
Biomass	Genotypic diversity	3, 59	4.403	0.007
	Time	3, 57	236.197	< 0.001
	Diversity x time	9, 138	2.332	0.017

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Table III-7. Separate one-way ANOVA results examining the effect of *S. altissima* genotypic diversity treatments on plot-level aboveground biomass within each of the four survey periods and on flower number in October.

Variable	Effect	DF	MS	*F*	*P*
Biomass	May	3, 59	275.428	0.656	0.582
	June	3, 59	5004.63	3.995	0.011
	July	3, 59	35176.7	5.156	0.003
	September	3, 59	47367.2	2.806	0.047
Flowers	October	3, 59	31895806	1.950	0.131

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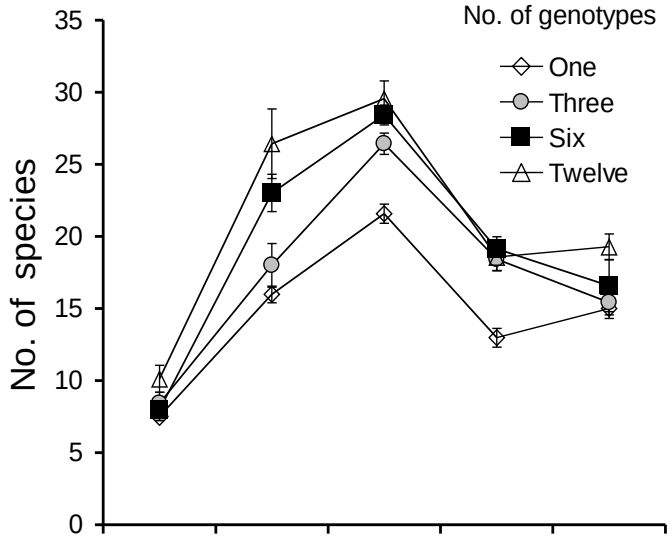
Table III-8. List of the most common herbivore species in experimental plots.

ORDER	
Coleoptera	*Chauliognathus pennsylvanicus*
	Chrysomelidae sp.
	Colaspis brunnea
	Conoderus sp.
	Curculionidae sp. 1
	Curculionidae sp. 2
	Diabrotica undecimpunctata howardi
	Epitrix sp
	Mordellistena sp.
	Olibrus sp.
	Systena elongata
Diptera	Agromyzidae sp. 1
	Asteromyia carbonifera
	Eurosta solidaginis
	Rhopalomyia solidaginis
Hemiptera	*Acanalonia bivittata*
	Acutalis tartarea
	Agallia constricta
	Anormenis chloris
	Clastoptera xanthocephala
	Coccus hesperidum
	Corythuca sp.
	Cuerna arida
	Empoasca fabae
	Entylia sp.
	Geocoris bullatus
	Graphocephala coccinea
	Gyponana sp.
	Lepyronia quadrangularis
	Lygus lineolaris
	Oncometopia sp.
	Philaenus spumarius
	Prosapia bicincta

	Scaphytopius sp. 1
	Scaphytopius sp. 2
	Scolops sp.
	Sibovia sp.
	Trialeurodes vaporariorum
	Uroleucon sp.
Hymenoptera	*Apis mellifera*
	Bombus sp.
	Halictus sp.
	Osmia sp.
Lepidoptera	*Cucullia asteroides*
	Gnorimoschema gallaesolidaginis

a)



b)

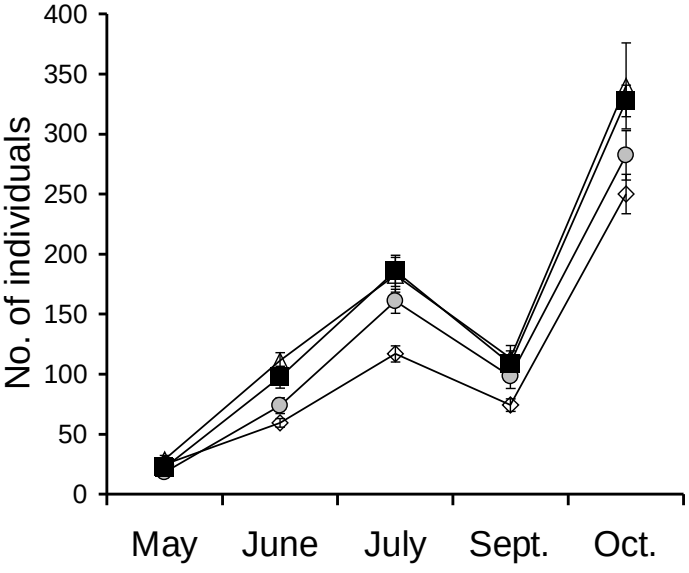


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Figure III-1. Effects of genotypic diversity in experimental plots of *Solidago altissima* on total arthropod richness **(a)** and total arthropod abundances **(b)** over the course of a growing season. Each point represents the plot-level mean ± SE for patches containing 1, 3, 6, or 12 *Solidago altissima* genotypes. The 1-genotype treatment consisted of all twenty-one genotypes with 2 replicates each and mixtures had 7 replicates each. A line connects each genotypic diversity level across survey periods.

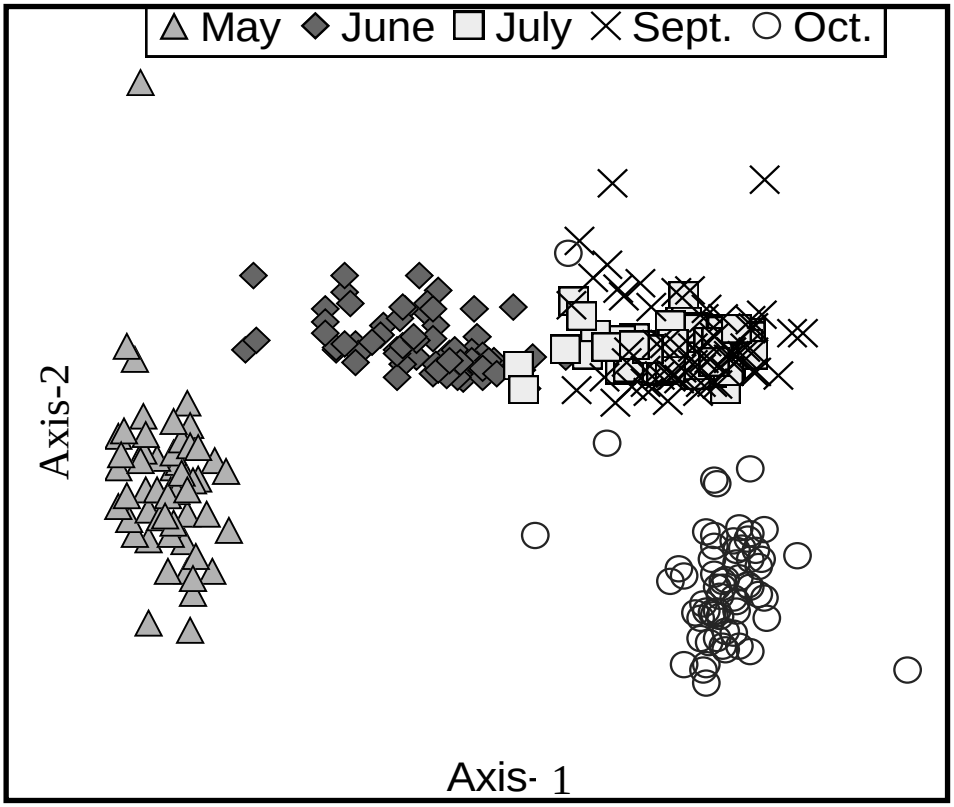

Figure III-2. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarities of plot-level arthropod communities in 63 experimental plots of *Solidago altissima* plants throughout a growing season. The five survey periods are represented by different shapes. Arthropod community composition differed among all survey periods indicating significant turnover in community composition throughout the growing season.

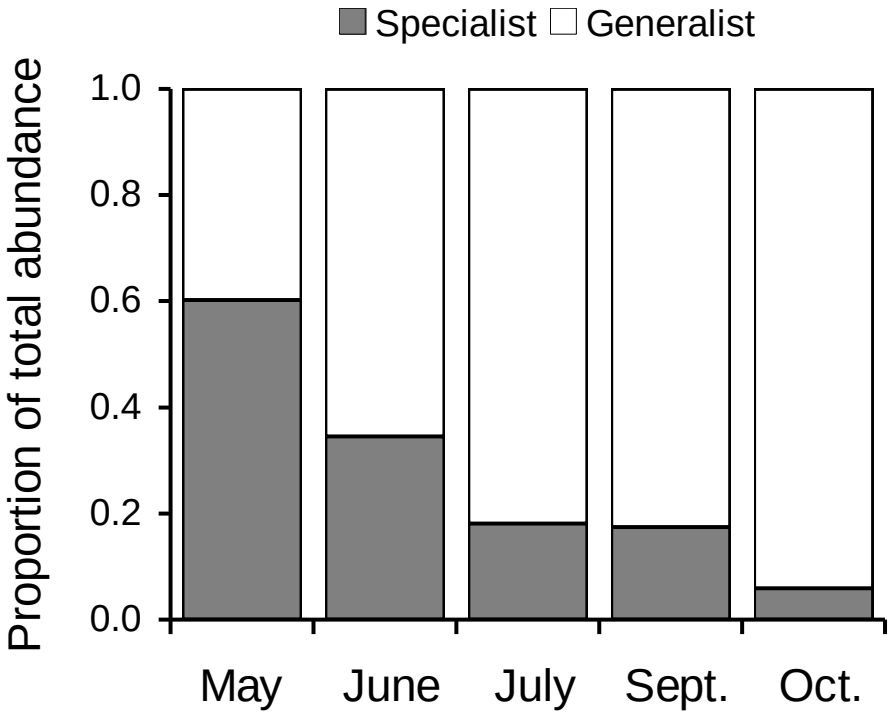

Figure III-3. Proportional abundances of generalist versus specialist herbivores throughout the growing season. Each bar represents the total arthropod abundance within a survey period and subsections indicate the percent of total made up by herbivore type.

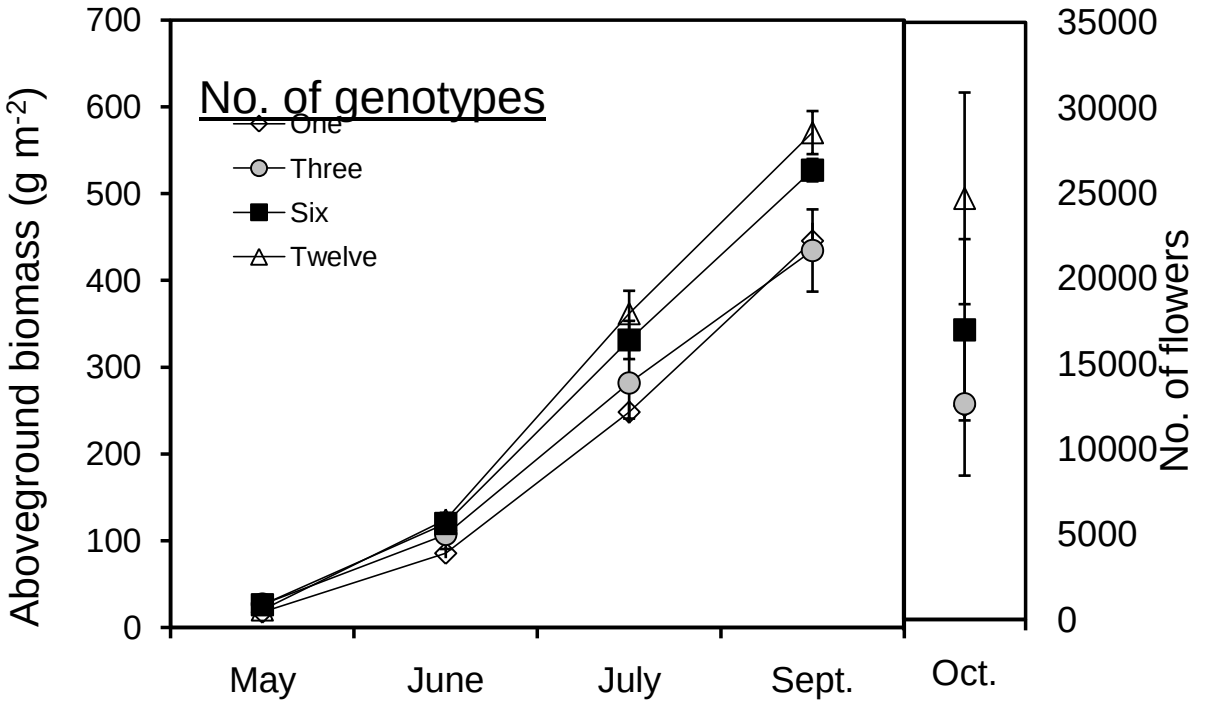

Figure III-4. Effects of genotypic diversity in experimental plots of *Solidago altissima* on plot-level aboveground biomass from May-September and on plot-level flower abundance in October. Each point represents the plot-level mean ± SE for patches containing 1, 3, 6, or 12 genotypes of *S. altissima* genotypes. A line connects each genotypic diversity level across all survey periods, except for October flower abundances.

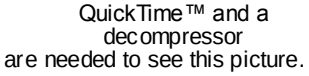

Figure III-5. Non-additive responses of plot-level arthropod richness **(a)** and plot-level aboveground biomass (May-September) and flower number (October only) **(b)** to mixtures of 3, 6, or 12 genotypes of *Solidago altissima* throughout the growing season. Zero indicates the number or amount predicted by summing the individual contributions of component host-plant genotypes grown in monoculture (additive richness/biomass/flowers). Bars indicate how many more or fewer arthropod species, grams of biomass, or number of flowers there are at each diversity level than the predicted additive amount for each of 5 sampling periods. * denotes significant non-additive responses ($P < 0.05$)

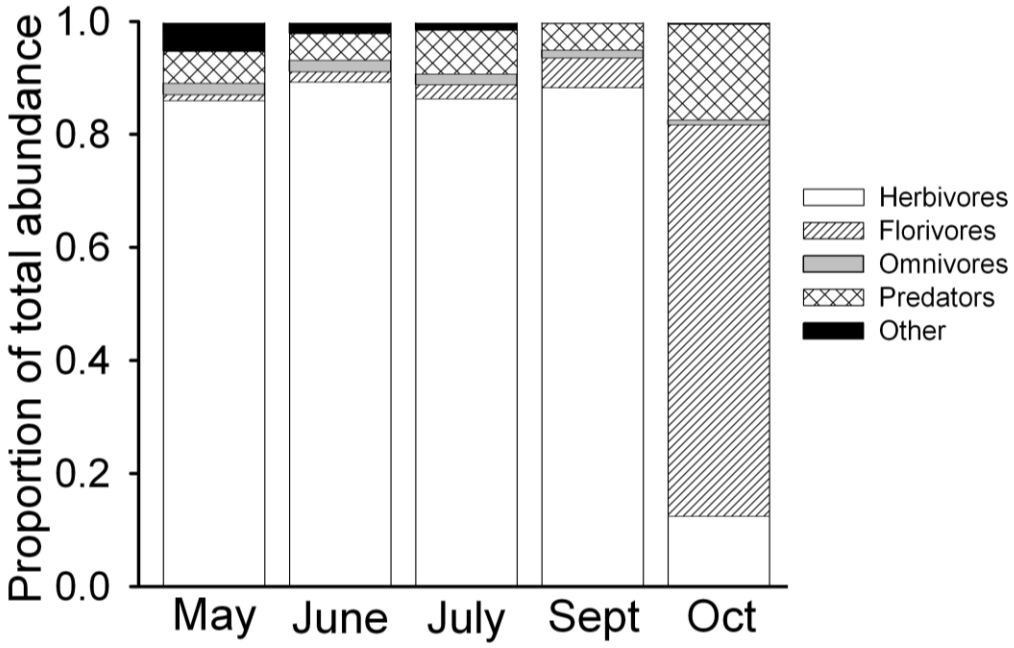

Figure III-6. Proportional abundances of arthropod feeding guilds throughout the growing season. Each bar represents the total arthropod abundance within a survey period and subsections indicate the percent of total made up by a particular feeding guild. Each guild is represented by a different color pattern.

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

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The following section is a slightly modified version of a paper published in the journal Oecologia.

Crutsinger G. M., N. Reynolds, A. T. Classen and N. J. Sanders. 2008. Disparate effects of host-plant genotypic diversity on above- and belowground communities. Oecologia 158: 65-75.

The use of "we" in this part refers to my co-authors and me. As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the design of the experiment, data collection and statistical analyses. I also wrote most of the paper.

Abstract

Intraspecific diversity can influence the structure of associated communities, though whether litter-based and foliage-based arthropod community 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.

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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 importance 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 within species is increasingly recognized as having 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; 2007). 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 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 inter-clonal 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 review). 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 2005-2006 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park near Oak Ridge, Tennessee (35º58'N, 84º12'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 US. Dominant species at the study site include *S. altissima, Verbesina occidentalis, V. 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 twenty-one *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 63 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 1-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 vacuumed sampled for 5 minutes, followed by 15 person-minutes of hand collection for larger arthropods. Vacuum and hand-collected samples were taken back to the laboratory and identified to species or morpho-species, counted, and assigned to trophic level based on feeding morphology, observations in the field (Crutsinger et al. 2006; 2007) 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, 2007). Both methods yielded similar numbers of arthropod species (94 species and 8,617 individuals in July of 2005 versus 104 species and 13,224 individuals in 2006). Species accumulation curves based on Chao 1 richness estimator (Chao 1984) plateaued in both years (Fig. IV-7), 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 of 2006, we harvested aboveground biomass from each plot, which was oven-dried at 60°C

and weighed.

We used two separate MANOVAs 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 (NMDS). ANOSIM and ordination procedures were run using Primer statistical package (Version 6, 21 Primer-E Ltd., 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.

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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 Corp, Lima, OH), filled with 4 g of air-dried litter, and sealed on the fourth edge. Four grams represents the natural inputs of leaf litter produced in a 0.0225 m^2 area in the field (Crutsinger unpublished data).

In spring 2006, we created mixtures of 1, 3, 6, or 9 genotypes in litterbags. The 1-genotype treatment consisted of 12 different *S. altissima* genotypes in monoculture with 3 replicates each. 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 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). 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 of individual paper bags and immediately returned them to the lab. We extracted litter microarthropods from each litterbag for 72 hours 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 25W light bulb was hung 10 cm above the litterbags and microarthropods were collected in plastic cups filled with 70% ethanol. Microarthropods were counted, assigned each to a trophic level, and identified to species or morpho-species. 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 collembola 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 carbon (C) and nitrogen (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 twelve 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. IV-1A) and predator composition also differed between years (Global $R = 0.483$, $P = 0.01$; Fig. IV-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.

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In 2006, S*olidago 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 ~2-fold (range: 20 – 38 species) and abundance by 3-fold (range: 97 – 304 individuals) among genotypes (Table IV-1). Genotype effects occurred across trophic levels: herbivore richness varied by 50% (Fig. IV-2A), herbivore abundance by 2.9-fold (Fig. IV-2B), predator richness by 4.6-fold (Fig. IV-2C), and predator abundance by 9-fold (Fig. IV-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. IV-4) and abundance was 34% higher in genotypically diverse plots relative to monoculture plots, though diversity effects saturated quickly at ~ 3 genotypes. Similar to genotype identity effects, genotypic diversity effects occurred across trophic levels. Herbivore richness (Fig. IV-5A) was 16% higher and abundance (Fig. IV-5B) was 34% higher in genotypically diverse plots. Predator richness (Fig. IV-5C) was 36% higher in genotypically diverse plots, but predator abundance (Fig. IV-5D) showed no significant response (Table IV-1).

Solidago altissima genotypes varied by ~ 5-fold in ANPP, but ANPP showed no response to genotypic diversity during the second year of this study (Table IV-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 monocultures 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.

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 ~ 4-fold difference among genotypes in collembolan abundance at 3 weeks (Table IV-2, Fig. IV-3), and ~ 2-fold difference in collembolan richness at 12 weeks (Table IV-2, Fig. IV-3). However, neither total microarthropod (Fig. IV-2) or mite richness and abundance were affected by leaf litter genotype at any time (Table IV-2 and IV-3). Host-plant genotype also had minimal effects on the richness and abundance of predators, herbivores, or detritivores (Table IV-4-6). 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 (Table IV-4).

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 5-

fold more collembolan individuals in 3-genotype mixtures compared to monocultures. At 12 weeks, there were 1.2-fold more mite individuals in 3-genotype mixtures. During the final collection at 24 weeks, there were 36% fewer total species in 9-genotype mixtures, but 30% more individuals in 3-genotype mixtures compared to monocultures (Table IV-2 and IV-3). There was no response of the different trophic groups to genotypic diversity (Table IV-6).

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. IV-6).

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 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. 2007) 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).

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 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 (Schuster 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 % 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 three-week collection date, higher colembolan richness occurred in 3-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 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 treatment 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.

Conclusions

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 communities 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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Appendix IV: Tables and figures

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

	df	MS	F	*P*-value
Genotype				
Total richness	20, 21	50.16	3.73	0.002
Total abundance	20, 21	6568.20	5.24	0.0002
Herbivore richness	20, 21	11.07	2.16	0.043
Herbivore abundance	20, 21	5031.05	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	2514924.00	5.82	<0.0001
Genotypic diversity				
Total richness	3, 59	125.37	5.07	0.003
Total abundance	3, 59	11960.40	3.53	0.020
Herbivore richness	3, 59	9985.88	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	78810.00	0.66	0.575

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Table IV-2. Summary of full model repeated-measure ANOVAs examining the effects of *Solidago altissima* genotype identity on total microarthropod, collembola, and mite richness and abundance over time. Significant *P*-values are shown in bold.

	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	<.0001
Genotype × time	33	1.17	0.26
Collembola richness			
Genotype	11	0.63	0.79
Time	3	11.79	<.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

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Table IV-3. Summary of full model repeated-measure ANOVAs examining the effects of *Solidago altissima* genotypic diversity on litter microarthropods over time. Significant *P*-values are shown in bold.

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

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Table IV-4. ANOVA summary of the effects of *S. altissima* genotype identity and genotypic diversity on litter microarthropods at each collection date. F-values are given with degrees of freedom immediately below. An asterix and bold text represents statistical significance (* $P < 0.05$, ** $P < 0.01$).

	3 weeks	6 weeks	12 weeks	24 weeks
Genotype				
Total richness	1.759 (11, 23)	2.198 (11, 24)	1.224 (11, 24)	1.461 (11, 24)
Total abundance	0.992 (11, 23)	1.510 (11, 24)	0.708 (11, 24)	1.277 (11, 24)
Collembolan richness	1.518 (11, 23)	0.949 (11, 24)	2.763* (11, 24)	0.721 (11, 24)
Collembolan abundance	2.269* (11, 23)	1.004 (11, 24)	1.975 (11, 24)	1.300 (11, 24)
Mite richness	1.845 (11, 23)	1.064 (11, 24)	0.473 (11, 24)	1.229 (11, 24)
Mite abundance	0.771 (11, 23)	1.517 (11, 24)	0.662 (11, 24)	1.151 (11, 24)
Genotypic diversity				
Total richness	0.420 (3, 74)	0.169 (3, 77)	0.255 (3, 77)	4.163** (3, 78)
Total abundance	0.864 (3, 74)	0.167 (3, 77)	0.162 (3, 77)	4.029* (3, 78)
Collembolan richness	3.620* (3, 74)	1.495 (3, 77)	0.742 (3, 77)	2.691 (3, 78)
Collembolan abundance	4.978** (3, 74)	0.814 (3, 77)	2.210 (3, 77)	1.713 (3, 78)
Mite richness	0.201 (3, 74)	1.707 (3, 77)	0.619 (3, 77)	1.051 (3, 78)
Mite abundance	0.376 (3, 74)	0.503 (3, 77)	1.387 (3, 77)	4.173** (3, 78)

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Table IV-5. Full model summary for repeated-measure ANOVAs examining the effects of *S. altissima* genotype identity on microarthropod predator, herbivore, and detritivore richness and abundance over time. Significant *P*-values are shown in bold.

	df	**F**	***P*-value**
Predator richness			
Genotype	11	1.14	0.37
Time	3	15.31	<0.0001
Genotype × time	33	1.69	0.03
Predator abundance			
Genotype	11	1.75	0.12
Time	3	30.73	<.0001
Genotype × time	33	1.27	0.20
Herbivore richness			
Genotype	11	1.02	0.79
Time	3	23.05	<.0001
Genotype × time	33	1.19	0.27
Herbivore abundance			
Genotype	11	2.82	0.02
Time	3	54.90	<.0001
Genotype × time	33	1.47	0.09
Detritivore richness			
Genotype	11	1.26	0.30
Time	3	7.69	0.001
Genotype × time	33	1.18	0.28
Detritivore abundance			
Genotype	11	2.20	0.055
Time	3	18.36	<0.0001
Genotype x time	33	0.92	0.58

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Table IV-6. Full model summary for repeated-measure ANOVAs examining the effects of *S. altissima* genotypic diversity on microarthropod predator, herbivore, and detritivore richness and abundance over time. Significant *P*-values are shown in bold.

	df	**F**	***P*-value**
Predator richness			
Genotypic diversity	3	0.49	0.68
Time	3	28.57	< 0.0001
Gen div × time	9	1.44	0.17
Predator abundance			
Genotypic diversity	3	0.96	0.41
Time	3	18.01	< 0.0001
Gen div × time	9	1.04	0.40
Herbivore richness			
Genotypic Diversity	3	0.16	0.91
Time	3	38.27	< 0.0001
Geno Div × time	9	1.60	0.11
Herbivore abundance			
Genotypic diversity	3	0.25	0.86
Time	3	49.59	< 0.0001
Gen div × time	9	0.56	0.82
Detritivore richness			
Genotypic diversity	3	0.30	0.82
Time	3	20.45	< 0.0001
Gen div × time	9	1.50	0.14
Detritivore abundance			
Genotypic diversity	3	1.91	0.13
Time	3	28.61	< 0.0001
Gen div × time	9	0.94	0.48

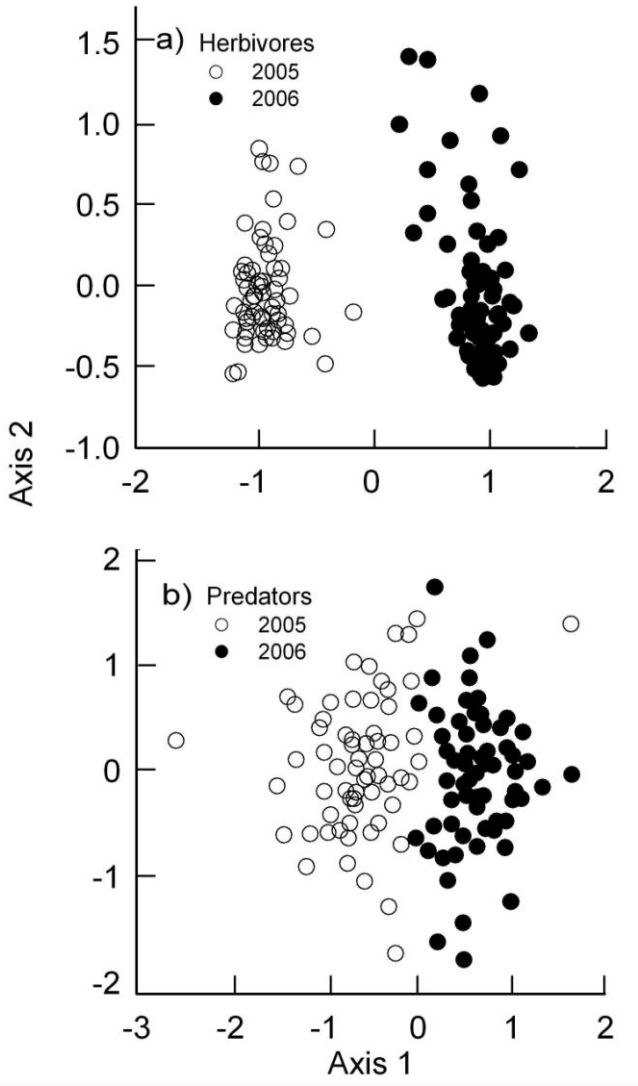

Figure IV-1. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarities of (a) foliage-based herbivore and (b) predator communities in 63 experimental plots of *Solidago altissima* plants in 2005 (open circles) and 2006 (filled circles). Each circle indicates a community 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).

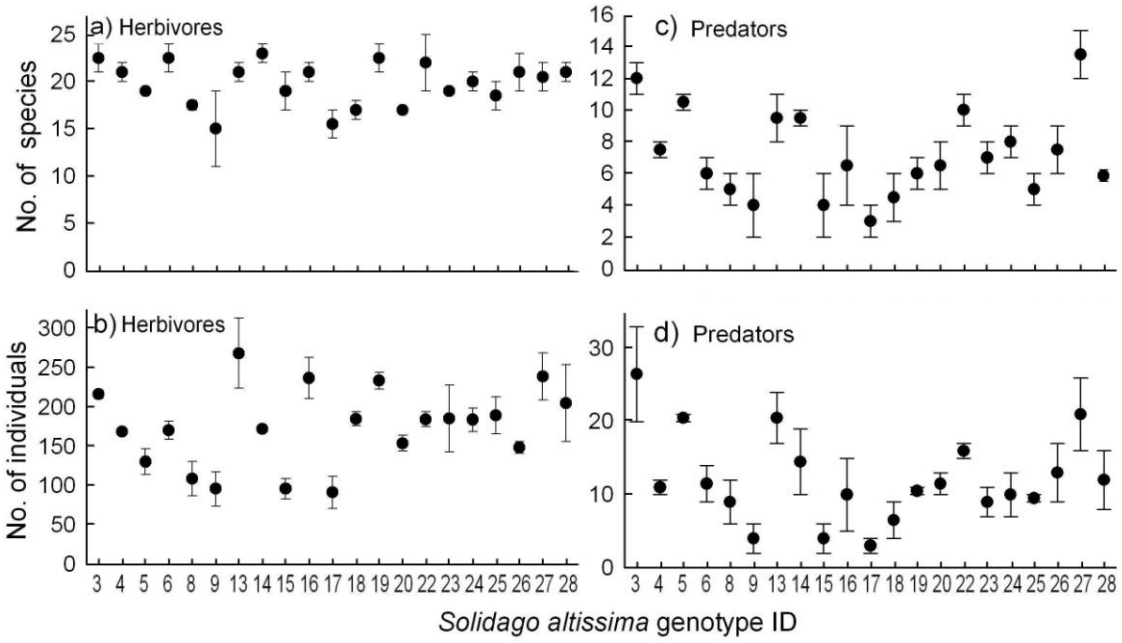

Figure IV-2. The relationship between (a) herbivore richness, (b) herbivore abundance, (c) predator richness and (d) predator abundance and genotype identity of *Solidago altissima* in 2006. Bars represent mean (±SEM) number of species and individuals in 1-m^2 experiment plots.

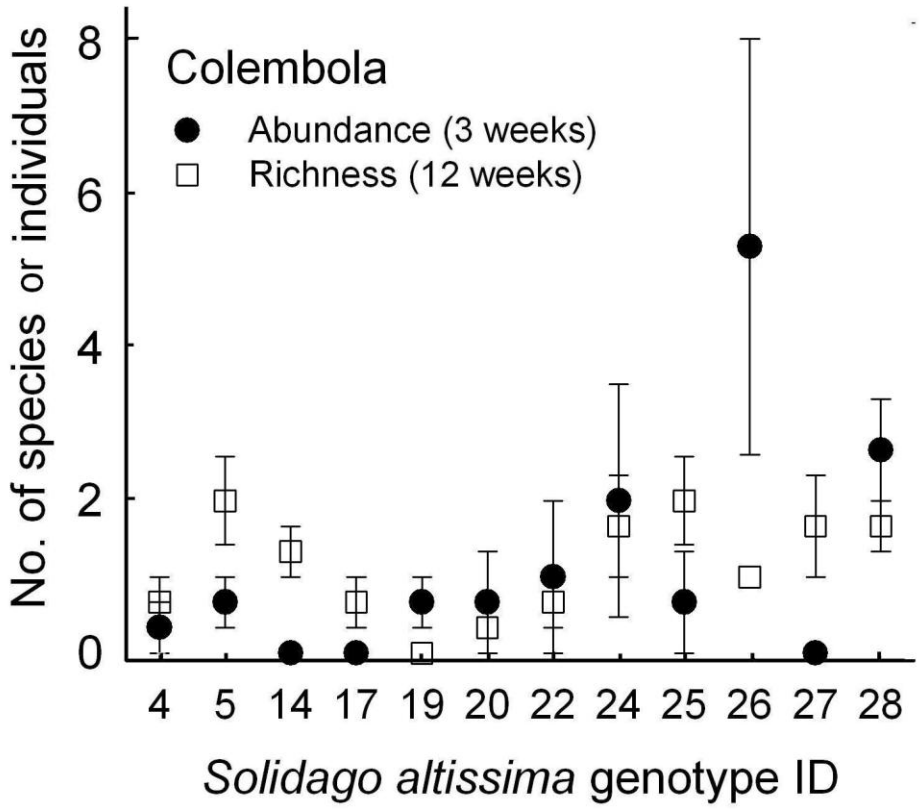

Figure IV-3. The relationship between collembola abundance at 3 weeks (open squares) and collembola species richness at 12 weeks into the experiment (closed circles) and genotype identity of *Solidago altissima*. Bars represent mean (±SEM) number of collembolan individuals or species in litterbags. Other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

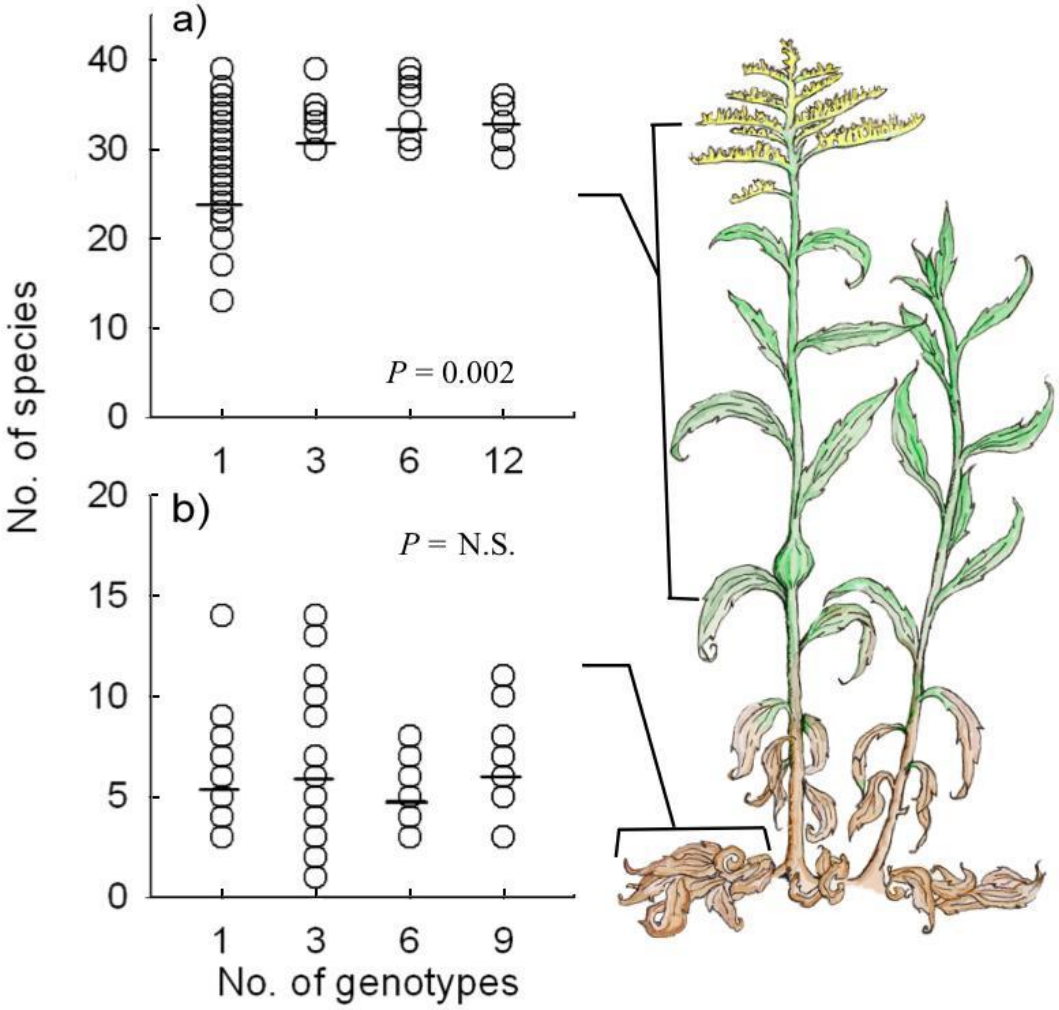

Figure IV-4. Relationship between population-level genotypic diversity of *Solidago altissima* and total species richness in (a) foliage- and (b) litter-based arthropod communities. Circles indicate plot-level observations and horizontal lines indicate treatment means. Note that the litter community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

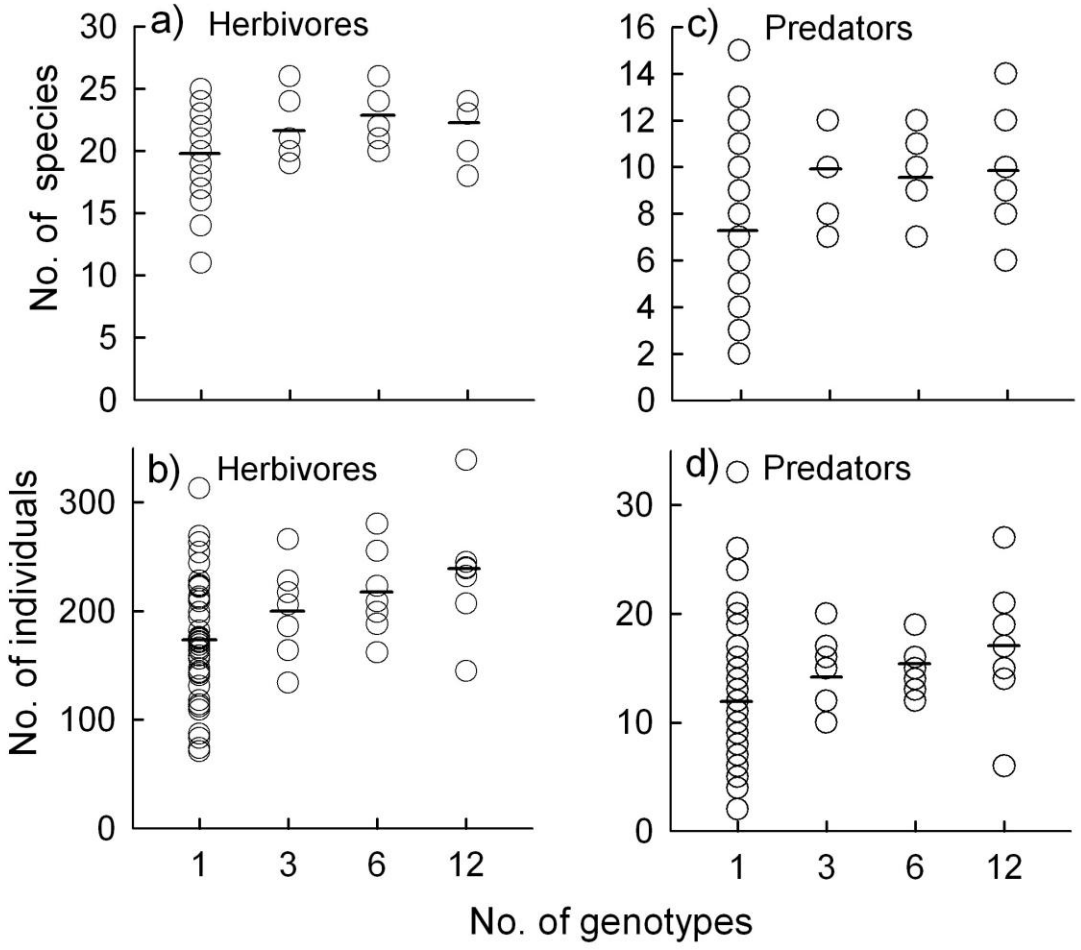

Figure IV-5. Relationship between population-level genotypic diversity of *Solidago altissima* and (a) herbivore richness, (b) herbivore abundance, (c) predator richness and (d) predator abundance. Circles indicate plot-level observations and horizontal lines indicate treatment means.

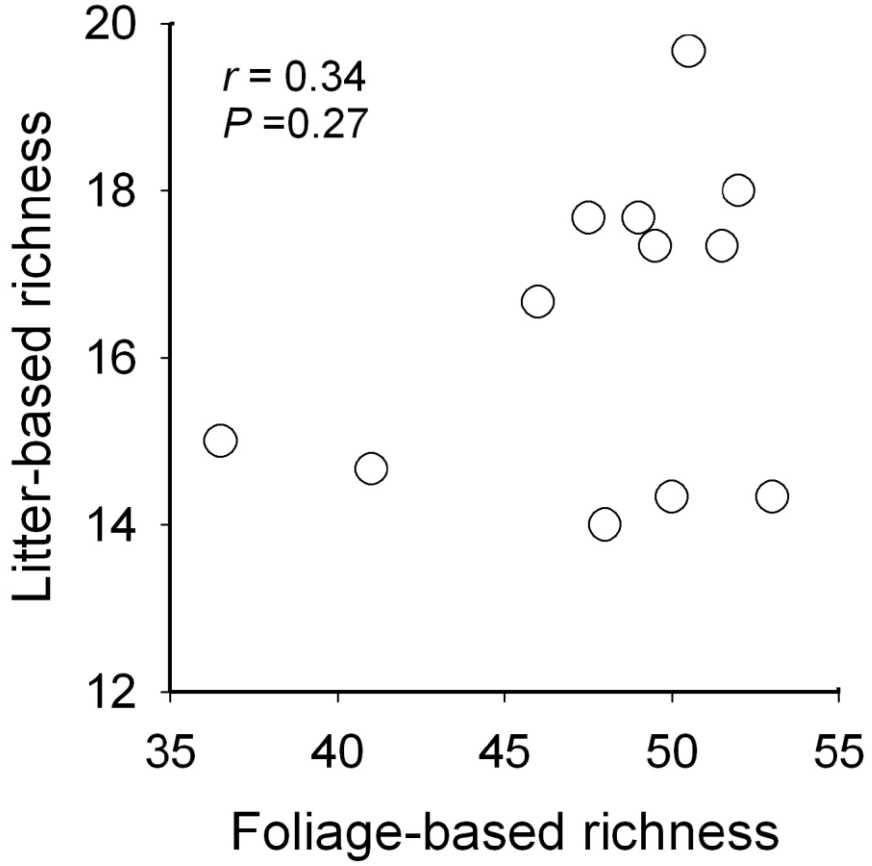

Figure IV-6. Relationship between foliage-based richness and litter-based richness for 12 *Solidago altissima* genotypes used in both the common garden and litterbag manipulations. Lack of a correlation indicates a decoupling in the responses of the two communities to variation among host-plant genotypes.

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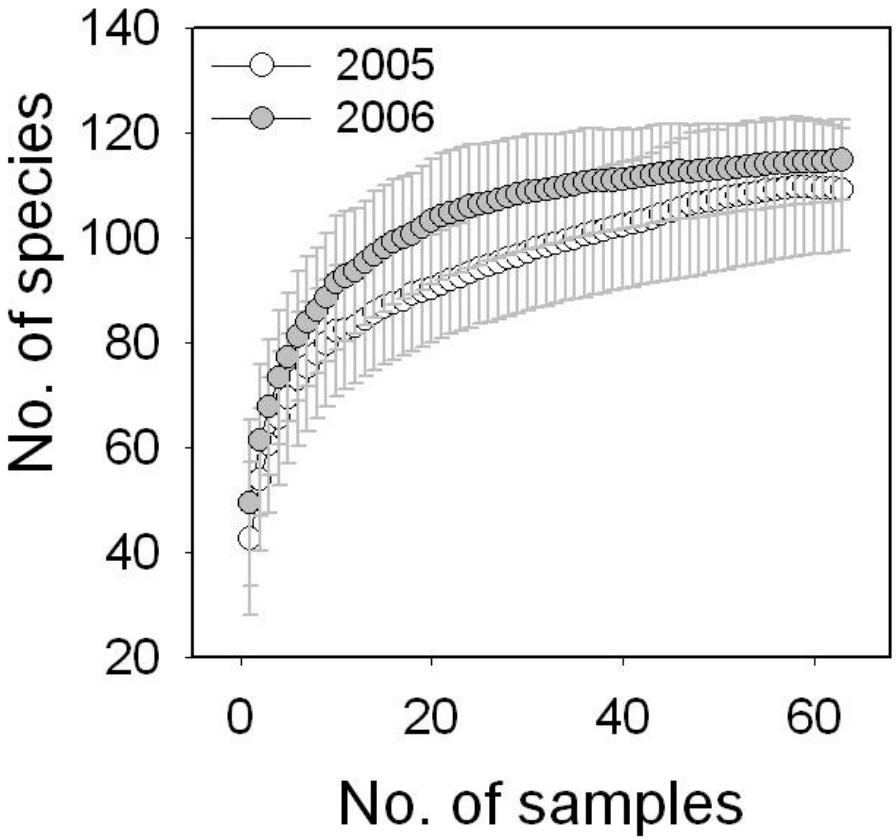
140
120
100
80
60
40
20
No. of species
2005
2006
0
20
40
60
No. of samples

.

Figure IV-7. Sample-based species accumulation curves (± SD) using Chao 1 richness estimator for 2005 and 2006.

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Chapter V. Intraspecific diversity and dominant genotypes resist plant invasions

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The following section is a slightly modified version of a paper published in the journal Ecology Letters.

Crutsinger G. M., L. Souza and N. J. Sanders N.J. 2008. Intraspecific diversity and dominant genotypes as a barrier to plant invasions. Ecology Letters 11: 16-23.

The use of "we" in this part refers to my co-authors and me. As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the design of the experiment, data collection and statistical analyses. I also wrote most of the paper.

Abstract

Numerous studies have asked whether communities with many species deter invasions more so than do species-poor communities or whether dominant species deter invasion by colonizing species. However, little is known about whether high intraspecific diversity can deter biological invasions or whether particular genotypes might deter invasions. In this study, we present experimental evidence that intraspecific diversity and particular genotypes of tall goldenrod, *Solidago altissima*, can act as a barrier to colonization by new species. We found that biomass of colonizing species was negatively correlated with genotypic diversity, and particular genotypes affected the richness, cover, and biomass of colonizing species. Stem density of *S. altissima* increased with genotypic diversity and varied among genotypes, suggesting that stem density is a key mechanism in limiting colonization dynamics in this system. Our results indicate that the loss of intraspecific diversity within a dominant plant species can increase susceptibility to plant invasions.

Introduction

Biological invasions threaten native biodiversity, alter the functioning of ecosystems, and cause substantial economic impacts (Vitousek et al. 1997, Mack et al. 2000, Lockwood 2006). Thus, it is critical to understand which species are likely to invade and which communities are likely to be invaded. One hypothesis, first formalized by Elton (1958), is that communities with more species should be more resistant to invasive species than are species-poor communities. Elton's diversity-resistance hypothesis has been supported by a number of studies, especially at local scales (Levine et al. 2004, Hooper et al. 2005, Srivastava and Vellend 2005, Fridley et al. 2007a), while positive relationships between diversity and invasion have been found at larger spatial scales (Fridley et al. 2007a). Though the theory has advanced since first posited by Elton, the general idea is that competition among species intensifies as communities become more species rich, leaving fewer available resources for colonizing species. However, many biodiversity studies confound diversity effects with the identity and/or abundance of a particular species (Hooper et al. 2005). In fact, the presence of competitively dominant species, rather than diversity *per se,* might be a key determinant of invasion resistance (Fridley 2001, Wardle 2001, Smith et al. 2004, Fargione and Tilman 2005).

Studies that link species diversity to invasion resistance are part of a larger body of work linking species diversity to the functioning of ecosystems (Hooper et al. 2005). A growing number of studies have shown that intraspecific diversity can also influence the structure of communities and the functioning of ecosystems (Hughes and Stachowicz 2004, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Whitham et al.

2006). Like diversity among species, diversity within species may play an important role in susceptibility or resistance to invasion, but this issue has been little explored (Weltzin et al. 2003, Hooper et al. 2005). For example, if genetic variation in the competitive ability of individuals within species occurs (Taylor and Aarssen 1990, Fridley et al. 2007b), then the colonization success of an invader may depend on both the genotypic and species identities of resident individuals (Vellend 2006). Therefore, the level of genotypic diversity within resident populations might ultimately determine species diversity, coexistence, and susceptibility to invasion within a community (Booth and Grime 2003, Vellend 2006, Whitham et al. 2006).

In this study, we ask whether local populations of a dominant species with higher genotypic diversity are more resistant to invasion than are those with lower genotypic diversity, and whether particular genotypes are more resistant to invaders than are others. We find that genotypic diversity and particular genotypes within populations deter biological invasion, much like species diversity and dominant species do.

Materials and Methods

Study site and natural history

We began this research in Spring of 2005 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park near Oak Ridge, Tennessee (35º58'N, 84º12'W). The site was abandoned from agricultural use in

1943. Plant community composition in the old fields surrounding the experimental area is typical of other old fields in east Tennessee. Besides *Solidago altissima,* common native plant species include *Verbesina occidentalis* L. (yellow crownbeard), *V. virginica* L. (white crownbeard), and *Rubus* spp. (blackberry). Out of the ~100 total plant species in neighboring fields, approximately 25% are exotic and invasive. Common invasive plant species at and near the experimental garden include *Microstegium vimineum*, *Lonicera japonica*, *Ligustrum sinense*, *Pueraria lobata*, *Rosa multiflora*, and *Lespedeza cuneata*.

Solidago altissima is a rhizomatous, out-crossing, perennial species that dominates old fields throughout eastern North America during the first 15-20 years following abandonment (Werner et al. 1980). Local populations of *S. altissima* can contain just 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, depending on how long an area has been left undisturbed (Maddox et al. 1989). Clones within a local area can exhibit considerable inter-clonal genetic variation in many plant traits, including those that might influence competitive ability, such as resistance to herbivores or biomass production (Crutsinger et al. 2006, Wise et al. 2006). In east Tennessee, *S. altissima* makes up, on average, 20 % (range = 5 – 47%) of the aboveground biomass and 0-43% of total plant cover in old-field ecosystems (Souza unpublished data).

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Experimental garden

In 2005, we collected 21 *S. altissima* ramets from local *S. altissima* patches growing 50-150 m apart in old fields near the experimental garden. Each ramet was identified as a unique genotype by means of amplified fragment length polymorphisms (AFLPs). All 21 genotypes were approximately equally related and so represent a local interbreeding population (Crutsinger *et al*. 2006). We propagated ramets for this experiment from rhizome cuttings grown in a greenhouse in the early spring of 2005.

In May 2005, we established 63 1 m^2 experimental plots in a 15 m × 20 m grid in the experimental garden. We cut 6 cm × 30 cm trenches around each of the experimental plots and lined them with heavy plastic to prevent spread of ramets among plots. Three weeks prior to planting the ramets, we sprayed all of plots with herbicide to eliminate previously established species. A 3-m tall fence was constructed around the experiment to exclude deer.

Each 1 m^2 experimental plot contained 12 *S. altissima* ramets and was randomly assigned to contain 1, 3, 6, or 12 genotypes, mimicking natural densities of genotypes (Maddox et al. 1989). We created genotypic mixtures by randomly sampling from the pool of 21 genotypes with the constraint that no two patches in a treatment could have identical composition. There were seven replicates for the 3-, 6-, and 12-gentoype treatments and two replicates of each of the 21 1-genotype treatments. For further details on the establishment of the experimental garden see Crutsinger et al. 2006.

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Invasion experiment

From spring of 2005 to the peak of the growing season in 2006, we hand-weeded each of the plots bi-monthly to exclude all other plant species, along with any *S. altissima* stems that might have colonized the plots from the seed bank. We were able to distinguish *S. altissima* seedlings from new ramets because seedlings are much smaller than new stems produced from rhizomes. In July 2006, we stopped weeding and allowed plant species to colonize the experimental plots, either from the seed bank or via dispersal from adjacent old fields into the plots for nine months, a duration similar to other invasion studies (e.g., Stachowicz et al. 1999, Levine 2000). Because of the initial treatments to the plots (e.g. spraying with herbicide and hand weeding the plots for two years), we are confident that most of the species that colonized the plots were derived from newly arriving seeds from adjacent old fields. Proximity to source pools of seeds should not affect our results because treatments were placed randomly within the experimental garden. We are confident of minimal disturbance effects of weeding because generally only small seedlings were removed and we did not weed the plots for 3 and 9 months prior to observations of colonists.

To test whether intraspecific diversity increased invasion resistance, we examined how variation in the number of genotypes of *S. altissima* affected the establishment and success of colonizing plant species in each of the 63 1-m^2 plots. We use "colonists" and "colonizing species" to refer to both native and non-native taxa that colonized the plots. In October of 2006 and April 2007, three and nine months after we terminated weeding, we recorded (1) richness and percent cover of exotic species, (2) richness and percent

cover of native species, (3) richness and percent cover of all colonists, (4) the biomass of colonists (April only), and (5) the number of *S. altissima* stems in each plot. To estimate percent cover, we overlaid a 20-cell grid (50 cm^2 per cell in a 4×5 grid or 5% cover for each square) over each plot and tallied the number of grid cells occupied by native and exotic species. High stem density and cover of *S. altissima* in many of the plots prevented us from using a higher resolution grid (e.g., a 100-cell grid). However, in a subset of the plots we were able to compare the results from 20-cell grids and 100-cell grids, and the results were not qualitatively different. *S. altissima* was excluded from all cover and biomass estimates. We estimated biomass of the colonizing species by harvesting all aboveground biomass of non-*S. altissima* species in each plot in April 2007. Plants were oven-dried at 60° C for 72 h and weighed to the nearest 0.01 g. We estimated plot-level *S. altissima* stem density at each time period by counting the total number of stems in each plot. We focused specifically on *S. altissima* stem density because it is positively and significantly correlated ($P < 0.001$ for all cases) with the aboveground biomass ($r = 0.54$), leaf area index ($r = 0.60$), and Normalized Difference Vegetation Index ($r = 0.60$) of *S. altissima*. Though other morphological characteristics that we did not measure could be important, we felt *S. altissima* stem density, or correlated traits, adequately represent competitive abilities of *S. altissima* genotypes and genotypic mixtures for abiotic resources (light, water, nutrients) and space.

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Statistical analyses

We used Pearson correlation coefficients to examine the relationships between genotypic diversity, stem density and each of the following response variables: native cover, exotic cover, the cover of all colonizing species (native + exotic), native species richness, exotic species richness, the richness of all colonizing species (native + exotic) in both October 2006 (three since weeding stopped) and April 2007 (nine months since weeding stopped), along with the biomass of colonizing species (native + exotic species biomass) in April (Table V-3). In addition, we used an all-possible regressions approach to model the relative effects of genotypic diversity and stem density on the variables listed above in both October 2006 and April 2007. We used Akaike's Information Criterion (AIC) to identify the best model.

To examine the effect of *S. altissima* genotype identity (in the monoculture plots) on the richness and percent cover of total, native, and exotic species, along with total colonizer biomass, we used separate ANCOVA models with genotype identity as the main effect in the model and stem density as the covariate. For all analyses, we analyzed the October and April data separately because the composition of the colonizing fauna differed substantially between October 2006 and April 2007 (data not shown). In all analyses, cover estimates were log-transformed prior to analysis to improve normality. However, for clarity, we show the untransformed values in all of the figures. We did not use Bonferroni corrections for any of the analyses because this would inflate the probability of committing Type II errors (Gotelli and Ellison 2004).

To test for non-additive effects of genotypic diversity on the number of *Solidago altissima* stems, we used Monte Carlo simulations using data from genotype monoculture plots to construct null genotype mixtures and their associated stem numbers. We then compared the observed stem abundances to these null mixtures. Each null mixture consisted of 3, 6, or 12 genotypes sampled to match the exact identities corresponding to a particular plot combination (e.g., for a 3-genotype plot containing G3, G13, and G19, we sampled only from monoculture plots containing these three genotypes) (Johnson et al. 2006). For each sampled genotype, the appropriate number of genotype individuals (4, 2, or 1), which also included all newly produced stems from rhizomes, was randomly sampled without replacement from a randomly selected replicate monoculture plot. This process was repeated 5000 times for every mixed genotype plot. To calculate statistical differences between stem numbers in observed and null mixtures, we used a bootstrap approach. For each of 10,000 iterations, we sampled seven null mixtures and calculated mean number of stems at the plot-level. We measured *P*-values as the fraction of iterations in which the null mean was equal to or exceeded the observed mean. We calculated 95% confidence intervals using percentiles (2.5^{th} and 97.5^{th} percentiles). If the effects of genetic diversity on stem number were additive, we would expect no difference between observed and predicted means ($P > 0.05$). All Monte Carlo simulations were coded in Microsoft Visual C++ 6.0 (Microsoft, Redmond, WA, USA).

Results and Discussion

In both October and April, genotypic diversity was not related to the richness or cover of colonizing plant species ($P > 0.23$ for total, exotic, or native richness and cover). However, genotypic diversity was negatively correlated with the biomass of colonizing plant species in April, nine months after the experiment was initiated ($r = -0.25$, $n = 63$, $P = 0.04$; Figure V-1A). Biomass of colonizing plants was 32% lower in 12-genotype plots relative to 1-genotype plots. In addition, total biomass (native + exotic species) of colonizing species in polyculture plots (those with at least three genotypes) was 17% lower than total biomass of colonizing species in 1-genotype plots. These results support Elton's (1958) original hypothesis that diversity deters invasions and agree with a growing list of empirical studies indicating that *among* species diversity can deter invasions at neighborhood scales (Levine et al. 2004, Fridley et al. 2007a). However, our results extend these studies by demonstrating that *within* species diversity can also deter plant invasions.

One criticism of many biodiversity studies is that they often confound diversity with the presence of a particular dominant species (Hooper et al. 2005). Indeed, many studies have shown that the presence of competitively dominant species, rather than diversity *per se*, can deter plant invasions (Crawley et al. 1999, Smith and Knapp 1999, Dukes 2002, Smith et al. 2004, Wilsey and Polley 2002, Emery and Gross 2006, Emery and Gross 2007). Here, we found that particular genotypes of *Solidago altissima* limited colonization. In October, total richness of colonizing species (native + exotic species richness) ($F_{20,21} = 2.14$, $P = 0.04$) and native richness ($F_{20,21} = 2.45$, $P = 0.04$), along with

total cover (native + exotic species cover) ($F_{20,21}$= 3.61, P = 0.002), varied by over two-fold among *S. altissima* genotypes. There was no effect of *S. altissima* genotype identity on exotic richness ($F_{20,21}$= 1.08, P = 0.42), and only marginal effects on native ($F_{20,21}$= 1.84, P = 0.08) and exotic cover ($F_{20,21}$= 1.87, P = 0.08). By April, after nine months of colonization, there was no longer any difference in the richness of colonizing species among genotypes (P > 0.45 for total, native, and exotic richness). However, particular genotypes still limited total cover of colonizing species (native + exotic) ($F_{20,21}$= 2.51, P = 0.02) and the cover of exotic species ($F_{20,21}$= 2.44, P = 0.02;), but not native cover ($F_{20,21}$= 2.51, P = 0.24). Total cover differed by 14% and exotic cover differed by 25% among genotypes. In April, there were also strong effects of *S. altissima* genotype identity on total biomass of colonizing species: total biomass ranged from 136 g m^{-2} to 445 g m^{-2} among genotypes ($F_{20,21}$ = 3.347, P = 0.004; Figure V-2).

The majority of colonizing plant species in both October (29 of 34 species) and April (21 of 38) were perennial species. While we did not separate colonizer biomass into native and exotic species, of the 38 species that colonized the experimental plots, 14 are exotic species (http://www.tneppc.org), and nine are considered invasive in Tennessee (Table V-4). Of the ten most common species that colonized our plots, seven are invasive species. Therefore, we are confident that our results reflect the potential role of intraspecific diversity in determining invasion dynamics of exotic and invasive species in this system. In biodiversity studies, it is often challenging to grow every genotype/species in monoculture that occurs in mixture plots while still obtaining high levels of replication. In this study, individual genotypes had only two replicate plots. Though we observed

strong effects of genotypic identity on colonizing plant species, the results should be interpreted cautiously because of the low replication.

The effects of both genotypic diversity and genotype identity on invasion resistance are likely mediated by the effects of genotypic diversity and genetic identity on stem density. Stem density increased with genotypic diversity ($r = 0.29$, $n = 63$, $P = 0.02$; Fig. V-1B) and was 45% greater in 12-genotype plots than in 1-genotype plots. In addition, stem density was 40% greater in plots with at least three genotypes relative to plots with only one genotype. Stem density varied by over ten orders of magnitude among genotypes ($F_{20,21} = 5.39$, $P = 0.0002$; Fig. V-4). The number of *S. altissima* stems was negatively correlated with total cover ($r = -0.30$, $n = 63$, $P = 0.02$; Fig. V-3A), native cover ($r = -0.38$, $n = 63$, $P = 0.002$), exotic cover ($r = -0.31$, $n = 63$, $P = 0.01$), and total biomass ($r = -0.78$, $n = 63$, $P < 0.0001$; Fig. V-3B) of colonizing plant species. All possible regressions indicated that stem density, rather than genotypic diversity, best predicted resistance to invasion in both October 2006 and April 2007 (Table V-1). Similarly, stem density, rather than genotype identity, limited the total biomass of colonizing species in the monoculture plots (Table V-2).

All of the experimental plots began with twelve stems. Our results suggest that stem density increased with genotypic diversity and that some genotypes produced more stems than did others. As a result, as stem density increased, space available for the establishment of colonizing species decreased. Increasing stem density may also lead to more intense competition between resident plants and colonizing individuals, thereby reducing the probability of their establishment and growth. For example, we observed no

difference in the cover of colonizing species among genotypic diversity treatments. However, there was an effect of the treatments on the biomass of colonizing species, indicating that the species that have established in diverse plots are not as productive. Interestingly, our results agree with other studies that have examined the relationships among species diversity, space use, and invasion success in plant communities (Knops et al. 1999, Levine 2000, Hector et al. 2001, Kennedy et al. 2002) and marine sessile invertebrate communities (Stachowicz et al. 1999, 2002). For example, at Cedar Creek in Minnesota, USA, Knops et al. (1999) found that total biomass of invaders was ~50% lower in plots with 12 species relative to plots with only one species. In a similar study at Cedar Creek, Kennedy et al. (2002) found a 94% reduction in the cover of invading plant species in plots with 12 species relative to monoculture plots. In addition, Hector et al. (2001) found that there was no effect of species richness (ranging from 1-12 species) on invader biomass during the first year the BIODEPTH experiment, but biomass of invading species and species richness were negatively correlated in later years. Of course, these studies all assessed the effects of interspecific diversity, whereas our focus is on intraspecific diversity. Thus, it is perhaps not surprising that the effects of intraspecific diversity are generally weaker than the effects interspecific diversity on invasibility. Nevertheless, our results indicate that plant invasions can be constrained by within species diversity.

Several mechanisms might explain why stem density increased with genotypic diversity, thereby deterring invaders. First, sampling effects, a contentious issue in biodiversity studies, might occur because high diversity plots have a greater chance of containing

more productive genotypes (Huston 1997, Hooper et al. 2005). Indeed, genotypes were highly variable in stem production and the most productive mixture was never greater than the most productive monoculture. Second, positive interactions, such as niche complementarity or facilitation, might occur among genotypes, resulting in greater stem production in mixtures relative to monocultures (i.e. interactive or non-additive effects). Disentangling sampling effects from non-additive effects requires comparing stem density of individual genotypes when growing in mixtures to the same genotypes growing in monocultures (Trenbath 1974). We grew all 21 genotypes that occur in mixtures in replicate monocultures, but could not confidently sample the same genotypes in mixtures after the first year of the experiment because of high levels of interdigitation among ramets within plots. Determining the identity of each ramet would require genotyping hundreds of ramets growing in individual mixtures, which was beyond the scope of this project. However, a previous study in this system (Crutsinger et al. 2006) indicated that positive interactions among genotypes in mixtures led to increased relative aboveground primary productivity (i.e. overyielding) during the first year of the study. In addition, other studies have also found support for positive interactions among genotypes leading to increased plant performance in mixtures (Reusch et al. 2005, Johnson et al. 2006). However, we did examine relative stem production from the first year of the study, when stems could still be assigned to particular genotypes. There were ~19% more ramets produced in 12-genotyple plots than the number predicted from component genotypes grown in monoculture (Fig. V-5). Our results are limited to only the early dynamics of plant colonization into the experimental plots, and determining whether this

mechanism and general patterns are consistent over multiple years requires further experimentation. But we conclude from the results from the first year that it is possible for facilitation or niche complementarity among genotypes, rather than sampling effects alone, to result in higher stem density in genotypically diverse plots.

Numerous studies have shown that *among*-species diversity and particular dominant species can limit biological invasions at small spatial scales (Fridley et al. 2007a). In a greenhouse study, Weltzin et al. (2003) found that the number of *Arabidopsis thaliana* genotypes did not affect emergence, survivorship, biomass, rosette area, or reproductive potential of the congener they introduced, *Arabidopsis suecica*. However, similar to our results, the density of *A. thaliana* had strong and negative effects on *A. suecica.* Collectively, our results demonstrate that *within*-species diversity and the identity of particular genotypes can reduce susceptibility to biological invasions. These results, in conjunction with a growing body of research (Wimp et al. 2005, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Whitham et al. 2006), illustrate that variation in intraspecific diversity can affect ecosystem processes and susceptibility to invasion. This suggests that the loss of intraspecific diversity could further exacerbate the impact of biological invaders on native biodiversity and ecosystems.

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Table V-1. All possible regression models using *Solidago altissima* stem density and genotypic diversity as predictors of total cover, exotic cover, and native cover of invading plant species for October 2006 and April 2007. Only models with lowest AIC are presented.

October 2006	Parameter	*P*	*AIC*	r^2
Total cover				
Stem density	-0.004	<0.0001	-203.72	0.31
Exotic cover				
Stem density	-0.067	0.003	208.39	0.13
Native cover				
Stem density	-0.0812	<0.0001	178.99	0.27
Total richness				
Stem density	-0.021	0.01	85.89	0.10
Exotic richness				
-	-	-	-	-
Native richness				
Stem density	-0.01	0.02	43.90	0.09
April 2007				
Total cover				
Stem density	-0.0002	0.008	-439.34	0.11
Exotic cover				
Stem density	-0.0004	0.01	-368.12	0.09
Native cover				
Stem density	-0.002	0.002	-224.10	0.14
Total richness				
Stem density	-0.01	0.06	99.00	0.06
Exotic richness				
-	-	-	-	-
Native richness				
Stem density	-0.01	0.008	48.84	0.11
Biomass				
Stem density	-1.62	<0.0001	519.08	0.61

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Table V-2. Results from ANCOVA with *Solidago altissima* genotype identity as the main effect and stem density as the covariate. Shown are the *F* values and *P*-values in parentheses.

October 2006	Total richness	Exotic richness	Native richness	Total cover	Exotic cover	Native cover	Total biomass
Genotype identity	1.68(0.13)	1.10(0.42)	1.63(0.14)	1.67(0.13)	1.14(0.39)	0.64(0.84)	
Stem density	1.04(0.32)	1.35(0.26)	0.08 (0.78)	1.65(0.21)	0.01 (0.95)	4.56(0.04)	
April 2007							
Genotype identity	0.75(0.74)	1.16(0.37)	0.86(0.63)	1.95(0.07)	1.81 (0.10)	1.14(0.38)	1.44(0.21)
Stem density	4.1(0.05)	2.02(0.17)	1.14(0.30)	0.66(0.43)	0.41(0.53)	1.70(0.21)	10.9(0.004)

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Table V-3 Correlation matrix of response variables for a) October 2006 and b) April 2007 datasets. Values are Pearson Correlation coeffiencents. '*' indicates P<0.05, '**' indicates P<0.01, and '***' indicates P<0.001.

(a) October 2006

	Total richness	Exotic richness	Native richness	Total Cover	Exotic Cover	
Exotic richness	0.71***					
Native richness	0.78***	0.11				
Total Cover	0.40**	0.19	0.39**			
Exotic Cover	0.24	0.18	0.17	0.75***		
Native cover	0.34**	-0.02	0.49***	0.64***		0.17

(b) April 2007

	Total richness	Exotic richness	Native richness	Total Cover	Exotic Cover	Native cover
Exotic richness	0.68***					
Native richness	0.73***	0.06				
Total Cover	0.09	0.08	0.04			
Exotic Cover	0.08	0.02	0.09	0.77***		
Native cover	0.11	0.03	0.04	0.19	0.17	
Weed biomass	0.15	0.00	0.21	0.38**	0.37**	0.39**

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Table V-4. Listed are the 38 species encountered in the experimental plots, whether they are native or exotic to east Tennessee, their invasion status, and the number of plots out of 63 in which the species was detected. Rank 1: Exotic plant species which possess characteristics of invasive species, spread easily into native plant communities, and displace native vegetation. Includes species which are or could become widespread in Tennessee (http://www.tneppc.org); Rank 2: Exotic plant species which possess some invasive characteristics, but have less impact on native plant communities. These plants may have the capacity to invade natural communities along disturbance corridors, or to spread from stands in disturbed sites into undisturbed areas, but have fewer characteristics of invasive species than Rank 1 above (http://www.tneppc.org).

Native or Exotic	Invasion status	Species	Total no. of Plots
Exotic	Rank 2	*Allium vineale*	49
Exotic	Rank 2	*Bromus spp.*	1
Exotic		*Cerastium glomeratum*	60
Exotic	Rank 2	*Cirsium vulgare*	41
Exotic		*Coronilla varia*	1
Exotic		*Dactylis glomerata*	3
Exotic		*Duchesnia Indica*	3
Exotic	Rank 2	*Festuca spp.*	1
Exotic		*Lamium amplexicaule*	5
Exotic	Rank 1	*Lespedeza cuneata*	18
Exotic	Rank 1	*Lonicera japonica*	2
Exotic	Rank 2	*Melilotus alba*	1
Exotic		*Oxalis stricta*	52
Exotic		*Paspalum dilatum*	1
Exotic		*Plantago lanceolata*	7
Exotic		*Potentilla spp.*	1
Exotic	Rank 1	*Sorghum halepense*	1
Exotic		*Stellaria media*	1
Exotic		*Taraxacum officionale*	52

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Exotic		*Trifolium campestre*	56
Exotic		*Trifolium repens*	19
Exotic		*Veronica spp.*	57
Exotic		*Viola arvensis*	23
Native		*Ambrosia artemisiifolia*	55
Native		*Symphyotrichum pilosum*	2
Native		*Carex spp.*	18
Native		*Desmodium spp.*	2
Native		*Erigeron strigosus*	31
Native		*Galium aparine*	1
Native		*Galium parisiense*	26
Native		*Geranium carolinianum*	41
Native		*Geum spp.*	23
Native		*Lactuca canadensis*	13
Native		*Ranunculus abortivus*	1
Native		*Salvia lyrata*	47
Native		*Setaria parviflora*	13
Native		*Triodanis perfoliata*	47
Native		*Verbesina spp.*	16

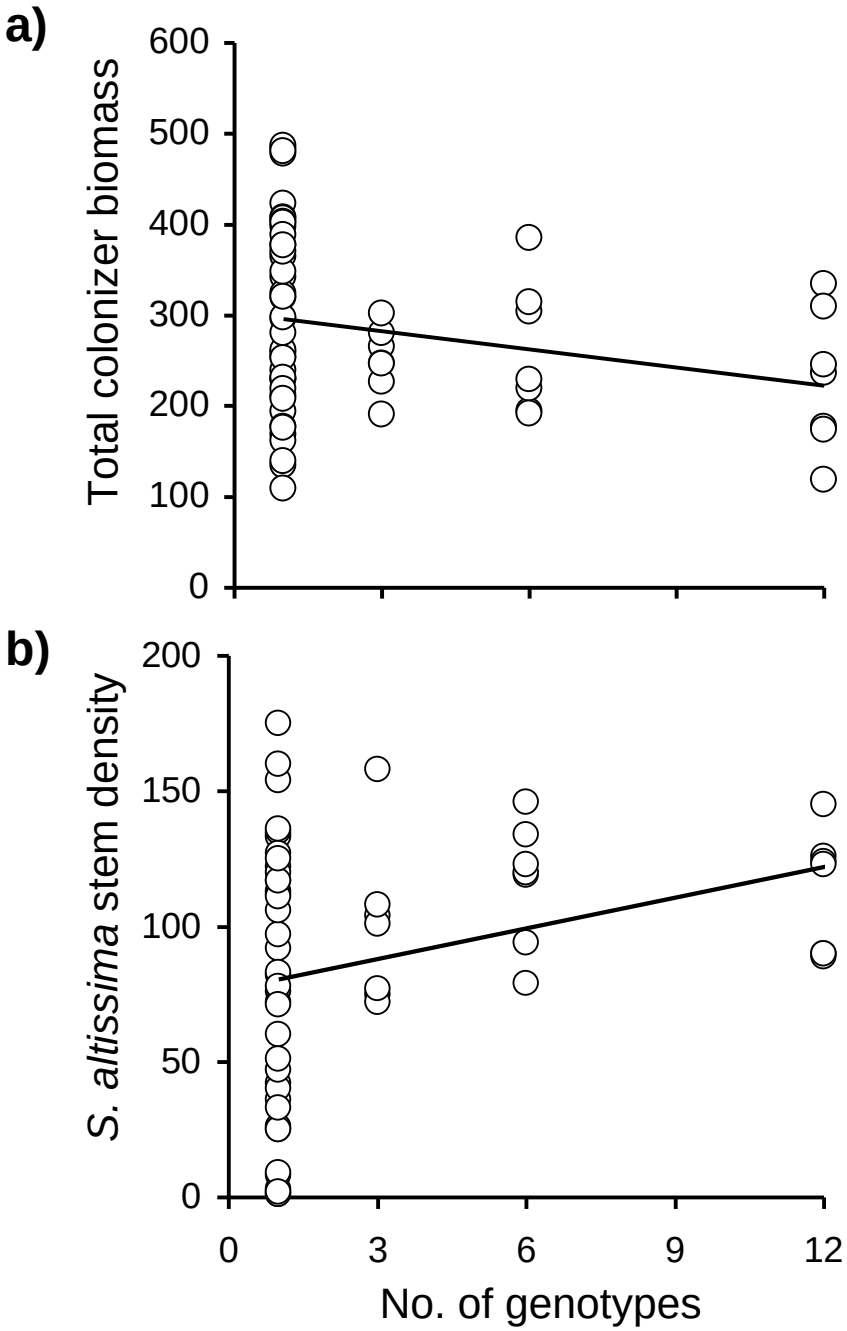


Figure V-1. The relationships between the number of *S. altissima* genotypes in 63 1-m^2 plots and the total aboveground biomass of colonizing plant species (a) and *Solidago altissima* stem density (b).

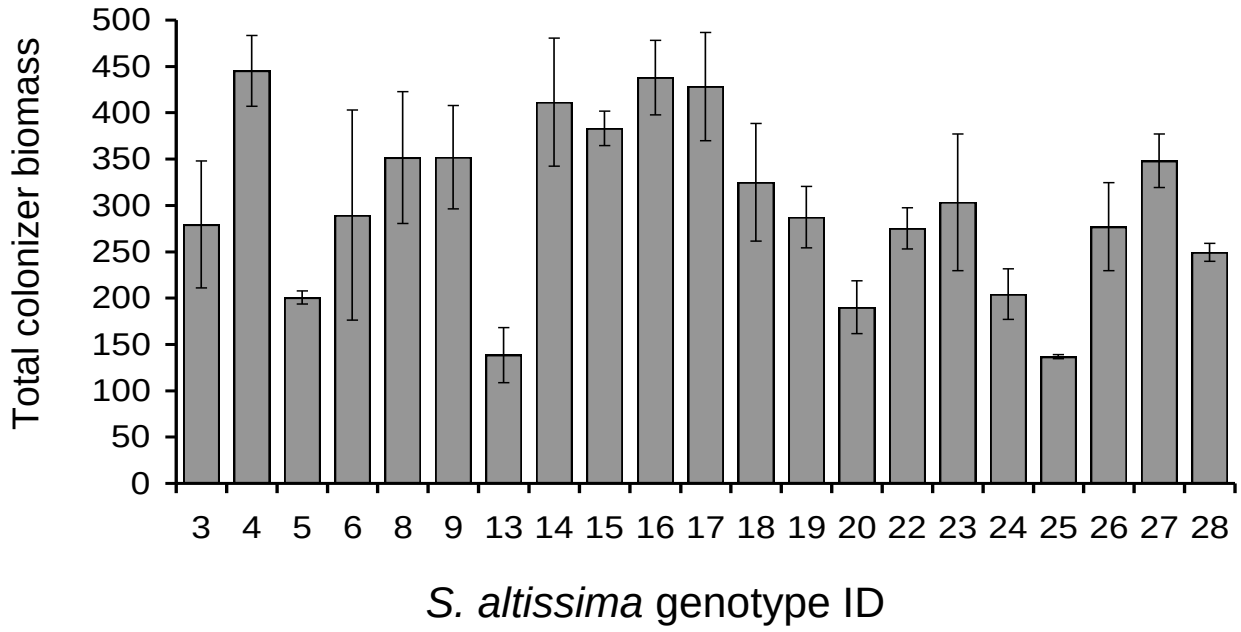
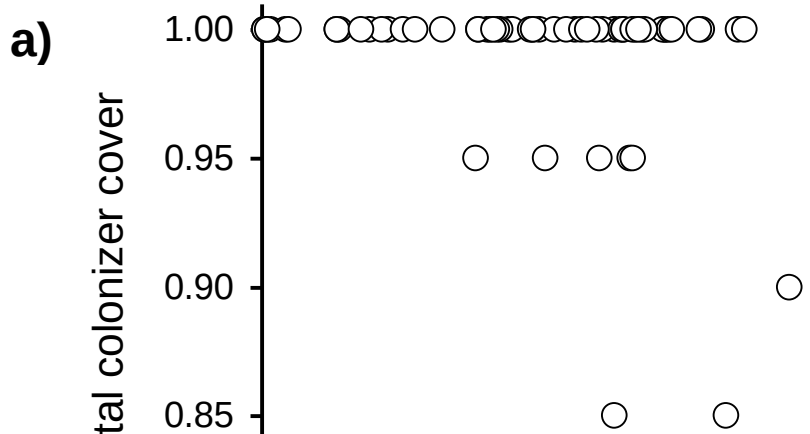


Figure V-2. The relationship between total aboveground biomass of all colonizing plant species (native + exotic species) and genotype identity of *Solidago altissima*. Bars represent mean (±SEM) biomass (g 1-m^2).



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b)

Figure V-3. The relationship between *Solidago altissima* stem density and total cover (a) and total biomass (b) of colonizing plant species.

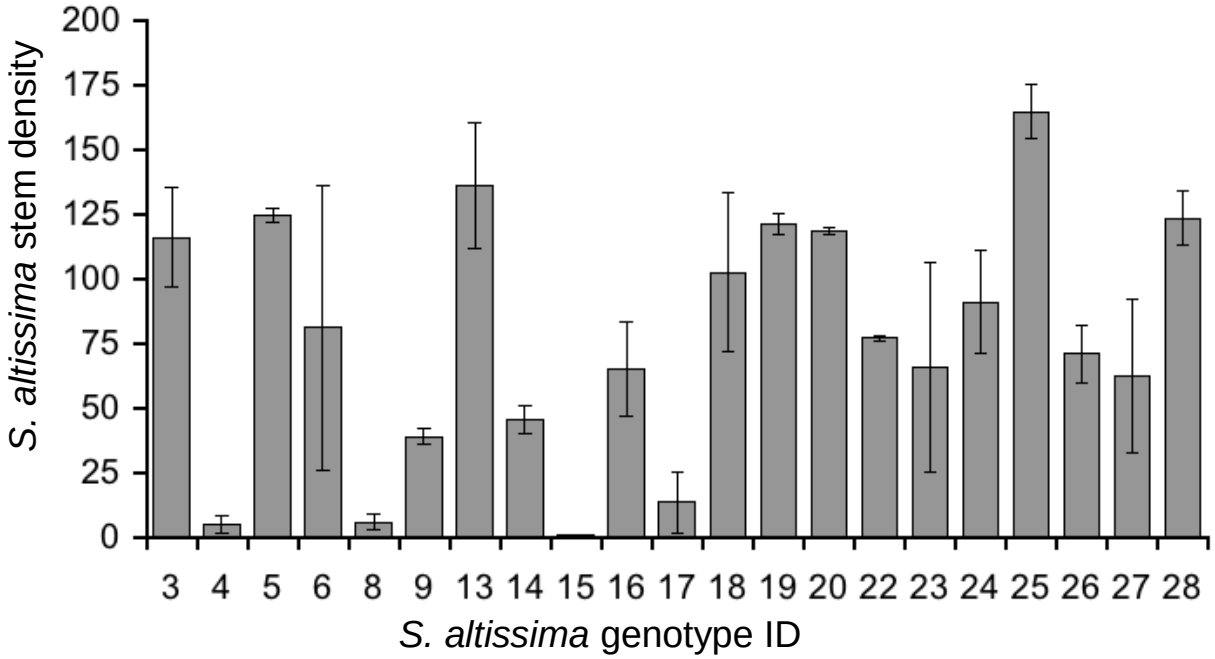

Figure V-4. The relationship between stem density and genotype identity of *Solidago altissima* after two years. All plots were started with 12 stems. Bars represent mean (±SEM) number of stems per 1-m^2 plot.

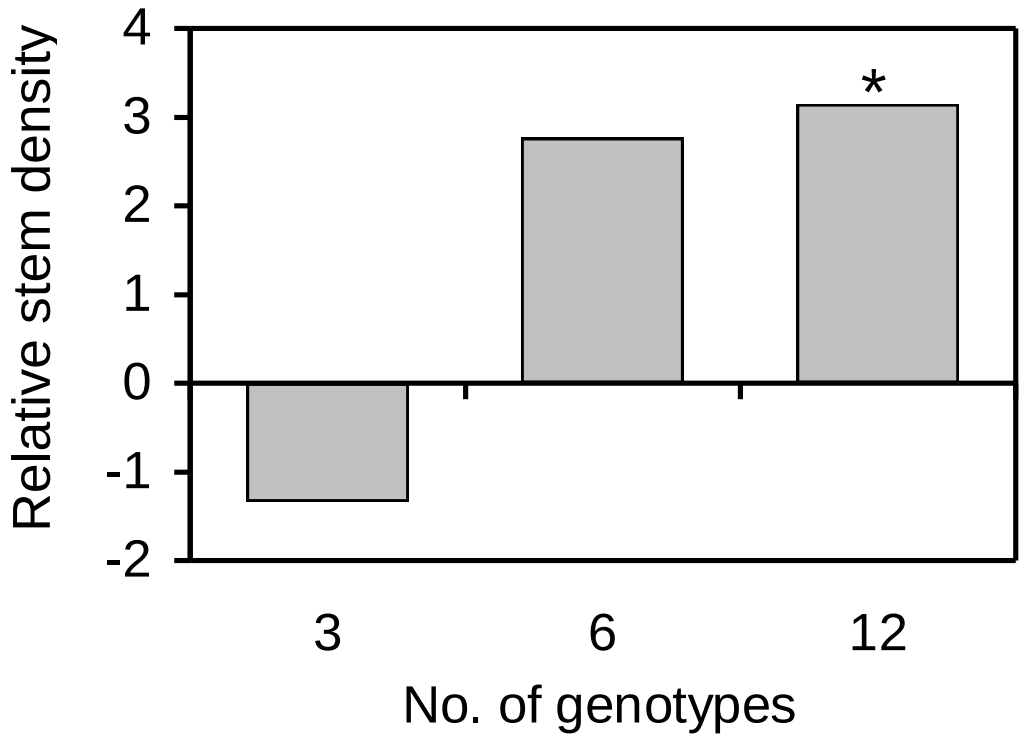

Figure V-5. Non-additive responses of plot-level stem density in mixtures of 3, 6, or 12 genotypes of *Solidago altissima.* Zero indicates the number of stems predicted by summing the individual contributions of component *S. altissima* genotypes grown in monoculture (i.e. additive stem number). Bars indicate how many more or fewer stems there are at a given diversity level than predicted. * denotes significant non-additive responses ($P < 0.05$).

Vita

Gregory M. Crutsinger was born in Portland, Oregon on July 23rd, 1980. He attended public school from 1985-1987 in Hinkley, California and from 1988-1998 in Findlay,

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