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POTENTIAL SELECTIVE PRESSURES BY PARASITOIDS ON A PLANT-HERBIVORE INTERACTION¹

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Abstract. The potential role of the third trophic level in the evolution of plant-herbivore relationships was examined in the case of the goldenrod *Solidago altissima*, and the fly *Eurosta solidaginis*, which forms a round stem gall. Previous observation had shown that galls attacked by parasites are significantly smaller than those in which the gall maker survives. Two different mechanisms could cause such a pattern: parasite attack could occur before galls reach full size and the attacks could cause early cessation of growth, or attack could occur after galls reach their mature size, but with inherently small galls being more prone to attack. In the first instance, parasite attack would diminish the cost of the gall to the plant, and thus favor plant genotypes that facilitate parasites. In the second instance, parasites would exert selection pressure on the gall maker to induce larger galls.

Monitoring of marked plants in the field, and field experiments in which parasites were excluded from gall-bearing plants except during controlled periods, showed that parasite attack does not stop gall growth. The parasitoid wasp *Eurytoma gigantea* is limited to attacking small galls because of the limited reach of its ovipositor. This created a selection intensity of 0.50, favoring *Eurosta* that induce larger galls.

Evolutionary response to selection could be realized directly through change in the gall maker's stimulus ability, or less directly through phenological changes. Plant reactivity to the gall maker declined with plant age, so that late-starting galls were more vulnerable to parasite attack.

Key words: *coevolution*; *Eurosta*; *Eurytoma*; *gall makers*; *herbivore*; *natural selection*; *parasitism*; *Pennsylvania*; *phenology*; *Solidago*; *species interactions*.

INTRODUCTION

Studies of plant-herbivore interactions have focused primarily on the direct effects that producer and consumer have upon the growth, survivorship, and reproduction of one another (for recent reviews see Thompson 1982, Crawley 1983, Futuyma 1983). However, direct effects may not be responsible for some of the adaptive traits involved in a species interaction. Species on higher trophic levels may exert selective pressures that cause evolution within an interaction between species on lower trophic levels (Bergman and Tingey 1980, Price et al. 1980). Influence by the third trophic level may be especially important to interactions between single plant species and monophagous, herbivorous insect species. The host plant is the habitat of the small, immobile, immature feeding stages of many insect species. Parasitoids and predators search for food within this "habitat," often using plant traits as cues (Vinson 1976). Herbivores may use structural features of the plant as refugia from attack, or plant morphology may simply impede search (Hulspas-Jordan and Van Lentre 1978, Price et al. 1980). Therefore, plant defenses against herbivory could include traits that facilitate attack by the herbivore's natural enemies. Conversely, herbivore defense against attack could include behavioral and physiological traits that take advantage of plant properties. The third trophic level may push

a plant-herbivore interaction in either direction; the direction taken will depend in large part on which of the interacting species is under stronger selection pressure.

Here we present a study on the interaction between tall goldenrod, *Solidago altissima* (Compositae)³, and the gall-making fly *Eurosta solidaginis* (Diptera: Tephritidae). We examined the potential selective pressures exerted by the parasitic natural enemies of the gall maker to determine if they can be a significant force in the evolution of either the goldenrod's responsiveness to the gall maker or *Eurosta*'s ability to stimulate gall growth in the plant.

The experiments and field observations we report test the hypotheses that (1) parasite attack on the gall maker arrests gall development, thereby reducing the plant's cost of gall formation and (2) small galls, by virtue of their size, are more likely to be victims of successful parasite attack. Previous work on the goldenrod-gall fly interaction by Stinner and Abrahamson (1979) raised the possibility of a selective advantage to goldenrod individuals that facilitate parasitoid attack on the gall maker. These authors found that galls attacked by parasitoids were smaller and drew less energy away from normal plant growth processes. If parasitoids cause this reduced energy flow (by killing the

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³ This goldenrod is also known as *Solidago canadensis* var. *scabra* (Werner et al. 1980, Abrahamson et al. 1983). In previous papers (Hartnett and Abrahamson 1979, Stinner and Abrahamson 1979) we have referred to this species simply as *S. canadensis*.

gall maker) the plant should benefit, since galls lower the production of fruits and reduce vegetative propagation (Hartnett and Abrahamson 1979). Alternatively, galls that are inherently small may be more vulnerable to penetration by parasitoid ovipositors. This would result in a selective advantage to gall makers inducing large galls. In other systems variation in parasitoid attack frequency has been linked to variation in gall size and morphology (Askew 1961, Weis 1982, 1983); parasitoids may have exerted a major influence in the morphological evolution of cynipid wasp galls (Price 1980, Cornell 1983).

The question of which, if either, selective regime can operate was engendered by another study, which showed that variation in gall size and growth rate is caused by genetic variance in both the goldenrod and the gall maker populations (A. E. Weis and W. G. Abrahamson, *personal observation*). Given heritable variation in gall traits, phenotypic evolution in either plant or insect is feasible if selective pressures are of sufficient magnitude.

NATURAL HISTORY OF THE SYSTEM

The larvae of *Eurosta* cause the growth of a spheroid-shaped swelling on the stem of tall goldenrod. Although the related goldenrods *S. canadensis* (sensu strictu) and *S. gigantea* are infested by northern and western populations of this insect, *S. altissima* is the sole host plant in central Pennsylvania (Givens 1982). It is a perennial, clonal herb commonly found in old fields and along roadsides (Werner et al. 1980).

The life history of the gall maker was detailed by Uhler (1951). The cycle begins in the spring when the larva, which has overwintered in the previous season's gall, pupates and then emerges to mate and oviposit. In mid-May the female injects an egg into the terminal bud through a tube-like ovipositor, leaving a scar. The first-instar larva tunnels through the bud and into the stem just below the apical meristem. Newly formed galls become apparent by mid-June and reach their mature diameter within 3 wk. The larvae feed on the inner tissues of the gall until October, when they enter diapause.

The primary natural enemies of *Eurosta* during its larval growth stage are the parasitoid wasps *Eurytoma obtusiventris* and *E. gigantea* (Hymenoptera: Eurytomidae) and the inquiline beetle *Mordellistena unicolor* (Coleoptera: Mordellidae) (Uhler 1951, 1961, Cane and Kurczewski 1976, Stinner and Abrahamson 1979, Abrahamson et al. 1983). *E. obtusiventris* is an internal parasitoid that delays development until September. By contrast, *E. gigantea* lays its egg within the gall's central cavity; the larva feeds externally on the gall maker larva, then consumes gall tissue (Uhler 1951). The beetle lays its egg just below the gall's epidermis; the larva then tunnels through the gall, eventually ending in the central chamber, where it consumes the gall maker.

MATERIALS AND METHODS

This study was conducted in the summers of 1982 and 1983 at the Bucknell University Chillisquaque Natural Area, Montour County, Pennsylvania, USA. The host plant grew in two fields removed from agriculture within the past 10 yr.

Phenology of the gall maker and its parasites

In 1983, daily emergence of gall maker adults was recorded from ≈ 1000 galls held in an outdoor screen cage. Median emergence date and first and third quartile dates, were determined from a plot of cumulative percent emergence vs. date. Emergence of the adult parasites was also monitored.

The timing of gall appearance in 1983 was determined from a group of 719 shoots bearing oviposition scars. In late May, these were marked with numbered tags and even-numbered stems were examined for gall appearance at 3–4 d intervals. Median and quartile dates of appearance were calculated. A sample of 54 punctured buds was collected in the 1st wk of June in 1983 and all buds were dissected to determine the depth to which the egg had been inserted into the bud.

Growth phenology of galls was determined from periodic destructive samples. In 1982, ≈ 250 newly formed galls were marked with numbered tags. At 3–7 d intervals, samples of 20 galls, chosen by a randomization computer program, were collected for measurement. In 1983, the 360 odd-numbered marked stems were sampled by the same procedure. We measured diameter at the equatorial plane. Galls were then cut in half at the equator, and the thickness of the gall wall was measured at four points and averaged. In 1982, outer dimensions were measured with calipers and inner dimensions with an ocular micrometer. In 1983, a dissecting microscope with a drawing tube attachment was used to superimpose the image of the gall on an APPLE II graphics tablet; the image was traced with a magnetic pen, and a computer program calculated the dimensions from the tracing.

Phenology of enemy attack was determined by a serial exclusion/exposure experiment. In each of the two years ≈ 700 galls were marked with numbered tags as soon as they became visible. Fifty galls (60 in 1983) were left unmanipulated as controls. The remaining galls were covered with parasitoid exclusion sleeves of nylon organdy (5 × 12 cm) secured with wire ties and paper clips. Immediately, a randomly chosen subsample of 50–60 galls was uncovered for 1 wk, during which time parasites were free to attack. At week's end galls were re-bagged and the next subsample was exposed. In each year, one additional group remained bagged for the entire season to test sleeve efficacy. At the season's end the galls were dissected and their contents identified. Comparison of mean diameters of the exposure groups to an unbagged control group showed that bagging had no effect on gall size.

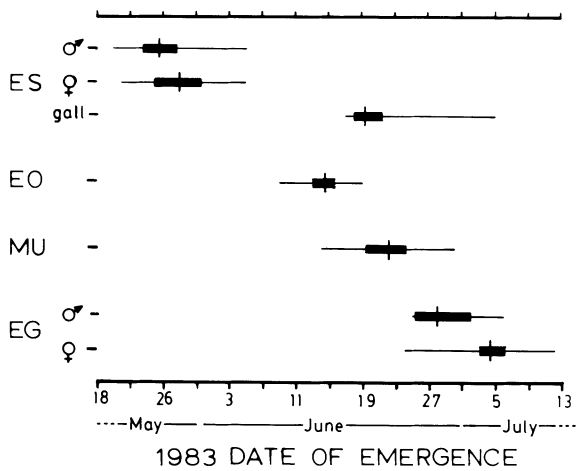


FIG. 1. Dates of emergence of *Eurosta* and its parasites and of the appearance of new galls. Overwintered insects were reared from their galls in an outdoor emergence cage; gall formation was monitored on marked plants. Vertical lines indicate medians, horizontal lines show ranges, and wide horizontal bars connect the first and third quartiles. Abbreviations (sample sizes in parentheses): ES = *Eurosta solidaginis* (92 ♂♂, 94 ♀♀, 195 galls); EO = *Eurytoma obtusiventris* (14 individuals); MU = *Mordellistena unicolor* (66 individuals); EG = *Eurytoma gigantea* (17 ♂♂; 31 ♀♀).

The exclusion/exposure experiment in 1983 was also used to determine if parasitoid attack stops gall growth. Gall diameters were measured at the beginning of each exposure interval, then again at the time of dissection. Mean postexposure growth increments of *E. gigantea*-attacked and unattacked galls were compared in each exposure group.

Plant age at gall appearance: effect on growth and survivorship

We tested whether plant age at the time of gall appearance has an effect on gall size by following the growth of age cohorts in the field. In 1982, 150 punctured stems were marked in late May; 359 stems (the even-numbered plants described above) were used in 1983. All stems were censused at 2–4 d intervals throughout June, then at 4–7 d intervals into August. Cohorts consisted of the set of galls first discovered on a census date. Diameters were measured on all galls on every census date. Final cohort mean diameters were compared with one-way analysis of variance and the Student-Newman-Keuls test for separation of means.

In October of each year, the galls were dissected to determine if the incidence of parasite attack varied with the date of gall appearance. In order to best meet the requirement of minimum expected values for a chi-square test, cohorts were pooled into early and late groups. Small sample sizes dictated the use of Fisher's Exact Test in some instances.

In both years, it seemed many of the galls on any one plant clone appeared on the same date. This led

us to suspect the diminished growth of late-starting galls to be due in part to clonal (genotypic) differences in plant reactivity rather than to plant age per se. Alternatively, "clusters" of galls could be the progeny of individual female flies, with each cluster inheriting genes for fast or slow gall formation. These possibilities were investigated in a greenhouse experiment in which plant genotype and age were crossed factors, and fly genotype was randomized. Plants were grown in 15-cm pots from 2-g rhizome cuttings taken from four *S. altissima* clones growing near Lewisburg, Pennsylvania. Three groups were started at 12-d intervals starting on 1 March 1983. Eight weeks after the first group was started, all groups were exposed to *Eurosta* oviposition by placing a plastic sleeve over the plant and introducing a randomly selected, mated female. All 108 shoots were punctured and 45 formed galls. Gall diameter was measured at four dates. Data were analyzed in a factorial, repeated-measure analysis of variance after logarithmic transformation to equalize variances.

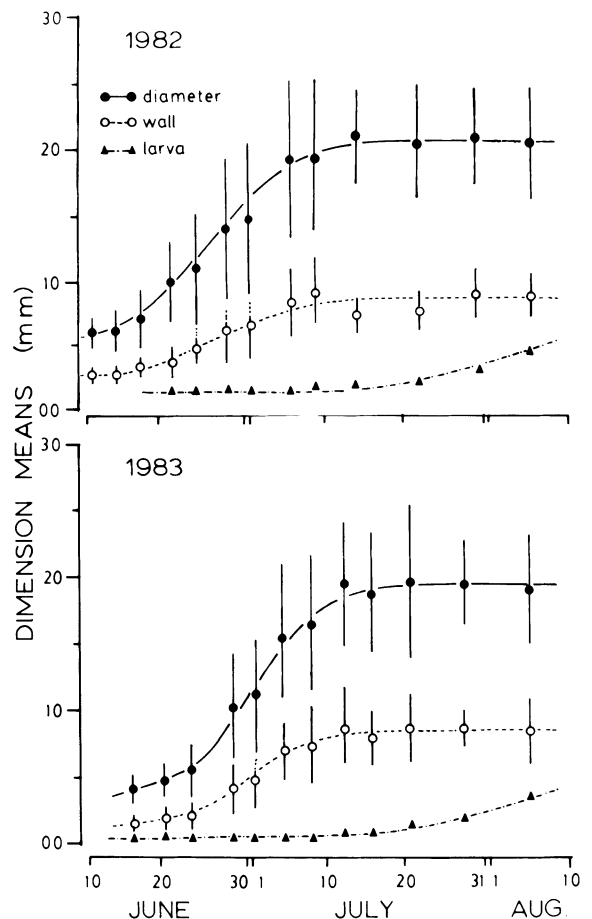


FIG. 2. Growth curves for ● gall diameter, ○ gall wall thickness, and ▲ *Eurosta* larval length. On each date 15–25 galls were collected, dissected, and measured. Points indicate means, and vertical lines indicate ± 1 SD. Curves were fitted by eye.

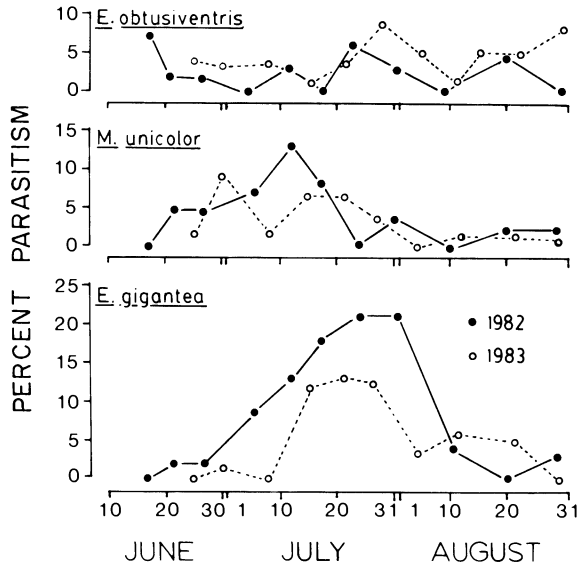


FIG. 3. Temporal dispersion of oviposition for the three insect parasitoids of *Eurosta*. Points indicate the percent of galls exposed to attack during a 7–10 d interval that were parasitized by the three species. Sample sizes ranged between 35 and 46 in 1982, and between 55 and 64 in 1983. The left-most points for each year in each graph are bagged control groups, i.e., they were exposed for the short period before the experiment began, but were then bagged for the rest of the season.

Size-dependent attack and survival

The functional relationships between gall size, enemy attack, and gall maker survival were determined from a field sample. Galls were measured using a template with circular holes in graduated 1-mm increments; the diameter was estimated as 0.5 mm less than the diameter of the smallest hole the gall would pass through. Galls were dissected to determine the percent survivorship and percent parasitism in each size-class. A regression of percent parasitism on gall size was performed where appropriate, but Spearman's rank correlation coefficient was used in other cases. Not all galls contained living insects, as some *Eurosta* die during development from fungal infection and other causes; these galls were excluded from the percent parasitism calculations, since they were presumably unsuitable for parasitoid oviposition, but were included when calculating size-dependent survivorship.

Data from this collection were also used to measure the selection intensity on gall size exerted by parasitism. The selection intensity is the difference between the mean phenotype of the selected individuals (i.e., the diameters of those that escaped parasitism) and the mean phenotype of the population as a whole, divided by the population standard deviation (Falconer 1981). This index is a measure of the magnitude and direction of a selective pressure but not of the evolutionary response to that pressure.

RESULTS

Phenology of insect emergence and gall appearance

The parasitoid *Eurytoma obtusiventris* emerges during the 3-wk lag between peak emergence of the gall maker and the appearance of new galls (Fig. 1). The other two parasite species emerge after peak gall appearance.

Gall growth and phenology of parasite attack

The *Eurytoma* wasps insert their eggs into the gall cavity or directly into the gall maker; thus gall size mediates host accessibility to these enemies. The thickness of the plant tissue that conceals *Eurosta* changes dramatically over the early summer (Fig. 2). In the sample of punctured buds, first-instar gall makers were found tunneling 1.79 ± 0.42 mm ($\bar{X} \pm SD$; $n = 36$) beneath the bud surface. On the first date that galls were visible, wall thicknesses were 2.48 mm and 1.59 mm in 1982 and 1983, respectively (Fig. 2). In both years gall growth reached its plateau near 10 July, when wall thickness averaged between 8 and 9 mm (Fig. 2).

To reach the host, the *Eurytoma* wasps need ovipositors at least as long as the depth of the intervening plant tissue. Ovipositor length ($\bar{X} \pm SD$) for *E. obtusiventris* was 2.69 ± 0.19 mm ($n = 9$). In both years gall walls quickly grew thicker than this (Fig. 2). Further, when the growth plateau was reached a substantial proportion of the gall population had walls thicker than the length of the average *E. gigantea* ovipositor, which was 8.77 ± 1.23 mm ($n = 35$). In 1983, for instance, mean wall thickness on the last sampling date exceeded the mean ovipositor length by 0.12 mm (Fig. 2).

Observing the potential change in accessibility of the gall maker over the course of development led to the formulation of the hypothesis that oviposition by the two *Eurytoma* species is timed to take advantage of the host's "window of vulnerability" (Washburn and Cornell 1981); that is, they should attack before galls grow too big. In the serial exclusion/exposure experiment we determined the temporal distribution of attack and the effect of attack on subsequent gall growth.

TABLE 1. Final mean diameters of galls containing normal *Eurosta* larvae or its various parasitoids. Data from the serial exclusion/exposure experiment.*

Gall content	Diameter (mm)		
	$\bar{X} \dagger$	SD	<i>n</i>
<i>Eurosta solidaginis</i> (gall maker)	20.90 ^a	3.31	393
<i>Eurytoma obtusiventris</i>	20.79 ^a	2.72	24
<i>Mordellistena unicolor</i>	20.42 ^a	3.65	19
<i>Eurytoma gigantea</i>	16.91 ^b	3.94	34

$F_{(3, 466)} = 15.16$; $P < .001$

* Bags on the galls had no significant effect on gall growth.

† Means with the same superscript letter do not differ significantly.

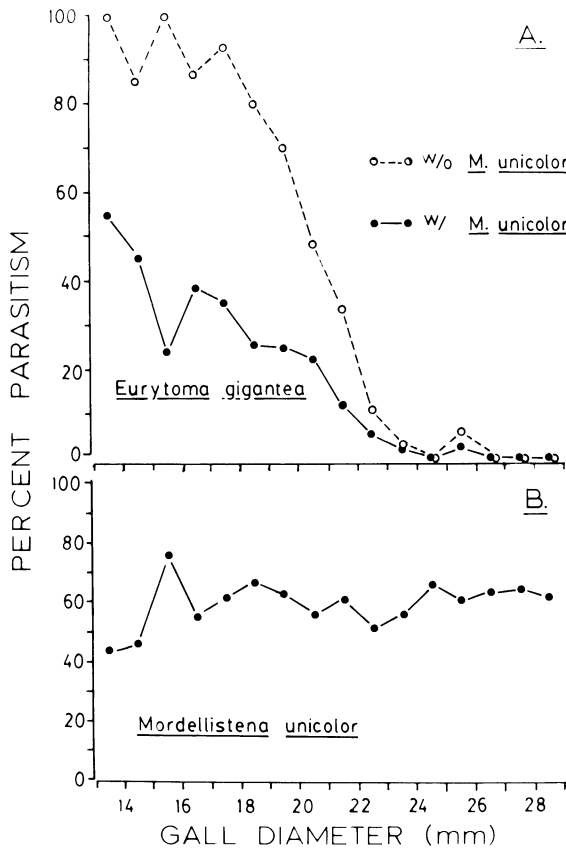


FIG. 4. Size-dependent parasitoid attack on *Eurosta*. (A) Parasitism by *Eurytoma gigantea*: ●—● percent of inhabited galls in each size-class that contained only this wasp ($r_s = -0.949$, $P < .001$). ○—○ percent of galls inhabited by species other than *Mordellistena unicolor* that contained the wasp ($r_s = -0.970$, $P < .001$). The upper curve thus estimates the size-dependent attack rates by *E. gigantea* in the absence of multiparasitism. (B) Parasitism by *Mordellistena unicolor*, calculated as the percent of inhabited galls in each size-class containing this beetle. The linear regression of parasitism vs. size was not significant ($Y = 47.5 + 0.006X$; $r^2 = 0.06$; $F_{(1,14)} = 1.99$; $P = .18$).

Results of the bagging experiment seem to indicate that oviposition by *E. obtusiventris*, the smaller parasitoid, is not affected by gall growth, since some galls were attacked in most exposure groups (Fig. 3). However, these results may reflect faults in experimental design. It is highly probable that *E. obtusiventris* attacked before galls were bagged; some hosts from galls in the control group (bagged at the beginning of the experiment and never exposed thereafter) were also parasitized by this species. Alternatively, this species may be able to penetrate the bags, oviposit, and escape. However, size considerations make early attack the more likely explanation. By the time of bagging, mean gall diameter (\pm SE) reached 6.28 ± 0.30 mm ($n = 45$) in 1982 and 9.01 ± 0.50 mm ($n = 58$) in 1983. Mean wall thickness at these times would have been 2.53 and 3.72 mm, respectively (A. E. Weis, *personal observa-*

tion). Galls attacked by *E. obtusiventris* did not differ in final size from unattacked galls (Table 1). It is unlikely that *E. obtusiventris*, with its mean ovipositor length of 2.69 mm, attacked galls later in the season.

In each year, attack by the larger parasitoid, *E. gigantea*, reached its peak after 10 July (Fig. 3), when galls had reached full size (see Fig. 2). Many if not most of the galls were unavailable to the average-sized female of this species during the time of peak attack. Consequently, *E. gigantea* successfully oviposited into galls significantly smaller than those in which hosts were unattacked (Table 1). This finding confirms that of Cane and Kurczewski (1976). Attack did not retard gall growth; comparison of the mean postexposure growth increment of *E. gigantea*-attacked galls and unattacked galls in each exposure group showed that all galls had completed growth by the time parasitoids oviposited. The "window of vulnerability" hypothesis can be rejected for this species.

Oviposition by the inquiline *Mordellistena unicolor* does not appear to be limited by gall size, because the egg is laid just below the gall epidermis. Attack by this beetle peaked in late June and early July (Fig. 3), but continued into August.

Gall size-dependent host mortality

Eurosta larvae inhabiting small galls were highly vulnerable to attack by *E. gigantea*, but vulnerability declined with gall diameter in a sigmoidal fashion (Fig. 4A, lower curve). The actual rate of attack by *E. gigantea* was probably underestimated in these data because *E. gigantea* itself can be killed by the beetle.

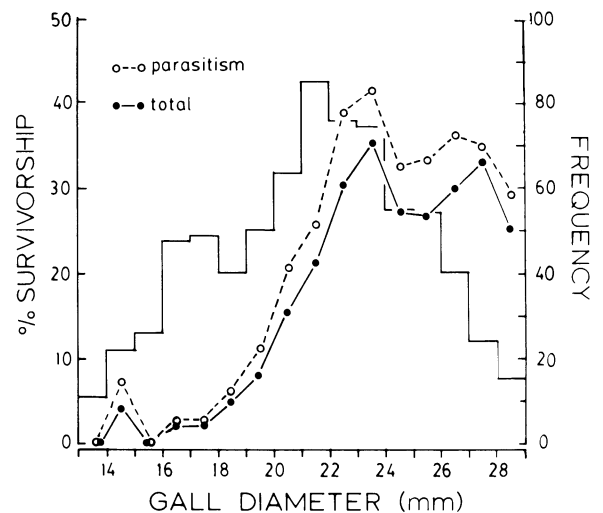


FIG. 5. Size-dependent survivorship of *Eurosta*, and the frequency distribution of gall diameter. ○—○ percent of inhabited galls in each size-class that contained surviving *Eurosta* ($r_s = 0.849$, $P < .001$). ●—● percent of all galls in each size-class that contained the surviving gall maker ($r_s = 0.830$, $P < .001$). The frequency histogram shows the number of galls in each size-class.

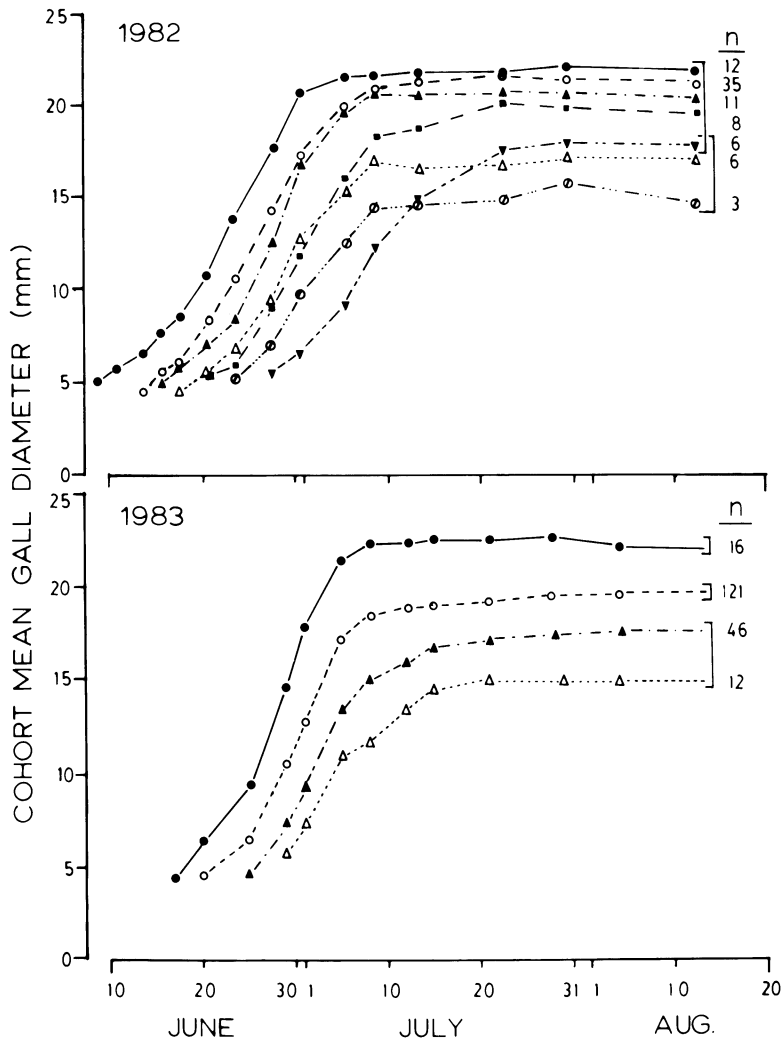


FIG. 6. Growth curves for age cohorts of galls. A cohort consisted of the set of newly formed galls first visible on a census date. Each gall was measured on the first date it was visible and on all subsequent census dates. Analysis of variance for final cohort mean diameters showed significant differences amongst cohorts in both 1982 ($F_{(6,75)} = 3.12$; $P = .009$) and 1983 ($F_{(3,191)} = 7.50$; $P = .0001$). Brackets enclose final means that did not differ significantly from one another.

Although *M. unicolor* oviposits in June and July, the larva burrows through the gall cortex until late in the summer and only then enters the central chamber, where it eats the resident: either a gall maker or a wasp larva (A. E. Weis, *personal observation*). When size-dependent attack rates were recalculated excluding galls attacked by the beetle, the sigmoidal shape of the curve was enhanced (Fig. 4A, upper curve). No pattern of gall size-dependent attack was seen in *M. unicolor* (Fig. 4B). Arcsine transformation of the percentage data did not remove the upper and lower plateaus; thus the sigmoidal shape is not simply a statistical artifact.

The pattern of *E. gigantea* attack resulted in increased survivorship of *Eurosta* with increased gall size. The two curves depicted in Fig. 5 show survivorship from insect enemy attack and survivorship from all the mortality factors that operate into the au-

turn. A histogram depicting the frequency distribution of gall diameter is also shown. These curves indicate that increased survival of the gall makers in large galls is primarily due to escape from *E. gigantea* attack. We conclude that large gall size confers a greater chance of survivorship upon *Eurosta* through its inhibitory effect on oviposition by the parasitoid *E. gigantea*.

Plant age at gall appearance: effect on growth and parasite attack

In 1982 and 1983 marked age cohorts of galls were regularly measured to determine if date of initiation affected gall growth and thereby affected vulnerability to attack. Fig. 6 shows that late cohorts tended to mature at smaller sizes. The trend was clearer in 1983, probably due to the more than doubled sample size. Just as the late cohort reached its growth plateau, stem

TABLE 2. Results of the greenhouse experiment to test the effects of plant clone (genotype) and plant age at oviposition on gall diameter growth.

A. Mean gall diameters by plant age at oviposition				
Plant age at oviposition (d)	Mean gall diameter (mm)			
	24 Apr	1 May	10 May	21 May
56	4.38	8.50	14.59	14.79
44	6.27	13.11	18.77	19.00
33	6.88	13.24	17.53	17.87

B. ANOVA table*				
Source of variation	df	MS	F	P
Within gall, among dates				
Plant clone	3	1.034	3.60	.023
Plant age (Clone × Age)	2	1.156	4.02	.027
Error	6	0.253	0.88	.519
Total				
Measuring date (Date × Clone)	3	8.156	254.02	<.001
(Date × Age)	9	0.106	3.29	.002
(Date × Clone × Age)	6	0.039	1.22	.302
Error	18	0.017	0.53	.935
Error	102	0.032		

* Using a repeated-measures design, with the data transformed to natural logs.

elongation paused as the meristem switched from the production of leaves only to the production of both leaves and floral branches (A. E. Weis, *personal observation*).

Our greenhouse experiment showed that increasing plant age had a negative effect on gall growth even when plant genotype (clone) was controlled for and insect genotype randomized. Over the four measuring dates, gall size was smallest for the oldest plant group (Table 2). Gall diameters differed significantly among measuring dates (i.e., the galls grew). The significant interaction effect among measuring dates and plant genotypes (Table 2) indicates that gall growth curves for the several clones were not of the same shape; the interaction between measuring date and plant age was not significant. Date of gall initiation did not differ significantly among clones or plant age groups. These results

indicate that in the field, plant age per se at the time of gall initiation affects gall growth, and is not simply a variable confounded with plant genotype.

Given the negative effect of a late start on gall growth, we predicted parasitism by *E. gigantea* would be higher in the late cohorts. We also suspected that incidence of *E. obtusiventris* could be different in early and late cohorts due to imperfect synchrony between gall appearance and oviposition activity. Table 3 shows that *E. gigantea* was disproportionately abundant in the late cohorts, while *E. obtusiventris* and *M. unicolor* were randomly distributed among cohorts. Although one of the parasites is more likely to attack late galls, total gall maker mortality due to parasitism does not necessarily increase in late cohorts. In 1982 early galls were less likely to be parasitized than later ones; this was not the case in 1983 (Table 3). When larval mortality due to all causes was considered, late-starting gall makers were found to suffer disproportionately (Table 4). We conclude that there is a selective advantage to early oviposition by the gall maker *Eurosta*, and that escape from parasite attack is at least occasionally an important component of this advantage.

DISCUSSION

There are two possible evolutionary changes in an interaction between a plant species and an insect herbivore when plant phenotypic variation causes variation in enemy attack. The first is a shift by the plant species toward a phenotype that facilitates enemy attack. The second is a change in the way the insect uses the plant so as to reduce risk. The direction in which the interaction evolves will depend upon the relative strengths of the selective pressures, and the existence of sufficient genetic variation in the appropriate species for the selected trait.

Parasites as a selective pressure on the plant

Our evidence shows that parasite attack does not stop gall growth, and thus does not benefit the plant. These results seem to conflict with the findings by Stinner and Abrahamson (1979) that the plant's energetic cost for parasitized galls was less than for galls with normal gall makers. They found that 6.72% of ramet

TABLE 3. Incidence of attack by the various parasitoids of *Eurosta* in early- and late-forming galls. Galls in which no species survived were excluded from the analysis.

Species	1982 date of gall formation				1983 date of gall formation			
	Before 11 June (n = 33)	After 11 June (n = 20)	χ ² *	P	Before 20 June (n = 112)	After 20 June (n = 46)	χ ² *	P
<i>Eurytoma obtusiventris</i>	2	2957†	7	1420†
<i>Mordellistena unicolor</i>	8	5	0.004	.945	54	19	0.624	.429
<i>Eurytoma gigantea</i>	2	6026†	11	13	8.600	.003
Total	12	13	4.098	.043	72	33	0.813	.436

* All chi-square values have 1 degree of freedom.

† By Fisher's Exact Test.

production was allocated to normal galls but only 5.33% (or 79.3% as much) when galls were parasitized. Energy values (joules per milligram) of the two types of galls were the same, so that gall volume should be proportional to energy content when equal density is assumed. A further examination of our data suggests that this energy "savings" to the plant is a consequence of the increased vulnerability of hosts in small galls. The mean volume of normal galls in the serial exclusion/exposure experiment was 5085.8 mm³ (based on their measured diameter and the formula $V = [4/3] r^3$) while that of parasitized galls was 3952.5 mm³. Thus, the mean volume of parasitized galls was only 77.7% as great as normal, which is very close to the previously observed difference in energy allocation. The greatest contributor to the apparent energy "savings" that comes with enemy attack is *E. gigantea*, whose average gall volume was 2848.4 mm³, or only 55.9% that of normal galls. The mean volume of galls attacked by the other two parasitoids is essentially the same as those unattacked. This suggests that the seeming diminution of energy loss to the plant in parasitized galls is a result of *E. gigantea*'s inability to penetrate large galls. The magnitude of the apparent "savings" will vary with the relative abundance of this wasp in the parasite guild.

Goldenrod individuals that produce penetrable galls will not necessarily realize greater fitness through the agency of parasites. Plant traits that decrease herbivory within a season by contributing to herbivore mortality by predators and pathogens have been shown theoretically (Moran and Hamilton 1980, Price et al. 1980) and empirically (C. E. Bouton et al., *personal communication*) to be favored by selection. Low reactivity of the plant to the gall maker would on average increase parasite attack on the gall maker, but the plant would still devote less energy to gall formation even when no parasite attacks. There is the further possibility that the alleles that code for high reactivity have favorable pleiotropic effects on general growth and reproductive characters in the plant. In such a case it would be possible that highly reactive clones have higher than average reproductive rates in spite of their production of large galls.

We conclude that phenotypic variation in the plant's reaction to the gall maker has a profound effect on the success or failure of parasitoid attack, but attack in and of itself is quite unlikely to be a direct cause of differential reproduction by plant phenotypes (and genotypes). Thus the natural enemies of *Eurosta* are not an immediate force in the evolution of goldenrod. This is not to say that the third trophic level can be of no consequence in goldenrod's evolution. As we argue in the next section, parasitoids exert a selective pressure on the gall maker to stimulate larger galls. Over the long run, parasitoids may place an indirect pressure on goldenrod, because evolution by *Eurosta* toward larger gall size could eventually place so great a drain on plant resources, including those devoted to reproduction (see

TABLE 4. Survivorship of *Eurosta* in early- and late-forming galls. Mortality due to all causes is considered.

	1982 date of gall formation		1983 date of gall formation	
	Before 11 June	After 11 June	Before 20 June	After 20 June
No. that died	15	18	85	56
No. that survived	21	7	40	13
	$\chi^2 = 5.46$ df = 1; P = .019		$\chi^2 = 3.87$ df = 1; P = .049	

Hartnett and Abrahamson 1979), that lower reactivity could be favored.

Parasites as a selective force on the gall maker

Our results present ample evidence that parasites are capable of acting as selective agents in the evolution of *Eurosta*'s ability to produce galls. The size-dependent survival rates (Fig. 5) indicate larvae in large galls are more likely to make genetic contributions to subsequent generations.

Our field experiments showed that *E. gigantea* is responsible for the increase in *Eurosta* mortality with decrease in gall size. Laboratory experiments by Weis et al. (1985) on the behavior of this wasp have confirmed the role of gall size in determining gall maker vulnerability to attack. An egg can be laid only when the thickness of the gall's wall is less than the length of the wasp's ovipositor. The greater frequency of *E. gigantea* in small galls is not due to a propensity of females to choose small galls, since large, impenetrable galls were equally attractive in the laboratory and were repeatedly probed by females despite the impossibility of success.

E. gigantea is generally not the most abundant enemy in the guild (Table 4). Incidence of attack by this species ranges from 2.2 to 26.7% (Ping 1915, Uhler 1951, 1961, Miller 1959, Cane and Kurczewski 1976, and Table 3). These figures may mean that this parasitoid has only a modest role in regulation of its host's population size, but the nonrandom distribution of attack with respect to gall diameter shows it can be a potent force in the evolution of the gall maker's stimulus ability. For instance, in the sample of galls used to detect size-dependent survivorship (Fig. 5), mean gall diameter was 20.62 mm (SD = 3.71 mm), while the *Eurosta* larvae that escaped parasitism had a mean gall diameter of 22.51 mm. Only 14.7% of the gall-makers were killed by *E. gigantea*, yet this level of attack was sufficient to create a selection intensity on gall diameter of 0.50. The rate of evolutionary response to selection of this magnitude also will depend upon the heritability of gall diameter under field conditions, but these data illustrate the importance of parasitoid attack for the evolution of the plant-gall maker interaction.

It appears that *E. gigantea* is also capable of exerting

selection upon the timing of gall maker emergence and oviposition, because of the decline in plant reactivity with age. Late-starting gall makers are less likely to survive to the end of the summer, in large part because they suffer greater parasitism. Climatic conditions may exert a counterbalancing selective pressure on emergence time; Uhler (1951) noted that *E. solidaginis* is inactive at temperatures below 18°C. The mother's energetic cost of flight at temperatures typical of April and early May might be prohibitive compared to the "cost" of losing a fraction of her offspring to parasitism.

In this paper, we have dealt with the effect of insect enemies of *Eurosta* and their effects on evolution of the plant-herbivore interaction. Our conclusion is that the wasp *E. gigantea* exerts an upward selective force on gall size, both for direct stimulus ability of the gall maker during the larval stage and for early eclosion and oviposition by adults. However, this upward selective pressure is not unopposed, since avian predators, specifically the Downy Woodpecker (*Picoides pubescens*) and the Black-capped Chickadee (*Parus atricapillus*) frequently peck open galls and eat the diapausing larvae during the winter (Milne 1940, Schlichter 1978). These predators are size selective, preferring large galls (Cane and Kurczewski 1976), presumably because they are more visible and because they are more likely to contain gall maker larvae. Stabilizing selection may thus favor an intermediate gall size that presents a trade-off in mortality risks from these two sources.

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