

Sink strength and clone size of sympatric, gall-forming aphids

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Abstract. The supply of carbohydrates to growing galls of four species of aphids (Pemphigidae: Fordinae) that co-exist on *Pistacia palaestina* trees was studied. Using ¹⁴C labelling we compared the sink strength of the gall of each species for its ability to manipulate the normal phloem transport from different sources. The results indicated that none of the galls had net photosynthetic ability and all of them imported assimilates according to their specific sink strength. The data also demonstrated a correspondence between the ability of galls to draw assimilates from wider sources (sink strength) and aphid reproductive performance. Furthermore, preliminary observations indicated that species which are stronger sinks have a negative impact over other galling aphids on the same leaf or shoot through withdrawal of assimilates and nutrients.

INTRODUCTION

Aphid galls act as sinks which sustain aphid nutrition by manipulation of phloem transport from different sources into the galls (Larson & Whitham, 1991). Mature leaves which export assimilates may serve as the sources. Although the mechanisms which regulate sink-source interactions are not fully known, it is generally accepted that phloem sap flows according to sucrose gradients and depends on the distance between the sink and the source, the vascular connections between them, and sink strength. Differences in source utilization and sink strength of four species of gall-forming aphids of the subfamily Fordinae, (Pemphigidae) which coexist on the same shoots of their primary host: *Pistacia palaestina* (Anacardiaceae) are described in this preliminary paper. The galls of *Baizongia pistaciae* (Bp) are formed near the terminal bud. *Geoica utricularia* (Gu) galls are located on the leaflet midrib. *Forda formicaria* (Ff) and *Paracletus cimiciformis* (Pc) galls are located on the leaflet margins. The three latter species may coexist on the same leaves or even the same leaflets, and share a similar life history (Koach & Wool, 1977).

MATERIALS AND METHODS

Sink strength of each gall was defined by its ability to draw assimilates from different sources. It was measured by ¹⁴CO₂ labelling technique during June–September 1992. Source organs (single leaves or leaflets) were enclosed in nylon bags tightly sealed with putty and thread. ¹⁴CO₂ gas was released by the reaction of sodium carbonate (Na₂¹⁴CO₃) solution with lactic acid injected into the bag. CO₂ fixation was allowed to take place under natural conditions for about four hours (10 am–2 pm). All shoots were removed two days after labelling and were deep frozen. Distribution of ¹⁴C in every shoot was first qualitatively estimated by autoradiography, then extracted for 24 h by DMF (N,N-Dimethylformamid). Radioactivity was determined by liquid scintillation counting. All ¹⁴C measurements are expressed as ratios of activity in the gall tissue (dpm/mg. dry weight) to activity (dpm/mg. dry weight) of the source tissue, after 48 h of transport. For brevity we refer to the measure as AR (assimilation ratio).

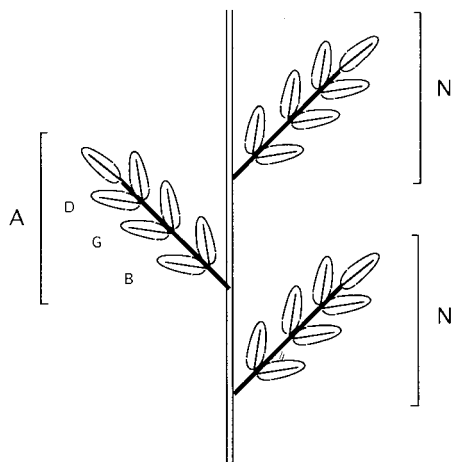


Fig. 1. Schematic presentation of different sources labelled in relation to the position of Gu, Pc, and Ff galls: A – galled leaf; N – un-galled (neighbouring) leaves; G – gall position; B – leaflet basal to the galled leaflet; D – leaflet distal to galled leaflet.

Shoots which carried Bp galls were labelled in June–September 1992. We labelled 4 types of source leaves: leaf on a neighbouring shoot, leaf at the base of the galled shoot (leaf positions 1–2), leaf at the middle of the galled shoot (leaf positions 4–6), and terminal leaves near the gall (leaves 10–12). Shoots which carried Gu, Pc and Ff galls were labelled in August and September. We selected for labelling only leaves on which the galls were located on the middle leaflets. On the galled leaves we labelled either leaflets distal to gall position, leaflets basal to the gall, or neighbouring leaves (Fig 1). In order to estimate photosynthetic ability of the gall tissue, we applied the label directly to the galls of each species (3 replicates). The morphological impact of Bp and Gu on leaves or leaflets was monitored on August 20 before leaf fall. We recorded the number of green (live) and brown (dead) leaves on shoots with and without galls of Bp, and the number of live and dead leaflets on leaves with and without Gu galls. Aphid clone size (performance) at the peak of reproduction (in autumn) was either measured, or obtained from previous data (Wool, unpublished data).

RESULTS

^{14}C labelling indicated that in August and September galls had a very low photosynthetic ability and all galls imported assimilates. Pc galls imported labelled assimilates from its own leaflet ($\text{AR} = 0.24 \pm 0.05$, $n = 7$) but neither from neighbouring leaves ($n = 41$), nor from neighbouring leaflets on the same leaf ($n = 8$). Clone size within these galls was 36 ± 12 ($n = 35$). Ff galls, which are located on leaflet margins like Pc, also did not import assimilates from neighbouring leaves ($n = 12$) nor from neighbouring leaflets ($n = 10$). Clone size of this species was 97 ± 25 ($n = 47$). Gu galls drew some assimilates from leaflets distal to gall position ($\text{AR} = 0.08 \pm 0.03$, $n = 5$) but more from leaflets basal to the gall on the same leaf ($\text{AR} = 0.3 \pm 0.14$, $n = 3$). Galls of this species did not import assimilates from neighbouring leaves ($n = 3$) on August 23, but Gu galls measured two weeks later imported labelled assimilates from leaves located one position below ($\text{AR} = 0.12 \pm 0.07$, $n = 4$), as well as one position above the galled leaves ($\text{AR} = 0.02 \pm 0.01$, $n = 5$). Clone size within these galls was 547 ± 216 ($n = 47$). By the end of August most of the leaflets galled by Gu, and most leaflets distal to them were brown and dead (Table 1). Pc

galls (n = 4) and 9 of 15 Ff galls which were located on the same leaflet with Gu were also dead.

TABLE 1. The impact of *Geoica utricularia* galls on leaflets of the occupied leaf. P is the proportion of the number of leaves of each category. Note that one gall may cause more than a single effect.

	tree 1 n	(n = 48) p	tree 2 n	(n = 116) p
Early senescence of occupied leaflet	22	0.45	73	0.68
Early senescence of distal leaflet	24	0.5	23	0.19
Early senescence of basal leaflet	2	0.04	3	0.02
No effect	5	0.1	18	0.15

Bp forms the largest galls and most powerful sinks. Clone size within these galls is around 10,000 aphids (and may reach 20,000). These galls manipulated more distant sources as the season advanced (Fig 2). In June they manipulated the closest terminal leaves, later they affected gradually the middle and basal leaves of the shoot. By the end of

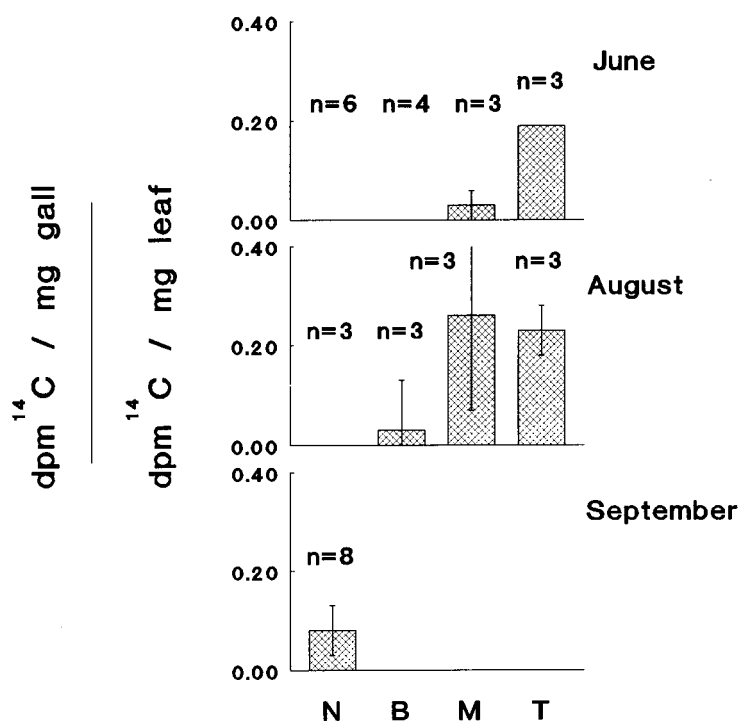


Fig. 2. Utilization of different sources by *Baizongia pistaciae* galls on different dates. Source leaves are: leaves on neighbouring shoots (N), basal leaves on galled shoots (B), middle position leaves on galled shoots (M), and terminal leaves (near the galls) of galled shoots (T). Note that in September galled shoots lost most of their leaves.

August most of the leaves on the galled shoots were dead (Table 2), and assimilates were imported to the galls from neighbouring shoots. Pc (n = 5) and Ff galls (2 of 6) which were located on the same shoots with Bp were dead. Anatomical changes in the vascular system of shoots galled by Bp extend to 50 cm below the gall (Aloni et al., 1989).

TABLE 2. The average number of undamaged leaves \pm SE on shoots galled by *Baizongia pistaciae* at end of August.

tree	with Bp		without Bp		t value	df
1	0.64 \pm 0.23	n = 11	8.86 \pm 0.98	n = 22	5.85	31***
2	1.50 \pm 0.7	n = 30	7.57 \pm 0.58	n = 35	6.73	63***
3	3.45 \pm 1.38	n = 11	4.53 \pm 0.94	n = 15	0.67	24 ns
4	1.33 \pm 0.69	n = 9	7.57 \pm 0.42	n = 23	7.93	30***
total	1.7	61	7.13	95		

Combining probabilities from independent tests: $X^2 = 51.8$, $df = 8$ ***

DISCUSSION

The photosynthetic ability of the gall tissue is limited and galls import assimilates from surrounding sources. Therefore, the correspondence between gall sink strength (the ability to use more distant sources of assimilates) of different aphid species, and aphid clone size in the galls (summarized in Table 3), could be expected. In the more powerful sinks (Bp and Gu galls) closer sources were used at the early stages, and wider and more distant sources were utilized later in the season. Bp first sequestered resources close to the gall, and at the end of the season it manipulated leaves of neighbouring shoots. Gu (probably) begins with the use of the leaflet it is on, then neighbouring leaflets, and later may use the resources from neighbouring leaves.

TABLE 3. Qualitative summary of sink strength and clone size of different galling species (names are abbreviated).

Species	Clone size	Ability to use source sites			
		occupied leaflet	leaflets within leaf	leaves within shoot	leaves of neighbouring shoot
Bp	10,000			+	+
Gu	574 \pm 216	+	+	+	-
Ff	97 \pm 25	+	-	-	-
Pc	36 \pm 12	+	-	-	-

The resources used by the different species of aphids on *Pistacia* seem to overlap when they are found together. Our results show that in such cases the most powerful sinks are dominant. Bp may cause early senescence of closest leaves and death of galls of Pc and Ff, which they may carry. Similarly, Gu causes death of Pc and Ff galls whenever they are found on the same leaflet with it. Thus, since resources are shared by several galls, exploitative competition over phloem assimilates or mineral nutrients may result. There are many examples of competition between different natural plant sinks such as fruits and young leaves (e.g. Ho, 1988). Our results indicate the possible existence of competition between sinks (galls) of different herbivore species.

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