G M. C , M D . C , A. N .

G. M. C e (@ .e), De E E B , 569 D e H , . e ee, K e, N 37996, A – M. D. C , De B , H e - e C e e, H e - e , A 23943, A – J. A. F e e N. J. e , De E E B , 569 D e H , . e ee, K e, , 37996, A.

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 , tall goldenrod, to contain 1, 3, 6 or 12 genotypes m^{-2}

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 *Solidago* 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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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), *Verbesina 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 interclonal 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 *Solidago* can vary considerably in their overall arthropod community compo-

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

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 . 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 . 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 3366f01T8ic

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.

This experiment showed that intraspecific genotypic diversity in experimental patches of 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 . 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 , 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

for an extended time, floral-associated arthropods in the . 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

either correlated or uncorrelated with the quantity of host

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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

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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.

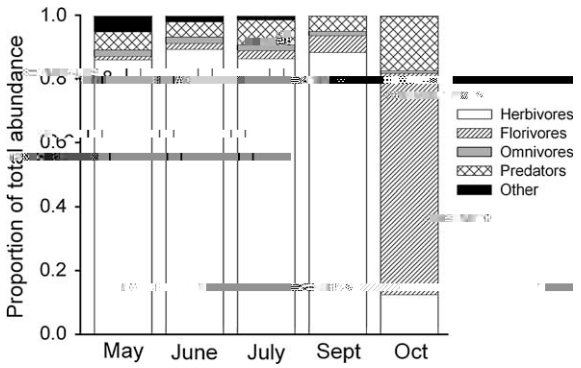

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Table 1. Repeated-measures ANOVA results examining plot-level

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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