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Temporal variation in herbivore host-plant preference and performance: constraints on host-plant adaptation

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Temporal variation in the acceptability or suitability of plant genotypes to an herbivore has seldom been considered as a possible constraint limiting the adaptation of herbivores to particular plant genotypes, or the occurrence of a positive correlation between host-plant preference and offspring performance. In this study, we used data spanning 12 yr from the same 20 clones of goldenrod (*Solidago altissima*) to examine the temporal variation in oviposition preference and offspring performance of a stem-galling fly, *Eurosta solidaginis*. We found that the stem galler's preference for, or performance on, the different clones was uncorrelated between years of this study. Furthermore, we found that the relative rankings of clones changed by an average of 31% between successive years. We suggest that these consistently high year-to-year fluctuations in preference and performance by *E. solidaginis* are likely due to environmental factors (e.g., water and nutrient levels, or abundance of interspecific herbivores) that fluctuate over time and are known to differentially affect the acceptability and suitability of clones to herbivores; i.e., genotype × environment interactions. These results are significant because temporal fluctuations in host-plant preference and performance are likely to favor a more generalized diet by herbivorous insects.

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Genotypes or clones of the same plant species can have drastically different effects on the fitness of herbivorous insects (Fritz and Simms 1992). As a consequence, natural selection may be sufficiently strong to favor the evolution of herbivore adaptations that are specific to certain plant genotypes or clones (for review, see Mopper 1996). Adaptations within an herbivore population to specific plant genotypes have been detected in a number of studies (e.g., Edmunds and Alstad 1978, McPheron et al. 1988, Karban 1989), including those involving mobile herbivores (Mopper et al. 1995, Stiling and Rossi 1997). The evolution of these adaptations can lead to the genetic substructuring of populations, i.e., deme formation, and may be the harbinger of macroevolutionary events such as sympatric and allopatric speciation and the diversification of herbivore taxa (Mitter et al. 1991, Mopper 1996, Farrell and Mitter 1998).

In situations where plant genotypes differ significantly in their suitability for herbivore growth, reproduction or survivorship, one adaptation that is expected to arise is a preference by ovipositing female herbivores for the plant genotypes that confer the highest fitness to their offspring (Thompson 1988). The positive correlation that should result between oviposition preference and offspring performance would serve to reinforce the reproductive isolation of herbivores associated with those most suitable plant genotypes. However, there are numerous possible constraints limiting the adaptation of herbivores to particular plant genotypes or the oc-

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currence of a positive correlation between preference and performance (Thompson 1988, 1996, Joshi and Thompson 1995, Mopper 1996). One constraint of potential significance is year-to-year variation in the relative preference and performance rankings of host-plant genotypes (here, ranking is the ordering of plant genotypes from the best to the worst in terms of herbivore preference or performance). Such temporal fluctuations in selection intensities are likely to favor a more generalized diet and a weak correlation between preference and performance (Futuyma 1976, Thompson 1988). Temporal variation in rankings is likely to arise because of annual or seasonal changes in the relative abundance, predictability, apparency or chemical composition of host-plant genotypes (Futuyma 1976, Thompson 1988, Chew and Courtney 1991). In particular, rank changes over time could be due to environmental factors or ontogenetic changes in the plant (for long-lived genotypes) that have differential effects among plant genotypes; i.e., genotype × environment or genotype × ontogenetic interactions. For example, some genotypes may be more resistant to attack by herbivores in dry years and other genotypes more resistant in wet years. The rankings of these plants would reverse between wet and dry years. In support of the latter possibility, genetic × environment interactions on herbivore preference or performance have been commonly reported in the literature (Via and Lande 1985, Weis 1992). To our knowledge, few studies have quantified temporal variations in the preference and performance rankings of host plants (e.g., Maddox and Root 1987, Fritz and Price 1988, Craig et al. 1999), and none for any significant duration of time; i.e., greater than a few years.

Herbivores with sedentary offspring are likely to be under the greatest pressure to evolve a tight linkage between oviposition preference and offspring performance (Craig et al. 1989, Larsson and Ekbom 1995, Abrahamson and Weis 1997), yet for the goldenrod stem galler, *Eurosta solidaginis* (Diptera: Tephritidae), a positive preference-performance correlation among goldenrod clones has generally not been detected (Horner and Abrahamson 1992, 1999, Craig et al. 1999, Cronin and Abrahamson 1999, 2001; but see Anderson et al. 1989). Temporal fluctuations in *Eurosta*'s rank preference and performance among the same collection of goldenrod clones have not been fully considered as a possible constraint on host-plant adaptation and the correlation between preference and performance. McCrea and Abrahamson (1987) have noted that *Eurosta* galling rates were strongly correlated among years in their three-year field study. However, Craig et al. (1999) reported no correlation in oviposition preference or offspring performance between two successive years or between two studies conducted six years apart but using the same goldenrod clones in a common garden.

Herein, we use 12 yr of data from the same long-lived goldenrod clones to examine the temporal variation in *Eurosta* oviposition preference and offspring performance. To our knowledge, this represents the first study to quantify the magnitude and address the possible causes and consequences of temporal variations in oviposition preference and offspring performance. We argue that substantial temporal variation in the relative preference and performance ranks among goldenrod clones is likely to have arisen as a consequence of genotype × environment or genotype × ontogenetic interactions that can affect the acceptability or suitability of long-lived or clonally growing plant species to their herbivores. We further argue that these large temporal fluctuations in rank preference and performance likely have constrained the evolution of a positive preference-performance correlation and limit the ability of this insect to locally adapt to specific goldenrod clones.

Materials and methods

Eurosta solidaginis is widely distributed throughout North America, producing galls on goldenrods (*Solidago*; Compositae) in all southern Canadian Provinces and in the continental United States except the Southwest (Uhler 1951, Foote et al. 1993, Abrahamson and Weis 1997). In the mid-Atlantic region of the United States, adult stem gallers eclose around mid- to late-May. Females are known to be very selective and oviposit into the terminal buds of genetically susceptible, tall or herbivore-free ramets of their primary host, tall goldenrod (*S. altissima*) (Anderson et al. 1989, Craig et al. 1999, Cronin and Abrahamson 1999, 2001). Within three weeks, the stem tissue shows signs of swelling and by mid-July the galls containing a single larva reach full size and are spheroid in shape. Larvae overwinter within the galls of senescent goldenrod ramets, then pupate and eclose the following spring.

Stem galler oviposition preference and offspring performance reported here are based on four different studies of the same 20 goldenrod clones. The first study was conducted in the field in 1985 by Anderson et al. (1989). All subsequent studies were performed over different years in the same common garden: 1990 and 1991 by Craig et al. (1999), 1995 by Cronin and Abrahamson (2001), and 1996 by us and reported for the first time in this paper. The measures of preference and performance were identical among studies and are reported on a per-plot (patch) basis. Stem galler oviposition preference was measured as the proportion of ramets ovipunctured per patch of a single clone. This metric has been commonly used in previous studies with this system (e.g., Anderson et al. 1989, Craig et al. 1999, Cronin and Abrahamson 1999, 2001). The measure of performance that was used was the proportion of plants that were ovipunctured that resulted in the formation of a mature gall. It accounts for the suitability of the host plant for the survival and development of the stem-galling fly (Anderson et al. 1989, Craig et al. 1999, Cronin and Abrahamson 1999).

Preference and performance measured on a per-ramet basis were available only from the 1995 and 1996 study years (Cronin and Abrahamson 2001, unpubl.). In those studies, we found that the effects of goldenrod clone and interspecific herbivores (1995 only) on preference or performance were the same whether analyzed on a per-ramet or per-plot basis. We therefore feel justified in the use of the plot-level measures of preference and performance outlined above.

In the study by Anderson et al. (1989), 38 goldenrod clones (> 300 ramets each) were located and marked approximately 6 km northeast of Bucknell University in Northumberland County, Pennsylvania, USA. Proportion of ramets ovipunctured by naturally occurring stem-galler females and the probability of gall formation were determined during that same year from a sample of 100 ramets per clone (1985). No information was available on the incidence of other herbivores that might affect stem-galler oviposition preference or offspring performance. Of the clones that were used by Anderson et al. (1989) a subset of 20 clones (1, 3, 4, 5, 6, 7, 8, 10, 13, 14, 15, 16, 17, 19, 24, 29, 33, 37, 38, and 40) were planted into a garden at Bucknell University by Craig et al. (1999) in 1989. Rhizomes from each genotype were planted in 1-m^2 plots that were arranged in four rows of 20 plots each. All 20 clones were represented within each row. 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 dehiscence. In 1990, Craig et al. (1999) stocked the garden with 320 adult stem gallers that were collected from the same general area from which the goldenrod genotypes were obtained. To enhance attack rates, Craig et al. (1999) enclosed a portion of the adult stem gallers in large cages over the garden. The use of the cages did not result in attack rates or survival rates that differed from those in the field study by Anderson et al. (1989). In 1991, Craig et al. (1999) repeated the same procedure, but also supplemented the garden with 750 galls collected from the previous year. Ramet numbers per plot were 17.4 ± 0.8 (mean ± se) for 1990 and 34.7 ± 2.4 for 1991. Over both years, few other herbivore species were present in the garden (T. P. Craig and W. G. Abrahamson pers. obs.).

The garden was subsequently used by Cronin and Abrahamson (2001) in 1995 to measure the change in stem-galler preference and performance in response to experimentally manipulated levels of several other goldenrod herbivores. Stem gallers and other herbivores were collected from the same location as the goldenrod clones, and were evenly distributed among plots (20 galls, 50 spittlebugs, 74 leaf beetle larvae and 140 aphids per plot). Thus, the effects of other herbivores (discounting possible genotype × environment interactions; see Cronin and Abrahamson 1999) on the rank ordering of host-plant clones by the stem galler should have been minimal. In the year following the herbivore introductions (1996), herbivore loads across plots fell to nominal levels. Cronin and Abrahamson (unpubl.) again stocked the garden with 20 galls per plot and subsequently recorded stem-galler preference and performance. Ramet densities per plot in these last two years averaged 58.9 ± 3.5 in 1995 and 60.3 ± 3.1 in 1996.

Overall, each of these separate studies described above generally revealed significant differences within years in host-plant preference and offspring performance among the 20 clones.

If the goldenrod clones remained unchanged with regard to their acceptability for oviposition or suitability for the development of stem-galler offspring, we would expect to find a positive correlation between years in both oviposition preference and offspring performance. Also, we may expect natural selection to have favored a positive correlation between preference and performance within, as well as between, years (see Thompson 1988). We therefore determined the correlation between all possible pairwise combinations of preferences and performances among the five separate studies spanning 12 yr. Because the mean and range of our preference and performance measures can vary among years as a result of differences in the density of ovipositing females (resulting in higher mean ovipuncture rates per plot) and larval offspring (resulting in greater intraspecific competition and lower survivorship), we standardized our measures for comparisons across years by computing their relative ranks. Within each year of the study, the clone with the highest preference was given a value of 1, the next highest a value of 2, and so on. A similar procedure was used to rank performances among clones. Clones that were tied shared the same average rank. We then used a Spearman's rank test (Sokal and Rohlf 1995) to assess whether there was a correlation among years in the preference or performance among clones (e.g., is the same clone always the most preferred among years), and within and among years between preference and performance.

Results

For the five different data sets that spanned a period of 12 yr, there was little evidence that preference or performance rankings of different goldenrod clones were consistent among years (Table 1). Even between succes-

Table 1. Spearman's rank correlation matrix for measurements of stem-galler oviposition preference and offspring performance among five different years. The sequential Bonferroni method (Rice 1989) was used to establish an overall error rate of 0.05 for each of three groups of pairwise correlations: preference-preference, performance-performance, and preference-performance.

		Preference					Performance				
		1985	1990	1991	1995	1996	1985	1990	1991	1995	1996
Preference	1985	1.000									
	1990	−0.063	1.000								
	1991	0.295	0.211	1.000							
	1995	−0.095	0.286	0.097	1.000						
	1996	−0.512*	0.177	−0.083	0.379	1.000					
Performance	1985	−0.126	−0.343	−0.766§	−0.359	−0.243	1.000				
	1990	−0.109	−0.052	−0.227	−0.047	0.181	0.237	1.000			
	1991	0.291	−0.592*	−0.086	−0.054	−0.047	0.168	0.296	1.000		
	1995	−0.306	−0.184	−0.354	−0.480	0.016	0.312	0.140	0.339	1.000	
	1996	−0.207	−0.460	−0.030	−0.424	0.108	0.074	−0.223	0.049	0.371	1.000

* $0.05 > P > 0.01$.
§ $P < 0.001$.

sive years in the common garden (1990–1991), where conditions and the experimental design were nearly identical, we were unable to detect a significant correlation in either of these two variables. Preference-performance correlations were also nonexistent, both within and among study years, with the exception of a single negative correlation between stem-galler performance in 1985 and oviposition preference in 1991 (Fig. 1, Table 1).

Despite the scarcity of significant correlations in Table 1, there do appear to be significant patterns with regard to the sign (positive or negative) of the correlations. Among the 10 possible inter-year comparisons of performance, 90% of those correlations exhibited a positive tendency (Table 2). This high frequency of positive correlations would not be expected by chance alone (Table 2), suggesting the possibility of an overall weak positive association among years in the suitability of goldenrod clones for stem-galler offspring survivorship. For preferences among years, we found no tendency for more positive or negative correlations. Finally, 84% of the 25 correlations between preference and performance were negative; a frequency that is not likely to have occurred by chance alone (Table 2).

From year to year there were significant changes in stem-galler rank preference and performance among the goldenrod clones (Fig. 1). In fact, between consecutive years of study, each goldenrod clone moved up or down in rank position by an average of 5.5 places out of 17–20 possible genotypes (a 31% change in rank; Table 3). While it would be meaningless to examine changes in raw preference for clones over time, because the magnitude of our measure of preference is so directly influenced by the abundance of stem gallers, raw performance (actual proportion of ovipunctured ramets that produced a gall) is less likely to be affected by density (Cronin and Abrahamson 1999). Between successive years, raw performance changed within a clone by an average of 0.21, which equates to a change in performance of 82% relative to the first year of the sequence pair. These results indicate that there are much more dramatic temporal changes in the stem-galler's response to a clone than are evident in the analyses of rank data. Although rank data are conservative in revealing the magnitude of change over time, we restrict subsequent analyses of our data to ranks to allow inclusion of the preference data.

In accordance with results from Table 1, performance rankings changed less between years than preference rankings (29% versus 34%; Table 3), but this difference was not significant (paired *t*-test, $t = 2.15$, df = 3, $P = 0.121$). Consecutive years (1990–1991, 1995–1996) had a mean percentage change in rank of 28%, which was not significantly lower than the 35% rank change between non-consecutive years (1985–1990, 1991–1995) ($t = 1.89$, df = 6, $P = 0.108$). There is,

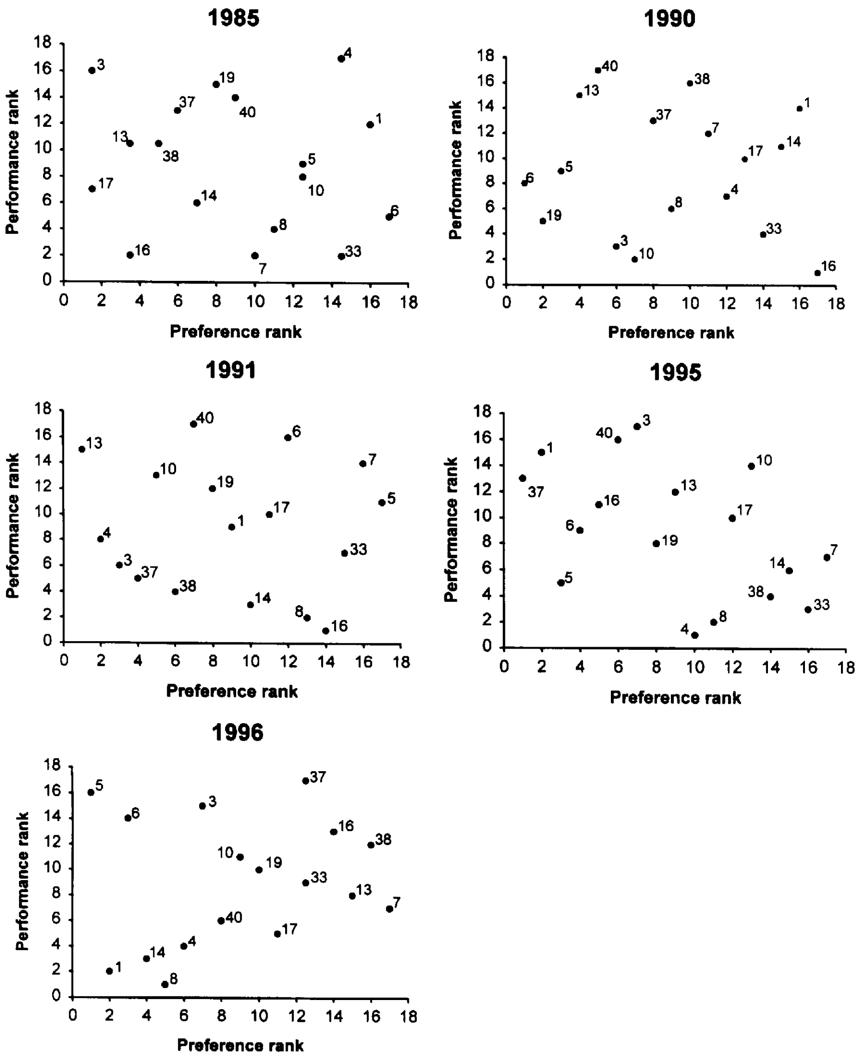

Fig. 1. The relationship between rank preference and rank performance of the goldenrod stem galler for different clones of *Solidago altissima* from five different years of study. Numbers indicate clone identification and only those clones that were common to all years were included. Correlation statistics are reported in Table 1.

therefore, no evidence to suggest that if our five years of preference-performance data were obtained from consecutive years, we would have significantly improved our chances of detecting positive correlations among years. In addition, there was no indication that the percentage rank change between 1985 and 1990 (when goldenrod genotypes were transferred from the field to the common garden; 36% change) or 1995 and 1996 (the garden with and without herbivores; 25%) was markedly different in magnitude from 1990 to 1991 (identical conditions in the garden; 32%); although, there were insufficient data to perform statistical tests. Finally, the magnitudes of the changes in rank performance above are probably an underestimate because the majority of data were collected from a garden that was designed to minimize differences in the environmental background.

Discussion

The evolution of herbivore adaptations that are specific to certain host-plant genotypes, particularly a preference by ovipositing female herbivores for plant genotypes that confer the highest fitness to their offspring, should be facilitated by temporal constancy in the relative suitability of host-plant genotypes to the herbivores (Thompson 1988, Mopper 1996). Across the 12-yr span of this study, we found very little evidence that goldenrod clones remained unchanged in terms of their relative acceptability (measured in terms of herbivore preference) or suitability (in terms of herbivore performance) to the stem galler: rank oviposition preference or offspring performance among goldenrod clones was uncorrelated between years. These results contradict the three-year studies by McCrea and Abrahamson (1987) and Maddox and Root (1987), which detected significant positive correlations between years in the galling rate per goldenrod clone. We do not have an explanation for the difference between their two studies and ours, but do note that McCrea and Abrahamson's (1987) and Maddox and Root's (1987) choice of measure, galling rate, is a composite of traits influencing both host preference and offspring performance.

Interestingly, we found a high frequency (84%) of negative correlations between host-plant preference and offspring performance within and between years, which runs contrary to the predictions of natural selection theory (Thompson 1988). We have argued previously (Cronin and Abrahamson 1999, 2001) that this result may be expected in light of the oviposition behavior of the stem galler. Adult female stem gallers are known to exhibit strong preferences for certain goldenrod clones and for tall, fast-growing, well-watered, herbivore-free ramets and those growing in nutrient-rich soils (Anderson et al. 1989, Walton et al. 1990, Horner and Abrahamson 1992, 1999, Cronin and Abrahamson 1999, 2001). Because female stem gallers do not discriminate amongst or avoid previously ovipunctured ramets (Craig et al. 2000), eggs can become strongly aggregated within the preferred ramets. Intraspecific competition among larvae within a ramet is known to be intense and can lead to drastic reductions in stem-galler survivorship and body size (Hess et al. 1996, Craig et al. 2000). As a consequence, as stem-galler density increases, we would expect stem-galler eggs to become increasingly more aggregated in those preferred ramets and the performance of the larvae to exhibit a concomitant decline (i.e., a negative preference-performance correlation; see Valladares and Lawton 1991, Cronin and Abrahamson 1999, 2001, Yamaga and Ohgushi 1999). If intraspecific competition among stem gallers affects the preference-performance relationship, we would predict that as the proportion of ovipunctured ramets per plot (a likely correlate of female stem galler density) increased among years, the slope of the regression line for the relationship between preference and performance would become more negative. Among the five years, we could detect no negative correlation between the mean proportion of ramets ovipunctured per plot and the magnitude of the slope of the preference-performance relationship ($R = 0.335$, df $= 5$, $P = 0.307$). An increase in statistical power (i.e., more years as data points) or higher stem-galler densities may have been necessary to detect a significant effect across years. In any event, this result suggests that the differences in density of stem gallers among years, due to differences in numbers released and those occurring naturally, did not significantly affect the preference-performance correlations reported in Table 1.

The magnitude of change in the rankings of goldenrod clones by the stem gallers was consistently high between years, averaging 34% in oviposition preference and 29% in offspring performance. What may be responsible for the consistently high change in ranking of goldenrod clones among years? Natural selection acting on the population of stem gallers over time cannot explain the temporal change in rank preference or performance during the 12-yr span of this study. Stem gallers were removed from the garden at the end of each year, and replenished the next year from galls harvested from distant sites; thus, there was no opportunity for the stem gallers to adapt over time to any particular garden condition or goldenrod clone. It is also unlikely that stochastic effects (i.e., genetic drift) associated with drawing a small number of gall insects from the local population and introducing them into the outdoor garden could explain the temporal fluctuations. Each year, the garden was stocked with a large number of stem gallers (320–1600 individual adults or larvae in galls) that were drawn from numerous sites adjacent to an 8-km stretch of road.

Temporal fluctuations in preference and performance rankings may have resulted from genotype × environment or genotype × ontogenetic interactions. Environmental factors such as crowding, nutrient and water levels, shading and herbivore loads can affect the acceptability and suitability of the host plant to the stem galler (Anderson et al. 1989, Walton et al. 1990, Horner and Abrahamson 1992, 1999, Cronin and Abrahamson 1999, 2001) and likely vary from year to year (see Sumerford et al. 1999). Provided that goldenrod clones differ in their response to these environmental fluctuations (i.e., the existence of genetic variation in reaction norms; Via and Lande 1985, Weis 1992, Gotthard and Nylin 1995, Abrahamson and Weis 1997) changes in preference or performance ranks among years would be expected. Several studies with goldenrods have detected

Table 2. Total number of positive and negative correlations for three categories of paired data: preference-preference, performance-performance and preference-performance correlations across studies (see Table 1). A *G*-test with William's correction (Sokal and Rohlf 1995) was used to determine if the occurrence of positive and negative correlations differed from an expected frequency of 0.50.

Category	Number of correlations	Positive correlations	Negative correlations	*G*-statistic	*P*
Preference-preference	10	6	4	0.384	0.536
Performance-performance	10	9	1	7.011	0.008
Preference-performance	25	4	21	12.424	0.004

Table 3. Mean and percentage change in preference and performance between successive years of study. For each goldenrod clone, the change in preference or performance rank was determined as the absolute difference in rank between two time periods. Similarly, change in raw performance on a clone (proportion of ovipunctured ramets that produced a visible gall) was determined by the absolute difference in performance between two years. Mean change in rank or raw performance was then determined as the average among the 17–20 clones. The percentage change in rank equals 100 × (mean rank/number of clones). The percentage change in raw performance is the average among clones of 100 × (change in raw performance/performance in the first year).

Trait	Years	Mean change in rank	Percentage change in rank	Mean change in raw performance	Percentage change in raw performance
Oviposition preference	1985–1990	6.294	37.0	—	—
	1990–1991	6.059	35.6	—	—
	1991–1995	6.353	37.4	—	—
	1995–1996	4.850	24.3	—	—
Offspring performance	1985–1990	5.794	34.1	0.194	58.8
	1990–1991	4.912	29.0	0.123	104.0
	1991–1995	5.000	29.4	0.283	115.2
	1995–1996	5.000	25.0	0.224	50.7

significant goldenrod clone × environment interactions affecting stem-galler preference and performance. These involve significant interactions between goldenrod clones and water availability (Maddox and Cappuccino 1986), nutrient levels (Horner and Abrahamson 1992) and the frequency of occurrence of other species of herbivores (Cronin and Abrahamson 1999). Genetic variation in host-plant reaction norms has not been well studied, but there is growing evidence for its occurrence (Weis 1992, Abrahamson and Weis 1997).

Host-plant genotype × ontogenetic interactions may similarly lead to temporal fluctuations in host-plant preference and offspring performance ranks. Often as clonal species age, connections among ramets can disintegrate, somatic mutations accumulate, and the clone's growth, vigor, reproduction and ability to defend itself against herbivores can change significantly (e.g., Price 1989, Hanzawa and Kalisz 1993, Falinska 1995, Tuskan et al. 1996, Kearsley and Whitham 1998). Changes such as these can have a great impact on the acceptability or suitability of a clone to an herbivore (e.g., Raupp and Denno 1983, Fritz 1992). If these ontogenetic changes in the plant were clone specific we would expect that the rankings among clones would vary from year to year. For example, resistance to herbivore attack may decrease with age for some plant clones, but increase with age for other clones. Our goldenrod clones were planted at the same time and were therefore similar in ontogeny throughout this study. At this point in time, there is no information on how goldenrod ontogeny affects its acceptability or suitability to the stem galler, or whether these ontogenetic effects on herbivores differ among clones. We can only conclude that for clonal or long-lived plant species, preference and performance ranks may commonly vary temporally in nature as a result of the interaction between host-plant genetics and the environment, plant ontogeny, or a combination of the environment and plant ontogeny.

Differential performance of herbivores among host-plant genotypes is expected to favor the evolution of behaviors in the herbivore that lead to the choice of plant genotypes that confer high offspring fitness (Thompson 1988) and other traits that improve overall fitness on those particular genotypes (for recent review, see Mopper 1996). Directional natural selection leading to the adaptation of herbivores to high quality host genotypes is likely to be constrained by temporal fluctuations in rank preference and performance of the magnitude reported here (Futuyma 1976, Thompson 1988, Chew and Courtney 1991). The optimal evolutionary strategy under these circumstances may be the inclusion of a broad range of host-plant genotypes into the herbivore's diet (Futuyma 1976). If there are no trade-offs associated with a generalist lifestyle, as much of the empirical evidence would suggest (Jaenike 1990, Via 1990, Joshi and Thompson 1995, Fry 1996), we might also expect only a weak correlation between host-plant preference and offspring performance. The absence of a preference-performance correlation in *E. solidaginis* (e.g., Horner and Abrahamson 1992, 1999, Craig et al. 1999, Cronin and Abrahamson 1999, 2001) and in many other plant-herbivore systems (e.g., Karban and Courtney 1987, Courtney and Kibota 1990, Larsson et al. 1995) may be attributed to these temporal changes in the host plant. Studies of the long-term temporal constancy of host-plant preference and performance characters, and the interactions between environmental and ontogenetic factors and plant genotypes would help bring into clearer focus the constraints on the evolution of diet breadth in herbivorous insects.

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