Plant module size and attack by the goldenrod spindle-gall moth

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Abstract—Larvae of the gall-inducing moth *Gnorimoschema gallaesolidaginis* (Riley) (Lepidoptera: Gelechiidae) attack ramets of *Solidago altissima* L. and *S. gigantea* Aiton (Asteraceae), initiating stem galls early in ramet growth. We examined the relationship between ramet size (as an indicator of plant vigour) and galling rate over 3 years at a field site in Toronto, Ontario, Canada. We marked *Solidago* ramets along line transects, measured their stem diameter, and recorded their fate (galled or ungalled) during the season. For *S. altissima*, galls were numerous enough for analysis in 2 years, and the frequency of galling increased monotonically with ramet stem diameter in both years. For *S. gigantea*, galls were numerous enough for analysis in all 3 years, but attack rate – stem diameter relationships were complex. In 2004 the galling frequency peaked at intermediate stem diameter, but in 2005 the galling frequency increased monotonically with stem diameter (and in 2006 the nonsignificant trend was similar). Overall, our data are most consistent with the plant-vigour hypothesis, but the 2004 data for *S. gigantea* lend some support to the suggestion that herbivore attack might sometimes be most intense on intermediate-sized modules.

Résumé—Les larves du papillon de nuit gallicole *Gnorimoschema gallaesolidaginis* (Riley) (Lepidoptera: Gelechiidae) attaquent les ramilles de *Solidago altissima* L. et de *S. gigantea* Aiton (Asteraceae), ce qui provoque la formation de galles sur la tige tôt dans la croissance des ramilles. Nous avons examiné la relation entre la taille de la ramille (comme indicateur de la vigueur de la plante) et le taux de formation des galles pendant trois années à un site de terrain de Toronto, Canada. Nous avons marqué des ramilles de *Solidago* le long de lignes de transect, mesuré le diamètre des tiges et déterminé leur sort (avec ou sans galles) au cours de la saison. Chez *S. altissima*, les galles étaient assez abondantes durant deux des années pour permettre l'analyse; la fréquence de formation des galles s'est accrue de façon monotone en fonction du diamètre des tiges pendant les deux années. Chez *S. gigantea*, les galles étaient assez abondantes durant les trois années, mais les relations entre le taux d'attaque et le diamètre de la tige étaient complexes. En 2004, le taux de formation des galles a atteint un maximum aux tailles intermédiaires des tiges, mais en 2005 le taux de formation de galles a augmenté de manière monotone en fonction du diamètre de la tige (et en 2006 la tendance était semblable mais non significative). Dans leur ensemble, nos données s'accordent avec l'hypothèse de la vigueur de la plante; cependant, les données de 2004 chez *S. gigantea* apportent un certain appui aux propositions selon lesquelles l'attaque des herbivores peut quelquefois être plus intense sur les modules de taille intermédiaire.

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Introduction

Feeding by phytophagous insects on their host plants has major ecological, evolutionary, and economic consequences (*e.g.*, McConnachie *et al.* 2003; Halpern and Underwood 2006; Maron and Crone 2006). Herbivory (which reflects both preference and performance) is often highly variable among individual plants within populations (*e.g.*, Wellings 1987; Eber 2004) and among modules (repeated morphological units such as leaves, branchlets, or ramets) within individual plants (*e.g.*, Gripenberg *et al.* 2007; Santos *et al.* 2008). This variation can

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have important consequences for the impact of herbivory on plants at the individual and population levels (*e.g.*, Heard and Remer 2008). Despite a wealth of studies examining herbivore load as a function of ecological, environmental, and spatial attributes of plants or modules, there remains considerable uncertainty about the generality of patterns in, and the ecological mechanisms behind, herbivore-load variation.

One interesting aspect of herbivore-load variation has been the relationship between herbivore attack and plant (or module) size. This relationship has important implications for the impact of herbivory on plant populations because larger plants or modules often contribute disproportionately to population-level reproduction — making attack on larger plants or modules likely to have more severe consequences at the population level. Furthermore, several hypotheses accounting for herbivore preference for (and performance on) individual plants or modules lead to predictions about the effects of module size on herbivore attack rates. Of these, the most obvious is the plant-vigour hypothesis (Price 1991), which suggests that herbivores should prefer, and (or) perform better on, plants or modules that through their vigorous growth represent a rich source of resources. Such vigorously growing modules should, all else being equal, have grown larger than their less vigorous neighbours and so, according to the plant-vigour hypothesis, the attack rate should increase with module size. The attack-rate pattern would be similar if larger modules were simply more apparent to searching herbivores. However, several hypotheses suggest roughly the opposite. For instance, the plant-stress hypothesis posits that plants or modules under stress are more suitable for attack because they are often nutritionally superior and less able to mount anti-herbivore defences (Rhoades 1979; White 1984). Modules experiencing stress during growth are, of course, likely to be smaller than their unstressed neighbours. For gall inducers (but not necessarily other herbivores), two other mechanisms might lead to better performance on smaller plant modules: vigorously growing modules may be unsuitable for attack because their tissues represent strong nutrient sinks that act in competition with gall growth and insect feeding (*e.g.*, Larson and Whitham 1997) or because gall induction on such a module requires a larger dose of the gall-inducing stimulus than an individual insect can provide (Bjorkman 1998; McKinnon *et al.* 1999).

Empirical data on module size – attack rate relationships are mixed, with some insect herbivores showing increased herbivory on larger (or faster growing) plants/modules, whereas others show the opposite pattern (Price 2003; Price *et al.* 2004; Quiring *et al.* 2006). Still others show parabolic relationships between plant/module size and herbivory (Quiring *et al.* 2006). The latter possibility is particularly interesting and suggests the possibility of a trade-off between vigour and stress, sink competition, or gall induction that creates an optimum module size for herbivore attack.

Gall inducers are particularly good model organisms for the study of herbivore–host interactions because they have very intimate relationships with their host plants and because each individual is unambiguously associated with a single host-plant module. Price (1991) has argued that gall inducers are particularly likely to conform to the plant-vigour hypothesis. However, because sink-competition and induction-stimulus mechanisms are specific to gall inducers among herbivores, and should lower realized attack on large modules, one could argue instead that gall inducers are particularly *unlikely* to conform to the plant-vigour hypothesis. Resolution of this conflict will require empirical data for a large and diverse set of gall inducer – host combinations, but unfortunately the set of studied gall inducers remains small and weighted heavily toward members of a few insect families (Quiring *et al.* 2006). Notably, few data exist for lepidopteran gall inducers (just two entries in the compilation of Quiring *et al.* 2006). We examined the relationship between module size and attack for larvae of the goldenrod spindle-gall moth, *Gnorimoschema gallaesolidaginis* (Riley) (Lepidoptera: Gelechiidae), on its two goldenrod hosts, late goldenrod, *Solidago altissima* L., and tall goldenrod, *S. gigantea* Aiton (Asteraceae). (Moths on *S. gigantea* have been treated as *G. jocelynae* Miller, although their status as a host race *versus* a cryptic species remains unclear; for simplicity we use the name *G. gallaesolidaginis* throughout.) Our study does not directly test the mechanistic basis of size-related patterns of attack and thus does not include direct tests of the plant-vigour and plant-stress hypotheses. However, we do document the effect of module size on attack in unmanipulated field populations of the two host species in 3 years and we provide a direct test of the optimal-module-size hypothesis.

Materials and methods

Study organisms and study sites

Solidago gigantea and *S. altissima* are clonal perennials, regrowing each spring from underground rhizomes. Many individual shoots (= ramets) generally arise from one genetic individual with or without persistent rhizome connections between shoots. Both species are primarily associated with grasslands and disturbed habitats such as abandoned fields and roadsides and are distributed over much of temperate North America. Their habitats overlap in most of their range (Semple and Cook 2006) and the two species are often densely intermixed in local populations.

Gnorimoschema gallaesolidaginis attacks both *S. altissima* and *S. gigantea*, but the subpopulation on each species is genetically distinct and likely constitutes either a well-developed host race or young cryptic species (Miller 2000; Nason *et al.* 2002; Stireman *et al.* 2005). Adults lay eggs in the fall, eggs overwinter and hatch in early spring, and hatchling larvae search (sometimes wandering for many hours) for newly emerged goldenrod shoots (Leiby 1922). After selecting a goldenrod ramet, a larva will feed its way through the terminal leaf bud into the stem and then, possibly after one or two moults, induce a gall. Gall induction is at least partly chemical (Beck 1953). Host-plant selection is very tight at the species level (*S. altissima vs. S. gigantea*), with individuals of each host-race found only rarely on the "wrong" host (Nason *et al.* 2002) despite rather weak effects of such mistakes on larval survival and growth (G.H. Cox, unpublished data). *Gnorimoschema gallaesolidaginis*, like other herbivores on *Solidago* L., also shows strong host preference (or perhaps strong performance differences) among ploidy races, at least of *S. altissima* (Halverson *et al.* 2008). However, data on the response of *G. gallaesolidaginis* to ramet size or vigour have not been available.

Our study site was a large mixed-species *Solidago* population at the northern end of Tommy Thompson Park, Toronto, Ontario, Canada (43°39′N, 79°19′W). The site is in secondary succession and is dominated by open fields and willow thickets. Both *S. altissima* and *S. gigantea* are present in mixed- and single-species stands of many tens of thousands of ramets.

Gall surveys

We surveyed goldenrod populations for the presence of *G. gallaesolidaginis* galls through the gall-initiation season in 2004, 2005, and 2006. In early spring of each year we laid line transects through mixed-species stands of *Solidago* and then marked with a numbered metal tag every *Solidago* ramet touching the transect. At the time of our first survey in each year (12, 5, and 13 May in 2004, 2005, and 2006, respectively) we measured stem diameter and ramet height as candidate measures of module (ramet) size and scored plants for the presence of *G. gallaesolidaginis* galls. We were able to detect galls that had been initiated but then failed shortly after (in as little as a few days) and we scored such cases as galled ramets, but we could not detect cases in which a gall inducer attacked but failed to initiate a gall. Therefore, our measure of attack combines preference and early-development performance. This measure is reasonable because galls that fail later in development have already had an impact on ramet growth — so from the perspective of the plant, measures of herbivore attack must account for galling even when the gall inducer does not survive.

Stem diameter was measured with a digital caliper 4 cm above the ground (or for shorter plants, as high up as possible) and ramet height was measured from the ground to the tip of the longest terminal leaves. We focused our analyses here on stem diameter. Although height is in many cases an appealing measure of overall ramet size (*e.g.*, Walton *et al.* 1990; Horner and Abrahamson 1992), height growth of both *Solidago* species is strongly impacted by *G. gallaesolidaginis* galling (Hartnett and Abrahamson 1979; Miller 2000; G.H. Cox, unpublished data). We expected stem-diameter growth to be less strongly impacted by galling and, to test this expectation, in 2006 we measured stem diameters of galled and ungalled ramets at the beginning and end of the season. We also assessed the correlation between ramet height and stem diameter for ungalled ramets for all six year × goldenrod species combinations.

We made our first survey in each year shortly after most or all galls were initiated on *S. gigantea* (66 of 92, all of 70, and all of 61 in our transects in 2004, 2005, and 2006, respectively) but before many galls had been initiated on *S. altissima* (0, 0, and 3 in 2004, 2005, and 2006, respectively). Thus, it is possible that for *S. gigantea* a few measured ramets had not been available for attack when gallmakers were searching for hosts but this was not the case for *S. altissima*. In 2004 and 2006 we resurveyed our plants for galls in late August, long after all galls had been initiated on both hosts. Our analyses used stem diameter from the first survey but galling-fate data from the end-of-season survey (so as to correctly identify the season-long galling fate of each ramet). In 2005 a severe drought damaged or killed many of the plants in our transects so we were not able to resurvey our original transects. However, we did survey a set of replacement transects in late spring (30 May – 30 June 2005) in which we measured only galled ramets.

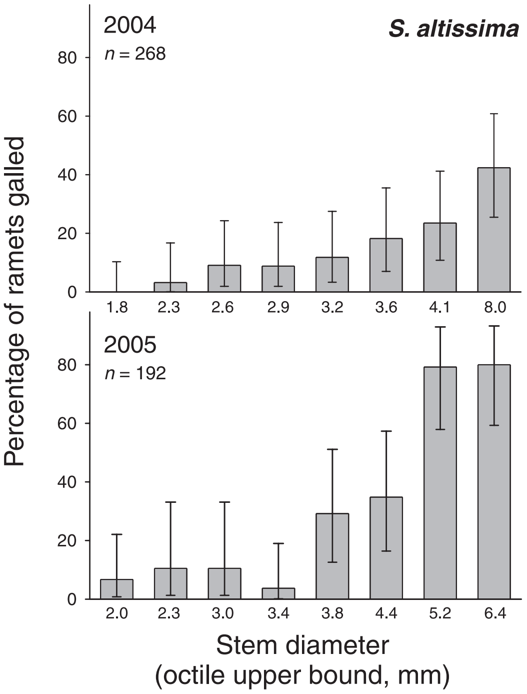
Statistical analysis

We tested the reliability of stem diameter as a measure of module size during gall inducer attack with two analyses. First, we used standard Pearson's correlation coefficients to measure covaration between stem diameter and module height of ungalled plants. Second, we used analysis of variance (ANOVA) to test for a difference in stem-diameter growth between galled and ungalled ramets over the entire season. This last analysis was conducted only on the 2006 data (for which we had end-of-season stem-diameter data).

We tested for dependence of the fate of a ramet (galled or ungalled) on its size (stem diameter) using logistic regression (PROC CATMOD; SAS Institute Inc.), including a diameter^2 term. Estimation of the diameter^2 term constitutes a direct test of the optimal-module-size hypothesis, which predicts a significant and concave-down quadratic effect of module size on galling. If the diameter^2 term was not significant we omitted it and reran the analysis to test for a linear effect of stem diameter on (logit-transformed) galling fate. To depict effects of stem diameter on galling rate graphically we calculated percent occurrence of galls for ramets in eight approximately equal-frequency diameter classes ("octiles"; Figs. 1, 2). However, all statistical analyses are based on the original, unaggregated data.

For 2004 and 2006 data our logistic regressions have a very straightforward interpretation: they test directly for effects of (early-season) stem diameter on per-capita galling risk. For 2005, because of loss of early-season transects to drought, the logistic regressions incorporate data from replacement transects and therefore work slightly differently. We used linear regression to test for an increase in stem diameter of ungalled plants over the period from the first surveys of the original (early-season) transects to the last surveys of the replacement transects. We reasoned that if stem-diameter growth was sufficiently slow we could combine data from the original and replacement transects even though the former included both galled and ungalled ramets and the latter only galled ramets. A stem-diameter effect in logistic regression would arise if the galled ramets from the replacement transects tended to sit at the high end of the module-size distribution assayed from the original transects. Although the 2005 data involve less direct inference than one might like, none of our results or interpretation are affected by their inclusion or exclusion.

Fig. 1. Rates of attack by *Gnorimoschema gallaesolidaginis* on *Solidago altissima* as a function of ramet stem diameter. Stem diameters are grouped by octile (upper bounds are indicated on the *x*-axis); error bars show confidence intervals calculated from a binomial distribution.

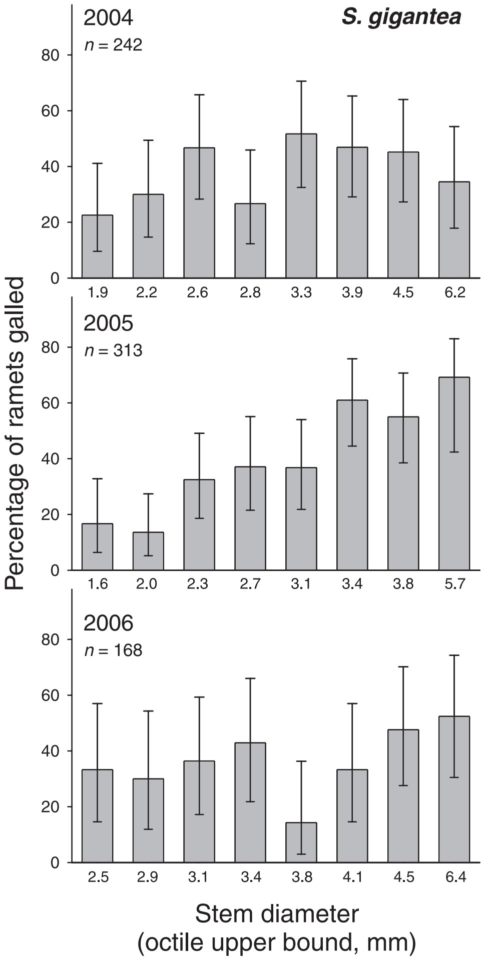


Results

Stem diameter as a measure of module size

Stem diameter proved to be a reliable measure of module size for both goldenrod species. Ramet height was strongly correlated with stem diameter for ungalled plants ($0.43 < r < 0.81$,

Fig. 2. Rates of attack by *Gnorimoschema gallaesolidaginis* on *Solidago gigantea* as a function of ramet stem diameter. Stem diameters are grouped by octile (upper bounds are indicated on the *x*-axis); error bars show confidence intervals calculated from a binomial distribution.



all $P < 0.0001$, for six year × goldenrod species combinations). Stem diameter increased very slowly over the growing season, and in 2005, average stem diameters of surveyed plants did not increase over the month that elapsed between the first and last surveys (regression, $F_{1,59} = 0.33$, $P = 0.57$, for *S. altissima*; $F_{1,54} = 1.45$, $P = 0.23$, for *S. gigantea*). This allowed us to combine data from replacement and original transects in the 2005 analysis of galling *versus* module size (see below). Finally, stem-diameter growth was unaffected by galling in 2006 (ANOVA, $F_{1,47} = 0.02$, $P = 0.89$, for *S. altissima*; $F_{1,60} = 1.02$, $P = 0.32$, for *S. gigantea*).

Module size and frequency of galling

For *S. altissima* the frequency of galling by *G. gallaeosolidaginis* increased sharply and significantly with ramet size in both 2004 and 2005 (Table 1, Fig. 1; only three galls were observed in 2006, too few for analysis). The term quadratic in ramet size was not significant in either year. For *S. gigantea*, trends in galling frequency with ramet size were more complex. In 2004, galling frequency peaked at intermediate ramet size (significant quadratic term; Table 1, Fig. 2). However, in 2005 galling frequency increased with ramet size, with no sign of leveling off. In 2006, galling frequency again tended to increase with ramet size, but this trend was not quite significant ($P = 0.07$).

Discussion

We were able to measure the relationship between module size (measured as stem diameter) and galling frequency in five data sets: for attack on *S. altissima* in 2 years and for attack on *S. gigantea* in 3 years. Overall, our data are most consistent with a positive module size – attack rate relationship (galling frequency increased significantly but monotonically with stem diameter in three data sets and trended the same way in a fourth) as predicted by the plant-vigour and apparency hypotheses. *Eurosta solidaginis* (Fitch) (Diptera: Tephritidae), another common gall inducer on the same hosts, shows a similar predilection for large and rapidly growing ramets (Abrahamson and Weis 1997) and this is a common pattern among gall-inducing insects in general (Price 2003; Price *et al.* 2004; Quiring *et al.* 2006). However, for attack by *G. gallaesolidaginis* on *S. gigantea* in 2004, we found a relationship consistent with the optimal-module-size hypothesis: a term quadratic in stem diameter explained significant variance in galling frequency, and galling peaked at intermediate stem diameter (Fig. 2).

Why might galling frequency have declined for the largest *S. gigantea* ramets in 2004? Two possible artifacts can be dismissed fairly easily. First, such a result might occur if there is an upper size limit beyond which ramets are invulnerable to galling and if phenological variation among years meant that ramets were unusually large in 2004. However, ramets were not unusually large in 2004, and the same large-diameter classes that incurred lower rates of attack in 2004 had higher rates of attack in 2005 (and

Table 1. Logistic regression analyses of galling fate (resulting from attack by *Gnorimoschema gallaesolidaginis*) as a function of stem diameter of *Solidago* spp. ramets.

	Source of variance*	df	Parameter estimate†	χ^2	*P*
Solidago altissima					
2004	Diameter	1	0.96	29.2	<0.0001
	Residual	184		147	0.978
2005	Diameter	1	1.22	42.2	<0.0001
	Residual	50		54.5	0.31
Solidago gigantea					
2004	Diameter	1	1.55	6.64	0.010
	Diameter^2	1	–0.19	5.21	0.022
	Residual	171		222	0.005
2005	Diameter	1	0.90	38.0	<0.0001
	Residual	36		35.5	0.49
2006	Diameter	1	0.32	3.2	0.07
	Residual	130		175	0.0053

Note: The χ^2 test associated with residual variance is a goodness-of-fit test for the overall model.

*All analyses began by including both linear and quadratic terms for stem diameter. When the quadratic term was not significant (all $P > 0.4$), results reported here are for an analysis run with only a linear term.

†For the linear term, a positive parameter estimate means that the attack rate increases with stem diameter. For the quadratic term, a negative parameter estimate means that the attack rate decreases for the largest ramets.

trended so in 2006; Fig. 2). Second, when module size is measured after attack begins, and if herbivore attack reduces plant growth, an apparent module-size optimum can arise simply because attacked modules cannot grow large. However, this artifact was not present in our study. Galls on *S. gigantea* were mostly initiated before our surveys, but stem-diameter growth was not affected by *G. gallaesolidaginis* attack (and galls on *S. altissima* were almost exclusively initiated after our module-size measurements were made). We also found that stem diameter predicted attack similarly when we separately examined galls initiated before and after our first surveys (analyses not shown). Therefore, gall inducer effects on plant growth are likely not responsible for the intermediate-sized peak in galling frequency for *S. gigantea* in 2004.

At least three other hypotheses are available to explain the low rates of galling on the largest ramets in 2004: competition between herbivore and plant resource sinks, dilution of the gall-induction stimulus, and release of plant stress effects on defence and nutrition. Of these, we suspect that competition between herbivore and plant sinks for photosynthates and nutrients is an unlikely explanation for module size-galling patterns in *G. gallaesolidaginis* because of the architecture of *Solidago* ramets. A *G. gallaesolidaginis* gall occurs midway along a single stem between the rhizome (and roots) and a terminal meristem that exhibits strong apical dominance; thus, more vigorous growth is likely to increase (not decrease) the levels of resources available to sustain the parenchyma tissue on which the insect feeds. Furthermore, if such a competitive effect existed it would be expected to act more strongly in *S. altissima* because ramets of that species are larger at the (later) time of attack (Seehawer 2002; G.C. Cox, unpublished data). However, our *S. altissima* data show no hint of an intermediate-sized peak in attack rate. The induction-stimulus-dilution and plant-stress hypotheses are less easy to dismiss in our system, and we have no data bearing directly on either. The induction-stimulus-dilution hypothesis holds that in the largest ramets the gall-inducing chemical produced by an attacking herbivore is diluted below the level required for successful gall initiation (Bjorkman 1998; McKinnon *et al.* 1999). Although the gall-induction stimulus for *G. gallaesolidaginis* is at least partly chemical (Beck 1953), the nature of the chemicals involved is completely unknown — as are the dosage required for gall formation and the dosage – ramet size relationship, if any. As for the plant-stress hypothesis, *S. altissima* and *S. gigantea* tissues include a wide variety of putatively anti-herbivore compounds, including mono-, di-, and sesqui-terpenes, phenolics, and polyacetylenes (*e.g.*, Cooper-Driver and LeQuesne 1987; Abrahamson *et al.* 1991; Kalemba *et al.* 2001; Johnson *et al.* 2007), at least some of which can reduce growth and increase mortality of generalist herbivores (Bosio *et al.* 1990; Hull-Sanders *et al.* 2007). Because their production is metabolically expensive (Gershenzon 1994), small and stressed ramets might well have lower concentrations of some or all compounds, although studies to date have focused on genetic rather than environmental influences on the defensive chemistry of *Solidago* spp. (Wise *et al.* 2006). Unfortunately, nothing is known of the response of *G. gallaesolidaginis* to any of these chemicals. Field and laboratory studies of *G. gallaesolidaginis* gall induction and fate under different plant stress conditions would be rewarding.

We do not know why the galling frequency – plant vigour relationship varied among years (for *S. gigantea*). Mean ramet diameter did vary slightly among years (ANOVA, $F_{2,388} = 15.2$, $P < 0.0001$), but size distributions overlapped extensively and the same large-diameter classes that incurred lower rates of attack in 2004 had higher rates of attack in 2005 (and trended so in 2006; Fig. 2). We suspect that *G. gallaesolidaginis* larvae are responding directly to plant traits for which stem diameter is an indirect and imperfect proxy. It would not be surprising to see shifts among years in the correlation between stem diameter and these hypothesized underlying traits; this could drive temporal heterogeneity in attack rate – stem diameter relationships. Importantly, many studies of attack rate – plant vigour relationships have had limited or no temporal replication and thus limited or no power to detect temporal heterogeneity in patterns of attack. Such heterogeneity may be very common in insect–plant interactions. Similarly complex spatial and temporal variation in attack-rate relationships has in fact been documented before in our goldenrod study system: insect herbivores vary spatially in their relative rates of attack on different host cytotypes (Halverson *et al.* 2008), and parasitoids vary spatially and temporally in their relative rates of attack on herbivores feeding on the two goldenrod species (Heard *et al.* 2006).

In general, patterns of herbivore attack reflect the interplay of preferences among available hosts and performance variation (including the action of natural enemies) among herbivores on different accepted hosts. We chose to examine the field distribution of herbivore attacks because this distribution is directly relevant to host-plant fitness and also reflects the joint effect of preference and performance. Empirically, it is often difficult to separate preference and performance effects on the distribution of herbivore attacks. Preference and performance are separable when the herbivore's attack is detectable before performance differences can arise — for instance, in gall inducers like *Eurosta solidaginis*, where ovipositing females leave distinctive scars (Abrahamson and Weis 1997). Unfortunately, in the field we cannot nondestructively identify attack by *G. gallaesolidaginis* until gall formation has begun because lepidopteran herbivores cause similar damage to the host goldenrod plants during feeding in the terminal bud. However, we suspect that if our results arise from performance effects, these effects must occur very early in larval attack. In laboratory studies of gall initiation by *G. gallaesolidaginis* larvae on the two alternative host-plant species (G.H. Cox, unpublished data), nonrandom patterns of herbivore attack are already evident at the very first sign of feeding damage, long before galls are initiated. Therefore, we hypothesize that host preference drives at least a large portion of the attack-rate pattern in our data. Further laboratory experiments will be necessary to fully untangle preference and performance effects in *G. gallaesolidaginis*. For the tephritid gall inducer *E. solidaginis* on the same goldenrod hosts, both adult-preference and larval-performance effects favour galls on larger, more vigorous ramets (in part because small ramets are likely to die before insect development is complete; Abrahamson and Weis 1997).

As attack rate – plant vigour data sets accumulate for more gall inducers, one obvious conclusion is that the relationship between plant vigour and herbivore attack is likely to vary among herbivore species (Quiring *et al.* 2006). Our results suggest that we might expect similar variation within herbivore species through time (and perhaps spatially) and that variation in herbivore attack rates among individual plants and modules will often be complex. As a result, such variation has the potential to be a rich source of interesting and important effects on herbivore-mediated natural selection and on plant and insect population dynamics (*e.g.*, Heard and Remer 2008).

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References

Abrahamson, W.G., and Weis, A.E. 1997. Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies. Princeton University Press, Princeton, New Jersey.

Abrahamson, W.G., McCrea, K.D., Whitwell, A.J., and Vernieri, L.A. 1991. The role of phenolics in goldenrod ball gall resistance and formation. Biochemical Systematics and Ecology, **19**: 615–622.

Beck, E.G. 1953. The nature of the stimulus in the *Solidago* gall induced by the larva of *Gnorimoschema gallaesolidaginis*. Brookhaven Symposia in Biology No. 6. pp. 235–251.

Bjorkman, C. 1998. Opposite, linear and non-linear effects of plant stress on a galling aphid. Scandinavian Journal of Forest Research, **13**: 177–183.

Bosio, C.F., McCrea, K.D., Nitao, J.K., and Abrahamson, W.G. 1990. Defense chemistry of *Solidago altissima* — effects on the generalist herbivore *Trichoplusia ni* (Lepidoptera, Noctuidae). Environmental Entomology, **19**: 465–468.

Cooper-Driver, G.A., and LeQuesne, P.W. 1987. Diterpenes as insect antifeedants and growth inhibitors — role in *Solidago* species. *In* Allelochemicals: role in agriculture and forestry. *Edited by* G.R. Waller. American Chemical Society Symposium 330, American Chemical Society, Washington, D.C. pp. 535–550.

Eber, S. 2004. Bottom-up density regulation in the holly leaf-miner *Phytomyza ilicis*. Journal of Animal Ecology, **73**: 948–958.

Gershenzon, J. 1994. Metabolic costs of terpenoid accumulation in higher plants. Journal of Chemical Ecology, **20**: 1281–1328.

Gripenberg, S., Morrien, E., Cudmore, A., Salminen, J.P., and Roslin, T. 2007. Resource selection by female moths in a heterogeneous environment: what is a poor girl to do? Journal of Animal Ecology, **76**: 854–865.

Halpern, S.L., and Underwood, N. 2006. Approaches for testing herbivore effects on plant population dynamics. Journal of Applied Ecology, **43**: 922–929.

Halverson, K.L., Heard, S.B., Nason, J.D., and Stireman, J.O., III. 2008. Differential attack on diploid, tetraploid, and hexaploid *Solidago altissima* L. by five insect gallmakers. Oecologia, **154**: 755–761.

Hartnett, D.C., and Abrahamson, W.G. 1979. The effects of stem gall insects on life history patterns in *Solidago canadensis*. Ecology, **60**: 910–917.

Heard, S.B., and Remer, L.C. 2008. Travel costs, oviposition behaviour and the dynamics of insect–plant systems. Theoretical Ecology, **1**: 179–188.

Heard, S.B., Stireman, J.O., III, Nason, J.D., Cox, G.H., Kolacz, C.R., and Brown, J.M. 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.

Horner, J.D., and Abrahamson, W.G. 1992. Influence of plant genotype and environment on oviposition preference and offspring survival in a gall-making herbivore. Oecologia, **90**: 323–332.

Hull-Sanders, H.M., Clare, R., Johnson, R.H., and Meyer, G.A. 2007. Evaluation of the evolution of increased competitive ability (EICA) hypothesis: loss of defense against generalist but not specialist herbivores. Journal of Chemical Ecology, **33**: 781–799.

Johnson, R.H., Hull-Sanders, H.M., and Meyer, G.A. 2007. Comparison of foliar terpenes between native and invasive *Solidago gigantea*. Biochemical Systematics and Ecology, **35**: 821–830.

Kalemba, D., Marschall, H., and Bradesi, P. 2001. Constituents of the essential oil of *Solidago gigantea* Ait. (giant goldenrod). Flavour and Fragrance Journal, **16**: 19–26.

Larson, K.C., and Whitham, T.G. 1997. Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. Oecologia, **109**: 575–582.

Leiby, R.W. 1922. Biology of the goldenrod gall-maker *Gnorimoschema gallaesolidaginis*. Journal of the New York Entomological Society, **30**: 81–95.

Maron, J.L., and Crone, E.E. 2006. Herbivory: effects on plant abundance, distribution and population growth. Proceedings of the Royal Society of London B Biological Sciences, **273**: 2575–2584.

McConnachie, A.J., Hill, M.P., Byrne, M.J., and de Wit, M.P. 2003. Economic evaluation of the successful biological control of *Azolla filiculoides* in South Africa. Biological Control, **28**: 25–32.

McKinnon, M.L., Quiring, D.T., and Bauce, E. 1999. Influence of tree growth rate, shoot size and foliar chemistry on the abundance and performance of a galling adelgid. Functional Ecology, **13**: 859–867.

Miller, W.E. 2000. A comparative taxonomic – natural history study of eight Nearctic species of *Gnorimoschema* that induce stem galls on

Asteraceae, including descriptions of three new species (Lepidoptera: Gelechiidae). Entomological Society of America, Lanham, Maryland.

Nason, J.D., Heard, S.B., and Williams, F.R. 2002. Host associated genetic differentiation in the goldenrod elliptical-gall moth, *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae). Evolution, **56**: 1475–1488.

Price, P.W. 1991. The plant vigor hypothesis and herbivore attack. Oikos, **62**: 244–251.

Price, P.W. 2003. Macroevolutionary theory on macorecological patterns. Cambridge University Press, Cambridge, United Kingdom.

Price, P.W., Ohgushi, T., Roininen, H., Ishihara, M., Craig, T.P., Tahvanainen, J., and Ferrier, S.M. 2004. Release of phylogenetic constraints through low resource heterogeneity: the case of gall-inducing sawflies. Ecological Entomology, **29**: 467–481.

Quiring, D.T., Flaherty, L., Johns, R., and Morrison, A. 2006. Variable effects of plant module size on abundance and performance of galling insects. *In* Galling arthropods and their associates: ecology and evolution. *Edited by* K. Ozaki, J. Yukawa, T. Ohgushi, and P.W. Price. Springer-Verlag, Sapporo, Japan. pp. 189–198.

Rhoades, D.F. 1979. Evolution of plant chemical defense against herbivores. *In* Herbivores: their interaction with secondary plant metabolites. *Edited by* G.A. Rosenthal and D.H. Janzen. Academic Press, New York. pp. 3–54.

Santos, J.C., Silveira, F.A.O., and Fernandes, G.W. 2008. Long term oviposition preference and larval performance of *Schizomyia macrocapillata* (Diptera: Cecidomyiidae) on larger shoots of its host plant *Bauhinia brevipes* (Fabaceae). Evolutionary Ecology, **22**: 123–137.

SAS Institute Inc. 2001. SAS/STAT version 8.2 [computer program]. SAS Institute Inc., Cary, North Carolina.

Seehawer, J.M. 2002. Impact of larval phenology and fitness trade-offs on the host races of *Gnorimoschema gallaesolidaginis* and host related population structure in one of its parasitoids, *Copidosoma gelechiae*. M.Sc. thesis, University of Iowa, Iowa City, Iowa.

Semple, J.C., and Cook, R.E. 2006. *Solidago*. *In* Flora of North America. *Edited by* Flora North America Editorial Committee. Oxford University Press, Oxford, United Kingdom. pp. 107–166.

Stireman, J.O., III, Nason, J.D., and Heard, S.B. 2005. Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod insect community. Evolution, **59**: 2573–2587.

Walton, R., Weis, A.E., and Lichter, J.P. 1990. Oviposition behavior and response to plant height by *Eurosta solidaginis* Fitch (Diptera: Tephritidae). Annals of the Entomological Society of America, **83**: 509–514.

Wellings, P.W. 1987. Spatial distribution and interspecific competition. Ecological Entomology, **12**: 359–362.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia, **63**: 90–105.

Wise, M.J., Fox, R.J., and Abrahamson, W.G. 2006. Disarming the paradox of sublethal plant defense against insects: *Trirhabda virgata* larval development time and leaf tissue loss on *Solidago altissima*. Entomologia Experimenta et Applicata, **120**: 77–87.