Research

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

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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 the genetic make-up of a host-plant patch.

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, Crutsinger et al. 2006, Johnson 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 Stachowicz 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, Johnson and Agrawal 2005, 2007, Whitham et al. 2006), and as the number of genotypes in a host-plant population increases, so should the number of corresponding arthropod species (Bangert et al. 2005, Wimp et al. 2005, Crutsinger et al. 2006, Johnson 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 (Reusch et al. 2005, Schweitzer 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 might 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?

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 (35°58′N, 84°12′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* (yellow crownbeard), *V. virginica* (white crownbeard) and *Rubus* spp. (blackberry); sub-dominants include about 60 other herbaceous and woody species (L. Souza et al. unpubl.).

Solidago altissima, or tall goldenrod, is a well-studied perennial that dominates old-field ecosystems throughout eastern North America (Werner et al. 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 et al. 1989). At the study site, *S. altissima* plants bolt in mid-April with leaf senescence and peak flowering occurring in early October (Crutsinger unpubl.).

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 15×20 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 22 May, 15 June, 23 July, 3 Sept and 3 Oct of 2005, and surveys lasted from one to four days. Between 09:00 and 16:00 h, 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 Appendix 5 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 (ver. 6). 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) (Crutsinger et al. 2006, Johnson 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 5000 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 (2.5th and 97.5th 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.

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 (see Crutsinger et al. 2006 for details), 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 h, 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 (ver. 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. 1a, Appendix 1, Table 1 and 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 and October survey periods (Fig. 1b, Appendix 1, Table 3 and 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 (Appendix 1, Table 1 and 3).

Though the effect of host-plant genotypic diversity on arthropod community composition varied at the end of the
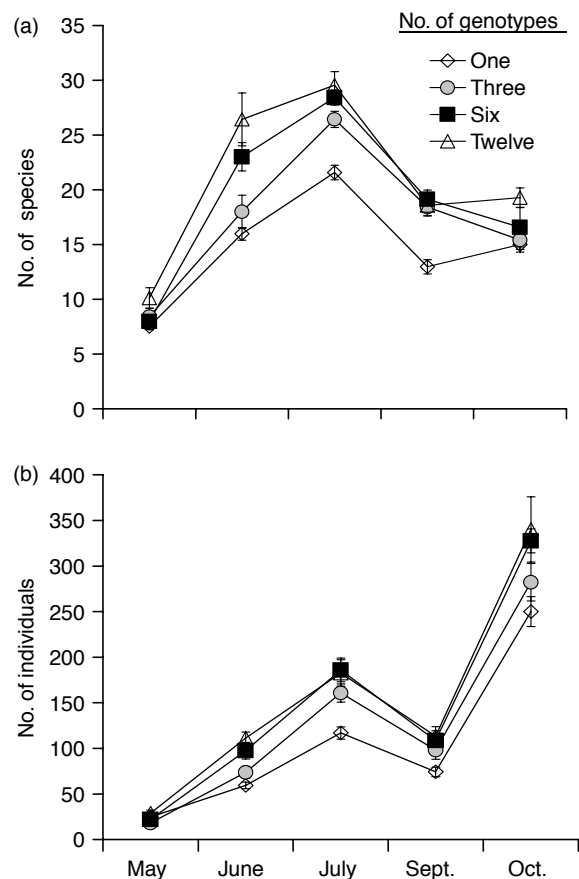

Fig. 1. Effects of genotypic diversity in experimental plots of *Solidago altissima* on total arthropod richness (a) and total arthropod abundances (b) over the course of a growing season. Each point represents the plot-level mean ± SE for patches containing 1, 3, 6 or 12 *S. altissima* genotypes. The 1-genotype treatment consisted of all twenty-one genotypes with two replicates each and mixtures had seven replicates each. A line connects each genotypic diversity level across survey periods.
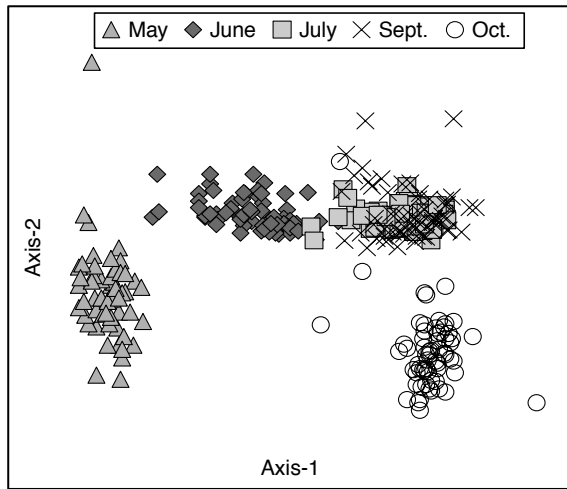
Fig. 2. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarities of plot-level arthropod communities in 63 experimental plots of Solidago altissima plants throughout a growing season. The five survey periods are represented by different shapes. Arthropod community composition differed among all survey periods indicating significant turnover in community composition throughout the growing season.

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. 2, Appendix 2), 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. 2, Appendix 2), 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 3). 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. 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. 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. 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. 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. 4, Appendix 4, Table 1 and 2). 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 4, Table 1).

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. 5b). The magnitude of non-additive effects was consistent from the May–July with up to ∼43% more biomass, and up to 29%
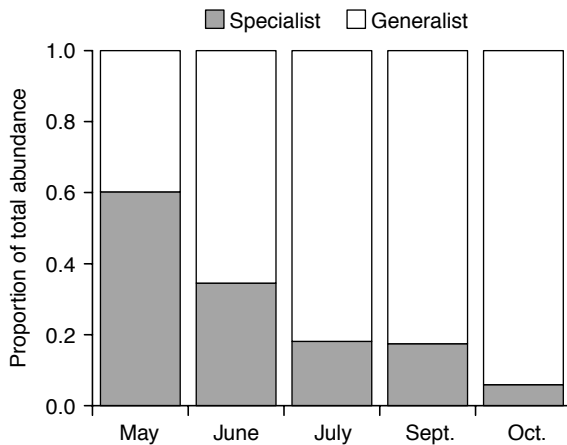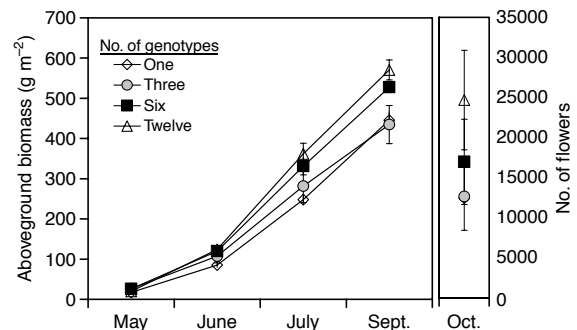

Fig. 3. Proportional abundances of generalist versus specialist herbivores throughout the growing season. Each bar represents the total arthropod abundance within a survey period and subsections indicate the percent of total made up by herbivore type.

Fig. 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.
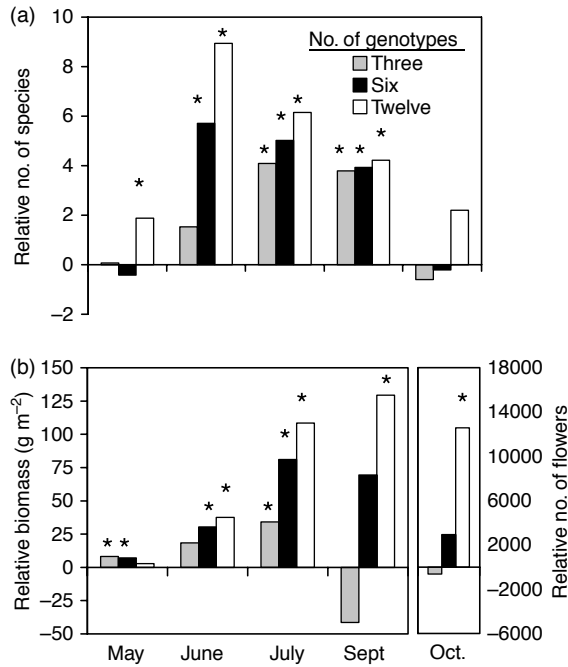
Fig. 5. Non-additive responses of plot-level arthropod richness (a) and plot-level aboveground biomass (May–September) and flower number (October only) (b) to mixtures of 3, 6 or 12 genotypes of *Solidago altissima* throughout the growing season. Zero indicates the number or amount predicted by summing 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).

more biomass than predicted by additive mixtures in September (Fig. 5b).

We detected no effect of genotypic diversity on the total number of flowers per plot in October (Fig. 4, Appendix 4, Table 2). 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. 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. 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. 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. 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. 1). During this time, the arthropod community consisted mostly of generalist, floral-associated species (Fig. 3, Appendix 3). 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. 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 hypothesized 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 (Crutsinger unpubl.). 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. 2 and 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. 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. 3, Appendix 2 and 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. 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. 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. 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.

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. 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 plays 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 Weis 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 ($\sim$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 vs 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*, which 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.

Conclusion

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 1.

Table 1. Results of repeated-measures ANOVA examining arthropod richness responses to manipulation 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 ×Time	12, 148	1.356	0.202

Table 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 3. Results of repeated-measures ANOVA examining arthropod abundance responses to manipulation 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 ×Time	12, 148	1.159	0.325

Table 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.

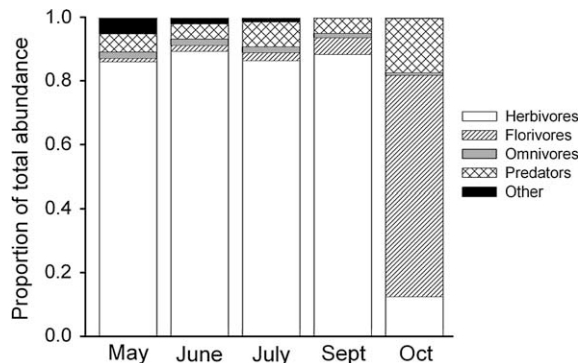| Variable	Effect	DF	MS	F	p
Abundance	May	3, 59	0.0573	0.887	0.452
	June	3, 59	0.0258	11.460	<0.001
	July	3, 59	0.1967	8.178	<0.001
	September	3, 59	0.1951	4.028	0.011
	October	3, 59	0.1157	2.233	0.093

Appendix 2.

Table 1. 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

Appendix 3.

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 pattern.

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Appendix 4.

Table 1. 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 × Time	9, 138	2.332	0.017

Table 2. Separate one-way ANOVA results examining the effect of *S. altissima* genotypic diversity treatments on plot-level above-ground 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

Appendix 5.

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