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Role of Host Plant Phenology in Host Use by *Eurosta solidaginis* (Diptera: Tephritidae) on *Solidago* (Compositae)

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ABSTRACT To assess whether plant phenology may affect potential for host shifts, *S. altissima* and *S. gigantea* were monitored in the field in Minnesota (both host races), in Pennsylvania (*S. altissima*, sole host), and in a Pennsylvania common garden of both host plants from both sites. Plant height was measured every other day, and growth rates were calculated through the oviposition period in the field and season-long in the common garden. Greenhouse-grown *S. gigantea* from both locations were subjected to oviposition by Minnesota *Eurosta* to compare galling susceptibility. Minnesota hosts had more comparable growth rates and more intraspecific variability than the same species in Pennsylvania. *S. gigantea* growth peaked earlier and fell more rapidly than that of *S. altissima* for all populations, suggesting an earlier, narrower window of host suitability. Pennsylvania *S. gigantea* will support gall formation, but ramet growth rate was significantly less than that of Minnesota *S. gigantea* under greenhouse conditions, and Minnesota *Eurosta* strongly preferred Minnesota ramets to those from Pennsylvania. Variations in daily growth rate fluctuations between species may confound *Eurosta's* detection of suitable hosts. These results indicate a higher probability of a host shift occurring in Minnesota than in Pennsylvania and may indicate why colonization of *S. gigantea* has not occurred in Pennsylvania.

KEY WORDS *Eurosta solidaginis*, galls, host plant phenology

ECOLOGICAL FACTORS may be critical to the interaction of a herbivore and host plant. Ecological monophagy (Gilbert 1976), a mode of host specialization brought about by extrinsic factors such as plant abundance or the opportunity a plant provides for escape from predation, may serve as catalyst to host specialization. Genetic adaptation to host plant chemistry could arise later as selection acts to increase the insect's growth efficiency on the host until the interaction becomes obligate monophagy (Smiley 1978).

Although plant chemistry is a widely cited source of host selection (e.g., Bosio et al. 1990, Abrahamson et al. 1991), careful consideration needs to be given to the sequence of the plant chemistry-host interface (i.e., following Smiley's [1978] proposed sequence of ecological monophagy evolving to obligate monophagy). Further, ecological factors (e.g., host phenology) may complement or hinder the herbivore's ability to select a host based on the finer scale of plant chemistry.

Numerous researchers have explored ecological factors that might contribute to host choice and specialization. Host phenologies (Holdren & Ehrlich 1982, Wood et al. 1990), host nutritional quality and resource reliability (Williams 1983), seasonal fluctuation in host quality and avoidance of natural enemies (Moran 1984), and plant apparency to herbivores and host growth habit (Rausher 1981, Singer et al. 1989) have all been cited as conditions affecting host selection by specialist insects.

Others cite variation within herbivore species as determining host choice (Wiklund 1981, Papaj 1986, Thompson 1988), but Thompson incorporated variation in herbivore host selection into the larger context of the variation encountered in host plant characters. Similarly, Thomas et al. (1987) found host preference to be the primary factor in initiating a host shift to an introduced plant species, but noted that plant characteristics such as drought tolerance might also have been a factor. Thomas et al. (1987) wrote, "At present, we have little idea whether the diet patterns of herbivore species that specialize on one or a few hosts in each population arise mostly from variation in traits of insects or of plants." Jaenike (1990) cited the importance of plant chemistry in determining the variety of plants on which an insect species can feed but noted that the actual

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diet may be significantly narrower because of the intervention of ecological variables.

Consequently, it seems critical to examine host shifts in light of ecological factors. We studied a host shift by *Eurosta solidaginis* (Fitch) (Diptera: Tephritidae), a gallmaker, found primarily on *Solidago altissima* (Compositae) (tall goldenrod) but observed in some locations (e.g., Minnesota, Illinois, Michigan, and New England) on *S. gigantea* (Waring et al. 1990). Despite the co-occurrence of *S. gigantea* with *S. altissima* throughout the latter's range, and the nearly universal distribution of *Eurosta* galls on *S. altissima*, galls are absent on many *S. gigantea* populations; e.g., in the mid-Atlantic, south central, and southeastern regions (Abrahamson et al. 1989).

The variation in *Eurosta* attack on the two *Solidago* species appears to be a host shift rather than polyphagy, possibly from *S. altissima* to *S. gigantea* with subsequent divergence. Genetic and behavioral data on *Eurosta* populations from the two hosts at sympatric sites indicate host race formation with limited gene flow (Waring et al. 1990, Craig et al. 1993).

One of Smiley's (1978) chief criteria for ecological monophagy is that larval performance does not closely parallel adult preference, indicating that factors other than host plant chemistry may determine host specificity. Such is the case for *E. solidaginis* preference and performance on *S. altissima* and *S. gigantea* (Craig et al. 1993; W.G.A., unpublished data) although early larval death is higher on *S. gigantea* than on *S. altissima* (Lichter et al. 1990).

Adult *E. solidaginis* females oviposit (puncturing of the bud with or without egg deposition, producing permanent scars in the folded leaves surrounding the apical meristem) into the apical bud of *Solidago* during an ≈2-wk period in mid-May to early June. Following oviposition, the larva hatches within 1 wk and feeds on the differentiating plant material produced by gall formation. At season's end, the larva burrows an exit to just beneath the gall's surface, then enters diapause as a third instar, to emerge as an adult fly after overwintering.

Following Smiley's (1978) logic in the contradictory nature of *E. solidaginis* oviposition preference versus larval performance, the objective of this study was to assess possible ecological host determinants by comparing *S. altissima* and *S. gigantea* host populations in Minnesota (where both goldenrod species are infested) with populations of the same *Solidago* species in Pennsylvania (where only *S. altissima* is attacked). Because previous studies by Abrahamson et al. (1988) and Horner & Abrahamson (1992) found no differences in galling success on *S. altissima* subjected to a range of nutrient availability and light treatments, this study of both *Solidago* species was concentrated on host plant phenology and within-species variation as factors influencing host use.

Materials and Methods

Field Phenology. Twenty-five clones (genets) each of *S. altissima* and *S. gigantea* located east of Lewisburg, PA, along a 4-km stretch from 0.5 km south of Highway 45 north to the State Road 1025 overpass along Highway 147, and 24 clones of *S. gigantea* and 15 clones of *S. altissima* located at or near the University of Minnesota Cedar Creek Natural History Area, Bethel, MN, were selected. A single ramet of each clone was tagged for repeated measurements. We used only spatially isolated genets with morphologically uniform ramets. Clones were a minimum 1 m in diameter to offer a representative sample size. Although individual clones grew under relatively uniform conditions, clone habitat varied from dry, well-drained slopes to poorly drained bottom lands.

The Pennsylvania habitat was an old-field road right-of-way disturbed in the late 1960s on loamy soil, including both dry slopes and wetlands. Cedar Creek Natural History Area is on the Anoka Sand Plain, a region of light, sandy soils, and clones grew in old fields abandoned over a period of years.

All clones at both locations were monitored before, during, and after the oviposition period every other day in Pennsylvania (24 April–5 June 1990) and every 3–5 d in Minnesota (23 May–18 June 1990). Measurements of plant height and change in height were used to determine growth rate.

High and low temperature readings and recorded precipitation for dates of observation for this and a following experiment were obtained from the nearest National Weather Service reporting stations at both locations (Selinsgrove, PA, and Cedar, MN).

Host Uniformity. During the 1990 oviposition season, 40 ramets in each of 10 large clones of each species in Minnesota and Pennsylvania were measured (14–17 May in Pennsylvania and 1–9 June in Minnesota) for plant height to compare within-species variation as a measure of availability for oviposition. These clones included some of those that were monitored for phenology, as well as other clones in the same immediate areas. To randomize any position effects, a transect was laid across each clone, and the two ramets closest to the transect at each 30-cm interval were measured, thus sampling ramets through a cross-section of the clone.

Host Genetic Variation. To separate genetic from environmental influences on plant populations from the two locations, rhizomes were collected from each clone used in the field phenology study (in Pennsylvania, 25 *S. altissima* and 25 *S. gigantea;* in Minnesota 15 *S.*

altissima, and 24 *S. gigantea*); a single replicate rhizome from each clone was weighed and planted 18 May 1990 in a common garden (1.8 m by 6.7 m) at Bucknell University, Lewisburg, PA. Rhizomes planted in a corresponding common garden in Minnesota failed to establish in sufficient numbers for analysis. At Bucknell, 79 of the 89 ramets survived (24 Pennsylvania *S. altissima*, 23 Pennsylvania *S. gigantea*, 11 Minnesota, *S. altissima* and 21 Minnesota *S. gigantea*) and were measured just as were the field plants every other day 13 June–21 July, then every 4 d until 11 September. The common garden was watered as needed, and weeds were controlled by hand cultivation and by sponge applications (wetting leaves only) of a 1.5% solution of Roundup herbicide (Monsanto Company Agricultural Products, St. Louis, MO).

Oviposition, Preference, and Galling Susceptibility. To determine if *Eurosta* would accept and produce larvae on Pennsylvania *S. gigantea*, a greenhouse experiment was conducted using 10 clones of Minnesota *S. gigantea* and 10 clones of Pennsylvania *S. gigantea* (collected from the same areas, but not necessarily the same genotypes as those used in other experiments). Thirty ramets of each clone were grown in standard pots (23 cm) from rhizome sections in ProMix BX (Premier Brands, Stamford, CT), and *Eurosta* reared from Minnesota *S. gigantea* galls were released in the greenhouse when ramets averaged 20 cm tall. Ramets of both populations were randomly distributed on benches. When a ramet bud showed multiple ovipositor scars, ramets were removed from the fly release area to protect ramets from excess bud damage. Ramet heights were recorded 1 d before flies were released, then twice more at 2-wk intervals to determine growth rates. Ramets were subject to natural light supplemented by high-pressure sodium vapor lamps (120 μE m^{-2} S^{-1} photosynthetically active radiation at plant level) in a photoperiod of 13:11 (L:D) h. A photocell turned off artificial lighting on bright days, but natural light was artifically supplemented on overcast days. Ramets were fertilized with 20 ml of full-strength Hoagland's solution (Hoagland & Arnon 1950) the day before first fly release. Flies were released 30 March, 6 April, and 12 April 1991 as blocks of ramets reached ideal oviposition height. Pots were randomized twice monthly to control for position effects.

The ramets matured to senescence, and aboveground biomass was harvested. Gall diameters and their fresh masses were determined, then galls were dissected to determine larval survivorship and larval fresh masses. Above-ground ramet mass, gall and larval dry masses, and total dry mass of ramets were determined.

Data Analysis. All statistical analyses were carried out using SPSS software (SPSS, Chicago, IL). Growth rates were measured as the changes in height from one observation to the next for field, common garden, and greenhouse ramets. Ramets were compared by species in the field, by species and origin in the common garden, and by origin in the greenhouse.

Student's t test was used to compare mean growth rates and physical dimensions by species for all field plants. No growth rate and dimension comparisons could be made between field locations because of the impossibility of determining comparable growth stage because of climatic differences. Coefficients of variation were used to determine height variability within populations.

Common garden measurements were analyzed with a one-way analysis of covariance (ANCOVA), using starting rhizome mass as covariate. A repeated-measures two-way ANCOVA, with starting rhizome mass as covariate, was used to assess the cumulative importance of species, origin, and species–origin interactions to growth rates.

Greenhouse measurements were analyzed with a one-way ANCOVA using starting rhizome mass as covariate with height and growth rates. Ovipositional preference was compared in the two populations (Minnesota and Pennsylvania) for the first two releases (combined) of flies. At the first release, there were 300 Minnesota ramets and 300 Pennsylvania ramets; at the second release, 274 Minnesota ramets and 297 Pennsylvania ramets. Thereafter, available ramets were biased toward smaller ramets and those from Pennsylvania, precluding free-choice comparisons. Chi-square analysis was used to compare ovipuncture rates and gall formation between origins.

One-way ANCOVAs assessed the influence of plant origin on gall characteristics and larval survival, using ramet mass as covariate where significant. Regression assessed the relationship of gall size and larval mass.

Results

Field Phenology. In Pennsylvania, *S. altissima* grew significantly faster than *S. gigantea* for 6 of 21 observations of which 3 significant observations occurred during the oviposition period (Fig. 1A). The cumulative growth rate of *S. altissima* was also significantly more rapid (t = 3.6, df = 42, P = 0.0008) during field observations than that of *S. gigantea* in Pennsylvania. In Minnesota, there were no significant differences in continuous or cumulative growth rates between species for any observation. Daily fluctuations in growth rate through the observation period at all locations roughly corresponded to temperature changes (Figs. 1–3).

Host Uniformity. Student's t tests were used to compare field ramets during the period of oviposition within each location. Mean height differences between *S. gigantea* and *S. altissima* in

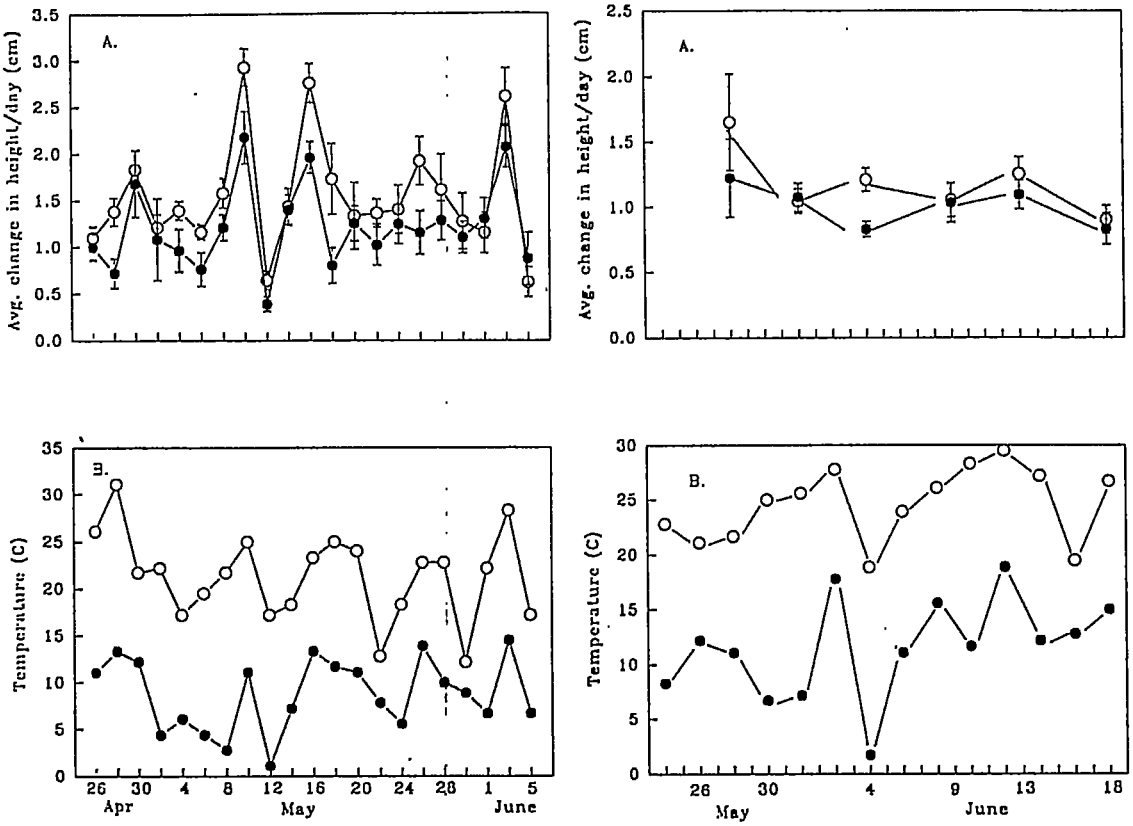

Fig. 1. (A) Mean growth rates (cm) ± SE calculated as change in height from one observation to the next (every other day) and averaged for daily rates from 26 April through 5 June 1990 for *S. altissima* (open circles) and *S. gigantea* (filled circles) in the field in Pennsylvania. (B) Corresponding weather readings for maximum (open circles) and minimum (filled circles) temperatures during the observation period from the National Weater Service reporting station, Selinsgrove, PA.

Fig. 2. (A) Mean growth rates (cm) ± SE calculated as change in height from one observation to the next (observation dates on the *x* axis) and averaged for daily rates from 26 May through 18 June 1990 for *S. altissima* (open circles) and *S. gigantea* (filled circles) in the field in Minnesota. (B) Corresponding weather readings for maximum (open circles) and minimum (filled circles) temperatures during the observation period from the National Weather Service reporting station, Cedar, MN.

Minnesota approached significance ($t = 1.75$, df = 798, $P = 0.08$), whereas in Pennsylvania, *S. altissima* was significantly taller than *S. gigantea* ($t = 9.94$, df = 778, $P < 0.001$) (Fig. 4). Height and growth rate comparisons could not be made between Minnesota and Pennsylvania populations because of the impossibility of determining comparable growth stage of ramets because of climatic (and hence phenological) differences. Pennsylvania *S. altissima* showed the most uniform height, as reflected in coefficients of variation, whereas Pennsylvania *S. gigantea* and the two Minnesota species showed comparable height variation (Fig. 4).

Host Genetic Variation.—In the common garden, where growth rates were followed all season, *S. altissima* from both locations showed the longest sustained positive growth pattern; *S. gigantea* growth patterns from both locations peaked earlier and fell more rapidly (Fig. 3). Starting rhizome mass, used as a covariate in analyzing growth rates in the common garden, was significant for all populations through the season until growth rates reached maximum and began to decline, indicating that plants with greater rhizome mass at planting had a stronger start and continued to benefit through most of the season.

Two-way repeated-measures MANOVA showed both species and origin were significant in differences in cumulative growth rate for ramets grown in the Pennsylvania common garden during the early part of the growing season (13–29 June) (species: $F = 4.9$; df = 1, 68; $P = 0.03$, origin: $F = 24.1$; df = 1, 68; $P < 0.001$), but the two-way interaction of species and origin was not significant. Because *Eurosta* attacks early in the growing season, these early season data are particularly important. For the remainder of the growing season (1 July–18 August), species was

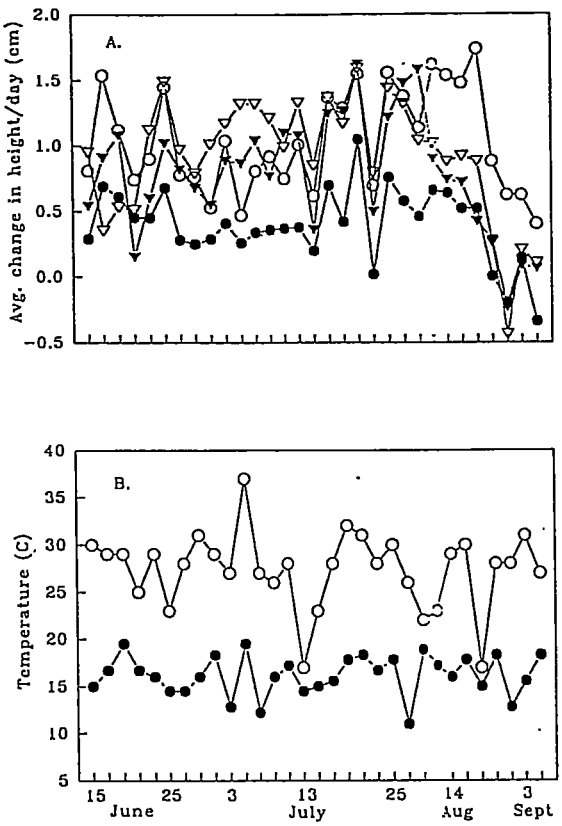

Fig. 3. (A) Mean growth rates (cm) calculated as change in height from one observation to the next (every other day, 15 June–21 July, then every 4 d 21 July–7 September 1990) and averaged for daily rates for *S. altissima* (circles) and *S. gigantea* (triangles) from both Minnesota (filled symbols) and Pennsylvania (open symbols) grown in a common garden at Bucknell University, Lewisburg, PA. (B) Corresponding weather readings for maximum (open circles) and minimum (filled circles) temperatures during the observation period from the National Weather Service reporting station, Selinsgrove, PA.

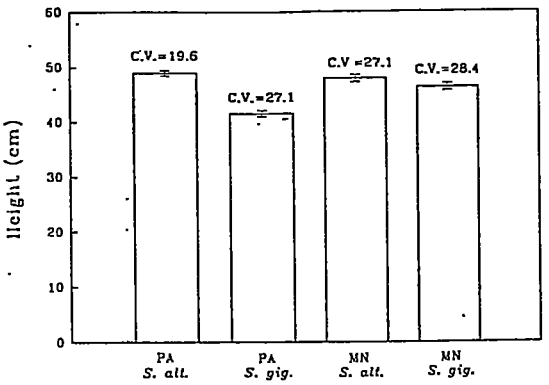

Fig. 4. Mean heights (cm) ± SE and coefficients of variation (C.V.) for goldenrod populations of the two host species in Pennsylvania and Minnesota fields during one-time measurements in each location's respective *E. solidaginis* oviposition period. *S. alt.*, *S. altissima*; *S. gig.*, *S. gigantea*.

not significant but origin (F = 10.3; df = 1, 69; P = 0.002) and species by origin (F = 8.0; df = 1, 69; P = 0.006) were significant to cumulative growth rate. In the latter part of the season, growth by species was not significantly different, but growth by origin was; considered together, ramets of different species and origins were significantly different in growth rate (Fig. 3A). Repeated measures "telescopes" growth over time, resulting in a measure of cumulative growth that averages fluctuations within the time period. Differences by species were significant for 14 and 18 August (F = 10.2; df = 1, 69; P = 0.002 and F = 5.4; df = 1, 69; P = 0.023, respectively) when *S. altissima* growth was sustained but *S. gigantea* growth declined.

Oviposition, Preference, and Galling Susceptibility. Minnesota *Eurosta* reared from *S. gigantea* galls showed strong preference for Minnesota rather than Pennsylvania *S. gigantea* ramets for ovipuncture (χ^2 = 58.2, df = 1, P < 0.001; n = 605 ramets). This comparison is based on total ramets punctured throughout the experiment, even after the ratio of Minnesota to Pennsylvania ramets available for attack had been reduced to 174 (Minnesota) and 252 (Pennsylvania). Minnesota ramets were significantly taller (F = 33.4; df = 1, 593; P < 0.001) and faster growing (F = 27.6; df = 1, 587; P < 0.001) and rhizome mass was a significant covariate (F = 67.6; df = 1, 593; P < 0.001 and F = 15.1; df = 1, 587; P < 0.001, respectively). Rhizome growth of Minnesota field clones was much more vigorous than Pennsylvania field clones, so that Pennsylvania starting rhizome mass averaged smaller than that of Minnesota. Minnesota ramets were larger and faster growing at oviposition. Minnesota ramets that were ovipunctured averaged greater growth than those not punctured for both origins (Table 1).

Pennsylvania ramets supported gall formation, although galling rates for all ramets from both origins were low (48 galls were formed from the 326 ramets punctured) (14.7%). Significantly more galls occurred on Minnesota ramets than on Pennsylvania ramets (χ^2 = 10.05, df = 1, P = 0.002; n = 605 ramets) with one Minnesota host genotype accounting for 17 galls (35% of total galls formed (n = 48)). Excluding this genotype, galling rates on ramets of both origins (n = 9 Minnesota genotypes, 10 Pennsylvania genotypes) were not significantly different.

All 11 Pennsylvania galls contained live larvae at ramet senescence. Of the 37 Minnesota galls, 18 held live larvae. Two larval mortalities were attributed to early larval death; the remaining 17 were destroyed by a predatory inquiline of ball

Table 1. Galling susceptibility in *S. gigantea* of colonized (Minnesota) and noncolonized (Pennsylvania) origin

Parameter[a]	Minnesota	Pennsylvania
Cumulative growth, cm		
Ovipunctured	13.7 ± 0.5 (n = 206)	9.5 ± 0.5 (n = 113)
Not ovipunctured	7.7 ± 0.6 (n = 88)	7.8 ± 0.5 (n = 181)
Height at first oviposition, cm		
Ovipunctured	12.9 ± 0.2 (n = 206)	10.4 ± 0.3 (n = 113)
Not ovipunctured	7.8 ± 0.4 (n = 88)	8.8 ± 0.2 (n = 181)
Growth rate at oviposition	7.2 ± 0.2 (n = 293)	5.1 ± 0.2 (n = 293)

[a] Height and growth expressed as means ± SE. Cumulative growth represents change in height throughout the observation period (1 mo). Growth rate at oviposition represents change in height during the 2 wk following first introduction of *E. solidaginis*.

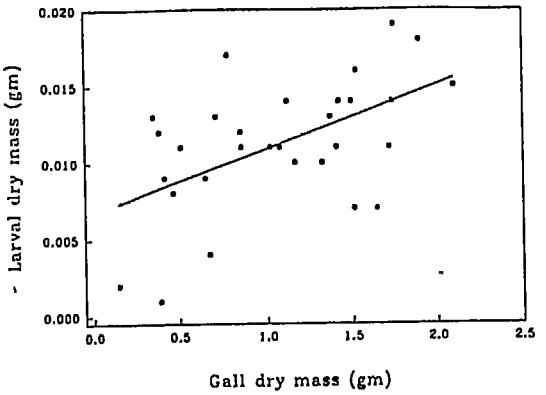

Fig. 5. Regression of all dry masses (Minnesota and Pennsylvania) for galls (x axis) and *Eurosta* larvae (y axis) where larval dry mass (g) = 0.004 gall dry mass (g) + 0.007, r = 0.53, P = 0.01.

galls, *Mordellistena unicolor* Lecoute (Coleoptera: Mordellidae), its source believed to be Minnesota plant material.

Gall diameter, gall fresh and dry mass, and larval dry mass from Minnesota clones were found to be significantly larger than those from Pennsylvania (Table 2). Above-ground biomass was a significant covariate for all gall characteristics but was not significant for larval fresh or dry mass. Using plant origin as the main effect with gall dry mass as covariate, gall dry mass was highly significant (F = 10.7; df = 1, 29; P = 0.003), whereas origin was not significant in its comparison with larval dry mass. In turn, gall dry mass varied significantly by origin (F = 15.8; df = 1, 47; P = <0.001), but gall mass corresponded more closely than host origin to larval dry mass. Regression showed a significant positive correlation (r^2 = 0.284, $P < 0.01$, n = 30) of larval dry mass and gall dry mass with a positive slope (Y = 0.004X + 0.007) (Fig. 5).

Table 2. Means ± SE for gall and larval characteristics by host origin

Parameter	Host origin	
	Minnesota	Pennsylvania
Gall diameter, mm	20.64 ± 0.77	14.76 ± 0.98
(F = 10.8, df = 1, 47, P = 0.002)	(n = 37)	(n = 11)
Gall fresh mass, g	3.54 ± 0.29	1.33 ± 0.20
(F = 10.6, df = 1, 47, P = 0.002)	(n = 37)	(n = 11)
Gall dry mass, g	1.23 ± 0.08	0.59 ± 0.07
(F = 12.3, df = 1, 47, P = 0.001)	(n = 37)	(n = 11)
Eurosta fresh mass, mg	31.5 ± 2.06	24.3 ± 3.25
(F = 3.9, df = 1, 30, P = 0.058)	(n = 20)	(n = 11)
Eurosta dry mass, mg	12.4 ± 0.78	9.2 ± 1.48
(F = 4.6, df = 1, 29, P = 0.041)	(n = 19)	(n = 11)

Statistical comparisons of host plant origin for gall and larval characteristics are from one-way ANCOVA using above-ground ramet biomass as a covariate (significant at least at $P <$ 0.05), except for *Eurosta* fresh and dry masses, which used one-way ANOVA.

Discussion

Variation in and between plant populations is well documented both by phenotype (Schlichting & Levin 1984) and genotype (Hamrick 1982, Antonovics 1984, Bradshaw 1984), and these differences affect the phytophagous insects which feed upon them (e.g., Linhart 1989). Our results suggest that several aspects of host plant phenology may pose obstacles to an herbivore's distribution. These elements, although individually subtle, may have a strong collective influence on immigration or host choice. Our findings suggest populations of the two *Solidago* species from different origins (in this case, Minnesota and Pennsylvania), by varying intraspecifically in growth habit, apparency, and galling susceptibility, alter conditions sufficiently to influence host use.

Although phenotypic plasticity may play a part in these host plant differences, comparisons in the common garden and the greenhouse indicate a contrasting genetic component expressed in growth rates. Growth traits of *S. altissima* and *S. gigantea* appear to converge in Minnesota and diverge in Pennsylvania. Pennsylvania *S. altissima* is larger and more uniform in size at time of oviposition than Pennsylvania *S. gigantea*, whereas the two species in Minnesota are comparable.

Although Pennsylvania *S. gigantea* supported gall formation, galling rates in the greenhouse were low for clones of both origins. This may be an artifact of experimental conditions or may indicate a growth pattern which limits the period of successful oviposition. A reduced window of vulnerability may limit host adoption or lead to temporal isolation of host races.

Ovipositional preference in the greenhouse indicated distinction by ramet origin. This may have been based on the greater height or faster growth rate of Minnesota ramets at oviposition, because Anderson et al. (1989) found in *S. al-*

tissima that *Eurosta* preferentially attacked ramets which were growing most rapidly at oviposition.

In the greenhouse, Pennsylvania *S. gigantea* yielded viable larvae, but Minnesota galls produced significantly larger larvae, and the mass difference may affect both larval survival to emergence and subsequent fecundity of the flies.

Our evaluation of ecological factors influencing the *Eurosta* host shift is necessarily based on current conditions that may or may not have been operating when the host shift occurred. However, considering the longevity of *Solidago* clones, which may persist for hundreds of years (Werner et al. 1980) and recorded host adoptions by introduced insect species in less than a century (Bush 1975, Thomas et al. 1987), it is conceivable that the *Eurosta* host shift occurred in conditions very similar to those we now observe.

Despite the high chemical specificity that is required for a gallmaker to induce galling (Abrahamson & Weis 1987), there is inherent flexibility in the host–herbivore interaction. *S. altissima* clones, and, in all probability *S. gigantea* clones, differ in resistance and susceptibility to the gallmaker (McCrea & Abrahamson 1987, Anderson et al. 1989), but larval survival is not closely correlated with oviposition preference among *S. altissima* clones (W.G.A., unpublished data).

In addition, Maddox & Root (1990) determined that suites of herbivores may be a far stronger selective force on *S. altissima* than any single herbivore. If the host responds to a suite of herbivores, it seems unlikely that a "gene-for-gene" interaction exists between *E. solidaginis* and *S. altissima*. The range of defenses with which *S. altissima* responds to a suite of herbivores may actually encourage variability and "sampling" by *E. solidaginis*.

For ovipositional "mistakes" or "samplings" to become a host shift, three conditions must be met: (1) the ovipositing female must identify a new host, (2) larval survival must result, and (3) assortative mating by host plant is necessary to limit gene flow (Futuyma 1986). Futuyma theorized that mutations occur in the herbivore to make these three steps possible, but by Smiley's (1978) reasoning, ecological conditions (e.g., plant abundance) may either supplement or precede mutation.

Eurosta ovipositional "mistakes" are likely, based on both genetic (Waring et al. 1990) and behavioral data (Craig et al. 1993). In the greenhouse experiment, although differences were intraspecific rather than interspecific, Minnesota *Eurosta* preferred Minnesota *S. gigantea* but increasingly punctured Pennsylvania *S. gigantea* as population numbers shifted in favor of the Pennsylvania ramets (personal observations). Although these observations were made on a single *Solidago* species, similar preference patterns may be exhibited interspecifically, particularly where the two species commonly grow interdigitated, as they do in Minnesota.

Given the obstacles to host adoption, it is expected to occur rarely and only under optimal conditions, which might include congruence of growth traits of the host and non host. The findings of Waring et al. (1990) suggest the shift was a one-time event, which may have occurred in the northern United States with subsequent immigration to other sites. Characteristics of the two *Solidago* species in Minnesota suggest their similarities may have at least facilitated ovipositional "mistakes." Both *Solidago* species are similar in growth rate and intraspecific variation. This similarity has also been noted (but not quantified) in New England near another sympatric site (Schmid et al. 1988).

The similarity of the two *Solidago* species in some locations may also affect their competitive interaction and subsequent availability to herbivores. Conversely, in Pennsylvania, where *S. altissima* appears to be a more rigorous and more uniform host (Figs. 1, 3, and 4), opportunities for alternate host colonization may be reduced below a necessary threshold. If *S. altissima* dominates, as it appears to, occurrence of *S. gigantea* may be so patchy as to discourage both host shift and immigration. Even if oviposition were to occur on Pennsylvania *S. gigantea*, the possibility of decreased larval size and lower fecundity could further limit chance of successful colonization. The uniformity of *S. altissima* in Pennsylvania may also act to keep the *Eurosta* population insular, and the variability of Minnesota *S. altissima* may lead to lower availability of the primary host during oviposition.

Jaenike (1990) noted environmentally based variation among insects could lead to geographical difference in host use. In areas where top-ranked hosts are abundant and oviposition frequent, he noted, thresholds for host acceptance may remain high, thus precluding use of low-ranking hosts. Where favored plants are rare or their *presence masked* (italics ours) by associated members of the plant community, thresholds for host acceptance are expected to fall, making the use of other plants more likely. Such a scenario may explain the distribution of *E. solidaginis* on *S. gigantea*.

Where the presence of *S. gigantea* is sufficient to encourage host acceptance by *Eurosta*, the difference in growth pattern of *S. gigantea* may have favored earlier oviposition on *S. gigantea* with subsequent temporal isolation and divergence of *Eurosta* populations.

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