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Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions

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Summary. We examined the capacity of the galling aphid, *Pemphigus betae,* to manipulate the sink-source translocation patterns of its host, narrowleaf cottonwood (*Populus angustifolia*). A series of ^{14}C-labeling experiments and a biomass allocation experiment showed that *P. betae* galls functioned as physiologic sinks, drawing in resources from surrounding plant sources. Early gall development was dependent on aphid sinks increasing allocation from storage reserves of the stem, and later development of the progeny within the gall was dependent on resources from the galled leaf blade and from neighboring leaves. Regardless of gall position within a leaf, aphids intercepted ^{14}C exported from the galled leaf (a non-mobilized source). However, only aphid galls at the most basal site of the leaf were strong sinks for ^{14}C fixed in neighboring leaves (a mobilized source). Drawing resources from neighboring leaves represents active herbivore manipulation of normal host transport patterns. Neighboring leaves supplied 29% of the ^{14}C accumulating in aphids in basal galls, while only supplying 7% to aphids in distal galls. This additional resource available to aphids in basal galls can account for the 65% increase in progeny produced in basal galls compared to galls located more distally on the leaf and limited to the galled leaf as a food resource. Developing fruits also act as sinks and compete with aphid-induced sinks for food supply. Aphid success in producing galls was increased 31% when surrounding female catkins were removed.

Key words: Galls – Herbivory – Sink-source – Translocation – Phloem-parasites

Two fundamentally different modes of herbivory are: (1) tissue-chewing by herbivores that crush and consume plant tissues, and (2) vascular-feeding by herbivores that tap into the stream of assimilates moving through host phloem or xylem. There is strong evidence that the secondary chemicals spilled from vacuoles, glands, and resin ducts when tissues are crushed play a major role in mediating the selection and consumption of plants and plant parts by chewing herbivores (Feeny 1976; Rhoades and Cates 1976; McKey 1979; Rosenthal and Janzen 1979; Berenbaum 1981). However, because the distribution of secondary chemicals is so strongly compartmentalized within plant tissues and cells (Conn 1984; Sharma and Strack 1985), it is likely that vascular feeders avoid ingesting most secondary chemicals (Raven 1983; Mullin 1986). Plant vascular systems are parasitized by an abundant and diverse group of herbivores including free-feeding homoptera and many gall-formers (Way and Cammell 1970; Billett and Burnett 1978; Harris 1980; Larew 1981; Wu and Thrower 1981; Raven 1983; Weis and Kapelinksi 1984; Rohfritch 1987). Because herbivores parasitizing host phloem usually do not directly kill plant tissue, but instead maintain long-term physiological relationships with their host plant, we examine the role of this physiological relationship in determining herbivore performance.

The vascular plumbing of a plant integrates non-photosynthetic regions of the plant body specialized for growth and reproduction with those regions specialized for net carbon gain, termed sinks and sources respectively. Growing meristems, flowers and fruits are examples of sinks, while sources are those regions of the plant with high concentrations of labile assimilates and include photosynthetic organs and storage tissues. The flow of assimilates from source to sink is influenced by vascular connections, distance between source and sink, and by sink strength (Larson and Dickson 1973; Cook and Evans 1983; Watson and Casper 1984). Sink organs drawing assimilates from the same source tissues compete for resources, and the relative strength of competing sinks appears to regulate allocation within a plant, with source tissues having no control over the destination of the assimilates they produce (Wareing and Patrick 1975; Cook and Evans 1983; Wyse 1986).

Within this dynamic system of host plant sinks and sources, phloem parasites must find and maintain sites with adequate food supplies. Factors likely to influence

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the capacity of phloem parasites to act as resource sinks include vascular connections and distance between plant source and herbivore sink, and potential competitive interactions between herbivore sinks and plant sinks. In this paper we examine the physiology of sink-source interactions between the galling aphid *Pemphigus betae* and its host plant, narrowleaf cottonwood, *Populus angustifolia*. The ecology of habitat selection by this aphid has been documented by Whitham (1978, 1986) and allows us to consider how sites of known quality in terms of aphid fitness differ in sink-source relationships. For example, *P. betae* shows a strong preference for initiating galls at the leaf base (84% of galls are basal). In comparison with galls formed further out on the leaf, stem mothers inducing galls at the base of a leaf produce 65% more progeny and they develop at a faster rate (Whitham 1978, 1986). To examine the relationship between ecology and sink-source physiology in this system we address the following questions: (1) What is the source for *P. betae* sinks, and how does the sink-source relationship change during the lifespan of the galling generation? (2) Does *P. betae* actively manipulate host transport? (3) How does gall position on the leaf affect sink-source relations? (4) Do strong plant sinks, such as developing fruits, compete with developing aphids for the same food resources?

Biology of the species

In spring, *P. betae* fundatrices (stem mothers) hatch from overwintered eggs laid beneath the bark of narrowleaf cottonwood and colonize leaves just as the buds begin to open. Galls are initiated by a single stem mother along the midvein of an expanding leaf. After two weeks of rapid gall growth, the stem mother inside matures and begins to parthenogenetically produce a generation of alate viviparae. The alates begin emigrating from the gall about six weeks after initiation. Each gall can contain up to 300 of the stem mother's progeny. The gall wall consists of a rich vascular network embedded in a matrix of parenchyma cells. The stylets of *P. betae* can be found inserted into phloem sieve tube elements (P.R. Larson, pers. comm.) and there is no evidence of feeding damage to the parenchyma cells separating the gall cavity from the vascular tissue (K.C. Larson, pers. observ.).

Patterns of phloem transport within cottonwoods are dynamic and dependent on season and developmental stage. Early in spring, expanding buds and leaves are strong sinks; their growth is supported by carbohydrates transported via the phloem from overwintered storage, and amino acids transported via the xylem from the roots (Larson and Dickson 1973; Dickson et al. 1985). Immature eastern cottonwood (*Populus deltoides*) leaves continue to import resources, as well as incorporating almost all current photosynthates directly into leaf growth, until they are about 50% expanded (Larson et al. 1980). The tip of the leaf matures first and begins to export while the leaf base is still immature and continues to import (Isebrands and Larson 1973; Larson and Dickson 1973). Once leaves are fully mature, they function exclusively as sources, exporting photosynthates to new leaves, elongating stems, axillary buds and fruits.

Methods

We conducted a series of ^{14}C-labeling experiments to study the sink-source relationship established between *P. betae* and narrowleaf cottonwood. $^{14}CO_2$ fed photosynthetically to eastern cottonwood leaves is incorporated into sugars, structural carbohydrates, proteins, and amino acids, with about 90% of the exported ^{14}C in the sugar fraction and the rest as organic and amino acids (Dickson and Larson 1975; 1981). Dickson et al. (1985) found that the distribution and accumulation of a ^{14}C-labeled amino acid was closely correlated with carbon sink strength. Thus, we are not simply measuring the distribution of sugar, but are measuring resources important to herbivores.

^{14}C Labeling and Quantification

We labeled whole shoots (shoots defined as the current year's growth from one apical bud) by enclosing them in a CO_2-impermeable mylar bag, releasing $^{14}CO_2$, and allowing leaves to photosynthetically fix the labeled carbon. A 3 ml plastic cup containing $Na^{14}CO_3$ precipitate was fastened to the shoot and the bag closed with twist-ties. $^{14}CO_2$ was released by injecting 2 ml of 20% lactic acid into the plastic cup with a syringe. The syringe hole was sealed immediately with tape and the leaves allowed to fix $^{14}CO_2$ for 30 min before the bag was removed (Isebrands and Nelson 1983). Immediately after the bag was removed a leaf punch was taken from the edge of a labeled leaf and frozen as an estimate of the amount of $^{14}CO_2$ fixed in each shoot. Shoots and leaves were allowed to transport ^{14}C-photosynthates for two days, then collected and immediately frozen.

Single leaves were labeled by enclosing them in small mylar bags with a plastic cup containing the $Na^{14}CO_3$ attached to the bag. Leaves were sealed in the bag with tape. Galls did not take up significant quantities of ^{14}C, so whole leaves, including the gall, could be exposed to $^{14}CO_2$ and only the leaf blade would be labeled. Other aspects of the labeling technique were the same as described above.

We used autoradiography to visualize the distribution of ^{14}C within leaves and shoots. We prepared shoots for autoradiography by freeze-drying to prevent diffusion of ^{14}C. Shoots were then rehydrated, pressed flat, and dried. Dried shoots were covered with cellophane and exposed to X-ray film for 10 days to visualize qualitatively the distribution of ^{14}C.

To quantify ^{14}C content, we divided shoots into component parts and processed them for scintillation counting according to methods in Dickson and Nelson (1982). The same shoots were used for both autoradiography and scintillation counting. All ^{14}C measurements are given as the ratio of disentegrations per min (dpm) per mg of sample to the dpm/mg of a leaf punch taken immediately after labeling. Thus, measurements are given as a proportion of the quantity of ^{14}C in a mg of sink tissue after transport to the quantity of ^{14}C per mg of source tissue at time zero. This measure, which we term "sink strength", quantifies the capacity of an aphid or plant part to accumulate labeled assimilates.

Field experiments

Food resources for P. betae. This experiment measured the seasonal dynamics of the source-sink relationship between cottonwood hosts and *P. betae*. Within a single tree growing under natural field conditions, we chose 30 similarly-sized shoots, 15 with a single basal gall on leaf #4 and 15 with a single basal gall on leaf #6

(with the most basipetal leaf as #1). At approximately 10 day intervals, three shoots with a gall on leaf #4 and three shoots with a gall on leaf #6 were ^{14}C-labeled, giving a total of four treatment times during the development and maturation of the gall aphids. At each treatment time, leaf #6 was labeled on all six shoots. After a two day transport period, we quantified the sink strength of galls for assimilates fixed in the galled leaf blade (shoots with galls on leaf #6) or for assimilates fixed in a single neighboring leaf (shoots with galls on leaf #4). In this experiment, "sink strength" was based on scintillation counting of whole galls, including gall tissue and the aphids inside.

Manipulation of host allocation. We first addressed the question of whether aphid galls increase spring allocation into galled shoots. Shoots were paired for size before bud burst in spring. One shoot of each pair was infested with 10 *P. betae* stem mothers. After four weeks of development, shoots were collected, dried, and component parts weighed. An average difference in weight of aphid-infested and control shoots was based on four pairs of shoots per tree, and replicated on ten trees.

Our second experiment to determine whether aphid-induced galls alter normal patterns of transport, compared the capacity of galled leaves and gall-free leaves to import ^{14}C from neighboring leaves. Five weeks after gall initiation, we selected seven shoots containing a single galled leaf at position #4, #5, or #6 and labeled all leaves on the shoot except for the galled leaf and an adjacent gall-free leaf. $^{14}CO_2$ uptake in these two leaves was prevented by sealing them in black plastic bags within the mylar bag into which $^{14}CO_2$ was released. To prevent overheating of unlabeled leaves, a layer of moist paper towel was wrapped around the leaves within the black plastic bag, and around the outside of the black bag. Three shoots were prepared for autoradiography. For all shoots, the difference in sink strength between the galled leaf (gall tissue plus leaf tissue) and the gall-free leaf was quantified by scintillation counting.

To determine if aphids could draw assimilates from all areas of the occupied blade, we labeled small areas of leaf tissue with $^{14}CO_2$ and determined ^{14}C accumulation in galls located basally or distally to the labeled tissue. Spot labeling of 1.2 cm^2 areas of leaf tissue was done by releasing $^{14}CO_2$ from a Warburg flask with a 1.2 cm^2 opening. The main opening of the flask was sealed to the underside of a leaf with lanolin and the ^{14}C was placed in the side arm (Isebrands and Larson 1977). Transport into a gall was determined qualitatively by autoradiography. Each gall was scored as labeled or not labeled as well as basal or distal to the labeled spot, and the results analysed with a chi-square test ($n=20$ galls).

Effect of gall position. This experiment measured the influence of gall position within a leaf on source-sink relationships. We compared the source of ^{14}C drawn into a gall located either at the base of a leaf or 12 mm distal to the base. Two potential sources were labeled: the galled leaf blade or the ungalled leaves surrounding a galled leaf. Twenty-seven similarly-sized shoots were selected and divided into three test groups: (1) The capacity of basal and distal galls to import ^{14}C from surrounding leaves was measured on nine shoots, each with one basally- and one distally-galled leaf. The galled leaves were bagged to prevent ^{14}C uptake and the remaining gall-free leaves of the shoot were labeled as described earlier. (2) The capacity of basal galls to intercept ^{14}C exported from the occupied leaf was measured by labeling a single, basally-galled leaf on nine shoots. (3) The capacity of distal galls to intercept ^{14}C was measured in the same way on nine additional shoots containing single distal galls located approximately 12 mm from the base of the leaf. In this experiment, "sink strength" was based on scintillation counting of the aphids contained within the gall.

Effect of flower removal. To determine if flower sinks compete with aphid sinks, we measured aphid responses to removal of flowers. Aphids were transferred to heavily-flowering shoots with all flowers removed, or controls with no flowers removed. One hundred aphids were transferred onto each of five trees (five aphids transferred to 10 treatment and 10 control shoots per tree, $n=5$ trees).

Results

Food resources for P. betae

Aphid-induced galls functioned as sinks throughout their development, while the source of phloem sap imported into aphid galls was dependent on seasonal development (Fig. 1). A two-way ANOVA showed that the sink strength of the gall was significantly affected by source (from the occupied leaf or a neighboring gall-free leaf, $F_{1,16}=94.9$, $p<0.001$) and the number of days since bud burst ($F_{3,16}=10.08$, $p<0.001$). The interaction of source and time was also significant ($F_{3,16}=6.37$, $p<0.005$) indicating that the relative contributions of different sources changed through time. Examination of these data indicate that: (1) one week after bud burst, developing galls were not strong sinks for photosynthates produced by the young leaves regardless of the source; (2) the occupied leaf blade became a strong source after 14 days but declined again after 41 days; and (3) contribution of ^{14}C-assimilates from a single neighboring leaf increased throughout the season. Estimating total ^{14}C allocation to galls by summing allocation from the occupied leaf and a neighboring leaf, shows that the contribution from a single, neighboring leaf increases from 0.05% seven days after gall initiation to 19.7% 41 days after initiation. The total allocation to a gall from all neighboring leaves is an estimated 38.3% (based on the number of vascular traces a gall shared with the labeled leaf #6 and unlabeled leaves #1 through #8).

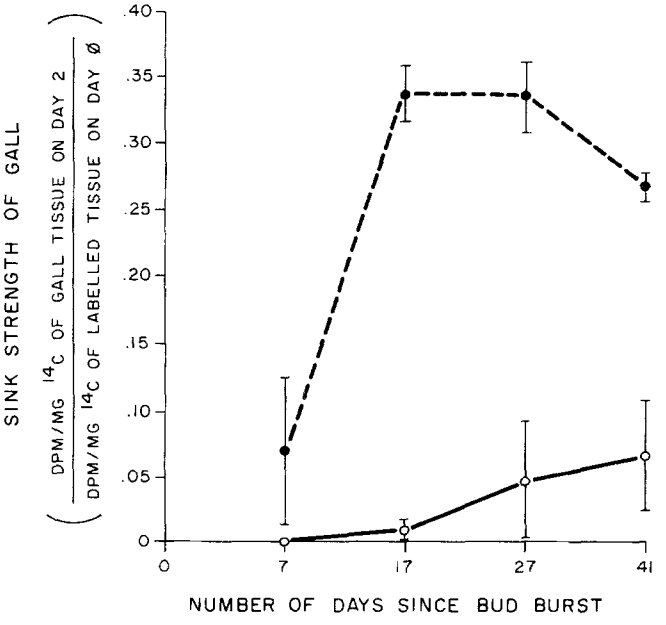

Fig. 1. Effect of seasonal development on sink strength of *P. betae* galls for ^{14}C-assimilates produced in the occupied leaf blade (*closed circles*) or in a neighboring, gall-free leaf (*open circles*). Vertical bars show ± 1 SE

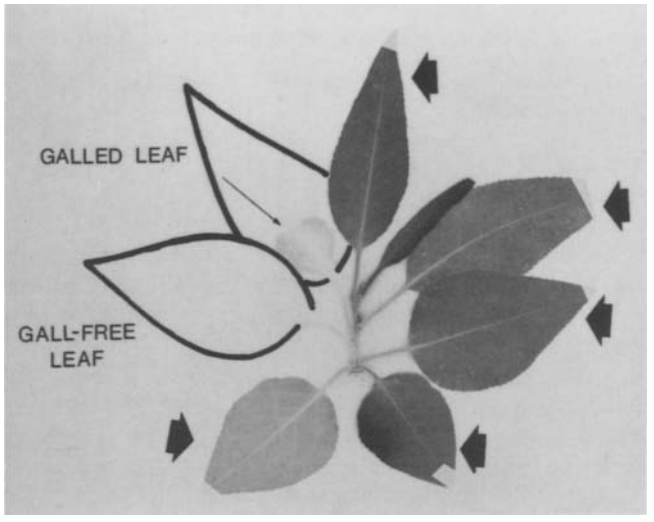

Fig. 2. Autoradiograph of translocation of ^{14}C-labeled assimilates from neighboring leaves into a galled and a gall-free leaf. ^{14}C-labeled assimilates were imported into the gall, but not the galled leaf blade or a gall-free leaf. All leaves of the shoot were labeled with ^{14}C except the galled leaf and a gall-free leaf. Heavy arrows show the locations of ^{14}C-label introduction (*dark exposing areas*), and dark areas outside these leaves show accumulation of ^{14}C-labeled products after 2 days of transport. The light arrow shows the location of the gall

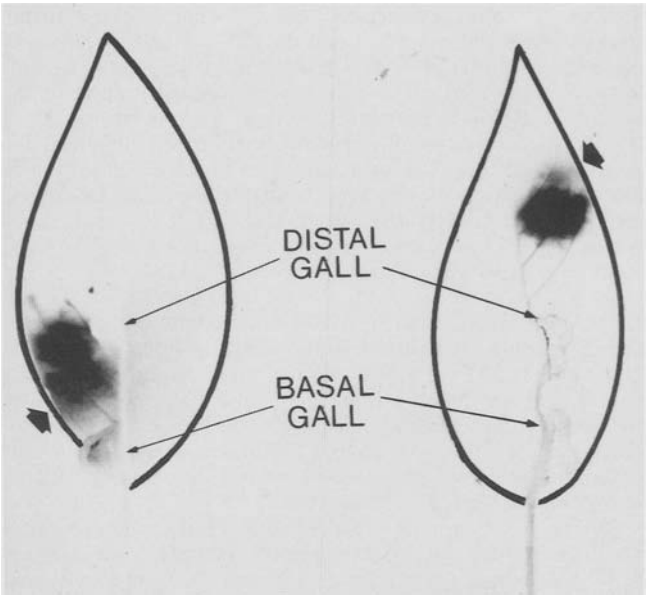

Fig. 3. Effect of gall position on capacity of galls to intercept photosynthates fixed in the occupied leaf. Each leaf was spot labeled with ^{14}C (*heavy arrows*), and dark areas outside of these spots indicate transport of ^{14}C-labeled assimilates after 2 days. The leaf on the right shows that ^{14}C-labeled assimilates are transported out of the labeled spot into the midvien and then into two galls (*light arrows*) located basal to the labeled spot. The leaf on the left shows that ^{14}C-labeled assimilates are transported out of the labeled spot into the gall located basally, but not into the gall located distally to the labeled spot (galls indicated by *light arrows*)

Manipulation of host allocation

The presence of developing galls resulted in significantly increased biomass allocation to aphid-infested shoots compared to gall-free control shoots. After four weeks of growth, galled shoots weighed on average 14.4% more than their gall-free controls (mean $\pm$1 SE: 0.804 ± 0.097 g for galled, 0.704 ± 0.090 for gall-free, $n=10$, $t=3.35$, $p<0.005$). The increased biomass of galled shoots was not the result of increased carbon fixation in galled compared to gall-free shoots (K.C. Larson unpub. data). These data indicate that aphids induced increased allocation of stored reserves into developing galls.

Aphid galls functioned as mobilizing sinks, able to import ^{14}C fixed in neighboring leaves. Normally, photosynthates were not transported among the equal-aged leaves of a shoot. The sink strength for assimilates fixed in neighboring leaves was virtually zero for gall-free leaves (0.001 ± 0.0005), while galled leaves imported significant quantities of labeled assimilates (0.053 ± 0.012) (Fig. 2, $p<0.005$, Wilcoxon Signed Rank Test, $n=7$).

Aphids also intercepted assimilates fixed in the galled blade before they could be exported from the leaf, but did not manipulate transport within the leaf (Fig. 3a, b). Aphids accumulated ^{14}C-photosynthates fixed in leaf tissues distal to the gall, but ^{14}C-photosynthates fixed in leaf tissues basal to the gall moved directly out of the leaf and were not drawn into more distal galls (chi square $=15.00$, d.f. $=1$, $p<0.001$).

Effect of gall position

Small differences in gall position on the leaf blade significantly affected the capacity of aphids to act as mobiliz-

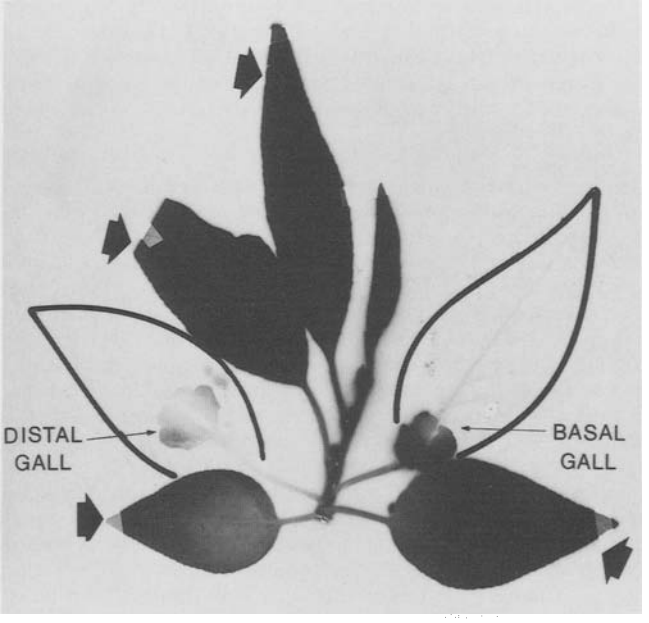

Fig. 4. Effect of gall position on capacity of galls to import ^{14}C translocated from surrounding leaves. The greater sink strength of the basal gall for the assimilates fixed in neighboring leaves is indicated by its darker exposure. All leaves of the shoot were labeled with ^{14}C (*heavy arrows*) except for a leaf containing a distal gall and a leaf containing a basal gall

ing sinks for assimilates fixed in neighboring leaves. Sink strength for assimilates fixed in neighboring leaves was significantly greater for aphids in basal galls (0.31 ± 0.103) than aphids in distal galls (0.07 ± 0.023) (Fig. 4, $t = 2.33$, $p < 0.05$, $n = 8$). Aphids in basal galls consumed 4.4 times more ^{14}C-labeled assimilates translocated from neighboring leaves than did aphids in galls just 12 mm distal to the base of the leaf.

In contrast, gall position did not significantly affect aphid capacity to intercept ^{14}C-assimilates exported from the galled blade. The sink strength of aphids in distal galls versus basal galls for assimilates fixed in the galled leaf blade was not significantly different (distal = 0.97 ± 0.064; basal = 0.77 ± 0.061; $t = 1.65$, $n = 17$, $p > 0.06$); although there was a trend toward greater sink strength for aphids in distal galls. Because aphids in distal galls do not draw in ^{14}C from basal sections of the galled leaf, these results may indicate that aphids in distal galls compensate for the reduction in source area by increasing sink strength within a leaf.

Effect of flower removal

Aphids transferred onto heavily-flowering control shoots had a mean survival of 58% ($\pm 4.8\%$) compared to 76% ($\pm 3.8\%$) for aphids transferred onto matched shoots with all flower buds removed ($F_{1,4} = 45.00$, $p < 0.005$).

Discussion

Colonizing stem mothers of *Pemphigus betae* strongly prefer to initiate galls at the bases of large leaves where their fecundity is greatest (Whitham 1978). Our results show that the sink-source relationship established between a gall and its host is strongly influenced by the location chosen by the stem mother. Regardless of the gall site selected, aphids intercept ^{14}C from the midvein that is exported from leaf tissue distal to the gall (non-mobilizing sink, McCrea et al. 1985). However, aphids colonizing leaf bases also have the capacity to actively manipulate transport and import ^{14}C fixed in surrounding leaves (mobilizing sink, McCrea et al. 1985). The most basal part of the leaf would appear to have two advantages in terms of sink-source relationships for *P. betae*: 1) resources produced in leaf tissues basal to the gall are not lost, and 2) aphids can tap into an additional food supply: the resources produced in neighboring leaves. Our quantitative ^{14}C labelling does not provide evidence that basal galls accumulate more label from the galled leaf than distal galls, and in fact shows a trend toward distal galls getting more. However, this experiment was done late in gall development, when ^{14}C from neighboring leaves was becoming increasingly important for basal galls, and may represent distal gall compensation for lack of resources imported from outside the galled leaf.

Aphid manipulation of normal transport patterns appears critical to maintaining food supplies. While free-feeding aphids often track the seasonal changes in host allocation patterns (Wratten 1974; Sutton 1984; Larsson 1985), immobility limits gall-formers' capacity to respond to seasonal changes. For example, early *P. betae* gall growth is fueled by allocation from stem reserves. As leaves become photosynthetically mature, they begin transporting ^{14}C to aphid sinks. Later still, before the aphids within the gall are mature, the galled leaf blade becomes chlorotic (Williams and Whitham 1986). Aphids in basal galls respond to the increasing food demands of a growing colony and decreasing supplies from the galled leaf by importing resources from neighboring leaves. Neighboring leaves supplied 29% of the ^{14}C accumulating in basal galls nearing maturity, while only supplying 7% to distal galls. Aphids in distal galls appear to suffer from a lack of food. Whitham (1986) has shown that basal galls produce 65% more aphids than distal galls, and that the aphids mature more rapidly.

The arrangement of vascular pathways within a plant will determine the potential food sources that herbivore sinks can draw upon. In our study, it was surprising that aphids in basal galls exerted a mobilizing effect on ^{14}C fixed in neighboring leaves, while aphids in distal galls did not even control the transport of ^{14}C fixed a few millimeters away in basal leaf tissue. The structure of vascular pathways can explain this result. Voglemann et al. (1982) mapped the vascular pathways of eastern cottonwood leaves (*Populus deltoides*), and found that the vascular bundles lie in distinct tiers within the midvein. Vascular bundles serving the base of a leaf entered the ventral part of the midvein and passed directly out of the leaf. Thus, aphids in distal galls have no possibility of tapping into the vascular bundles serving the base of a leaf. On the other hand, the vascular bundles leading out of a leaf join common orthostichies shared with other leaves of the shoot, even though the direction of assimilate flow normally prevents mature leaves from importing (Larson and Dickson 1973). By inducing a reversal of assimilate flow aphids were able feed on the assimilates produced in neighboring leaves.

There is a strong potential for competition between sinks within the same vascularly integrated unit. There are numerous examples of competition between a plant's natural sinks for the available sources (Thrower 1974; Wareing and Patrick 1975; Blechschmidt-Schneider 1984; Egli et al. 1985; Ho 1988). However, only rarely has competition between plant sinks and herbivore-induced sinks been considered. We find evidence of competition between aphid-induced sinks and flower/fruit sinks. First, both aphid galls and developing fruit accumulate ^{14}C from the same leaves (K.C. Larson, unpub. data). Second, the experimental removal of the flower buds subtending a shoot resulted in a 31% increase in successful gall formation relative to controls. In this experiment, removal of flower buds clearly increased the resources available for aphid gall development, but we cannot conclude that aphids should avoid inducing galls on shoots subtended by flowers. In fact *P. betae* prefers mature reproductive trees over young, rapidly-growing trees (Kearsely and Whitham 1989). We conclude that aphids interact with surrounding plant parts acting as sinks, and that the sink strength of near-by plant parts should influence *P. betae* success. As of yet, however, we have not ranked various plant parts on young and

mature plants in terms of sink strength. It is possible that vigorously growing shoots of young trees are stronger competitors than flowers of mature trees.

Sink-source interactions between herbivores and their host plants provide an alternative to plant chemistry in explaining the distribution and fitness of phloem parasites. Zucker (1982) found a gradient of increasing phenolic concentration from the base to the tip of week-old narrowleaf cottonwood leaves and proposed that this could account for the preferrence of *P. betae* for basal sites within leaves. However, he does not consider that the phenolic gradient in young cottonwood leaves could be due to the gradient in leaf maturation (Isebrands and Larson 1973), with the early maturing tip having higher phenolic contents than the younger, and still developing base. It is unknown whether a phenolic gradient is maintained as leaves mature. While phenolic content may serve as a cue for location within a leaf, it is unclear how local tissue phenolic content would influence a phloem parasite feeding on resources drawn from the entire galled leaf, neighboring leaves, and stem reserves. A lack of interaction between secondary metabolites and phloem parasites is supported by other cases in which the distribution and concentration of secondary metabolites have been poor predictors or positively associated with the distribution and abundance of free-feeding homoptera or galling herbivores (Wratten et al. 1984; Taper and Case 1987; Waring and Price 1988).

Understanding food resources, and the role of sink-source interactions, is fundamental to gall-herbivore ecology. We found that herbivores acting as mobilizing sinks may be especially affected by competitive interactions with surrounding plant sinks, or by minor differences in gall position. Competitive interactions between herbivore-induced mobilizing sinks and plant sinks may be often overlooked. The chalcidoid wasp, *Hemadas nubilipennis* destroys the terminal bud following oviposition, presumably to eliminate it as a competitor (Shorthouse et al. 1986). Another galler, *Rhabdophaga strobiloides,* exerts apical dominance over subtending lateral buds and thus may reduce competition (Weis 1984). Non-mobilizing herbivore sinks may maximize resource supply by selecting the largest plant parts available and by precise positioning of the gall. Gall-formers often prefer large parts (Whitham 1978; Weis and Kapelinksi 1984; Craig et al. 1986; Price et al. 1987). Hartnett and Bazzaz (1984) have previously stressed the importance of factors other than chemistry when examining feeding-site selection and patterns of herbivory for phloem feeders. The results of our study support their hypothesis that plant-phloem parasite interactions can be influenced by the dynamics and physiological activity of the plant parts surrounding the parasite.

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