



## The influence of oviposition phenology on survival in host races of *Eurosta solidaginis*

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### Abstract

Phenological differences between host plants can contribute to allochronic isolation of host races of phytophagous insects. Host races of the gallmaking fly, *Eurosta solidaginis*, that live on different species of goldenrod (*Solidago altissima* and *S. gigantea*) exhibit different emergence phenologies. These differences could result from adaptation to corresponding phenological differences between the hosts in periods of optimal suitability for gall formation and survival to adulthood. In order to test this, some flies of each host race were allowed to emerge naturally while the emergence times of others were manipulated to correspond to the emergence and oviposition periods of the other host race. Percent gall formation and survival to adulthood were examined for three oviposition periods: the peak time of emergence and oviposition of the earlier-emerging host race (that from *S. gigantea*), that of the later-emerging host race (that from *S. altissima*), and a week after the peak emergence of the host race from *S. altissima*. Flies of both host races were allowed to ovipuncture plants of the appropriate species during each of these periods. Plant relative growth rates were measured during each of these periods. The experiment was repeated twice over a two-year period. Relative growth rates of both host species were highest during the earliest oviposition period (the period during which the host race from *S. gigantea* normally emerges). Percent gall formation was significantly correlated with plant relative growth rate, but the coefficient of determination was low. In both years of the study, percent gall formation of both host races was highest during the earliest oviposition period (the period during which the host race from *S. gigantea* normally oviposits). Likewise, percent survival to adulthood in both host races was highest during the earliest oviposition period. There was no significant effect of oviposition period on the percent of larval death due to parasitism by *Eurytoma gigantea* or predation by *Mordellistena unicolor*. These results suggest that the host race from *S. altissima* does not emerge at the time that its host is optimally suited for gall formation or survival to adulthood. Therefore, differences in emergence phenologies do not appear to be due to corresponding phenological differences between the host species in suitability for gall formation or survival to adulthood.

### Introduction

The expansion to new host species has been suggested to be an important mechanism leading to the proliferation of species in parasites, including phytophagous insects (Bush, 1969, 1975; Diehl & Bush, 1984; Bush & Howard, 1986). In order for the populations to develop into two species rather than a single species with an expanded host range, the expansion must be followed by reproductive isolation of the races utilizing the different hosts (Bush, 1975;

Diehl & Bush, 1984, 1989; Bush & Howard, 1986). A number of factors could contribute to this reproductive isolation, including adaptation to phenological differences in the two hosts that result in temporal isolation in emergence and mating periods (Bush, 1975; Wood, 1980; Wood & Guttman, 1982; Wood & Keese, 1990; reviewed in Tauber & Tauber, 1989). Phenological differences in host-plant species may include differences in their periods of growth or suitability for attack by phytophagous insects. These types of differences in host-plant phenologies have in fact been

shown to be related to reproductive isolation in some phytophagous insects (e.g., Wood, 1980; Wood & Guttman, 1982; Wood & Keese, 1990; Komatsu & Akimoto, 1995). Furthermore, differences in duration of diapause and the concomitant effects on emergence phenology have also been shown to influence reproductive isolation and genetic differentiation in other species of phytophagous insects (e.g., *Rhagoletis*; Feder et al., 1997a,b, 1998). Nevertheless, the prevalence and importance of these differences in contributing to reproductive isolation has not been widely studied among species of phytophagous insects.

The goldenrod ball gallmaker, *Eurosta solidaginis* (Diptera: Tephritidae), is a narrowly oligophagous insect that occurs on two species of goldenrod, *Solidago altissima* and *S. gigantea*. The populations on the two host plants have been identified as host races (*sensu* Bush, 1975; Craig et al., 1993). It has been hypothesized, based on allozyme and mitochondrial DNA data, that *S. altissima* was the original host (Waring et al., 1990; Brown et al., 1996). Although capable of interbreeding and producing viable offspring (Craig et al., 1994, 1997; Itami et al., 1998), the insects on these two host plants are known to be partially genetically differentiated from each other, even when they occur sympatrically (Waring et al., 1990; Brown et al., 1996; Itami et al., 1998). Several factors, including strong preference for mating on their natal host and different patterns of emergence of adult insects, contribute to the partial reproductive isolation between these host races (Craig et al., 1993, 1994; Itami et al., 1998). Adult *Eurosta* of the race from *S. gigantea* emerge, on average, about seven days earlier than the race from *S. altissima*, but there is some annual variation in the emergence phenologies (Craig et al., 1993; Itami et al., 1998).

Although differences in emergence are influenced by both genetic and environmental factors (Abrahamson et al., 1994), the ultimate factors that have brought about these differences are not known. We hypothesized that the host plants differ in their optimal periods of suitability for attack (e.g., Bush, 1969). In this study, we tested the hypothesis that each host race emerges during the period when its host plant is optimally suited for gall formation and survival to adulthood. In addition, we examined the role of host growth rate in these differences. Growth rate may be associated with overall plant vigor and with suitability of the plant for survival of herbivore offspring (Price et al., 1987). Furthermore, oviposition preference in *E. solidaginis* has been found to be significantly corre-

lated with growth rate (Horner & Abrahamson, 1992). Therefore, we further hypothesized that larval success was related to plant growth rate, and that growth rate in the two host plants would be maximal during the period in which they are normally attacked. If these hypotheses were correct, we would expect each host race to emerge during the period that their host plant exhibited the highest growth rate and was most suitable for gall formation and survival to adulthood. Finally, we examined differences in rates of parasitoid attack and predation on larvae as factors that might influence emergence patterns.

## Materials and methods

*Natural history.* *Solidago altissima* and *S. gigantea* are perennial clonal herbs common in disturbed areas in the eastern and northern United States. Adult *Eurosta solidaginis*, which do not feed, emerge in early spring and have an adult lifespan of approximately five days (Uhler, 1951). After mating, females oviposit into the apical bud of their natal host species. When females insert their ovipositor into a bud, they leave a visible scar (an 'ovipuncture'). Females do not oviposit every time they ovipuncture a bud, and it is not possible to determine whether oviposition has occurred without destructively sampling the bud. However, in a separate study we have shown that a female will oviposit an average of one egg during each oviposition bout, regardless of the number of ovipunctures (Craig et al., in press). Therefore, we assumed that each ovipunctured stem contained at least one egg. Larvae tunnel toward the apical meristem and induce the formation of a gall, which grows only in the presence of a living larva. Larvae feed within the gall throughout the growing season and overwinter in the gall on the senescent stem. Plant genotype, among other factors, has been shown to influence the interaction between *E. solidaginis* and *Solidago* (e.g., McCrea & Abrahamson, 1987; Horner & Abrahamson, 1992). *Eurosta solidaginis* larvae are attacked by a number of parasitoids and predators, principally two parasitoids (*Eurytoma gigantea* and *E. obtusiventris*), an inquiline beetle (*Mordellistena unicolor*), black-capped chickadees (*Parus atricapillus*), and downy woodpeckers (*Picoides pubescens*; reviewed in Abrahamson & Weis, 1997).

*Experimental design.* Plants were propagated from rhizomes. Four well-isolated clones of both *S. al-*

*tissima* and *S. gigantea* were identified in the field within ten kilometers of our study site at Cedar Creek Natural History Area (CCNHA), Bethel, Anoka County, MN, USA (T34N, R23W, center of quadrant 28; 49.6 km N of Minneapolis/St. Paul, MN, USA). Although we could be relatively certain that these clones represented different genotypes because of their isolation from one another, we could not be certain that each clone represented a single genotype. We therefore will refer to plants propagated from these clones as clonal fragments. However, our interest in this study was to examine the phenological differences across a range of genotypes, not the effect of genotype *per se*. Forty-eight replicates of each of the four clonal fragments of each species were propagated into individual standard 20-l nursery pots in the field one year prior to this study to allow the number of stems per pot to proliferate. In order to prevent frequent freeze/thaw cycles in the potted plants, and in order to ensure that potted plants did not warm and sprout prematurely relative to field-grown plants, we consolidated the pots, placed them in trenches, and covered the pots and their sides loosely with hay during each fall of the study. Pots were uncovered and removed from the trenches during the second week in May (1–2 weeks prior to the study) each year. One replicate pot of each of the four clonal fragments of each species, each with a minimum of five stems, was randomly assigned to each of 48 enclosure cages constructed of nylon mesh and located in the field. Each cage then contained eight pots: one pot of each clonal fragment of each of the two species. The 48 cages were then randomly assigned to one of three oviposition periods (treatments; 16 cages per treatment). These oviposition periods corresponded to the date of peak emergence and oviposition of the earlier-emerging host race (that from *S. gigantea*), that of the later-emerging host race (that from *S. altissima*), and one week after the peak emergence of the later-emerging host race.

Flies were reared from galls collected in the field within a 66-km radius of CCNHA. Although the host races exhibit different emergence phenologies (Craig et al., 1993; Itami et al., 1998), and although environmental factors (especially temperature differences) lead to annual differences in these emergence patterns (reviewed in Itami et al., 1998), the emergence phenologies were similar within host races and within years for the populations that we sampled (J.V. Craig, unpubl.). For the earliest oviposition period (that in which the race from *S. gigantea* normally emerges and prior to normal emergence of the race from *S. al-*

*tissima*), galls of the race from *S. gigantea* were unmanipulated. Emergence time of the race from *S. altissima* was accelerated by maintaining the galls at room temperature during nights and cold periods in early spring. For the second oviposition period (that in which the race from *S. altissima* normally emerges, but that is after the date on which the race from *S. gigantea* normally emerges), galls of the race from *S. altissima* were unmanipulated. For this oviposition period, emergence time of the race from *S. gigantea* was delayed by refrigerating galls. For the third oviposition period, emergence time of the host race from *S. gigantea* was delayed by refrigerating galls, and we used late-emerging flies from unmanipulated galls of the host race from *S. altissima*. Thus, the earliest oviposition period served as the control for emergence of the race from *S. gigantea*, while the second oviposition period served as the control for emergence of the race from *S. altissima*. Since emergence dates of the two races differ somewhat between years (Itami et al., 1998), the experiment was repeated twice over a two-year period. Dates for the oviposition periods in 1993 were 1 June, 8 June, and 15 June. Dates for the oviposition periods in 1994 were 26 May, 1 June, and 8 June.

At each oviposition period, two to six mated and marked females of each host race were released into each cage assigned to that treatment. Ovipositing females show a strong fidelity to their natal host plants (Craig et al., 1993). Cages were constantly monitored while flies remained in the cages. Flies were allowed to ovipuncture freely until most stems within all pots were ovipunctured, then were repeatedly placed on the remaining unattacked stems of their natal host until ovipuncture was observed. Flies were then removed from the cages and plants were censused for the number of ovipunctures. Cages were removed during the third week in June.

Plant relative growth rate (cm/cm/day) was measured on one randomly selected stem in each pot over a one-week period encompassing the period of oviposition. Relative growth rate was used instead of 'simple' growth rate (cm/day) because the former controls for effects of initial differences in plant size and is often a better index of plant vigor. In order to ascertain that the potted plants in our experiment were demonstrating a similar phenology to plants grown in the ground, we also measured the heights and relative growth rates of plants in an adjacent experimental garden (Craig et al., 1997) during the first year of our study (1993).

Since the ability to form galls is one of the principle factors determining survival to adulthood in host races of *Eurosta* (Craig et al., 1997), and since gall formation gave us a larger sample size than did survival to adulthood, we used gall formation as one index of success. Galls were collected from senescent stems in the fall (October) of both years of this experiment, and the percent of ovipunctured stems that formed galls was determined. All galls from each pot were placed in nylon screen bags and the bags were placed in wire exclosures to exclude bird predation over winter. Galls were shipped to TCU in late March and gall diameter was measured. Adults were reared in controlled environment chambers (21 °C, L16:D8). We used the percent of ovipunctured stems from which an adult fly emerged as another index of survival. Because our interest was to examine the effects of oviposition phenology across several genotypes and not in the differences between genotypes *per se*, the mean percent gall formation and the mean percent survival to adult across all four clonal fragments of each species within a cage were used in the analyses.

Finally, galls from which no adult *Eurosta* emerged were dissected to determine the cause of mortality. We categorized mortality as larval death from unknown causes (attributed to differences in host-plant suitability and/or response; Abrahamson & Weis, 1997), parasitism by *Eurytoma* species, and predation by *Mordellistena*. The percent mortality due to each factor in each host race in each cage was determined.

**Statistical analysis.** Plant relative growth rate, the mean percent gall formation, mean percent ovipunctured stems from which an adult fly emerged, gall diameter, percent galls attacked by *Eurytoma gigantea*, and percent galls attacked by *Mordellistena unicolor* were analyzed by separate three-factor analyses of variance. Factors and levels used in each analysis were year (2 levels), oviposition period (3 levels), and host species (2 levels). All factors were treated as fixed factors. Percent data were arcsine-transformed to enhance normality.

Relative growth rates of potted plants in our experiment were compared to those in the experimental garden by three-factor analysis of variance. Factors and levels used in the analysis were location (pot or garden; 2 levels), oviposition period (2 levels), and host species (2 levels).

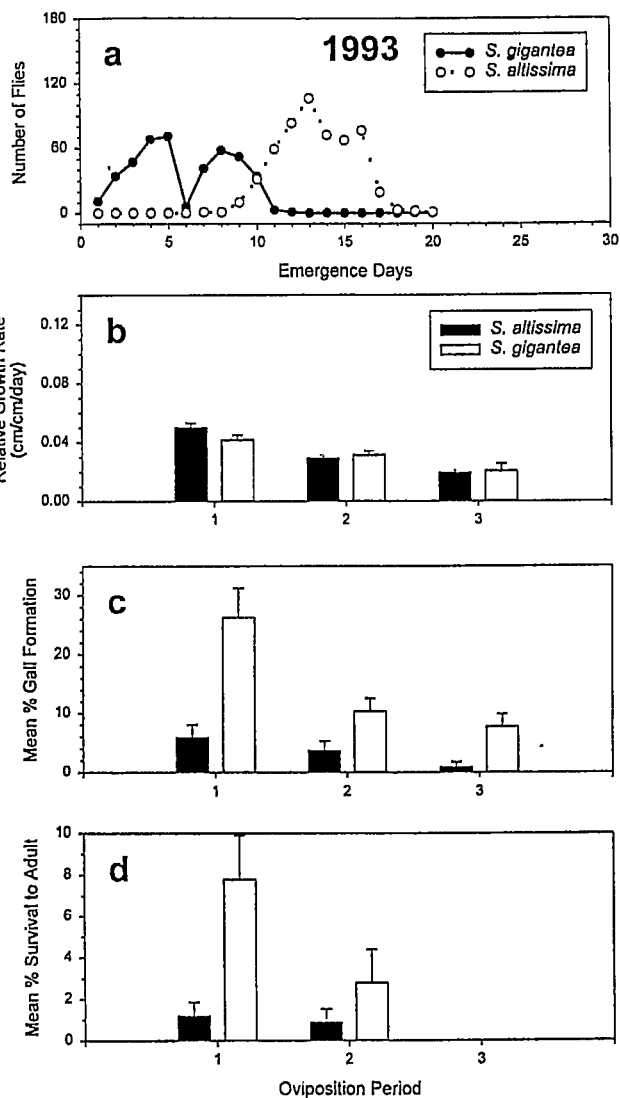


Figure 1. Emergence of flies from unmanipulated (control) field-collected galls (a), mean relative growth rates (+1 S.E.) of *Solidago altissima* and *S. gigantea* (b), mean percent gall formation (+1 S.E.) of host races of *Eurosta solidaginis* from *Solidago altissima* and *S. gigantea* (c), and mean percent survival to adulthood (d) at different oviposition periods in 1993. Oviposition period '1' (+1 S.E.) coincides with the date of peak emergence of the host race from *S. gigantea*, oviposition period '2' coincides with the peak emergence of the host race from *S. altissima*, and oviposition period '3' coincides with a period late in the emergence period of the host race from *S. altissima*.

## Results

In 1993, natural emergence (i.e., emergence of adult flies from unmanipulated galls) of the race from *S. gigantea* extended from 25 May to 6 June, with the peak of emergence on 29 May (Figure 1a; there was no emergence on 30 May, on which the maximum temperature was 8 °C). Emergence of adults of the race from unmanipulated galls of *S. altissima* extended

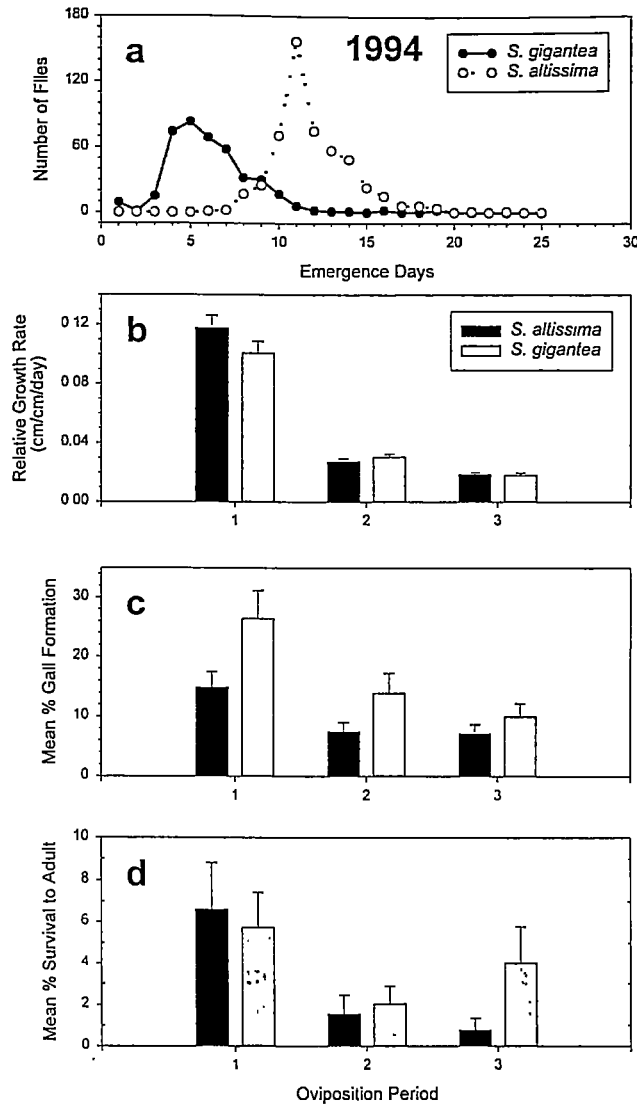


Figure 2. Emergence of flies from unmanipulated (control) field-collected galls (a), mean relative growth rates (+1 S.E.) of *Solidago altissima* and *S. gigantea* (b), mean percent gall formation (+1 S.E.) of host races of *Eurosta solidaginis* from *Solidago altissima* and *S. gigantea* (c), and mean percent survival to adulthood (+1 S.E.) (d) at different oviposition periods in 1994. Oviposition periods are described in Figure 1.

from 31 May to 13 June, with peak emergence on 8 June. In 1994, emergence of adult flies from unmanipulated galls of the race from *S. gigantea* ranged from 19 May to 6 June, with a peak on 23 May (Figure 2a). Emergence of the race from *S. altissima* extended from 26 May to 10 June, with a peak on 29 May.

Plant relative growth rate was significantly affected by year and oviposition period (Table 1). In addition, there were significant effects of the interaction between year and oviposition period and of the interaction between oviposition period and species. In

Table 1. Summary of analysis of variance of the effects of year (Y), oviposition period (P), and species (S) on relative growth rates of host plants

Source	SS	df	F	P
Year	0.008	1	25.68	<0.001
Period	0.084	2	126.06	<0.001
Species	0.001	1	3.03	0.084
Y × P	0.025	2	37.29	<0.001
Y × S	0.000	1	0.76	0.385
P × S	0.003	2	5.07	0.007
Y × P × S	0.000	2	0.53	0.590
Error	0.059	178		

Table 2. Summary of analysis of variance of the effects of year (Y), oviposition period (P), and host species (S) on mean gall formation in host races of *Eurosta solidaginis*

Source	SS	df	F	P
Year	0.55	1	14.18	<0.001
Period	1.27	2	16.42	<0.001
Host Species	1.23	1	31.91	<0.001
Y × P	0.01	2	0.18	0.837
Y × S	0.18	1	4.69	0.032
P × S	0.13	2	1.69	0.188
Y × P × S	0.02	2	0.23	0.798
Error	6.94	180		

general, relative growth rates were higher in 1994 than in 1993 and were higher during the earliest oviposition period and decreased in the latest periods (Figures 1b and 2b). However, the trend for decreasing relative growth rate in later oviposition periods was weaker in 1993 than in 1994. Of the two host plant species, *S. altissima* had a higher relative growth rate at the earliest oviposition period, but the differences between species diminished in the later oviposition periods. We found no significant differences ( $P > 0.05$ ) between the relative growth rates of the potted plants in our experiment and plants growing in our experimental garden.

Cages were constantly monitored while flies remained in the cages and, although we observed females ovipuncturing their own host, no females were observed to ovipuncture the alternate host. In 1993, 138 of the 1376 ovipunctured stems formed galls, while in 1994, 213 of the 1415 ovipunctured stems formed galls. The mean percent of ovipunctured stems forming galls was significantly affected by

Table 3. Summary of analysis of variance of the effects of year (Y), oviposition period (P), and host species (S) on mean survival to adulthood in host races of *Eurosta solidaginis*

Source	SS	df	F	P
Year	0.09	1	5.23	0.023
Period	0.58	2	17.10	<0.001
Host Species	0.17	1	10.24	0.002
Y × P	0.04	2	1.15	0.319
Y × S	0.02	1	1.15	0.285
P × S	0.03	2	0.90	0.410
Y × P × S	0.15	2	4.44	0.013
Error	3.05	180		

year, oviposition period, host species, and the interaction between year and host species (Table 2). Percent gall formation was higher in the race from *S. gigantea* than in the race from *S. altissima*, higher in both host races in 1994 than in 1993 (especially for the host race from *S. altissima*), and tended to decrease from the first oviposition period to the later periods in both host races (Figures 1c and 2c). The percent of ovipunctured stems forming galls was correlated with plant relative growth rate ( $r = 0.09$ ,  $P = 0.01$ ). Gall diameter was not significantly affected by any main factor or interaction ( $P > 0.05$ ).

Twenty-five adult flies emerged from the stems ovipunctured in 1993, while 44 emerged from those ovipunctured in 1994. The mean percent of ovipunctured stems from which adults emerged was significantly affected by year, oviposition period, and host species (Table 3). There was also a significant effect of the year × oviposition period × host species interaction. In 1993, the mean percent survival to adulthood decreased from the first oviposition period to the last for the host race from *S. gigantea* (Figure 1d). In the host race from *S. altissima*, there was no significant difference between the first two oviposition periods in the mean percent survival to adult. No adults emerged from the stems ovipunctured in the third oviposition period from either host plant. In 1994, the mean percent survival to adult was significantly higher in the first oviposition period than in the last two oviposition periods for the host race from *S. altissima* (Figure 2d). In the host race from *S. gigantea*, the mean percent survival to adult was highest for the first oviposition period, intermediate for the third oviposition period, and lowest for the second oviposition period.

Dissection of those galls from which no adult *Eurosta* emerged showed that most larval mortality was due to unknown causes. In 1993, 60 of 112 (53.6%) larvae died of unknown causes, and 52 (46.4%) were attacked by *Eurytoma gigantea*. In 1994, 97 of 168 (57.8%) larvae died of unknown causes, 43 (25.6%) were attacked by *E. gigantea*, and 28 (16.7%) were attacked by *Mordellistena unicolor*. There was a significant effect of host species on the percent galls attacked by *E. gigantea*; a significantly greater proportion of galls on *S. gigantea* than on *S. altissima* were attacked by *E. gigantea* ( $33.4 \pm 3.8$  and  $16.9 \pm 4.2$ , mean  $\pm$  SE, respectively;  $F_{1,127} = 9.43$ ,  $P = 0.003$ ). There were no significant effects of year, oviposition period, or any interaction on parasitism by *E. gigantea*. The percent of *Eurosta* preyed upon by *M. unicolor* was significantly higher in 1994 than in 1993 (there was no attack in 1993; in 1994, the percent galls attacked by *M. unicolor* was  $12.4 \pm 2.6$ , mean  $\pm$  SE;  $F_{1,126} = 11.48$ ,  $P = 0.001$ ). There were no significant effects of oviposition period, host plant, or any interactions on predation by *M. unicolor*.

## Discussion

There was no significant difference between the relative growth rate of the potted plants in our experiment and that of plants growing in the adjacent experimental garden, suggesting that the phenology of the potted plants was similar to plants growing in the ground. The relative growth rate of both host species in this experiment was highest at the earliest oviposition period and decreased during later periods. Therefore, the hypothesis that the relative growth rate of the two host species would be maximal during the period in which they are normally attacked was supported in *S. gigantea*, but not in *S. altissima*. Instead, the highest relative growth rate in *S. altissima* occurred before natural emergence of the host race from this species. Percent gall formation was significantly correlated with growth rate, as hypothesized. However, the coefficient of determination was very low, suggesting the overwhelming influence of other, undetermined factors on survival.

Percent gall formation in both host races was highest during the earliest oviposition period and decreased during later periods. Therefore, emergence of adult flies from control (unmanipulated) galls of the host race from *S. gigantea* occurred at a time corresponding to the period of optimal suitability for gall formation. In contrast, the emergence of adult flies from con-

trol galls of the host race from *S. altissima* occurred later than the period during which their host was optimally suited for gall formation. In fact, gall formation was higher in the host race from *S. altissima* when adult emergence was manipulated such that adult flies emerged earlier than normal, during the time that the race from *S. gigantea* normally emerges.

The mean percent survival to adulthood was highest during the earliest oviposition period and decreased in later oviposition periods in both years for the host race from *S. altissima*. The mean percent survival to adulthood was also highest during the earliest oviposition period in both years for the host race from *S. gigantea*. However, in 1994, an intermediate level of survival to adulthood was observed in the last oviposition period in the host race from *S. gigantea*. Because the total number of ovipunctured stems that produced an adult fly was small, and because we used the mean percent ovipunctured stems from each cage, a small difference in the number of adults strongly influences the results. Therefore, the data for the mean percent survival to adulthood should be interpreted with caution. In any case, survival to adulthood in the host race from *S. altissima* was highest during the earliest oviposition period in both years. This is inconsistent with the hypothesis that this host race emerges at a time that its host is most suitable for survival to adulthood.

Observed patterns of gall formation and survival to adulthood were inconsistent with the hypothesis that differences in patterns of emergence in host races of *E. solidaginis* are the result of adaptation to differences between their respective host plants in periods of optimal suitability for attack. With regard to host-plant suitability, both percent gall formation and survival to adulthood in the host race from *S. altissima* were higher when the emergence of adult flies was manipulated so that they emerged at the same time as those from the host race from *S. gigantea*. If the differences in emergence and oviposition phenologies are not due to adaptation to differences between the respective host plants in periods of optimal suitability for gall formation, why might these differences in emergence and oviposition phenologies exist? Several alternative explanations are possible: (1) the observed differences in patterns of emergence are the result of selection against the production of hybrids between the host races; (2) the observed patterns are the result of selection due to attack by parasitoids or predators; or (3) the observed patterns are the result of differential gene flow in the absence of selection.

Selection against the production of hybrids between the host races might be responsible for the observed differences in emergence phenology. We have shown elsewhere that hybrids between the host races exhibit low rates of gall induction (Craig et al., 1997). This low rate of gall induction in hybrids could serve as a strong selection pressure causing divergence in emergence times. Parasitism, which has been implicated in the initial separation of these host races (Brown et al., 1995), may also select against the production of hybrids between the host races. Hybrids appear to form smaller, misshapen galls (Craig, Horner, and Itami, unpubl.). As a result, larvae in these galls may be more susceptible to attack by the parasitoid wasp, *Eurytoma gigantea*. *Eurytoma gigantea* attacks galls after they have reached their maximum size, and the diameter of galls that can be successfully attacked is constrained by the length of the ovipositor (Weis & Abrahamson, 1985; Weis et al., 1985; reviewed in Abrahamson & Weis, 1997). Therefore, the seemingly smaller galls of hybrids may be more susceptible to attack by *E. gigantea*. The observed differences in emergence phenologies may therefore be the result of selection against the production of hybrids. Whether there is sufficient genetic variation in emergence time and whether selection pressures are sufficient to produce allochronic isolation between these races are yet to be determined.

Selection pressure imposed by parasitism and/or predation could also lead more directly to delayed emergence in the host race from *S. altissima*. We found no significant effect of oviposition period on attack by *Eurytoma gigantea* or *Mordellistena unicolor*. However, selection due to two other causes of larval mortality were not examined in this study. Bird predation was prevented by storing the galls in wire enclosures. However, bird predation is not a likely selection factor affecting emergence phenology. Downy woodpeckers and black-capped chickadees preferentially attack larger galls, but we found no significant effect of oviposition period on gall diameter. We can not, however, exclude the selection pressure caused by the parasitoid, *E. obtusiventris*. *Eurytoma obtusiventris* searches oviposited stems before galls have reached their maximum diameter, preferentially searches and attacks larvae on *S. altissima*, and may have exerted a strong selection pressure resulting in the initial shift from *S. altissima* (Brown et al., 1995). Likewise, attack by *E. obtusiventris* could result in directional selection on oviposition phenology, and may explain the delayed emergence of the host race from *S. al-*

*tissima* relative to host-plant suitability. Decreased mortality due to temporal escape from the parasitoid *E. obtusiventris* could more than offset the increased mortality due to the delay of emergence/oviposition relative to the optimal suitability of the host plant. However, although *E. obtusiventris* occurs over much of the range of *Eurosta solidaginis*, it does not occur in the area in which this study was conducted. Therefore, we can not know how differences in oviposition phenology might affect attack by this parasitoid. In areas in which *E. obtusiventris* occurs, this parasitoid may provide sufficient selection pressure to have caused a shift to a later oviposition period in the host race from *S. altissima*.

Finally, observed differences in emergence phenologies may be the result of differential gene flow in the absence of selection. Models produced by Stam (1983) for flowering time in plants and by Butlin (1990) for emergence time in insects show that differences in phenology can come about by differential gene flow among populations in the absence of selection. Early emerging phenotypes have the opportunity to mate only with others of the same phenotype, and vice versa. The characteristics of *Eurosta* make it a good candidate for this type of divergence in emergence time in the absence of selection: there is phenotypic variance in emergence times both within and between the host races that is partially under genetic control (Abrahamson et al., 1994; Itami et al., 1998), the adult lifespan is only a few days (Uhler, 1951), and the difference in peak emergence time between the races can exceed the adult lifespan (Craig et al., 1993; Itami et al., 1998). However, the model by Butlin (1990) requires, among other factors, that there is an *initial* difference in emergence times. This initial difference in emergence time may be brought about, for example, by environmental differences or differences in suitability of the two host plants. In *Eurosta*, a potential cause for this initial difference in phenology is unclear. Attempts to identify factors that could lead to this initial difference in emergence time have been unsuccessful. For example, differences in gall characteristics (size, color, and shape) of the races on the two host-plant species that might lead to differences in larval temperature and degree-day accumulation have not proven to have a significant effect on date of emergence (Abrahamson et al., 1994). Therefore, to date, we have no evidence of any environmental factors that might have led to an initial difference in emergence phenology. Nevertheless, other factors

need to be considered before this hypothesis can be discounted.

In summary, differences in emergence times of the two host races of *Eurosta solidaginis* do not seem to be related to differences in the time that their respective host plants are most suitable for gall formation or survival to adulthood. Percent gall formation and survival to adulthood of both host races were highest during the period that the host race from *S. gigantea* normally oviposits (the earliest oviposition period in this study). Percent gall formation is related to plant relative growth rate, but the growth rate of both host plants is highest earlier in the growing season. Differences in emergence times may be due to (1) selection against the production of hybrids, (2) selection caused by parasitism by *E. obtusiventris*, or (3) differential gene flow in the absence of selection.

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