Oecologia (2008) 154:755–761
DOI 10.1007/s00442-007-0863-3

COMMUNITY ECOLOGY - ORIGINAL PAPER

Differential attack on diploid, tetraploid, and hexaploid *Solidago altissima* L. by five insect gallmakers

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Received: 8 May 2007 / Accepted: 7 September 2007 / Published online: 9 October 2007

Abstract Genetic variation among plants can influence host choice and larval performance in insect herbivores. Ploidy (cytotype) variation is a particularly dramatic form of plant genetic variation, and where diploid and polyploid cytotypes of a species occur in sympatry, they may provide herbivores with choices that are distinguished by profound and genome-wide genetic differences. We tested for non-random attack by five gallmaking insect herbivores on diploid, tetraploid, and hexaploid cytotypes of the goldenrod *Solidago altissima* L., working in seven midwestern US populations where the ploidies co-occur on spatial scales relevant to insect host choice. For four of the five herbivores, attack was non-random with respect to ploidy at one or more sites. Ploidy effects on attack were complex: the ploidy subjected to highest attack varied both across herbivores within sites and (for most herbivores) across sites within herbivores. Ploidy effects on attack will alter rates of encounter between insect herbivores—either increasing or decreasing the likelihood of two herbivores sharing a host plant ramet, compared with the case with no effects of ploidy. Plant ploidy variation appears likely to have a major impact on insect community organization, and perhaps on plant–herbivore coevolution, but that impact is likely to be spatially heterogeneous.

Keywords Polyploidy · Insect–plant interactions · Herbivory · Goldenrod

Communicated by Richard Karban.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0863-3) contains supplementary material, which is available to authorized users.

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Introduction

Interactions between phytophagous insects and their host plants are often influenced by intraspecific variation in plant genotype, with consequences for insect community organization and ecosystem function (Crutsinger et al. 2006; McGuire and Johnson 2006; Whitham et al. 2003; Wimp et al. 2005). Variation in cytotype, and particularly in ploidy, is a widespread evolutionary phenomenon in plants, and rates of polyploidization are high enough to produce frequent intraspecific variation in ploidy (Ramsey and Schemske 1998; Soltis and Soltis 1993). Still, this important form of plant genetic variation has not been fully integrated into our understanding of the evolutionary ecology of plant–insect interactions. Only a few studies have examined the impact of polyploidy on interactions between plants and their insect herbivores (Münzbergová 2006; Nuismer and Thompson 2001; Thompson et al. 1997). Each of these studies found significant differences in herbivore attack among intraspecific ploidy forms. However, just one

study (Nuismer and Thompson 2001) asked whether different insect herbivores showed concordant responses to ploidy variation (they did not, for three herbivores at one site) and just one study (Thompson et al. 1997) has asked whether herbivores show concordant ploidy effects across multiple sites (they did, for one herbivore at three sites). These results indicate that polyploidy may indeed be an important factor influencing phytophagous insect communities and setting the stage for their coevolution with their host plants. However, these studies say little about whether such effects are rare or common, whether they are representative of the taxonomic diversity of insect herbivores, or whether we should generally expect a geographic mosaic in insect responses to plant polyploidy as we do in many other ecological interactions (Thompson 2005; e.g., Heard et al. 2006).

In this study, we take a spatially extensive and community-based approach to investigate the influence of ploidy variation in late goldenrod (*Solidago altissima*) on attack by five gallmaking insect herbivores. We document ploidy effects on attack rates for all of the herbivores, and show that for four of them ploidy effects vary in intensity and even in direction among sites. Our data therefore suggest that, for plant species with co-occurring ploidy forms, ploidy variation and associated genetic variability could have a major impact on insect community organization. Our data also suggest that we should often expect responses to plant ploidy to be spatially complex and discordant among herbivore species.

Materials and methods

Study system

Solidago altissima L. (Asteraceae: Astereae) is a rhizomatous perennial with a native distribution over much of temperate North America (Nova Scotia to Florida, and west to Texas and Alberta; Semple and Cook 2006). Its original habitats likely included prairies and forest openings but, since European colonization, *S. altissima* has become an abundant plant of roadsides, old fields, and other disturbed or successional areas. There are three known cytotypes that differ in ploidy (henceforth, just "ploidies"): diploid (2n = 18), tetraploid (2n = 36), and hexaploid (2n = 54). *S. altissima* is predominantly diploid in the west (treated as ssp. *gilvocanescens* by Semple and Cook 2006) and hexaploid in the east (ssp. *altissima*), with a broad zone of overlap in the Midwest where tetraploids are also found. In the overlap zone, all three ploidies co-occur on very fine spatial scales in some local populations (Halverson et al. 2007). Despite previous assignment of western diploids and eastern hexaploids to separate subspecies, Halverson et al. (2007) argue that ploidies in the overlap zone are not ancient, monophyletic lineages; instead, higher ploidies appear to be multiply derived.

Many insect herbivores (>100 spp.) attack *S. altissima* (Fontes et al. 1994; Root and Cappuccino 1992). These herbivores of *S. altissima* vary in their degree of host specialization, with some feeding broadly on many herbaceous plants, others restricted to Astereae, and many specific to *S. altissima* and the closely related and widely co-distributed *Solidago gigantea* Ait and *Solidago canadensis* L. No data on preference or performance patterns across ploidies have been available for any of these herbivores. In this study, we focus on five common gallmaking herbivores of *S. altissima*. Two are stem gallers [*Eurosta solidaginis* Fitch (Diptera: Tephritidae) and *Gnorimoschema gallaesolidaginis* Riley (Lepidoptera: Gelechiidae)], two are meristem gallers [*Rhopalomyia solidaginis* Loew (Diptera: Cecidomyiidae) and *Procecidochares atra* Loew (Diptera: Tephritidae)] and one is a leaf galler [*Asteromyia carbonifera* Osten Sacken (Diptera: Cecidomyiidae)]. Only *Eurosta* has described subspecific variants on *S. altissima*: two subspecies differing in wing coloration meet and hybridize in Iowa (Brown and Cooper 2006), at the western end of our sampling transect (see below). We focused on gallmakers for two reasons. First, presence of a gall indicates unambiguously that a herbivore individual developed and fed on a particular plant genotype (unlike sightings of herbivores that are mobile among plants). Second, gallmakers experience highly intimate interactions with their host plants, and so they may be more likely than other herbivores to be sensitive to host genetic variation (including ploidy variation).

Sampling of goldenrod populations

We scored plants for ploidy and herbivore attack in seven *S. altissima* populations along a 570-km east–west transect through Illinois, Iowa and Nebraska (Electronic Supplementary Material I). We had previously established that these populations included *S. altissima* ramets of more than one ploidy, and that on spatial scales of 5–10 m ramets show no sign of clumping by ploidy (Halverson et al. 2007). As in previous studies of herbivory and polyploidy (Nuismer and Thompson 2001; Münzbergová 2006), we measured herbivore attack. Patterns in relative attack across ploidies will be influenced by herbivore preference for, and performance on, the different ploidies, and potentially by other ecological factors. Separating these influences on attack rate would require common-garden experiments, which we have not yet performed.

We established a 40 × 120-m grid in each population, with the grid defining forty-eight 10 × 10-m quadrats. We sampled *S. altissima* ramets in two phases: phase I served to assay available ploidy variation in each population,

while phase II served to assay ploidy variation among herbivore-attacked ramets. In phase I, we sampled the ramet closest to each gridline intersection, whether or not it had been attacked. In phase II (late July 2004, when herbivore activity was apparent), we sampled further ramets that we could see had been attacked by the herbivores of interest. For each herbivore species, we sampled up to four attacked ramets in each quadrat, selected haphazardly but with the constraint that each was at least 1 m away from other sampled ramets. Many quadrats yielded fewer than four sampled ramets, either because fewer than four ramets in the quadrat were attacked, or because attacked ramets were closer together than 1 m. We are confident that we did not inadvertently bias our sampling by ploidy, because we sampled without regard for plant or gall size or other observable variation; in any event, there are no known morphological correlates of ploidy that are apparent at the time that we sampled (pre-flowering).

For each sampled ramet, we collected leaves for ploidy analysis. Leaf tissue was wrapped in aluminum foil, flash-frozen in liquid N_2, and stored at −80°C until analyzed for ploidy. We also scored each sampled ramet for the presence of the six insect herbivores. When there were multiple galls of one species on a ramet, we scored this as a single occurrence, as we were unable to determine whether two galls on the same ramet represented offspring of the same female (one host choice decision) or two females (two host choice decisions). Furthermore, in phase II sampling, a ramet selected based on the presence of one herbivore often hosted galls of another herbivore as well. In such cases, to avoid non-independence we do not include the latter "incidental" herbivores in our analyses. In some cases, a gall might have been initiated but the gallmaker failed to survive; we scored such ramets as "under attack".

Flow cytometric determination of ploidy

We chopped each leaf sample until homogenized in a chilled petri plate with ~25 µl of Galbraith buffer (Galbraith et al. 1983). We then added ~2 ml of buffer, filtered through 50 and 20 µm microfilters, and centrifuged (800 × *g*, 4°C) for 8 min. After removing the supernatant, we added ~1 ml of 100 µl/ml propidium iodide (PI) to each pellet and vortexed to mix. We used a Beckman–Coulter Epics XL–MCL flow cytometer (Iowa State University Flow Cytometry Facility) to measure the DNA content of ~3,000 nuclei as a function of their PI fluorescence intensity under 488 nm excitation. We converted fluorescence to ploidy using 2n, 4n, and 6n *S. altissima* standards (determined via root-tip squash chromosome counts by J. Semple, University of Waterloo, Canada). Ploidy standards displayed the expected pattern of relative fluorescence, making scoring of ploidy for our sampled ramets straightforward.

Quantifying ploidy effects on host use

If a herbivore either prefers or performs better on one ploidy than another, we will see a distribution of ploidies among attacked ramets that differs from the distribution available for attack (Table 1). For each herbivore, we tested fit between available (phase I sampling) and attacked (phase II sampling) ploidy frequencies at each site in turn (ignoring herbivore/site combinations for which we collected less than seven attacked ramets). Because expected counts were sometimes <6, we used Fisher's exact tests, applying them to contingency tables in which the rows corresponded to ploidy and the columns to available versus attacked ramets (2 × 3 or 2 × 2 tables, depending on the number of ploidies present). Unattacked ramets at the time of phase II sampling provide no information about ploidy effects, were not sampled, and do not enter into the statistical tests. To protect against inflation of type I error when performing tests for multiple sites, we checked all *P*-values for significance following sequential Bonferroni correction (Rice 1989; *P*-values in bold in Fig. 1). This procedure can be criticized for being too conservative (Moran 2003; Nakagawa 2004), and we suggest cautious interpretation of the single case in which a test was significant before, but not after, Bonferroni correction (*Gnorimoschema* at McFarland Park).

We were particularly interested in whether, for each herbivore, ploidy effects on attack rate varied across sites. (We emphasize that we are *not* interested in comparing absolute attack rates, on any ploidy or on the total population,

Table 1 Ploidy frequencies for *Solidago altissima* at our seven study sites[a]

Site (site abbreviation in parentheses)	n	Diploid	Tetraploid	Hexaploid
Rest Area, Lincoln, Nebraska (RAL)	33	0%	33%	67%
Smith Wildlife Area, Council Bluffs, Iowa (SWA)	34	15%	35%	50%
Beaver Lake, Dexter, Iowa (BVL)	32	16%	34%	50%
McFarland Park - Ames, Iowa (MFP)	66	85%	15%	0%
Conard Environmental Research Area, Grinnell, Iowa (CER)	83	45%	5%	51%
Norton Nature Area - Durant, Iowa (NNA)	36	72%	17%	11%
Johnson Sauk Trail State Park, Annawan, Illinois (JST)	21	24%	19%	57%

[a] Full site details are in Appendix I of Halverson et al. (2007)

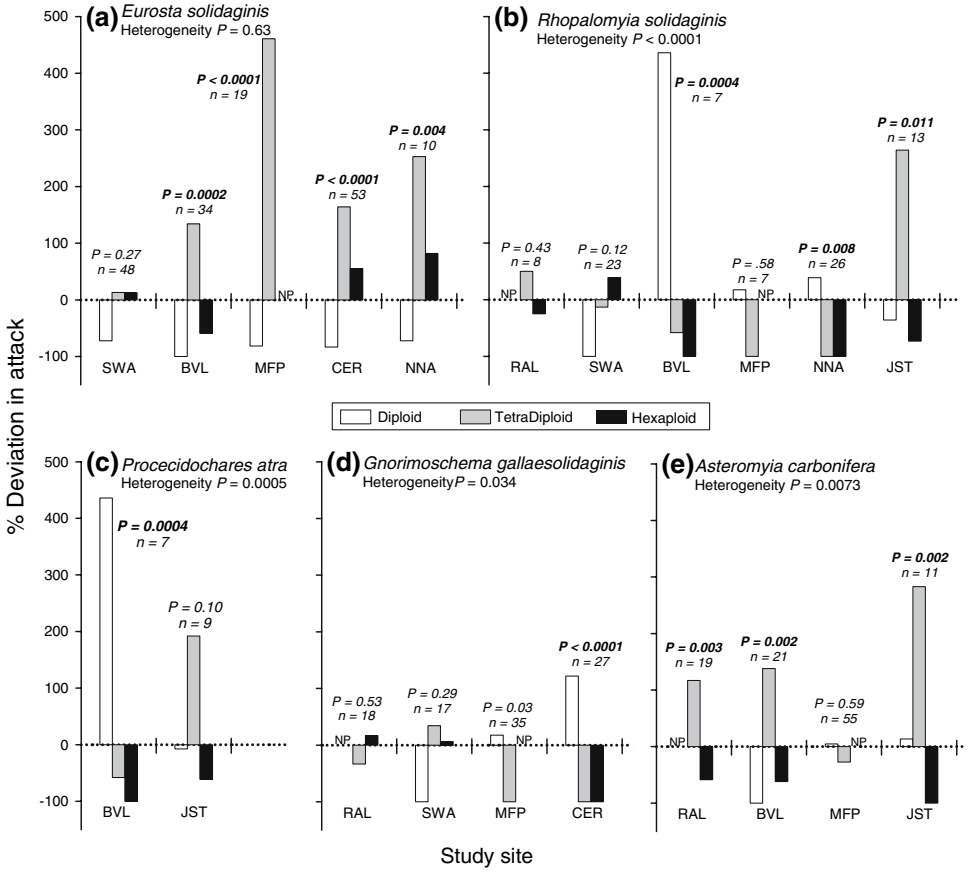

Fig. 1a–e Ploidy effects on attack rates by five herbivores of *Solidago altissima* at seven study sites. *% Deviation in attack* compares the observed counts of herbivore-attacked ramets to counts expected based on the available ploidy distribution (Table 1), and is calculated as [100 × (observed−expected)/expected]. Scale is the same on all panels. Note that while this calculation assumes that the available ploidy distribution is known, statistical analyses actually recognize that it is estimated. Site-by-site *P*-values are from Fisher's exact tests; those in *bold* remain significant after sequential Bonferroni correction. Heterogeneity *P*-values are from the Monte Carlo test (Electronic Supplementary Material II). Sample sizes are total numbers of attacked ramets, per site and herbivore. Sites are arranged from west to east. *NP* Ploidy not present at a site; for site abbreviations see Table 1

among sites; such comparisons would risk confounding effects of ploidy with environmental and other influences on attack. Instead, we ask whether *relative* attack rates on the three ploidies are the same across sites.) For each herbivore with data for multiple sites, we tested for among-site heterogeneity in ploidy effects using a Monte Carlo test implemented in Microsoft QuickBASIC (Microsoft, Redmond, Wash.). For each herbivore, this test estimates ploidy effects on attack using data pooled across all sites, uses these pooled estimates to simulate attack at each site, and then compares actual to simulated variation in ploidy effects among sites. The Monte Carlo test takes into account sampling uncertainty in our estimate of available ploidy frequencies at each site, as well as sampling uncertainty in our estimate of ploidy frequencies among galled ramets. This test is described in more detail in Electronic Supplementary Material II.

Results

Our seven sites had varying proportions of diploid, tetraploid, and hexaploid ramets (Table 1). Five sites had ramets of all three ploidies, one lacked diploids, and one lacked hexaploids.

All five herbivores showed significant ploidy effects on attack rates for at least one site, and four (all but *Eurosta*) showed significant among-site heterogeneity in ploidy effects. The ploidy with the highest attack rate was sometimes the most common one (six cases), but often was not (15 cases).

For *Eurosta*, tetraploids were significantly overrepresented, and diploids underrepresented, among attacked ramets at four sites (Fig. 1a). At the fifth site, trends in the same direction were not significant. Although we did not rear *Eurosta* to identify subspecies affiliations and test for subspecific affiliations with ploidy, there is no evidence of a shift in ploidy effects in the region of contact between the subspecies (western Iowa).

Rhopalomyia galls were common enough for analysis at six sites. Diploids were strongly overrepresented among attacked ramets at one site [Beaver Lake (BVL); Fig. 1b] and mildly so at another (Norton Nature Area), while tetraploids were strongly over-represented at a third site (Johnson Sauk Trail State Park; JST). At the remaining three sites, ploidy usage did not differ from random expectation. The test for among-site heterogeneity strongly rejected the hypothesis of common ploidy effects for *Rhopalomyia* ($P < 0.0001$).

Procecidochares galls were common enough for analysis at two sites. At one of these (BVL; Fig. 1c), diploids

were strongly over-represented among attacked ramets. However, at the other (JST), no such pattern was observed, and the hypothesis of common ploidy effects was rejected ($P = 0.0004$).

Gnorimoschema galls were common enough for analysis at four sites. At one site [Conard Environmental Research Area (CER); Fig. 1d], only diploids were attacked, with tetraploids and hexaploids present but unattacked. At a second site (McFarland Park, MFP), diploids were again over-attacked and tetraploids ignored (here hexaploids were not available). At the remaining two sites, no ploidy effects were observed, and we rejected the hypothesis of common ploidy effects among sites ($P = 0.034$).

Finally, *Asteromyia* galls were common enough for analysis at four sites. At three sites, tetraploids were overrepresented among galled ramets (Fig. 1e); but at the fourth (MFP), no such pattern was observed, and we again rejected the hypothesis of common ploidy effects among sites ($P = 0.0073$).

Discussion

Host–plant ploidy significantly affected attack rates for all five of our gallmakers (Fig. 1). Because ramets of different ploidies were thoroughly interspersed at each site (Halverson et al. 2007), patterns in attack rate among ploidies are not likely to reflect environmental variation within sites.

The ploidy effects we observed were often extremely strong. In some cases, ramets of one ploidy were completely ignored by herbivores despite being common in the population (e.g., hexaploids at BVL ignored by *Rhopalomyia* and *Procecidochares*; Fig. 1b, c). In other cases, ramets of one ploidy were attacked more than 4 times as often as expected based on their frequency in the population (e.g., tetraploids attacked by *Eurosta* at MFP and diploids attacked by *Rhopalomyia* at BVL; Fig. 1a, b).

Ploidy effects on insect attack have been demonstrated for only a few other insect herbivores (Münzbergová 2006; Nuismer and Thompson 2001; Thompson et al. 1997). With respect to our study system, plant-genotype effects on larval preference and performance have previously been demonstrated for *Eurosta* by Craig et al. (1999, 2000), and probably for at least some of our herbivores by Crutsinger et al. (2006; this study considered insect community-wide responses to plant genotype without identifying any particular herbivore species). However, plant ploidy was not considered in either of these studies, and no data concerning plant ploidy effects on attack have been available for any of our herbivores.

Beyond the simple demonstration of plant-ploidy effects, the most striking aspect of our data is the strong heterogeneity we observed in those effects—there is no single preferred (or optimal-performance) ploidy for most herbivores. Of our five herbivores, four (all but *Eurosta*) showed strong and significant heterogeneity in ploidy effects among sites. This result contrasts sharply with the only other study to have evaluated ploidy effects across multiple mixed-ploidy populations: Thompson et al. (1997) found consistently higher attack by *Greya politella* on tetraploid versus diploid *Heuchera grossulariifolia* across three Idaho sites.

Herbivore attack-rate differences among plant ploidies could arise in two fundamentally different ways. First, herbivores could be responding to plant characteristics that are direct consequences of ploidy variation. For instance, plant polyploids typically have larger cells, slower growth rates, and (after time for mutation accumulation) more alleles per gene than their lower-ploidy ancestors (Otto and Whitton 2000), and any of these characteristics could affect (directly or indirectly) insect preference and/or performance. Alternatively, ploidy forms may evolve differences that are not functionally related to ploidy, but can persist simply because gene flow between ploidies is reduced or eliminated. If insects respond to differences of this latter sort, attack will be statistically associated with ploidy, but ploidy is best seen simply as a marker by which we recognize favored or disfavored plant lineages. The *S. altissima* system is ideal for resolving this distinction, because tetra- and hexaploids in our study area appear to have evolved repeatedly from lower ploidies, with each ploidy including genetically dissimilar lineages (Halverson et al. 2007). If a herbivore responds to direct consequences of polyploidy (cell size, etc.,) then we would expect it to show a consistent ploidy effect across sites despite the multiple origins of higher ploidies. This was the case for *Eurosta* (Fig. 1b), which was consistently associated with tetraploids despite their likely multiple origins. All four other herbivores, however, showed significant heterogeneity in ploidy effects (Fig. 1c–f). These species were likely not responding to ploidy per se, but rather showing responses to trait variation among plant lineages for which ploidy acts as a marker. Unfortunately, we are not yet able to document the specific plant traits of *S. altissima* lineages that underlie the ploidy effects we have observed. Finally, it is conceivable that heterogeneity in ploidy effects arises as a result of genotype × environment interactions under which ploidies differ in vulnerability to attack, but do so differently at each site. Testing this hypothesis would require reciprocal-transplant experiments, which we have not yet attempted.

It is also possible that the ploidy effects we see are a function not only of plant genotype, but also of genotypic variation in the insects themselves. For example, *Asteromyia* consists of several genetically distinct "gall morphs" that coexist on *S. altissima* (Crego et al. 1990; J. O. Stireman, unpublished data), and we do not know whether these morphs respond differently to host ploidy.

Furthermore, both *Gnorimoschema* and *Rhopalomyia* from *S. altissima* include divergent clades of mitochondrial DNA haplotypes that cannot be explained by geographic isolation (Stireman et al. 2005). These clades could represent ploidy-specific races, although we have no data yet with which to assess this hypothesis. Certainly, the potential for herbivores to make relatively fine genetic distinctions is well established for our herbivores: several exhibit cryptic host races on the closely related and sympatric goldenrod species *S. altissima* and *S. gigantea* (Stireman et al. 2005). If insect genetic structure associated with plant ploidy does exist, then interaction between these two genetic assemblages (insect and plant) could lead to complex coevolutionary dynamics, including ploidy-associated evolutionary diversification.

Our data can also be interpreted with respect to concordance or discordance among herbivore species at a given site, and this perspective too reveals considerable complexity. There are sites where different herbivores are largely concordant in their responses to plant ploidy (e.g., JST, tetraploids significantly over-attacked by two herbivores, with another trending in the same direction). However, there are also sites where herbivores show sharply differing ploidy effects (e.g., BVL, tetraploids over-attacked by two herbivores, but diploids by two more). Similar local discordance in ploidy effects among herbivores was reported by Nuismer and Thompson (2001) for three moths on *Heuchera grossulariifolia*, albeit for just a single site. Such complexity may have important consequences for herbivore communities, because community organization can be strongly affected by concordant or discordant ploidy preferences among species. For instance, at CER and MFP (but not at Smith Wildlife Area, SWA), *Gnorimoschema* and *Eurosta* are much less likely to occur on the same ramet than one would predict without knowledge of ploidy effects (Fig. 1b, f). In contrast, at both BVL and JST, *Procecidochares* and *Rhopalomyia* share a ploidy preference (for diploids at BVL and tetraploids at JST; Fig. 1c, e) and thus are much more likely to co-occur on a ramet than expected by chance. These patterns of association can even display striking shifts between sites: for instance, *Asteromyia* and *Rhopalomyia* are more likely than expected to co-occur at JST (where both are overrepresented on tetraploids; Fig. 1d, e); but much less likely to at BVL (where they differ in the effect of ploidy on attack). Ploidy effects can thus alter the likelihood or strength of interspecific competition among herbivores, and could change the net impact of herbivory if fitness consequences of different herbivores are non-additive.

Our results for the *Solidago*–herbivore system add force to the growing realization that host–plant genetic variation can play an important role in driving patterns in insect herbivore distribution and abundance. Effects of plant genotype on herbivore attack are common (see review by McGuire and Johnson 2006), and these genotype effects may vary among habitats (Johnson and Agrawal 2005) or among herbivore species (e.g., Nuismer and Thompson 2001; Rudgers and Whitney 2006; Wimp et al. 2005). Insect responses to plant genetics can have important impacts on the organization of the arthropod communities (parasitoids, predators, and pollinators as well as herbivores) associated with plants (Whitham et al. 2003), and even on ecosystem processes such as primary and secondary production (Crutsinger et al. 2006). Most studies have considered variation in insect attack either among clones within populations (e.g., Crutsinger et al. 2006; McGuire and Johnson 2006) or among parental classes in hybrid zones (e.g., Dungey et al. 2000; Hochwender et al. 2005; Wimp et al. 2005). Our study, together with a few others (Münzbergová 2006; Nuismer and Thompson 2001; Thompson et al. 1997), demonstrates that the co-occurrence of ploidy forms can represent an important kind of plant genetic variation for insect herbivores. Since polyploidization has been an important force in the evolution of angiosperm diversity (Otto and Whitton 2000), and since it has become increasingly clear that polyploidization rates are often high and ploidies often codistributed (Soltis and Soltis 1993; Ramsey and Schemske 1998), understanding insect responses to plant polyploidy should be a high priority in the study of plant–insect interactions.

Acknowledgements We thank Iowa DNR, Nebraska DOT, Story and Cedar County Conservation Boards, Illinois State Parks and Grinnell College for permission to collect on their property. K. Day, J. Doll, T. Nowak and K. Tarvin assisted with field work. F. Williams conducted proof-of-concept work and provided pilot data, and J. Semple graciously shared chromosome-count standards and expertise. R. Karban and an anonymous reviewer made helpful comments on the manuscript. Our work was funded by the National Science Foundation (USA; DEB 0107752 to S. B. H. and DEB 0107938 to J. D. N.) and the Natural Sciences and Engineering Research Council (Canada; Discovery Grant to S. B. H.). All work herein complied with the current laws of the countries in which it was performed.

References

Brown JM, Cooper I (2006) Evolution of wing pigmentation patterns in a tephritid gallmaker: divergence and hybridization. In: Ozaki K, Yukawa J, Ohgushi T, Price TW (eds) Galling arthropods and their associates. Springer Japan, Tokyo, pp 253–263

Craig TP, Abrahamson WG, Itami JK, Horner JD (1999) Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. Oikos 86:119–128

Craig TP, Itami JK, Shantz C, Abrahamson WG, Horner JD, Craig JV (2000) The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. Ecol Entomol 25:7–18

Crego CL, Weis AE, Polans O, Bretz CK (990) Sympatric sibling speciesfrom three phenotypically distinct *Asteromyia* (Diptera: Cecidomyiidae) galls on thesame host plant species. Environ Entomol 83:149–154

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

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

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

Galbraith DW, Harkins KR, Maddox JM, Ayers NM, Sharma DP, Firoozabady E (1983) Rapid flow cytometric analysis of the cell cycle in intact plant tissues. Science 220:1049–1051

Halverson K, Heard SB, Nason JD, Stireman JO III (2007) Origins, distribution and local co-occurrence of polyploid cytotypes in *Solidago altissima* (Asteraceae). Am J Bot (in press)

Heard SB, Stireman JO III, Nason JD, Cox GH, Kolacz CR, Brown JM (2006) On the elusiveness of enemy-free space: spatial, temporal, and host-plant-related variation in parasitoid attack rates on three gallmakers of goldenrods. Oecologia 150:421–434

Hochwender CG, Janson EM, Cha DH, Fritz RS (2005) Community structure of insect herbivores in a hybrid system: examining the effects of browsing damage and plant genetic variation. Ecol Entomol 30:170–175

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

McGuire RJ, Johnson MTJ (2006) Plant genotype and induced responses affect resistance to herbivores on evening primrose (*Oenothera biennis*). Ecol Entomol 31:20–31

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405

Münzbergová Z (2006) Ploidy level interacts with population size and habitat conditions to determine the degree of herbivory damage in plant populations. Oikos 115:443–452

Nakagawa S (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol 15:1044–1045

Nuismer SL, Thompson JN (2001) Plant polyploidy and nonuniform effects on insect herbivores. Proc R Soc Lond B 266:605–609

Otto SP, Whitton J (2000) Polyploid incidence and evolution. Annu Rev Genet 34:401–437

Ramsey J, Schemske DW (1998) Pathways, mechanisms, and rates of polyploid formation in flowering plants. Annu Rev Ecol Syst 29:467–501

Rice W (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Root RB, Cappuccino N (1992) Patterns in population change and the organization of the insect community associated with goldenrod. Ecol Monogr 63:393–420

Rudgers JA, Whitney KD (2006) Interactions between insect herbivores and a plant architectural dimorphism. J Ecol 94:1249–1260

Semple JC, Cook RE (2006) *Solidago*. In: Flora North America Editorial Committee (ed). Flora of North America. Oxford University Press, Oxford, pp 107–166

Soltis DE, Soltis PS (1993) Molecular data and the dynamic nature of polyploidy. Crit Rev Plant Sci 12:243–273

Stireman JO III, Nason JD, Heard SB (2005) Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod insect community. Evolution 59:2573–2587

Thompson JN (2005) The geographic mosaic of coevolution. University of Chicago Press, Chicago, Ill.

Thompson JN, Cunningham BM, Segraves KA, Althoff DM, Wagner D (1997) Plant polyploidy and insect/plant interactions. Am Nat 150:730–743

Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, Shuster SM, Wimp GM, Fischer DG, Bailey JK, Lindroth RL, Woolbright S, Kuske CR (2003) Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84:559–573

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