

## INTERSPECIFIC COMPETITION BETWEEN ROOT-FEEDING AND LEAF-GALLING APHIDS MEDIATED BY HOST-PLANT RESISTANCE<sup>1</sup>

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**Abstract.** While the competitive interactions of herbivores are often debated, rarely have the resistance traits of their host plants been considered as an important factor that might determine the outcome of an interaction. In the study reported here, host-mediated interactions were explored for two aphid species that feed on plants of the genus *Chenopodium*. *Pemphigus betae* feeds underground on roots, while *Hayhurstia atriplicis* feeds aboveground where it forms leaf galls. Although they never encountered one another directly, these two aphid species shared a common resource, the phloem sap of their host.

We examined the effects of each of these herbivore species on their host plants and on one another through several garden and growth chamber experiments. Four major results emerged. First, the root-feeding aphid *P. betae* had no significant effects on its hosts. In contrast, leaf galling by *H. atriplicis* reduced overall host mass by an average of 54% and seed set by an average of 60%. Second, competitive interactions between the herbivore species depended on the level of host resistance to leaf galling by *H. atriplicis*. On susceptible plants, leaf-galling colonies of *H. atriplicis* reduced *P. betae* numbers by an average of 91%, often eliminating the root feeders entirely. In contrast, on plants resistant to galling, *H. atriplicis* colonies were smaller and did not affect *P. betae* infesting roots of the same hosts. Third, the interaction was asymmetrical; although *H. atriplicis* had a strong negative effect on *P. betae*, the latter showed no measurable effects on *H. atriplicis*. Censuses indicated that the strong negative effects of *H. atriplicis* on *P. betae*, as found in the growth chamber and garden experiments, also take place naturally in the field. Fourth, although one might expect plants resistant to one aphid species to be resistant to other aphids also, resistance to leaf-galling aphids is not correlated with resistance to root-feeding aphids in this system.

**Key words:** aphids; *Chenopodium*; gall formation; *Hayhurstia atriplicis*; herbivore interactions; herbivore/plant interaction; host-plant resistance; interspecific competition; lamb's-quarters; *Pemphigus betae*; root feeders.

### INTRODUCTION

Interspecific competition among herbivorous insects has often been discounted as a widespread or important phenomenon (Andrewartha and Birch 1954, Hairston et al. 1960, Lawton and Strong 1981). Recently, however, a number of studies have documented strong negative interspecific effects (e.g., Stiling and Strong 1984, Karban 1986). These effects differ from those emphasized by classical competition theory. While the classical view would suggest that competition is severe between closely related species using similar niches, competing herbivorous insects may be very distant taxonomically (Karbon 1986) and may utilize their shared host in very different ways, feeding on different tissues (Karbon 1986) or at different times of the season (Faeth 1986, Harrison and Karban 1986). A further charac-

teristic of the interspecific effects occurring among herbivorous insects is that they are typically asymmetrical (Faeth 1986, Karban 1986). These characteristics of interactions among herbivores arise from the fact that tissues of an individual plant depend on a common resource budget, as pointed out by Janzen (1973) and refined by Whitham et al. (1990). Thus, species feeding at different times or on different parts of a plant may strongly affect the quality or quantity of resource available to one another.

Since interactions among herbivores appear frequently to be mediated through the chemistry and physiology of the host plants, the outcomes of herbivore-herbivore interactions are likely to depend on the level of host resistance to each herbivore species. Recent studies on a wide variety of plants suggest that variation in resistance to herbivore attack is widespread within natural plant populations (e.g., Edmunds and Alstad 1978, Moran 1981, Whitham 1983, Karban 1987, Maddox and Root 1987, Fritz and Price 1988,

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Moran and Whitham 1990). This variation often involves different levels of susceptibility to herbivore manipulation of host chemistry, morphology, and physiology (McCrea and Abrahamson 1987, K. C. Larson and T. G. Whitham, *personal observation*).

Here, we characterize the interaction occurring between a root-feeding aphid species, *Pemphigus betae* (Aphididae: Pemphiginae), and a shoot-feeding aphid species, *Hayhurstia atriplicis* (Aphididae: Aphidinae), feeding on a shared host plant, *Chenopodium album* (lamb's-quarters), that varies in resistance. These two species are spatially separated on their hosts, never encounter one another directly, and do not share any natural enemies. However, they both feed on the phloem sap of the same plant species and thus might be expected to compete. The host species includes two genetically different types, susceptible genotypes upon which *H. atriplicis* successfully forms galls and resistant genotypes upon which *H. atriplicis* forms colonies but not galls. All host genotypes are susceptible to *P. betae*. We examined the consequences of resistance for the outcome of the interaction between these two insects. Specifically, we addressed the following questions: (i) How do these two aphid species affect the relative fitness of susceptible and resistant host plants? (ii) How does host resistance affect aphid performance? (iii) If these aphid species compete are their interactions symmetrical or asymmetrical? (iv) Does host resistance affect the outcome of interspecific competitive interactions?

#### *Natural history*

*Pemphigus betae* typically shows a complex life cycle in which it alternates between the roots of a herbaceous summer host and the leaves of a woody spring and fall host (narrowleaf cottonwood, *Populus angustifolia*). However, the woody hosts are commonly omitted from the life cycle, particularly at sites where these hosts are resistant and aphid performance is low (Moran and Whitham 1988a). In our northern Utah study sites along the Weber River, the summer hosts include *Chenopodium* (lamb's-quarter) species, *Polygonum* (smartweed) species, and *Rumex* (dock) species. Of these, the most commonly occupied host is *Chenopodium album*, upon which we focus in this study. *Chenopodium album* is an introduced, annual weed associated with disturbed sites (Arnold et al. 1980). When these aphids do not alternate hosts, roots are colonized early in the spring by wingless females that overwintered as adults in the soil. However, when they do alternate hosts, winged migrants fly in June from narrowleaf cottonwood to *C. album* where they deposit active nymphs on leaves. These nymphs crawl through crevices in the soil to colonize roots or rootlets. The root-feeding phase consists of a series of wingless parthenogenetic generations. First-instar nymphs are small and mobile and are probably responsible for most movement between feeding sites within the root system of an individual

plant. The life cycle does not include any winged morphs able to fly from one root host to another. Thus, all dispersal is local or occurs via the winged autumn migrants that initiate the cottonwood phase of the life cycle.

*Hayhurstia atriplicis* feeds on leaves of *C. album* and several other *Chenopodium* species in our study area and elsewhere is known from *Atriplex* and *Beta* species (Hayhurst 1909). It spends its entire life cycle on these hosts. On most *Chenopodium*, it typically feeds on the upperside of the leaf and induces longitudinal folding to form a pod-shaped pseudogall. During the summer, both wingless and winged parthenogenetic females are produced. The latter fly to new plants to initiate colonies. Nymphs born in one gall frequently walk to additional, younger leaves to initiate further galls. Consequently, once colonized by a single winged female, all of the new leaves on a plant may be attacked and galled by her descendants. Wingless sexuals are produced in autumn, and the sexual females deposit overwintering eggs near the seed heads (Hayhurst 1909, N. A. Moran, *personal observation*).

Feeding and reproduction by *H. atriplicis* can also occur without gall formation; nongalling colonies develop on older leaves, on stems, and, in our study area, on certain *C. album* that are resistant to gall formation. Although some plants are resistant to galling by *H. atriplicis*, and others are susceptible, all plants are susceptible to root infestations of *P. betae*. These resistance and susceptibility traits are central to our study because they allow us to critically examine how host resistance might mediate the competitive interactions of two aphid species exhibiting very different life histories.

While the mechanism of resistance is now known, it results in complete suppression of the leaf-galling response (to *H. atriplicis*), even when aphids occur on young leaves at stages that would be susceptible in other *Chenopodium*. Resistant and susceptible *C. album* genotypes occur in the same sites and may frequently be found growing in mixed stands. Both are colonized by both aphid species, but only on the susceptible types does colonization by leaf aphids result in the production of galls. In our study area in the lower Weber Canyon, resistant and susceptible plants differ in branching pattern and leaf shape and, in the absence of aphids, can be distinguished within 3 wk of germination. At other sites in Utah and Arizona, this correlation between architecture and resistance is absent (N. A. Moran, *personal observation*). Specimens of resistant and susceptible plants from several sites have been confirmed as *C. album* (S. Welsh, *personal communication*). The susceptible state is probably ancestral, based on the observation that susceptibility is widespread in other *Chenopodium* species and other *C. album* populations (Hayhurst 1909, Smith and Parrott 1978, N. A. Moran, *personal observation*). While a genetic or cytoplasmically inherited basis to the dif-

ference seems certain, details of the genetic mechanism are currently unknown. The two types may be part of a single interbreeding population or may be effectively independent lineages, with little or no gene flow due to extensive selfing or other barriers. Whether or not the variation is intra- or interspecific does not fundamentally affect conclusions from the experiments reported in this paper, which examine the consequences of variation in resistance among closely related plants for interactions among herbivores.

## MATERIALS AND METHODS

### *Garden experiments*

Field-collected seeds of *C. album* hosts were planted in 4-L pots. Following seedling establishment, they were thinned to one plant per pot. Between 28 and 31 May 1985, pots were inserted up to their rims in a plot in the Weber Canyon, eliminating substantial differences in temperature between soil in and outside of pots. Differences between natural conditions and those in pots appeared to be minor with respect to aphid performance, based on observations of naturally occurring colonies. Totals of 64 resistant and 108 susceptible plants were intermixed randomly in a grid at 0.2-m intervals, together with *Rumex crispus* planted for another experiment. Plants were watered enough to prevent wilting (approximately every 3 d depending on weather) throughout the season. Between 13 and 17 June, all plants were inoculated with *P. betae* from leaf galls of *Populus angustifolia*. Transfers were made by isolating migrants in Petri dishes where they deposited 12–24 nymphs on moist filter paper. The filter paper was then inserted in loosened soil in the pots. Nymphs tended to walk down and away from light into crevices where they began to feed on roots.

In the garden, *C. album* was naturally colonized by winged *H. atriplicis* migrants beginning  $\approx$  10 July. By 7 August, 92% of *C. album* in the garden had at least some *H. atriplicis*. Susceptible plants colonized by early August had a large proportion of their leaves galled. If colonized later, after flowers and fruits began to develop, few galls developed since leaves were beyond the susceptible stages. Susceptible plants were categorized as "galled" (>25% of leaves galled) or "ungalled" (<2% of leaves galled).

To determine the consequences of galling for success of *H. atriplicis* colonies, we collected infested ( $\geq$  1 aphid) leaves from resistant plants and from galled and un-galled susceptible plants. Each leaf was placed in a closed container and examined in the laboratory. Numbers of live *H. atriplicis*, presence of one or more predators (including syrphid fly larvae, lacewing larvae, and coccinellid beetle larvae), and numbers of individuals killed by hymenopterous parasitoids ("mummies") were recorded for each leaf.

To determine the success of *P. betae* colonies on galled and un-galled susceptible plants and on resistant

plants, all *P. betae* colonies were destructively censused on 21–30 September. Censuses were accomplished by removing each pot from the soil and immersing the contents in water. Aphids floated to the surface and were counted and removed to be preserved in individual vials of alcohol. Mean adult body length was calculated from four specimens per plant, or from all adults collected if fewer than four were present.

Roots were carefully washed free of soil and plants dried in presses. Seeds were removed from shoots, and roots were cut off at the soil line. After drying each plant to constant mass, masses of seeds, shoots, and roots were obtained.

The relationship between *P. betae* success and host growth was obtained from the correlations between numbers of *P. betae* and masses of host plant parts. In order to examine these relationships independently of the impact of *H. atriplicis* galling, only resistant plants were included in these analyses.

### *Screen cage experiment to test for interspecific competition*

To test for the presence or absence of competitive interactions between aphid species we conducted a screen cage experiment. Both types of host were subjected to four infestation treatments: both aphid species, neither aphid species, *H. atriplicis* only, and *P. betae* only. This design constitutes the equivalent of a removal or addition experiment for demonstration of interspecific effects. The common garden results as well as the censuses of naturally occurring colonies (see below, Materials and Methods: Field Censuses of Natural Populations) provide quantitative information concerning the importance of the interaction for *P. betae* population size in the field.

In May 1986, 12 susceptible and 12 resistant plants were grown from seed in pots in a greenhouse in Flagstaff, Arizona. Seeds were from the same maternal plants used for the common garden of the previous year, from two maternal parents for the resistant plants, and from four maternal parents for the susceptible plants. On 2 June, plants were infested with *P. betae*, using the same procedure as described above for the garden experiments. On 20 June, half of the *P. betae*-infested plants were infested with *H. atriplicis*. The treatments, aphid-free, *P. betae* only, and both *H. atriplicis* and *P. betae*, were isolated in four separate screen cages outdoors, combining resistant and susceptible plants in each cage. Within 4 d, *H. atriplicis* galls began to develop on susceptible plants. On 15 July, all plants were destructively censused for *P. betae*.

### *Growth chamber experiment to test for aphid impacts on hosts*

A growth chamber experiment was performed to determine whether infestation by root feeders early in the spring reduces growth of *C. album* hosts. Such an effect could reduce the rate of increase of *H. atriplicis* later

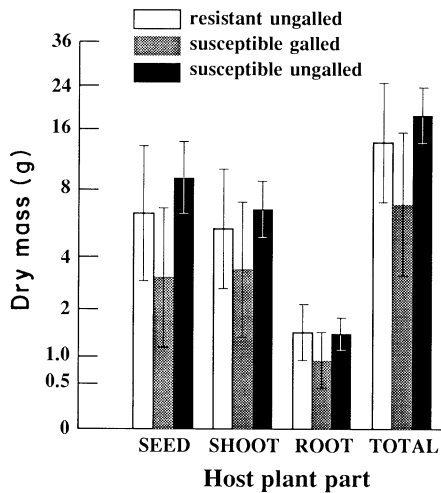


FIG. 1. Consequences of infestation by the leaf feeder *Hayhurstia atriplicis* for growth of *Chenopodium album* in common garden experiment. Galled susceptible plants showed significantly lower seed, shoot, root, and total mass. Error bars give  $\pm 1$  SD from the means. Sample sizes are 63 resistant, 82 galled susceptible, and 9 ungalloped susceptible plants. Analyses are given in Table 1.

infesting leaves of the same plants. Totals of 24 resistant and 35 susceptible plants were grown from seed in pots in a greenhouse starting in April 1986. On 15 May, 12 of the resistant and 18 of the susceptible plants were infested with root aphids, using the procedure outlined for the previous experiments. Root aphid-infested plants and noninfested plants were kept in two separate growth chambers under identical conditions (constant temperature of 20°C, photoperiod of 14L:10D). On 5 July, when plants were just beginning to flower, height of each plant was measured from soil line to the tip of the longest stem.

#### Field censuses of natural populations

To determine whether the effects of leaf-galling aphids on root aphids observed in the common garden and screen cage experiments also occur in nature, we destructively censused both aphid species on naturally occurring *C. album*. The census was conducted on 8 August 1986 on 62 plants that were growing at a site in the Weber Canyon near the common garden of the previous year. Each plant was scored as galled or ungalloped by *H. atriplicis* (plants with intermediate levels of galling were excluded) and was then excavated and numbers of *P. betae* recorded.

## RESULTS

### Comparison of resistant and susceptible hosts in the absence of aphids

In the absence of aphid infestations, resistant and susceptible plants have indistinguishable allocation patterns. Allocation to different tissues and overall growth were similar for uninfested resistant plants, in-

TABLE 1. One-way ANOVAs for differences in growth between resistant, ungalloped susceptible, and galled susceptible *Chenopodium album* host plants. Data were log transformed before analysis.

Mass	df	F	P <
Seeds	151, 2	21.6	.0001
Shoots	151, 2	7.89	.0006
Roots	151, 2	13.67	.0001
Total	151, 2	15.80	.0001

festated resistant plants, and uninfested susceptible genotypes. Resistant genotypes, which showed variable levels of *H. atriplicis* infestation but no galling, were not significantly different from ungalloped susceptible genotypes in masses of any parts or in overall mass (Fig. 1).

### Impact of *H. atriplicis* on resistant and susceptible hosts

In comparison of galled and ungalloped susceptible plants in a common garden, infestation by leaf-galling aphids greatly reduced overall growth and altered allocation to roots, shoot, and seeds. Susceptible genotypes suffered severely reduced size when attacked by *H. atriplicis*, with an average reduction in mass of 39% for shoots, 21% for roots, 60% for seeds, and 54% overall (Fig. 1, Table 1).

### Impact of *P. betae* on *C. album* host plants

Two lines of evidence suggest that *P. betae* has little or no impact on its host plants. First, in common garden experiments using plants of the same ages and with no leaf-galling aphids, regression analyses show no relationship between the numbers of *P. betae* on the root system of a plant and the plant's subsequent performance. Even though individual plants supported from 17 to 3236 aphids on the root systems, this variation in densities was not significantly related to the mass of the shoot, mass of the root, mass of the seed crop, nor the total mass (Table 2).

Second, in growth chamber experiments, infested and noninfested plants showed no significant differ-

TABLE 2. Pearson correlation coefficients for relationships between numbers and sizes of *Pemphigus betae* per plant and the mass of the plant part, for plants resistant to galling by *Hayhurstia atriplicis*.\*

	N	Mass (g)		
		Seed	Shoot	Root
No. <i>P. betae</i> per plant	63	-0.12	0.06	-0.02
Average length of <i>P. betae</i> adults	60	0.12	0.04	-0.04

\* Numbers of aphids per colony, average adult length within a colony, and masses of plant parts were log transformed before analysis.

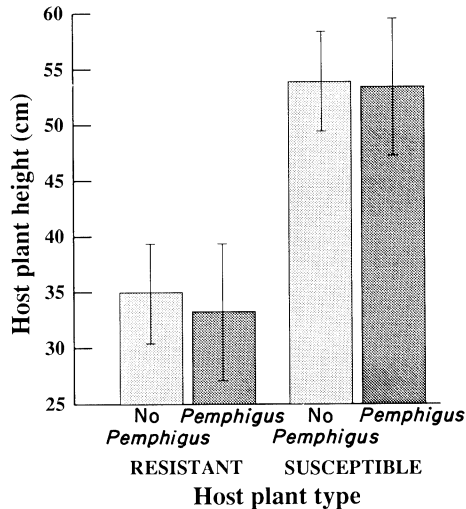


FIG. 2. Effects of root aphids on *Chenopodium album* growth in growth chamber experiment. Error bars give  $\pm 1$  SD. Numbers of plants in each category were 7 resistant, no *Pemphigus betae*; 17 resistant, *P. betae*; 7 susceptible, no *P. betae*; and 28 susceptible, *P. betae*. ANOVA:  $F(\text{root aphid infestation}) = 0.29$ ,  $df = 1,51$ ,  $P > .5$ ;  $F(\text{host susceptibility}) = 138.2$ ,  $df = 1,51$ ,  $P < .0001$ ;  $F(\text{susceptibility} \times \text{root aphid interaction}) = 0.10$ ,  $df = 1,51$ ;  $P > .7$ .

ences in height. In the growth chamber, several lines of each type of plant (leaf-galler resistant and susceptible) were experimentally infested with the root-feeding aphid, *P. betae*. Six weeks after inoculation, colonies were well established on treatment plants of both types as determined by carefully removing intact soil masses and observing root colonies. Plants with roots infested with *P. betae* showed no difference in height from noninfested plants (ANOVA:  $F = 0.29$ ;  $df = 1,48$ ;  $P > .5$ ; Fig. 2). Host height was not affected by interaction between *P. betae* infestation and host susceptibility (ANOVA:  $F = 0.10$ ;  $df = 1,48$ ;  $P > .7$ ) or between *P. betae* infestation and host genotype (ANOVA:  $F = 0.36$ ;  $df = 3,48$ ;  $P > .7$ ).

The only significant difference in height occurred between resistant and susceptible host types (ANOVA:  $F = 138.2$ ;  $df = 1,48$ ;  $P < .0001$ , Fig. 2). This difference reflects the correlation between branching architecture and resistance categories that occurred in the Weber Canyon sites.

#### Advantages of leaf galling for leaf-feeding aphids

Although *H. atriplicis* can either live freely on the leaves of its hosts or live within galls that it stimulates the plant to produce, performance is superior for colonies associated with galls (Fig. 3A). Mean leaf aphid densities on leaves of galled susceptible plants are almost five times as great as densities on leaves of ungalled susceptible plants (mean = 69.8 aphids/galled

leaf, mean = 14.3 aphids/ungalled leaf; Student's  $t = 7.25$ ,  $df = 60$ ,  $P < .0001$ ).

Comparisons of performance on resistant and susceptible plants suggest that resistance to gall formation is important in determining performance of leaf aphids. Densities on ungalled leaves of susceptible and resistant plants showed no significant differences (mean density on susceptible = 14.3 aphids/leaf, on resistant = 12.1 aphids/leaf; Student's  $t = 0.77$ ,  $df = 61$ ,  $P > .4$ ). While not conclusive, this pattern suggests that the main difference between performance on resistant and susceptible plants is the ability to form galls successfully.

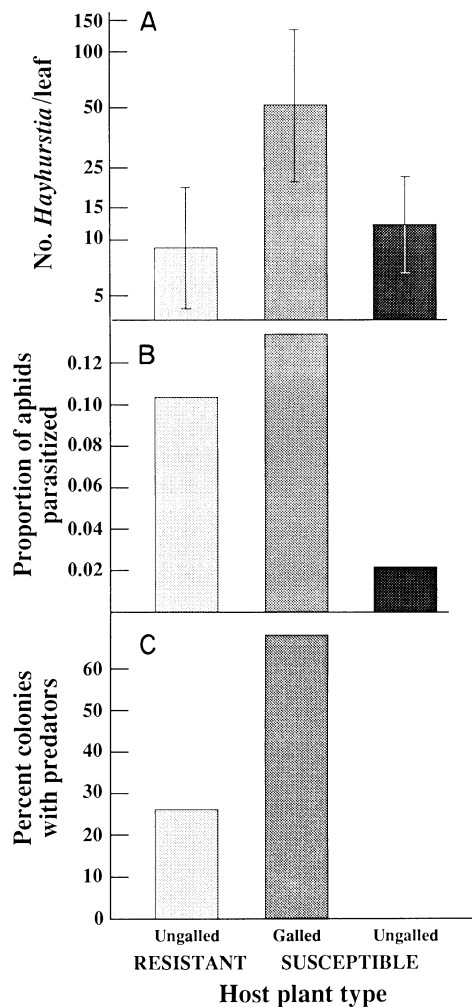


FIG. 3. Consequences of galling for success of leaf aphids in common garden. (A) Mean number of live *H. atriplicis* on leaves of resistant plants ( $N = 41$  leaves), on galled leaves of susceptible plants ( $N = 40$  leaves), and on ungalled leaves of susceptible plants ( $N = 22$  leaves). Error bars give  $\pm 1$  SD. ANOVA:  $F = 50.8$ ,  $df = 2,100$ ,  $P < .0001$ . (B) Percent of aphids per leaf that are dead from parasitization. Kruskal-Wallis:  $H = 27.1$ ,  $df = 2$ ,  $P < .0001$ . (C) Proportion of leaves with predators. Chi-square:  $\chi^2 = 29.7$ ,  $df = 2$ ,  $P < .0001$ .

This greater abundance on galled leaves most likely reflects a greater reproductive rate. An alternative hypothesis that would predict the same differences in densities is that predators and parasites selectively forage on ungalled leaves of susceptible and resistant plants, where aphids are more exposed than on galled leaves. However, just the reverse was observed in censuses of parasitoids and predators on galled and ungalled leaves. The proportion of aphids killed by parasitoids was higher on galled leaves than on ungalled leaves of resistant or of susceptible plants (Fig. 3B; Kruskal-Wallis:  $H = 27.1$ ,  $df = 2$ ,  $P < .0001$ ). Similarly, the proportion of leaves with predators such as coccinellid beetles and syrphid fly larvae was greater for galled leaves than for ungalled leaves of either susceptible or resistant plants (chi-square:  $\chi^2 = 29.7$ ,  $df = 2$ ,  $P < .0001$ ). The cause of the greater attack rate of galled leaves was not identified. Because leaf curl galls are not closed and afford little protection from natural enemies, the greater concentrations of aphids on susceptible plants may attract more parasitoids or predators. Furthermore, the galls may produce some visual or chemical cues that attract certain natural enemies, paralleling the attraction of leaf miner parasitoids to leaf mines and other damage on oak leaves (Faeth and Bultman 1986).

#### Effects of host resistance type on root aphids

Root-feeder densities did not differ significantly between resistant and susceptible plants in the absence of leaf galls (Student's  $t = 1.890$ ,  $df = 71$ ,  $P > .4$ ; Fig. 4A). In addition, lengths of adult root aphids were similar on ungalled, susceptible hosts and on hosts resistant to leaf galling (mean = 1.78 mm for ungalled susceptible plants vs. 1.76 mm for resistant plants; Student's  $t = 0.29$ ,  $df = 66$ ,  $P > .9$ ; Fig. 4B).

#### Interspecific competition

In the common garden, the root-feeding aphid was strongly suppressed when leaf galls were present on the same plant (Fig. 4A). On susceptible plants, densities of root-feeding aphids were 14 times as great when leaf galls were absent as when they were present (mean = 16.6 root-feeders/susceptible plant with leaf galls vs. 225 root-feeders/susceptible plant without leaf galls; Student's  $t = 4.36$ ,  $df = 1-6$ ,  $P < .0001$ ). Root-feeders were 28 times as abundant on plants resistant to leaf galling as on susceptible, galled plants (mean = 466 root-feeders/resistant plant vs. 16.6 root-feeders/susceptible plant with leaf galls;  $t = 18.6$ ,  $df = 161$ ,  $P < .0001$ ). Furthermore, on 28% of the plants with leaf galls ( $n = 99$ ), root-feeding aphids went locally extinct. In contrast, when leaf galls were absent on either resistant ( $n = 64$ ) or susceptible plants ( $n = 9$ ), root-feeding aphids always survived. The lower densities of the root-feeding aphids on plants with leaf galls do not reflect differences in colonization rates, since all plants were experimentally inoculated with the same numbers

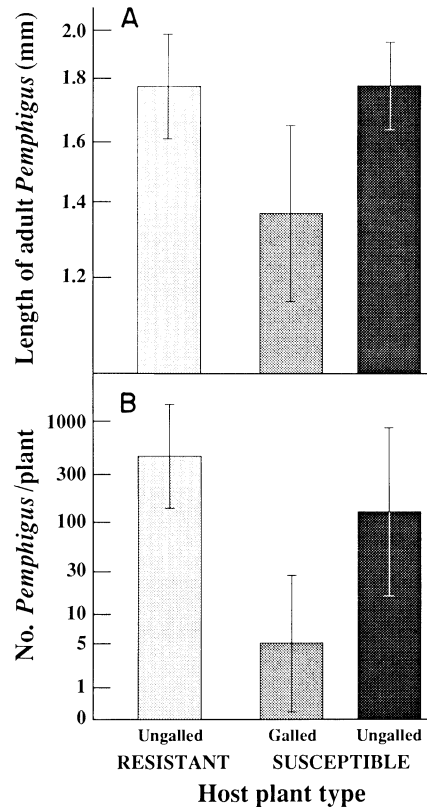


FIG. 4. Consequences of galling by *H. atriplicis* for growth and reproduction of *P. betae* on roots of the same plant. Error bars given  $\pm 1$  SD. (A) Log<sub>10</sub>-transformed numbers of *P. betae* on roots of resistant plants ( $N = 64$ ), galled susceptible plants ( $N = 99$ ), and ungalled susceptible plants ( $N = 9$ ). ANOVA:  $F = 152.1$ ,  $df = 2, 169$ ,  $P < .0001$ . (B) Means of log-transformed body lengths of adults for resistant plants ( $N = 60$ ), galled susceptible plants ( $N = 54$ ), and ungalled susceptible plants ( $N = 8$ ). ANOVA:  $F = 42.2$ ,  $df = 2, 119$ ,  $P < .0001$ .

of root-feeding aphids before any leaf aphids were present.

Not only did leaf galls depress root-feeder abundances, they also negatively affected their sizes (Fig. 4B). Mean lengths of adult root feeders were decreased by 22% on galled plants compared to ungalled susceptible plants (mean = 1.39 mm on susceptible plants with galls vs. 1.78 mm on susceptible plants without galls; Student's  $t = 6.06$ ,  $df = 60$ ,  $P < .0001$ ). Root feeders on galled susceptible plants were 21% smaller than those on resistant plants (mean = 1.39 mm for galled plants vs. 1.76 mm for resistant plants; Student's  $t = 6.26$ ,  $df = 112$ ,  $P < .0001$ ).

The pattern established in the common garden experiments was further supported by screen cage experiments that were designed to examine competitive interactions. When all combinations of presence and absence of leaf aphids and resistance and susceptibility to leaf galling were experimentally established and their consequences for root aphid densities examined, root

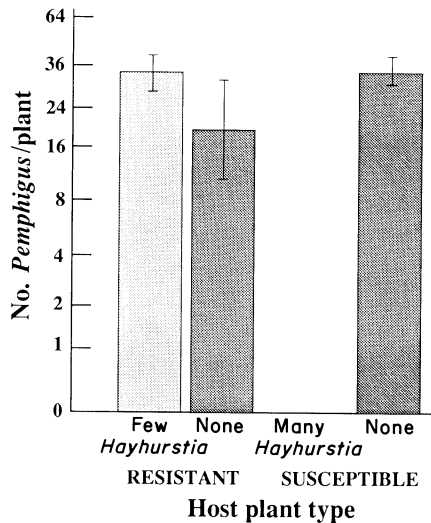


FIG. 5. Exclusion of *P. betae* by *H. atriplicis* in screen cage experiment. Numbers of *P. betae* were log transformed. Error bars give  $\pm 1$  SD from the means. Number of plants in each category was six. ANOVA:  $F = 196.3$ ,  $df = 3, 20$ ,  $P < .0001$ .

aphids were completely excluded on all galled plants (Fig. 5). In contrast, root aphids persisted on all ungalled plants, including plants susceptible to leaf galls (mean = 36.7 root aphids/plant), resistant plants with leaf aphids (mean = 20.8 aphids/plant), and resistant plants without leaf aphids (mean = 36.7 root aphids/plant), with no significant differences among these categories (ANOVA:  $F = 2.61$ ,  $df = 2, 15$ ,  $P > .2$ ).

#### Censuses of aphids on naturally occurring hosts

Censuses of aphids on naturally occurring hosts confirmed our experiments. In comparisons of resistant and susceptible plants growing intermixed at the same site, infested plants without the leaf galler, *H. atriplicis*, had significantly more *P. betae* on their roots than did plants with leaf galls (ANOVA on  $\log_{10}$  [number of *P. betae*/plant]:  $F = 22.3$ ;  $df = 1, 60$ ;  $P < .0001$ ; Fig. 6). Thus, the effect of leaf galls on root aphids observed in the common garden and growth chamber experiment appears to play a role in the distribution and abundance of *P. betae* on naturally occurring host plants.

## DISCUSSION

### Interspecific competition

Observational data and two separate experiments show that, when these two aphid species occur together on the same susceptible plant, leaf galling by *H. atriplicis* reduces or excludes *P. betae* on the roots. The consequences of this interaction for the larger scale dynamics of *P. betae* populations are unknown. Several factors are likely to affect the importance of *H. atriplicis* for *P. betae* distribution and population size. First, if *P. betae* is able to avoid plants infested with *H. atri-*

*plicis*, then it may partially circumvent the negative consequences of cohabitation. However, several facts suggest that such avoidance does not occur. *Pemphigus betae* colonizes its hosts before mid-July, the latest time at which migrants from cottonwoods move to summer host plants. The subsequent generations are subterranean and sedentary, as no winged migratory forms are produced that can fly to other root host plants. *Hayhurstia atriplicis* produces winged colonizers throughout the season, and most infestations are initiated in late July and August, after *P. betae* is already committed to its root host plants (N. A. Moran, *personal observation*). Thus, *P. betae* chooses hosts before most *H. atriplicis* colonies are present. Furthermore, there is no evidence to suggest that *P. betae* migrants from cottonwoods avoid *C. album* hosts that are susceptible to galling by *H. atriplicis*.

The negative effects of competition on *P. betae* populations could also be limited by the fact that the leaf-galling *H. atriplicis* feeds only on a subset of the plant taxa used by the root-feeding generations of *P. betae*. *Pemphigus betae* colonies on *Rumex* and *Polygonum* species are not subjected to competition from *H. atriplicis*. However, several other herbivores, including several aphid species, do feed on the aerial parts of these plants (N. A. Moran, *personal observation*). Whether these species affect *P. betae* feeding on roots of the same hosts is unknown.

Finally, the influence of leaf galls on *P. betae* population size may be mediated by the effects of weather on host plant growth and on aphid colonies. Moran and Whitham (1988b) showed that *P. betae* population size during the root-feeding phase is affected by rainfall patterns during the growing season. Possibly, rainfall affects *P. betae* numbers directly and through interaction with leaf-galler abundance.

### Host resistance as a mediator of competitive interactions

Few investigators have attempted to examine the consequences of variable host-plant resistance for in-

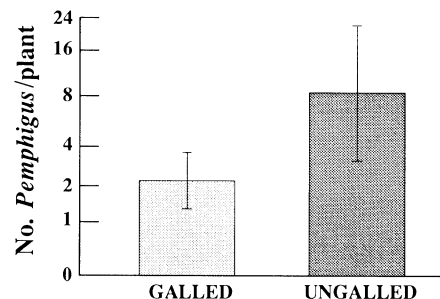


FIG. 6. Log-transformed numbers of *P. betae* on naturally occurring galled and ungalled *C. album*. Error bars give  $\pm 1$  SD from the means. Sample sizes were 20 galled and 42 ungalled plants. ANOVA:  $F = 22.3$ ,  $df = 1, 60$ ,  $P < .0001$ .

teractions among herbivores. In studies of the leaf-galling stages of *P. betae* that occur on cottonwood, T. G. Whitham (*personal observation*) found that the negative effects of intraspecific competition were more severe on resistant clones than on susceptible ones.

Interspecific competition is likely to be strongly affected by host plant resistance traits. In this study we experimentally show that when plants are susceptible to the leaf-galling aphid, *H. atriplicis*, this aphid can completely exclude the root-feeding aphid, *P. betae*. However, if the host plant is resistant to *H. atriplicis*, a refugium is available to *P. betae* where its performance is just as high as on susceptible plants without a competitor. Similarly, in natural populations, *P. betae* was almost never found in association with *H. atriplicis* on the same susceptible plant, while *P. betae* was abundant on roots of nearby susceptible plants where *H. atriplicis* did not co-occur. Thus, both in common garden experiments and under natural conditions in the field, host resistance determines which aphid species will be on a plant.

While our study concentrates on the interactions of two species, a few other studies have examined broader assemblages (e.g., Fritz et al. 1986, Maddox and Root 1987, Fritz and Price 1988) and have shown that host clone or genotype can be correlated with specific herbivore species. While these broader studies did not experimentally examine competition in terms of differential insect performance, our study shows that one species suppresses the other and that host resistance creates a refugium where the inferior competitor can thrive in the absence of competition.

#### *Resistance to one but not to all*

A critical issue in ecology and agriculture is whether the impacts of diverse pests on plants act in concert or whether they cancel one another out (Drake 1981a, b, Fritz et al. 1987, Karban et al. 1987, Maddox and Root 1987, Whitham et al. 1990). For example, if we select for a strain resistant to one herbivore will it also be resistant to other herbivores or does resistance to one come at the expense of increased susceptibility to others? This fundamental question has important implications for any crop improvement program and for our understanding of the evolution of plant defenses to herbivores and pathogens.

Although the studies cited above present conflicting answers to this question, the study presented here clearly shows that plants that were highly resistant to the leaf-galling aphid were also highly susceptible to the root-feeding aphid. Thus, increasing resistance to one species may confer no advantages of increased resistance to another herbivore, even when both use the same component of the host plant, in this case, the vascular sap. However, these two aphids fed in different regions, and only one was a galler. The latter is probably the most important difference, since plant resistance prevented gall formation and gall formation

was strongly associated with subsequent performance of both aphid species.

#### *Advantages of galling in host-mediated interactions*

The ability of gall formers to divert nutrients within a plant (e.g., Llewellyn 1982, McCrea et al. 1985, Abrahamson 1987, K. C. Larson and T. G. Whitham, *unpublished manuscript*) suggests that they may frequently affect food availability for other co-occurring species on the same host. Nongalling species may sometimes take advantage of this nutrient diversion by feeding on the enriched tissues themselves, provided that they are sufficiently mobile. For example, *Chaitophorus* aphids on *Populus* feed preferentially in or near leaf galls formed by *Pemphigus* species (N. A. Moran, *personal observation*). An extreme case is seen in *Eriosoma yangi*, another pemphigine aphid, which does not form galls itself but is obligately parasitic upon the galls of other *Eriosoma* species (Akimoto 1981). Herbivores with restricted mobility, such as the root-feeding phases of *Pemphigus* species, do not have the option of exploiting nutrient sinks formed by galling species on the same plant. Because there are no dispersive morphs during the summer phase of the life cycle, *P. betae* cannot escape competition by abandoning galled plants for ungalled ones.

Other cases of interspecific effects among aphids are known (e.g., Antolin and Addicott 1988). In fact, sap feeders, such as *P. betae*, *H. atriplicis*, and other aphids, are involved in a disproportionate number of cases in which competitive effects have been shown between herbivorous insect species (Strong et al. 1984, Karban 1986). It is not clear why sap-feeding species might compete more often than other insects. Karban (1986) suggests that homopterans are often sedentary and thus cannot move to escape the effects of competition. Another possibility is that homopterans are sharing the most mobile component of their host plant and thus even spatially separated species may compete directly for nutrients. Both of these factors appear to contribute in the case of *H. atriplicis* and *P. betae*.

These results add to the growing documentation that asymmetrical competition, mediated by changes in shared host plants, is frequent among herbivorous insects. As with leaf miners attacking oaks at different times of the season (Faeth 1986) or moths feeding on lupines at different times (Harrison and Karban 1986), *P. betae* and *H. atriplicis* never encounter one another directly. In their case, the species arriving first, *P. betae*, is subjected to severe negative effects from the later arrival of *H. atriplicis*.

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