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POPULATION ECOLOGY AND EVOLUTIONARY CONSIDERATIONS

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SUMMARY

In most gall-forming aphids, only the fundatrix is able to induce a gall on the host plant. In *Smynturodes betae* Westw. (and a few other species), F_2 descendants emerge from the mother gall and induce their own, morphologically different galls. This constitutes an added complexity to the already very complex life cycle of gall-forming aphids.

We investigated the ecology of *S. betae* on marked trees and shoots at four sites in Israel. Gall initiation, gall distribution and density, and temporal changes in clone size within the galls were investigated during two consecutive years. We discuss the possibility that the two-gall life cycle evolved from the typical one-gall system of most gall aphids, and the possible selective advantage of this added complexity in the life-history strategy of gall aphids. Although the total reproductive output of *S. betae* is not higher than in related species with a single gall per life cycle, there seems to be an advantage in the subdivision of each aphid clone into several galls, thus reducing the risk of the accidental extinction of the clone (genotype) by environmental factors, including parasites and predators.

KEY WORDS: *Smynturodes betae* Westw., gall aphids, life cycle, ecology, evolution

INTRODUCTION

The term "life-history strategy" is used to describe an array of fitness related characteristics of a strain or a species, and is often used in insect ecology (Price, 1984). It may include parameters such as age-specific fecundity, developmental time variation and diapause, and dispersal tendency—all of which may have a profound effect on the chances of survival and reproduction. Comparisons of life-history strategies have led to the classification of species as r - or K -selected (e.g., Ricklefs, 1984). Reproductive strategies often, if not always, correspond to the pattern of some external, climatic factor—notably the pattern of geographical or temporal changes in temperature, rainfall, or daylength. Research on several organisms demonstrated

that life-history strategies varied among populations and strains within species (examples in Goldschmidt, 1940 for the Gypsy moth *Lymantria dispar*, Bell et al., 1979, 1983 for differences in diapause tendency among strains of the stored-products moths *Ephestia cautella* and *Plodia interpunctella*, and Istock, 1981 in the picher-plant mosquito *Weinomyia smithii*). That such differences in life-history strategies could be caused by selection was demonstrated experimentally by Wool and Sverdlov (1976) with populations of the flour beetle *Tribolium castaneum*.

In aphids, which are the subject of the present investigation, the existence of within-species differences in life-history characteristics is well known, leading to the concept of aphid "biotypes" (Eastop, 1973; Blackman, 1972, 1974; Leather, Wellings and Dixon, 1983; Muller 1985; Dohlen and Gill, 1989). The parthenogenetic reproduction of aphids makes it likely that "biotypes" are formed and maintained, since a single individual may give rise to a large clone of genetically-identical offspring.

Among aphid species, gall-forming aphids are strictly host-specific in the gall stage (review in Wool, 1984), and the primary host trees of almost all species in the largest family (Pemphigidae) are deciduous. In temperate climate, the winter is the most difficult time of the year for these herbivores. Their typical life-history involves a diapausing, overwintering egg stage on the primary host, as an escape strategy from unfavourable conditions. In the warmer parts of their distribution range there also exist active, subterranean winter generations on the roots of secondary hosts.

The complexity of life-history strategies of aphids, particularly gall-forming species, with host-alternation and sexual as well as parthenogenetic reproduction within one life cycle, prompted Mordwilko (1924, 1928) and Moran (1988) to consider

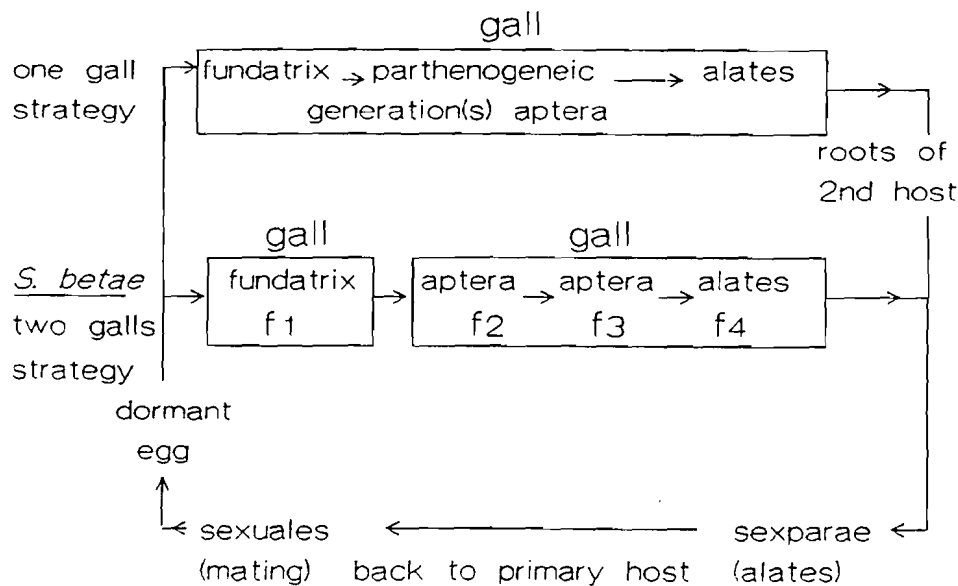


Fig. 1 Typical life-history strategy of the Fordinae (top and bottom lines) and the two gall system of *S. betae* (middle). The typical cycle in the figure begins in the spring (left hand top corner) and continues clockwise. The vertical lines represent winters. Sexuparae and sexuales are formed in the second spring.

aspects of the evolution of life-history strategies in aphids.

Typically, the fundatrix of gall-forming aphids belonging to the family Pemphigidae induces a single gall in the spring. Inside the gall, the fundatrix matures and reproduces parthenogenetically. The aphids of the second and later generations are unable to induce gall formation (Wool, 1984; Moran 1988). This is so in *Pemphigus* species in Europe and North America, where their life cycle is typically one year long, and in most species belonging to the subfamily Fordinae (Pemphigidae) in the Mediterranean region including in Israel, on 3 primary *Pistacia* hosts (Anacardiaceae) (Koach and Wool, 1977), where their life cycle (Fig. 1) is typically two years long (Bodenheimer and Swirski, 1957; Wool, 1984)

Among the Fordinae, species belonging to the tribe Fordini induce two types of galls on the same host (Wertheim, 1954; Bodenheimer and Swirski, 1957; Wool, 1984 and references there). This is illustrated in Fig. 1. One of these species is *Smynthuroides betae* West., which colonizes *P. atlantica* exclusively. The fundatrix forms a small (5–7 mm long) red gall on the midrib of the leaflet. The apterous second

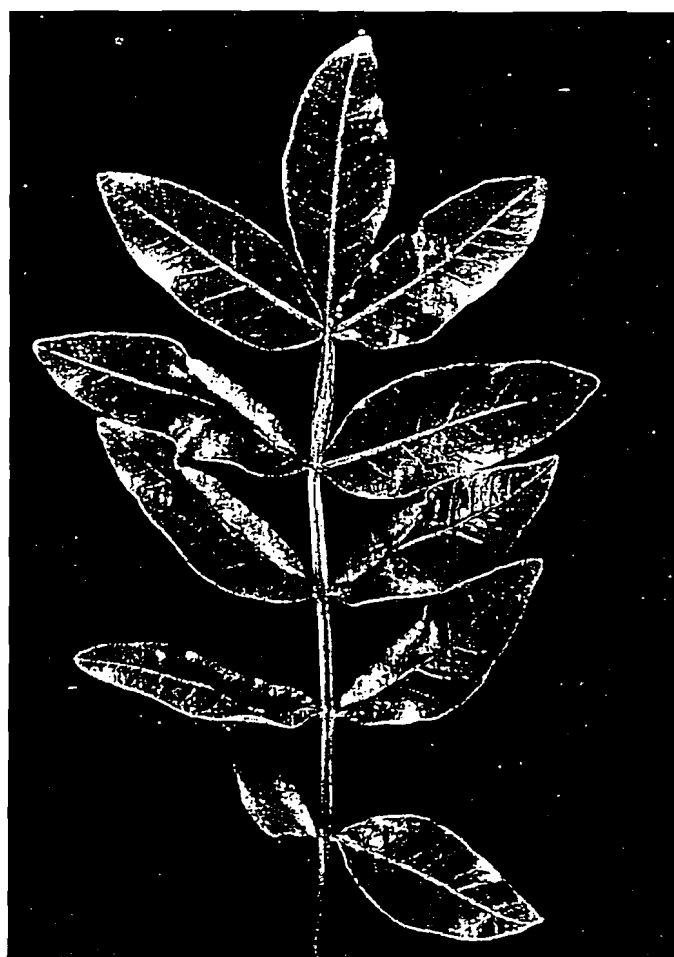


Fig. 2. A *Pistacia atlantica* leaf carrying final galls of *S. betae* (Photograph by A. Shouy).

generation nymphs induce the final, spindle-shaped galls (about 20 mm long), on the leaflet margin (Koach and Wool, 1977) (Fig. 2).

The present study is the first detailed ecological research on the gall generations of an aphid which induces two types of galls. We shall address the following issues:

- a) What are the major characteristics of the two-gall life history strategy?
- b) What are the stages contributing to clone-size increase and the main mortality factors in the gall stage?
- c) What could have been the selective advantages of the two-gall system in the evolution of the two-gall life-history strategy in the Fordinae?

MATERIALS AND METHODS

Study Sites

Galls of *S. betae* were studied intensively from 1988–1990. The main study sites were: 1) Tel-Aviv University Botanical Gardens (TA). 2) Old Botanical Gardens in Abu-Kabir (AK). 3) Kibbutz Givat Brenner, about 35 km south of Tel-Aviv (GB). 4) Kibbutz Gvaram, about 70 km south of Tel-Aviv (G). At TAU and AK the trees were planted as seedlings 15 and 40 years ago respectively, and are tended to at times by gardeners. GB is an old, abandoned plantation of the edible *Pistacia vera* grafted on *P. atlantica* stocks, but the grafts failed and the stocks were left unattended for 40 years or more. Similarly G is an abandoned ruin, uninhabited for at least 40 years, with some much older trees. GB and G may be considered natural sites from the point of the populations of *S. betae*, since the infestations must have occurred naturally, and the sites were unattended by humans for a long time.

We monitored the timing and rate of formation of galls in the field on individually marked trees and shoots (since galls are formed each year exclusively on new shoots, a shoot is a logical and convenient sampling unit). The number of trees and shoots varied among localities and years (see Results). These data gave information on the density of galls each year and the numbers of clones reaching maturity on each tree at each site.

Clone Size and Reproductive Success

Fundatrix and final galls were collected at least once a month each year between March and November. Gall content was examined in the laboratory and the aphids counted. In September, before alate migration, individual final galls were enclosed in nylon screen bags. Twice a week the alate aphids were removed from the bags by aspiration and were counted. This procedure enabled us to study the rate, timing and number of alate aphids migrating from individual galls. Clone size, especially at its peak, and the numbers of migrating alates give a measure of reproductive success at the gall stage. In addition, the presence of parasites and predators in the galls was recorded, to give a measure of mortality levels and percentage of surviving clones. In

early March 1989 several large branches (more than 1 m long) carrying a single fundatrix gall were isolated from neighbouring galls by smearing tanglefoot at the base of the branch. In this way we were able to determine the number of successful final galls induced by the descendants of each fundatrix, the timing and rate of final gall formation, and the distances between fundatrix and final galls.

Statistical Analysis

Conventional statistical methods were used in data analysis (Sokal and Rohlf, 1981). Differences among sample means were tested by *t*-tests or single-classification ANOVA, depending on the numbers of means to be compared. Linear regression and "Nested" ANOVA were used to test specific hypotheses.

RESULTS

Fundatrix Gall Stage

Gall initiation. The fundatrices (F1) hatch from the overwintering eggs in early March before the buds break. The fundatrix galls are formed on the midrib of the leaflet. Usually only one gall is found on each leaflet, but occasionally 2–5 galls were found.

Colonization success rate and gall density. If feeding and gall formation are discontinued, a red scar remains on the leaflet for several weeks. To obtain an estimate of fundatrix success in colonization, we counted the number of red scars on the leaflets. In 3 samples of leaves collected in 1988, on average 24.3% of aphid feeding attempts resulted in gall initiation (Table 1), but the rate of success was significantly different among localities ($\chi^2=14.9$, $df=2$, $P<0.001$).

Fundatrix gall density varied widely (range: 0–29 galls/shoot). Significant differences were found among localities, among trees, and between shoots within trees. In 1988 the average density was significantly higher than in 1989 (Table 2, $t=2.5$, $df=28$, $P<0.05$).

Fundatrix survival and longevity. In early April the number of galls with live fundatrices declined and most were dead by mid-April. The parasitoid *Monoctonia*

Table 1. Successful and unsuccessful fundatrix galling attempts (1988).

locality	no. leaves	no. scars	no. galls	% successful attempts
TA	37	316	119	27.3
GB	12	65	29	30.8
AK	6	163	27	14.2
Total	55	544	175	24.3

Table 2. Density of fundatrix galls in 1988 and 1989.

year	locality	no. trees	no. shoots	density-galls/shoot
1988	TA	6	55	7.2
	GB	10	80	6.7
	AK	2	8	1.6
	pooled	18	143	5.1
1989	TA	3	28	4.5
	GB	6	52	2.5
	G	3	27	2.9
	pooled	12	107	3.3

pistaciicola Stary (Aphidiidae) killed about 23% of the fundatrices (Wool and Burstein, 1991). Although the fundatrices die, the galls remain on the trees until the leaves are shed in the fall, and are invaded by inquilines such as free living aphids, psyllids and spiders. In some of the fundatrix galls F2 nymphs continue the life cycle (see below).

*Final Gall Stage

Formation of the final galls. As soon as the fundatrices mature in their galls, their F2 offspring disperse and form the final galls. The first final galls appear in early April on leaflet margins, and infestation of any individual shoot was completed in 10 days or less (range 4–14 days). Each final gall is formed by a single F2 aphid. Infrequently (24 of 1500 galls), we found final galls with two or more-sometimes many-F2 aphids. Such galls remained small, had a distorted shape, and all the aphids were found dead. Galls with live aphids invariably contained only one F2 female.

Final gall density. Gall density was significantly different between years (Table 3) (in TA, $F=6.12$, $df=2,169$, $P<0.001$; in GB, $F=34.07$, $df=2,178$, $P<0.001$, Table

Table 3. Final gall density at two sampling sites in 3 consecutive years.

		no. trees	no. shoot	no. galls	galls/shoot	SE
TA	1988	4	65	1625	25.0	2.9
	1989	3	41	581	24.1	1.8
	1990	6	66	1371	20.8	0.45
	Total	13	172	3577	21.8	
GB	1988	5	29	609	21.0	2.3
	1989	6	62	558	9.0	1.6
	1990	9	90	390	4.3	0.51
	Total	20	181	1557	8.6	

3).

Final gall density per shoot is related to the numbers of fundatrices which colonized that shoot earlier. Our observations show that F2 nymphs spread out to new leaves toward the tips of the growing shoots: this behaviour will create non-random gall distribution. The distances between fundatrix and final galls were measured on 12 long isolated shoots, each carrying a single fundatrix gall. Most of the final galls were formed on young leaflets 15–55 cm away from their fundatrix source galls, two-thirds of them distal (peripheral) to it (Fig. 3).

The numerical relationships between the numbers of fundatrix and final galls were investigated in order to estimate the reproductive success of fundatrices. The two types of galls were counted on eight large branches from TA, AK and GB carrying many shoots. The eight branches carried 226 fundatrix galls and 1946 final galls of *S. betae*. On average, each fundatrix gave rise to about 9 successful F2 descendants. Linear regression of final galls on fundatrix gall density (Fig. 4), yielded a smaller estimate (about 5 successful F2). The difference may be due to a density dependent decrease in final gall density when fundatrix gall density increases. This suggestion is supported by data from the experimentally isolated shoots in TA. When all but a single fundatrix gall per shoot were removed, each fundatrix produced as many as 20 successful F2 descendants (mean = 20.2, SE = 2.19, $n = 25$). Shortage of leaves seems to limit final-gall density in *S. betae*. More than 50% of the F2 aphids seem not to find suitable leaves to form galls.

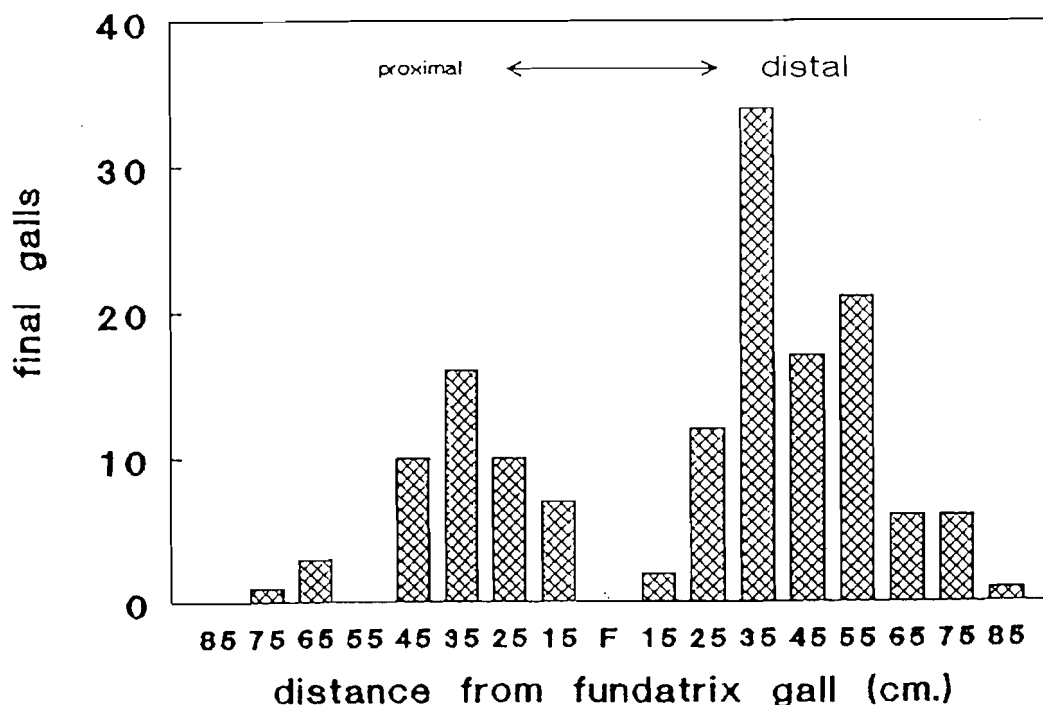


Fig. 3. Distribution of final galls of *S. betae* relative to the fundatrix source gall (marked F), in isolated branches carrying a single fundatrix gall (data of all branches pooled).

50%

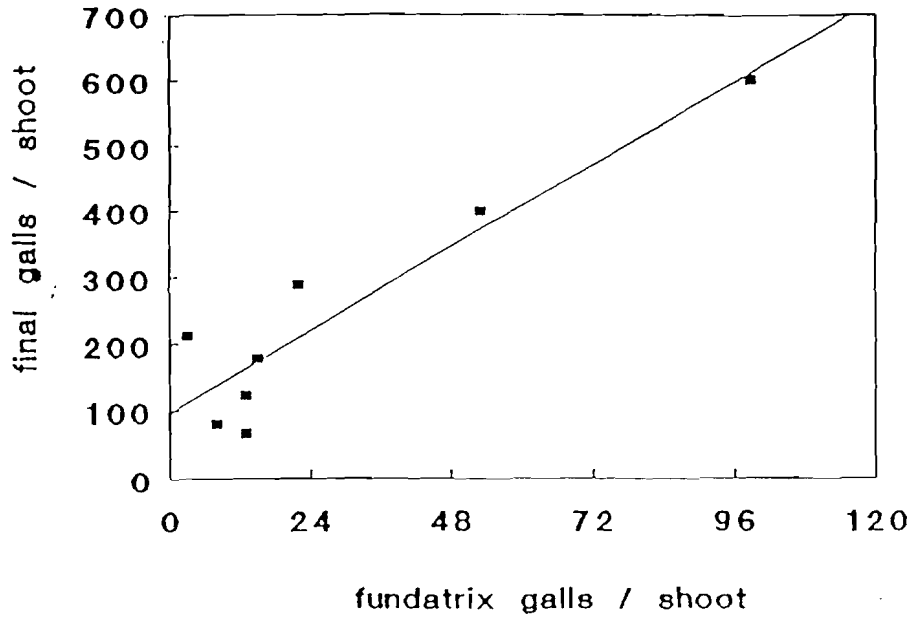


Fig. 4. Relationship between the numbers of fundatrix and final galls on 8 large branches (see Table 4). A linear regression line is plotted through the data points.

Clone Size Variation

Temporal variation. Each final gall contains at first a single F2 fundatrix. In late

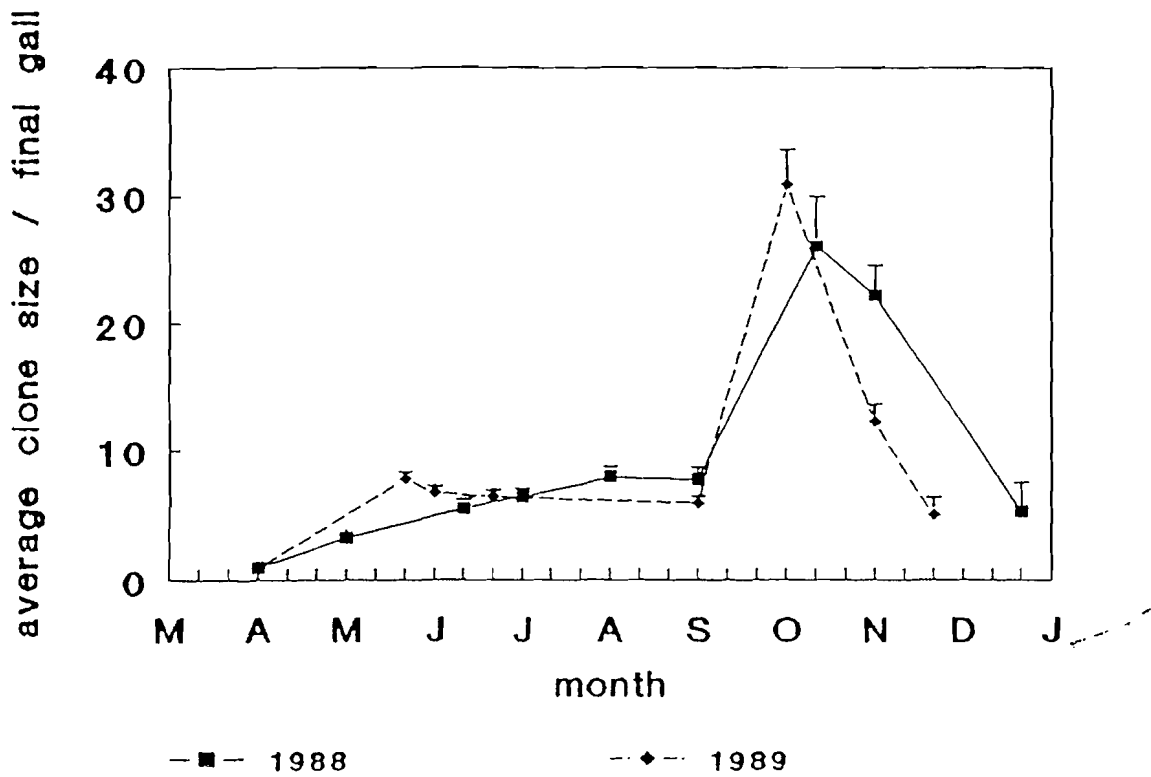


Fig. 5. Temporal changes in clone size in *S. betae* final galls in TA. The same pattern was observed in all localities.

April, on average, seven (range 1-21) apterous F3 females are produced parthenogenetically. Clone size in the gall remains at this level through July and August. In late August through October, about 30 F4 aphids are produced per gall (the number varied to a maximum of 120) and become alates (or eventually die). Clone sizes declined rapidly in October due to migration of the alates to the secondary hosts (Fig. 5). As indicated by the counts of the alates in bagged galls, most of the alates left the galls in the last two weeks of October. However, the emergence from the galls is not synchronized. Differences of up to 4 weeks were recorded between the beginning of migration in the earliest and latest galls. In some galls migration was completed in two weeks, but in others it continued for two months. This sequence of events was similar at all sites in both years. The galls are shed with the leaves in the fall.

Spatial variation. Two level "nested" ANOVA (Sokal and Rohlf, 1981) was used on data from TA, AK and GB in 1988, and data from TA, G and GB in 1989 to calculate variance components of clone size among sites, trees within sites, and galls within trees. The results show that variation among sites was small and non-significant in all cases. Differences among trees within sites were highly significant ($P < 0.001$) and accounted for about 35% of the variation. About 60% was due to variation among galls on the same tree (Table 4).

Reproductive success in the final galls. The ultimate measure of reproductive success in the gall stage is the number of alates which leave the galls in the fall. In our sample of 23 bagged galls, the cumulative numbers of alates ranged from 4 to 75 (mean \pm SE: 35 ± 4.8).

Loss of entire clones in final galls. Not all final galls produce alates: many clones are lost to predators, parasites and other (unknown) causes. Rates of loss of entire galls

Table 4. Summary of nested ANOVA on clone size. Data were square-root transformed before analysis.

source of variation	df	MS	variance components (%)
<i>1988</i>			
sites	2	24.4 ^{ns}	1.9
trees within sites	9	20.9 ^{***}	36.0
galls within trees	120	2.6	62.1
<i>1989</i>			
sites	2	32.0 ^{ns}	7.5
trees within sites	15	15.4 ^{***}	32.3
galls within trees	174	2.2	60.2

*** $p < 0.001$; ns, not significant.

varied among years and sites, and also among trees within sites, and ranged from 10% to 50% (up to 95% on one tree).

Complete Life Cycle within the Fundatrix Galls

In some of the fundatrix galls, some F2 larvae matured and reproduction continued to F3 and F4. "Complete life cycle" (=CLC) galls were darker, 25% larger and became harder than normal galls during the summer. CLC galls were found at all sites, and comprised between 3-24% of the fundatrix galls. In 1989, tree no. 1 in GB with 24% CLC galls was studied in detail. F3, F4 production and alate migration occurred at the same time in CLC and final galls, but CLC galls had smaller mean clone sizes than final galls: 12.8 and 32.8, respectively ($t=4.6$, $df=19$, $P<0.01$, data were square-root transformed before analysis). The CLC galls indicate that the fundatrix galls, referred to in the literature as "temporary galls" (see Wertheim, 1954, citing older authors) are in fact not always temporary.

DISCUSSION

Gall Initiation and Density

Whitham (1978, 1980) and Zucker (1982) suggested that fundatrices of *Pemphigus betae* choose an optimal spot for gall formation, and that they use the concentration of phenolic compounds as a measure of leaf suitability. Other gall forming insects select leaves or leaf nodes (generally the largest ones) for gall formation (e.g., Fritz and Price, 1988). Mouthpart penetration without feeding were observed in free living aphids (McLean and Kinsey, 1964; Nault and Styer, 1972), and interpreted as indicating substrate inspection. In *S. betae* we have no evidence that site selection by fundatrices involves a search for optimal leaf quality.

Whitham (1978) considered that a "census of aborted and successful galls (in *Pemphigus betae*) accurately reflects the number of stem mothers that survived dispersal from tree trunks to developing leaf buds" (p.1167). In *S. betae*, the red scars may not be equivalent to Whitham's aborted galls. Scars are found on the leaflet blade and not on the midrib, where galls are formed. This may suggest that the red scars simply indicate misses. The first instar fundatrix may find it technically difficult to locate the midrib of the primordial leaflet in the bud. Furthermore, during the initiation of the final galls which takes place when the leaves are completely unfolded, no scars are found.

Moran and Whitham (1988) showed that in *Pemphigus betae*, gall density is affected by the availability of sexuales, which develop on the secondary hosts. This, in turn, is affected by environmental conditions, in particular, rainfall. We do not have comparable data for *S. betae*.

Density of final galls, as well as the fundatrix galls, in 1989 was lower than in 1988 at both localities. In 1990, gall density was even lower than in 1989. However, only

long-term studies (e.g., Wool, 1990) can tell whether the observed fluctuations are random or periodic, and whether they are correlated with some environmental factor.

Final gall distribution on shoots within trees was not random. Non random infestation of shoots was also found in *Aploneura lentisci* (Wool and Manheim, 1986). Differences in gall density among shoots, however, do not necessarily imply differences in shoot quality: ecological factors such as the timing of leaf emergence and aphid attack could lead to the same result.

Reproductive success. It is reassuring that reproductive success at the garden sites (TA and AK) were similar to natural, unattended sites, so that we can regard our study as that of natural populations. The among-tree, within-site variance component shows that the growth conditions of the host tree may be an important regulator of clone size (see also Wool and Manheim, 1988). Variation among galls on the same tree may have a genetic component—fecundity variation among fundatrices—as well as micro-environmental and/or genetic differences among shoots of the host tree (Whitham, 1980; Lamarck, 1809).

Life Cycle complexity

Aphid life cycles are among the most complex in the insect world. The alternation of hosts, the occurrence of sexual and parthenogenetic reproduction, and the presence of anholocyclic populations where the primary host is absent, prompted Mordwilko (1924, 1928) to speculate on the evolution of these cycles. For a modern review of the subject see Moran (1988, 1989). (A different unique case of an evolutionary change in the life cycle of a galling aphid is described by Akimoto (1988, 1989): *Eriosoma yangi*, an obligatory parasitic aphid in the leaf roll pseudogalls on Japanese elm, probably evolved from a founder population which migrated from Chinese elm. On the latter host, *Eriosoma* races still form their own galls, but facultatively invade other *Eriosoma* galls (Akimoto, 1988)). In most aphids only one life-history stage—the fundatrix—evolved to maintain tight relationships with the host plant, and can form galls (Moran, 1988). (Many free-living aphids modify the plant tissues by causing leaf rolls and other deformations, which are sometimes referred to as pseudogalls or galls, but do not form true galls).

Smythurodes betae is one of a small group of gall-forming aphids which produce two types of galls on the same host, within a few weeks of each other. In the life cycle of *S. betae* there are thus two colonization events (the fundatrices attack the buds, and F₂ attack the unfolding leaves on the growing shoot), and two dispersal events: F₂ aptera disperse away from the fundatrix galls, and F₄ alates disperse to the secondary hosts (Fig. 1). Apart from *S. betae*, species which are known to produce 2 galls are three species of *Forda* on *Pistacia* (Wertheim, 1954; Bodenheimer and Swirski, 1957), two *Pemphigus* species in South East Asia (Aoki, 1975) and two species of *Thecabius* in North America (Maxson and Knowlton, 1929; Harper, 1959; Palmer, 1952) on

species of *Populus*. We suggest that the primitive life cycle of these species involved a single (fundatrix) gall. F2 aphids acquired the ability to form galls only later in their evolution. (The occurrence of this phenomenon on two different host plant families in different parts of the world may indicate that it evolved independently at least twice). Three facts support this suggestion: First, that in most Pemphigidae, only the fundatrix forms the gall. Second, the entire life cycle of *S. betae* on *Pistacia atlantica* can still be completed in some fundatrix galls (see section on CLC galls). Third, the fundatrix galls of the five different species of Fordini are morphologically similar, but the final galls of these species are very different in structure and morphology (photographs in Koach and Wool, 1977).

What could have been the advantages of making the life history strategy more complex? to answer this question we need to compare *S. betae* with a closely-related species that has a one-gall strategy. This comparison is difficult to make because Fordinae galls are very different in shapes and sizes, and quantitative data on life-history parameters are lacking. There is no comparable species among the Fordini, but we have ecological data on *Aploneura lentisci* (Pass.), which occurs in similar habitats and coexists with *S. betae* in TA, AK and GB (Wool and Manheim, 1986, 1988). Although its host, *P. lentiscus*, is not deciduous, the gall stage in the life cycle of *A. lentisci* begins and ends at the same time as in *S. betae*. This is perhaps dictated by the need to colonize new leaves which appear on both hosts only in the spring, and to find annual secondary hosts to continue the cycle in the winter: these are unavailable in the summer in Israel and only appear after the first winter rains.

We now look for possible advantages in reproductive output between the two strategies. In *A. lentisci*, average clone sizes per gall may be higher than 250 and galls with more than 500 aphids were recorded (Wool and Manheim, 1986). Clone sizes depend among other factors on the physiological conditions of the tree (Wool and Manheim, 1988). In *S. betae* (present study) the average output from a single final gall was about 40, but a gall-for-gall comparison is unjustified: we should take into account the fact that each *S. betae* fundatrix produces, on average, 5 to 9 final galls (and may produce 20 if enough leaves are available for galling). So each fundatrix produces 200-400 offspring by the season's end. There seems to be no advantage in the two-gall system when total reproductive output of the two extant species is compared. Nonetheless, in comparison with a CLC gall (if that was the primitive strategy), the ability to produce final galls must have been a major advantage.

However, there is a further advantage to the two-gall system in terms of clone survival. Once the gall is formed, the gall former cannot change its location to escape deteriorating conditions, predation or parasitism. Many insect galls are destroyed by predators and parasites (Price, Fernandes and Waring, 1987; Hawkins, 1988; Cornell, 1990). Differences in plant quality among buds and shoots (Whitham, 1980) may affect gall survival. A tendency of premature abscission of galled *populus* leaves was observed in a study of *Pemphigus betae* (Williams and Whitham, 1986; see also Stiling

and Simberloff, 1989). Our observations on the Fordinae indicate also that many galls are lost every year: depending on year and site, 10–50% of final galls of *S. betae* may on average be lost before alate dispersal. Parasitoids (*Monoctonia pistaciaecola* Stary) take 23% of fundatrix galls, but after subdivision, less than 2% of the much more numerous final galls are parasitized (Burstein and Wool, 1991; Wool and Burstein, 1991). Among the known sources of final-gall destruction in *S. betae* and other Fordini, predacious larvae of Lepidoptera (Pyralidae) and Diptera (Chamaemyiidae) are prominent (Wool, 1984; Wool and Manheim, 1988; Wool, Burstein and Shenkar, unpubl.).

Due to the parthenogenetic reproduction in the galls, the genotype of the fundatrix is reproduced intact in her F₂ offspring. The partitioning of the clone into 5–20 subclones, dispersing away from the original site and subverting more of the plant resources for their separate maintenance, reduces considerably the probability of accidental destruction of the fundatrix genotype by environmental factors, predation and parasitism. Similarly, Setzer (1980) suggested that intergall migration of F₂ in *P. betae*—which makes one gall per life cycle—is an evolved response which increases fitness.

In the invading behavior of *Eriosoma* aphids described by Akimoto (1988, 1989) this explanation is less likely, since invaders suffer a great decrease in fitness (Akimoto, 1989). But the invaders are F₁ fundatrices; therefore each represents a different genotype, unlike Setzer's (1980) *Pemphigus* and our *S. betae*.

Spreading the risk by clone subdivision may have been the main advantage in the evolution of the extra complexity in the already complex life history of the Fordini.

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