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Host-plant genotype and other herbivores influence goldenrod stem galler preference and performance

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Abstract Ecologists have labored to find an explanation for the lack of a positive correlation between host preference and offspring performance in herbivorous insects. This study focuses on how one herbivore species can influence another herbivore species' ability to accurately assess the suitability of different host-plant genotypes for larval development. In particular, we examined the role that an early season xylem-feeding homopteran (meadow spittlebug, *Philaenus spumarius*) has on the preference-performance correlation of a late-season dipteran stem galler (*Eurosta solidaginis*) among different goldenrod genotypes. In a greenhouse, we released adult stem gallers into replicate cages that contained ramets from four different goldenrod genotypes crossed with three densities of spittlebugs (0, 1, or 8 nymphs placed 2 weeks previously on each ramet). Spittlebug feeding caused a density-dependent decline in ramet growth rates, which in turn caused a corresponding decrease in host-plant preference by the stem gallers (number of ovipunctures per bud or proportion of ramets attacked). Goldenrod genotype and the interaction between spittlebugs and genotypes also influenced host-plant preference by the stem galler. Goldenrod genotype had the greatest impact on stem galler offspring performance (gall size or survivorship). Spittlebug density also affected performance, but only through its interaction with goldenrod genotype. On some genotypes, the survivorship of stem-galler larvae decreased with increasing spittlebug density, while on other genotypes, survivorship remained unchanged, or actually increased, with increasing spittlebug density. This suggests that there was genetic variance among goldenrod genotypes in their norms of reaction for their suitability as a host to the stem gallers. One possible explanation for why spittlebugs caused a significant reduction in preference, but not in performance, was that spittlebugs had very few long-term effects on the host plant. Flower number, flowering phenology, and the allocation of the ramet's biomass to different structures (belowground organs, stems, leaves, and flowers) were unchanged with respect to spittlebug density. The only effect of spittlebugs was a 3–4% decrease in ramet height at the end of the growing season. We argue 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. The damage to goldenrods caused by spittlebugs prior to attack by the stem gallers is similar in effect to potentially innumerable other causes of goldenrod stress (e.g., reduction in ramet growth rates). As a consequence, stem gallers may not be able to discern the subtle differences among stresses that identify those that will negatively affect the fitness of stem-galler offspring. The fact that goldenrod genotypes differ in their response to stresses would only further complicate the host-selection process. We propose that the stem gallers may have evolved a strategy that uses simple cues as the basis for rejecting similarly stressed plants, whether all of those plant genotype-stress combinations reduce performance or not.

Key words *Eurosta solidaginis* · Host choice · Plant stress · Plasticity variation · Preference-performance correlation

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Introduction

Within a plant species there can be considerable variation in the effect that different plant genotypes have on the performance (growth, survival, and fecundity) of herbivorous insects (e.g., Moran 1981; Craig et al. 1989; Preszler and Price 1995). In response to this variation, natural selection should favor herbivores that feed, or oviposit preferentially on, those plants yielding highest

performance. The expected consequence is a positive correlation between preference and performance among the available host genotypes (Thompson 1988). From an ecological viewpoint, the observed relationship between host preference and larval performance can play a critical role in the distribution and abundance of an herbivore population (e.g., Price 1991, 1994; Ohgushi 1995; Bigger and Fox 1997). Evolutionarily, the relationship between these two variables has been linked to understanding host-plant specificity, diet breadth, host-race formation, sympatric speciation, life-history evolution and the adaptive radiation of herbivore taxa (e.g., Bush 1975; Futuyma and Meyer 1980; Mitter et al. 1991; Joshi and Thompson 1995; Thompson 1996).

Strong, 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; Hanks et al. 1993). However, this pattern is far from ubiquitous: many insects preferentially oviposit on plant genotypes that do not yield highest fitness (see Karban and Courtney 1987; Courtney and Kibota 1990; Horner and Abrahamson 1992; Fox 1993; Larsson et al. 1995; Craig et al. 1999a). In response to these inconsistent results, a broad range of hypotheses have emerged to explain the lack of a positive preference-performance correlation. Factors such as plant apparency (Feeny 1976; Rhoades and Cates 1976; Wiklund 1984; Chew and Courtney 1991), novel association between host plant and herbivore (Chew 1977; Thompson 1988, 1996; Joshi and Thompson 1995; Larsson and Ekbom 1995), phenology of herbivore oviposition (Straw 1989; Briese 1996), herbivore abundance (Wiklund 1982), environmental predictability (Futuyma 1976; Cates 1981; Chew and Courtney 1991; Lalonde and Roitberg 1992), parasites and predators (Lawton and McNeill 1979; Strong and Larsson 1994; Stiling and Rossi 1996), and limited discriminatory ability of herbivores ("host confusion" hypothesis of Fox and Lalonde 1993; Larsson and Ekbom 1995) may all subvert the occurrence of a one-to-one correspondence between preference and performance.

Most studies of preference and performance focus only on the relationship among plant species or genotypes. In nature, many other variables that occur prior to, or at the time of host-plant selection, can affect the plant's phenotype; and consequently its acceptability (=preference) or suitability (=performance) as an ovipostion or feeding site for an herbivore. The list of variables is infinite, but includes water or nutrient availability (Maddox and Cappuccino 1986; Horner and Abrahamson 1992; Preszler and Price 1995; Ruohomaki et al. 1996), wind exposure (Cipollini 1997), amount of shade (Ruohomaki et al. 1996; Horner and Abrahamson 1992), or the presence of other herbivores (Lewis 1984; Faeth 1986; McMillin and Wagner 1997). If a plant genotype's suitability is phenotypically plastic in response to each of these environmental variables, the types of hosts (in terms of suitability) that are available to an herbivore would be increased potentially by orders of magnitude. This would add tremendously to the difficulty an herbivore faces in selecting a suitable oviposition or feeding site. To further complicate the issue, host acceptability or suitability may depend on interactions that occur between the plant genotype and various aspects of the environment (Maddox and Cappuccino 1986). That is, each genotype may respond differently to the environmental variable, implying genetic variance in phenotypic plasticity (Via and Lande 1985; Via 1987; Scheiner and Lyman 1989; Gotthard and Nylin 1995). Host confusion, or constraints on the ability to discriminate among the plethora of host types (i.e., all the particular environment-by-genotype combinations), seems likely under these circumstances (Fox and Lalonde 1993; Larsson and Ekbom 1995). This may be especially true because many of the environmental variables have similar effects on the plant phenotype at the time of host selection (e.g., cause a reduction in plant height), yet have variable long-term effects on plant and herbivore performance. Complexity in the plant's environment, therefore, can render the selection of suitable host plants a daunting task. More studies are needed that account for the effects of important environmental variables, including their interaction with plant genotype on the preference-performance relationship.

In this study, we tested the hypothesis that early-season herbivores can obscure the expected positive correlation between adult oviposition preference and offspring performance. In particular, we determined the effect of the meadow spittlebug, *Philaenus spumarius* L. (Homoptera: Cercopidae), goldenrod genotype, and the interaction between spittlebugs and genotypes on the oviposition behavior and offspring performance of the stem galler, *Eurosta solidaginis* Fitch (Diptera: Tephritidae). This was accomplished by releasing adult stem gallers into cages that contained four goldenrod genotypes crossed with three densities of spittlebugs. Although spittlebug density, goldenrod genotype, and their interaction strongly affected stem galler oviposition preference and offspring performance, stem gallers showed no tendency toward ovipositing on plants that yielded highest performance. We argue that this result is due to the inability of the stem galler to discriminate among the large suite of plant stresses (spittlebugs included) that interact differentially with the available plant genotypes.

Materials and methods

Natural history of herbivores

The life history, ecology and evolution of the tephritid stem-galling fly, *E. solidaginis*, are detailed in Uhler (1951) and Abrahamson and Weis (1997), so we provide only a brief description here. *E. solidaginis* attacks and induces gall formation on the goldenrod, *Solidago altissima*. In Pennsylvania, adult stem gallers oviposit into the terminal buds of goldenrod around mid to late May. Within 3 weeks the stem tissue shows signs of swelling, and by mid-July the galls reach full size and are spheroid in shape. The larvae overwinter in the third stadia within the galls of senescent goldenrod stems, 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 a positive correlation between the two traits has been rarely observed (Anderson et al. 1989; Horner and Abrahamson 1992; Abrahamson and Weis 1997; Craig et al. 1999a; but see M. Eubanks and W.G. Abrahamson, unpublished work).

The suite of herbivores that feed on goldenrod is extremely diverse. According to Root and Cappuccino (1992), 129 species of insects are capable of completing their development on *S. altissima*. All but a few of these species are rare, or only sporadically abundant. In addition to *E. solidaginis*, two species of leaf beetle (*Trirhabda virgata* and *T. borealis*), two aphids (*Uroleucon nigrotuberculatum* and *U. caligatum*), and the meadow spittlebug (*Philaenus spumarius*) make up the vast majority of the total herbivore biomass (Cappuccino 1987; Root and Cappuccino 1992; Meyer 1993). Of these herbivores, the spittlebug is the first to attack the goldenrods and is typically in high abundance at the time when *E. solidaginis* adults are searching for oviposition sites (J.T. Cronin, personal observation). The other species appear later than the spittlebugs, but a few days before the stem galler emerges, and do not normally reach high abundance until later in the season.

The cosmopolitan meadow spittlebug feeds on the xylem fluids of more than 500 species of dicots (Weaver and King 1954; Owen 1988), but in the northeastern United States, early instar nymphs tend to prefer *Solidago* spp. (Lavigne 1959). In Pennsylvania, overwintering eggs hatch from the senescent vegetation in early spring (Ahmed and Davidson 1950; Lavigne 1959), and the larvae ascend the emergent goldenrod stems to feed at the base of newly flushed leaves (J.T. Cronin, personal observation). Approximately 2 weeks later, when spittlebugs are in their second nymphal instar, stem-galler adults begin the process of selecting oviposition sites. The relatively immobile spittlebugs develop through three additional instars, and then moult into an adult around the end of July (Lavigne 1959). At this point, adults quickly disappear from goldenrod fields, presumably emigrating to areas with more succulent herbs (J.T. Cronin, unpublished data). In September, adults migrate back to the goldenrod fields where they lay their eggs.

Nymphal spittlebug densities generally range from 0–12 (mean ≈4) individuals per goldenrod ramet (Meyer 1993; J.T. Cronin, unpublished work), but have been known to occur at epidemic levels in some localities and years (Wiegert 1964; Whittaker 1973; Root and Cappuccino 1992). Even at very low spittlebug densities, goldenrods show measurable signs of stress. After just 3 weeks of exposure to spittlebug feeding, plant biomasses, specific leaf areas, growth rates, photosynthetic rates, numbers of lateral stems and seed production were all lower than for plants that were free of spittlebugs (Meyer and Whitlow 1992; Meyer 1993; Meyer and Root 1993). A change in any one of these variables could potentially have a tremendous impact on host choice and larval performance of *E. solidaginis*. For example, goldenrod ramets that have slower growth rates and are shorter in height are less preferred by the stem galler than faster-growing, taller ramets (Anderson et al. 1989; Walton et al. 1990; Horner and Abrahamson 1992; How et al. 1993; Craig et al. 1999a, 1999b).

Methods

Plant genotype and spittlebug treatments

The goldenrod clones used in this study were selected from a common garden that was established in 1985 at Bucknell University, Lewisburg, Pennsylvania, United States. Anderson et al. (1989) and Craig et al. (1999a) determined experimentally the oviposition preference and offspring performance rankings of the 40 goldenrod genotypes that were originally planted in the garden. We selected four genotypes that differed markedly in their rankings. Of the 40 genotypes, genotype 85-3 was ranked 26.5 for preference and 2 for performance, genotype 85-5 ranked 9.5 and 14, genotype 85-6 ranked 2 and 19, and genotype 85-16 ranked 24.5 and 26. Lower rankings indicated higher relative preference or performance.

In March 1996, rhizomes from each of the four genotypes were excavated from the common garden, cut into 5-cm lengths and planted in vermiculite in shallow trays. Trays were then placed in a greenhouse at Bucknell University. Once goldenrod shoots reached a height of about 10 cm, the individual ramets were transferred to separate 20-cm diameter standard pots containing Pro-Mix BX potting soil.

First and second instar spittlebug nymphs, and the stems on which they were attached, were collected from the field and immediately transferred to the potted ramets. For the experiment, we established in the greenhouse three densities of spittlebug nymphs (0, 1, 8) on each of the 4 goldenrod genotypes. The experiment was divided among seven experimental blocks, with blocks dispersed in space (among greenhouse benches) and in time (spanning a 3-week period). Within each block, the 12 spittlebug density-by-goldenrod genotype combinations were replicated six times for a total of 72 potted ramets per block (placed in a 12×6 array on each greenhouse bench). Because ramet height has been shown to be an important predictor of plant preference by the stem galler (Anderson et al. 1989; Walton et al. 1990; Horner and Abrahamson 1992; How et al. 1993; Craig et al. 1999a, b), we selected ramets so that the range in height within a block spanned only 5 cm (absolute heights varied from 17–22 cm to 30–35 cm, depending on the block).

The spittlebug density treatment levels were established by gently transferring nymphs from chilled goldenrod cuttings to the potted ramets using a small camel's-hair paintbrush. Within minutes spittlebugs began feeding, as evidenced by the formation of frothy spittle around the insect. Spittlebugs were then left alone to feed on the ramets for 14 days. Plants were checked daily for loss of nymphs and spittlebugs were replaced as necessary to maintain designated density levels. Ramets were spaced far enough apart that there was no contact among them; we never observed the relatively sessile nymphs to move between plants. All density fluxes were a consequence of nymphal disappearance (i.e., death or failed emigration).

Rearing stem gallers

Eurosta solidaginis were collected in January and February of 1996 and maintained in diapause by storing them in a non-frost-free freezer at –10°C. To break diapause, galls were transferred to small screen cages placed within an environmental chamber set at a constant 26°C, 85% relative humidity (RH), 14:10 h light:dark (L:D) photoperiod. Emerging adults were removed daily and stored in a separate growth chamber set at 10°C (all other conditions identical). For the following experiments, we used adult flies that were <3 days old. Flies experiencing this developmental regime show no detectable difference in oviposition behavior from flies reared under natural conditions (W.G. Abrahamson and J.T. Cronin, personal observations).

Oviposition preference

After spittlebugs had been feeding on the ramets for 2 weeks, the pots were randomly re-distributed within the bench and a fiberglass-screen cage was placed over them. A total of 20 male and 20 female flies were released into each cage to mate and select oviposition sites among the 72 host plants. Apical buds were examined every 4–6 h and the trial was terminated once 50–60% of the buds had evidence of oviposition scars. This was to ensure that sufficient numbers of ramets had been visited, yet not all buds had been attacked. On average, it took flies about 3–4 days to achieve this level of oviposition. Upon termination of the experiment, the flies and cage were removed. The height of each ramet was measured and all spittlebugs were counted and removed. The total period of the ramet's exposure to spittlebugs was 17–18 days; at which time, nymphs were already beginning their final moult into adults.

Our measure of host-plant preference was the number of ovipuncture scars found in the apical buds of each ramet. There are

several reasons that justify the use of this measure. First, there is a strong positive correlation between number of eggs laid and number of ovipuncture scars (Abrahamson and Weis 1997, Fig. 5.6: r^2=0.61, P<0.001; see also Horner and Abrahamson 1992; Hess et al. 1996; Craig et al. 1997, 1999b). The presence of an egg is clearly an indication that the host plant has been accepted by a searching stem galler and it is logical to assume that the greater the number of eggs laid, the more acceptable is the host (i.e., has a high preference). Second, there is no evidence of a plateau in this relationship (even with more than 40 punctures), suggesting that the acceptability of the host as an oviposition site does not diminish with an increase in the number of eggs previously laid or traces left behind by other flies (e.g., punctures, chemical markers). This conclusion is supported by Craig et al. (1999b), who demonstrated that the presence of ovipunctures has no effect on the acceptance of a bud as an oviposition site by female stem gallers that subsequently visit that bud. These data provide strong support for the use of this singular measure as a proxy for host preference. Other studies with this stem galler have opted to use the proportion of ramets that were ovipunctured as a measure of preference (Anderson et al. 1989; Horner and Abrahamson 1992; Craig et al. 1999a). For comparative purposes, we also include an analysis of this preference measure.

Spittlebug and genotype impact on goldenrod fitness

If there is an effect of spittlebugs on the performance of the stem galler, it is possible that it would be indirect and mediated through the spittlebug's effect on host-plant quality. We therefore determined the relationship between spittlebug density and plant fitness using only gall-free ramets. To this end, we reared the potted ramets used in the previous experiment through the flowering stage and to senescence.

On 5 July we recorded whether or not ramets had begun to flower, and the approximate stage of flowering (0, 25, 50, 75, and 100% of buds in flower). We then harvested flower heads from a ramet when all the flowers had opened, but before any of them had lost sepals, petals, or seeds. In addition, we measured the terminal height of each ramet (to the nearest 1 cm). For each of 26 ramets, chosen to represent a broad range of flower production, we counted the number of flower heads, dried those heads in an oven at 65°C for 4 days, and then determined their mass (to the nearest 1 mg). We used these data to determine the relationship between total flower-head mass and head number per ramet (using least-squares regression).

Flower heads from the remaining ramets were harvested in the same manner; except that head counts were omitted. Five flower heads were haphazardly chosen and later dissected to determine the mean number of flowers per flower head. The remaining flower heads were dried and the total dry mass determined. We then used the regression model from above to translate mass into the number of flower heads, and then by multiplying this number by the mean number of flowers per head, we determined the total number of flowers per ramet.

In mid-December, after ramets had completely senesced, we harvested the vegetation from each ramet in the first three experimental blocks (the other four blocks were omitted due to labor constraints) and divided it into three categories: stems, leaves, and below-ground organs (roots and rhizomes). Vegetation from each category was dried and then weighed to the nearest mg. Thus, for each ramet we obtained data on the allocation of biomass to below-ground organs, stems, leaves, and reproduction (from flower weights above).

Offspring performance

We used the galls that were produced from the stem-galler preference experiment to determine the effect of spittlebugs and goldenrod genotypes on stem-galler performance. Galls that were stored in the freezer in December 1996 were removed on 15 February 1997, placed in individual small plastic cups, and transferred to a growth chamber (28°C, 80% RH, 14:10 h L:D photoperiod). Every day, we removed emerged adult flies from the incubator and recorded their (1) post-diapause development time (i.e., time spent in the growth chamber), (2) sex, (3) gall diameter, (4) thorax length, (5) wing length, (6) wing width, (7) mean hind tibia length (8) biomass, and (9) egg load. We consider each of these nine variables to be potential measures of stem-galler performance.

Another performance measure used in this study was stem-galler survivorship. Direct measurement of survivorship from egg to adult eclosion was impossible because the number of eggs laid per ramet could not be ascertained without permanently damaging the bud. Consequently we obtained an indirect estimate of the number of eggs laid per ramet by making use of the strong linear relationship between the number of ovipunctures and number of eggs laid per ramet [see Abrahamson and Weis 1997; eggs=0.20(ovipunctures)+1.59, r^2=0.61, P<0.001]. For each experimental block and goldenrod genotype-by-spittlebug density combination, we estimated egg-to-adult survivorship as the total number of adult flies emerged divided by the total number of eggs laid among the six ramets. We also include for comparison, a direct measure of survivorship: the proportion of offspring surviving from the first appearance of the gall (*c*. 3 weeks post-oviposition) to adult eclosion.

Statistical analysis

Preference data from host-choice experiments are often plagued by a dependent variable that has a bivariate distribution (accept or reject a host) and a lack of independence in the choice among plant groups (Singer 1986; Barker 1992). This was unlikely to be a problem in our analysis of stem-galler preference. First, our primary measure of preference, the number of ovipunctures, was a relatively continuous trait that ranged from 0 to 40 per bud in this experiment. Second, we released 20 female stem gallers into a cage and allowed them sufficient time to sample and oviposit in many ramets. Thus, acceptance of one ramet did not preclude the acceptance of another ramet. Finally, because stem gallers are not influenced by the ramet's prior history with regard to other searching stem gallers (Abrahamson and Weis 1997; Craig et al. 1999b), the results are likely the summation of many independent oviposition events.

Based on the above considerations, we analyzed the effects of spittlebug density and goldenrod genotype on host-plant preference (number of ovipunctures per ramet) with ANOVA. A two-way completely randomized block factorial design was used in which spittlebug density and genotype were treated as the main (fixed) effects, and the seven greenhouse benches (cages) served as the block effect. Even though variation in ramet height within a block was minimized in the experiment by using similarly sized ramets, we also included ramet height at the time of stem-galler release as a covariate in the model. For ease of reference, we designate the above design ANOVA model I. The natural-log transformation was used to normalize ovipuncture data. For analysis of the proportion of ramets ovipunctured, the unit of replication was no longer each ramet, but each block (n=7). This was necessary because each experimental block provided only one estimate of the proportion for each spittlebug-goldenrod genotype combination. Hence, the model was reduced to a two-way factorial design (ANOVA model II). To normalize the distribution of proportions, we used the angular transformation (Sokal and Rohlf 1995).

To determine the effect of spittlebugs on goldenrod ramet fitness, we performed the following analyses. First, we examined the effect of spittlebug density and goldenrod genotype on the terminal height of ramets. The ANOVA model had the same sources of variation as described for the analysis of ovipuncture number (model I), except that initial ramet height was excluded in this model. Second, we determined whether the flowering phenology of the ramets varied with respect to our two main treatment effects. Here, the proportion of ramets of a given genotype and spittlebug density treatment that had begun flowering on 5 July was

used as the dependent variable in a two-way factorial ANOVA (model II). Third, we examined whether the proportional allocation to each of the four plant structures, below-ground organs, stems, leaves and flowers, varied among treatments. A separate ANOVA was performed for each plant structure using a design similar to model I from above. In all cases, the percentages allocated to each plant structure were approximately normally distributed and required no transformation. Finally, we performed a two-way factorial randomized block ANOVA on the natural log of the number of flowers produced per ramet (model I).

To determine the effect of spittlebugs and genotypes on stem-galler offspring survivorship (egg-to-adult and first appearance of the gall-to-adult), we used a model II design. Both measures of survivorship required an angular transformation to normalize the data and separate ANOVAs were used for each. A model II design was also used to analyze all other measures of stem-galler performance (e.g., gall diameter, mass, and egg number). For these individually based characters, there were too few spittlebug density×goldenrod genotype combination cells complete to retain the block effect in the model. Finally, the relationships among performance variables were determined using Pearson's product-moment correlations (Sokal and Rohlf 1995). The distribution of all variables were examined visually and none required a transformation to achieve normality.

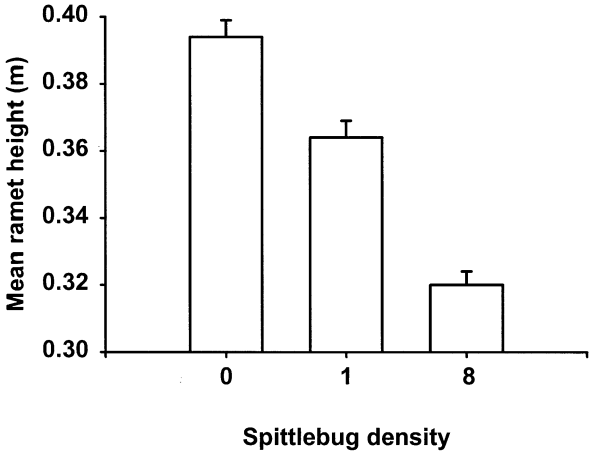

Fig. 1 Mean (±SE) goldenrod ramet heights immediately preceding stem-galler release into oviposition cages. Spittlebug nymphs were exposed to the ramets for 2 weeks before measurements were taken. Increasing spittlebug density caused a significant decline in ramet height ($F_{2,420}$=220.75, P<0.001): means for each density were significantly different from all other means (P<0.001 for all pairwise comparisons; Tukey's HSD test)

Results

Oviposition preference

After feeding for 2 weeks, spittlebugs caused a strong density-dependent reduction in goldenrod ramet height (Fig. 1). Ramets with no spittlebugs were 8% and 20% taller than ramets with one and eight spittlebugs, respectively. The growth rates [(final height–initial height)/initial height)] of ramets during this 2-week period were also similarly affected by spittlebug density ($F_{2,483}$= 273.28, P<0.001). Based on these results, we incorporated ramet height as a covariate in the analysis of stem-galler preference, keeping in mind that this variation in height was induced by the spittlebugs. We also note here that spittlebug feeding caused the goldenrod leaves to become twisted and deformed; although no quantitative data on this were collected.

Over the seven experimental blocks, 61.6±1.7% of the ramets were ovipunctured with an average of 8.9±1.2 ovipunctures per ramet (range: 0–40). Numbers such as these are well within the range found in nature. Anderson et al. (1989) found 53.5±2.9% of all ramets attacked in their field study of 30 goldenrod genotypes (range: 20–90% per genotype), and Hess et al. (1996) found an average of 5.8±2.2 ovipunctures per ramet (range: 0–18.55) among 10 field-sampled goldenrod genotypes.

Host-plant choice by the stem galler, as measured by the number of ovipunctures per ramet, was influenced by almost all factors examined (Table 1, Fig. 2A). In order of decreasing importance (based on the percentage of the total variation in number of ovipunctures that was explained by each factor; Table 1), the choice of a ramet as an oviposition site was influenced by ramet height, followed by experimental block, spittlebug density, spittlebug density×genotype interaction, goldenrod genotype, and finally, the spittlebug×block interaction. Female stem gallers made fewer oviposition attempts on goldenrods inhabited by eight, than by one or no, spittlebugs; however, there was no difference in number of ovipositions between the 1- and 0-spittlebug density treatments (Fig. 2A). Among goldenrod genotypes, only genotype

Table 1 Results of ANOVA on the effect of spittlebug density, goldenrod genotype, experimental block, and ramet height (covariate) on stem-galler preference (log-transformed number of ovipunctures)

Source of variation	*df*	MS	*F*	*P*	%Var[a]
Spittlebug density	2	7.281	7.936	<0.001	14.3
Goldenrod genotype	3	3.738	4.074	0.007	7.3
Block	6	11.998	13.077	<0.001	23.5
Spittlebug density×genotype	6	3.874	4.222	<0.001	7.6
Spittlebug density×block	12	3.246	3.538	<0.001	6.4
Genotype×block	18	0.889	0.969	0.495	1.7
Spittlebug density×genotype×block	36	0.792	0.864	0.696	1.6
Ramet height	1	18.353	20.004	<0.001	35.9
Error	419	0.917			1.8

[a] Percentage of the total variance in stem-galler preference that was explained by each source of variation (source sum-of-squares/total sum-of-squares)

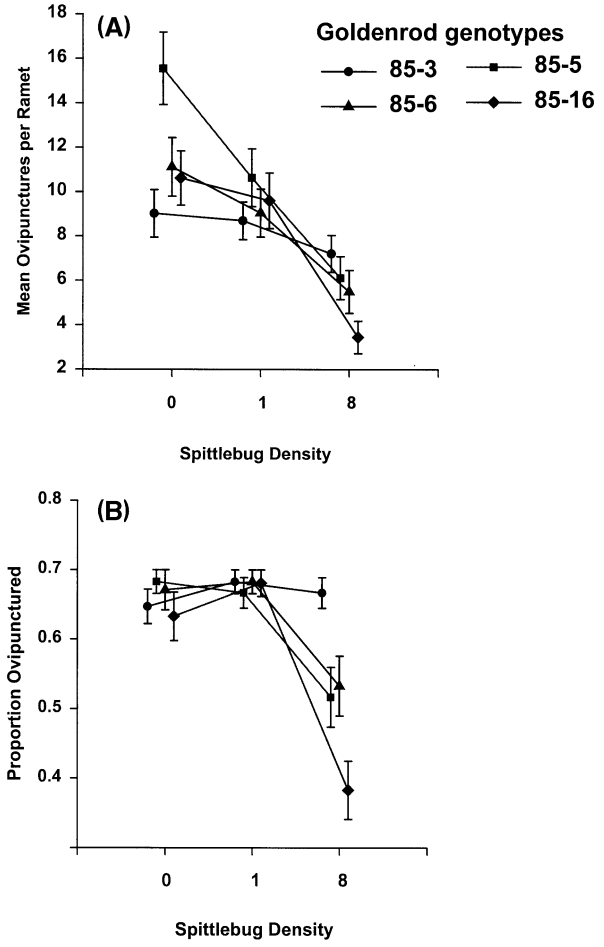

Fig. 2 The effect of spittlebug density and goldenrod genotype on two measures of host-plant preference: **A** number of ovipunctures per ramet and **B** proportion of stems ovipunctured. **A** Mean (±SE) number of ovipunctures was similar between ramets with spittlebug densities of 0 and 1 (Tukey's HSD, P=0.889), but was significantly greater for plants with 0 versus 8 spittlebugs and 1 versus 8 spittlebugs (P<0.001 and P=0.004, respectively). Among genotypes, only 85-5 and 85-16 differed significantly in number of ovipunctures (P=0.003). **B** Mean (±SE) proportion of ramets ovipunctured showed the same pattern with respect to spittlebug density: proportions were similar between the two lowest densities (P=0.627), but both differed from the highest density (P<0.001). Only goldenrod genotypes 85-3 and 85-16 differed significantly in proportions ovipunctured (P=0.002). To increase clarity, means for each spittlebug density level were separated along the x-axis

85-5 and 85-16 differed significantly (Fig. 2A). We found the same qualitative pattern with respect to the proportion of stems ovipunctured (Fig. 2B): there was a highly significant effect of spittlebug density ($F_{2,71}$=29.61, P<0.001), goldenrod genotype ($F_{3,71}$=4.94, P=0.004), and their interaction ($F_{6,71}$=5.55, P<0.001) on host preference.

Spittlebug and genotype impact on goldenrod fitness

Terminal ramet height (i.e., height at the end of the growing season) decreased with increasing spittlebug density; although, the only significant differences in height occurred between the 1- and 8-spittlebug-density treatments (Fig. 3). We also found significant differences in height between genotype 85-3 and all other genotypes (Fig. 3). Overall, the effects of goldenrod genotype were two times greater than the effects of spittlebug density on terminal ramet height (Table 2). Experimental block, genotype×block interaction, and spittlebug×block interaction also had a significant influence on terminal ramet height (see legend, Fig. 3).

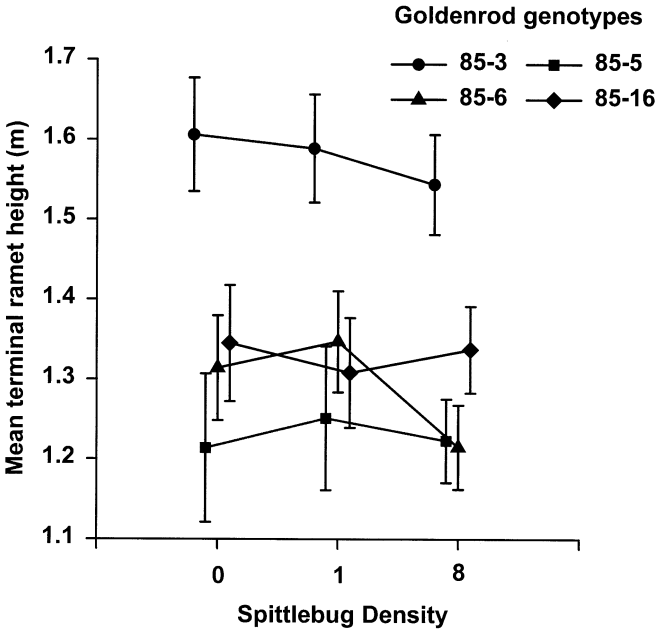

Fig. 3 Terminal ramet height (mean±SE) was influenced by spittlebug density and goldenrod genotype ($F_{2,193}$=3.28, P=0.040 and $F_{3,193}$=5.25, P=0.002, respectively). Statistically significant differences occurred only between genotype 85-3 and each of the other three genotypes (Tukey's HSD, P<0.05); whereas only spittlebug densities of 1 and 8 were different (P=0.033). Based on an ANOVA model similar to the one presented in Table 1, experimental block ($F_{6,193}$=16.07, P<0.001), spittlebug density×block ($F_{12,193}$=3.41, P<0.001) and genotype×block ($F_{18,193}$=1.73, P=0.037) also influenced terminal ramet height

The proportion of ramets that had initiated flowering on 5 July (arcsine-square root transformed) was strongly dependent upon plant genotype ($F_{3,66}$=30.34, P<0.001), but not upon spittlebug density or the spittlebug density×genotype interaction ($F_{2,66}$=1.58, P=0.214 and $F_{6,66}$=1.93, P=0.089, respectively) (see also Table 2). A similar pattern was observed for the allocation of biomass to the four reproductive structures (Table 3). For all four plant structures, spittlebug density had no significant effect on proportionate allocation, but genotype had a significant effect on all structures but the below-ground organs (Table 3). On average, the proportion of variance in the model explained by spittlebug density and genotypes was 8 and 62%, respectively (Table 2). There were no other factors that influenced biomass allocation.

Ramet reproductive success (measured as the number of flowers produced) was also strongly influenced by goldenrod genotype, but not spittlebug density (Fig. 4).

Genotype explained over 50% of the variation in reproductive success among ramets (Table 2), and there were significant differences in flower number between all possible genotype pairs except 85-3 and 85-5, and 85-6 and 85-16 (Fig. 4).

Offspring performance

Egg-to-adult survivorship of the stem gallers was most strongly influenced by goldenrod genotype (Fig. 5). In particular, stem gallers on genotype 85-16 had significantly lower survivorship than on the three other genotypes, and those on 85-5 had lower survivorship than on 85-3. Spittlebug density affected survivorship primarily through its interaction with goldenrod genotype: survivorship on 85-16 decreased ($F_{1,71}$=7.728, P=0.007), while on genotypes 85-3 and 85-6 ($F_{1,71}$=12.55, P=0.001 and $F_{1,71}$=10.29, P=0.002, respectively) it increased between ramets with 0 and 8 spittlebugs. These opposing patterns may explain why we found only a marginally significant (Fig. 5, P=0.060) spittlebug density main effect in the analysis of stem-galler egg-to-adult survivorship. We found the same qualitative pattern for the effect of goldenrod genotype ($F_{3,72}$=10.87, P<0.001), spittle-

Table 2 Summary of the effects of spittlebug density and goldenrod genotype on four performance characters of individual ramets. Numbers represent the proportion of variation explained by these two treatments in separate ANOVA's and asterisks denote level of significance. Percentages associated with biomass ratios are based on the means for all four plant structures (below-ground organs, stems, leaves, and flowers)

Ramet character	Percent variation explained by	
	Spittlebug density	Goldenrod genotype
Terminal height	10.5*	18.0**
Biomass ratios	8.0	62.2**
Flowering phenology	4.5	87.1**
Flower number	5.7	56.5**

*P<0.01, **P<0.001

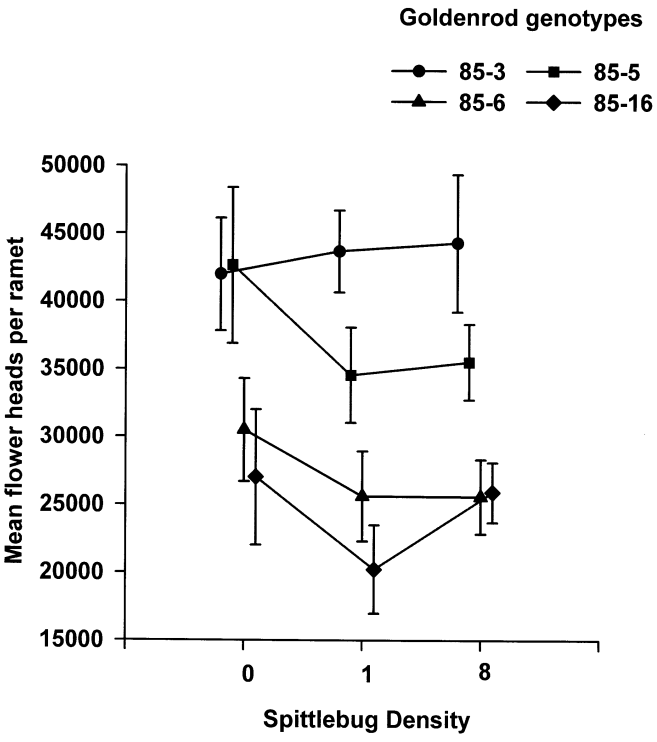

Fig. 4 Goldenrod ramet reproductive success (mean flower number ±SE) varied with respect to plant genotype ($F_{3,180}$=10.01, P<0.001), but not to spittlebug density ($F_{2,180}$=1.01, P=0.367). The analysis was based on the ANOVA model reported in Table 1 using natural-log transformed numbers. All genotypes differed significantly from each other (Tukey's HSD, P≤0.015), except for the pairs 85-3 and 85-5 and 85-6 and 85-16. No other factors had a significant effect on mean flower number

Table 3 The influence of spittlebug density and goldenrod genotype on the proportionate allocation of energy to below-ground organs (rhizomes and roots), stems, leaves and flowers. Separate ANOVAs were performed on each plant structure. In the complete model (see Table 1), the block effect and its interactions with other factors had no significant effect on allocation, therefore these sources of variation were omitted from the table below

Plant structure	Source of variation	*df*	MS	*F*	*P*
Below-ground organs	Spittlebug density	3	0.050	0.076	0.927
	Goldenrod genotype	2	0.684	1.043	0.375
	Spittlebug density×genotype	6	0.522	0.795	0.575
	Error	175	0.656		
Stems	Spittlebug density	3	0.249	1.169	0.313
	Goldenrod genotype	2	0.606	2.844	0.039
	Spittlebug density×genotype	6	0.215	1.011	0.420
	Error	175	0.213		
Leaves	Spittlebug density	3	0.091	0.679	0.509
	Goldenrod genotype	2	1.168	8.713	<0.001
	Spittlebug density×genotype	6	0.091	0.675	0.670
	Error	175	0.134		
Flowers	Spittlebug density	3	0.068	0.625	0.536
	Goldenrod genotype	2	1.519	13.997	<0.001
	Spittlebug density×genotype	6	0.047	0.434	0.855
	Error	175	0.109		

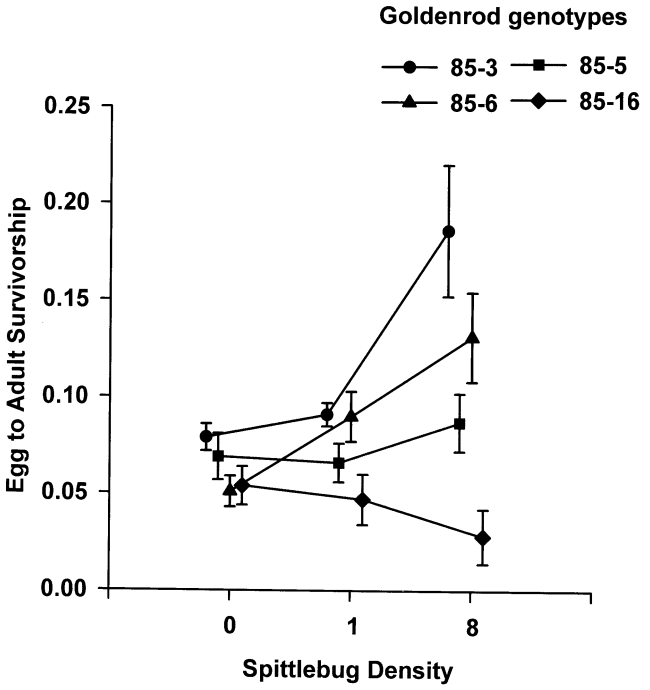

Fig. 5 Egg-to-adult survivorship (mean±SE). Based on ANOVA, there was a significant effect of goldenrod genotype ($F_{3,71}$=15.478, P<0.001) and genotype×spittlebug interaction ($F_{6,71}$=4.687, P=0.037) on survivorship, but not of spittlebug density on survivorship ($F_{2,71}$=2.93, P=0.060). Among genotypes, survivorship on 85-16 was significantly lower than on all other genotypes (Tukey's HSD, P≤0.003), and 85-5 was lower than 85-3 (P=0.020)

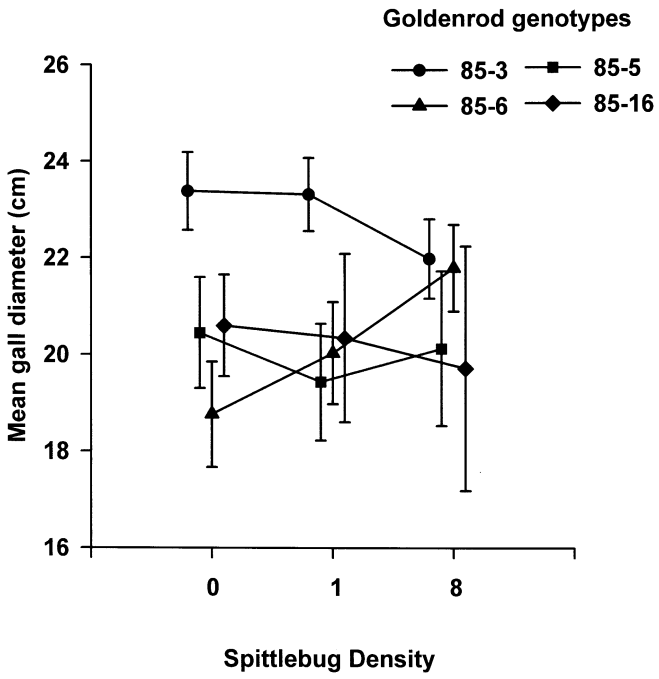

Fig. 6 Stem-galler mean gall size (±SE) in response to spittlebug density and goldenrod genotype. Plant genotype had a significant effect on performance ($F_{3,262}$=5.598, P=0.001), but there was no effect of spittlebugs or the interaction between genotypes and spittlebugs ($F_{2,262}$=0.002, P=0.998 and $F_{6,262}$=0.993, P=0.43, respectively). Among genotypes, 85-3 yielded significantly higher performance than any of the other genotypes (Tukey's HSD, P≤0.027)

bug density ($F_{2,72}$=0.10, P=0.902), and spittlebug density×goldenrod genotype ($F_{6,72}$=2.39, P=0.037) on the survivorship of offspring from the first appearance of the gall to adult eclosion.

Of the 280 ramets that produced a visible gall, 13.9% bore ≥2 galls (maximum 3 galls). The probability of occurrence of multiple-galled stems increased linearly with the number of ovipunctures (r^2=0.487, P=0.006). Greater numbers of ovipunctures were associated with spittlebug-free ramets (Fig. 2A); yet we could detect no difference in proportion of stems with multiple galls on spittlebug-free versus spittlebug-infested ramets (χ^2=3.20, P=0.202). Because there appeared to be little bias in the distribution of multiple galls among spittlebug treatments, the individually based performance measures (development time, gall diameter, thorax length, wing length, wing width, hind tibia length, biomass and egg load) were analyzed using all galls combined. We note, however, that an analysis using ramets with single galls only provided qualitatively similar results.

For both male and female stem gallers (analyzed separately), there was a significant positive correlation among all size-related performance variables (gall diameter, biomass, wing length, wing width, hind tibia length, and thorax length; Pearson's correlation, P≤0.05); with the exception of a marginally significant correlation between female gall diameter and tibia length (P=0.085). Stem-galler size characters were also positively correlated with female egg load (P≤0.035), but not with development time. Because gall diameter is well correlated with adult size and female fecundity, we use this one variable as a representative measure of stem-galler performance (see also Anderson et al. 1989; Craig et al. 1999a; M. Eubanks and W.G. Abrahamson, unpublished work). Based on an ANOVA, we found that goldenrod genotype was the only factor that affected gall size (Fig. 6). As with the survivorship data, genotype 85-3 yielded significantly higher stem-galler performance than all other genotypes. No other differences among genotypes were found.

Adult preference and offspring performance

There was very little evidence of a correlation between host preference (number of ovipunctures or the proportion of ramets ovipunctured) and offspring performance (gall size, egg-to-adult survivorship, or gall-to-adult survivorship) within any of the seven cages (experimental blocks). Of the 42 correlation analyses possible (7 blocks×6 preference-performance comparisons), there were only 2 in which the level of significance, P, was ≤0.05: a positive correlation between proportion of ramets ovipunctured and gall size for block 4 (r=0.81, P=0.01), and a negative correlation between the number of ovipunctures and egg-to-adult survivorship in block 3

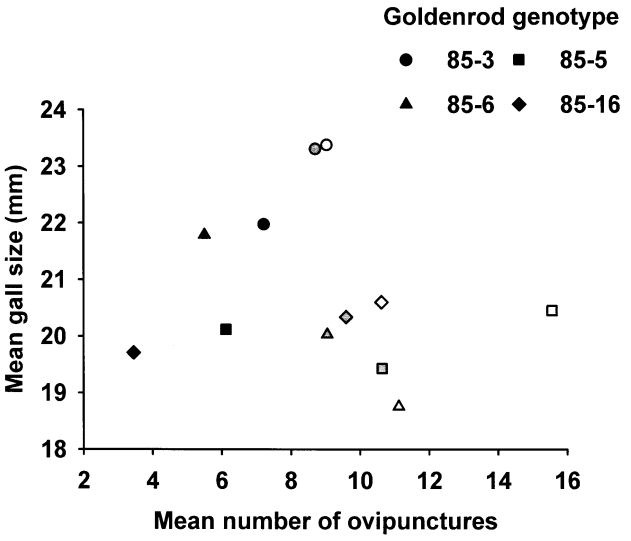

Fig. 7 Stem galler mean host preference and offspring performance among the 12 different spittlebug density×goldenrod genotype combinations. Genotypes are denoted by different symbols and spittlebug densities by degree of shading (*open symbols* 0, *lightly filled symbols* 1, *filled symbols* 8 bugs per ramet). No significant correlation between preference and performance was observed (r=0.152, P=0.638)

(r=–0.65, P=0.024). However, after adjusting for an inflated type I error rate brought about by multiple tests (using the Dunn-Šidák correction; Sokal and Rohlf 1995), none of these possible correlations were deemed significant. Pooling all seven cages did not change these results; no significant correlation was evident between any measure of preference and performance (P>0.05). Alternatively, we examined the relationship between mean preference and performance among the 12 spittlebug density×genotype combinations. From this viewpoint, there was again no apparent relationship between preference and performance (Fig. 7: only the relationship between ovipuncture number and gall size is presented; all other preference-performance measures showed the same nonsignificant pattern). There are several points to note from Fig. 7: (1) while ramets with high spittlebug densities were strongly avoided or overlooked, it was not because those ramets were of poor quality as a host; (2) even though clone 85-3 yielded highest stem-galler performance (both in terms of survivorship and gall size), its preference was intermediate among the other genotypes; and (3) the overall trend among these 12 treatment combinations was not significant (Fig. 7).

Discussion

Previous studies by Anderson et al. (1989), Horner and Abrahamson (1992), Craig et al. (1999a) and M. Eubanks and W.G. Abrahamson (unpublished work) showed that goldenrod genotype influences host-plant preference by *E. solidaginis*. We also found an effect of genotype on preference, but it was small relative to the effect that the meadow spittlebug, a common early-season herbivore of goldenrod, had on stem-galler preference. Spittlebugs caused a density-dependent reduction in the proportion of ramets ovipunctured and the number of ovipunctures per ramet by female stem gallers. However, the effects of spittlebug density on preference did not translate into a similar effect on stem-galler survivorship or gall size, our two measures of performance. In fact, the only effects of spittlebugs were manifest in the interaction between spittlebug density and goldenrod genotype on survivorship. The interaction was striking: survivorship decreased with increasing spittlebug density on one goldenrod genotype (85-16; Fig. 5), but increased on two others (85-3 and 85-6). This implies that at least for some genotypes in nature, there was evidence of competition between spittlebugs and stem gallers (see also Faeth 1986; Harrison and Karban 1986; Karban and Adler 1996). In a common-garden experiment using 16 goldenrod genotypes and three species of herbivores, the spittlebug, a leaf beetle (*Trirhabda* spp.) and an aphid (*U. nigrotuberculatum*.), we found similar effects on stem-galler preference and performance (J.T. Cronin and W.G. Abrahamson, unpublished work). The presence of all three herbivores significantly reduced preference, but had very little impact on performance.

Spittlebug nymphs directly and indirectly reduced stem-galler preference for goldenrod ramets. The indirect effects on preference arose because spittlebugs significantly reduced the growth rate and height of ramets at the time of exposure to adult stem gallers. Our results indicated that ramet height was the most important predictor of stem-galler preference: shorter ramets were much less preferred by stem gallers than taller ramets. This positive correlation between ramet height and oviposition preference by *E. solidaginis* was found previously with this system (e.g., Anderson et al. 1989; Walton et al. 1990; Craig et al. 1999a, 1999b) and a similar relationship has been observed in several other gall-inducing insects (e.g., Craig et al. 1986, 1989; Fondriest and Price 1996; Price et al. 1997). The direct effects of spittlebug density were revealed by ANOVA (Table 1), which partitioned the effects of ramet height (covariate) from the effects of spittlebug density alone (main effect) on the number of ovipunctures per ramet. After accounting for the effects of ramet height, we still detected an effect of spittlebug density on host preference; although the direct spittlebug effects were approximately 2.5 times less than the indirect effects (Table 1). This suggests that either the direct presence of spittlebugs and/or their traces (e.g., spittle, frass), or spittlebug-induced short-term changes in plant chemistry or morphology (leaves become twisted and distorted), also contributed to a reduction in the preference of goldenrod ramets occupied by spittlebugs. It remains unclear whether the lower preference for spittlebug-infested plants is a consequence of female stem gallers having a reduced encounter rate or a higher rejection rate of ramets with, versus without, spittlebugs. Casual observations (J.T. Cronin, personal observation) suggest the former scenario.

One likely explanation for why the spittlebug-induced reduction in preference did not translate into a corresponding reduction in performance is that the spittlebugs had very few long-term effects on the fitness of goldenrod ramets. Potted ramets showed visible signs of stress within 2 weeks after spittlebugs were released onto them (misshapen leaves and up to a 20% reduction in height), but by the end of the growing season, we found little evidence of the spittlebug's presence. There were no detectable effects of spittlebug density on ramet flower production, flower phenology, or biomass ratios. Even the differences in ramet height had abated over the season, resulting in only ≈3–4% difference in height between ramets with and without spittlebugs.

The general lack of a spittlebug effect on goldenrod ramet fitness contradicts the findings of Meyer and Whitlow (1992), Meyer (1993), and Meyer and Root (1993). In their studies, spittlebugs had a strong negative effect on goldenrod growth rates, biomass allocation, photosynthetic rates, and seed production. The deviation in our studies is probably due to the difference in range of spittlebug densities used. Densities in these other studies ranged from 2 to 30 (depending on the study), although Meyer and Whitlow (1992) point out that densities of 20 and above rarely occurred in nature. We used lower densities because we wanted our range to be centered around the natural mean. Field estimates of spittlebug densities during the year of this study averaged 2.3±0.3 (range 0–14, and heavily skewed to the right; J. Cronin, unpublished work).

Finally, we note that our measure of stem galler egg-to-adult survivorship excluded the effects of natural enemies and competitors that would have been otherwise present in nature. Certainly, these factors would lower survivorship rates in the field, but the important question is whether natural enemies or potential competitors would interact with goldenrod genotypes to affect stem-galler survivorship rates. If so, our conclusions about the effects of spittlebugs and goldenrod genotypes on survivorship in the greenhouse may be inapplicable to field situations. To address this problem, we (J.T. Cronin and W.G. Abrahamson, unpublished work) released stem gallers into an outdoor garden consisting of multiple goldenrod genotypes that were infested with several dominant goldenrod herbivores (including spittlebugs). While stem galler egg-to-adult survivorship was lower in the garden than in the greenhouse, mortality from natural enemies (*Eurytoma* parasitoids and a mordellid beetle) and competitors did not vary significantly among goldenrod genotypes. This suggests that the inclusion of field-based sources of mortality would likely not alter the conclusions drawn from the present study.

Absence of a preference-performance correlation

Intuitively, natural selection should favor the evolution of a 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). In this study, we found a strong preference for spittlebug-free ramets, but these ramets did not consistently yield higher offspring performance than ramets infested with spittlebugs. On the contrary, it is possible that by more strongly aggregating their eggs on uninfested ramets (1.1 and 1.5 times as many eggs as in the low and high spittlebug treatments, respectively), stem gallers may have actually decreased the survivorship of their offspring on those ramets. According to Hess et al. (1996) and Craig et al. (1999b), intraspecific competition among early instar larvae within the same bud is usually intense, with the death of all but one or two larvae a common outcome. Consequently, stem gallers within spittlebug-free ramets may suffer proportionately greater losses due to intraspecific competition than those within spittlebug-infested ramets. This may explain why there was a trend toward higher egg-to-adult survivorship in the 8- relative to the 0-spittlebug density treatments (for all genotypes except 85-16). Therefore, as a result of intraspecific competition among first instars, aggregating eggs onto spittlebug-free hosts may actually involve fitness costs that are ultimately higher than any potential costs associated with spittlebug-infested plants. We would predict that as the proportion of ramets with spittlebugs increases, stem-galler ovipositions will become increasingly more aggregated on spittlebug-free ramets; which in turn, will result in decreasing stem-galler performance on the preferred ramets. Given the relatively high mean number of eggs laid per ramet within some genotypes in nature (up to 5.3 eggs; Hess et al. 1996), this is likely to be a common occurrence whenever spittlebugs are prevalent. As a consequence, a tradeoff may be favored by natural selection in which lesser quality hosts are adopted in favor of reduced intraspecific competition (see Anderson et al. 1989).

It is also possible that the lack of a positive preference-performance correlation could have been due to a methodological constraint in our experimental design: inherent differences in ramet growth rate and height were reduced by selecting ramets of similar height at the start of the experiments (time of spittlebug introduction). If taller, faster-growing, ramets yield higher stem-galler performance, we may have reduced the variation in host quality to the point where ovipositing flies could not distinguish among ramets based upon these characters. Thus, a positive correlation may have been obscured. This is unlikely for two reasons. First, Walton et al. (1990) demonstrated that ramet height is not correlated with stem-galler performance. Second, in a common-garden study in which we (J.T. Cronin and W.G. Abrahamson, unpublished work) manipulated goldenrod genotype and herbivore abundances (including spittlebugs), but did not control for ramet heights, we also found no correlation between preference and performance (see also Anderson et al. 1989; Horner and Abrahamson 1992; Craig et al. 1999a).

Because there are few fitness benefits, and indeed there are likely costs associated with the aggregation of offspring onto spittlebug-free ramets, why do stem gallers show such a strong preference for them? Alternatively, why have the stem gallers not evolved to utilize spittlebug-infested plants? We offer a possible scenario that could answer these questions; one which takes into account only the indirect effects of spittlebugs on goldenrod preference (as stated earlier, direct effects are 2.5 times lower in magnitude). In many respects, the damage by spittlebugs to their host plant is similar to that caused by innumerable other plant stresses such as nutrient or water deficiencies (Horner and Abrahamson 1992; Meyer and Root 1993), presence of other herbivores (Hartnett and Abrahamson 1979; McBrien and Harmsen 1987; Meyer and Whitlow 1992; Pilson 1992; Meyer 1993; Meyer and Root 1993; Root 1996), and goldenrod competition with other species (Goldberg 1987). Each of these stresses can cause qualitatively similar changes in the plant's height, growth rate, branching pattern, photosynthetic rates, turgidity, and potentially other unexplored chemical and physiological changes. While countless differences may exist among the various types of stresses, the stem gallers may not have the ability to discriminate among them, especially when plant genotypes also differ in their responses to these stresses (see interactions in Figs. 2, 5). If some stresses negatively impact stem-galler performance while others do not (e.g., spittlebugs on genotype 85-16 vs. 85-3), an inability to discriminate among the many stress-plant genotype combinations can result in a poor correlation between host preference and offspring performance. This point has been previously raised by Fox and Lalonde (1993), Larsson and Ekbom (1995), and Abrahamson and Weis (1997).

Confronted with imperfect discriminatory ability, the stem-galler's assessment of a ramet may have to be based on a relatively simple set of cues that are indicative of a poor-quality (e.g., stressed) host plant (Fox and Lalonde 1993; Larsson and Ekbom 1995; Abrahamson and Weis 1997). One possible indicator might be short ramet height. In this case, all plants stressed in the same generalized way, whether those stresses are transient (and have little or no impact on stem-galler performance) or long-term (and negatively impact performance), would be rejected. This would serve to simplify the discrimination process (fewer recognizable categories) and be an effective (optimal) solution if the transient stresses are in the minority (Fox and Lalonde 1993; Larsson and Ekbom 1995). We agree with Larsson and Ekbom (1995) that "host confusion" would be particularly likely with gall insects, because of their generally short lifespans and intimate relationships with their host plants. To test the oviposition hypothesis we outlined above, we will need to determine the precise cues used in the selection process, the changes in the host-plant genotype induced by each stress, the effect of each stress on stem-galler preference and performance on each plant genotype, and the relative frequency of occurrence of each source of stress and genotype. This is a daunting task, but would provide valuable insight into the oviposition behavior of herbivores in general.

Goldenrod resistance plasticity

From the perspective of the plant, there was considerable plasticity within genotypes for their acceptability to stem-galler attack (preference) and suitability for offspring survivorship (performance). Furthermore, goldenrod genotypes displayed different degrees of plasticity which was indicated by a significant genotype×spittlebug (=genotype×environment) interaction (for example, compare the survivorship of stem gallers on genotype 85-3 and 85-16 with respect to spittlebug density in Fig. 5). The presence of genotype-specific differences in plasticity is thought to be a pre-requisite for the evolution of plasticity (Via and Lande 1985; Via 1987; Scheiner and Lyman 1989; Gotthard and Nylin 1995). To date, there have been only a few other studies that have found evidence for genetic variance in the norm of reaction to potential environmental stresses (e.g., Maddox and Cappuccino 1986; Horner and Abrahamson 1992; Pigliucci et al. 1995).

Within the spectrum of the environmental conditions provided in this study, no single goldenrod genotype was the most adaptive. For example, in the absence of spittlebugs, genotype 85-3 would be the least acceptable (i.e., most resistant) genotype to stem-galler oviposition (Fig. 2A), but would confer the highest survivorship, body size and fecundity (i.e., least resistant) to the stem galler's offspring (Figs. 5, 6). In the absence of spittlebugs, no one goldenrod genotype stands out as the most resistant to the stem galler. On the other hand, genotype 85-16, which is moderate in its resistance in the absence of spittlebugs, is the least acceptable and confers the lowest survivorship at high spittlebug densities. This resistance in the presence of spittlebugs is beneficial to the plants because even our highest density of spittlebugs had little impact on the plants, while only a single gall can detrimentally affect goldenrod growth and reproduction (Hartnett and Abrahamson 1979; Stinner and Abrahamson 1979; McCrea et al. 1985; Abrahamson and McCrea 1986). We conclude that unless spittlebug densities in nature are relatively constant from year to year, no single genotype will be most advantageous. Relative to the other major herbivores of goldenrod (Root and Cappuccino 1992), spittlebugs appear to be common and less variable from year to year; thus it is possible that genotypes such as 85-16 would be at some advantage. Furthermore, spittlebug-dependent variability among genotypes with regard to resistance to stem gallers can greatly amplify the difficulty in stem gallers evolving adaptations to certain genotypes (i.e., specializing on those genotypes).

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References

Abrahamson WG, McCrea KD (1986) Nutrient and biomass allocation in *Solidago altissima*: effects of two stem gallmakers, fertilization, and ramet isolation. Oecologia 68:174–180

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

Ahmed DD, Davidson RH (1950) Life history of the meadow spittlebug in Ohio. J Econ Entomol 43:905–908

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

Barker JSF (1992) Genetic variation in cactophilic *Drosophila* for oviposition on natural yeast substrates. Evolution 46:1070–1083

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

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

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

Chew FS (1977) Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31:568–579

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

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 (1999a) Oviposition preference and offspring performance of *Eurosta solidaginis* on genotypes of *Solidago altissima*. Oikos 86:119–128

Craig TP, Itami JK, Shantz C, Abrahamson WG, Horner J, Craig JV (1999b) The influence of host-plant genotype, plant growth, and intraspecific competition on oviposition preference and offspring performance in host races of *Eurosta solidaginis*. Ecol Entomol (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

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

Gotthard K Nylin S (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. Oikos 74:3–17

Hanks LM, Paine TD, Millar JG (1993) Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. Oecologia 95:22–29

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

How ST, Abrahamson WG, Craig TP (1993) Role of host plant phenology in host use by *Eurosta solidaginis* (Diptera: Tephritidae) on *Solidago* (Compositae). Environ Entomol 22: 388–396

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 107:379–385

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

Lavigne R (1959) Biology of *Philaenus leucophtalmus* (L.), in Massachusetts. J Econ Entomol 52:904–907

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
McBrien HL, Harmsen R (1987) Growth response of goldenrod, *Solidago canadensis* (Asteraceae), to periodic defoliation. Can J Bot 65:1478–1481
McCrea KD, Abrahamson WG, Weis AE (1985) Goldenrod ball gall effects on *Solidago altissima*: C^{14} translocation and growth. Ecology 66:1902–1907
McMillin JD, Wagner MR (1997) Chronic defoliation impacts pine sawfly (Hymenoptera: Diprionidae) performance and host plant quality. Oikos 79:357–362
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
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
Moran N (1981) Intraspecific variability in herbivore performance and host quality: a field study of *Uroleucon caligatum* (Homoptera: Aphididae) and its *Solidago* hosts (Asteraceae). Ecol Entomol 6:301–306
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
Owen DF (1988) Native and alien plants in the diet of *Philaenus spumarius* (L.) (Homoptera: Cercopidae). Entomol Gaz 39: 327–328
Pigliucci M, Whitton J, Schlichting CD (1995) Reaction norms of *Arabidopsis*. I. Plasticity of characters and correlations across water, nutrient and light gradients. J Evol Biol 8:421–438
Pilson D (1992) Aphid distribution and the evolution of goldenrod resistance. Evolution 46:1358–1372
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
Rhoades DF, Cates RG (1976) Toward a general theory of plant anti-herbivore theory. Rec Adv Phytochem 10:168–213
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). Ann 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
Singer MC (1986) The definition and measurement of oviposition preference in plant-feeding insects. In: Miller J, Miller TA (eds) Insect-plant interactions. Springer, Berlin Heidelberg New York, pp 65–94
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
Stinner BR, Abrahamson WG (1979) Energetics of the *Solidago canadensis*-stem gall insect parasitoid guild interaction. Ecology 60:918–926
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
Uhler LD (1951) Biology and ecology of the goldenrod gall fly, *Eurosta solidaginis* (Fitch). Memoir 300:1–51
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
Weaver CR, King DR (1954) Meadow spittlebug. Res Bull Ohio Agric Exp Stat 741
Whittaker JB (1973) Density regulation in a population of *Philaenus spumarius* (L.) (Homoptera: Cercopidae). J Anim Ecol 42:163–172
Wiegert RG (1964) Population energetics of meadow spittlebugs (*Philaenus spumarius* L.) as affected by migration and habitat. Ecol Mongr 34:217–241
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
Wiklund C (1984) Egg laying patterns in butterflies in relation to their phenology and the visual apparency of their host plants. Oecologia 63:23–29