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Autecology of *Baizongia pistaciae* (L.): a monographical study of a galling aphid

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ABSTRACT

This paper is an overview of the information concerning the biology and ecology of *Baizongia pistaciae*, the most conspicuous species of gall-forming aphids on *Pistacia palaestina* in Israel. My intention was to gather together the scattered pieces of information that were published in different journals in different years, and present a complete picture (as of 2012) of the state of knowledge on the complex biology of this species. References to other galling aphids on the same host are made in the paper but more detailed information about them is beyond the scope of this paper. The bulk of the published data was accumulated during more than 30 years of research by myself and my students. The work of colleagues in other countries was added, as well as references to older literature. Some unpublished data, which were the basis for some of the statements in the review, are included in an appendix.

KEYWORDS: aphids, *Baizongia*, galls, ecology, life history

INTRODUCTION

Gall-inducing aphids (Aphididae: Fordinae) constitute a major and conspicuous part of the herbivore insect fauna on *Pistacia* trees and shrubs. Some 15 species induce their galls on three common species of *Pistacia* in Israel—*Pistacia atlantica*, *P. palaestina*, and *P. lentiscus*—and were studied intensively in the last 40 years. The biology and ecology of these aphids and their complex life cycles were recently reviewed (Wool 2004, 2005). Autecological reports on the most common species were published (see reference list in Wool, 2005). Strangely enough, the reports on the most conspicuous of these galling aphids—*Baizongia pistaciae* (L.)—were not collected together to form a general picture of its biology and ecology.

Every traveler in the Mediterranean forests of Israel in the Galilee or on Mount Carmel, must have noticed the large galls of *B. pistaciae*. In the summer, they are often red (when exposed to the sun). In winter the empty, dry galls remain attached to the bare branches of the tree and are even more conspicuous (Fig. 1). My purpose in this review is to bring together the scattered information on this species, as a “flag” species which represents the complexity of the entire group of galling aphids.

Fig. 1. Old empty galls of *Baizongia pistaciae* on upright shoots near the base of a tree, indicating heavy infestation in the previous year.

In addition to a summary of published research on *B. pistaciae*, carried out by my students and myself at the Department of Zoology, Tel Aviv University, since 1971, I include—and acknowledge—unpublished material collected by some of my students, particularly O. Shukry, as part of their M.Sc. theses.

HOST PLANTS AND DISTRIBUTION

Baizongia pistaciae (L.) induces a very conspicuous gall, usually on the terminal bud of new shoots of its specific host plant, *P. palaestina*, in the Mediterranean forest of Israel. It was formerly known in the literature as *Pemphigus cornicularius* Pass., a very appropriate descriptive name referring to its large, horn-shaped gall.

Several characteristics contribute to the conspicuous appearance of *B. pistaciae* in the Mediterranean forests of Israel. First, their size and galling sites: large galls may reach 35 cm in length (Fig. 2). They are most often formed on the apical buds of the shoots on the tree. Further, when exposed to sunlight galls tend to become red (Fig. 3). Old galls, vacated by the aphids at the end of the summer, remain attached to the branches and the black, dry shells may serve to identify the host tree species when the leaves are shed (Fig. 4).

The galls of *B. pistaciae* are known from countries around the Mediterranean and in the Middle East. In Israel, Lebanon and Syria it colonizes exclusively *P. palaestina*

Figs. 2–4. 2. A large, horn-shaped gall of *Baizongia pistaciae* collected at Baram, Galilee, by J.J.Y. Martinez. Photo: A. Shoob; 3. A red *Baizongia pistaciae* gall, “stamped” by the shadow of a nearby leaf. Collected at Bet Shemesh by O. Shukry. Photo: A. Shoob; 4. A living record of the history of colonization of a tree by *Baizongia pistaciae*. The buds at the tips of side shoots are beginning to grow (current year). The side shoots grew in year 1 due to the relaxation of apical dominance when the main shoot died for some unknown reason (dead shoot seen in the middle). The old gall marks the terminal bud site in year 2. Photo: O. Shukry.

(Wool 1984, Swirski and Amitai 1999) although in the Botanical Gardens of the Hebrew University on Mount Scopus, Jerusalem, galls were found on *P. khinjouk* trees (of Egyptian origin). In Turkey, Italy, and Greece it occurs on *Pistacia terebinthus* (Bodenheimer and Swirski 1957). Galls were found on *P. terebinthus* at Mirando do Duoro (eastern Portugal) in 1997 and in Montserrat (Spain) in 1999 (Wool, unpublished.). Galls were recorded on *P. khinjouk* in Iraq (Bodenheimer and Swirski 1957) and on *P. terebinthus* in Iran (Davatchi 1958). In India and Western Himalaya, *B. pistaciae* galls were recorded on *Pistacia integerrima* (Chakrabarti 1987, 2001). Anholocyclic populations of *B. pistaciae* were found on herbaceous secondary hosts in Europe where no *Pistacia* grows (Zwölfer 1958).Wertheim (1950, 1954) provided the first ecological data on this species in Israel.

More than one species?

Identification of *B. pistaciae* in its geographical range is based on gall characteristics as well as on aphid morphology (the identification of the host tree may suffer from uncertainties in plant taxonomy). The morphological characters used for identification of the species, and some biological data, are given by Roberti (1939, 1983), Zwölfer (1958), Davatchi (1958), Del Campo *et al.* (1990), and Zhang (1995).

A photograph of a shoot of *P. palaestina* carrying galls of *B. pistaciae* appeared on the front page of the Israel Journal of Entomology,Vol. 33, announcing an annotated list

Fig. 5. A crowded group of atypical, blunt-ended, galls of *Baizongia pistaciae*. Bet Shemesh site. Photo: O. Shukry.

of Israeli aphids (Swirski and Amitai, 1999). Although the caption described them as "hornlike galls", the photograph showed galls with a blunt apex—not at all hornlike. In response to the photograph, Prof. G. Remaudiere of the Natural History Museum in Paris—a veteran in the taxonomy of the Fordinae—suggested that these galls may be induced by a new species of *Baizongia* (DW, personal communication). Unfortunately the material provided upon his request was insufficient. Blunt galls were often encountered at several research sites, notably near Bet Shemesh—Bet Guvrin road (Fig. 5), and the form was discounted as a deformation due to some disturbance during gall growth.

A recent molecular analysis of aphids from galls collected in Spain, France, and Israel shows that the aphids are very similar genetically (T. Fukatsu, unpublished data referred to in Wool, 2005), although the collection sites are separated by the entire length of the Mediterranean sea. The aphids at these sites were considered as belonging to one and the same species.

LIFE CYCLE

Baizongia pistaciae shares with most of the galling aphids a life cycle that includes host alternation (reviews in Wool 2004, 2005). MacKenzie and Dixon (1990) used the life cycle of *B. pistaciae* as an illustration of their optimality hypothesis of the evolution of aphid life cycles and host alternation. Briefly, the typical holocycle involves parthenogenetic reproduction in the gall during the summer, on the primary host tree (In Israel: *Pistacia P. palaestina*), followed by colonization of secondary hosts. The alternation of hosts is accomplished by alate morphs. Fall migrants emerge from the galls in the

Figs. 6–7. 6. Longitudinal section through a bud of *Pistacia palaestina* showing early stages of gall initiation of *B. pistaciae*; 7. Details of Fig. 6 enlarged.

autumn and disperse. Their offspring colonize the roots of the grasses and resume parthenogenetic reproduction. In the spring a second alate form appears (sexuparae). These aphids fly back to *Pistacia* and deposit sexual males and females. After mating, fertilized eggs remain on the tree and gall fundatrices hatch in the next spring. This life cycle is common to most Pemphigidae (Moran and Whitham, 1988; Moran, 1992) and has been described in detail (Wool, 1984; Blackman and Eastop, 1994).

GALL INITIATION AND GROWTH

Many fundatrix nymphs of *B. pistaciae* can be found—upon close examination—on the apical buds of *P. palaestina* in late March—mid-April, when the dormant buds begin to grow. Quite frequently, several leaves are colonized on the same or closely-adjacent buds. The result is a cluster of galls—up to 14 were recently counted—attached to the same shoot (e.g., Fig. 5). Each gall is induced by a single fundatrix. The aphid first settles on the small, elongating shoot inside the bud, and her activity causes it to bend at an angle of 60–90 degrees. This is the first external indication of the induction of a gall (Wertheim 1954). Then the fundatrix moves to a primordial leaf and settles inside a folded leaflet. This is where the gall is induced (Figs. 6, 7). The growing plant tissues form a depression which encloses the aphid and extends as a tube—sealed at its distal end—to the underside of the leaflet. Within the tube the aphid matures and reproduces. The other leaflets on the attacked leaf eventually wilt and drop, the petiole thickens and the gall remains attached to the shoot.

Fig. 8. Fall dispersal: alates emerge from a gall.

Fig. 9. Cross section of a *B. pistaciae* gall early in development. Note the two rows of latex ducts and the reversed order of the vascular elements. Phloem is formed closer to the inner gall surface in the row closer to the gall cavity (Photo: R. Aloni).

In most cases, the galled shoot does not elongate, and the gall appears attached to the previous year's growth. In some cases, a secondary apical bud is infested, apical dominance is partially maintained, the shoot does elongate, and the gall appears to be attached to the middle of the current year's shoot. The loss of apical dominance stimulates the growth of side-shoots from secondary buds (Fig. 4). This contributes to the naturally bush-like phenotype of heavily-infested trees of *P. palaestina* in the Mediterranean forests of Israel (Martinez and Wool 2003; Kurzfeld-Zexer et al., 2011).

The gall increases continuously in size throughout the summer so long as the aphids inside are alive. Death of the aphids stops gall growth. At the end of the summer (October–November) cracks appear in the gall wall from which resin oozes–then the gall cracks open—at one or both ends—and the alate aphids (fall migrants) emerge (Fig. 8), disperse, and reproduce to start the subterranean part of the life cycle (see below). Galls varied in length already in the first sampling date (Fig. 10). This variation could be due to differences in bud burst, shoot growth rate, or differences in fundatrix arrival and gall initiation times. Gall length increased in a more or less linear fashion during the summer, but galls varied in elongation rate (as illustrated by the slopes of the lines in Fig. 10). In

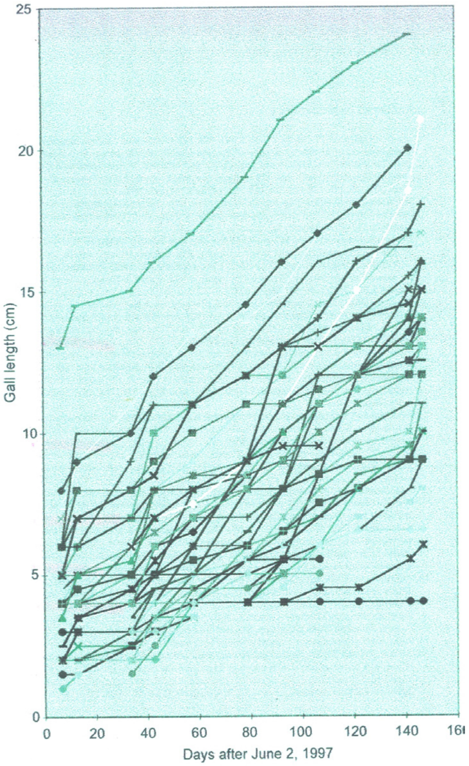

Fig. 10. Plot of repeated measurements of lengths of marked galls at the Bet Shemesh site in 1997. Each line describes a different gall. Abscissa is in days after the first measurement (June 2, 1997).

the early phase of gall development, galls elongated with little change in circumference (gall diameter remains <5mm while gall length increases to 100 mm). The aphids were located and seemed to feed in the distal end of the gall near the apex. Only later, with the appearance of the 3rd aphid generation, the galls began to increase in circumference (Appendix 1).

The temporal patterns of gall size changes when measured on the tree without disruption were not the same as the changes in mean size of sampled galls.

Contrary to the linear growth curves of individual galls (Fig. 10), there seem to have been two or three phases of fast mean gall elongation. The pattern illustrated by the means is not obscured by the wide range of variation among galls within samples (Fig. 11). The mean gall length remained almost unchanged for six weeks after a short initial gall growth phase in June. A period of gradual growth began in mid-July and lasted until early September, again followed by a three-week stasis. Fast growth was again resumed in October and lasted until the termination of sampling. These phases, if

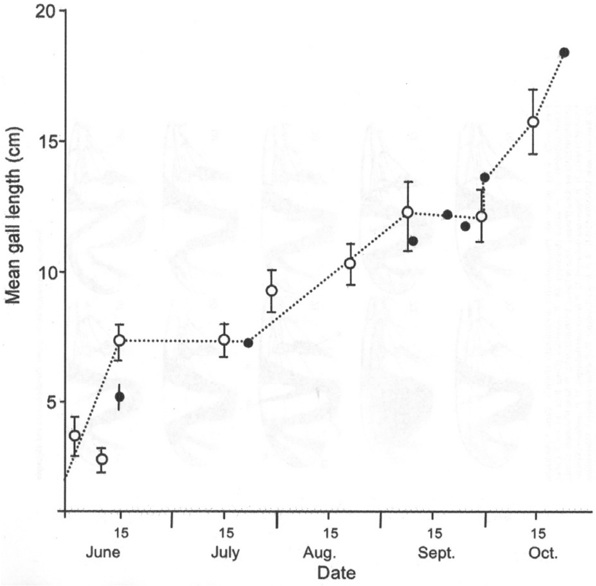

Fig. 11. Temporal pattern of mean gall elongation (black dots: galls sampled in 1996; hollow circles: galls sampled in 1997).

real, seem to correspond to the reproductive schedule in the galls, when the daughters and granddaughters of the fundatrix matured and began to reproduce.

The temporal plot of gall volume showed little change from July to September, followed by a fast-increasing phase in late September–early October (Fig. 12, Appendix 1).

Clone size estimation

Studies of population dynamics of gall-inducing insects—galling aphids are no exception—almost always require destructive sampling: it is not possible to census the inhabitants of the gall without collecting and opening it and thus disrupting the process under observation. To obtain an estimate of the continuous process, samples are taken periodically and their means are plotted sequentially—but this requires the assumption that reproduction occurs at the same rate in different galls. On the other hand, sampling different galls at successive points in time has the advantage that the measurements are statistically independent (Appendix 1).

The youngest galls contain the fundatrix, and few of her daughters. Later, clone size increases dramatically. (Wertheim (1950) measured gall lengths and clone sizes of *B. pistaciae* in Jerusalem. The galls contained only 1–3 individuals in early May, 5–30 in June, less than 100 in July—and thousands in August–October). In 1996 and 1997, mean clone sizes increased slowly between June and August, and much more quickly in October (Fig. 12)—in parallel to the growth of gall volume (Appendix 1).

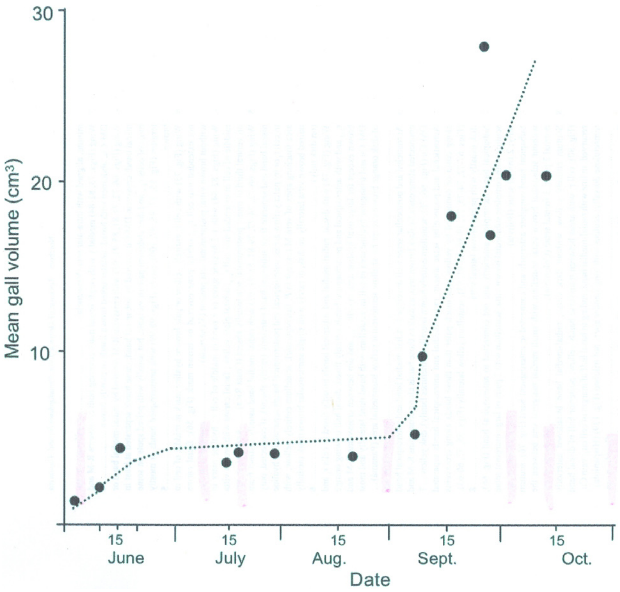

Fig. 12. Temporal pattern of increase in gall volume (dipping estimates) in 1996 and 1997. Note the stasis in July and the acceleration in September.

Predicting clone size from gall dimensions. The clone sizes and gall dimensions of the sampled galls in 1996 were used to find a best-fit function from which to predict clone size (O. Shukry, unpublished). Linear and quadratic functions of gall length gave the poorest fit ($R^2 = 0.45$). Gall volume (dipping estimates) and calculated surface area gave better fit to the logarithm of clone size ($R^2 = 0.6$ and $R^2 = 0.69$, respectively). However, no single gall measurement turned out to be a useful predictor of clone size. The calculated internal surface area (Appendix 1) increased steadily from July to October, 1996. The fast growth of the clone at the end of the summer catches up with the increase in surface area: when the two curves are plotted together, they intersect in early October (Fig. 13). This may be an illustration of the Malthusian principle. At about the same time, the aphids in the galls become alate, ready to leave the galls, apparently because density (aphids/cm^2 of internal gall surface) reaches a critical value. A similar phenomenon was observed in the marble galls of *Geoica wertheimae* on the same host (Wool and Ben Zvi, 1998).

COMPETITION FOR RESOURCES

Galls of eight species of Fordinae may be found on the shoots of *P. palaestina* in Israel (Wool 1995). *B. pistaciae* is the only species which evolved the ability to take over the terminal buds of *P. palaestina* (Inbar et al., 2004), and interspecies competition for this galling site can be ruled out. However, when several fundatrices occur on the same bud

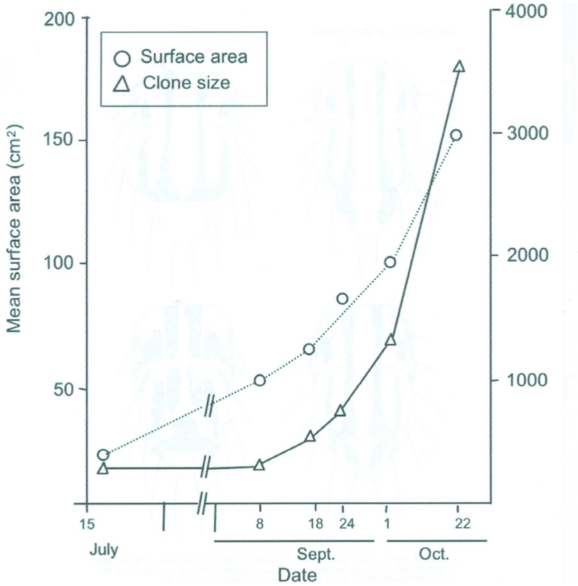

Fig. 13. Temporal pattern of clone size estimated from sampled galls in 1996, and the changes in calculated gall inner surface area. Note that the clone increases faster than the surface available for feeding. The curves intersect at the time that alates were found in the galls.

—as is frequently the case—intra-specific competition for suitable leaflets may take place within the bud, as described for other Fordinae (Inbar 1998). Moreover, once the galls are initiated, competition for plant resources occurs, mediated by the nutrient sinks caused by the galls (Inbar et al., 1995). To colonize a shoot, the fundatrices must induce a stronger sink than plant parts like buds, flowers and fruit competing for the same resources (Larson and Whitham, 1991, 1997). Sink strength may be estimated by the ability of the gall to divert nutrients from distant sources like other leaves or shoots. This is measured in translocation experiments using $^{14}CO_2$. The amounts of photosynthates translocated into the gall—relative to the source leaf may be estimated by scintillation counting as a quantitative measure of sink strength (Inbar et al., 1995).

Field experiments were carried out on *B. pistaciae* at Canada Park, Israel in 1992. Galls of *B. pistaciae* induced the most powerful sink of four Fordini on *P. palaestina*. The galls mobilized sugars from more distant sources as they increased in size during the summer. Small galls only used photosynthates from neighboring leaves on the same shoot, but larger galls diverted sugars from adjacent shoots (Burstein et al., 1994). Gall sink strength is probably due to the increased demand for nutrients by the growing plant tissues, but may be indirectly affected by the increased utilization of the sugars by the multiplying aphid clone. At the end of summer, the sink created by the *B. pistaciae* gall may cause early abscission of leaves below the gall—with the consequent premature mortality of galls of other Fordinae that happen to be located on them.

THE GALL ENVIRONMENT

One of the proposed advantages of the gall, apart from facilitating aphid feeding, is perhaps isolating the aphids from unfavorable external environments (Price et al. 1987). Chemicals in the gall wall of *B. Pistaciae* may provide some protection from insect attack (Martinez 2009a). The galls of *B. pistaciae* were described as incubators, enabling the aphids to reproduce in a favorable environment (Mackenzie and Dixon 1991). The aphids reproduce in the galls in the summer, when the air temperature at some sites may approach 40°. How well does the gall wall moderate the internal gall temperature is poorly documented. In a small-scale experiment, internal and external temperatures were recorded for 28 hours in five *B. pistaciae* galls on a tree in sunlight. In the daytime, gall temperatures were 1 °C lower than the ambient. At night, the temperature in the galls exceeded the ambient temperatures by 1–2 °C. Aphid respiration may increase the internal gall temperature during the night or in cold weather (Martinez, 2009b). Humidity in the sealed gall must be high—especially with the respiration of many aphids inside—but no accurate measurements have been published.

Gall functional anatomy

Cross sections of galls of *B. pistaciae* at different stages of gall growth (Alvarez, 2011; Wool, unpublished) reveal that the internal structure of the galls is very different from the normal leaf. The fundatrix settles on the adaxial side of the embryonic leaflet and induces an invagination of leaflet tissues, which extends like a finger in a glove to the abaxial side (Wertheim, 1954). As a result, the internal gall surface is continuous with, and homologous to, the adaxial surface. The process of gall formation is similar to that described for *Geoica wertheimae* on the same host plant (Wool et al., 1999; Alvarez, 2012), although the resulting gall shapes of the two species are very different.

The epidermis, palisade tissue, and parenchyma are modified or missing in the gall. The vascular elements—especially the phloem—show the greatest modification. The phloem is associated with and develops in latex ducts, which are characteristic of *Pistacia* (Sawidis et al., 2000). As a result of the invagination, a secondary layer of latex ducts is formed below the internal gall surface. While normally in the ungalled leaf, phloem is produced toward the periphery and xylem towards the inside of the vascular bundle, in the secondary layer of latex ducts the order of the tissues in the vascular bundles is reversed: phloem is closer to the internal surface area of the gall and xylem is produced toward the periphery (Fig. 9). The aphids need only to insert their stylets through a small number of cell layers (3–5) to reach their feeding sites in the phloem. In *B. pistaciae,* similar to *G. wertheimae*, the vascular system develops into an elaborate network of feeding tubes for the multitude of aphids inside the gall.

When galls are cut open early in the season, all aphids seem to be attached to the gall wall and appear to be feeding. In mid- or late-summer, many aphids seem to be detached and occupy the gall cavity, dropping out easily when the gall is opened. It is possible that as aphid size and density in the gall increase during the summer, some of the aphids are shoved off the feeding sites. This may be one trigger for the induction of the alate morph and fall dispersal (see below).

The arrest of shoot elongation when galled by *B. pistaciae* and the consequent loss of apical dominance modifies the tree architecture (Kurzfeld-Zexer et al., 2011). Furthermore, the presence of a gall induces changes in the anatomy of the shoot bearing the gall. Anatomical changes in the vascular system—in particular the xylem—were detected 10 cm below the *B. pistaciae* gall. More xylem with numerous wide vessels is deposited in the galled branch at the end of the growth season, compared with paired ungalled branches. This makes possible a substantial increase of water transport into the gall-carrying branch when both the gall and the aphid clone are at their peak size (Aloni, 1991).

Feeding and honeydew

The aphids feeding in the gall seem to excrete smaller quantities of honeydew, compared with similar numbers of free-living aphids. The honeydew accumulates in the gall in the form of wax-coated droplets (Inbar and Schultz, 2001) which coalesce at the bottom of the gall. The wax coating enables the aphids to walk on the honeydew without getting trapped in it (Pike, et al., 2002). In the past, aphid honeydew was considered an excretion of surplus sugars: plant sap is rich in sugars—particularly sucrose—but poor in amino acids, and the phloem-feeding aphids must ingest a large quantity of plant sap to get the needed proteins (Dixon, 1998). Recent research, however, discovered that the honeydew contained little sucrose but mainly monosaccharides and oligosaccharides (references in Wool, et al., 2006). This suggested that the aphids—perhaps with the help of their symbionts—use the breakdown products of sucrose (glucose and fructose) to synthesize the more complex sugars.

Honeydew was collected from individual *B. pistaciae* in 1997–1998 (See methods in Wool, et al., 2006). Twenty-six different sugars were detected in the 58 samples of *B. pistaciae*. The two most frequent sugars—present in 82 and 92% of the galls sampled, respectively—were glucose and fructose. Together these two sugars constituted 23–26% of the total sugar content in these samples. Honeydew composition varied among samples taken in different times of the year. These temporal differences could be due to seasonal changes in the sugar content of the plant sap, or to changes in aphid metabolism as the temperatures changed (Wool, et al., 2006).

GALL ABUNDANCE

The abundance of *B. pistaciae* at a site can be estimated by two parameters: the proportion of occupied trees may vary due to the geographical distribution of the aphids. Locally, the probability of colonization of a tree may be affected by the location and distance of the sources of migrant sexuparae (see below) and their colonization success. The conditional abundance of galls on occupied trees reflects the density of colonizing fundatrices, their survival and reproductive potential. The two parameters are not independent and may be affected in different degrees by the same factors.

The proportion of occupied trees

Although *B. pistaciae* may occur in all sites where *P. palaestina* grows (Koach and

Wool, 1977), the proportion of occupied trees varied greatly among sites in Israel (Table 1). Trees marked “selected” were used for a long-term study (see below) and were not initially a random sample. Of particular interest is the difference among habitats: a higher proportion of trees growing in roadsides were occupied compared with trees within the forest or in open fields. Roadsides seem to be a better habitat both for the trees and for the aphids—perhaps due to the rainwater runoff from the paved road surface, which is favorable to the trees as well as the secondary host grasses. Another advantage may be easier access to colonizing aphids in an otherwise forested area. Trees located at the ecotone between forest and pasture, were more likely to be colonized by the aphids, than in either of these habitats. Older trees, with rough bark and lichen-covered trunks, were colonized more often than young trees with smooth bark. Tree sex and the number of trees in a patch did not affect the probability of colonization (Martinez and Wool, 2006).

Gall abundance on occupied trees

A long-term study of gall abundance on marked trees was initiated in 1978 at three sites in Israel. Only trees already occupied by *B. pistaciae* were initially selected for study. The sites were: 1) Mount Carmel, along the road from Bet Oren to Damoun, 2) along the Bet Shemesh–Bet Guvrin road, already mentioned, and 3) trees at the Tel Aviv University Botanical Gardens. Each site was visited once a year after leaf fall, usually in December, when the galls are very conspicuous on the leafless branches. Repeated censuses of the marked trees continued for 20 years. All galls on each tree were counted. (Some dry galls may remain on the trees for more than one year. In the analysis the probability of counting the same galls twice was considered negligible).

Table 1
Percent of *Pistacia palaestina* trees colonized by *B. pistaciae* at different sites (a compilation of unpublished records)

Site	habitat	# of trees	Occupied (%)	Author
Galilee–road	roadside	44	91%	Martinez
Galilee–field	field	44	64%	Martinez
Galilee 2000	roadside	70	62.9%	Martinez
Galilee 1999	roadside	60	62%	Martinez
Har Halutz	bush	38	60%	Wool
Carmel -East	bush	100	21%	Wool and Shmida
Bet Oren	road–selected	16	100%	Wool
Jerusalem		50	16%	Shmida
Canada Park	bush	21	20%	Wool
Bet shemesh	road- selected	35	84%	Wool
Bet Shemesh	roadside	39	79.5%	Martinez
Bet Shemesh	field	40	12.5%	Martinez
Yehiam	lakeside	15	0	Wool

Censuses at the end of the summer must be an underestimate of gall survival rates, because galls which were aborted or parasitized early in the season are not counted. It is difficult to estimate how many such galls were initially present. The proportions of galls marked in June which reached the aphid-dispersal stage near Bet Shemesh, were 61% in 1996 and 70% in 1997 (O. Shukry, unpublished).

Temporal trends in gall abundance (1978–1998)

Gall abundance of *B. pistaciae* varies from site to site, from tree to tree and from year to year (Wool, 1990, 2002). In the first 10 years, peaks and troughs in abundance on any given tree fluctuated with a two-year period (Wool, 1990), similar to the alternate yield pattern of the host tree. The pattern was largely lost in the later years of the study (Wool, 2002). The mean long-term number of galls varied greatly among trees. The range of gall abundance per tree was very wide and varied among sites (Table 2). Variation among sites could be caused by differences in the growth conditions of the trees. Factors associated with the aphid populations on the secondary hosts at each site, as well as genetic differences among odd-and even-year populations of the aphids, cannot be excluded (see discussion in Wool, 2002).

The raw data collected in the 20-year continuous study were further analyzed with emphasis on the patterns of population variability and stability (Lamb et al., 2011). Although protected in large galls on persistent trees, population variability of *B. pistaciae* was similar to that in free-living aphids on herbaceous hosts. Despite the great variation in abundance, a positive correlation was found between the variability in odd- and even-year cohorts on individual trees—a pattern not detected in the earlier analysis—which indicates either some genetic similarity of clone characteristics or the host-tree growth pattern.

The trees at sites located near roads—Carmel and Bet Shemesh—carried higher numbers of galls than sites away from the roads (Martinez and Wool, 2006; table 2). The peaks and troughs in gall abundance were not synchronized among trees, and no significant correlations were found between abundance and temperature and rainfall variables during the 20 study years. This result negates the possibility of abundance regulation by climate (Wool, 2002). In particular, the absence of significant correlation of abundance with rainfall was surprising, because precipitation was expected to be important in the relatively dry climate of Israel. The fact may in part be explained by noting that the trees grow in a micro-habitat of roadsides with a better water supply than the surrounding fields (Martinez and Wool, 2006). It is possible that different stages of the complex life cycle of these aphids (see below) may respond differently to climatic variables and the effects cancel each other, or that the "noise" may be too large to detect the effect of any single variable - except perhaps in exceptionally wet or dry years, an extension of the "density-vague" ecology (Strong, 1984, Wool, 2002).

HOST ALTERNATION

Like most species of Fordinae, *B. pistaciae* alternates between hosts (reviews in Wool,

Table 2
Means and ranges of long-term gall abundance per tree at the research sites

Site	Mean gall abundance	# of trees	Years per tree
Carmel	5.7 to 138.7	17	2 to 20
Tel Aviv (TAU)	0.0 to 44.9	33	11 to 17
Bet Shemesh–Bet Guvrin			
Road	3.7 to 280.3	17	3 to 19
Hilltop	3.5 to 55.3	12	2 to 16

2004, 2005), and this alternation requires two stages of dispersal, each carried out by a special alate morph.

Terminology

The life cycle of most European gall-inducing aphids (Pemphigidae) is completed in a single year. Most of the Fordinae in Israel take two years to complete the cycle. This causes some terminological confusion. Because in Europe the alates vacate the galls and colonize the secondary hosts in early summer, these alates are referred to as “spring migrants”, while the sexuparae, which migrate from the secondary to the primary hosts and arrive at the trees in Europe just before winter, are referred to as “fall migrants”. For the Fordinae, this terminology is inappropriate. Galls are vacated at the end of the summer, and the alates dispersing from the galls deserve to be called “fall migrants”. I refer to the alates migrating from the secondary to the primary hosts in the spring as “sexuparae” to avoid confusion with the European terminology.

Fall dispersal

B. pistaciae galls in Israel begin to open in October (Wertheim, 1950, 1954), the same holds true for *B. pistaciae* on *Pistacia terebinthus* in western Spain and Portugal. (Del Campo, et al., 1985). The first indication of the imminent opening of the galls is the appearance of cracks in the gall wall, from which some resin often oozes. The gall opens from the top or from both ends and the alate disperse (Fig. 8). Some apterous aphids remain in the gall after the alates have left, but they eventually perish.

In the laboratory the alates are attracted to light and otherwise appear to disperse randomly (Wertheim, 1950). They do not fly toward secondary hosts but find refuge under stones and other sheltered places on the ground, where they give birth to their offspring (crawlers). These crawlers may survive without feeding for days or weeks (many of the secondary host plants may not yet have germinated at dispersal time before the first rains (Wertheim, 1950)). The reproductive potential of the fall migrants, i.e., the numbers of crawlers per isolated alate, varies considerably. Alates sampled later in the year produced significantly fewer offspring than alates sampled earlier (Table 3).

Sexuparae migration (spring migration)

The sexuparae develop during the winter on the roots of secondary hosts, and fly to

Table 3
Mean numbers of crawlers per isolated alate in 1996 and 1997. N = 20 in each sample

Sampling date	Mean ± SE
Early Nov. ’96	11.4 ± 1.82
mid-Nov. ’96	8.7 ± 4.36
Dec. ’96	5.5 ± 3.10
Early Nov. ’97	11.9 ± 1.64
mid-Nov. ’97	8.95 ± 3.46
Dec. ’97	5.9 ± 2.87

Pistacia in the spring (see the following section). Unlike the dispersal of the alates in the fall, the spring migration must be directional. The Fordinae are host-specific, and the role of the sexuparae is to identify and land on the correct host tree on which their sexual offspring will mate, and deposit fertilized eggs. Correct identification increases the chance that the fundatrices, hatching from these eggs a year later, will succeed in inducing a gall. To study the migration of sexuparae to their primary hosts, sticky traps were placed on branches of marked trees at two sites (Canada Park and TAU Botanical Gardens; Wool, et al., 1994, 1997). The traps were designed to intercept the sexuparae as they walked down from the foliage to the trunk, along the main branches, larvipositing the sexuals in crevices.

The evidence suggested that the sexuparae land quite frequently on an unsuitable host when more than one *Pistacia* species grow at a site (as is often the case in the Mediterranean forests of Israel). Although most of the sexuparae were caught on their true host, *P. palaestina*, a noticeable minority landed and reproduced on *P. atlantica* and *P. lentiscus*, non-hosts of *B. pistaciae*—a waste of reproductive effort (Wool, et al., 1994, 1997). This was one reason for the conclusion that the host specialization of galling aphids was driven by selective removal of aphid genotypes which failed to adjust to the properties of the host tree, rather than by improving host detection by the aphids (Wool, 2005a).

THE SUBTERRANEAN GENERATIONS

Until recently, information on the subterranean stage in the life cycle of *B. pistaciae* (and other Fordinae) was mostly of taxonomic value (e.g., Roberti, 1939, 1983) and emphasized data from studies of agricultural crops (Harpaz, 1953; Bodenheimer and Swirski, 1957). Wild host plants infested with Fordinae rarely show external signs of the presence of aphids on their roots, and their detection was based on haphazard pulling out of suspected plants. We have not yet found *B. pistaciae* populations on secondary hosts in the field. This is hard to explain because in laboratory cultures, these aphids tend to aggregate and to produce long white wax threads, and should be recognizable (Wool, 1998; Wool and Kurzfeld-Zexer, 2008). Although we did succeed in rearing *B. pistaciae* in the laboratory, we can only guess at the natural secondary host of this species.

Laboratory cultures

The construction of simple root cages from disposable, 9-cm standard petri dishes made possible successful rearing of *B. pistaciae* in the laboratory (Wool, 1998). Early attempts to rear *B. pistaciae* in the laboratory were summarized by Wool and Kurzfeld-Zexer (2008). Briefly, the crawlers, born to field-collected fall alates, settled on the roots in aggregates, and produced long, white wax threads from glands on their dorsum (Roberti, 1939, 1983; Wool and Kurzfed-Zexer, 2008). The green crawlers started to feed immediately, and after one molt their color changed to creamy yellow. Feeding aphids excreted large quantities of honeydew, which soon became coated with wax.

Newborn nymphs often settled near their mothers, and the entire colony became covered with wax (we observed that once they commenced feeding, aphids tended not to change their feeding sites: colonization of new seedlings was mostly by newborn 1st-instars. Colonies persisted for 14 generations when newborn 1st-instars were transferred twice weekly to new cages, but no sexuparae were formed.

The colony maintenance procedures were changed: fresh seedlings were added periodically, while the old seedlings with the aphids were left in the cages. Consequently aphid density was higher in the cages, which probably contributed to the induction of alate sexuparae in colonies in 2005. Other species of Fordinae, when handled similarly, produced sexuparae (Wool and Sulami, 2001; Wool and Kurzfeld-Zexer, 2008).

This suggested that the expression of the alate phenotype and the initiation of the sexual cycle were triggered by the increased density in the cages, since other factors known to induce this change—temperature and light—were held constant. Wool and Sulami (2001) suggested that the stimulus for the change from parthenogenetic to sexual reproduction was probably received by the embryonic crawlers when their mothers dispersed from the galls in the previous fall, as is the case in the European Pemphigidae. The delay of several months in the expression of the alate phenotype may be due to some (yet unknown) “interval timer” (Lushai, et al., 1996; Campbell and Tregidga, 2006). The production of sexuparae which fly to the primary host—marks the end of the parthenogenetic phase and the initiation of the sexual phase in the aphid life cycle.

Differential success on different herbaceous hosts

Zwölfer (1958) listed many Fordinae as polyphagous at the subterranean stage. Surprisingly, *B. pistaciae* crawlers did not colonize wheat or barley roots (of the cultivars used) but did very well on both wild (*A. sativa*) and cultivated oats (*Avena*). A likely reason for the failure of *B. pistaciae* to colonize wheat seedlings may be the presence of hydroxamic acids (HX, also referred to as DIMBOA) in variable quantities in wheat cultivars but not in oats. HX are well-known aphid deterrents and fitness reducers (Niemeyer, 1988). *B. pistaciae* seems to be particularly sensitive to these alkaloids, because other species of Fordinae—notably *Aploneura lentisci*—readily colonized wheat roots (Wool and Sulami, 2001; Wool and Kurzfeld-Zexer, 2008).

PARASITES AND PREDATORS

Little attention was paid in past studies of the Fordinae in Israel, to the presence of natural enemies in *B. pistaciae* galls. The large galls are sealed until alate emergence, and *Leucopis* flies (Chamaemyiidae) and Anthocorid bugs (*Anthocoris* sp.), which are very common on other Fordinae on the same trees (Steinitz, unpublished) were not found in the sealed galls of *B. pistaciae*. The larvae of the pyralid moth, *Alophia combustella,* bore holes in the gall wall and prey on the aphids (see Bodenheimer and Swirski, 1957). In late summer, mature larvae exit the gall through the holes to pupate in the ground (DW, personal observation).

The larva of the gelechid moth, *Palumbina guerrini* (Sattler, 1982) seems to be a common predator of *B. pistaciae* early galls. This kleptoparasite feeds on the gall tissues and thereby destroys the aphid habitat. The mature moth larva prepares an exit hole for the adult moth, and pupates in a frass-covered silk bag with its head towards the hole (DW, personal observation). If the gall is attacked early, the entire aphid colony may be destroyed by this predator. If the gall is attacked later in the season, gall growth and aphid reproduction may allow the moth to complete its development without killing the clone. (The mean number of aphids in parasitized galls sampled in June 2002 was reduced to only 1/5 of the contents of the unparasitized galls in that sample, see Appendix 1).

Many small, black and shriveled galls of *B. pistaciae* are often seen on crowded shoots in early season. The reasons for the early mortality were never properly investigated. Many of these may be victims of predator attack—each of a small sample of these galls contained a moth larva (DW, personal observation). A single "mummy"—skin of a parasitized fundatrix—was found in one of 139 early galls collected in June 2002. The parasitoid *Monoctonia pistaciaecola* Stary may have parasitized the fundatrix before the gall was sealed, as is the case in the fundatrix galls of *Smynthurodes betae* (Wool and Burstein, 1991a,b).

Two species of Syrphid flies were reported from *B. pistaciae* galls in south-eastern Spain (Rojo and Marcos-Garcia, 1997). The adults of these non-specific aphid predators probably lay their eggs when the galls open to release the aphids at the end of summer, and do not do much damage to the clone at that stage. Up to 25 maggots were found in large galls. The syrphids presumably were first attracted to the galls as shelter, and only secondarily as a food source (Rojo and Marcos-Garcia, 1997). Syrphid maggots were occasionally found in galls of *B. pistaciae* in Israel (Wool, unpublished). Insectivorous birds (*Phylloscopus* spp.)—especially migrating birds—were often seen preying on alates emerging from the galls in the autumn (D. Wool and M. Inbar, unpublished; Burstein and Wool, 1992).

GEOGRAPHIC VARIATION IN MORPHOLOGY OF FALL MIGRANTS

B. pistaciae may be found in Israel wherever its primary host, *P. palaestina*, occurs, from the Golan Heights to the southern slope of the Judean Hills (Koach and Wool, 1977). In the autumn of 1972 and 1973, 161 mature galls containing alates were collected throughout this range (Koach, 1976, unpublished). Samples of alates—usually nine per gall—were mounted on microscope slides. Nineteen morphological characters were measured on each alate (Wool, 1977).

The largest variance component in *B. pistaciae* was variation among galls on the same tree. In most characters, it contributed 50% or more of the total variance and was always highly significant statistically (Table 3 in Wool, 1977). This component estimates mostly genetic variation among fundatrices, since each gall is induced by a different single fundatrix. Variation among aphids within the same gall (12–26% of the variance) estimates non-genetic differences among individuals, since reproduction within galls is clonal (it also includes measurement error). Variation among aphids on different trees within sites contributed 6–15%, and variation among collection sites often less than 15% (ibid.). These results suggest that *B. pistaciae* populations are not geographically differentiated in Israel (see next section).

Manheim (1996, unpublished) and Manheim and Wool (2004) compared the morphology of fall migrants and sexuparae of the same species. Contrary to the majority of the Fordinae, wing length and femur length in *B. pistaciae* were longer in the fall migrants than in the sexuparae, and there was no difference in antennal characters (Table 4).

B. PISTACIAE AS A META-POPULATION

Meta-population theory is popular among contemporary ecologists, as it helps to describe population dynamics on a large geographical scale. A meta-population consists of geographically-separated sub-populations (patches) embedded in an uninhabitable habitat (matrix), but connected by migration and gene flow. Some patches may in time become extinct, and others may occasionally be re-colonized by migrants from other patches. The meta-population structure is thus maintained despite the turnover of its parts.

The geographical distribution of *B. pistaciae* in Israel is patchy, because the landscape has been subject to human interference over centuries (Martinez 2002, unpublished). The natural forest in particular was grazed, cut and burned, leaving patches of *P. palaestina* trees geographically separated, with intervening areas where no hosts are available for galling by *B. pistaciae*. The population of *B. pistaciae* in Israel may justly be referred to ecologically as a meta-population.

Wool and Inbar (1998) considered each tree as an island, which must be recolonized each year, because the galls die every winter with leaf abscission. But the tree is only a part of the patch. To survive at a site, the aphids also need grasses as secondary hosts. A patch may be composed of more than one tree, sharing the same secondary hosts. Also, the population on the grasses is not bound by leaf abscission and may persist longer than the gall population on the trees (see Moran, 1992 in *Pemphigus*). This makes the country a collection of patches which can become extinct locally and be re-colonized as the case may be.

Patch size depends on dispersal ability of the aphids and consequently on gene flow. Aphids are poor fliers, but can be carried over large distances by wind (Hille Ris Lambers, 1957). If long-distance dispersal is frequent, the entire country may become one

Table 4
Morphological dimensions of *alate B. pistaciae*. Means and standard errors in microns. Sample sizes in parentheses. (WTL = wing total length; F2, Ti2 are leg characters; A12 and S12 are antennal characters; URS is the terminal rostral segment). Extracted from Manheim (1996)

Character	Fall migrants	Sexuparae	t =
WTL	3147 ± 44.8 (15)	2746 ± 52.6 (10)	5.67***
F2	347 ± 6.4 (15)	430 ± 10.4 (10)	7.24***
Ti2	534 ± 2.3 (15)	618 ± 19.9 (10)	3.85***
URS	103 ± 1.9 (14)	139 ± 1.9 (10)	12.88***
A12	251 ± 5.8 (15)	260 ± 9.2 (10)	0.9 ns
S12	7 ± 0.34 (15)	7.1 ± 0.26 (10)	0.17 ns

panmictic population. The colonizing ability of *B. pistaciae* in nature was demonstrated when a forest fire destroyed the occupied trees and the grasses in section of the Carmel National Park. Re-sprouting trees provided vacant niches for the aphids in the blackened landscape. Two years after the fire, 37 of the 39 burned and resprouting *P. palaestina* trees were recolonized by *B. pistaciae* (while less than half the trees were colonized by other Fordini after six years (Wool and Inbar, 1998). *B. pistaciae* seems to be a very good colonizer. This may not be surprising, considering that each gall may release far larger numbers of dispersing alates at the end of summer than any other species of Fordinae on the same trees.

Persistence of patches

Once a tree is colonized, it remains colonized for years—presumably from nearby grasses in the patch (Wool and Inbar, 1998). That some patches persist for a long time is shown by long-term observations. Persistence of populations on individual trees was confirmed by detailed analysis, and was positively correlated with abundance (Lamb, Mackay, and Wool, 2011). The great majority of the marked trees on the south-facing slope of Mt. Carmel and the Bet Shemesh—Bet Guvrin road were continuously occupied in the 20 years of study (Wool, 1990, 2002).The probability of a tree being "vacant" (no galls) in any given year was as low as 6% at the Carmel site, and 13% at the Bet Shemesh site. The fact that the trees at both sites grew in roadsides may have improved the chance of colonization by *B. pistaciae* (Martinez and Wool, 2006).

Genetic differentiation of subpopulations and patch size

Whether the patch distribution of *B. pistaciae* has genetic consequences required detailed examination. Martinez (2002) used 42 molecular markers, obtained by RAPD-PCR, from DNA of *B. pistaciae* to estimate gene flow, using Wright's F-statistics. Two or three trees were marked at each of four sites in Israel: Upper Galilee, Western Galilee, Carmel, and Bet Shemesh. Calculations of genetic differentiation (Fst) were based on the frequency of the markers in DNA samples from individual galls. The mean number of migrants exchanged per generation was calculated by the relation Nm = (1–Fst)/4–Fst.

Values of Nm smaller than 1 indicate that genetic drift alone can account for the observed differences in marker frequency between the compared landscape units, be it trees or sites. Values >1 indicate that other forces, like selection, are necessary to explain the differences among sites (see review in Wool, 2006).

The results suggested that between trees more than 200 m apart, less than 1 migrant was exchanged per generation. Thus *B. pistaciae* populations on individual trees within sites may be genetically different (Martinez et al., 2005). The authors suggested that patch size for *B. pistaciae* may be as small as a single tree with its surrounding grasses (Martinez et al., 2005).

The study by Martinez et al. (2005) stimulated further research on the molecular variation in populations of *B. pistaciae*. Ben-Shlomo and Inbar (2012) extended their study to 78 trees in eight geographical populations in Israel and one in Turkey, and used more sensitive molecular methods than did Martinez in 2002, which yielded 248 molecular markers. They found no evidence for genetic differentiation among populations on different trees—regardless of the distance between them—in contradiction to the previous study (but in line with the morphological analysis reported above).

Although the patchy ecological distribution of *B. pistaciae* and its host trees strongly suggest that deme formation is likely, these authors concluded that gene flow by the dispersing alates swamps any local differentiation of patches (trees and adjoining grasses) and no deme formation is detectable (Ben-Shlomo and Inbar, 2012).

REFLECTIONS AND CONCLUDING REMARKS

In reviews and discussions of the life cycle of the Fordinae (of which *B. pistaciae* is a prominent example)—as well as other Pemphigidae galling aphids, it is often emphasized that the clone in the gall is the issue of a single parthenogenetically-reproducing fundatrix, representing a single maternal genotype. This implies that the fact that the clone in the gall is composed of thousands of individuals can be ignored; they are nothing but redundant, “xerox” copies of the one genotype.

Ecologically, however, it may be misleading to ignore the fact that *B. pistaciae* galls contain 10,000–30,000 individual aphids. Once the fundatrix begins to reproduce, each individual aphid in the gall interacts with the gall environment—including other clone mates—individually. Although they are born parthenogenetically, and live in the same space, aphids within the gall are not ecologically identical and do not develop synchronously. They differ in age, size, and reproductive potential. The developmental processes in the gall, such as change of instars and the formation of alate fall migrants, occur individually.

This ecological variation among genetically-identical clone mates is reflected, among other variables, in the numbers of individuals remaining apterous in the galls at the end of the fall migration, when all alates have left: whether few or numerous, these “late developers” demonstrate within-gall variability in developmental rates. Similar variation is detectable when individual fall migrants from a single gall are caged and their offspring are counted (e.g., Table 3). Is it reasonable to assume that this variation does not mean anything for the clone?

These late developers eventually must die as there is nothing in the dry galls for them to feed on, and do not contribute genetically to the future of the clone, being of the same genotype as the dispersing alates, but the proportion of late-developers affects the number of dispersing alates—and thus the reproductive success of the fundatrix!

The "late developers" are outliers in the distribution of individuals within the clone, as are those with low or high reproductive potential (be it because they fed better or were born earlier). While the gall colony lasts, these outliers must consume resources and compete for food and space with other individuals. Their relative numbers—which are seldom if ever reported—are a measure of the "developmental noise" tolerated by the clone genotype of the fundatrix. This margin may (probably does) differ from gall to gall, i.e., from one fundatrix to another. It may affect the relative success of different clones if some environments give an advantage to clone genotypes with more canalized (or less canalized) development. This argument seems superficially to lead to group selection, but remember that genetically the clone is one unit. Late developers do not contribute to the genetic pool of the clone as the fall migrants start their own colonies on the grass roots, but they must do something when the gall is in existence. The gall acts as a sieve, and in a way synchronizes the characteristics of the individuals destined to represent the clone in future generations. We need to investigate the role of these ecological outliers in more detail. This is one of the issues that need to be explored in the future.

Nearly sixty years of research have passed since G. Wertheim first studied the biology of galling aphids on *Pistacia* in Israel. *B. pistaciae* is no doubt the most conspicuous one on its host, *P. palaestina*. It is perhaps disappointing that we do not yet have a clear concept of the mechanism of gall induction by the aphids—although this was addressed in studies of other aphid species: What does the fundatrix do to induce the gall? Is it a chemical component of the saliva, or the mechanical damage to the cells at the inserting point of the tiny mouthparts (as seems to the present author more likely), which mobilizes plant hormones to begin tissue growth? A related controversial issue is the determination of gall shape: is it only an "extended phenotype" of the fundatrix genotype, or is it modified by the anatomy of the host plant organ on which the gall is induced? All these issues are not restricted to the biology of *B. pistaciae*, and thus outside the scope of the present review. Some answers should be provided in the future.

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APPENDIX 1

Miscellaneous Comments

Temporal patterns of gall growth. Gall growth was studied quantitatively during two summers (1996–1997) at a long-term study site along the Bet Shemesh–Bet Guvrin Road, about 40 km southeast of Tel Aviv (Israel grid 148 128). This site is exceptionally favorable for *P. palaestina* as well as the galling aphids (Martinez and Wool, 2006). Fifty-nine labeled galls were measured repeatedly six times in 1996 and 49 galls were measured 12 times in 1997 (Unpublished data, O. Shukry, 2001). On each visit to the site, samples of galls were taken haphazardly from unmarked trees. At the end of the summer (November) all surviving labeled galls were harvested and taken to the laboratory for measurements of gall volume and clone size.

Calculated variables: Efforts were made to find a variable that will enable the estimation of temporal changes in clone size without opening the galls. Gall volume measured volumetrically—by dipping in a water-filled graduated cylinder—may be a good descriptor of changes in gall size because galls were often irregular.

Gall volume was estimated from its length and circumference for comparison with the direct volumetric method. Assuming the gall to be a perfect cylinder with length h and circumference $2\pi r$, the radius was estimated as $r = \text{circumference}/2\pi$, and gall volume as $V = \pi r^2 h$ (these are overestimates. The calculated volumes, assuming a perfect cylinder, were in most cases approximately twice as large as the measured values (data not shown)). The internal surface area of the gall is an important biological variable for the aphids, a measure of their potential feeding area: as phloem-feeders, aphids must have access to the gall wall to feed. Surface area was estimated as $S = 2\pi rh$ if the gall is assumed to be a perfect cylinder.

Clone size estimation. Clone size in sampled galls in 1996 and 1997 was estimated by direct count so long as the number of aphids was small enough. Later, three samples of 100 aphids were weighed on a Mettler-Toledo AE50 balance and the mean aphid weight was used to estimate clone size from the total biomass. Clone size estimates continued as long as the aphids remained apterous (until October) (O. Shukry, unpublished data).

The regression equation of log clone sizes on calculated surface area in the sampled galls was used to predict clone sizes in the repeatedly-measured galls. These predictions were compared with the actual clone sizes in the same galls when they were opened at the end of the season. This empirical relationship gave poor predictions especially for large galls, when the logarithms were back-transformed to actual numbers.

Predators: Six of 16 galls collected at Even-Sapir, Judean Hills on May 25, 2002, contained *P. guerrini* larvae (L. Kurzfeld, unpublished). Fifty of 139 galls collected from the Bet Shemesh–Bet Guvrin site (June 16, 2002) contained *P. guerrini*.