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Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling

Abstract Gall forming herbivores induce sinks and act as phloem parasites within their host plants. Their performance on the host plant can depend on the sink-source relationship they establish with the plant. Because sink-source relationships within a plant are reflected in its architecture, we examined how architectural differences among cottonwoods might influence the success of the galling aphid, *Pemphigus betae*. Using cloned cottonwoods in common garden studies, we found three major patterns. First, there is a significant clonal or genetic component to tree architecture; cloned trees grown in a common garden maintain the architecture of parental trees. Second, resistant tree genotypes have more natural sinks (i.e., buds) relative to sources (i.e., stem volume) than susceptible trees. Third, these differences in architecture result in greater competition among sinks on aphid-resistant trees than on aphid-susceptible trees. Sink competition within a tree was estimated by the Gini coefficient which quantifies the size inequality of a shoot population (i.e., competition among sinks is low when shoots are nearly equal in size, and great when a few shoots are large and most are small). Aphid death through gall abortion increased significantly ($r^2 = 0.65$) on garden-grown trees as competition among sinks within a tree increased. Based on these observations we proposed the "sink competition hypothesis" to account for the performance of gall formers on their host plants. To test this hypothesis, we experimentally reduced sink densities (i.e., buds) on branches of resistant tree genotypes to resemble the bud densities of susceptible genotypes. By reducing the number of competing sinks, we predicted that aphid survival would increase. As predicted, aphid survival significantly increased. For example, in one removal experiment, aphid survival increased from 20% on control branches to 55% on branches with the highest level of bud removal. Similar bud removals on susceptible trees did not increase aphid survival, indicating that competition is relaxed on susceptible hosts. With the exception of the plant vigor hypothesis, most current hypotheses explaining herbivore distributions in nature focus on the importance to leaf-chewing herbivores of variation in chemistry. We believe that a sink competition model is needed to explain the distributions of the diverse group of herbivores that act as phloem parasites. The sink competition model is more mechanistic than the vigor hypothesis, and may account for apparent contradictions because it more clearly quantifies the resource base and the potential interactions that occur when sinks, either herbivore-induced or natural, compete for sources.

Introduction

While competition has often been viewed as being strongest among closely related species, recent work has shown strong competition between unrelated species (e.g., Karban 1986), or between species that occupy different parts of a plant (e.g., Moran and Whitham 1990a). One competitive interaction that has been largely overlooked is competition between plant parts and herbivore-induced galls or other phloem feeders. Galling herbivores feed on the photoassimilates and nutrients moving through the plant from sites of production or storage (sources) to sites of active use or growth (sinks) by tapping into the host vascular system and creating a sink (Billett and Burnett 1978; Weis and Kapelinski 1984; McCrea et al. 1985; Abrahamson and Weis 1987; Larson and Whitham 1991). Gall formers such as the

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aphid, *Pemphigus betae*, tap directly into host phloem, but gallers with chewing mouthparts can also act as phloem sinks when they feed on nutritive layers that function to transfer nutrients from the phloem to the larval chamber (Rohfritsch 1987, 1988; Bronner 1992). Thus, most gallers are functioning within the plant as phloem parasites by acting much like the plant sinks (i.e., buds, fruits, or young shoots). While competition among these natural plant sinks is well documented (Ho 1988) and forms the basis of allocation theory within plants (Bazzaz et al. 1987; Lubbers and Lechowicz 1989), the potential impacts of competition between plant sinks and herbivore-induced sinks have rarely been examined.

The strength of any sink (i.e., a natural plant part or herbivore-induced gall) is dependent on the availability of surrounding sources and competitive interactions with surrounding sinks (Wareing and Patrick 1975; Cook and Evans 1983; Watson and Casper 1984; Wyse 1986; Ho 1988; Wardlaw 1990). Any change in plant form, whether genetically based or manipulated through physical removal of parts, changes the arrangement and ratio of sinks and sources and influences the outcome of competition between sinks (Gifford and Evans 1981; Blescschmidt-Schneider 1984; Egli et al. 1985; Waller 1986). For example, genetic variability in the architecture of rice cultivars results in plants with different ratios of sink organs to source organs, and thus different sink-source relationships (Lafitte and Travis 1984). Architectural modifications of plants through the removal of parts can also significantly impact sink-source relationships within plants (Egli et al. 1985; Lehtilä 1994). Gottlieb (1984, 1986) provides many examples of architectural traits, such as internode length and branching patterns, that are variable within populations and appear to be under simple genetic control at one or two loci. Because the architecture of a plant is reflected in its sink-source relationships (Waller 1986), the architectural form of a plant can be expected to be a significant aspect of host quality for gall formers. This paper examines the significance of intraspecific variation in modular architecture of cottonwoods on the galling success of *P. betae*.

Genetically diverse populations of cottonwoods occur in the western United States, where narrowleaf cottonwood (*Populus angustifolia*) and Fremont cottonwood (*P. fremontii*) form large, hybrid swarms (Eckenwalder 1984; Keim et al. 1989). Narrowleaf cottonwood and hybrids with Fremont cottonwood are galled by the aphid *P. betae* (Paige and Capman 1993). Aphid survival on naturally growing trees within the hybrid zone ranges from 0% to 75% and these resistance traits are maintained in clones growing in common gardens ($r^2 = 0.81$; Whitham 1989). Furthermore, colonizing aphids discriminate between trees and selectively recolonize those trees where survival is greatest (Moran and Whitham 1990b). Here we examine how the modular architecture of cottonwoods affects sink-source relationships; and how this in turn is related to tree resistance to galling by *P. betae*.

We find that on susceptible trees, aphids induce a strong sink that functions much like the plant's own sinks, drawing in assimilates from surrounding parts. However, on resistant trees, few aphids succeed in producing a gall, and those that do fail to induce a strong sink. We examine the hypothesis that the genetically determined architecture of the tree affects the intensity of intraplant competition such that sinks, whether they are plant reproductive and vegetative buds or aphid galls, compete with one another for limited sources (i.e., from leaves and storage tissues). To address this hypothesis, we ask the following specific questions: (1) Is tree architecture correlated with degree of aphid resistance? (2) Is tree architecture genetically determined? (3) Is intraplant sink competition greater on resistant trees? (4) Is aphid survival increased by removing competing plant sinks?

Biology of the species

In spring, *P. betae* fundatrices (stem mothers) hatch from overwintering eggs laid beneath the bark of cottonwoods and colonize leaves just as the buds begin to open (Whitham 1978). Galls are initiated by a single stem mother along the midvein of an expanding leaf. Gall growth is rapid and the stem mother is completely enclosed within a few days. Inside the gall, stem mothers parthenogenetically produce a generation of alate viviparae which begin emigrating from the gall about 6 weeks after initiation. Each stem mother continually produces nymphs throughout gall maturation, with up to 300 progeny produced over her lifetime. The gall wall consists of a rich vascular network embedded in a matrix of parenchyma cells.

[14]C translocation studies showed that the gall induced by *P. betae* functions as a strong sink (Larson and Whitham 1991). In spring, resources for gall development are imported by *P. betae* into the galled leaf from stem storage tissue through active manipulation of host transport patterns. After leaves have matured, aphids draw food from the galled leaf blade and from surrounding leaves of the shoot (Larson and Whitham 1991). These aphid-induced sinks function within the plant in much the same way as the plant's own natural sinks. For example, when sinks are released from competition following the removal of a competing sink (i.e., flower buds), the performance of the remaining sinks (i.e., aphid galls and vegetative buds) increases.

Materials and methods

A common garden of clones vegetatively propagated from a haphazardly selected set of parent trees growing in the hybrid zone was started in 1982. The susceptibility of the clones used in this study to aphid attack ranged from 11.2% to 65% stem mother success in producing a gall. RFLP genetic analyses have shown that of the nine genotypes used in this study, one is pure narrowleaf cottonwood, while the rest are complex backcrosses (Keim et al. 1989). This garden provided uniform conditions of age and environment

for making comparisons among clones. At the time of this study, the clones produced almost exclusively vegetative buds, and any branches that did produce reproductive buds were not sampled. Approximately five asexually propagated clones of each parent tree are growing in the common garden. While both parent trees and derivative clones were measured for genetic comparisons (see next section), most architectural measurements and manipulations used the common garden clones.

Architecture of resistant and susceptible genotypes

To determine the ratio of sinks to sources at bud break in spring, we quantified bud density relative to stem volume for 15 first order laterals on each of the nine garden genotypes. Each replicate branch was a 1-year-old first-order lateral from the main trunk of a 5-year-old clone. We estimated the volume of a branch by measuring its total length and its basal diameter, and used the equation: volume = basal radius$^2 \cdot \pi \cdot$ stem length $\cdot 0.70$. This non-destructive estimation of branch volume was strongly correlated with branch biomass measured on 25 cut and dried samples ($y = -1.58x + 1.89$; $r^2 = 0.97$; $n = 25$; $p < 0.001$). The total number of buds per branch was counted and added to the calculation to determine the number of buds per cubic centimeter of stem volume. In cottonwoods, the largest laterals are those produced from the most apical buds of the growth increment in any one year, with more basal buds producing smaller laterals (Isebrands and Nelson 1982). Because larger branches have lower bud densities, regardless of genotype (unpublished data), we sampled only the five most apical (largest) laterals for each replicate clone.

During midsummer we quantified the growth of the buds described above. We measured the length of each shoot developing from the spring buds on the 15 first-order laterals. Because we were interested in the interactions among the shoots within a plant, each genotype was analyzed as a population of shoots. Populations of plants usually show strong size hierarchies, with a few large individuals and many smaller ones. To express the inequality of shoot sizes within a clone, we calculated the Gini coefficient (Weiner and Solbrig 1984). This statistic is equal to one-half of the relative mean difference, i.e., the arithmetic average of the differences between all pairs of shoots.

To examine the genetic basis of these modular differences, we compared the shoot populations of the garden clones with their parent trees still growing in their native field site. We carried out the same shoot length measurements as described above for 20 branches on each parental clone.

Experimental changes in tree architecture

To test the hypothesis that architecture determines the level of resistance to galling by *P. betae*, we removed buds from branches of resistant clones to give them a similar architecture to susceptible clones. Before bud burst in spring, we removed 0%, 25%, 50%, or 75% of the buds from 23 branches of the most resistant genotype in the common garden (13 experimental branches from one clone and 10 from a second clone). When buds began to open in spring, we transferred 2–4 stem mothers onto each remaining bud on these experimental branches. Stem mothers were transferred as they hatched from eggs collected from under the bark of cottonwoods growing along the Bear River in southwestern Wyoming. For each branch we calculated the stem volume per bud and the rate at which stem mothers successfully produced a gall containing offspring, and used these data in a regression analysis.

To test the generality of the results of the above study on a single genotype, we compared the survival of aphids on bud removal versus control branches on four resistant and four susceptible trees growing in the field. In this experiment, aphid survival was compared on control versus 50% bud removal branches. Stem mothers were transferred onto control and experimental branches as in the previous experiment. Data were analyzed as a two-way ANOVA.

Results

Architecture of resistant and susceptible genotypes

Aphid-resistant and -susceptible clones differed in modular architecture, with aphid-resistant genotypes having either shorter or thinner internodes than aphid-susceptible genotypes. Thus, before bud break in spring, the three most resistant common garden genotypes (those with aphid survival < 35%) averaged twice as many buds per cubic centimeter stem volume as did the three most susceptible genotypes (aphid survival > 60%; Fig. 1). This difference represents a greater sink (buds) to source (stem) ratio on resistant than on susceptible clones and, consequently, the potential for greater competition between sinks for limited sources on resistant clones.

The greater sink demand relative to source supply within resistant genotypes was reflected in the distribution of shoot sizes in midsummer. The buds on the three most resistant genotypes developed into a skewed population of mostly short shoots and a few large terminals. In contrast, buds on the three most susceptible genotypes developed into a population more uniform in size containing longer shoots (Fig. 2). Thus, on aphid-resistant clones a smaller proportion of the developing buds capture most of the available stored resources required for shoot elongation. On susceptible clones, these resources are more equitably distributed among the elongating buds. This not only affects tree architecture, but likely affects other organisms such as aphids that attempt to induce sinks. If the latter is true, we would expect aphid survival to be correlated with the Gini coefficient (G), a statistic that measures the inequality within a population and ranges from 0 for a uniform population to 1 for maximum inequality (Weiner and Solbrig 1984).

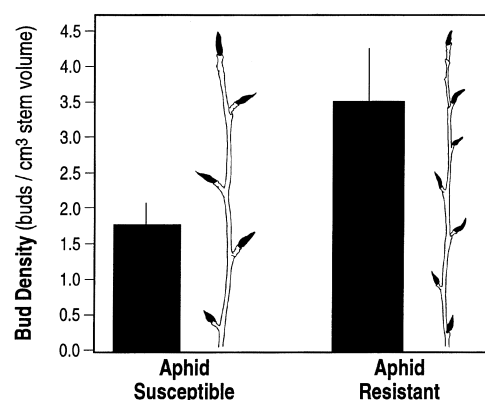In agreement with our prediction, we found that among the garden genotypes, G was strongly correlated

Fig. 1 Bud density (buds/cm^3 stem volume) for the three most susceptible genotypes (aphid stem mother survival >60%) and three most resistant genotypes (aphid stem mother survival <35%) growing in a common garden. The *shoot icons* are computer-scanned images of a shoot from a resistant and a shoot from a susceptible tree
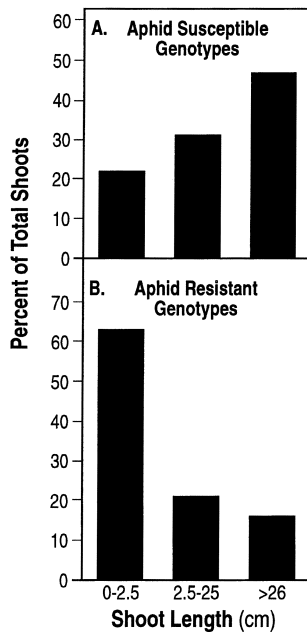
Fig. 2A,B Distribution of shoot lengths on three susceptible clones **(A)** and three resistant clones **(B)**

Fig. 3 Regression between the percent stem mother survival and the Gini coefficient (G) for the mid-summer shoot population for each clone. G ranges from a minimum of 0 for a population of uniformly sized individuals to 1 at maximum inequality in size. Each *point* represents the average values of 3–5 clones of nine genotypes grown in the common garden

Fig. 4 Survival of aphid stem mothers to produce a successful gall on architecturally modified branches of a resistant clone. Each *point* represents one branch with from 0 to 75% of the buds removed (*crosses* on the *shoot icons* indicate buds which were removed to lower bud density)

with aphid survival, with the most susceptible clones having the most uniform size distribution (Fig. 3; $r^2 = 0.69$; $n = 9$; $F = 18.12$; $p < 0.005$). The greater inequality among shoots on aphid-resistant trees than on susceptible trees supports the conclusion that resources were most limiting on resistant genotypes, such that only a few buds had the resources necessary for elongation.

A genetic basis to modular architecture was indicated by the strong correlation between shoot lengths on the derived common garden clones and that of their parents still growing in the field ($r^2 = 0.81$; $n = 5$; $p < 0.01$). In addition, the different replicates or clones of the same parental genotype showed no significant differences in morphological traits such as leaf size, shoot size, bud size, or bud density. For this reason, measurements on clones of the same genotype were pooled.

Experimental changes in tree architecture

We predicted that removing buds before the spring allocation of stored reserves would increase allocation to developing aphid galls and thus increase stem mother survival. Removing from 0% to 75% of the buds from branches of an aphid-resistant clone (i.e., average pretreatment aphid survival of 11.2%) resulted in branches with a posttreatment range of architectures from those typical of resistant trees to those typical of susceptible trees. The mean length of shoots resulting from the remaining buds increased from 3.26 ± 0.55 cm on control branches to 21.68 ± 2.17 cm on the branches with the highest removal, and the percentage of short shoots decreased from 66.7% on the former to 20.37% on the latter (contrast to Fig. 2). The survival of stem mothers
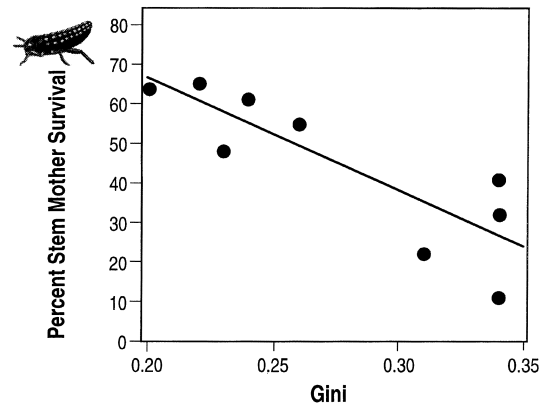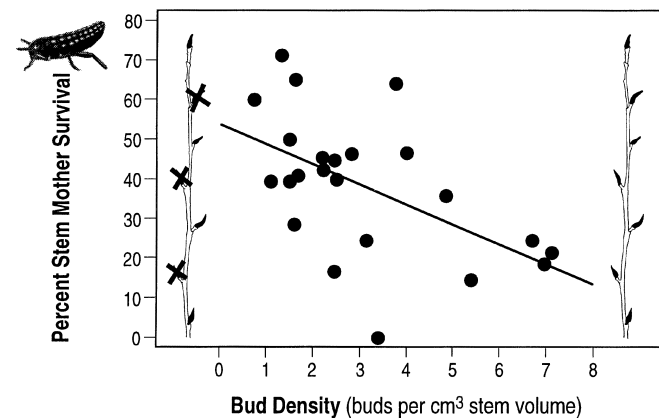
transferred to architecturally modified branches significantly increased on branches with bud densities lowered by removals (Fig. 4, $F = 8.49_{1, 21}$; $r^2 = 0.29$; $p = 0.008$). In this experiment, stem mother survival never exceeded 25% on branches with bud densities typical of resistant clones, but averaged 55% on branches with bud densities modified to give susceptible-type architectures.

Transfer of aphids onto four additional resistant genotypes showed the same pattern as the above experiment on a single genotype. Survival of stem mothers on the branches of resistant trees with 50% bud removal was significantly increased over survival on control branches (Fig. 5A; $F = 10.61$; $p < 0.005$).

While bud removal experiments were successful in making resistant trees more susceptible, identical bud removal experiments on susceptible trees resulted in no
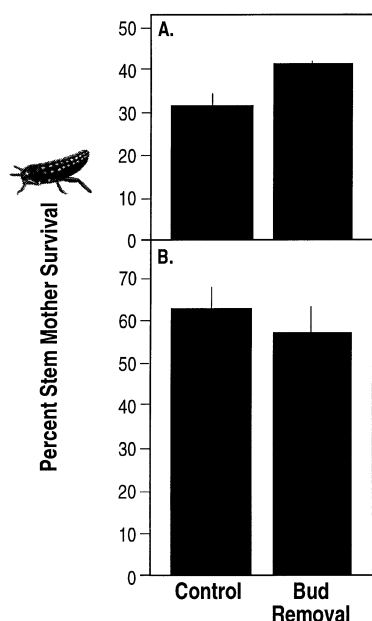
Fig. 5A,B Survey of aphid responses to architectural modifications on four resistant trees (**A**) and four susceptible trees (**B**). Aphid survival was determined on control branches versus branches with 50% bud removal

change in aphid survival (Fig. 5B; $F = 4.27$; $p > 0.05$). The factors that limit stem mother survival on susceptible clones do not appear to be due to resource limitation or sink competition within the plant. However, a major factor limiting stem mother survival below 30% on resistant clones appears to be due to competition between sinks for limited sources and consequently a failure of *P. betae* to manipulate host allocation.

Discussion

Architecture and sink competition

The galls induced by *P. betae* act as strong sinks, and their early growth depends on resources redirected into the galled shoot from reserves stored over winter in the stems (Larson and Whitham 1991). We found that stem mother success in producing a gall is limited by competition with surrounding plant sinks, specifically neighboring vegetative buds, and that variation between trees in susceptibility to galling (Whitham 1989) can be accounted for by variation in the intensity of intraplant sink competition during gall formation. Our conclusions are based on two main results: (1) individual clones of hybrid cottonwoods differed in their architecture, and thus in the ratio of sinks to sources, and (2) manipulation of sink to source ratios through architectural modifications decreased intraplant sink competition and increased stem mother success.

The architectural difference we found between resistant and susceptible cottonwoods cannot be divorced from underlying sink-source allocation patterns. With

resistant trees having almost twice as many buds per unit of stem volume as susceptible trees, aphid stem mothers inducing galls on resistant trees face a higher ratio of sinks to sources and the potential for stronger competition among sinks during spring allocation of stored reserves than on susceptible trees. From the perspective of a sink-inducing galler, our resistant cottonwoods appear to have more competing sinks in early spring, when an increased allocation to the galled shoot is required to produce a gall (Larson and Whitham 1991).

Competition among expanding buds during early spring can be expected to affect their final size (i.e., shoot size), just as competition among plants in a population impacts their final size. The impacts of competition on size are not usually uniformly distributed across individuals, and it is typical for strongly skewed or bimodal size distributions with mostly small individuals and a few large individuals to develop under strong competition (Harper 1977; Weiner and Thomas 1986; Huston and DeAngelis 1987). The developing buds within a tree compete for access to vascular connections to storage reserves in the stems or roots (Sachs et al. 1993), and we expect the outcome of this competition to be similar to the pattern documented among individuals in a population, i.e., to be expressed in terms of size inequality. By midsummer, the population of shoots that make up an aphid-resistant cottonwood resemble a population of plants suffering density stress and strong competition: both show strong size inequality indicated by a relatively high Gini coefficient (see Weiner 1985 for examples of plant size distributions under different densities). However, the shoots of the susceptible cottonwoods were much more uniform in size, resembling populations of plants not suffering strong competition.

We hypothesized that stronger sink competition due to the greater bud density on resistant cottonwoods caused aphids to be inferior sinks such that they lost out in competition with natural plant sinks and suffered higher rates of gall failure. If true, then by experimentally reducing the number of competing sinks, we hypothesized that aphid survival should be enhanced. By reducing the bud density on branches of an aphid-resistant genotype, we produced branches within resistant clones that had bud densities and levels of sink competition typical for a susceptible tree. Our predictions were confirmed. On branches with high bud densities most stem mothers aborted and died in the gall attempt. However, with the removal of competing sinks, stem mothers were more successful in forming galls, with successful gall development increasing as bud density decreased.

The sink competition model of plant-gall former interactions

Although competition among sinks within a plant has been well studied (Wareing and Patrick 1975; White

1980; Ho 1988; Solomon 1988a, b), it has rarely been examined from the perspective of the herbivore. We found that the aphid gall former, *P. betae*, faced strong competition from natural plant sinks, significantly reducing gall success. For example, the survival of gall-forming stem mothers on all resistant trees in this study increased by an average of 33% following vegetative bud removal. Similarly, in another study, aphid survival increased 31% following flower bud removals (Larson and Whitham 1991). When more than one gall occupies the same leaf, these gall aphids also suffer strong intraspecific competition which significantly reduces their survival and reproduction (Whitham 1978, 1980, 1986). For example, when one of two competing stem mothers is experimentally removed, the average reproductive success of the survivor increases by 34% (Whitham 1986). These studies and the data presented here demonstrate that on resistant trees, aphids suffer not only strong intraspecific competition, but also strong interspecific competition from natural plant sinks.

Studies of gall former–plant interactions will benefit from the application of a sink competition model that focuses on gall formers as sink-inducing phloem parasites and mechanisms specific to this mode of herbivory. Most major hypotheses that account for patterns of herbivory are based on variation in the nutritional or secondary metabolite chemistry of tissues due to stress, genetics, or induced responses (Coley et al. 1985; Karban 1986; Mattson and Haack 1987; Hunter et al. 1992; Ohgushi 1992). However, tissue chemistry is not likely to be as important to phloem parasites as it is to tissue-chewing herbivores, and in several cases gallers have been found to be positively associated with higher levels of secondary metabolites (Waring and Price 1988; Taper and Case 1987).

Price et al. (1990) and Price (1991) have found that gall formers exhibit a strong pattern of preference for the largest plants or parts of individual plants. Because a major contributor to sink strength is sink size, or perhaps more accurately relative growth rate (Wardlaw 1990; Farrar 1993), vigorously growing plant parts will be large sinks during their development, and in the case of leaves, become large sources at maturity. Thus, increased gall former performance on relatively large parts is predicted by both Price's vigor hypothesis (Price et al. 1990; Price 1991) and the sink competition hypothesis we document here. However, the sink competition hypothesis can be more comprehensive than the vigor hypothesis in recognizing that the size of the sink is only one aspect of sink strength and that two other factors, competition from surrounding sinks and vascular connections between sinks and sources, also have major impacts on sink strength.

The significance of sink competition and vascular connections will depend on whether the gall former induces mobilizing or nonmobilizing sinks. Gall formers producing nonmobilizing sinks do not manipulate normal host allocation patterns, but instead just intercept a portion of the assimilates flowing past or through the gall (McCrea et al. 1985). For nonmobilizing gall sinks we expect a strong positive association between vigorous growth and gall former performance because the vigor of the galled plant part will strongly impact sink strength and determine food availability for the gall inhabitants. However, gall formers inducing mobilizing sinks manipulate normal host transport patterns and divert assimilate flow from neighboring plant parts to the gall (McCrea et al. 1985). For gall formers such as *P. betae* that create mobilizing sinks, competitive interactions and vascular connections with neighboring parts, as well as the size of the galled part, will impact food availability for the gall inhabitants. Gall formers do not have to be either nonmobilizing or mobilizing sinks. As we have found with *P. betae*, they may act as mobilizing sinks for some sources (storage reserves in the stems and from neighboring leaves) and nonmobilizing sinks for other sources (current photosynthesis from the galled leaf blade) (Larson and Whitham 1991), thus making simple predictions difficult.

While the sink competition hypothesis is more complex than the vigor hypothesis, we believe it provides a better framework to understand both the mechanisms involved and the exceptions to the pattern. In general we predict that phloem parasites acting as mobilizing sinks will be influenced by competitive interactions with surrounding natural plant sinks. In our study, lower bud density resulted in larger shoots and lower sink competition between natural sinks and gall sinks, but large plant parts may not always be associated with lower sink competition. Three examples demonstrate this point. First, Tscharntke (1988) found that midge larvae forming galls in the stem internodes on large, vigorous reed shoots had lower survival than on thin, stressed shoots. However, when the shoot apex of a large shoot was destroyed by stem-mining caterpillars, survival on large shoots increased, and performance was greater than on thin shoots. It is possible that sink competition was limiting gall formation by the larvae in the presence of the vigorously growing shoot tip. A second example also suggests that the stem apex may be an especially strong sink competitor. Shorthouse et al. (1986) observed a cynipid wasp that actually destroyed the stem apex following oviposition in the stem, presumably to eliminate it as a competitor for source allocation. Third, although most of our studies have reported increased aphid performance on the largest leaves and shoots (e.g., Whitham 1978, 1980), we have found that strong competition from rapidly growing shoots may limit gall success. Stem mothers placed on shoots of trees that had been heavily grazed by large ungulates during winter and were experiencing very rapid shoot regrowth had decreased survival despite larger leaf sizes (Larson, unpublished data). Thus, nonmobilizing sinks are predicted to perform better on larger plant parts, but for gallers that depend on mobilizing as well as intercepting resources, exceptions to the general pattern of preference for the most vigorous parts can be expected.

The significance of vascular integration between plant parts on galler-host relationships has not been examined, but the concept of integrated physiological units (IPUs) (Watson and Casper 1984) is important to understanding the relationships between phloem parasites and their hosts. Gall sinks will potentially interact with all other sinks within the IPU, and will not be impacted by sinks outside the IPU. For example, using ^{14}C labeling experiments we have found that *P. betae* galls can import assimilates from the galled leaf blade and neighboring leaves, but that their ability to act as mobilizing sinks is constrained by vascular connections (Larson and Whitham 1991, unpublished data)

Regardless of whether gallers are mobilizing or non-mobilizing, as phloem parasites they will be influenced by any of the factors that impact plant architecture. Variability in plant architecture among natural plant populations is common and widespread, and can be due to genetics, age, environmental stress, or herbivore damage (Kramer and Kozlowski 1979; Gottlieb 1984, 1986; Craig et al. 1986; Maillette 1987, Whitham and Mopper 1985). In our study, aphid stem mothers responded similarly to differences in architecture due to genetic differences between trees and experimentally manipulated differences among the branches of a single genotype. Variability in modular architecture due to any of the reasons cited above will be reflected in variability in the sink-source relationships within the plant and thus in different physiological environments for galling herbivores.

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