James T. Cronin · Warren G. Abrahamson

Goldenrod stem galler preference and performance: effects of multiple herbivores and plant genotypes

Abstract Few studies have examined how the preference-performance relationship of an herbivore for different genotypes of its host plant is affected by the presence and/or feeding activity of other members of the herbivore assemblage. In an outdoor garden, we manipulated the abundance of three common herbivores, the meadow spittlebug, a leaf beetle, and an aphid, on replicate 1-m^2 plots of 16 different genotypes of tall goldenrod, *Solidago altissima*. Adults of the goldenrod stem galler, *Eurosta solidaginis*, were subsequently released into the garden to oviposit among the host plants. Oviposition preference was strongly influenced by plant genotype and the presence of two of the herbivores, spittlebugs and leaf beetles. The effects of the herbivores were additive: the presence of leaf beetles reduced preference by 6%, spittlebugs by 18%, and both herbivores combined by 25%. Plant genotype-herbivore species interaction effects on stem-galler preference, which would indicate the presence of genetic variation among goldenrod genotypes in their norms of reaction for their acceptability as a host to the stem galler, were absent in this study. The performance of the stem galler was also significantly affected by goldenrod genotype, but in general was not affected by the presence of herbivores early in the season (the exception was a positive correlation between the proportion of ramets infested by all herbivores and gall size). Overall, we could find no correlation between preference and performance. This is in accord with results from previous studies on this system that were performed in the absence of herbivores, suggesting that the presence of herbivores in this study did not qualitatively alter the preference-performance relationship. We suggest that the lack of a positive correlation between host-plant preference and larval performance may reflect a constraint on the discriminatory ability of female stem gallers preventing them from selecting the best hosts among plants that differ in genotype and level of environmental stress (e.g., presence of interspecific herbivores).

Keywords *Eurosta solidaginis* · Gall insect · Herbivore assemblage · Host choice · Preference-performance relationship

J.T. Cronin (✉)
Department of Biology, P.O. Box 9019,
University of North Dakota, Grand Forks, ND 58202-9019, USA
e-mail: james_cronin@und.nodak.edu

W.G. Abrahamson
Department of Biology, Bucknell University, Lewisburg,
PA 17837, USA

Introduction

A simple expectation from evolutionary theory is that natural selection should favor an herbivore that preferentially oviposits on plant genotypes that yield high performance for their offspring (Thompson 1988). Positive preference-performance correlations have been found in a number of herbivorous insects (e.g., Craig et al. 1989; Price et al. 1990; Rossi and Strong 1991), but exceptions are common (e.g., Karban and Courtney 1987; Courtney and Kibota 1990; Fox 1993; Larsson et al. 1995). Factors promulgated to explain these inconsistent results have run the gamut from differences in plant apparency (Feeny 1976; Chew and Courtney 1991), novel associations between host plant and herbivore (Thompson 1988, 1996; Joshi and Thompson 1995), phenological differences in herbivore oviposition (Straw 1989; Briese 1996), variations in herbivore abundance (Wiklund 1982), environmental predictability (Futuyma 1976; Cates 1981; Chew and Courtney 1991; Lalonde and Roitberg 1992), and limited discriminatory ability of herbivores (host confusion hypothesis of Fox and Lalonde 1993; Larsson and Ekbom 1995). Regardless of the form, the preference-performance relationship can greatly influence the distribution and abundance of herbivore populations (e.g., Price 1991, 1994; Ohgushi 1995; Bigger and Fox 1997), as well as the evolution of host-plant specificity, diet breadth, host-race formation, and sympatric speciation (e.g., Bush 1975; Futuyma and Meyer 1980; Mitter et al. 1991; Joshi and Thompson 1995; Thompson 1996).

The presence of extrinsic factors that affect host-plant preference and performance differentially may also alter the preference-performance relationship. Water or nutrients (Maddox and Cappuccino 1986; Horner and Abrahamson 1992, 1999; Preszler and Price 1995; Ruohomaki et al. 1996), wind exposure (Cipollini 1997), amount of shade (Ruohomaki et al. 1996; Horner and Abrahamson 1992), presence of parasites and predators (Lawton and McNeill 1979; Strong and Larsson 1994; Stiling and Rossi 1996), or the presence of other herbivores (Lewis 1984; Faeth 1986; McMillin and Wagner 1997; Cronin and Abrahamson 1999) may change through time or affect preference and performance in qualitatively different ways. One common situation might involve the presence of an herbivore assemblage that feeds on the plant prior to the occurrence of the target herbivore. This assemblage might induce chemical changes in the plant (e.g., Faeth 1986; Harrison and Karban 1986; Karban and Adler 1996), alter plant apparency (e.g., by stunting growth), or directly deter the colonization of the plant by the target herbivore, and so alter host-plant preference. Unless offspring performance is similarly affected, the preference-performance relationship may be fundamentally altered. For example, in a greenhouse study (Cronin and Abrahamson 1999), we found that meadow spittlebugs (*Philaenus spumarius* L.; Homoptera: Cercopidae), which feed on goldenrods early in the season, drastically reduced host-plant preference by the goldenrod stem galler (*Eurosta solidaginis* Fitch; Diptera: Tephritidae). In contrast, stem-galler survivorship (a measure of performance) tended to increase on spittlebug-infested plants. As a consequence of these opposing trends, the relationship between preference and performance went from no, to a slightly negative, correlation in the absence and presence of spittlebugs, respectively. We are aware of no other studies that have addressed this issue, particularly with regard to assemblages of herbivores that may act in concert to affect the preference-performance relationship of another member of that assemblage.

In this study, we examined whether the assemblage of herbivores that feed on tall goldenrod (*Solidago altissima*) early in the season has an effect on the preference-performance relationship of the stem galler (*E. solidaginis*) among different goldenrod genotypes. The herbivore assemblage includes the meadow spittlebug, *P. spumarius*, two leaf-chewing beetles, *Trihrabda borealis* Blake and *T. virgata* LeConte (Coleoptera: Chrysomelidae), and an aphid, *Uroleucon nigrotuberculatum* (Homoptera: Aphididae). These herbivores were introduced into an outdoor garden that consisted of 16 goldenrod genotypes and subsequently we released adult goldenrod stem gallers to oviposit on the available plants. We tested whether stem-galler oviposition preference and offspring performance were affected by (1) presence/absence of each herbivore species in the assemblage, (2) goldenrod genotypes, (3) interaction between early-season herbivores and goldenrod genotypes (a genotype-by-environment interaction), and (4) interactions among early-season herbivore species. The effect of the herbivore assemblage on the preference-performance relationship was also examined. Finally, we discuss how these herbivores may affect the distribution of, and what role they may have played in the evolution of host-plant choice by, the stem galler.

Materials and methods

Natural history of herbivores

The life history, ecology and evolution of the goldenrod stem galler are detailed in Uhler (1951) and Abrahamson and Weis (1997); only a brief description is provided here. In Pennsylvania, adult stem gallers oviposit into the terminal buds of the goldenrod, *S. altissima*, around mid- to late May. Stem tissue shows signs of swelling within 3 weeks and by mid-July the gall, harboring a single larva, reaches full size and is spheroid in shape. Larvae overwinter within the galls of senescent goldenrod ramets, then pupate and eclose the following spring. In the absence of any other herbivores, stem gallers show strong differences in preference and performance among goldenrod genotypes, but no positive correlation between the two traits has been found (Anderson et al. 1989; Horner and Abrahamson 1992, 1999; Craig et al. 1999).

The suite of herbivores that feed on goldenrod is extremely diverse. According to Root and Cappuccino (1992), 138 species of insects are capable of completing their development on *S. altissima*. In addition to *E. solidaginis*, two species of leaf beetle (*T. virgata* and *T. borealis*), two aphids (*U. nigrotuberculatum* and *U. caligatum*), and the meadow spittlebug (*P. spumarius*) comprise the vast majority of the total herbivore biomass (Cappuccino 1987; Root and Cappuccino 1992; Meyer 1993). The spittlebug tends to be the first herbivore to begin feeding on goldenrods in the spring and all of these herbivores are present on goldenrods before stem-galler adults begin to emerge (J.T. Cronin personal observation).

Several studies suggest that these herbivores can significantly affect the quality and fitness of goldenrods, and consequently stem-galler preference and performance. Goldenrods that were exposed to feeding by either spittlebugs, leaf beetles or aphids for a 3-week period had biomasses, specific leaf areas, growth rates, photosynthetic rates, and seed production that were lower than plants that were free of herbivores (Meyer and Whitlow 1992; Meyer 1993; Meyer and Root 1993). However, the effects of each herbivore on goldenrod ramets were not the same. For example, spittlebugs, but not the other two herbivores, reduced the production of lateral stems; and spittlebugs and leaf beetles, but not aphids, delayed flowering. In general, the magnitude of effects on the host plant were greatest for the spittlebugs, followed by leaf beetles; and to a much lesser extent, aphids. It remains untested how each of these main herbivores of goldenrod affect the preference-performance relationship of the stem galler among different goldenrod genotypes in a field situation. Because of their varied effects on host plant performance, it is possible that these three herbivores would have different and non-additive effects on stem-galler preference or performance.

Common garden

The oviposition preference and offspring performance of the stem galler was determined within a goldenrod garden that was established in 1989 at Bucknell University, Lewisburg, Pennsylvania, United States (Craig et al. 1999). Of the 38 genotypes that were used to measure stem galler ovipuncture and survivorship rates in the field by Anderson et al. (1989), a subset of 20 genotypes were planted into the garden. These genotypes were chosen to represent a broad range of susceptibility to stem-galler attack and suitability for stem-galler survivorship. Rhizomes from each genotype were

planted in 1-m² plots that were arranged in four rows of 20 plots each. Within each row, all 20 genotypes were represented; thus there were a total of four plots per genotype. The spread of rhizomes and seed between plots was prevented by a 30-cm deep aluminum flashing that formed the border of each plot, and by cutting and removing ramets before seed set and dehisced. Four genotypes were removed for a separate study (Cronin and Abrahamson 1999); thus, only 16 genotypes spread over 64 plots were available for this study.

Herbivore introductions

Herbivores used in this experiment were obtained from fields of goldenrods in the area surrounding Lewisburg, Pennsylvania. During the middle of May 1995, we collected aphid colonies, leaf beetle larvae, and first/second instar spittlebug nymphs. *T. borealis* and *T. virgata* are indistinguishable as larvae (Messina 1982) and so were treated as one species in these collections. The only aphids found were *U. nigrotuberculatum*. To each of the 64 plots we added approximately 50 spittlebugs, 74 leaf beetles and 140 aphids (distributed evenly within the plot).

Corresponding with the release of herbivores, ball galls containing *E. solidaginis* larvae from the previous year were collected from the same sites and transferred to the common garden. Each plot was stocked with a total of 20 galls. Twelve days later the first adult stem gallers began to emerge; thus, the other herbivores had been feeding for at least 12 days prior to the occurrence of stem gallers. Because adult flies have a median range of dispersal of 7 m day^{-1} (Cronin et al. 2001), stem gallers were expected to be able to completely redistribute themselves within the garden following emergence.

Herbivore loads

During the first week of June, stem gallers began to emerge from the galls placed within the common garden, and within a week, the emergence period had passed. At this time, we haphazardly selected 25 ramets from each of the 64 1-m² plots and recorded herbivore loads. For herbivore loads, we recorded the presence/absence of spittlebug nymphs, leaf beetle larvae and aphids on each ramet. Based on counts from a subset of five ramets per plot, spittlebugs averaged 0.67 ± 0.04 (SE; range: 0–8, $n=288$), leaf beetles 2.11 ± 0.09 (range: 0–6), and aphids 1.16 ± 0.13 (range: 0–68) per ramet. The densities of these herbivores are comparable to those found in natural goldenrod habitat (Sholes 1982; Cappuccino 1988; Meyer and Whitlow 1992; Meyer 1993; Brown 1994; Cronin and Abrahamson 1999). At the same time that herbivore loads were determined, we also recorded the presence of stem-galler ovipunctures in one of three categories: 0, 1–3, or ≥4 ovipunctures per ramet (visible as scars in the developing buds). To monitor the fate of goldenrod ramets with varying herbivore species and ovipuncture histories, ramets were individually labeled with color-coded wires. Because spittlebug nymphs, leaf beetle larvae and aphids are very sedentary (Meyer and Whitlow 1992; Meyer 1993; Brown 1994; Cronin and Abrahamson 1999), we expected little redistribution of herbivores in the interim between the release of herbivores and the completion of the stem-galler's oviposition period.

Stem-galler preference and performance

Stem-galler preference was measured in two ways: the proportion of ramets ovipunctured per 1-m² plot (out of the 25 ramets marked), and the likelihood that an individual ramet was ovipunctured (1 or more ovipuncture scars). Both measures have been used with this system (Anderson et al. 1989; Horner and Abrahamson 1992, 1999; Craig et al. 1999; Cronin and Abrahamson 1999). The latter measure has a clear advantage in that stem-galler preference can be directly related to the presence of other herbivores on that same ramet. However, because ramets within a plot may have interconnecting rhizomes, each ramet may not represent an independent replicate; thus, the plot-based measure of preference may be more appropriate. We report both measures and note any discrepancies in results between the two.

Stem-galler performance was obtained in the following way. In December 1996 we collected all the galls produced from the 25 marked goldenrod ramets per plot and reared out adults the following spring. Gall diameter, which is positively correlated with measures of body size and fecundity (Cronin and Abrahamson 1999), was used as one measure of stem-galler performance. Another measure of offspring performance that we employed was the survivorship of stem gallers from 3 weeks post oviposition (when developing galls become visible) to adult emergence the following spring. Egg-to-adult survivorship was impossible to assess directly because number of eggs laid per ramet could not be ascertained without permanently damaging the bud. However, the strong linear relationship that exists between the number of eggs laid and the number of ovipunctures per ramet (Hess et al. 1996; Abrahamson and Weis 1997; Craig et al. 1997, 2000) made it possible to use ovipuncture number as a relative measure of the number of eggs laid. Stem-galler survivorship within a plot was then computed by summing the number of ovipunctures among the twenty-five marked ramets and dividing that number by the total number of stem gallers that completed development to adult eclosion (see Craig et al. 1997, 1999; Cronin and Abrahamson 1999). This measure may be biased if the relationship between ovipunctures and eggs laid varies among genotypes or herbivore treatments, but studies by Craig et al. (1997) have shown that this relationship does not change in a qualitative way among different treatments.

Statistical analyses

Ovipuncture preference

For stem-galler preference at the scale of the 1-m² plot, we used ANCOVA to test the effects of garden row (the garden was divided into four rows; block effect), goldenrod genotype (random effect), the proportion of ramets infested by each herbivore species (covariate), and plot density (covariate) on the proportion of ramets per plot with at least one ovipuncture scar. A separate ANCOVA was performed for the effects of spittlebugs, leaf beetles and all three herbivores combined. The effect of aphids alone was not assessed because plots had a low proportion of ramets infested by aphids (<15%) and one-third of all plots contained no aphids at all. For all analyses performed, the proportions of ramets infested by each herbivore category did not require a transformation to achieve normality.

To determine which factors influence stem-galler preference among individual ramets, we used logistic regression (Hosmer and Lemeshow 1989). Here, we tested if garden row, goldenrod genotype, presence of spittlebugs, presence of leaf beetles, presence of aphids, or plot density influenced whether or not a ramet was ovipunctured (binary dependent variable). Significance levels for each component of the model were determined with a *G*-test (Hosmer and Lemeshow 1989).

Offspring performance

At the plot scale, we used an ANCOVA design identical to the one described for stem-galler ovipuncture preference to determine which factors affect mean gall size per plot. At the ramet scale, we used a nested ANCOVA to determine the effect of goldenrod genotype, plot within goldenrod genotype (nested factor), presence of spittlebugs and leaf beetles and plot density on the gall size per ramet. With the nesting factor, we were able to partition the variation in mean gall size that is attributed to differences among the four plots per goldenrod genotype.

The effects of goldenrod genotype and herbivores on stem-galler survivorship among plots (gall-to-adult and egg-to-adult)

were analyzed with separate tests because the shortage of surviving adults in each genotype-herbivore species combination (20% of the plots had zero survivorship) rendered it impossible to use standard parametric tests. Gall-to-adult and egg-to-adult survivorship among the 16 goldenrod genotypes were analyzed with separate Kruskal-Wallis nonparametric tests (Sokal and Rohlf 1995). The relationship between herbivore infestation rates and stem-galler survivorship among plots was determined using Spearman's rank correlation (Sokal and Rohlf 1995). Among ramets, we used a logistic regression model analogous to the one described previously to determine whether goldenrod genotype and the different herbivore species affected stem galler offspring survival (gall-to-adult only).

Preference-performance relationship

The relationship between stem-galler oviposition preference (proportion of ramets ovipunctured) and offspring performance (mean gall size or survivorship) among the 64 plots and among the 16 goldenrod genotypes was determined using Pearson's product moment correlations (Sokal and Rohlf 1995). A relationship between preference and performance among ramets could not be determined because our measure of preference was a bivariate response (ovipunctured or not), and therefore only for the preferred (ovipunctured) ramets were their data for performance.

Results

The mean number of goldenrod ramets (±SE) among the 64 1-m^2 plots was 58.9±3.5. Of those ramets, an average of 53.7±2.4% were infested with leaf beetles, 41.6±2.2% with spittlebugs, and 3.0±0.6% with aphids (the low percentage for aphids is attributed to the colonial behavior of

this species). Overall, 73.6±1.8% of the ramets were infested by at least one of these herbivores. The stem gallers ovipunctured 49.8±1.9% of the ramets in each plot on average, a rate of attack similar to the levels found among goldenrod genotypes in nature (53%; Anderson et al. 1989).

E. solidaginis oviposition preference, measured as the proportion of ramets ovipunctured per 1-m^2 plot, was strongly influenced by position in the garden (block), goldenrod genotype and the presence of spittlebugs, leaf beetles and all herbivores combined (Table 1). In contrast, the density of ramets per plot had no effect on the proportion of ramets that were ovipunctured. In general, goldenrod genotype had a stronger effect on oviposition preference (explaining 34.5% of the model variation on average; as determined by the ratio of the genotype to total mean squares) than each herbivore species (20.6% of the variation on average). For spittlebugs, leaf beetles and
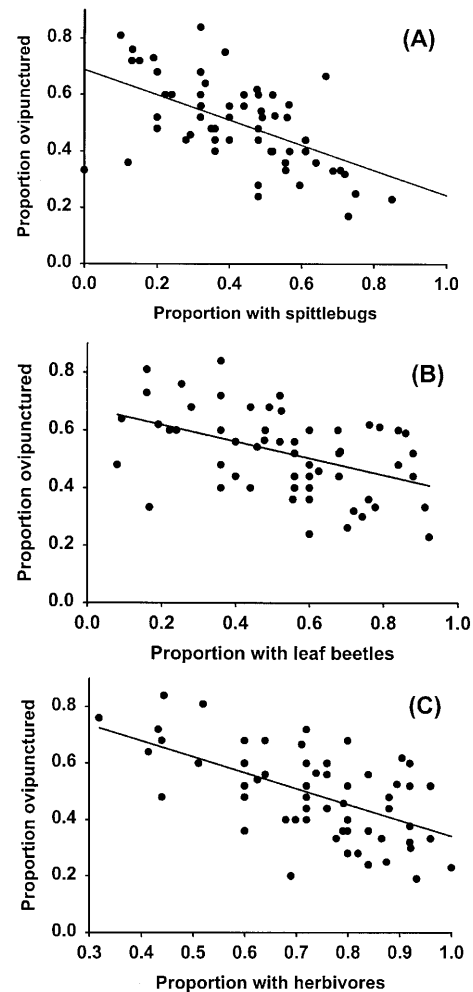
Table 1 ANOVA results for the effect of garden row (block effect), goldenrod genotype (fixed factor), proportion of ramets attacked by each herbivore species (covariate) and plot density (covariate) on the proportion of ramets that were ovipunctured per plot by the stem galler. A separate ANOVA was performed for each herbivore and for all herbivores combined

Source of variation	df	MS	F	P
Spittlebugs				
Garden row	3	0.066	5.294	0.005
Goldenrod genotype	15	0.049	3.756	0.001
Spittlebugs	1	0.010	5.611	0.032
Genotype×spittlebugs	15	0.018	1.470	0.181
Plot density	1	0.001	0.034	0.854
Error	28	0.013		
Leaf beetles				
Garden row	3	0.099	9.048	<0.001
Goldenrod genotype	15	0.180	16.074	<0.001
Leaf beetles	1	0.166	7.909	0.013
Genotype×beetles	15	0.021	1.931	0.063
Plot density	1	0.001	0.078	0.782
Error	28	0.011		
All herbivores				
Garden row	3	0.086	5.596	0.004
Goldenrod genotype	15	0.046	3.866	<0.001
Herbivores	1	0.082	6.824	0.020
Genotype×herbivores	15	0.012	0.753	0.714
Plot density	1	0.001	0.010	0.928
Error	28	0.015		

Fig. 1A–C The relationship between the proportion of ramets with an herbivore present and the proportion of ramets ovipunctured by the stem galler (ovipuncture preference) per plot. *Lines* are fit by least-squares regression and indicate that an increase in the proportional abundance of **A** spittlebugs (r^2=0.281, P<0.001), **B** leaf beetles (r^2=0.199, P<0.001), and **C** all herbivores combined (r^2=0.321, P<0.001) caused a decrease in ovipuncture preference

all herbivores combined, an increase in the proportion of ramets with herbivores caused a significant decline in the oviposition preference per plot (Fig. 1). Based on the slopes of the relationships, spittlebugs had a stronger negative effect on stem-galler preference than leaf beetles (-0.42 ± 0.09 vs. -0.29 ± 0.07), although the slopes were statistically indistinguishable ($t=1.58$, $P=0.070$). Moreover, the effects of spittlebugs and leaf beetles are generally additive. When summed, the slopes for spittlebugs and leaf beetles overlapped with the slope for all herbivores combined (including aphids; -0.56 ± 0.10). Finally, there was no correlation between the proportion of ramets with spittlebugs and leaf beetles among plots ($r=0.024$, $P=0.852$).

Qualitatively similar results were found when oviposition preference was assessed among ramets. Based on a logistic regression, we found that goldenrod genotype and the presence of spittlebugs or leaf beetles had a significant impact on the likelihood that a ramet would be ovipunctured (Table 2). Aphids had no significant effect on ovipuncture preference. Relative to herbivore-free ramets, the presence of spittlebugs alone or leaf beetles alone on a ramet reduced the likelihood of ovipuncture by 18.2% and 6.1%, respectively. The absence of a spittlebug×leaf beetle interaction in the regression analysis (Table 2) indicates that their combined effects were generally additive. Together on the same ramet, spittlebugs and leaf beetles reduced the likelihood of ovipuncture by 24.5%, relative to herbivore-free ramets. In contrast to above, this analysis revealed a significant effect of plot density on the preference (Table 2). The likelihood of ovipuncture tended to increase with density, but the fit was quite poor ($r=0.110$).

A total of 743 galls developed on the 3769 ramets within the common garden (a galling rate of 20%). Among plots, mean gall size was significantly affected by goldenrod genotype, but not by spittlebugs or leaf beetles that infested the ramets earlier in the season, or any other factor in the model (Table 3). The combined action of all herbivores, however, did significantly impact mean gall size per plot. Surprisingly, mean gall size per plot increased with an increase in the proportion of
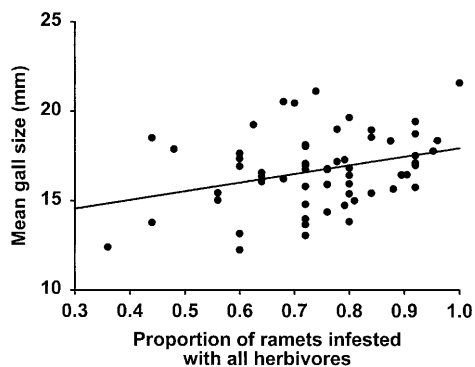
ramets infested by herbivores (Fig. 2). In addition, mean gall size tended to decrease as gall density per plot increased ($r=0.332$, $df=62$, $P=0.008$). Finally, among individual ramets, we found no effect of goldenrod genotype or other herbivores on gall size (Table 4).

Egg-to-adult (indirect measure) and gall-to-adult (direct measure) survivorship among plots were unaffected by goldenrod genotype (Kruskal-Wallis test: $H=18.21$, $P=0.252$, $df=15$ and $H=15.53$, $P=0.414$, $df=15$; respectively) and were not correlated with the proportion of ra-

Table 2 Results from logistic regression analysis for the effects of garden row, goldenrod genotype, the presence of spittlebugs, leaf beetles and aphids, and the density of ramets per plot on the likelihood that a ramet was ovipunctured by the stem galler

Predictor[a]	df	G-statistic[b]	P
Garden row	3	38.00	<0.001
Goldenrod genotype	15	71.76	<0.001
Spittlebugs	1	30.74	<0.001
Leaf beetles	1	7.49	0.006
Aphids	1	3.02	0.082
Goldenrod genotype×Spittlebugs	15	2.64	0.98
Goldenrod genotype×Leaf beetles	15	9.90	0.826
Goldenrod genotype×Spittlebugs× Leaf beetles	15	0.01	1.00
Spittlebugs×Leaf beetles	1	0.14	0.704
Plot density	1	8.59	0.003

[a] Because of the relative scarcity of aphids, no interactions between aphids and other herbivores, and aphids and goldenrod genotype could be tested
[b] G-statistic is approximately chi-square distributed

Table 3 ANCOVA results for the effect of garden row (block effect), goldenrod genotype (fixed factor), proportion of ramets attacked by each herbivore species (covariate) and plot density (covariate) on mean gall size per plot. A separate ANCOVA was performed for each herbivore, and for all herbivores combined

Source of variation	df	MS	F	P
Spittlebugs				
Garden row	3	0.164	0.045	0.987
Goldenrod genotype	15	11.667	3.185	0.005
Spittlebugs	1	5.294	1.445	0.240
Genotype×spittlebugs	15	2.478	0.676	0.783
Plot density	1	2.447	0.668	0.421
Error	26	3.663		
Leaf beetles				
Garden row	3	6.114	2.173	0.115
Goldenrod genotype	15	7.471	2.655	0.014
Leaf beetles	1	5.257	1.868	0.183
Genotype×beetles	15	3.837	1.364	0.237
Plot density	1	5.596	1.989	0.170
Error	26	2.814		
All herbivores				
Garden row	3	3.428	1.261	0.308
Goldenrod genotype	15	7.510	2.763	0.011
Herbivores	1	13.489	4.963	0.035
Genotype×herbivores	15	3.974	1.462	0.192
Plot density	1	2.146	0.790	0.382
Error	26	2.718		

Fig. 2 Proportion of ramets infested with all herbivores (spittlebugs, leaf beetles, and aphids) and its effect on gall size. *Line* is fit by least-squares regression ($r^2=0.101$, $P=0.012$)

92

Table 4 Results from a nested ANCOVA for the effect of golden-rod genotype, plot within goldenrod genotype (nested factor), presence of spittlebugs, presence of leaf beetles and plot density (covariate) on the gall size per ramet

Source of variation[a]	df	MS	F	P
Goldenrod genotype	15	29.510	2.080	0.031
Plot within goldenrod genotype	43	14.184	2.054	<0.001
Spittlebugs	1	0.405	0.029	0.864
Leaf beetles	1	2.457	0.179	0.672
Spittlebugs×Leaf beetles	1	4.186	0.305	0.581
Plot density	1	0.106	0.008	0.930
Error	466			

[a] Data were insufficient to evaluate interaction effects between goldenrod genotype and the two herbivores

mets infested by spittlebugs, leaf beetles or all herbivores combined (r_s<0.200, P>0.36). These results are in accord with our findings regarding survivorship among individual goldenrod ramets. The likelihood that a stem galler survived from the first visible signs of gall formation to adult eclosion was independent of goldenrod genotype (G=24.10, df=15, P=0.063), spittlebugs (G=0.40, df=1, P=0.527) and leaf beetles (G=2.79, df=1, P=0.095).

Because the number of ovipunctures (and therefore eggs laid) was generally higher for herbivore-free ramets (Fig. 1), measures of performance may have been confounded by different levels of intraspecific competition in herbivore-free, versus herbivore-infested, ramets. That is, greater intraspecific competition within preferred ramets may have lowered offspring performance on those ramets to levels comparable to, or below, the levels for the less-preferred, herbivore-infested, ramets. There is evidence that intraspecific competition is occurring among stem-galler larvae within a single ramet. In the absence of other herbivores, ramets with low (1–3), relative to high (≥4), numbers of ovipunctures had significantly higher egg-to-adult survivorship (27.4% vs. 9.6% survival, respectively; χ^2=6.47, P=0.011, df=1) and larger, but not quite significant, gall diameters (17.24±0.54 mm vs. 16.18±0.36 mm, respectively; t=1.50, df=144, P=0.068). To minimize the potential bias in survivorship and gall size that may have been brought about by the differential effects of intraspecific competition among treatments, we re-analyzed these data sets using only ramets that had low numbers of ovipunctures [1–3; corresponds to <2 eggs laid on average (Abrahamson and Weis 1997)]. This, however, did not change our results. Among ramets, gall-to-adult survival remained unaffected by goldenrod genotype (G=23.11, df=15, P=0.082), spittlebugs (G=0.009, df=1, P=0.924) and leaf beetles (G=0.005, df=1, P=0.944). Gall size also remained unaffected by goldenrod genotype ($F_{15,39}$=1.146, P=0.351), spittlebugs ($F_{1,255}$=0.262, P=0.609) or leaf beetles ($F_{1,255}$=1.265, P=0.262).

There was no relationship between stem-galler oviposition preference (proportion of ramets ovipunctured) and offspring performance (gall size or survivorship) among the 64 1-m^2 plots (Fig. 3). Among the 16 golden-
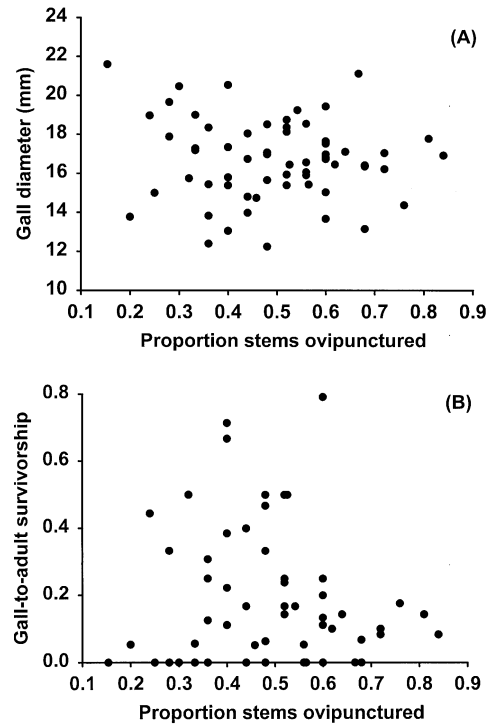

Fig. 3 Relationship between preference (proportion of ramets ovipunctured per plot) and two measures of performance: **A** mean gall size per plot (Spearman's rank correlation: r_s=0.067, P=0.605) and **B** gall-to-adult survivorship per plot (r_s=–0.065, P=0.608)

rod genotypes (plots averaged within genotypes) we also were unable to detect a relationship between the proportion of ramets ovipunctured and gall size (r=–0.074, P=0.785) or survivorship (r=–0.302, P=0.769).

Discussion

In accordance with other studies (e.g., Anderson et al. 1989; Craig et al. 1999), host-plant genotype significantly affected ovipuncture preference by the stem galler. Preference was further modified by two members of the herbivore assemblage, spittlebugs and leaf beetles, which indicates that the acceptability of these plant genotypes is phenotypically plastic. However, there was no interaction between genotypes and herbivore abundance that would indicate genetic variability for phenotypic plasticity (Via and Lande 1985; Via 1987; Scheiner and Lyman 1989). This is in contrast to a greenhouse study of ours that found strong variation in plasticity among goldenrod genotypes for stem-galler acceptability in the presence of different spittlebug densities (Cronin and Abrahamson 1999).

The presence of herbivores significantly reduced stem galler ovipuncture preference. Spittlebugs had a negative effect on oviposton preference that was 35% stronger than the negative effects of leaf beetles (based on a comparison between slopes of the relationship in Fig. 1). Overall, the combined effect of these two herbivores on

stem-galler preference was additive. While the precise cause for the reduction in preference due to the presence of spittlebugs and leaf beetles is unknown, there is evidence that these two species significantly alter the physiology, morphology, and growth of their host plant (Meyer and Whitlow 1992; Meyer 1993; Meyer and Root 1993; Cronin and Abrahamson 1999). This herbivore-induced change in the plant may consequently change the acceptability of that plant to adult female stem gallers. Inducible responses of this type have been reported with increasing frequency in the literature (see Karban and Baldwin 1997; Tollrian and Harvell 1999), and have also been demonstrated to occur between *Trirhabda* spp. and later-arriving *U. nigrotuberculatum* (I. Seidl-Adams and W.G. Abrahamson, unpublished work).

The particular attributes of the ramet that the stem galler bases its oviposition decisions upon is incompletely known. One contributing factor involves plant growth: stem gallers are less likely to ovipuncture shorter, slower growing goldenrod ramets (e.g., Walton et al. 1990; Craig et al. 1999, 2000; Cronin and Abrahamson 1999). Discrimination on the basis of plant height or growth rates has been observed in several other gall-inducing insects (e.g., Craig et al. 1986, 1989; Fondriest and Price 1996; Price et al. 1997). Because spittlebugs and leaf beetles reduce goldenrod growth rates and height at the time of stem-galler attack (Meyer 1993; Meyer and Root 1993; Cronin and Abrahamson 1999), they indirectly alter plant acceptability to the stem gallers (mediated through changes in plant growth rates).

In spite of the significant effects of spittlebugs and leaf beetles on stem-galler preference, there was no corresponding effect on stem galler offspring performance (measured in terms of gall size or survivorship). These herbivores are very sedentary (Meyer and Whitlow 1992; Meyer 1993; Brown 1994; Cronin and Abrahamson 1999; J.T. Cronin and W.G. Abrahamson, unpublished work) and spent at least 3 weeks on the same goldenrod ramets. Spittlebugs began to moult into adults within a week after we examined plots for herbivore movement (4 weeks after initial release) and the adults quickly disappeared from the study area (most likely in search of more succulent herbs; see Cronin and Abrahamson 1999). Therefore, plot infestation rates by spittlebugs likely remained constant while spittlebugs were present in the garden. Leaf beetles also began moulting into adults within a week after our movement census was complete, but adults were found at low numbers throughout the summer in our plots. Even though larval leaf beetle infestation rates per plot remained unchanged throughout the experiment, adults were more mobile and likely fed within more than one plot. Thus, the effects of leaf beetles on stem-galler performance can be ascertained only for the larvae. It is possible, however, that adult leaf beetles, by feeding on all plants, may have obscured any effects of larval leaf beetles on stem-galler performance.

The 4- to 5-week period that spittlebug nymphs and leaf beetle larvae were feeding on the goldenrods was more than sufficient to have a significant long-term neg-ative impact on their host-plant's fitness (Meyer and Whitlow 1992; Meyer 1993; Meyer and Root 1993; Cronin and Abrahamson 1999). However, the expected herbivore-induced reduction in plant fitness did not translate into a corresponding reduction in stem-galler performance (see also Cronin and Abrahamson 1999). In fact, we detected a positive overall effect of herbivores on gall size (Fig. 2). The cause for this unexpected result is discussed in the next paragraphs.

Intuitively, natural selection should favor the evolution of a positive correlation between host preference and offspring performance (Thompson 1988), and this should be especially true of species with sedentary offspring such as gall insects (Craig et al. 1989; Larsson and Ekbom 1995; Abrahamson and Weis 1997). It is now widely recognized that the preference-performance relationship can be constrained or influenced by a variety of environmental factors (see Introduction), although to our knowledge few studies have examined the effects of other herbivores on this relationship (Lewis 1984; Cronin and Abrahamson 1999). In this study, we found that spittlebugs and leaf beetles caused a significant reduction in host-plant preference by the stem galler, but not a corresponding reduction in stem-galler offspring performance – there was no correlation between preference and performance. Using the same garden site and goldenrod genotypes, Craig et al (1999) found no preference-performance correlation in the absence of herbivores. This suggests that the presence of other goldenrod herbivores, at densities comparable to those used in our study, does not qualitatively alter the preference-performance relationship of the goldenrod stem galler.

Our results, however, suggest a mechanism by which spittlebugs and leaf beetles may indirectly affect the relationship between stem-galler preference and performance. Herbivore-free plants were more strongly favored and thus, on average, were more likely to receive ovipunctures and eggs. Intraspecific competition among early larval stem-gallers is particularly intense, leading to the death of supernumery larvae (Hess et al. 1996; Craig et al. 1997, 2000). Our results support this conclusion: ramets with more than four ovipunctures had lower survivorship than ramets with one to three ovipunctures, and as gall density per plot increased, gall size decreased. Consequently, stem gallers within herbivore-free ramets were expected to have suffered proportionately greater levels of intraspecific competition (i.e., higher mortality, smaller body size, reduced fitness) than those within herbivore-infested ramets. If intraspecific competition is stronger than interspecific competition, as many studies have shown (Connell 1983), stem galler performance may actually be higher in plots that are more heavily infested with other herbivore species. This scenario would explain the paradoxical increase in gall size (a correlate of stem galler size and fecundity; Cronin and Abrahamson 1999) as the proportion of ramets infested by all herbivores increased (Fig. 2).

In this study, over 70% of the goldenrod ramets were infested with at least one of the three herbivores we stud-

ied. It is presently unclear what consequences might unfold when infestation rates by these other herbivores increase (near 100% infestation rates are possible; Root and Cappuccino 1992), or ovipositing stem-galler female densities increase (up to 100% infestation rates with an average of 5 eggs laid per ramet; Hess et al. 1996) within an area. One possibility is that herbivore-free host plants will receive proportionally more stem-galler eggs laid (increased over-aggregation of eggs) than the herbivore-infested ramets. Absolute preference rankings for the herbivore-free ramets would remain high, but the performance on those ramets would decline due to increasing intraspecific competition, possibly to levels low enough that the correlation between preference and performance would become negative (see also Valladares and Lawton 1991; Yamaga and Ohgushi 1999). An alternative possibility is that the preference of hosts may be initially in favor of herbivore-free ramets, but as intraspecific competition increases within those ramets, inherently lesser quality hosts, i.e., herbivore-infested ramets, may become acceptable. If this is true, preference rankings of initially low-quality hosts (herbivore-infested) should increase with increases in either the infestation rates by other herbivores or the density of ovipositing female stem gallers. For any infestation rate or stem-galler density, the distribution of stem-galler eggs among ramets would be expected to approach an ideal-free distribution (Fretwell and Lucas 1970; Milinski and Parker 1991; Tregenza 1995). Even if female stem gallers are capable of assessing host suitability perfectly, this behavior may also lead to no, or a negative, correlation between preference and performance. Anderson et al. (1989) observed a tendency by the stem gallers to increase oviposition rates on resistant goldenrod genotypes as the oviposition period progressed, thus supporting the possibility of an ideal-free distribution of ovipositions among ramets. Considering these observations, the assessement of stem-galler preference and performance rankings across a range of infestation rates or stem-galler densities is warranted.

One question that remains to be answered is why stem gallers show a low preference for herbivore-infested ramets when there appears to be little or no difference in performance on herbivore-infested, versus herbivore-free, ramets (even when differences in intraspecific competition are controlled). We have argued previously (Cronin and Abrahamson 1999) that the stem-galler's inability to correctly assess the quality of its host plant may be due to limited discriminatory powers (Fox and Lalonde 1993; Larsson and Ekbom 1995). Spittlebugs and leaf beetles cause many of the same physiological and morphological changes to their host plant, including biomass allocations, growth rates and ramet heights (Meyer and Whitlow 1992; Meyer 1993; Meyer and Root 1993; Cronin and Abrahamson 1999). Other sources of stress such as nutrient or water deficiencies, presence of other herbivores, and goldenrod competition with other species have similar effects on goldenrods (Goldberg 1987; Hartnett and Abrahamson 1979; Horner

and Abrahamson 1992, 1999; Meyer and Root 1993; Root 1996). While countless differences may exist among ramets stressed by these different agents, the stem gallers may not have the ability to discriminate among them. An inability to distinguish among the many stress inducers may also lead to a poor correlation between host preference and offspring performance (Fox and Lalonde 1993; Larsson and Ekbom 1995; Abrahamson and Weis 1997). Larsson and Ekbom (1995) have argued that this "host confusion" is most likely to occur with gall insects, which are characterized by generally short lifespans and intimate relationships with their hosts. More work is clearly needed to assess the validity of the host-confusion hypothesis in this gall-insect system.

References

Abrahamson WG, Weis AE (1997) The evolutionary ecology of a tritrophic-level interaction: goldenrod, the stem gallmaker and its natural enemies. Princeton University Press, Princeton

Anderson SS, McCrea KD, Abrahamson WG, Hartzel LM (1989) Host genotype choice by the ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). Ecology 70:1048–1054

Bigger DS, Fox LR (1997) High density populations of diamondback moth have broader host plant diets. Oecologia 112:179–186

Briese DT (1996) Oviposition choice by the *Onopordum capitulum* weevil *Larinus latus* (Coleoptera: Curculionidae) and its effect on the survival of immature stages. Oecologia 105:464–474

Brown DG (1994) Beetle folivory increases resource availability and alters plant invasion in monocultures of goldenrod. Ecology 75:1673–1683

Bush GL (1975) Modes of animal speciation. Annu Rev Ecol Syst 6:339–364

Cappuccino N (1987) Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. Ecology 68:1634–1646

Cappuccino N (1988) Spatial patterns of goldenrod aphids and the response of enemies to patch density. Oecologia 76:607–610

Cates RG (1981) Host plant predictability and the feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores. Oecologia 48:319–326

Chew FS, Courtney SP (1991) Plant apparency and evolutionary escape from insect herbivory. Am Nat 138:729–750

Cipollini DF (1997) Wind-induced mechanical stimulation increases pest resistance in common bean. Oecologia 111:84–90

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Amer Natur 122:661–696

Courtney SP, Kibota TT (1990) Mother doesn't know best: selection of hosts by ovipositing insects. In: Bernays EA (ed) Insect-plant interactions. CRC, Boca Raton, pp 161–188

Craig TP, Price PW, Itami JK (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. Ecology 67:419–425

Craig TP, Itami JK, Price PW (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology 70:1691–1699

Craig TP, Horner JD, Itami JK (1997) Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. Evolution 51:1552–1560

Craig TP, Abrahamson WG, Itami JK, Horner JD (1999) Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. Oikos 89:119–128

Craig TP, Itami JK, Shantz C, Abrahamson WG, Horner J, 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

Cronin JT, Abrahamson WG (1999) Host plant genotype and other herbivores influence goldenrod stem galler preference and performance. Oecologia 121:392–404

Cronin JT, Hyland K, Abrahamson WG (2001) Within-patch movement of a stem-galling fly: implications for host-plant choice. Ecol Entomol 26 (in press)

Faeth SH (1986) Indirect interactions between temporally separated herbivores mediated by the host plant. Ecology 67:479–494

Feeny PP (1976) Plant apparency and chemical defenses. Rec Adv Phytochem 10:1–40

Fondriest SM, Price PW (1996) Oviposition site resource quantity and larval establishment for *Orellia occidentalis* (Diptera: Tephritidae) on *Cirsium wheeleri*. Environ Entomol 25:321–326

Fox CW (1993) A quantitative genetic analysis of oviposition preference and larval performance on two hosts in the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Evolution 47:166–175

Fox CW, Lalonde RG (1993) Host confusion and the evolution of insect diet breadths. Oikos 67:577–581

Fretwell SD, Lucas HL Jr (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor 19:16–36

Futuyma DJ (1976) Food plant specialization and environmental predictability in Lepidoptera. Am Nat 110:285–292

Futuyma DJ, Meyer GC (1980) Nonallopatric speciation in animals. Syst Zool 29:254–271

Goldberg D (1987) Neighborhood competition in an old-field plant community. Ecology 68:1211–1223

Harrison S, Karban R (1986) Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sim. Oecologia 69:354–359

Hartnett DC, Abrahamson WG (1979) The effects of stem gall insects on life history patterns in *Solidago canadensis*. Ecology 60:910–917

Hess MD, Abrahamson WG, Brown JM (1996) Intraspecific competition in the goldenrod ball-gallmaker (*Eurosta solidaginis*): larval mortality, adult fitness, ovipositional and host-plant response. Am Midl Nat 136:121–133

Horner JD, Abrahamson WG (1992) Influence of plant genotype and environment on oviposition preference and offspring survival in a gallmaking herbivore. Oecologia 90:323–332

Horner JD, Abrahamson WG (1999) Influence of plant genotype and early-season water deficits on oviposition preference and offspring performance in *Eurosta solidaginis* (Diptera: Tephritidae). Am Midl Nat 142:162–172

Hosmer DW, Lemeshow S (1989) Applied logistic regression. Wiley, New York

Joshi A, Thompson JN (1995) Trade-offs and the evolution of host specialization. Evol Ecol 9:82–92

Karban R, Adler FR (1996) Induced resistance to herbivores and the information content of early season attack. Oecologia 107:379–85

Karban R, Baldwin IT (1997). Induced responses to herbivory. University of Chicago Press, Chicago

Karban R, Courtney S (1987) Intraspecific host plant choice: lack of consequences for *Streptanthus tortuosus* (Cruciferae) and *Euchloe hyantis* (Lepidoptera: Pieridae). Oikos 48:243–248

Lalonde RG, Roitberg BD (1992) Host choice behavior of a thistle-feeding fly: choices and consequences. Oecologia 90:534–539

Larsson S, Ekbom B (1995) Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? Oikos 72:155–160

Larsson S, Glynn C, Hoglund S (1995) High oviposition rate of *Dasineura marginemtorquens* on *Salix viminalis* genotypes unsuitable for offspring survival. Entomol Exp Appl 77:263–270

Lawton JH, McNeill S (1979) Between the devil and the deep blue sea: on the problem of being a herbivore. In: Anderson RM, Turner BD, Taylor LR (eds) Population dynamics (20th Symposium of the British Ecological Society). Blackwell, Oxford, pp 223–244

Lewis AC (1984) Plant quality and grasshopper feeding: effects of sunflower conditions on preference and performance in *Melanoplus differentialis*. Ecology 65:836–843

Maddox GD, Cappuccino N (1986) Genetic determination of plant susceptibility to an herbivorous insect depends on environmental context. Evolution 40:863–866

McMillin JD, Wagner MR (1997) Chronic defoliation impacts pine sawfly (Hymenoptera: Diprionidae) performance and host plant quality. Oikos 79:357–62

Messina FJ (1982) Comparative biology of the goldenrod leaf beetles, *Trirhabda virgata* LeConte and *T. borealis* Blake (Coleoptera: Chrysomelidae). Coleopt Bull 36:255–269

Meyer GA (1993) Comparison of the impacts of leaf- and sap-feeding insects on growth and allocation of goldenrod. Ecology 74:1101–1116

Meyer GA, Root RB (1993) Effects of herbivorous insects and soil fertility on reproduction of goldenrod. Ecology 74:1117–1128

Meyer GA, Whitlow TH (1992) Effects of leaf and sap feeding insects on photosynthetic rates of goldenrod. Oecologia 92:480–489

Milinski M, Parker GA (1991) Competition for resources. In: Krebs JR, Davies NB (eds) Behavioural ecology. An evolutionary approach, 3rd edn. Blackwell, Boston, pp 137–168

Mitter CB, Farrell B, Futuyma DJ (1991) Phylogenetic studies of insect-plant interactions: insights into the genesis of diversity. Trends Ecol Evol 6:200–203

Ohgushi T (1995) Adaptive behavior produces stability in herbivorous lady beetle populations. In: Cappuccino N, Price PW (eds) Population dynamics. Academic Press, San Diego, pp 303–319

Preszler RW, Price PW (1995) A test of plant-vigor, plant-stress, and plant-genotype effects on leaf-miner oviposition and performance. Oikos 74:485–492

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Price PW (1994) Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. Res Popul Ecol 36:1–12

Price PW, Craig TP, Fernandes GW, Itami JK, Mopper S, Preszler RW (1990) Insect herbivore population dynamics on trees and shrubs: new approaches to latent and eruptive species and life table development. In: Bernays EA (ed) Insect-plant interactions. CRC, Boca Raton, pp 1–38

Price PW, Roininen H, Tahvanainen J (1997) Willow tree shoot module length and the attack and survival pattern of a shoot galling sawfly, *Euura atra* (Hymenoptera, Tenthredinidae). Entomol Fenn 8:113–119

Root RB (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77:1074–1087

Root RB, Cappuccino N (1992) Patterns in population change and the organization of the insect community associated with goldenrod. Ecol Monogr 62:393–420

Rossi AM, Strong DR (1991) Effects of host-plant nitrogen on the preference and performance of laboratory populations of *Carneocephala floridana* (Homoptera: Cicadellidae). An Entomol Soc Am 20:1349–1355

Ruohomaki K, Chapin FS, Haukioja E, Neuvonen S, Suomela J (1996) Delayed inducible resistance in mountain birch in response to fertilization and shade. Ecology 77:2302–2311

Scheiner SM, Lyman RF (1989) The genetics of phenotypic plasticity. I. J Evol Biol 2:95–107

Sholes ODV (1981) Herbivory by species of *Trirhabda* (Coleoptera: Chrysomelidae) on *Solidago altissima* (Asteraceae): variation between years. Proc Entomol Soc Wash 83:274–282

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stiling P, Rossi AM (1996) Complex effects of genotype and environment on insect herbivores and their enemies. Ecology 77:2212–2218

Straw NA (1989) The timing of oviposition and larval growth by two tephritid fly species in relation to host plant development. Ecol Entomol 14:443–454

Strong DR, Larsson S (1994) Is the evolution of herbivore resistance influenced by parasitoids? In: Hawkins B, Sheehan W (eds) Parasitoid community ecology. Oxford University Press, Oxford, pp 261–276

Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol Exp Appl 47:3–14

Thompson JN (1996) Trade-offs in larval performance on normal and novel hosts. Entomol Exp Appl 80:133–139

Tollrian R, Harvell CD (eds) (1999) The ecology and evolution of inducible defenses. Princeton University Press, Princeton

Tregenza T (1995) Building on the ideal free distribution. Adv Ecol Res 26:253–307

Uhler LD (1951) Biology and ecology of the goldenrod gall fly, *Eurosta solidaginis* (Fitch). Memoir 300:1–51

Valladares G, Lawton JH (1991) Host-plant selection in the holly leaf-miner: does mother know best? J Anim Ecol 60:227–240

Via S (1987) Genetic constraints on the evolution of phenotypic plasticity. In: Loeschke V (ed) Genetic constraints on adaptive evolution. Springer, Berlin Heidelberg New York, pp 41–71

Via S, Lande R (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505–522

Walton R, Weis AE, Lichter JP (1990) Oviposition behavior and response to plant height by *Eurosta solidaginis* Fitch (Diptera: Tephritidae). Ann Entomol Soc Am 83:509–514

Wiklund C (1982) Generalist vs. specialist utilization of host plants among butterflies. In: Visser JH, Minks AK (eds) Plant-insect relationships (Proceedings of the 5th International Symposium). Pudoc, Wageningen, pp 181–191

Yamaga Y, Ohgushi T (1999) Preference-performance linkage in a herbivorous lady beetle: consequences of variability of natural enemies. Oecologia 119:183–190