

# Gall aphids do not select optimal galling sites (*Smynthuroides betae*; Pemphigidae)

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**Abstract.** 1. In studies of insect–host plant interaction it is often suggested that insects preferentially colonize host plants (or sites within plants) on which their fitness is maximized (a positive covariance of preference and performance). This suggestion stems from the assumption that natural selection has driven the system toward optimal use of resources.

2. Our study of the galling aphid *Smynthuroides betae* Westw. demonstrates that the distribution of galls on leaves is not due to preference, and can be altered by manipulating the aphid arrival time or the shoot growth rate.

3. We found no correlation between gall density and performance (aphid clone size) at different positions along the shoot.

4. Because leaves on the growing shoot are not equally responsive to aphid stimulation, the colonizers have no choice but to settle on leaves that are at the right stage when they arrive.

5. *S. betae* colonizers did not discriminate between shoots of their host and a congeneric non-host, on which their fitness is invariably zero.

6. Synchronization between galler and host plant phenologies seems to be the key to the observed distribution of galls on the tree. The data give no support to the preference–performance hypothesis.

**Key words.** Gall aphids, galling site selection, preference–performance covariation, aphid–host synchronization, *Smynthuroides betae*.

## Introduction

A positive covariance of host preference and herbivore performance is often assumed, or suggested, in studies of insect–plant interactions. Many examples are available of insect ability to choose among different species of potential host plants (recent examples: Dodge & Price, 1991; Dodge *et al.*, 1990; Ferguson *et al.*, 1991; Leather, 1985, 1986; Via, 1986, 1991), although experimental proof is sometimes equivocal (Singer *et al.*, 1988). Natural selection is assumed to increase preference–performance covariance during coevolution of plants and herbivores (review in Thompson, 1988). Models of habitat selection assume that organisms should select (prefer) the best habitat unless forced to accept suboptimal ones, e.g. by competition (see discussion of Fretwell & Lucas (1970) model in Price, 1984; Ward, 1987). To exercise preference the insects must be able to evaluate the quality of potential hosts.

Active host selection has been demonstrated experimentally in many cases (e.g. Craig *et al.*, 1986, 1988, 1989; Fritz & Nobel, 1989; Leather, 1985; Roininen & Tahvanainen, 1989).

Another, less well documented aspect of host selection is colonization of specific leaves or shoots within hosts. Such discrimination is very important for insects which have but a short mobile stage and do not change location once settled, such as scales (Coccidae), leaf miners, and in particular, for galling insects, since not all plant parts can respond to the insect attack by forming a gall. Within plant site ‘preference’ is often inferred indirectly from differential colonization of shoots or leaves, in particular when insect within-plant distribution is correlated with performance (e.g. Whitham, 1978; Itoika & Inoue, 1991).

Many studies provide information on site preference by leaf miners (e.g. Gracillariidae) (Hespenheide, 1991). In the two most intensively studied moth species, *Lithocalletis quercus* (Auerbach & Simberloff, 1989) and *Cameraria* sp. (Faeth, 1990a, 1991), mines tend to aggregate on large leaves, apparently due to female oviposition

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preference (Bultman & Faeth, 1986), but female discrimination between leaf sizes (and ages) is not perfect, and leaf size (at least in *L. quercus*) explains but a small fraction of the variation in mine density among leaves.

Price (1991) cites a number of examples in support of the 'plant vigor hypothesis', which suggests that herbivores (gallers in particular) preferentially colonize fast-growing parts of the host plants (which consequently are larger at the end of the growth season). Some examples are the galling sawflies *Euura mucronata* (Price *et al.*, 1987b) and *E. lasiolepis* (Craig *et al.*, 1986) on willows; *Phylloxera* on wild grapes (Kimberling *et al.*, 1990), and the cecidomyiid galler *Radobhaga* on *Salix* (Ahman, 1984).

One of the most often cited examples is the galling aphid *Pemphigus betae* on *Populus*. In *P. betae*, galler fitness is maximized on the largest leaves compared with smaller ones on the same shoot (Whitham, 1978, 1980). Zucher (1982) suggested that colonizers selected a galling site even within a single leaf, and their selection was related to a concentration gradient of phenolic compounds, from the base to the tip of the leaf. Rhomberg (1984) challenged Whitham's interpretation of the data, and showed that it is not necessary to invoke preference in order to account for the distribution of galls on the shoot. This challenge remained unanswered and *P. betae* data continue to be cited as an example of positive covariance of preference and performance (Price, 1984; Whitham, 1992).

Wool & Manheim (1988) working with a related gall aphid, *Aphloneura lentisci* (Fordinae, Pemphigidae), argued that high density of galls at particular sites may be unrelated to preference and that, at such sites, gall density in *A. lentisci* is inversely related to performance.

Gall forming aphids are particularly suitable for preference/performance studies because they are often specific to particular species of hosts and colonization sites within hosts (Weis *et al.*, 1988), while colonization is limited to a short 'time window' during leaf expansion. In addition, it is easy to monitor the performance of an individual clone within a closed gall.

We present here observational and experimental data on a galling aphid, *Smynthuroides betae* Westw. (Pemphigidae). Our objective was to study the determinants of intraplant site colonization and their relation to aphid performance.

## Materials and Methods

*The insect.* The aphid *Smynthuroides betae* West. (Homoptera, Pemphigidae) is one of fifteen species of the subfamily Fordinae which induce galls on *Pistacia* trees in Israel (Wertheim, 1954; Bodenheimer & Swirski, 1957; Koach & Wool, 1977). The life cycle of *S. betae* lasts 2 years (Wool, 1984) and is more complex than in other related aphids in that two different galls are sequentially formed on the same host tree, within 2–3 weeks of each other, by each aphid lineage (family) (Wool & Burstein, 1991b). The cycle begins when the fundatrix nymph (F1) emerges in the spring from an overwintering egg in bark crevices on the primary host *P. atlantica* and forms a small, red gall

on the midvein of the leaflet. Three weeks later the F1 mature and commence parthenogenetic reproduction. Each fundatrix may produce about twenty second-generation (F2) offspring. The F2 nymphs disperse and induce their own spindle-shaped, final galls on the leaflet margins. F3 and F4 are produced during the summer in the galls. In autumn clone size in the final gall reaches its peak – on average thirty-five alate aphids per gall (Wool & Burstein, 1991b). Clone size decreases rapidly when the alates disperse from the galls to larviposit near the secondary hosts (Leguminosae, Solanaceae and Graminae). Their offspring penetrate the soil and feed on the roots. In the next spring alate sexuparae are produced, fly back to the primary host and viviparously produce males and females. These mate and produce the overwintering eggs in bark crevices on the trunk and major branches of the tree. The ecology of this aphid and its parasitoids has been described in detail (Wool & Burstein, 1991a, b).

Ideally, we would like to have data on preference and performance of both F1 and F2. However, F1 is much more difficult to manipulate in the field before their galls are induced. Moreover, reproductive success (performance) of an F1 clone depends primarily on the selection of galling sites by F2. The bulk of the experimental work was therefore done with this colonization stage.

*Field observations.* The present study was carried out in the spring and autumn of 1991, at two of the sites where most of our previous work on this species was carried out: Tel Aviv University Botanical Gardens (TAU) and Givat Brener (GB), about 35 km south of Tel Aviv (Wool & Burstein, 1991b). These sites were chosen for reasons of convenience. Both sites have been colonized annually by large populations of *S. betae* (D. Wool, unpublished). We examined intensively two *P. atlantica* trees (nos. 6 and 7) at TAU, which bear many final galls every year (our personal observation), and two trees (nos. 4 and 9) at GB. The latter trees produced very few final (F2) galls in 1988 and 1990, although fundatrix galls were abundant on them every year since 1988. A fifth tree (no. 10) at TAU was used for aphid transfer experiments (see below). Previous observations indicated that tree 10 breaks its buds about 10 days later in the spring than trees 6 and 7. About forty shoots were marked on each tree at TAU, and about twenty on each tree at GB. During the gall initiation stage we monitored the trees twice a week. Each time we measured shoot length, counted the numbers of leaves and of fundatrix and final galls, and noted gall positions on the shoot (the oldest leaf near the base of each shoot was numbered 1).

As a measure of aphid preference we used the density of final galls at each leaf position (as in Whitham, 1978). *Pistacia* leaves are compound: the number of leaflets per leaf varies (from three to twelve). *S. betae* normally forms no more than two galls per leaflet (Wool & Burstein, 1991b). Mean gall density per leaflet is therefore a measure of occupancy of galling sites.

In October, when clone size in the galls was at its peak, galls were collected and opened in the laboratory and all aphids were counted. We used gall survival (percentage of

galls with at least one live aphid) and mean clone size as measures of performance at each leaf position.

*Field experiments.* (a) F1 galls were collected from early shoots on trees 6 and 7 at TAU, and held in the laboratory. The emerging F2 aphids were transferred to marked aphid-free shoots on tree 10 (TAU). Shoots with transferred aphids were isolated with tanglefoot to confine the aphids.

(b) During the colonization phase of the trees in 1991, F2 aphids were transferred to marked aphid-free shoots on the source trees (sixteen shoots per tree) and confined to leaves 1–6 at the base of the shoot. Similarly, F2 aphids from TAU were transferred to trees 4 and 9 at GB (fourteen and ten shoots, respectively).

(c) Since pruning causes an extension of shoot growth period in *Pistacia* (Wool & Manheim, 1988; Burstein & Wool, unpubl.), we pruned and marked several branches on tree 9 in GB in December 1990. In 1991 we compared shoot length, number of leaves, and gall distribution on shoots near the pruning site with normal shoots on the same tree.

*Galling-site preference.* It is extremely difficult to test directly for the ability of aphid colonizers to select optimal galling sites, because the quality of a site is evaluated by the insect performance and is unknown to us at settling time. In the literature, variables such as shoot length, leaf size, etc., have been used to estimate leaf quality. These are not necessarily relevant for the colonizing insects (see, for example, Faeth, 1991) (although they are to the human observer). In the absence of measurements of plant quality relevant to the insect, it is impossible to match pairs of suitable leaves or shoots for the aphid to choose from. We therefore used a method based on our knowledge of the *S.betae*–*P.atlantica* interactions. We know, from previous observations (Wool, unpubl.) and transfer experiments (Burstein, unpubl.) at TAU, that *S.betae* F2 can induce final galls on the wrong host, *P.palaestina*. These galls begin to develop, but are aborted at an early stage and no reproduction takes place in them.

Our test for F2 galling site preference was designed as follows. Fresh shoots of *P.atlantica* and *P.palaestina* with young, unfolding leaves, were brought into the laboratory and held in water. Pairs of shoots, one of each host, were matched as near as possible by age and numbers of leaves, intertwined, and held together with strips of masking tape. Small groups (four to ten) of neonate F2 aphids – taken

from F1 galls – were transferred to the tape between the two shoots, and were free to select young leaves of either host for galling. The lower part of both shoots was smeared with tanglefoot to prevent escape. The numbers of galls induced on each host were recorded 48 h later. This would represent an extreme case of discrimination ability.

The null hypothesis was that if F2 do not discriminate between the correct and incorrect host plants species, they probably cannot detect the much smaller differences between adjacent leaves on the same tree.

*Data analysis.* Standard techniques of statistical analysis were used (Sokal & Rohlf, 1981). We calculated correlations between preference and performance variables. Regression analyses were used to test for the relationship between shoot length and final gall density. Since each shoot bore a different number of fundatrix galls (which are the source of F2) we corrected for the differences in fundatrix gall density by using this variable as the covariate in ANCOVA. Nested ANOVA was used to calculate the proportion of variation in clone size among galls on the same leaf, leaves on the same shoot, and shoots on the same tree. Numbers of leaves, numbers of galls and clone size were square-root transformed before analysis.

## Results

Most final galls were formed in early April (Wool & Burstein, 1991b). The increase in final gall numbers coincided with shoot elongation and hence gall density was highly correlated with the number of new leaves available (Fig. 1). The average numbers of fundatrix and final galls per shoot, shoot length (at the end of the growth season) and the numbers of leaves per shoot on the four trees are given in Table 1. GB and TAU were very different in tree growth variables – trees at GB grew less and had fewer leaves per shoot than ones at TAU. At GB, very few final galls were produced on the marked shoots in 1991, although these shoots carried many fundatrix galls (Table 1). (On tree 4, only one marked shoot of twenty carried final galls. This tree is no more genetically aphid-resistant than any other at the site – the densities of final galls in the preceding and subsequent years on this tree were similar to other trees at GB). Therefore, our analysis of clone size and gall survival will be limited to the trees at TAU.

At the end of the growth season, final gall density at

**Table 1.** Average numbers of F1 and F2 galls per shoot, leaves per shoot and average shoot length in mm ( $\pm$  standard errors) on marked shoots on each tree ( $n$  = number of shoots; ranges of variation in parentheses).

	F1 galls	F2 galls	Shoot length	Leaves
TAU tree 6 ( $n = 39$ )	7.48 $\pm$ 0.98	17.15 $\pm$ 2.7	118.88 $\pm$ 15.19 (11.1–366.4)	10.64 $\pm$ 0.51 (6–17)
TAU tree 7 ( $n = 42$ )	4.95 $\pm$ 0.77	20.61 $\pm$ 3.1	198.01 $\pm$ 26.04 (2.9–463.9)	10.95 $\pm$ 0.63 (4–17)
GB tree 4 ( $n = 20$ )	5.42 $\pm$ 0.86	0.65 $\pm$ 0.63	23.86 $\pm$ 3.56 (7.4–66.4)	5.35 $\pm$ 0.22 (4–8)
GB tree 9 ( $n = 19$ )	7.86 $\pm$ 1.30	3.78 $\pm$ 1.25	90.91 $\pm$ 20.15 (5.6–166.4)	7.75 $\pm$ 0.52 (5–10)

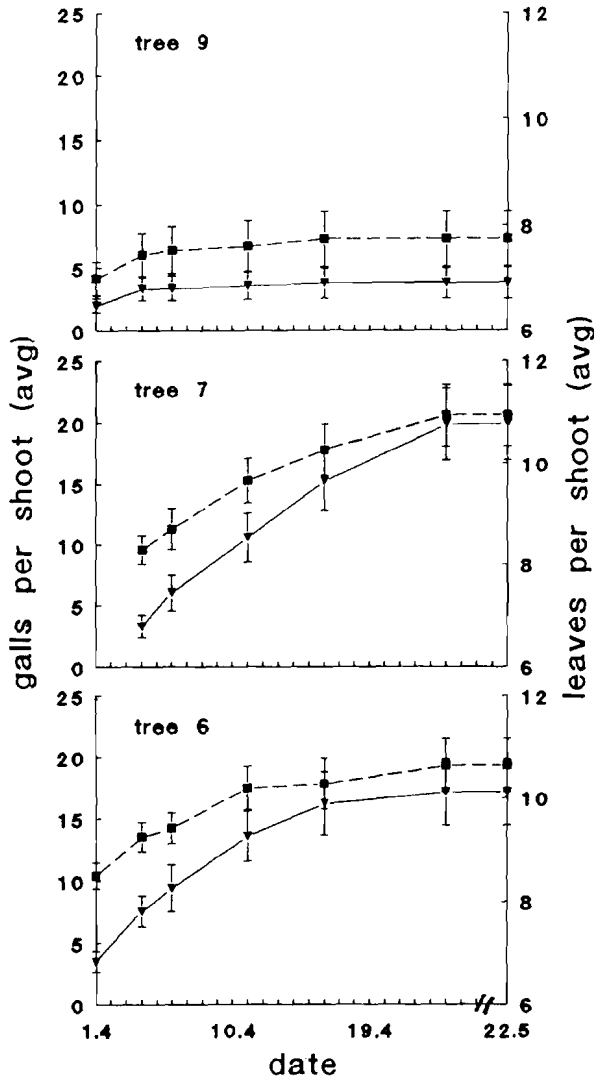


Fig. 1. Cumulative mean numbers of galls (▼) and leaves (■) on the marked shoots at different sampling dates. Correlations between the two variables are: tree 6 (TAU):  $r = 0.99$ ,  $df = 5$ ,  $P < 0.01$ ; tree 7 (TAU):  $r = 0.99$ ,  $df = 4$ ,  $P < 0.01$ ; tree 9 (TAU):  $r = 0.96$ ,  $df = 4$ ,  $P < 0.01$ .

TAU was positively correlated with shoot length and with the number of leaves on the shoot (as expected, the latter two variables were intercorrelated). In contrast, fundatrix gall density was not correlated with shoot length (Table 2).

Possible dependence of final gall density per shoot on the number of fundatrix galls on the same shoot was tested by regression, separately in trees 6 and 7 (slopes were  $b = 0.54$ ,  $SE = 0.25$ ; and  $b = 0.139$ ,  $SE = 0.34$ , respectively). Although the slope for tree 6 (but not for tree 7) was significantly different from zero at the 5% level, both regression lines explained very little of the variation ( $r^2 = 0.10$ ,  $0.004$ , respectively). These results suggest that high fundatrix density does not necessarily translate to high density of final galls (see Discussion).

Table 2. Correlation coefficients of fundatrix and final gall densities with shoot length and the numbers of leaves on trees 6 and 7 (TAU). Correlations of shoot length and number of leaves: tree 6:  $r = 0.943$ ,  $df = 37$ ; tree 7:  $r = 0.922$ ,  $df = 40$ ;  $P < 0.001$  in both cases.

	F1 galls tree 6	F2 galls tree 6	F1 galls tree 7	F2 galls tree 7
Shoot length	0.319 NS $df = 37$	0.741*** $df = 37$	0.061 NS $df = 40$	0.824*** $df = 40$
No. of leaves		0.794*** $df = 37$		0.678*** $df = 40$

#### Gall distribution

The fundatrix galls of *S. betae* were formed on leaves 1–8 on the shoot, while the final galls were formed on the distal leaves 7–17 on both trees (Fig. 2). (Some final galls were found on lower leaves which developed from lateral buds several days later than the apical buds). This distribution may create the impression that F2 preferentially colonize distal leaves, and that the most desirable leaves (indicated by the highest density) are leaves 11–13. We show below that this is not necessarily so.

#### Performance and preference

Nested ANOVA on aphid clone size (a measure of performance) showed that variation among galls within leaves contributed 40–60% of the variation (Table 3). A significant variance component was added by variation among leaves at different positions on the shoot (about 30%). The among-shoot variance component was not significant (Table 3). Therefore, in the following analysis of performance variables we combined all shoots for each tree.

Figs 3(a) and 3(b) show the relationship between final

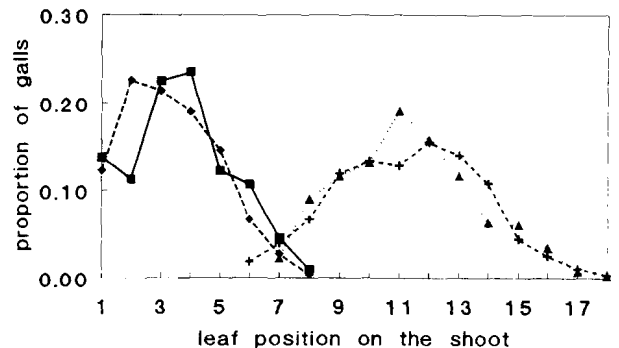
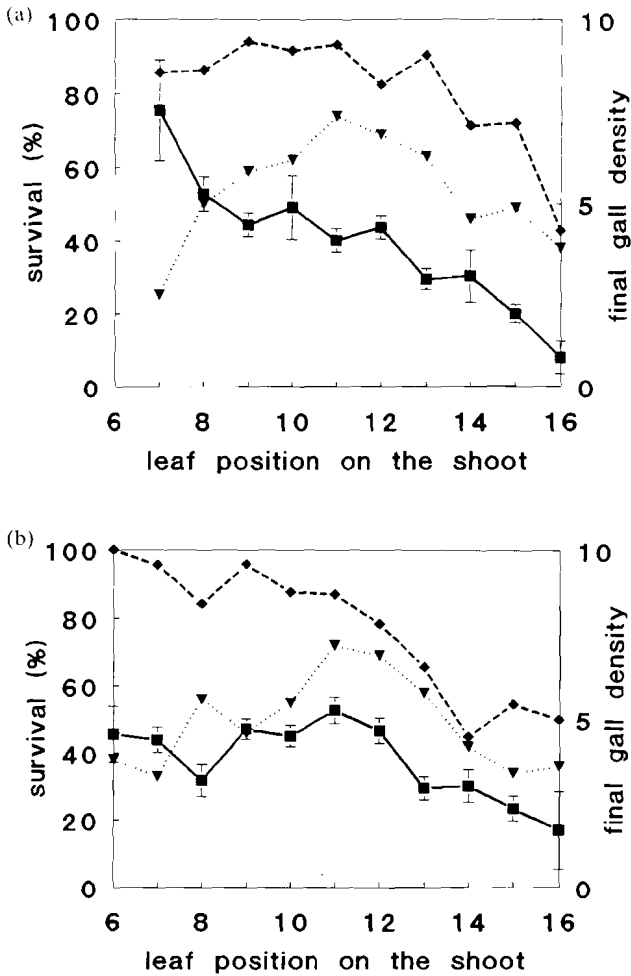


Fig. 2. Fundatrix and final gall distribution at different leaf positions on the shoots. ■, F1 gall, tree 7; +, F2 gall, tree 7; ◆, F1 gall, tree 6; ▲, F2 gall, tree 6. Pooled data of all marked shoots on tree 6: 195 fundatrix galls and 658 final galls on tree 6; 195 fundatrix galls and 783 final galls on tree 7).



**Fig. 3.** Final gall density ('preference') (▼, galls/shoot) and performance variables (clone size, ■ and gall survival, ◆) at different leaf positions on the shoot on tree 6 (Fig. 3a) and tree 7 (Fig. 3b) at TAU.

gall density ('preference') and gall survival and clone size = reproductive success (performance) at different leaf positions along the shoot for trees 6 and 7. The relationships between the variables were not identical on the two trees, but they showed a similar trend. On both trees gall survival and clone size decreased with increasing leaf

position: performance was lower on the more distal leaves. Final gall density (preference) on the other hand, showed a symmetrical distribution with a peak at leaves 11–13 (Fig. 3a, b). Correlations between preference and performance variables were low and nonsignificant. (Density with clone size:  $r = 0.13$ ,  $df = 8$  and  $r = 0.47$ ,  $df = 9$  on trees 6 and 7, respectively. Density with survival:  $r = 0.53$ ,  $df = 8$  and  $r = 0.20$ ,  $df = 9$ , respectively,  $P > 0.05$  in all cases.)

Clone size was independent of gall density per leaf at all leaf positions but one (tree 7, leaf 12) (Table 4). Although the number of degrees of freedom for each position is small due to the narrow range of gall densities, there was no indication that the aphids suffer reduced fitness at the observed densities.

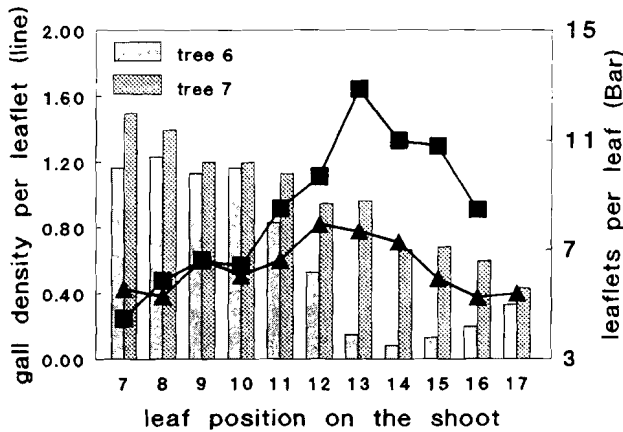
Gall density per leaflet is a measure of the degree of occupancy of galling sites on the leaves. Even on the most crowded leaves (nos. 11–13) not all the galling sites were occupied by F2 aphids: on average about half of the sites remained free (Fig. 4). Gall density per leaflet was strongly skewed to the left, with the highest densities on the distal leavae of the shoot. This is, at least in part, due to the fact that the most distal leaves were often composed of fewer leaflets (Fig. 4).

**Table 4.** Regression statistics of average clone size in final galls on gall density per leaf, at different positions along the shoot, on trees 6 and 7 at TAU.

Position	<i>b</i>	SE	df	<i>r</i> <sup>2</sup>	<i>P</i>
Tree 6					
8	-1.47	1.47	3	0.24	>0.05
9	-8.12	3.65	2	0.71	>0.05
10	1.24	2.83	3	0.06	>0.05
11	-0.73	1.48	3	0.07	>0.05
12	0.40	0.17	3	0.62	>0.05
13	0.14	0.59	2	0.03	>0.05
14	0.03	0.08	2	0.05	>0.05
15	0.08	0.28	2	0.04	>0.05
Tree 7					
8	-7.02	7.14	2	0.32	>0.05
9	-2.92	3.00	5	0.15	>0.05
10	1.45	2.53	5	0.06	>0.05
11	7.42	1.90	3	0.83	>0.05
12	4.67	0.90	5	0.84	<0.001
13	5.03	3.01	3	0.49	>0.05

**Table 3.** Nested analysis of variance of clone size at TAU.

Source of variation	SS	DF	MS	F	Variance component (%)
Tree 6					
Among shoots	267.48	22	12.15	1.64 NS	10.60
Among leaves	235.94	32	7.37	3.1***	29.88
Within leaves	441.82	186	2.37		59.49
Tree 7					
Among shoots	323.63	20	16.18	2.62 NS	27.02
Among leaves	203.25	33	6.10	3.9***	31.69
Within leaves	242.88	154	1.57		41.27

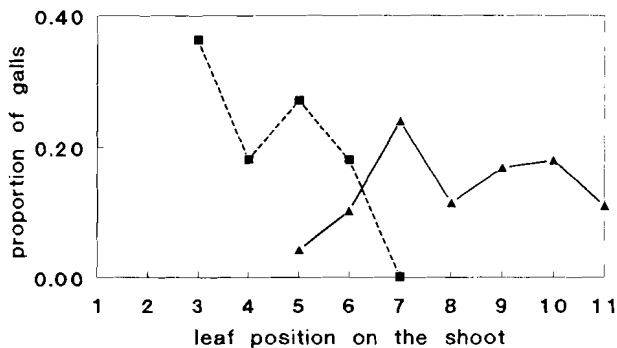


**Fig. 4.** Average final gall density per leaflet at different leaf positions (■, tree 6; ▲, tree 7). The maximum number of final galls per leaflet is normally two. The number of leaflets per leaf (bars) decreases towards the tip of the shoot. The space below the lines indicates occupied galling sites. (The total number of galls at each leaf position was divided by the average number of leaves times the average number of leaflets at each position.)

#### Colonization experiments

F2 aphids from trees 6 and 7 were transferred to isolated shoots on the late-budding tree 10 about 10 days before the native F2 aphids were born. These aphids successfully colonized the lower leaves (nos. 3–6) of the shoots (positions which are normally colonized by F1) and produced final galls there (Fig. 5). In contrast, F2 which were confined to the lower leaves at their normal colonization time (thirty-two shoots at TAU and twenty-four at GB) were unsuccessful: although we have seen them crawling around on the shoots, not a single final gall was formed on the lower leaves.

Trees at GB carried much smaller numbers of F2 galls than trees at TAU, although the numbers of fundatrices (F1) were similar (Table 1). To eliminate the possibility that F2 aphids from GB and TAU are different in colon-



**Fig. 5.** Location of final galls induced by transferred aphids (■) on tree 10 (TAU) 10 days before local aphid infestation (▲).

ization success, we reciprocally transferred F2 aphids between GB and TAU. None of TAU aphids transferred to GB succeeded in gall formation on tree 4, and only four of twenty-five induced galls on tree 9. By contrast, twenty-two of twenty-eight aphids from GB tree 9 succeeded in forming galls on tree 10 at TAU, as did eight of ten local aphids transferred from tree 6 to tree 10 as control ( $\chi^2 = 0.059$ ,  $df = 1$  NS). Thus, colonization success of F2 from GB and TAU seems to be the same, and does not explain the difference in F2 gall density between TAU and GB.

#### Pruning

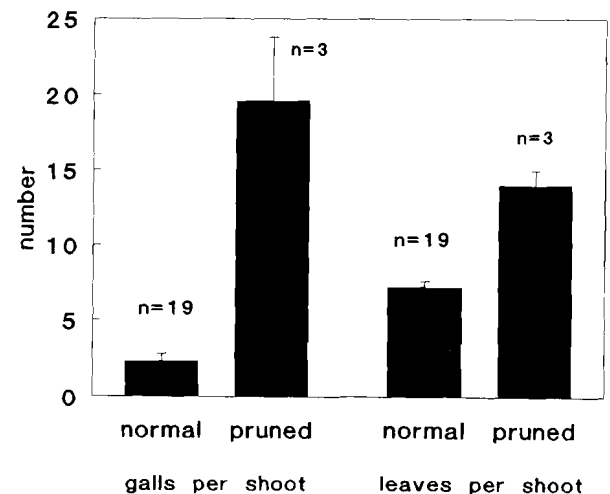
Ten pruning cuts were made on tree 9 in 1990, but only three shoots grew there in the spring of 1991. Shoots that grew near the pruning cuts were more than 3 times longer (mean length = 355 mm,  $SE = 32.04$ ,  $n = 3$ ) than normal shoots on that tree (data in Table 1) ( $t = 4.92$ ,  $df = 20$ ,  $P < 0.01$ ), and bore more leaves than normal shoots (Fig. 6;  $t = 5.83$ ,  $df = 20$ ,  $P < 0.001$ ). They also carried more final galls per shoot ( $t = 7.81$ ,  $df = 23$ ,  $P < 0.001$ ) (Fig. 7).

Fundatrix gall distributions on normal and pruned shoots on tree 9 were the same (Fig. 7). In contrast, final galls on pruned shoots were located on more distal leaves than on normal shoots (nos. 8–13). No leaves beyond no. 10 occurred on normal shoots at GB, while pruned shoots grew longer and carried more leaves (Fig. 7).

#### Galling-site preference experiments

Forty-three of sixty-eight F2 aphids induced galls on the experimental shoots (in eleven trials). The twenty-five which did not either dropped off the plants or died.

Twenty-four of the galls were induced on the true host, *P. atlantica*. Nineteen were induced on the wrong host,



**Fig. 6.** Mean numbers of leaves per shoot (right) and final galls per shoot (left) on normal and pruned shoots on tree 9.

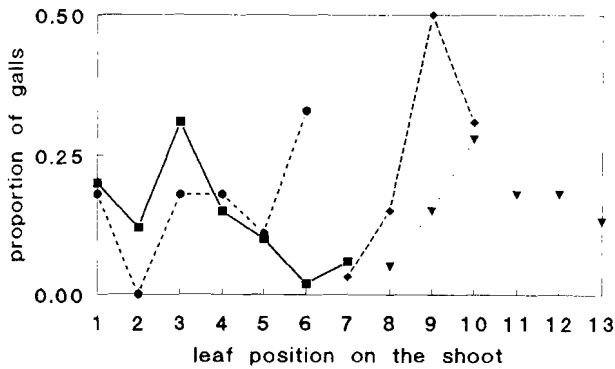


Fig. 7. F1 and F2 gall distributions on shoots on tree 9 (GB). Data are from normal shoots (■, F1; ◆, F2) and from shoots that grew after pruning (●, F1; ▼, F2).

*P. palaestina*. These results are not significantly different from 1 : 1 ( $\chi^2 = 0.58$ ;  $P > 0.05$ ). We are unable to reject our null-hypothesis that F2 aphids cannot discriminate host from non-host tissues (and therefore probably cannot detect more subtle differences between different shoots or leaves of the same host).

## Discussion

The ways and means by which insects recognize and select their host plants are central to many ecological, physiological and behavioural studies of insects. Within this framework, the question of whether or not females select plants (or sites within plants) which are best for the survival and reproduction of their offspring has been controversial.

In their review of host-selection models, entitled 'Mother doesn't know best', Courtney & Kibota (1990) summarily dismiss the possibility of choice by ovipositing females, of hosts most suitable for their offspring: a most important condition in their model is that female preference is independent of offspring performance. Quite the opposite attitude, however, can be found in other studies of insect-plant coevolution (e.g. Thompson, 1988; Via, 1986; Singer *et al.*, 1988; Roininen & Tahvanainen, 1989). The strongest expression of the belief that 'mother knows best' may be found in Whitham (1992, p. 233): 'Organisms that face variable environments should become evolutionarily adapted to discriminate between the mosaic patterns of variation and selectively settle where their reproductive success or fitness is highest. The decision whether to settle should be based on the fitness to be expected in a given habitat.'

The reasons for the different attitudes of Courtney & Kibota (1990) and Whitham (1992) to this question may stem from the differences in biology of the insects from which the evidence was collected. The former authors used mainly data from the Lepidoptera (at least fifty-five of 172 references in their review) and fruit flies (about thirty additional references) and consequently considered cases of selection among host plant species. Whitham's

work concerned aphids, and selection not merely within host species but between sites on the same individual tree or shoot.

Because our own work concerns a related gall-forming aphid, our experiments are important for testing this possibility.

Whitham (1978, 1980) observed that (a) many fundatrices of *P. betae* settle and form galls on the largest leaves on the shoot (at an early stage of shoot growth), (b) that galls formed on large leaves contain more aphids than do galls on smaller leaves, (c) that fundatrices tend to settle at the base of the leaf blade and to defend the site against intruders, and (d) that galls formed at these sites contain more aphids than do galls located away from the leaf base.

Facts (a) and (b) were interpreted to indicate selection of optimal leaves, and (c) and (d) were interpreted as indicating optimal site selection within leaves. Due to the detailed studies of the biology and ecology of *P. betae* on its host by Whitham and his associates, this system became known as one of the best examples of positive covariance of preference and performance and is widely cited as such (e.g. Price, 1984).

Our results with the gall aphid *S. betae* are in line with the title of Courtney & Kibota's review. We failed to detect a significant correlation between final gall density per leaf ('preference') and reproductive success ('performance').

In the Pemphigidae each gall is founded by a single fundatrix, and the number of her offspring in the gall (clone size) truly reflects its performance. We came to the conclusion that the interpretation of gall density as a measure of preference is incorrect, at least in the case of *S. betae* on *Pistacia* (see also Rhomberg, 1984). Our galling site preference experiments demonstrate that F2 colonizers do not show preference for their true host when matched with the (congeneric) unsuitable host on which their fitness is invariably zero. This experiment has been criticized as irrelevant, because, like the galling stages in other gall-forming aphids, the fundatrices of *S. betae* (both F1 and F2) do not face a choice between hosts in nature. They are born on the host selected a year before by another life-history stage, the sexupara, and must either make a gall there or die. However, we consider this experiment as both relevant and important, a test of the discriminatory ability of the F2 nymphs in search of a galling site. Their inability to choose between host and non-host makes it very unlikely that they can detect differences in quality between two leaves of the same host.

The life cycles of *P. betae* and *Populus* and *S. betae* on *Pistacia* differ in some important details. One relevant difference is that the latter species forms two types of galls within 3 weeks of each other (Wool & Burstein, 1991b). The colonization stage of *Pemphigus* involves fundatrices hatching from overwintering eggs. Most of them infest the shoots within 3 days (Whitham, 1978, 1980). This stage is equivalent to the *fundatrix* gall stage in *S. betae* which is likewise very short, and coincides with the early leaf flush of *P. atlantica*. The short infestation period species makes it difficult to discern any temporal pattern, and therefore all leaves may seem to be simultaneously available. Differ-

ences in gall density among leaves could be interpreted as reflecting active preference. The limited data we have on this stage (Table 1, and Wool & Burstein, unpubl.) show that the F1 density on different trees was independent of their reproductive success (= the density of F2 galls) later in the season.

Whether or not the aphids have a choice when they arrive at a shoot and actively show preference for an optimal leaf can be evaluated by choice experiments only if different usable leaves are simultaneously available. This is hardly the case in rapidly elongating shoots, because new leaves are available for a rather short time (1–2 days), while lower leaves mature and lose their ability to respond to aphid probing. Leaves that cannot respond to the aphid stimulation are not available as galling sites.

Final galls of *S. betae* are not formed on leaves 1–6, because these leaves are already too old at the time that the first F2 arrive. These same leaves responded by forming galls when F2 aphids were artificially introduced to them 10 days earlier (Fig. 5). Leaf position on the shoot provides a time scale, since more distal leaves are necessarily younger than proximal ones. Leaf position (age) affects insect distribution especially in gall formers that exclusively exploit immature plant organs (Mani, 1964; Weis *et al.*, 1988). Differences in fitness between galls at different positions were observed in *Pemphigus populicaulis*; the gall distribution was shown to result from differences in arrival time of the fundatrices (Faith, 1979).

Shoots which grow faster, or for a longer time, carry more leaves and more galls than shorter shoots. This is in accord with the 'plant vigor hypothesis' (Price, 1991). The low density of final galls in GB (Table 1) is also explained by the plant vigour hypothesis: shoots on GB trees (especially tree 4) bore very few leaves in 1991. When we removed the limiting factor, and induced further shoot growth by pruning tree 9, the numbers of final galls per shoot increased significantly (Fig. 6). Natural factors such as massive grazing by mammals can cause similar effects (Danell & Huss-Danell, 1985).

If site selection is based on 'fitness to be expected in a given habitat', then gall density should be positively correlated with clone size. We find no significant correlation between the two variables. The highest F2 gall density was found on leaves 11–13 and decreased almost monotonically on lower and higher leaves (Fig. 3a, b). However, clone size and survival, our measures of performance, were equally high (or higher) at lower positions on the shoot (Fig. 3a, b) and only declined towards the tip. It could be claimed that the colonizers go to suboptimal leaves when all the better sites are occupied [as suggested by Fretwell & Lucas' model (1970) and Whitham (1980)]. However, our data show that many sites on the 'superior' leaves remained unoccupied. Later-arriving colonizers, which cannot occupy the free sites on lower leaves (those are already too old), either congregate near the tip (if young leaves are still available), or die (Burstein & Wool, unpubl.).

Clone size was independent of gall density at each position (Table 4). Therefore, no support for intraspecific exploitative competition is suggested by the data. The

differences in performance among leaf positions are not due to competitive interactions.

As we stated above, leaf position provides a time dimension for aphid colonization. Rhombert (1984) suggested that the availability of susceptible leaves at the right time, and not leaf selection, could determine the distribution of *Pemphigus populicaulis* galls on *Populus deltoides*. Independently of our work, Akimoto & Yamaguchi (unpublished) arrived at conclusions similar to ours with the galling aphid *Tetraneura* sp. on *Ulmus* in Japan. The timing of insect and host phenology in determination of herbivore distribution seems very important for aphids (e.g. Dixon, 1976), and also in Lepidopterous herbivores (Feeny, 1970, 1976; Mitter *et al.*, 1979). Hunter (1990, 1992) emphasized the importance of the bud burst phenology of the host tree in the population dynamics of oak-feeding Lepidoptera.

Whitham (1978) found that leaf size of *P. betae* strongly affected aphid performance. This seems to be true in *S. betae* as well. The number of leaflets per leaf is a good estimate of leaf size. In *Pistacia* distal (late) leaves are composed of fewer leaflets (Fig. 4). We found that the number of leaflets per leaf was positively correlated with clone size (tree 6:  $r = 0.8$ ,  $df = 8$ ,  $P < 0.01$ , tree 7:  $r = 0.75$ ,  $df = 9$ ,  $P < 0.01$ ).

It is unclear what variables determine the quality of a leaf for the aphids, and whether large leaves differ from smaller ones in these variables. Zucker (1982) claimed that *P. betae* selects sites with low concentration of phenolic compounds within a leaf. Larson & Whitham (1991) argued that nutrition and availability of assimilants (sink–source relationship) is the main factor which affects preference (and performance). Hartnett & Bazzaz (1984) showed that leaves with a higher rate of photosynthesis at the time of colonization may not be optimal leaves for the aphids in the long run. In *Cameraria* sp. (a leaf miner), an intensive study revealed that density was unrelated to phytochemical variables measured in the leaves (Faith, 1990a, 1991). Thus, there seems to be no reason to assume that females select high quality ('best') leaves for oviposition.

We believe that aphid colonizers do not search for optimal sites at all at the time of site 'selection'. Success of F2 in formation of final galls is in many ways unpredictable: the number of suitable leaves, their distance from the source (F1 gall), and the number of conspecific aphids competing for galling sites cannot be predicted. In such circumstances, aphid 'optimal' behaviour should be to form galls on the first usable leaf they can find and not search for the best one. We further suggest that within-host leaf (site) colonization strategy of gall formers, which can use only a small fraction of the host plant, should emphasize synchronization with the host and not preference and evaluation of leaf chemical or nutritional quality. (Incidentally, colonization at different times may affect not only fitness variables but also the shape of the gall, as demonstrated by Faith (1979) in *Pemphigus populitransversus*.) If the time of aphid emergence, maturation and reproductive rate are under genetic control, stabilizing selection should have operated on these variables towards synchronization



with the host plant because insects arriving too early or too late do not find a galling site. There seems to be no published evidence on the heritability of any of the fitness traits in gall aphids. The fact that we do not find total synchrony between aphid and tree phenology (see also Dixon, 1976) may suggest that genetic variation plays a minor part in determination of timing. One important reason may be that bud-burst phenology varies among trees and among years (Hunter, 1990).

The ability of insects, including aphids, to discriminate between different host plant taxa has been often documented (e.g. Thompson, 1988; Leather, 1986). Differences among leaves on the same shoot, however, must be much more difficult to detect (except perhaps between a young and an old leaf) and, as our data show, it is not necessary to invoke active selection to explain gall distribution patterns within a host tree.

In ecological studies of site selection by insects within host plants, *performance* variables are readily measurable (e.g. survival and clone size within galls). This is not so with *preference*. It is difficult to be certain that the insect has a choice and that a real decision is made to prefer certain sites. Inferring preference from density data may not be valid because, as we show in the present work, aggregation at certain sites may be caused by external factors, such as the availability of colonizable sites on the host plant and the presence of colonizers at the right time, involving no preference at all.

We believe that the hypothesis of a positive covariance between preference and performance should be regarded as the *alternative* hypothesis in the statistical sense. The null hypothesis should be that the two variables are unrelated. Only when all other explanations are rejected, should the alternative hypothesis be accepted. The hypothesis of positive covariance between preference and performance is too important for evolutionary ecology to be accepted on faith.

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