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Population ecology and clone dynamics of the galling aphid *Geoica wertheimae* (Sternorrhyncha: Pemphigidae: Fordinae)

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Galls, aphids, Fordinae, *Pistacia*, population ecology

Abstract. *Geoica wertheimae* induces spherical galls on its primary host, *Pistacia palaestina* (Anacardiaceae). We studied the temporal changes in gall size and aphid clone size, as well as gall distribution and abundance on marked trees during two consecutive years. The density of galls (per shoot and per leaf) was low during the study period, and gall distribution was clumped. Gall abundance varied greatly among trees, but gall abundance and tree budburst phenology were uncorrelated. Galls increased eight-fold in volume during the season, in parallel with the increase in aphid clone size, from one individual to several hundred aphids per gall. The trigger for the induction of the alate morph in the galls in late summer seems to be an abrupt change in aphid density within the galls, which occurs when aphid reproductive rate exceeds the rate of change in gall internal surface area.

Two species of Lepidopterous larvae were present in about one-third of the galls. They occasionally destroyed the aphid clone, but many aphids often remained alive. However, the volume of parasitized galls was significantly smaller than that of unparasitized galls, illustrating the dependence of gall size on aphid clone size.

INTRODUCTION

Geoica wertheimae Brown & Blackman (Pemphigidae: Fordinae) is one of approximately 15 gall-forming aphids on *Pistacia* trees (Anacardiaceae) in Israel (Koach & Wool, 1977). In previous publications, all aphids inducing spherical galls on *Pistacia* were referred to as *G. utricularia* Passerini (Wertheim, 1954; Bodenheimer & Swirski, 1957; Koach & Wool, 1977), and were reported by that name from many countries around the Mediterranean and in the Middle East to Iran. The primary hosts of *G. utricularia* were recorded as *P. terebinthus*, *P. mutica*, *P. atlantica* and *P. palaestina* (Bodenheimer & Swirski, 1957). Brown & Blackman (1994) considered that *G. utricularia* is a species complex, and gave the form on *P. palaestina* species status, naming it *G. wertheimae*.

G. wertheimae induces marble-shaped galls on the leaflets of its primary host *P. palaestina* (Fig. 1). The aphid has a typical 2-year holocycle involving alternation between *P. palaestina* and the roots of secondary hosts, various grasses (Zwölfer, 1958). Galls first appear at the end of March and continue to grow throughout the summer while the numbers of parthenogenetically-produced female aphids in the gall increase from one to several hundred (see results). In September–November, the galls crack open and the alate aphids of the last generation disperse. Their offspring develop on the roots of the secondary hosts in winter. In the following spring and early summer, alate sexuparae are formed on the roots and fly back to *Pistacia* where they produce sexual males and females (Wool

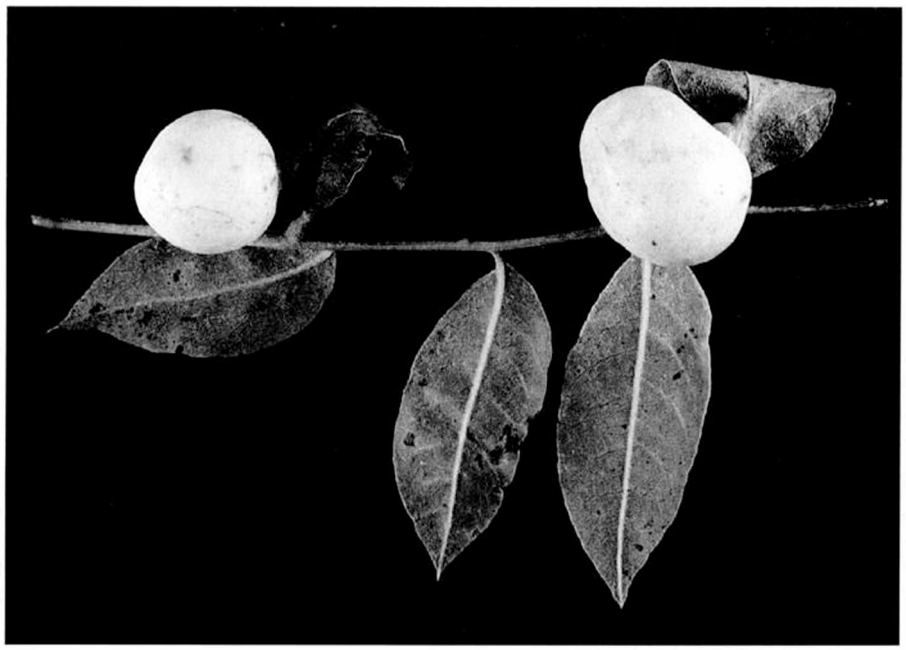

Fig. 1. Spherical galls of *G. wertheimae* on a leaf of *Pistacia palaestina.*

et al., 1994, 1997). A single egg develops in each fertilized female and overwinters on the tree, and a new fundatrix hatches in the following spring.

G. wertheimae galls were previously collected throughout their range in Israel for a detailed study of alate (fall migrant) geographic variation in morphological characters (Wool, 1977). A recent ecological work, using labelled CO_2, showed that the gall is a nutritional sink, and photosynthetic products are translocated from the leaves into the galls (Burstein et al., 1994). The position of *G. wertheimae* galls on the leaf, and its sink strength, are such that it outcompetes other species of galling aphids that happen to occur on the same leaflet (Inbar et al., 1995).

The present study is the first detailed investigation of the gall stage of *G. wertheimae* in Israel. Its emphasis is on population ecology and clone-size dynamics in the gall. (The changes in gall and leaf anatomy due to gall formation will be reported elsewhere).

The fundatrix, her daughters, and granddaughters are wingless. Alate (winged) individuals are formed towards the end of the summer. In free living aphids, a short photoperiod, lower temperatures, and an increase in crowding induce the formation of winged individuals (a recent example: Vaz Nunes & Hardie, 1996). This is also the case in the subterranean generations of gall forming *Pemphigus* on the roots of their secondary hosts (Judge, 1968; Moran et al., 1993a,b).

No information is available on the induction of alates in aphids within the gall. The aphids in the closed gall may, nonetheless, perceive changes in temperature or photoperiod either directly or indirectly through changes in the host tree. Each gall of the Fordinae begins with a single aphid. Further reproduction may increase crowding, even though the

gall increases in size. Crowding can be defined as aphids per unit gall volume, but a more meaningful measure would be aphids per unit internal gall-surface area, since the aphids must have access to the gall tissues in order to feed. (We often observed, while opening *Geoica* galls, that the aphids were closely packed on the gall walls). We suggest that crowding may be the most important determinant of alate formation within the galls.

MATERIAL AND METHODS

Research site

Most of the research was carried out at Canada Park, a public recreation site about 30 km east of Tel Aviv, at the foot of the Judean Hills. Twenty five *P. palaestina* trees were tagged and numbered in 1991. These trees appear to be survivors of the natural forest which was destroyed by humans in the past. The area is now tended by the Park Authority of the Jewish National Fund and the trees are protected from destruction, but are occasionally subjected to heavy pruning.

The trees were visited twice a month from March to September 1995, and less regularly in 1996. Galls were sampled randomly from 5–12 trees each time, depending on availability.

Galls were measured and dissected in the laboratory. Gall diameter was measured with Mitutoyo (Japan) calipers. (In later samples, gall volume was measured instead by the volume of water displaced when the gall was dipped in a water-filled graduated cylinder). Gall wall thickness was measured (in some galls) with the calipers to the nearest 0.01 mm. The aphids were removed from the gall and counted (in the early season). Later, when their numbers increased to several hundred, three samples of 100 aphids were weighed each time and aphid numbers were estimated from the average weight and the total aphid biomass in the gall. The empty galls were dried at 70°C for 48 h and weighed. The presence of parasites, predators and inquilines was noted (parasitized or predated galls were not used for clone size estimation).

To estimate the surface area of the internal gall cavity, we assumed that the *Geoica* gall is a perfect sphere. From the measured gall diameter D, we calculated the internal radius (R = D/2 minus gall wall thickness). Alternatively, from gall volume (V) we calculated R from the relation $V = 4/3\ \pi R^3$ for a sphere (rearranging $R = \sqrt[3]{3V/4\pi}$ minus the gall wall thickness). Using R we calculated the internal surface area as $S = 4\pi R^2$ and crowding was calculated as N/S (aphids per sq. mm of surface area) where N = the number of aphids in the gall.

Tree phenology and gall abundance

Rough estimates of gall abundance per tree were obtained by inspection on a scale of 1 to 10, where 10 represents many galls on the tree. Gall abundance was also estimated as the mean number of galls per shoot since a shoot is a biologically meaningful sampling unit in galling aphids (Wool & Bar El, 1995). In early spring – from 12 March to 27 April 1996 – we estimated the bud burst status of each of 10 trees five times on a scale of 1 to 8 : 1 represents a dormant tree and 8 a tree growing vigorously. All estimates were obtained by the same observer (O.B.-Z.).

Statistical analysis

Conventional statistical procedures were followed (Sokal & Rohlf, 1995). For clone size and gall weight we used parametric ANOVA and t-tests as appropriate. For comparisons of gall distribution on shoots to expected Poisson frequencies, we used Chi-square tests. We used non-parametric correlation (Spearman's) to test for association between the status of budburst and gall abundance on trees, and Mann-Whitney U tests for comparisons of volumes of parasitized and unparasitized galls.

RESULTS

The earliest galls of *G. wertheimae* were detected at Canada Park in March (24.iii.95 and 12.iii.96), as small – usually red – swellings at the base of young leaflets (e.g., Fig. 5 in Wertheim, 1954). In early April some galls already had a clear spherical shape.

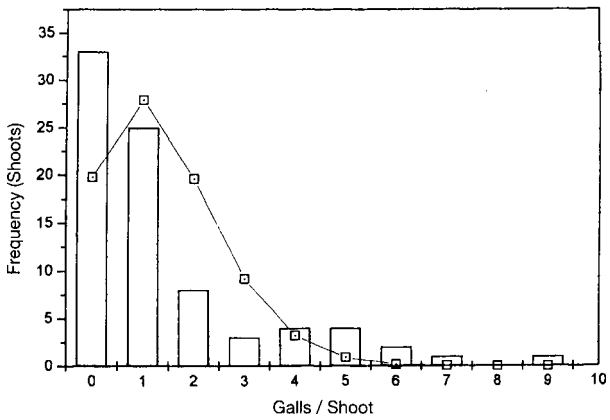

Fig. 2. Frequency distribution of *G. wertheimae* galls on 79 galled shoots sampled when at least one gall of any species was present. Canada Park, 1996. The line connects expected Poisson frequencies.

Gall distribution and abundance

The distribution of galls on 79 shoots in 1996 is illustrated in Fig. 2. The distribution was distinctly clumped (deviation from Poisson distribution; $x^2 = 19.4$; 8 df; $P < 0.05$). The mean number of galls per shoot in both years was rather low. Shoots were sampled when at least one gall of any aphid species was present (Wool & Bar-El, 1995) and the mean of 1.4 galls/shoot is, therefore, an overestimate (corresponding means calculated by the same method from samples on the same trees were 3.6 galls/shoot in 1993, and 2.4 galls/shoot in 1994). Mean numbers of galls per leaf in 1993–1995 were similar (1.42, 1.23. 1.3 galls/leaf): most galls occurred singly, but some leaves carried 3–9 galls.

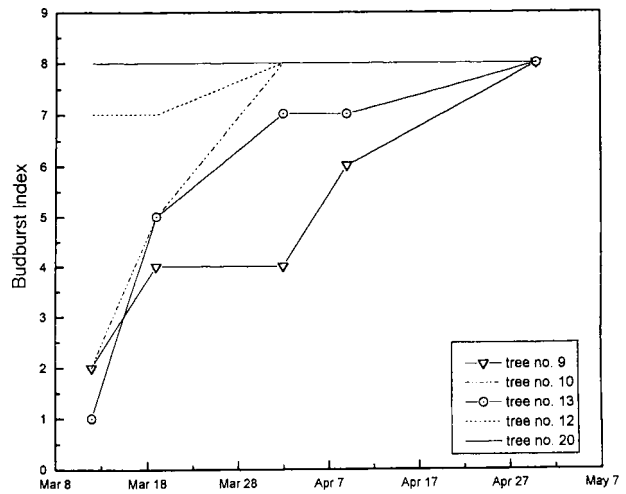

Fig. 3. Examples of differences among trees in budburst phenology at Canada Park, 1996. Dormant trees were scored 1, vigorously growing trees were scored 8. Trees were scored 5 times in spring. Only 5 trees are illustrated.

Tree phenology and gall abundance

There were differences in phenology among individual trees. For example, tree 20 scored 8 and tree 12 scored 7, on the budburst scale, on the first visit, while trees 8 and 13 were almost dormant on that date and burst their buds gradually (Fig. 3). A single measurement of budburst (at a specific date) may not sufficiently describe the differences among trees. A composite measure of growth status is the sum of the scores per tree in the five consecutive visits. Since the maximum score is eight, the total maximum in five visits is 40.

Gall abundance per tree was not correlated with this measure of budburst phenology. Spearman's non-parametric correlation coefficient was very low and not significantly different from zero ($r = 0.15$; 8 df; $P >> 0.05$).

Gall volume

Gall volume increased from less than 0.5 cm^3 in April to about 4 cm^3 in August (Fig. 4). As expected, gall volume was significantly correlated with gall dry weight ($r = 0.77$; df = 289; $P < 0.001$). Mean gall volume in 1995 shows two periods of abrupt, increased growth rate – one between 9 and 30 June (75–90 days) and another between 1–15 August (130–145 days after first sighting of galls) (Fig. 4). It is probable that these periods of fast gall growth correspond to changes in aphid clone size in the galls. Sampling in 1996 was less intensive than in 1995, and the intervals between samples were too wide to detect abrupt changes. Mean gall volumes in 1996 were similar to the 1995 values (Fig. 4).

Clone size

Mean aphid clone size failed to show abrupt changes corresponding to gall volume increase. Clone size increased geometrically in 1995 and linearly in 1996 (Fig. 5). The geometric growth curve can be expected from the reproductive biology of the aphids in the gall in which the number of mothers multiplies each generation when daughters mature.

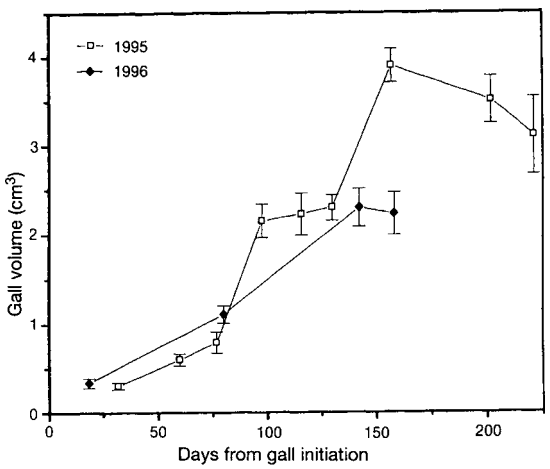

Fig. 4. Temporal changes in mean gall volume of *G. wertheimae* in 1995 (open squares) and 1996 (filled diamonds). Note the "steps" in gall volume in 1995 (see text). Abscissa is in days since the detection of the first galls (24.iii.95 and 12.iii.96).

Aphid density

Because both variables increase with time, it is not surprising that gall volume and clone size are correlated. However, taking gall volume as the independent variable, the slopes of the regression lines of clone size on gall volume are estimates of aphid density (aphids/cm^3).

TABLE 1. Slopes (± SE) of the regression lines of clone size on gall volume in galls sampled at different dates. All slopes but one were significantly different from 0 ($P < 0.01$ at least); ns = not significant.

Sampling date	Slope (aphids/cm^3 gall)			n	R^2
	b	±	SE		
April 25	11.9		2.62	45	0.32
April 30*	7.0		7.0	14	0.08 ns
May 23	28.9		3.52	41	0.63
June 9	32.4		6.74	32	0.43
June 30	59.3		5.08	45	0.76
July 1*	70.5		8.47	49	0.60
July 18	89.9		12.87	38	0.61
August 1	93.9		6.92	88	0.68
August 27	168.3		35.92	90	0.20
September 2*	105.0		10.10	28	0.81
September 18*	69.4		16.50	9	0.72
October 1*	70.0		16.70	10	0.69

* Date of 1996 (all others in 1995).

The slopes of the regression lines show a clear temporally increasing trend from April through August (Table 1; two early samples are omitted because in March and early April only a single aphid occupied each gall). Two samples in April and July 1996 match well with those in 1995. No samples were taken in September 1995, the majority of the galls having been evacuated by the alates at that time.

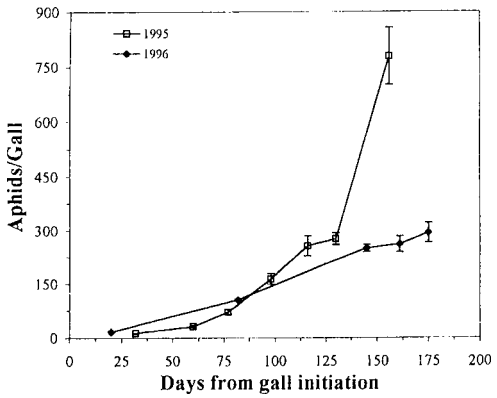

Fig. 5. Temporal changes in mean clone size in *G. wertheimae* galls in 1995 (open squares) and 1996 (filled diamonds). Abscissa in days after the detection of the first galls (24.iii.95 and 12.iii.96).

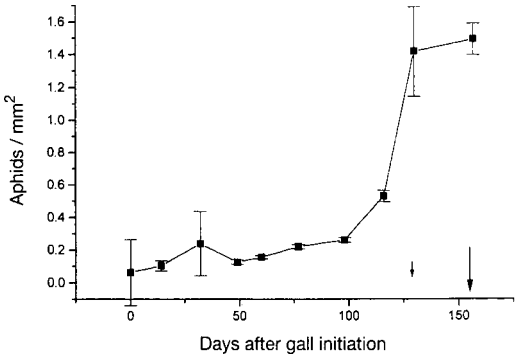

Fig. 6. Temporal changes in density (aphids/mm^2 of internal gall surface area; means ± SE) in 1995. The small arrow indicates the earliest finding of alates in *G. wertheimae* galls (in Jerusalem) in that year. The large arrow marks the timing of alate occurrence in most galls at the study site (Canada Park). Note that the first alates were found in the galls when density showed a rapid increase.

Aphid crowding calculated as aphids per mm^2 remained stable and low until the end of June at about 0.2 aphids/mm^2 (Fig. 6). Crowding increased steeply in July: by the middle of the month crowding was still only about 0.5 aphids/mm^2, but increased three-fold in the next two weeks to almost 1.5 aphids/mm^2 (1.viii.95). Very little change occurred after that (Fig. 6).

The first alate aphids in 1995 were found in *Geoica* galls on *P. palaestina* (in the Botanical Gardens of the Hebrew University on Mount Scopus, Jerusalem) on 3 August. On 20 August, many galls in Canada Park contained alate aphids. Assuming that there is a 2–3 weeks' interval between the induction of wing development and the actual appearance of alate individuals, it seems that alate induction occurred in mid July – perhaps just as crowding exceeded 0.5 aphids/mm^2.

A slight but clear tendency of the gall wall becoming thinner towards the end of the summer was noticed in both 1995 and 1996, prior to the opening of the gall wall to release the aphids (Table 2).

TABLE 2. Gall wall thickness (in mm) in samples of mature galls at the end of the season.

Year	Date	Mean ± SE	(n)
1995	August 27	1.99 ± 0.097	(26)
	October 6	1.64 ± 0.045	(42)
	October 20	1.61 ± 0.070	(28)
1996	September 2	1.83 ± 0.058	(28)
	September 18	1.54 ± 0.111	(13)
	October 1	1.42 ± 0.075	(12)

Predators and parasites

Two species of lepidopterous caterpillars were found frequently in the galls. *Palumbina guerinii* (Gelechidae) (Sattler, 1982) larva bores into the gall and feeds on the plant tissues, indirectly causing aphid death. Ito & Hattori (1982, 1983) used the term "kleptoparasite" to describe a moth, *Nola innocua* (Nolidae), which destroys aphid galls in Japan by

feeding on the gall tissue, like *P. guerinii* in the present study. *Alophia combustella* (Pyralidae) is a known aphid predator (Bodenheimer & Swirski, 1957). Both moths are not host-specific and were found in the galls of several Fordinae (e.g., *Forda formicaria* (Wool & Bar-El, 1995) and *Aploneura lentisci* (Wool & Manheim, 1986). Before pupation each larva prepares an exit hole (sealing it with a white plug) through which an adult escapes. Several holes may be found in a single gall, probably inhabited by several larvae. The biology of these moths has not been investigated in any detail in Israel, and it is unclear whether a larva changes galls during its growth.

Moth larvae were found in galls on all sampling dates throughout both study years. About one third of the 834 galls sampled contained caterpillars or showed distinct evidence of their presence (frass, pupal skins). *P. guerinii* seemed to be more frequent than *A. combustella* in *G. wertheimae* galls (100 of the 264 infested or damaged galls contained a live larva of the former species; only 14 contained the latter. It was not possible to identify the species in the other 150 galls). The amount of damage to the aphids by *P. guerinii* seemed to depend on the time of caterpillar entry relative to aphid reproductive stage. Galls attacked early remained extremely small, and contained no aphids. Galls attacked later persisted to the end of the season and many contained live aphids, so that the moths did not destroy the aphid clone entirely. However, parasitized galls were smaller than unparasitized galls, illustrating that gall growth depends on aphid clone size (Table 3).

TABLE 3. Volume (in ml) of moth-parasitized and unparasitized galls in June and October 1995, means ± standard errors (n). The significance of the differences was tested by the non-parametric Mann-Whitney test.

	Parasitized		Not parasitized
June	0.84 ± 0.288 (20)		1.15 ± 0.144 (31)
		$Z = 2.209, P < 0.05$	
October	2.13 ± 0.209 (27)		4.43 ± 0.327 (43)
		$Z = 4.820, P < 0.01$	

One ichneumonid and one braconid hymenopterous parasites of the moths were also found in the galls. There was no evidence of parasitization of *Geoica* by dipteran or hymenopteran parasites, which are common in other Fordinae galls (Wool & Manheim, 1986; Wool & Burstein, 1991a; Wool & Bar-El, 1995).

DISCUSSION

Each gall of *G. wertheimae* contains the offspring of a single female, and clone size at the end of the summer is a measure of the fundatrix' reproductive success. This value may reach several hundred to over a thousand. The fact that gall abundance in our study area in three consecutive years remained low (Wool & Bar-El, 1995), illustrates that this species – like other Fordinae – faces severe population bottlenecks during its life cycle. These may occur during the two dispersal stages (fall and spring migration) and the two winter exposure periods – as live aphids on the roots of secondary hosts, and as dormant overwintering eggs on the primary host, which must hatch and find a suitable galling site for the

female genotype to survive. So far, only the spring migration was investigated in detail (Wool et al., 1994, 1997).

The abrupt changes in mean gall volume are probably related to the aphids' reproductive pattern within the galls. In March and April, only the single fundatrix was found in each gall. Her offspring (F2), were few in number and gall growth was slow. When these individuals began to reproduce, perhaps simultaneously, they seemed to cause a "burst" of growth stimuli on the plant. A similar burst may have occurred when the F3 began to reproduce, accellerating gall growth. The dependence of gall size on clone size in *G. wertheimae* is further illustrated by the smaller size of galls parasitized by moth larvae compared with unparasitized galls (Table 3).

Pattern of changes in clone size

It is instructive to compare the temporal pattern of changes in clone size of *G. wertheimae* with that of other Fordinae: *Smynthurodes betae* (Wool & Burstein, 1991b), *Forda formicaria* (Wool & Bar-El, 1995), *Aploneura lentisci* (Wool & Manheim, 1986), and *Slavum wertheimae* (Wool & Bogen, in press). The galls of the first 3 species are formed on leaflet margins of their host plants and attain their final size early, when the galls are occupied only by the single fundatrix. After an initial production of 5–20 daughters, the clones of *F. formicaria* and *S. betae* remain unchanged for some weeks until the end of the summer. Then they increase rapidly with the appearance of the last (alate) generation. *A. lentisci*, which colonizes the evergreen host plant *P. lentiscus*, shows a gradual increase in clone size (Wool & Manheim, 1986). These patterns of clone size increase contrast sharply with the exponential growth patterns of clones in *G. wertheimae* (this study) and *S. wertheimae* (Wool & Bogen, in press).

Aphid crowding and alate induction

Alate formation is not synchronized among galls, showing that in *G. wertheimae* alate induction in the gall is not triggered by an abiotic, external factor.

The dates of detection of the first alates suggest that alate induction occurred in midsummer. If this interpretation is correct, then we can rule out aphid reliance on any external clues for alate formation: high summer temperatures and day length do not change much in July, and the trees do not show any evidence of senescence and abscission, which begins in September. We suggest that crowding within the galls is the trigger which induces alate morphogenesis in the galls of *G. wertheimae*.

Interestingly, our data show a classical Malthusian phenomenon. Since aphid parthenogenetic reproduction within the gall results in geometric increase in clone size, and the gall surface area grows linearly, there should come a point where crowding is too high. At or near this point, clone size increase ceases. The aphids become alates and migrate as soon as the gall opens, and the next reproductive stage occurs outside of the galls, free of the limitations of space.

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