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Colonization of ecological islands: Galling aphid populations (Sternorrhyncha: Aphidoidea: Pemphigidae) on recovering *Pistacia* trees after destruction by fire

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Abstract. *Pistacia palaestina* (Anacardiaceae) is a common tree in the natural forest of Mt. Carmel, Israel, and the primary host of five common species of gall-forming aphids (Sternorrhyncha: Aphidoidea: Pemphigidae: Fordinae).

After a forest fire, resprouting *P. palaestina* trees, which are colonized by migrants from outside the burned area, become "ecological islands" for host-specific herbivores.

A portion of the Carmel National Park was destroyed by fire in September of 1989. The same winter, thirty-nine resprouting trees that formed green islands in the otherwise barren environment were identified and marked. Tree growth was extraordinarily vigorous during the first year after the fire, but shoot elongation declined markedly in subsequent years. Recolonization of the 39 "islands" by the Fordinae was studied for six consecutive years. Although the life cycle of the aphids and the deciduous phenology of the tree dictate that the "islands" must be newly recolonized every year, the results of this study show that trees are persistently occupied once colonized. This is probably due to establishment of aphid colonies on the roots of secondary hosts near each tree following the first successful production of a gall.

Differences in colonization success of different species could be related to both the abundance of different aphid species in the unburned forest and the biological characteristics of each aphid species.

INTRODUCTION

The effects of fire on natural and planted forests has been the subject of numerous publications and books (e.g., Koslowski & Ahlgren, 1974; Walstad et al., 1990; Moreno & Oechel, 1994). Many of these studies examined the question of whether fires are destructive or beneficial to the ecosystem as a whole, and how prescribed burning can be used to maintain ecosystem diversity. Many authors agree that fire is a natural component of the ecosystem, particularly in Mediterranean forests (e.g., Moreno & Oechel, 1994), although most, if not all, fires in the region are the result of human activities.

When a natural forest is burned, the insect fauna associated with it can be destroyed. Insects which live on plants can be killed even by a brief flash fire. Those that live inside plant tissues or in protected enclosures such as galls may endure longer exposures, but will succumb to longer-burning fire. Depending on the surface temperature, subterranean organisms can also be killed. Surviving organisms starve to death after destruction of their food plants.

Fires can create patchy habitats where plant communities can differ from those of unburned sites. Some plant species ("resprouters") respond to fire by growing new and vigorous shoots. In the USA, the cynipid wasp, *Xanthoteras politum*, frequently colonizes

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burn sites in huge numbers, although the location and extent of vegetated patches are probably, for the most part, unpredictable (Washburn & Cornell, 1981).

Several tree species in Mediterranean forests are "resprouters". Insect fauna associated with these plants can only be reestablished by immigration from surrounding unburned areas. Host-specific herbivores are particularly susceptible to decimation by fire and are, perhaps, the most difficult populations to reestablish. Thus, recovering host trees become "ecological islands" that are scattered in an inhospitable area that the immigrants must traverse.

On Mt. Carmel, Israel, the natural vegetation is predominantly typical Mediterranean forest. The dominant species are evergreen oak, *Quercus calliprinos*, and two species of *Pistacia* (Anacardiaceae): *P. lentiscus* (evergreen) and *P. palaestina* (deciduous). A variety of bushes are characteristic of this forest: *Crataegus azarolus* (Rosaceae), *Phillyrea media* (Oleaceae), *Rhamnus palaestina* (Rhamnaceae), *Calycotome villosa* (Papilionaceae), *Poterium spinosum* (Rosaceae), and two species of *Cistus* (Cistaceae): *C. salvifolius* and *C. villosus*. Some stands of *Pinus halepensis* occur naturally, but large areas have been planted with pine trees over the last 70 years to provide shade and recreation. Part of the area, the Carmel National Park, is a public recreation park.

In the long, hot, dry Israeli summer (no rain usually falls between May and October), annual vegetation dries up and provides ample fuel for occasional fires. In September of 1989, fire destroyed a large portion of the Carmel National Park. All above-ground vegetation was completely burned and only charred stumps of dead pines were left standing (Neeman et al., 1995).

Pistacia trees on Mt. Carmel are primary hosts for "guilds" of specialist, host-specific, gall-forming aphids (Pemphigidae: Fordinae) (Koach & Wool, 1977; Wool, 1984, 1996). *P. lentiscus*, a common shrub species, is host to only one gall-forming species, the ecology of which was studied in detail by Wool & Manheim (1986, 1988). *P. palaestina* hosts galls of the following five common species: *Baizongia pistaciae* (L.) (Wool, 1990), *Geoica wertheimae* Brown & Blackman (referred to as *G. utricularia* in previous work, e.g., Wool & Koach, 1976), *Forda formicaria* von Heyden (Wool & Bar-El, 1995), *F. marginata* Koch, and *Paracletus cimiciformis* von Heyden. This "guild" is the subject of the study presented herein.

The life cycle of the Fordinae is very complex (Wool, 1984; Wool & Burstein, 1991). Briefly, the aphids alternate between their primary host (*Pistacia*) and secondary hosts (grasses). Galls are induced on the primary host in the spring by fundatrices that emerge from overwintering fertilized eggs. All further reproduction is parthenogenetic. Two or three generations reproduce in the gall during the summer. Host alternation is accomplished by the last generation which becomes alate (winged). Their descendants develop on grass roots during winter without inducing galls. A second alate form (sexuparae) emerges from the roots the following spring and returns to *Pistacia* to reproduce sexual males and females (Wool et al., 1994). Fertilized eggs are sheltered in bark crevices and new galls are induced in the following spring.

Not a single branch of *Pistacia palaestina* survived in the burned area, and all galls were destroyed. In September, during the time the fire occurred, the galls contained the last summer generation and alate fall migrants were about to disperse to secondary hosts. Moreover, overwintering eggs in bark crevices were also destroyed, so two aphid generations were eliminated. It is unclear whether the fire affected subterranean, root-feeding stages on grass roots within the burned area. Almost no Sternorrhyncha were recovered during intensive sampling of soil arthropods in both burned and unburned control plots in the first two years after the fire (Broza et al., 1993).

Just six months after the fire, during March through April of 1990, oak and, in particular, *Pistacia* trees in the burned area began to resprout from subterranean buds. In this paper, we describe recolonization by host-specific, gall-forming aphids on *Pistacia palaestina* trees that recovered from fire. Recolonization was monitored for six years after the fire.

MATERIAL AND METHODS

In March of 1990, six months after the fire, we visited the burned area and mapped and marked 39 *P. palaestina* trees that had started to produce new shoots with numbered stakes. (At the time, surviving trees were easily perceived as green islands in the barren black landscape.)

The 39 trees were scattered throughout the burnt area: six were in the south, 15 in the north, six in the east and 12 in the centre. Almost all trees that had resprouted at the time of the visit were included. (We suspected that trees on the periphery of the burned area would be colonized more easily than those in the center. These suspicions were not confirmed by the study results). During subsequent census visits, nearly all marked trees were revisited, although locating the trees became increasingly difficult because they were obscured by *P. lentiscus* bushes, *Cistus* seedlings and pines that colonized the area.

Marked trees were visited four times in 1990, three times in 1991, twice in 1992, 1994 and 1996, and once in 1993 and 1995. One annual visit took place in winter of each year, and we counted galls of *B. pistaciae* during this visit. These galls remain attached to branches and can be seen and easily counted during the winter when leaves have been shed (Wool, 1990). Since recovering trees grow slowly and are still small (approx. one meter above ground), it was possible to count all galls on each tree. During each winter visit, growth measurements were recorded to document the previous year's shoot elongation. The three longest shoots on each tree were measured. Other visits took place during spring and summer in order to survey leaf galls of *G. wertheimae*, *F. formicaria*, *F. marginata* and *P. cimiciformis*. During the first two spring visits, the first week of April of 1990 and 1991, trees were classified into three categories by the status of the buds: dormant, swelling buds, or elongating shoots.

Two sets of data are available for use in estimating tree occupancy by Fordinae *before* the fire. The southern border of the burned area is less than 1 km away from an unburned site (Area A) that contains 16 *P. palaestina* trees that were tagged in 1979 and annually censused for *B. pistaciae* (Wool, 1990). Since this species is best surveyed in winter (Wool, 1990), tree occupancy by the other leaf-galling species may have been underestimated. The second data source (Area B) is located about 2 km northeast of the burned area on the northern slope of Mt. Carmel. Thirty-six trees in Area B were censused in April of 1991 for use in *F. formicaria* research. *B. pistaciae* galls may not have been noticed at the time of the census because April is early in the season for this species.

Data analysis

Hierarchical ("nested") analysis of variance (Sokal & Rohlf, 1995) was used to test for differences in tree growth (shoot elongation) in different locations within the burned area. Differences in the frequency distribution of gall abundance between trees in control and burned areas were tested by use of χ^2-tests.

Two techniques were used to examine temporal trends in the data. Correlation analysis was used to examine gall abundance on the same trees between years; a series of McNemar's tests was used to indicate the significance of changes (Sokal & Rohlf, 1995). Both analyses were run for each gall-forming species and each pair of years (1990–91, 1991–92, etc.). We noted the numbers of trees (a) occupied in both years, (b) occupied in the first but not in the second year, (c) occupied in the second but not in the first year or (d) not occupied in either year. The null hypothesis was that no changes took place from year to year: i.e., trees that were colonized in one year remained colonized, and those that were free of galls remained uncolonized in the next year. The test criterion was calculated as $\chi^2 = (b-c)^2/(b+c)$, with 1 df. We used the BIOM program package (Rohlf, 1987).

To test for differences in gall abundance of one species (*B. pistaciae*) between burned and control areas, we employed a randomization (bootstrap) test. The variable used was the sum of galls on each tree from 1991–95. There were no *B. pistaciae* galls on burned trees in 1990. The five-year sum was considered a better estimate of abundance than each separate year because gall abundance is known to fluctuate widely between years. We calculated the difference between median gall abundances for the 39 recovering burned trees and the 16 control trees in area A (data for the latter were available since 1979 (Wool, 1990) but only 1991–95 data were used). The median rather than the mean value was used in the comparisons because gall frequencies were strongly skewed to the right. After the observed "diff" was calculated, data from both groups were combined and reshuffled, then randomly divided into two groups of 16 and 39 trees, and the difference between the two medians ("diff") was recalculated. This resampling was repeated 1,000 times. The distribution of the random "diff" values provided a test of significance for the observed "diff" (Sokal & Rohlf, 1995). We modified a routine in the "Resampling Stats" programs (Simon et al., 1995), for our purpose.

RESULTS

Recovery of the trees

Initially, growth of new shoots was very rapid. When first measured in March of 1990, some shoots were already 60 cm long or more. Annual shoot elongation at the end of summer in 1990 was ten times greater than shoot elongation in unburned trees in the control area (Fig. 1) [means ± SE (n) are 80.7 cm ± 3.58 (n = 38) vs 8.4 cm ± 1.35 (n = 51)]. This extraordinary growth rate declined by half in the next year and steadily thereafter in subsequent years, approaching the "normal" growth rate (Fig. 1).

A hierarchical ("nested") analysis of variance (Sokal & Rohlf, 1995) was used to analyse measurements from each year in order to partition the variation of shoot length into the following components: sections within the burned site, trees within these sections, and shoots within individual trees. The results (Table 1) show that most of the variation was contributed by differences among individual trees (P < 0.001). No significant differences in tree growth rates were found among trees in different sections of the burned area and all trees were grouped together in the following analyses.

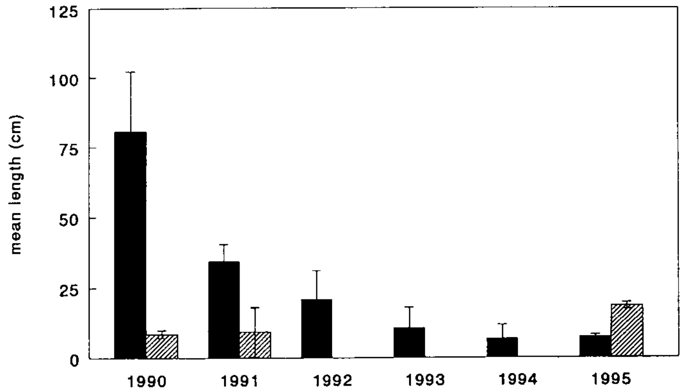

Fig. 1. Mean shoot elongation per year (in cm, ± SE) of 39 "resprouting" *Pistacia palaestina* trees following destruction by 1989 fire (black bars). The three longest shoots on each tree were measured at the end of each summer. Measurements of shoots on unburned trees in "control" Area A (see text) at indicated years are shown for comparison (cross-hatched bars).

TABLE 1. Variation in tree growth (shoot elongation) – results of "Nested" ANOVA: Variance components contributed by different levels of hierarchy. "Sections" refers to the position of the trees within the burned area – south, north (2 samples), east or centre.

Year measured	Variance components (%) among sections (df = 4)	among trees (df = 32)	shoots within trees (df = 74)
1991	7.0 ns	61.3*	31.7
1992	0	64.1*	35.9
1993	6.5 ns	69.5*	24.0
1994	0.06 ns	73.5*	26.5
1995	7.9 ns	63.4*	28.6

* $P < 0.001$; ns = not significant.

Colonization of the trees by different species

To our surprise, we found *F. marginata* galls on the foliage of seven *P. palaestina* trees in 1990. This species induces two galls in its life cycle, referred to as F_1 (fundatrix) and F_2 (final) galls (similar to *Smynthurodes betae*; Wool & Burstein, 1991). The curious thing about the presence of galls on the recovering trees was that only F_2 galls were found (a few galls per tree). It is unlikely that we missed the fundatrix galls because new shoots were small and few in number, and were thoroughly searched.

As expected, all other species were absent in 1990, and the first galls were found in 1991 (Table 2). One F_1 gall of *F. marginata* was found on tree # 10, along with a typical dense population of F_2 galls on the same tree. A few F_2 galls were found on seven other trees. Twenty-two trees were colonized by *B. pistaciae* and one by *P. cimiciformis*. Additional trees were colonized by all species except *F. formicaria* in subsequent years (Table 2). By 1995, at the end of this six-year study, all 39 trees were colonized by *B. pistaciae* (at least one gall per tree), and about half of the trees were colonized by *F. marginata* and *P. cimiciformis*. However, only seven trees were colonized by *G. wertheimae*, and none of the recovering trees were colonized by *F. formicaria* (Table 2).

TABLE 2. Numbers of colonized trees of the total 39 studied. A tree was considered colonized if it carried at least one gall. By the end of 1994, all 39 trees were colonized by *B. pistaciae*.

Species	1990	1991	1992	1993	1994	1995
B. pistaciae	0	22	35	29	39	39
G. wertheimae	0	0	5	no data	7	no data
F. marginata	7	8	12	no data	17	no data
P. cimiciformis	0	1	15	no data	15	no data
F. formicaria	0	0	0	no data	0	no data

Persistent occupation of trees after colonization

"Occupation" is defined herein as the presence of at least one gall on a tree at observation time. Although the life cycle of the Fordinae involves, or imposes, repeated colonization of all trees every year (because the aphids must leave the galls in the fall), the presence of galls on trees was not random and, once colonized, trees also tended to be colonized in subsequent years. This trend is particularly clear for *B. pistaciae*; almost all of the trees were colonized in 1992 and remained colonized throughout the study. We tested for persistence of occupation by using a series of McNemar's tests for significance of changes (Sokal & Rohlf, 1995). Each species was tested separately for each pair of years (1990–91, 1991–92, etc.) (Table 3 summarizes the results.)

For *B. pistaciae*, a significant χ^2 value was obtained only from 1991–1992 data: this was the year that 15 new trees were colonized. No additional significant changes in occupation occurred in later years. In 1993, seven additional trees were colonized, but this change did not result in a significant χ^2 value. No significant changes were observed for *G. wertheimae*, *P. cimiciformis* or *F. marginata* except in the 1992–94 subset. However, this subset is composed of a two-year interval and is not comparable to the others (leaf galls were not counted in 1993 or 1995).

TABLE 3. Summary of McNemar's tests for significance of changes in occupation of the same trees over consecutive years: a = number of trees occupied in both years; b + c = number of trees occupied in one year but not in the other; d = trees not occupied in either year. Total number of trees 39.

Species	Years	a	b	c	d	χ^2 1df	P
B. pistaciae	1991–92	19	3	15	2	8.0	< 0.001
	1992–93	26	8	2	3	3.6	> 0.05
	1993–94	23	4	10	2	2.6	> 0.05
G. wertheimae	1992–94	2	3	2	32	0.2	> 0.05
F. marginata	1990–91	4	4	4	27	0	
	1991–92	5	3	7	24	1.6	> 0.05
	1992–94	4	0	8	27	8.0	< 0.001
P. cimiciformis	1992–94	2	12	0	25	12.0	< 0.001

Control trees

The percentage of "control" trees occupied by each galling species in Areas A and B is presented in Table 4. The first column for each area is data from old field records (the mean for 1988–91 in Area A, and the 1991 survey in Area B). On 3 July of 1996, we recensused both control areas. All trees in Areas A and B were examined. (In A, nine additional unmarked trees were added to increase the sample size). The results show a clear difference between Areas A and B. In Area A, *B. pistaciae* galls were significantly more frequent than in Area B, whereas the reverse was true for *F. formicaria* and *F. marginata* (G tests of independence on the numbers of trees from Table 4; P < 0.001, P < 0.001, and P < 0.05, respectively).

TABLE 4. Percentage of "control" trees occupied by Fordinae species in control Areas A and B (in 1996, sample size in Area A was increased from 15 to 24).

Species	A			B		
	No. trees	1988–91 (mean)	1996	No. trees	1991	1996
B. pistaciae	15 (24)	66.7	70.8	36	not recorded	16.7
G. wertheimae		6.7	29.2		not recorded	0.0
F. formicaria		20.0	13.3		33.3	50.0
F. marginata		13.3	58.3		25.0	25.0
P. cimiciformis		15.3	4.2		0	8.3

Gall abundance

The factors regulating gall abundance are complex and may involve, apart from colonization success, other properties of the aphids (e.g., number of arrivals, fecundity and survival of fundatrices) and individual host plants (Wool et al., 1997). Since non-destructive means of estimating abundance of leaf-galls has not yet been developed (see Wool & Bar-El, 1995), quantitative data are only available for *B. pistaciae*.

TABLE 5. *B. pistaciae* gall abundance on 39 recolonized trees and 16 nearby unburned (control A) trees (sum for 5 years, 1991–1995).

Galls per tree	Number of trees (burned area)	Control
1–10	8	2
11–50	13	1
51–100	6	2
101–150	1	2
151–200	4	3
201–250	1	2
251–300	2	1
301–350	1	2
351–400	0	0
401–450	0	0
>451	3	1
Total	39	16

There were large differences in the numbers of *P. pistaciae* galls hosted by different trees. A frequency distribution of trees characterized by the total number of galls they hosted (sum for five years, 1991–95) is provided in Table 5. Twenty-one hosted less than 50 galls over the five year period (eight of these hosted less than 10). In contrast, seven trees hosted more than 200 galls each. The results show that the trees that hosted numerous galls were the same individuals throughout the five observation years; gall abundance on the same individual trees (in different years) was significantly correlated once colonizers were established in 1992 (Table 6). It is important to note that the highest correlation coefficient exists between 1992 and 1994 data (two years apart), although two other values are also highly significant. This is consistent with the two-year periodical changes in gall abundance that is characteristic of this species (Wool, 1990; Wool et al., 1997).

TABLE 6. Pearson's Product-moment correlations of *B. pistaciae* gall abundance on the same trees in different years.

Year	1991	1992	1993	1994
1992	-0.8 ns	–		
1993	0.17	0.53 *	–	
1994	0.08	0.84 **	0.63 *	–

* $P < 0.01$; ** $P < 0.001$; ns = not significant.

Temporal patterns were not the same for all trees, and were similar to those observed in 1982 on four burned trees in Beit Guvrin (Wool, 1990). After one year without galls, gall abundance first increased to high levels and then began to exhibit periodical cycles. Although a five-year period is too short for temporal pattern analysis, some of the trees in the present study exhibited a fluctuating pattern, while others appeared to continue to increase in gall abundance (examples in Fig. 2).

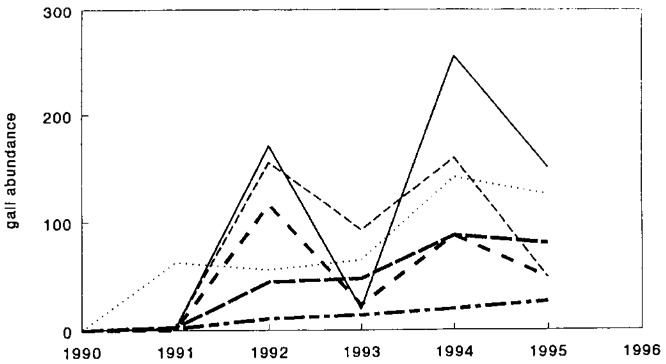

Fig. 2. Examples of fluctuations in *Baizongia pistaciae* gall abundance on six of the "resprouting" trees. No galls were found in 1990, as expected. Some trees show characteristic bi-annual alteration of high and low abundance. Each line represents a single tree.

Comparison of *B. pistaciae* gall abundance in the burned and control areas

B. pistaciae abundance was measured herein as the five-year sum of galls per tree during 1991–1995. The median of the 16 control trees in Area A was 169.5, whereas the median of the 39 recovering trees was 38, thus yielding a "diff" value of 131.5.

The distribution of the simulated "diff" values, the difference between the medians of 1,000 randomly resampled groups of 16 and 39 values from the combined data in one of

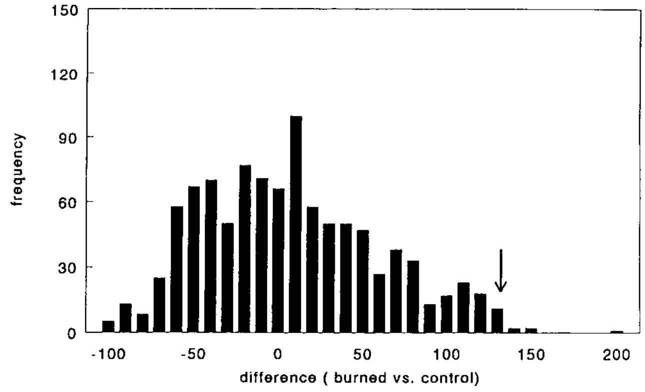

Fig. 3. Simulated distribution of the difference ("diff") of mean *Baizongia pistaciae* gall abundance between 39 "resprouting" and 16 control (Area A) trees. Data were 5-year sums of galls per tree. Values were combined, reshuffled and randomly sampled with replacement 1,000 times. The observed "diff" is indicated by the arrow. The probability of values as large or larger to be obtained by chance is very small (0.008).

the two runs, is illustrated in Fig. 3. The position of the observed "diff" is indicated by the arrow. The proportion of values equal to or greater than the observed "diff" was 0.008. No values of absolute magnitude similar to the observed were found in the left tail of the distribution. Thus, the two medians are significantly different, and we can conclude that, five years after the fire, abundance of the most successful colonizer, *B. pistaciae*, is still, on average, lower than in the control area.

Correlation of tree growth with *B. pistaciae* colonization success

No significant correlation was found between tree growth increments and *B. pistaciae* gall abundance in the same year. Moreover, tree growth in year y was not correlated with *B. pistaciae* in year $y+1$ or in year $y-1$ (data not shown).

DISCUSSION

Extinction of local populations, followed by recolonization, is an integral process in natural systems. Major catastrophes like volcanic eruptions destroy plants and animals within large tracts of habitat in some parts of the world (e.g., Hawaii). Recolonization of new lava flows by endemic *Drosophila* species occurs after their specific host plants are reestablished on new lava. The process of extinction and recolonization is determined by the population structure and genotype frequencies of the extant populations (Carson et al., 1990). Although local extinctions must frequently occur after small, naturally occurring and man-made catastrophes (fire is one of the most common of the latter), few of these extinctions have been documented and published. Unusual weather conditions caused total destruction of a population of the bug *Lygaeus equestris* in part of Sweden and repopulation was a slow process that was dependent on colonists from neighboring areas (Solbreck, 1991). One year after a fire, Ehnström et al. (1995) studied recolonization of burned pine forests in Finland by bark and wood beetles, and found that the common bark beetle species preferentially colonized dead, dying, or severely damaged trees. However, bark beetles do not normally attack healthy trees, thus, no direct comparison to our gall-forming aphids is appropriate. We know of no long-term observations of aphid recolonization on trees after a fire.

One characteristic of galling aphids (Fordinae) that is advantageous to recolonization studies is that colonization is part of their normal life cycle. In the natural forest, specific, primary host plants may be few and far apart, yet aphids must newly colonize each tree every year. Fire is a common occurrence in Mediterranean forests. Although one author suggested that galls may have evolved as an adaptation to protect their inhabitants from fire (Koteja, 1986), this was certainly not the case for the Fordinae. In our study, both galls and overwintering eggs on the bark were totally destroyed by the 1989 fire at the Carmel National Park. Even if the gall had offered some protection to the aphids, they would have starved to death when the tree died.

Burned areas are rich in mineral nutrients, and recovering trees have a favourable root/shoot ratio for shoot elongation. This was evidenced in our study by the fast growth rate of recovering *Pistacia* trees in the first year after the fire. These conditions may also indirectly benefit insects that colonize these plants (Washburn & Cornell, 1981). In a previous study, gall midges were abundant in a previously burned area in which shoots were growing rapidly, and abundance remained high the second year after the fire (Price et al., 1995).

In our study, tree growth rate declined rapidly and reached "normal" rates after four years (Fig. 1). In contrast, more trees were occupied by the aphids and gall abundance levels increased in later years after the fire. Similarly, *B. pistaciae* gall abundance on four *P. palaestina* trees that were recovering from a 1982 fire reached unprecedented levels three years after the fire (Wool, 1990).

Tree age may affect colonization by insects. Moran & Whitham (1990) reported that young *Populus* trees are not colonized by *Pemphigus betae.* No information is available regarding the chronological age of the 39 trees in our study. Most trees in Mediterranean forests in Israel are estimated to be less than 50 years old due to widespread anthropogenic disturbances, although, in some sites, protected trees exist that are up to 600 years old (Y. Waisel, pers. comm.). Regardless of the age of the roots, the above-ground portions of all trees in this study were the same age after the fire. At colonization time in 1990, all shoots were approximately six months old. In 1996, 19 of the trees bore fruit and were thus identified as female. The other 20 trees were either male or "immature". (No male inflorescences were seen on recovering trees). Both male and female trees were colonized.

Persistent occupation of the same trees in consecutive years

Although the biology of the Fordinae imposes repeated recolonization of the trees every year with host alternation, in our study the same trees were colonized every year. Our long-term observations of *B. pistaciae* since 1980 in other parts of Israel confirm this conclusion (Wool, 1990 and later unpublished data). It is likely that the persistence of galls on individual trees from year to year is due to the establishment of colonies on secondary hosts near a colonized tree. Once the first successful colonizers produce a gall, it is likely that some emerging alates will larviposit on secondary hosts near the host tree, thus increasing the likelihood that sexuparae will arrive at the same tree in subsequent years. We reached a similar conclusion during a study of sexuparae remigration (Wool et al., 1997).

Colonization success: comparison of different species

A species' colonization success was estimated by counting the number of trees (islands) that carried at least one gall. We considered colonization of the same tree by different species to be independent events because each species occupies a different gall location on the tree (Inbar & Wool, 1995).

Colonization success differed between different species. *B. pistaciae* occupied all trees just three years after the fire. A preliminary analysis indicated that bud-burst status of the trees may have affected colonizing success of this species (Wool & Burstein, 1992). *F. formicaria* seems to be the least successful colonizer; no *F. formicaria* galls were found on any of the trees during the study. *G. wertheimae* was a poor colonizer; only seven trees were colonized in five years. The other two species were intermediate in terms of colonization success.

Mayr (1965) emphasized two characteristics of a good colonizer (plant or animal) species: (a) good dispersal ability and survival until a new favourable habitat is found; and (b) ability to become established when a favourable site is found. In the latter category, the advantage of reproductive systems that do not require mating, or tolerate self- fertilization (in plants) was indicated.

Galling aphids have both a mobile colonizing stage (the sexuparae) that are apparently able to find their primary hosts (Wool et al., 1994), and the ability to reproduce parthenogenetically in the major part of their life cycle. However, they normally have a sexual stage which is critical in holocyclic populations on the primary host.

Why is *B. pistaciae* a good colonizer and *F. formicaria* a bad one? The absence of galls on recovering trees could be because sexuparae of the species have not yet arrived there, but could also be due to unsuccessful establishment of aphids on individual trees (tree resistance). Colonization success also depends on the synchronization of aphid arrival with tree bud-burst (Akimoto & Yamaguchi, 1994; Komatsu & Akimoto, 1995; Wool & Burstein, 1992; Wool et al., 1997).

B. pistaciae has the highest reproductive output of the Fordinae in this study: this species produces thousands of fall migrants per gall. Limited observations of winter generation indicate that *B. pistaciae* can be successfully reared on any seedling of Graminae, and may reproduce several generations during the winter (Wool, unpublished). *B. pistaciae* sexuparae do not usually land on unsuitable plants (Wool et al., 1994). However, *P. cimiciformis* and *F. formicaria* do not make landing "mistakes" either, yet seem to be much less successful as colonizers.

The temporal pattern of *B. pistaciae* colonization was similar to expectation: no galls were found in 1990, but sexuparae of this species (migrating from the periphery) must have located recovering trees (that were very small but quite conspicuous on the black background) and deposited some sexuals, resulting in fertilized eggs from which fundatrices emerged in 1991. Twenty-two of the 39 trees were colonized in 1991.

The case of *F. marginata*, which colonized seven trees in 1990, is particularly curious. The ecology of *F. marginata* is poorly understood. This species characteristically attacks small trees that have been subjected to grazing or other disturbances, and low branches of other trees (Inbar & Wool, 1995). Its fundatrices (F_1) are particularly large as compared with other species, and their fecundity seems exceptionally high (unpublished data). The only probable way that the tiny, wingless F_2 fundatrices of this species could have arrived at the study trees during the summer of 1990, when no F_1 were found, is by wind transport. Their chance of hitting a *P. palaestina* tree in the dense vegetation of a normal forest is probably close to zero, but they may have a better chance over bare ground after a fire. No record of wind dispersal of apterous fundatrices of Pemphigidae is known to us; this was, however, demonstrated in Adelgidae (McClure, 1990) and *Phylloxera* (Hawthorne & Dennehy, 1991).

Comparison of gall abundance in the burned and "control" areas

There is no way to know which species colonized the trees in the burned area before the fire. We used the term "control" to designate unburned trees, and assumed that, before the fire, the composition of species that formed galls in the area was similar to that of the surrounding Carmel National Park. However, we found that species composition in Areas A and B was not the same. Which of the two sets of data, A or B, better represent the burned area before the fire? It seems to us that Area A is a better approximation of the pre-fire composition. The Area is situated on the south-facing slope of Nahal Oren, and is characterized by a less humid habitat than the north-facing slope of Area B. Most of the burned area is on a gentle, south-facing slope of Nahal Kelach. Although dense Mediterranean forest covers both of the unburned areas, we believe that the Area A control gives a better approximation to the pre-fire proportions of the Fordinae. If this is true, the fact that *F. formicaria* has not yet colonized any of the recovering trees may be due to its relative scarcity on that side of the mountain, rather than an indication of poor colonization ability.

Since it is not possible to anticipate when and where the next ecological disturbance may occur, this study stresses the need for long-term routine sampling of natural forests in order to obtain the baseline information, which can be used to detect changes in populations.

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