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INTERSPECIFIC COMPETITION AMONG PHLOEM-FEEDING INSECTS MEDIATED BY INDUCED HOST-PLANT SINKS[1]

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Abstract. The role of interspecific interactions among herbivorous insects is considered to be limited, especially in specialist communities. In the current study we report on exploitative interspecific interaction between two closely related phloem-feeding species of gall-forming aphids (Homoptera; Pemphigidae; Fordinae), mediated by the supply of photoassimilates from the host plant.

Geoica sp. forms a spherical gall on the leaflet midrib of *Pistacia palaestina* (Anacardiaceae), while *Forda formicaria* forms crescent-shaped galls on the leaflet margin of the same host plant. Using ^{14}C labeling, we were able to trace the food supply (assimilated carbohydrates) from the leaves to galls of each species. We found that *Geoica* galls are strong sinks. These galls divert the normal phloem transport of the plant and reduce the amount of assimilates imported by *F. formicaria,* especially when they are located on the same leaflet. By the end of the season *Geoica* caused death of 84% of *F. formicaria* galls that were located on the same leaflet, and reduced reproductive success in the surviving galls by 20%. This is because the presence of *Geoica* causes early senescence (but not abscission) of the leaflet it is on (whether or not *F. formicaria* is present). The interaction is asymmetrical: *F. formicaria* did not affect reproductive output of *Geoica* nor did it cause visible damage to the leaflets. To our knowledge, this is the first demonstration of exploitation competition for plant assimilates between two insect-induced sinks.

This exploitative competition, mediated by manipulation of plant phloem transport, stands in contrast to the absence of interference competition for galling sites between the two aphid species. Although their spatial distributions partly overlapped, the niche breadth of each species (measured from gall positions on leaves along the shoot axis) was not affected by the presence of the other. Moreover, when both species were located on the same leaf, they formed galls independently on the same or different leaflets, and there was no indication of interference competition over galling sites.

Key words: aphids; carbohydrate sinks; Fordinae; galls; interspecific competition; phloem transport.

INTRODUCTION

Carbon partitioning between sources (organs that export assimilates) and sinks (organs that import assimilates) and its regulation are critical aspects in plant biology and crop production. In plants, sugar is produced photosynthetically, mostly in the mature leaves. Carbohydrate reserves in storage organs (tubers, bulbs, etc.) or the trunk and branches of trees may serve as important sources of assimilates early in the growth season. Sink organs are lateral meristems, developing buds, young leaves, fruits, roots and—at the end of the growth season—storage organs (review in Ho 1988). In many cases carbohydrates are in short supply, facilitating sink competition (Gifford and Evans 1981, Ho 1988, Wardlaw 1990). This competition may result, for example, in alternate-year bearing of fruits and seeds, differential fruit size, or reduction of vegetative growth. Sink competition is also correlated with senescence of leaves and reproductive organs (Gifford and Evans 1981, Watson and Casper 1984, Ho 1988, Nooden 1988). The mechanism(s) of regulation of carbon partitioning between plant sinks are far from being conclusively determined (e.g., Wyse 1986, Wardlaw 1990, Sonnewald and Willmitzer 1992).

Various parasitic organisms induce sinks that utilize host-plant carbon resources. Strong sinks are induced by pathogenic viruses (Burdon 1987), bacteria (e.g., *Agrobacterium* sp., which induce "crown galls"; Mani 1964), fungi (Hall et al. 1992), and parasitic plants (Seel et al. 1992). These organisms compete with host-plant sinks and change carbon allocation, in many cases severely damaging the host plant. In addition, many invertebrates induce galls (Mani 1964), which may function as sinks. An extensive resource allocation

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analysis in *Solidago* indicated that galls are sinks for assimilants and nutrients (e.g., Stinner and Abrahamson 1979, Weis et al. 1988, and references therein). Using ^{14}C labelling to trace phloem transport of sugars into galls, it was found that galls may be nonmobilizing sinks, which intercept and partly block the normal carbon translocation (e.g., McCrea et al. 1985). Other galls may alter the normal phloem flow and import assimilants from neighboring leaves and other plant sources (Jankiewicz et al. 1970, Larson and Whitham 1991). Carbohydrate supply may become a limiting resource, for which competition between a variety of sinks may take place within the plant. The importance of sink–source regulation in plant response to herbivory was emphasized by Whitham et al. (1991). Larson and Whitham (1991) showed that aphid-induced galls may compete for assimilates with plant sinks such as flowers and fruits. It has been suggested that stronger sinks induced by phloem-feeding herbivores import large amounts of assimilates via the phloem system, and thus may dominate other sinks. For example, Moran and Whitham (1990) described competitive interactions between two aphid species attacking different plant organs, and suggested as one possibility that they may compete for nutrients. However, as far as we know, there is no published report of interspecific or intraspecific exploitative competition between insects, in which plant-assimilates were shown to be a limiting factor.

Competition among herbivores may be of two kinds: interference (=contest) and exploitative (=scramble) (for definitions see Price 1984: 418). Interspecific competition is thought to be infrequent and unimportant in shaping community structure among insect herbivores. This view is supported by the fact that herbivores seem rarely to be resource limited (Hairston et al. 1960), and many empty niches are available in particular for herbivorous specialists (Price 1984, Strong et al. 1984). On the other hand, Janzen (1973) argued that all plant parts are a common resource budget, and herbivores that share the same plant automatically compete ("the process is true competition in the sense that the presence of each species lowers the availability of resources for the other." Janzen 1973: 786). Few plant-mediated interspecific interactions among herbivores have been detected (e.g., Karban 1986, Moran and Whitham 1990, Hunter 1992). However, mobilizing sinks induced by herbivores may result in such interactions.

*Intra*specific interactions were documented in the galling aphid *Pemphigus betae,* which forms galls on poplar (Whitham 1978). This aphid induces mobilizing sinks that draw assimilates from neighboring leaves. Galls located at basal leaf position induced more powerful sinks than more distal galls on the same leaf (Larson and Whitham 1991). Competition among the gall-inducing herbivores, however, was not studied.

Gall-forming aphids (review in Wool 1984) are particularly suitable organisms for the study of exploitative competition for plant assimilates. Aphids are sap-feeding herbivores that feed directly on the sieve elements. Galling (Larson and Whitham 1991, Burstein et al. 1994), as well as free-living aphid aggregations (Peel and Ho 1970, Way and Cammell 1970, Dixon 1975, Veen 1985, Hawkins et al. 1987, Thomas and Lombard 1991), and even single aphids (Canny and Askham 1967), induce sinks for plant assimilates. Galls provide superior nutrition for the aphids in them (Forrest 1971, Llewellyn 1982). Dixon (1985) suggested that interspecific exploitative competition over phloem sap may be important in some aphids. In a preliminary study on the sources of assimilates imported into galls of a guild of aphid species (Homoptera; Pemphigidae) that forms galls on *Pistacia palaestina* Boiss., we found indications for exploitative competition, since the source of assimilates of different species may overlap (Burstein et al. 1994).

In the current study, which involves two of these species, we ask the following questions: (1) What are the sources of assimilates of each species when it is found alone or together with the other species? (2) Do these species (sinks) compete for assimilates that they import into the galls? (3) What are the effects of the sink relationships on the fitness of each species? (4) If the gallers negatively affect each other's performance, do they avoid one another when choosing galling sites?

Materials and Methods

The system

The two species studied are *Geoica* sp. and *Forda formicaria* von Heyden. These are two of 15 gall-forming aphids (Homoptera; Pemphigidae; Fordinae) that form galls on *Pistacia* (Anacardiaceae) trees in Israel (Koach and Wool 1977). Both species use as primary host *P. palaestina,* a deciduous, pinnate-leaved tree, commonly found in the natural forests. (*Geoica* was referred to in previous publications as *G. utricularia* Pass. [Wool and Koach 1976, Koach and Wool 1977, Wool 1977, 1984], but we have evidence that more than one species of this genus is present in Israel, and the taxonomy of the complex is problematic.) We chose these species because they are quite common and may occupy the same shoot, leaf, or even leaflet of the same individual tree (Inbar and Wool 1995). The life history of these and related gall-forming aphids was described in previous studies (e.g., Wool and Burstein 1991). Briefly, galls are formed by a fundatrix nymph in the spring. Within each gall, 2–3 generations of aphids are produced parthenogenetically. In autumn galls open and alate (winged) aphids disperse to secondary hosts. The rest of the cycle involves a return flight to the *Pistacia* trees and sexual reproduction on them (Wool 1984), but it is irrelevant for the present paper, which deals with the gall stage only. The two species are different in their galling strategy. *Geoica* forms a single globular (1–3 cm in diameter) gall on the leaflet midrib,

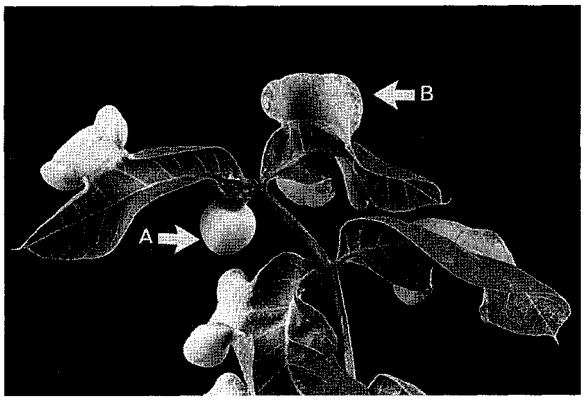

FIG. 1. Young spherical galls of *Geoica* sp. (A) and crescent galls of *F. formicaria* (B) on a leaf of *Pistacia palaestina*. One leaflet had both species, other leaflets had only crescent galls. Note the position of the spherical gall on the leaflet vein.

while *F. formicaria* forms two types of galls: a fundatrix (F_1) gall, ≈5 mm long, is formed early in the spring on the leaflet midrib, and ≈3 wk later a second, crescent-shaped final gall is induced on leaflet margins by the descendents of the fundatrix (F_2) (Fig. 1). Within these galls two generations are produced (F_3) and (F_4); the latter is the winged, migratory form (Wool and Barel 1995). The fundatrix (F_1) galls die after ≈4 wk. In this paper we discuss only the final galls. We shall use the terms "spherical gall" and "crescent gall" to refer to *Geoica* sp. and *Forda formicaria* galls, respectively.

Study site

All experiments and observations were conducted in 1993 on a single naturally growing *P. palaestina* tree, at Canada Park, 30 km southeast of Tel Aviv. The tree was chosen because it carried large populations of the two species, which were needed for the extensive labeling experiments. We have preliminary evidence from other trees and locations (Burstein et al. 1994) that justifies drawing general conclusions from the present results, although quantitative differences in response may be expected among trees.

^{14}C labeling procedure and analysis

The source organ (one or more leaflets) was enclosed in a transparent plastic bag, sealed tightly as in Burstein et al. (1994). Into the bag, we injected $^{14}CO_2$ released by lactic acid from sodium carbonate solution (American Radiolabeled Chemicals Limited, St. Louis, Missouri) ≈1.85 MBq/leaflet. The bags remained in situ for 4 h (1000–1400), to allow photosynthetic fixation of labeled CO_2. Then the bags were removed. The shoots with the labeled leaves remained in situ for a further 48 h for natural translocation of assimilates. After 48 h the shoots were cut off and kept deep frozen (at −20°C) in the laboratory until analysis.

In order to quantify the distribution of ^{14}C, we extracted each leaf part (source (labeled) leaflets, nonlabeled leaflets, galls, and leaf petioles) separately for 24 h in N,N-dimethylformamide. Scintillation counting (Packard 1500 Tri-Carb liquid scintillation analyzer) was done with 0.1 mL of extract in 4 mL scintillation liquid (Safe Fluor, Lumac Company).

Sink strength

The definition of sink strength and the way to measure it are controversial issues among plant physiologists (see Farrar 1993 for an extensive review and references). We follow Larson and Whitham's (1991) definition. Sink strength is expressed as the "specific radioactivity" of gall tissue (becquerels per milligram dry mass) divided by "specific radioactivity" of source tissue. All measurements are per tissue dry mass (oven dried at 70°C for 24 h) after 48 h of natural transport.

Sink strength does not reflect the actual quantity of assimilates incorporated in the gall, since it is a ratio of specific radioactivities. As an alternative measure, we also calculated PL (proportion of labeled assimilates) in the gall, PL = (specific radioactivity of gall tissue × gall mass) ÷ [(specific radioactivity of gall tissue × gall mass) + (specific radioactivity of source tissue × leaflet mass)]. (In calculations of PL for galls on cohabited leaflets, the second gall was included as part of the source.) PL is the proportion of carbon translocated to the gall in 48 h of the amount remaining in the source leaf. PL ranges between 0 and 1. PL = 0 indicates that no labeled assimilates were imported into the gall.

Field labeling experiments

Experiments were carried out approximately once every 3 wk, May–October 1993. On each visit to the tree, six treatments were set up. Each treatment was replicated five times. Treatments differed in the position of the source leaflet relative to the gall (sink) and the species of galls involved (Table 1). Galls may be found on different leaflets within a leaf, but for convenience we selected leaves where spherical and crescent galls were located on the basal leaflets. Although leaves may carry many galls of each species, only

TABLE 1. Treatments in field-labeling experiments. Each treatment was replicated on five different shoots on each sampling date.

Treatment	Aphid species on galled (sinks) leaflet	Position of source leaflets relative to the sinks
1	Gsp	same leaflet*
2	Ff	same leaflet*
3	both Bsp and Ff	same leaflet*
4	Gsp	more distal leaflet(s)
5	Ff	more distal leaflet(s)
6	both Gsp and Ff	more distal leaflet(s)

* Excluding the galled area.

leaves carrying a single crescent, a single spherical, or one gall of each species were used.

When galled leaflets were labeled (treatments 1–3), the galled area was covered with putty to prevent direct carbon fixation by the gall tissue itself, although we have evidence that the photosynthetic ability of the gall tissue is very limited and there is no net CO_2 fixation in the gall (M. Inbar, *unpublished data*).

In nature, the leaves of *Pistacia palaestina* are sometimes skeletonized by caterpillars of the procession moth, *Thaumetopoea solitaria.* The galls, however, are not eaten and develop normally (Wool and Barel 1995). In order to measure the ability of *F. formicaria* to use alternative carbohydrate sources in such situations, we labeled in September 1993, as an additional treatment, leaflets located distal to crescent galls (as in treatment 5), but the blade of the galled leaflet itself was removed so that distal leaflets were the only labeled sources.

Niche breadth

The possibility that *Geoica* sp. and *F. formicaria* compete for galling sites was examined as in Burstein and Wool (1993) and Inbar and Wool (1994). The relevant dimension of the niche of the two species is the location of the galls on different leaves along the shoot.

We examined the distribution of spherical and crescent galls on 48 shoots carrying at least one gall of either species. The location and number of galls on each leaf were recorded (the oldest, basal leaf was numbered 1). We calculated niche breadth (B) by Levins' formula (Price 1984: 395)

$$B = 1/(\Sigma P_i^2 S),$$

where P_i is the proportion of galls on leaf i, and S is the number of leaves on the shoot. B ranges from 0 to 1. B was calculated separately for three categories of shoots: shoots with only spherical, only crescent, and shoots with both galls. We also calculated proportional similarity (PS) between the species in leaf (habitat) occupation (Price 1984):

$$PS = 1 - \tfrac{1}{2}\Sigma|P_{ik} - P_{jk}|,$$

where P_{ik} and P_{jk} are the proportions of species i and j on resource unit k (a leaf within shoot). PS ranges between 0 (no overlap) and 1.

Reproductive fitness of F. formicaria *and* Geoica

Samples of leaflets with solitary crescent galls, and with both spherical and crescent galls (10 each), taken at random, were examined in the laboratory approximately once a month from April to November 1993. We recorded clone size and the number of dead galls (which did not contain any live aphids). In addition, since galled-leaf position on the shoot may affect aphid reproductive success (Burstein and Wool 1993), we collected 42 leaves that carried a solitary crescent gall on one leaflet, and both species on another leaflet in October 1993. We compared clone size and survival in the crescent galls in the two situations, counting F_3 and F_4 generations separately.

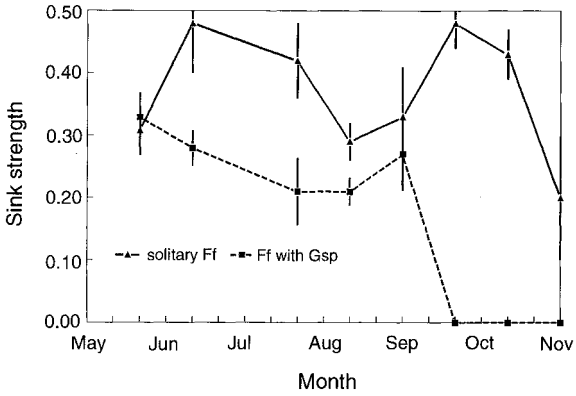

FIG. 2. Competition for resources drawn from the galled leaflet: temporal changes in sink strength of *F. formicaria* (Ff) crescent galls (Bq/mg gall)/(Bq/mg source leaf), when solitary and cohabiting with spherical *Geoica* galls (Gsp) (mean ± 1 SE, n = 5, at each sampling date).

On 1 May 1993, at an early stage of *Geoica* development, we carefully removed 40 spherical galls from the leaflets: 20 of them were located on the same leaflet with crescent galls. The leaflet blade and crescent galls were not damaged. Each leaflet was marked with a plastic tag, and the effect of killing the spherical gall on clone size in crescent galls was monitored 5 mo later, at the peak clone size of this species. (Crescent galls were not treated in this experiment, because we had evidence at that stage that the presence of *F. formicaria* galls on the same leaflet does not affect the fitness of *Geoica.*)

Statistical analysis

Analysis of ^{14}C translocation and niche breadth data was carried out by nonparametric tests because these complex variables cannot be assumed to have normal distributions. Friedman's nonparametric randomized-block test was used to test for differences in sink strength between solitary crescent galls and those cohabiting with spherical galls on a leaflet. (Sampling dates were taken as blocks.) Chi-square tests were used for differences of observed and expected frequencies of galls on leaflets. Mann-Whitney U tests were used to compare mean niche breadth between treatments. Parametric paired-comparison t tests were used to analyze aphid reproductive success (numbers of aphids per gall = clone size) (normal distribution expected after square-root transformation). All tests were carried out according to Sokal and Rohlf (1981).

RESULTS

Import of assimilates from the galled leaflet

The galled leaflet is a very important source of assimilates for both species. The temporal changes in sink

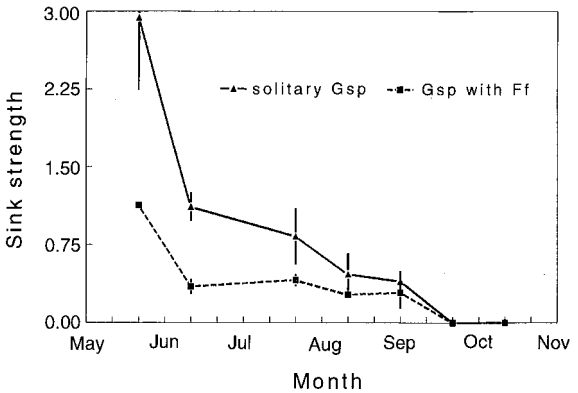

FIG. 3. Competition for resources drawn from the galled leaflets: Temporal changes in sink strength of spherical *Geoica* galls (Gsp) (Bq/mg gall)/(Bq/mg source leaf) when solitary and cohabiting with *F. formicaria* crescent galls (Ff). (Note that the ordinate scale is different from Fig. 2; mean ± 1 SE, $n = 5$, at each sampling date.)

strength of crescent galls are illustrated in Fig. 2. In May, sink strength of crescent galls cohabiting with spherical galls on the same leaflet was the same as in solitary crescent galls, but in June and later, sink strength in cohabiting galls for assimilates from their own leaflet was considerably lower. In October, on most of the leaflets that carried spherical galls, the leaflet blade distal to the gall was dry, and therefore could not serve as a source. For this reason, all crescent galls on these leaflets died, while solitary crescent galls were still importing assimilates from the leaflet even in early November. Friedman's randomized blocks test indicated that sink strength of crescent galls with and without cohabiting spherical galls was significantly different ($\chi^2 = 5.14$, df = 1, $P < 0.05$. Treatment means in Fig. 2 used as data).

Spherical galls induce strong sinks for assimilates from their leaflet (Fig. 3). In May, these sinks were six times stronger than crescent gall sinks (compare ordinates of Fig. 3 and Fig. 2). Sink strength decreased until the death of the leaflet in October. In the presence of crescent galls on the same leaflet, the sink strength of spherical galls was reduced by half in early June and remained at this level until September, when the declining sink strength of solitary spherical galls approached this low level. During most of the summer, the sink strength of solitary spherical galls remained higher than on cohabited leaflets (Friedman's randomized blocks, $\chi^2 = 4.16$, df = 1, $P < 0.05$).

Both species were negatively affected (incorporated smaller quantities of assimilates) when they cohabited the same leaflet (Fig. 4). We plotted PL (the proportion of total assimilates located in the gall) for each species when alone and when cohabiting with the other. All but two of the means, regardless of species, were located below the diagonal, showing that both species imported less assimilates from the leaflet when they occurred together. This shows that for galling species that depend solely on the galled leaflet, the supply of assimilates may become limiting.

Import of assimilates from distal leaflets

Spherical galls induced strong sinks toward distal leaflets by May. Sink strength of solitary, spherical galls towards distal leaflets was quickly reduced in later samples (Fig. 5). However, cohabiting spherical galls maintained high import levels until September. The proportion of assimilates drawn into the spherical gall from distal leaflets tended to be higher in cohabiting than in solitary galls (5 of 7 bivariate means above the diagonal in Fig. 6), although only two of the differences were significant statistically. This may indicate some compensation for the loss of assimilates from the presence of the other species. On the other hand, the galled leaflet normally appears to be the only source of assimilates for crescent galls. We detected no import into the crescent galls at any date when labeling was applied

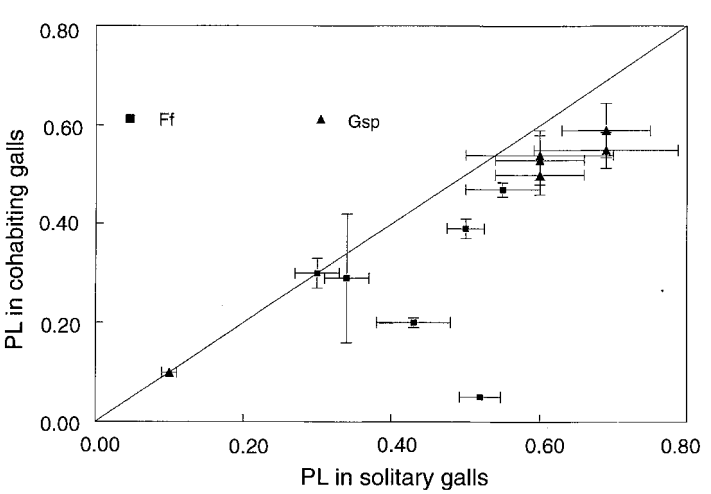

FIG. 4. Resources drawn from the galled leaflet: Proportion of labeled assimilates (PL) in solitary and cohabiting galls. Each point represents the bivariate mean of all galls sampled at a given date: 5 solitary galls (abscissa) and 5 cohabiting galls (ordinate) of a single species. Bars are ± 1 SE. Almost all points are located below the diagonal, indicating lower PL in cohabiting galls of both species.

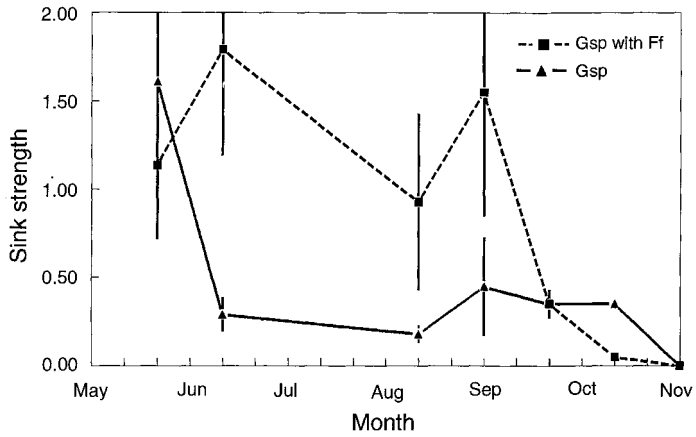

FIG. 5. Competition for resources drawn from distal leaflets: Temporal changes in sink strength of spherical *Geoica* galls (Gsp) when solitary and cohabiting with crescent galls (Ff) [(Bq/mg gall)/(Bq/mg source leaf), mean ± 1 SE, n = 5 at each sampling date]. Note that sink strength of Gsp towards distal leaflets tends to be stronger when cohabiting with Ff than when solitary.

distally to the galled leaflet, whether solitary or cohabiting with spherical galls (6 sampling dates, 2 treatments × 5 galls each time; in all cases PL near 0).

Unlike galls on intact leaflets, crescent galls that had their leaflet blades removed (simulating insect herbivory) drew assimilates from distal leaflets on the same leaf when tested in October. Their mean sink strength was 0.17 ± 0.1 (mean ± 1 SE, n = 10) which was not significantly different from sink strength of control crescent galls toward their own leaflets at that time (0.19, see last point in Fig. 2: Mann-Whitney test, U = 79.5, NS). We found no transport of assimilates between ungalled leaflets within leaves. We conclude that, in the absence of the leaflet blade, solitary crescent galls can import assimilates from other sources.

Gall location on the shoot

Spherical galls and the fundatrix (F_1) galls of *F. formicaria* are found on the basal (early) leaves while the crescent galls are located on the more distal (late) leaves on the shoot (Fig. 7). Proportional similarity between spherical and crescent gall distributions in the present study was 0.27 ± 0.04 (n = 48 shoots). The niche breadth (in terms of using different leaves along the shoot) of one species was not affected by the presence of the other (Table 2).

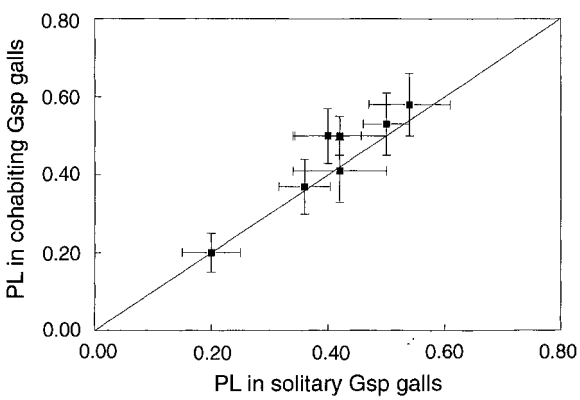

FIG. 6. Resources drawn from distal leaflets: Proportion of labeled assimilates (PL) in spherical *Geoica* galls (Gsp), solitary and cohabiting with *F. formicaria* crescent galls. Each point is the bivariate mean of 5 solitary (abscissa) and 5 cohabiting galls (ordinate) sampled on a given date. Five of the seven points lie above the diagonal, indicating that cohabiting *Geoica* galls imported more assimilates from distal leaflets than did solitary galls.

Distribution of galls on different leaflets within leaves

In order to search for possible interactions at the leaf level, we deliberately searched for leaves with both species, and noted gall positions on all leaflets. Crescent and spherical galls were counted on 63 leaves, which bore 531 leaflets. The frequencies of leaflets occupied by the species either separately or together on the same leaflet were not significantly different from the expected frequency of occurrence of the two independent events (Table 3).

Reciprocal effect of crescent and spherical galls on each other's reproductive success

Thirty-two leaves were used to examine the effect of the presence of a crescent gall on clone size in the

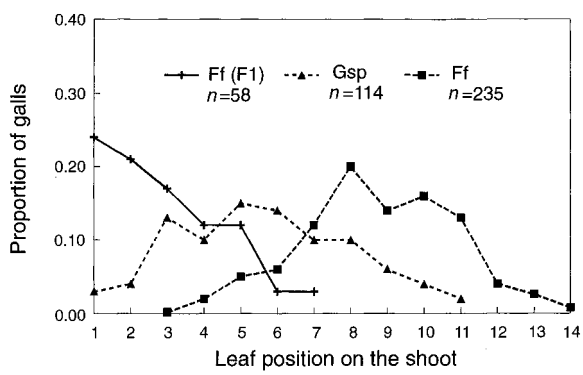

FIG. 7. Distribution of galls on leaves along the shoot axis (Leaf 1 is the oldest). The distributions of spherical *Geoica* (Gsp) and *F. formicaria* (Ff) crescent galls overlap considerably. (F_1 is the fundatrix generation of *F. formicaria*.)

TABLE 2. Niche breadth (B) calculated for *F. formicaria* (crescent galls) and *Geoica* sp. (spherical galls) alone and together on shoots of *Pistacia palaestina*.

	Crescent galls			Spherical galls		
	B	SE	n	B	SE	n
Shoots with one species	0.22	0.03	16	0.38	0.05	19
Shoots with two species	0.27	0.025	27	0.33	0.042	27
Mann-Whitney U test	$U = 108$	NS		$U = 91.5$	NS	

spherical gall. Each of these leaves carried, on one leaflet, both spherical and crescent, and on at least one other leaflet a solitary spherical gall. Average clone size in spherical galls cohabiting a leaflet with crescent galls was 627 ± 83.70 aphids per gall ($n = 32$). Solitary spherical galls on another leaflet but on the same leaf contained on average 639 ± 55.87 aphids ($n = 32$). This difference was not significant (paired $t = 0.39$, df = 30, $P > 0.05$). Crescent galls did not affect the survival of cohabiting spherical galls: gall survival remained around 85%. By contrast, survival of crescent galls cohabiting with spherical galls was severely reduced (Table 4). By the end of October, 84% of these galls, and the leaflets carrying them, were dead.

Spherical galls caused early senescence (but not abscission) of the galled leaflet (Table 4). Thus, the death of the crescent galls on leaflets galled by both species was a consequence of the damage to the leaflet (see also in Burstein et al. 1994). These deleterious effects were not observed before August (M. Burstein et al., *personal observation*). Ungalled leaflets located distally from spherical galls also suffered the same effect (Table 4).

Clone size in solitary and cohabiting crescent galls was practically identical until late summer: the second generation of apterous aphids (F_3), which were born in May–June, was not affected by the presence of cohabiting spherical galls. At that time, sink strength of crescent galls was still relatively high (Fig. 2). However, the last winged migrant generation (F_4) in cohabiting crescent galls that survived until September–October suffered 20% reduction in clone size compared with solitary crescent galls on the same leaves (Table 5).

Spherical gall removal experiments

Removal of spherical galls in the spring completely eliminated the early leaflet senescence, which is a characteristic effect of intact spherical galls. Crescent galls that were found on the same leaflet with the removed spherical galls developed normally. Mean clone size was 9.8 ± 0.6 galls (mean ± 1 SE) and 76.9 ± 7.4 galls in the third and fourth generations, respectively (compare with Table 5). Similarly, spherical galls ($n = 35$), which were naturally aborted or parasitized early in the season, showed no evidence of early leaflet death.

TABLE 3. Observed and expected frequencies of leaflets carrying solitary and cohabiting galls of the two species (531 leaflets observed on 63 leaves with both species present).

	Solitary crescent	Solitary spherical	Cohabiting	Unoccupied
Obs. frequency	140	62	20	309
Exp. frequency	135.3	57.3	24.7	313.7
Obs. proportions	0.263	0.116	0.037	0.581
$\chi^2 = 1.514$, 2 df; NS				

DISCUSSION

We demonstrated, for the first time, that interspecific exploitative competition for plant assimilates occurs between two aphid-induced sinks. Sink-competition might be added to the list of recently documented mechanisms of plant-mediated interspecific interactions among herbivores (e.g., Karban and Myers 1989, Faeth 1992, Hunter 1992, Masters et al. 1993). Because carbon translocation within plants is often sectorial (Watson and Casper 1984, Jones et al. 1993) it may be difficult to measure such interactions, especially when the system involves large host plants (such as trees) that bear many sinks and sources.

All labeling experiments were carried out on a single tree. The frequency of cohabiting galls of the two species on the same leaflet was too small for adequate sampling on most trees (4% on the most crowded tree). However, there is no reason to doubt that when the crescent galls cohabit with spherical galls on any tree, competition for assimilates is the mechanism behind the (often observed) mortality of the crescent galls. Although host-plant genotype may affect the outcome of insect–plant interactions (e.g., Moran and Whitham 1990), we believe that inter-tree differences would be quantitative, not qualitative. We have some preliminary published evidence from trees at other sites documenting the sink strength of these Fordinae galls and the effect of spherical galls on senescence of galled leaflets and mortality of cohabiting species (Burstein et al. 1994; M. Inbar, *unpublished observations*).

Both crescent and spherical galls can be described as mobilizing sinks (McCrea et al. 1985), facilitating the movement of assimilates among mature leaflets and leaves, a phenomenon that does not occur in ungalled *Pistacia* shoots (Takeda et al. 1980; M. Inbar, *unpublished data*). Crescent galls were relatively weak mobilizing sinks, and normally imported assimilates only from the galled leaflet itself. However, when the leaflet blade was removed, these galls imported assimilates

TABLE 4. The effect of spherical galls on galled and ungalled (distal) leaflets, and on crescent galls on the same leaves, in October 1993.

	Number of leaves	Percent dead	χ^2
Galled leaflet (spherical)	109	85.3	11.98, $P < 0.01$
Distal leaflet	109	39.7	
Cohabiting crescent galls	78	84.6	21.11, $P < 0.001$
Solitary crescent galls	55	12.73	

from more distal leaflets. This ability to switch sources must be important for crescent galls in nature, for example, when the young leaves are skeletonized by caterpillars of the procession moth (*Thaumetopoea solitaria*).

The fact that the spherical and crescent gall makers competed for phloem assimilates is illustrated by our finding that both species' galls imported less assimilates when they cohabited than when they did not (Fig. 4). Being stronger sinks, spherical galls diverted assimilates away from cohabiting crescent galls on the same leaflet, eventually causing their death. Despite the clear correlation between aphid clone size, gall mass, and sink strength (see Burstein et al. 1994), we do not know what makes spherical galls stronger sinks. Spherical galls cause the early senescence and death of the leaflet blade beyond the gall, whether or not it is occupied by the competitor. Positioned on the leaflet midvein, a spherical gall thus prevents a cohabiting crescent gall from using nutrient sources other than the galled leaflet, by blocking the flow of assimilates, water, and minerals to the rest of the leaflet blade. Spherical galls may also benefit from the mobilization of nutrients out of the senescing sources (Thomas and Stoddart 1980, Douglas 1993). The loss of the galled leaflet as a source of assimilates for spherical galls (Fig. 2) does not affect their reproductive success, since they are able to compensate for these losses by importing assimilates from other leaflets (Figs. 5 and 6). Crescent galls are formed in April and accumulate most of their mass until mid-June. Up to this time spherical galls are small, and cohabiting crescent galls seem to be getting assimilates most of the summer (Fig. 2). As a consequence, the numbers of second-generation aphids within crescent galls (F_3), which are produced by mid-June, were similar in cohabiting and solitary galls (Table 3).

TABLE 5. Mean numbers of descendents in solitary crescent galls and cohabiting with spherical galls on the same leaf.

	F3		F4	
	Solitary	Cohabiting	Solitary	Cohabiting
Clone size	9.8	9.3	78.8	62.0
SE	0.5	0.7	7.6	4.1
n	42	42	42	42
	Paired $t = 1.05$, $P > 0.05$, NS		Paired $t = 3.7$, $P < 0.001$	

Only the production of the last winged generation (F_4) within these galls at the end of August was affected by the cohabiting spherical galls. The negative effect was reversible if the spherical galls were destroyed experimentally or naturally (by predators and parasitoids) early enough in the season.

Previous studies involving free-living insects, gall formers and leaf miners showed early leaf abscission following herbivore stimuli (e.g., Faeth 1992). However, other galling aphids (Williams and Whitham 1986) and free-living aphids (e.g., Petitt and Smilowitz 1982) do not prevent (or even enhance) premature abscission. Despite the accelerated senescence in the galled leaflets, the presence of spherical galls did not cause early abscission. It is likely that the same plant growth regulators that govern the strength of plant sinks (Kuiper 1993) affect the development of aphid (and other insects) galls. Auxin (Miles 1989, Aloni 1991, Hori 1992) and cytokinins (Elzen 1983) are found in large quantities in insect galls, although their origin is not clear. Auxin flux from the leaf blade eliminates the formation of the abscission zone in the petiole during the abscission process, and cytokinins also delay senescence and prevent abscission (e.g., Mattoo and Aharoni 1988).

In this study we measured the flow of assimilates to the gall sink via the phloem. It is reasonable to assume that galls manipulate the xylem transport as well. Aloni et al. (1989) demonstrated that the coral-like galls of the aphid *Slavum wertheimae* H.R.L. on *Pistacia atlantica* Desf. induced more xylem differentiation in the shoot below the gall compared with ungalled shoots. These changes may increase the supply of water and minerals into the galls. Similar effects of wider vessel differentiation were found in branches below the galls of *Baizongia pistaciae* on *P. palaestina* (Aloni 1991). The galls of this species may reach the size of a banana and house several thousand aphids. We found that these galls manipulate phloem assimilates from leaves and even other shoots on the tree (Burstein et al. 1994).

Interspecific interference competition for galling sites (e.g., Whitham 1979, Fritz et al. 1986, Akimoto 1988, Craig et al. 1990) appears to be unlikely in our Fordinae (Inbar and Wool 1995). Many galling sites on galled leaves remain empty. Even when they occur on the same leaf, we found in this study that crescent galls are formed independently of spherical galls and the two species co-occur on the same leaflet no more and no

less frequently than expected by chance (Table 3). The interactions between the two species at the colonization period are probably minimized due to the difference in galling sites (Inbar and Wool 1995). Spherical galls tend to be located on the more basal leaves of the shoot and crescent galls are mostly on more distal ones (Fig. 7), further reducing the chance of interference. Our data show that when spherical and crescent galls do occur together, about 85% of the crescent galls die (Table 4). But only about 4% of all crescent galls were killed due to such interspecific interactions, a small loss compared with other risks in the aphid life cycle. Therefore, interspecific exploitative interaction in this system is probably not important in shaping current populations despite its unequivocal results when it does occur. Nevertheless, our demonstration that plant-mediated competition does operate among aphid gall sinks (and was asymmetrical, harming one competitor more than another) should encourage further investigation of the possibility that such competition might have stronger effects in other systems.

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