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Herbivore abundance is independent of weather? A 20-year study of a galling aphid *Baizongia pistaciae* (Homoptera: Aphidoidea)

Received: January 7, 2002 / Accepted: October 8, 2002

Abstract The gall abundance of *Baizongia pistaciae* (L.) (Pemphiginae: Fordini) on marked *Pistacia palaestina* trees (Anacardiaceae) was monitored for 20 years at two natural sites in Israel (Carmel, in the center of the host distribution, and Beit Guvrin, near its southern limit), and in the botanical gardens of Tel Aviv University. Gall abundance varied between zero and 500 galls/tree and fluctuated from year to year. The analysis aimed at a diagnosis of the underlying causes of the temporal changes in gall abundance. Weather variables were expected to synchronize gall abundance on most trees on the same site. There was little indication of synchrony among trees in most years. Correlations of mean gall abundance with weather variables were low (<0.4 , explaining $<16\%$ of the variation) and almost none were significant. The temporal pattern of gall abundance was analyzed for every tree separately (the “autecological” paradigm). There was no convincing evidence of self-regulation (density-dependence) in gall abundance on any tree, although the rate of change in abundance tended to decrease with increasing density on some trees. At one site (Carmel), significantly more abundance peaks (1 SD above the mean) occurred in “wet” years (precipitation above average) than in “dry” years. This pattern was not observed at the other sites. The biannual fluctuations in abundance, observed in the first 10 years of the study, were far less clear when the 20-year sequence was analyzed. If the causative mechanism is tree stress – as assumed previously – then the biannual pattern may not be expected except in years of favorable conditions, when gall abundance is high enough to drain the tree of resources and cause a lower gall abundance the following year. The life cycle of galling aphids is very complex. A clone enclosed in a gall on a tree alternates with a subterranean population on the roots of herbaceous plants, with two migratory phases in between. Moreover, a sequence of parthenogenetic generations is interrupted by a

single event of sexual reproduction. In *B. pistaciae*, this cycle takes two years to complete. Regulating mechanisms of gall abundance at the different stages may work in different directions, canceling each other out. I suggest that direct effects of weather on the aphids at any stage of their complex life cycle may be obscured when the net result (gall abundance) is studied. Weather effects may be detectable only when it is extremely favorable or unfavorable for the aphids (or the host plant).

Key words Fordini · Autecological paradigm · Temporal variation · Long-term study · Insect–plant interaction

... (diagnosis is) the art of detecting the cause of a particular condition from observations of its symptoms... Even though the diagnostician may use sophisticated techniques, the final diagnosis is no more than an educated opinion. (Berryman, 1999, p. 93)

Introduction

Much has been written about factors regulating fluctuations in insect population size. The majority of studies on population fluctuations last no more than 5 years, but when perseverance (and perhaps financial support) is sufficient for long-term research, patterns are discovered which may shed light on the underlying mechanism. Some notable examples of long-term studies are Den Boer (1988, 1990) on populations of winter moth (19 years) and of Carabidae (23 years), respectively, Clarke et al. (1985) on the decline in frequencies of melanic moths (25 years), and Redfern and Cameron (1998) on yew midge galls (27 years). Whittaker and Tribe (1998) reported on 37 years of observations of spittlebugs in Scotland, and Ylioja et al. (1999) reconstructed the abundance of an agromyzid fly from feeding scars in sections of tree trunks, providing data for 47 and 65 years at two localities.

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The authors of these studies suggested possible mechanisms to account for the observed patterns. These mechanisms ranged from self-regulation (density-dependence) to the effects of external variables; temperature (Whittaker and Tribe 1998), and tree age and the disturbance history of the stand (Ylloja et al. 1999) are two recent examples. Jarosik and Dixon (1999) recorded the abundance of an oak-feeding aphid on two trees by biweekly sampling for 19 years. The pattern of abundance on the two trees was very different: on one tree, the aphids seemed to respond to density at all seasons of the year, while on the other they responded when the density was low ("curvilinear density dependence"; Jarosik and Dixon 1999).

Gall-forming insects on trees are convenient organisms for long-term studies on abundance patterns (Yukawa 2000). The galls are often large and conspicuous, and remain on the tree for weeks or months (in some cases for more than a year). Trees are convenient sampling units since they are long-lived, providing replication in both space and time. Since each species of galling insect makes a species-specific gall (Mani 1964; Wool 1997), it is possible to identify the organism unambiguously. Moreover, the presence of the gall is evidence of the presence of the galler, even when it is long gone at the time of inspection. If the galler died, the cause of its mortality can sometimes be ascertained (e.g., Weis et al. 1992; review in Price et al. 1987).

In 1978, I started what became a long-term study of the abundance of the galling aphid *Baizongia pistaciae* (L.) (Fordini; Pemphiginae) on *Pistacia palaestina* (Anacardiaceae) in Israel. Galling aphids present some of the most complex life cycles in the insect world (review in Wool 2003). *B. pistaciae* induces large, horn-shaped galls, sometimes more than 20cm long (Fig. 1). Like most Fordini, *B. pistaciae* alternates between the primary host (*P. palaestina*), on which the galls are formed, and the roots of herbaceous secondary hosts (Graminae). Galls are induced in the spring by fundatrix nymphs emerging from overwintering, fertilized eggs. Three generations of parthenogenetic reproduction in the galls during the summer may result in a clone of more than 20000 aphids. Alate (winged) aphids of the final generation disperse and reproduce on the ground. Their offspring find their way to the roots of grasses, where they feed and reproduce during the winter and spring. Alate sexuparae fly from the secondary hosts back to *Pistacia* in the spring (Wool et al. 1994, 1997) and produce sexual males and females. A single fertilized egg overwinters until the following spring, when the fundatrix hatches and induces a new gall. The 2-year cycle is illustrated by Blackman and Eastop (1994, Fig. 2). The galls remain attached to the branch when the leaves are shed, and can be conveniently counted in early winter after leaf fall.

In the first 10 years of the study, high and low gall abundance on many individual trees alternated within a 2-year period (Wool 1990). I suggested that a heavy load of galls in one year may have depleted the tree of some resources, making it less favorable for gall induction or aphid success the following year (alternate fruit bearing in cultivated pistachio, *Pistacia vera*, is explained likewise (Crane and



Fig. 1. Gall induced by *Baizongia pistaciae* on *Pistacia palaestina*. A gall this size may contain a clone of 20000 aphids (photo A. Shoob)

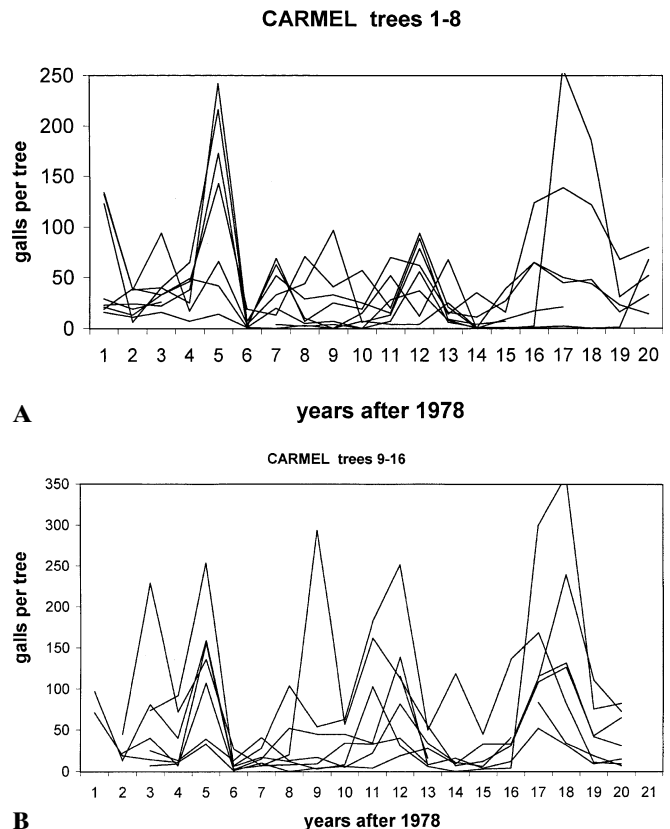


Fig. 2. Gall abundance of *B. pistaciae* at the Carmel site. Each line represents a different tree. The 16 trees are plotted in 2 groups, shown in **A** and **B**. Note that peaks and troughs are only rarely synchronized

Table 1. Stages in its life cycle when *B. pistaciae* may be particularly exposed to risks

Period	On the tree	On the roots
Spring	Eggs fail to hatch Fundatrices fail to induce galls Predation on arriving sexuparae	Predation on the root aphids
Summer	Parasitism and predation in galls	Mortality due to high temperatures (may survive in ant nests?)
Fall	Gall loss with leaf abscission Bird predation on emerging fall migrants	Crawlers fail to find roots and establish colonies
Winter	Mortality of overwintering eggs	Destruction of root colonies by excess moisture

Iwakiri 1981, 1987; Weinbaum et al. 1994). Unlike tree resources, which may vary individually among trees, a weather factor could synchronize gall abundance on different trees, as the climate is the same for all trees at a site (Wool 1990). In a 17-year study, Hunter and Price (1998) found that abundance of galling sawflies on many willow trees in Arizona was mainly explainable by changes in rainfall.

The aphids may be relatively protected from the elements inside the galls (Price et al. 1987), but may be directly or indirectly affected by weather at other stages in the life cycle (Table 1). For example, rainfall may improve the growth conditions of the tree, which may in turn facilitate gall induction by more fundatrices, and/or allow better feeding and reproduction in the gall. Similarly, rainfall may improve the growth of grasses and allow better survival and the production of more sexuparae on the secondary hosts, which in turn may increase gall abundance in the following year (e.g., Moran and Whitham 1988). On the other hand, excess soil moisture may be harmful for the aphids on the roots. Conversely, a dry year may cause a crash of the root populations, negatively affecting abundance on all trees. High summer temperatures may facilitate plant growth, but may be harmful for the root generations since ground temperatures in the summer may exceed the physiological limits of some species (Harpaz 1953). Antagonistic effects at different stages of the life cycle may cancel each other out, and the net response to climatic variables may be too low to be detectable.

The *B. pistaciae* study was continued until 1998. Weather variables (temperature and rainfall) for the same 20-year period were examined in a search for possible factor(s) controlling the peaks and troughs in gall abundance on different trees.

Methods

Study sites

Site selection depended on the accessibility of *P. palaestina* trees carrying galls of *B. pistaciae*. The trees at sites 1 and 2

are located along roads (later research revealed that galls are bigger and more abundant along roads than in the “natural” forest away from the road [Martinez and Wool 1999]). There may have been an unconscious bias toward trees that were galled in 1978. At the third site, all trees were used. The three sites are described below.

1. Mount Carmel (CAR). This site is near Kibbutz Beit Oren (Israel Grid 151 237), in a typical Mediterranean forest composed of *Quercus calliprinos*, *Pistacia lentiscus*, *Calycotome villosa*, and two species of *Cistus*. Sixteen *P. palaestina* trees were tagged in 1978. The trees varied in size, and are characteristic of the natural forest on the south-facing slope of Mt. Carmel (Wool 1990; Wool and Inbar 1998).
2. Beit Guvrin (BG). This site is along a stretch of the road from Beit Shemesh to Beit Guvrin, about 40 km SE of Tel Aviv (Wool 1990) (Israel Grid 148 128). The area is near the southern limit of the distribution of *P. palaestina* (and, of course, its galling aphid fauna). Sixteen trees were tagged in 1979. The trees seem to be survivors of the natural forest, which was burned, cut, and grazed upon for many years.
3. Tel Aviv University (TAU) Botanical Gardens. Unlike the other two, this site is man-made. *P. palaestina* seedlings, from seeds collected in nature, were planted in 1974. The gardens represent Israeli habitats, and the trees are surrounded by grasses and shrubs that occur with them in nature. Twenty-four trees were tagged in 1979, and this number increased to 32 when small trees, overlooked in the first survey, were added.

All trees at CAR were colonized by *B. pistaciae* every year. At the other sites, some trees were not colonized by this species in some years. At TAU, some trees were not colonized at all in the 20 years of study, or bore only 1–2 galls occasionally, although they are located a few meters away from colonized trees (Wool 1990).

Measured variables

All the galls on each tree were counted once every year, between November and January, after leaf fall. The trees were 2–6 m tall. Counts were made with a hand counter while walking around the tree. When the numbers were large, independent counts were made by two observers and averaged.

Calculated variables

The mean number of galls per tree (*gallmean*) was used to represent the aphid population in each year and at each site. This variable should reflect the influence of external weather factors, which affect all trees synchronously.

Climatic variables

Data for 1978–1998 from weather stations near the research sites were obtained from the Israel Meteorological Service.

Table 2. Means (\pm SE) of the climatic variables at the three sites, 1978–1998

Variable	Carmel	Beit Guvrin	TAU
RainFall (mm)	268.7 \pm 30.5	192.0 \pm 32.1	248.0 \pm 38.7
RainWint	351.1 \pm 23.5	327.3 \pm 24.6	280.5 \pm 23.5
RainSprg	29.7 \pm 4.5	None	16.8 \pm 4.2
TminFall ($^{\circ}$ C)	13.7 \pm 0.16	14.2 \pm 0.18	14.9 \pm 0.20
TminWint	8.7 \pm 0.22	9.0 \pm 0.24	10.1 \pm 0.23
TminSprg	15.1 \pm 0.23	15.5 \pm 0.24	17.2 \pm 0.13
TminSumm	20.5 \pm 0.10	20.2 \pm 0.09	22.8 \pm 0.11
TmaxFall ($^{\circ}$ C)	23.1 \pm 0.23	23.1 \pm 0.24	23.3 \pm 0.21
TmaxWint	17.1 \pm 0.28	17.1 \pm 0.34	18.0 \pm 0.22
TmaxSprg	27.3 \pm 0.19	27.7 \pm 0.28	24.9 \pm 0.17
TmaxSumm	31.3 \pm 0.10	31.8 \pm 0.14	29.4 \pm 0.14
CoolMar	56.1 \pm 3.33	53.4 \pm 3.09	46.9 \pm 2.90

The weather station nearest to CAR was at Kibbutz Even Yitzhak (Gal-Ed, 20km southeast of the site; Israel Grid 157 218). Rainfall data for BG were available from two stations: Beit Gimal, 1.5km north of the site (Israel Grid 147 125), and Kibbutz Beit Guvrin, 15km south of the site (Israel Grid 140 113), from which temperature data were also available. The weather station for TAU was at Sde Dov airport, barely 1 km from the site. Rainfall data were monthly precipitations (in mm). Temperatures were monthly averages of daily minimum and maximum.

I pooled the raw climatic data into four 3-month periods, roughly corresponding to biologically meaningful stages in the life history of the aphids: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). Precipitation was summed for three periods because there is no summer rain in Israel (Table 1, and Wool and Koach 1976).

P. palaestina is deciduous and may require winter chilling to break its buds in spring, as do many fruit trees grown commercially in the country. I acquired data of a cumulative chilling index (analogous to the cumulative number of degree-days below a threshold temperature; Erez et al. 1990). The index was provided for the end of January, February and March of each year.

Means and standard deviations of the weather variables at the three sites are given in Table 2. Codes for the variables have a suffix indicating the period (e.g., *RainWint* = rainfall in the winter period; *TminSprg* = minimum temperature in the spring period; *CoolMar* = cumulative chilling index to the end of March).

Data analysis

There are two possible approaches to the analysis of these data. The “demographic” paradigm (Hengeveld and Walter 1999) considers the mean of all trees at a site as being representative of the population. Since climate should be the same for all trees at a site, temporal changes in climate should affect *gallmean*. Alternatively, each tree can be treated as a separate ecological unit (the “autecological” paradigm; Hengeveld and Walter 1999).

Density dependence

Gall abundance on individual trees may be self-regulated (density-dependent). A number of methods have been published for testing this suggestion (Holoak 1993). Nearly all tests use the slope of the regression of N_{t+1} on N_t , where N_t is the abundance at time t (e.g., Whittaker and Tribe 1998). Slopes significantly smaller than 1 indicate density-dependence. It may also be useful to examine the rate of change in abundance, $K = \ln(N_{t+1}/N_t)$ in response to N_t .

Periodicity

As a follow-up to previous reports (Wool 1990; Wool and Inbar 1998), I tested for any regular biannual fluctuation in gall abundance on individual trees. First, I used the non-parametric “runs up or down” test (Sokal and Rohlf 1995). The “null” hypothesis was that the distribution of peaks was random. The alternative hypothesis was one-tailed: only cases of *too many* runs resulted in rejection of the null hypothesis (suggestive of a biannual pattern). The analysis was carried out on 34 individual trees at the three sites. Second, I used time-series analysis. If there was a regular 2-year periodicity, gall abundance in consecutive years (lag of 1 year) should be negatively autocorrelated, and should show positive autocorrelation with a lag of 2 years. I performed this analysis on all trees at CAR, and on all trees with sufficient data at the other sites.

Correlation with climate

I calculated standard Pearson’s correlation coefficients (Sokal and Rohlf 1995) between abundance and weather variables at each site and period. I started with the “demographic” approach, using *gallmean*. This analysis yielded very low correlations, which did not reach statistical significance. I then did the same with the data for some individual trees. The correlations were not improved (see results).

Final analysis

Driven by my belief (perhaps shared by many colleagues, and supported by published cases such as Hunter and Price 1998) that weather must have some effect on gall abundance, I tried a different approach. I looked at the 20-year temporal pattern of each tree and focused on years of exceptionally high or low abundance (the terms “peaks” and “troughs” will be used throughout this paper). For these years only, I looked for any association with weather variables. Peaks and troughs on different trees differed greatly in amplitude and were only rarely synchronized (Wool 1990, and see results). The selection of peaks and troughs used for this study may introduce personal bias, so statistically valid rules were called for to define them. The steps taken in the final analysis are listed below.

1. The 20-year mean gall abundance and standard deviation were calculated for each tree.

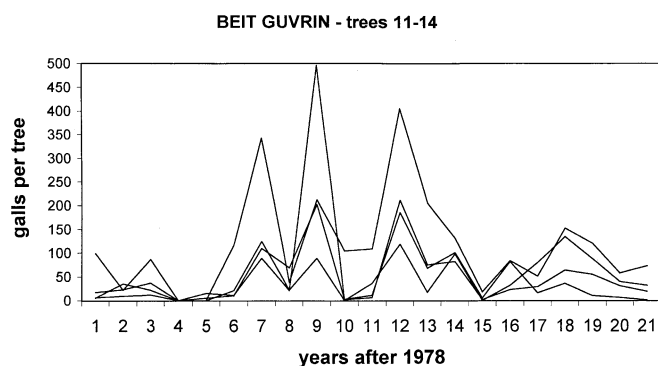


Fig. 3. Gall abundance at the Beit Guvrin site. Four trees (11–14) which were destroyed by fire in 1982 resprouted and were recolonized by *B. pistaciae*. Peaks and troughs are synchronized for some years after recolonization. Most other trees at the site show no synchrony and low gall abundance (not illustrated)

- When the abundance in any year was greater than 1 SD above the long-term mean, it was considered to be a “peak” year. Similarly, when the abundance was less than 1 SD below the long-term mean, it was considered to be a “trough” year. When the lower limit was a negative value (a situation which arose when the mean was small and the SD large, in particular at TAU), years with zero galls were considered to be troughs.
- After defining peak and trough years, long-term means and SD were calculated for the weather variables. For each year, I noted whether each variable was above or below the long-term average. (The use of the ± 1 SD rule for weather proved to be impractical since the variation in most weather variables did not exceed these limits.)
- The frequencies of peaks (and troughs) which occurred in “above-average” years versus “below-average” years for each weather variable were tested for departure from the “null” expected frequencies by χ^2 tests.

Results

The raw data

The gall abundances of *B. pistaciae* for each of the three research sites are illustrated in Figs. 2–4, respectively. Each line shows the data for one tree. For clarity, not all trees at a site are illustrated.

CAR

The abundance on individual trees fluctuated from almost zero to 350 galls. Peaks and troughs on different trees were not synchronized except for a peak in 1983 (year 5) and a trough in 1984, shared by all trees at the site. In the first 8 years, the abundance on many trees showed a biannual pattern, as reported earlier (Wool 1990), but the periodicity was disrupted after 1988, and the intervals between peaks became longer (Fig. 2)

TEL AVIV trees 1-10

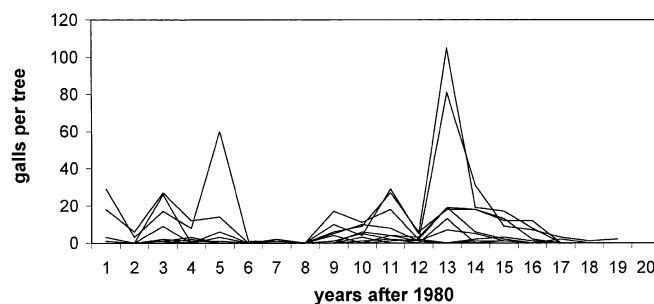


Fig. 4. Gall abundance of some trees at the Tel Aviv site which show synchronized peaks and troughs. Some of the other trees at this site were never colonized in the 20-year study

Table 3. Correlations of climatic variables with gallmean at the three sites

Variable	Carmel	Beit Guvrin	BGI ^a	TAU
RainFall	0.125	0.366	0.409*	-0.128
RainWint	-0.025	0.029	0.149	0.063
RainSprg	-0.255	None		-0.054
TminFall	-0.403*	-0.109		-0.103
TminWint	0.004	-0.218		-0.260
TminSprg	0.139	0.229		0.236
TminSumm	0.346	-0.129		-0.022
TmaxFall	-0.374	-0.260		0.204
TmaxWint	-0.069	0.232		0.038
TmaxSprg	-0.171	-0.156		0.421*
TmaxSumm	0.060	0.010		0.267
CoolJan	-0.294	0.287		0.172
CoolFeb	-0.187	0.277		0.199
CoolMar	-0.132	0.328		0.109

^a Rainfall data in this column are from Beit Gimal

* $P < 0.1$

BG

The gall abundance on most trees at this site was considerably lower than at CAR, and fluctuated between zero and 50 galls, except on four trees (Nos.11–14) which had peaks as high as 500 galls/tree. These trees were burned to the ground in 1982 and had resprouted. Galls reappeared in 1984 and peaks and troughs were synchronized, but with very different amplitudes (Wool 1990). No clear pattern was observed after 1993 (Fig. 3).

TAU

Gall abundance at this man-made site was rather low on most trees and in most years. However, the abundance on some trees alternated biannually for part of the time (Fig. 4).

Correlations of gall abundance with climatic variables

Correlations of *gallmean* with climatic variables were low (Table 3). The highest correlation explained only 16% of the variation. Only 3 of 43 values approached, but did not

Table 4. Correlations of gall abundance on four trees, with some climatic variables, at Beit Guvrin. None of the correlations are statistically significant ($P > 0.05$, $df = 18$)

	Tree number			
	11	12	13	14
RainFall	0.393	0.235	0.266	-0.067
RainWint	-0.219	-0.035	-0.202	-0.140
RainTotal	0.192	0.225	0.119	-0.056
TminFall	-0.354	-0.321	-0.153	-0.115
TminWint	0.154	0.044	0.167	0.255
TminSumm	0.283	0.342	0.311	0.279
TmaxWint	0.112	0.054	0.089	0.230

quite reach, statistical significance, regardless of the season of the year or the weather variable employed.

To test whether the low correlations with climate are due to the asynchrony among trees, I looked at the group of four trees at BG mentioned above. These trees grow side by side, not more than 50m from each other. The three clear peaks on these trees are well synchronized (see Fig. 3). Neither the annual means of the four trees (data not shown) nor gall abundance on each tree separately were significantly correlated with weather variables (Table 4). The correlations were not improved by log- or square-root transformation of the gall counts.

Some general impressions may be reached from observation of the *signs* of the correlation coefficients in Table 3. Gall abundance was negatively correlated with *TminFall* at all three sites, and with *TmaxFall* at CAR and TAU. Correlations with *TminWint* at TAU and BG were also negative. Since there are no live galls on the trees in winter, it is possible to deduce that cooler weather may be favorable for the growth and reproduction of root generations. This idea is supported by the positive correlations of *CoolJan*, *CoolFeb*, and *CoolMar* with gall abundance at BG and TAU: a higher value of the index indicates a colder year. On the other hand, at CAR the correlations with the chilling indices were negative. As the correlations were not significant in any case, the interpretation remains speculative.

Self-regulation of abundance (density-dependence)

Regression analysis was carried out on all individual trees with a sufficiently long sequence of data (>15 years). About half the slopes were negative, but only two of 27 regression slopes were significantly different from zero (Table 5). These two slopes were also significantly smaller than 1, as expected from density-dependence, but these results do not provide a convincing indication of a density-dependent regulation of *B. pistaciae* gall abundance.

The rate of change in gall abundance, K , gave different patterns on different trees. When plotted against N_t , there was a wide scatter of points, albeit with a tendency for a decreasing K with increasing N_t (Fig. 5A is typical of many trees). When plotted against time, in many cases alternating peaks and troughs resulted in the early years of the study.

Table 5. Tests for the density-dependence of gall abundance. Slope \pm SE of the regression of $\ln N_{t+1}$ on $\ln N_t$ (N_t = observed number of galls on the tree in year t). The significance of the slope was first tested against the null hypothesis $|\beta| = 0$. Only the two significant slopes were tested for density-dependence

Site	Slope	SE	Significance $H_0 = \beta = 0$	Density $H_0 = \beta = 1$
CAR				
1	-0.239	0.250	ns	
2	-0.019	0.242	ns	
3	-0.264	0.278	ns	
4	0.011	0.241	ns	
7	-0.181	0.268	ns	
8	0.235	0.250	ns	
9	0.393	0.231	ns	
10	0.518	0.192	$P < 0.05$	$P < 0.05$
11	0.301	0.254	ns	
12	-0.191	0.277	ns	
13	-0.045	0.305	ns	
14	0.029	0.375	ns	
BG				
7	-0.273	0.276	ns	
8	-0.452	0.284	ns	
11	-0.133	0.253	ns	
12	0.128	0.242	ns	
13	0.088	0.242	ns	
14	0.322	0.204	ns	
15	0.532	0.206	$P < 0.05$	$P < 0.05$
16	0.043	0.228	ns	
TAU				
2	0.124	0.310	ns	
6	0.214	0.295	ns	
10	0.261	0.265	ns	
15	-0.173	0.261	ns	
20	-0.449	0.236	ns	
27	-0.077	0.342	ns	
28	-0.579	0.325	ns	
29	0.310	0.331	ns	

ns, not significant

Interestingly, many of the peaks occurred in even-numbered years and many of the troughs in odd-numbered years (Fig. 5B is an extreme example).

Two-year periodicity of gall abundance on individual trees revisited

Since the first report of 2-year periodicity in gall abundance (Wool 1990), ten more years of observation have been added, but not all trees provided an unbroken sequence of data for a quantitative analysis of periodicity. The runs tests found an indication of biannual periodicity (at $P < 0.05$) in only 9 of the 34 trees tested (Table 6).

A few trees showed the expected negative autocorrelations with a lag of 1 year in the time-series analyses, and almost all of those were at CAR. None of the negative correlations were statistically significant. The majority of the trees tested (29 of 41) showed positive autocorrelations with a lag of 2 years, and 13 of them were statistically different from zero at $P < 0.05$ (Table 7). It seems that the biannual pattern did not persist when a longer sequence of years was considered.

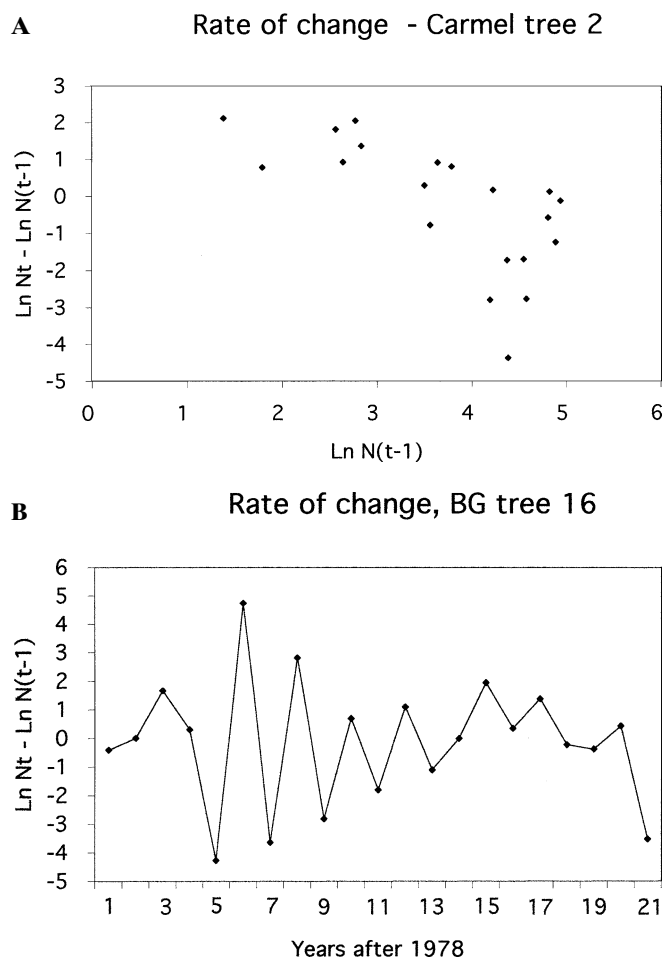


Fig. 5. The rate of change in abundance, $K = \ln(N_{t+1}/N_t)$ **A** The scatter of points when plotted against N_t (CAR tree 2 as an example). Note the decreasing tendency of the cloud of points. **B** Alternating fluctuations when plotted against time (BG tree 16 as an example)

Gall abundance and rainfall: a reevaluation

Although 12 weather variables were originally analyzed (see Table 2), it appeared that many of them were not likely to explain the peaks or troughs of gall abundance because they varied within very narrow limits. The range of differences between +1 SD and -1 SD of the mean of temperature variables was no more than 2–3°C, while gall abundance varied by two orders of magnitude. Only precipitation data seem to qualify as possible regulators of gall abundance.

At CAR, significantly more peaks occurred in above-average rainfall (W) years than expected (using *rainWint* and total rainfall as variables, Table 8). Nevertheless, some peaks did occur in below-average rainfall (D) years. No significant pattern emerged when the fall and spring precipitations were analyzed separately.

BG is a drier locality (see Table 2) and I expected a stronger dependence of gall abundance on rainfall than at CAR. Contrary to my expectation, no significant pattern emerged. At TAU also, no difference was found between gall abundance frequencies in D and W years (Table 8).

Table 6. Runs tests for nonrandom (biannual) patterns of gall abundance

Site	Total number of trees	Number analyzed	H_0 rejected
Carmel	15	15	4
Beit Guvrin	28	9	3
TAU	33	10	2

Table 7. Time-series analysis: numbers of trees with positive and negative autocorrelations of gall abundance with a lag of 1 and 2 years (the numbers of correlations are significantly different from zero in parentheses)

Site	Trees analyzed	Negative lag 1	Positive lag 2
Carmel	15	7 (0)	7 (1)
Beit Guvrin	15	1 (0)	14 (7)
TAU	11	1 (0)	8 (5)

More unexpected results were obtained from the analysis of the frequency of troughs. I expected that troughs would be associated with years of drought, in particular at BG. There was no deviation in the observed frequency of trough abundance (considering total rainfall) between W and D years at any site.

Discussion

The purpose of this study was to understand the causal mechanism(s) regulating temporal fluctuations in abundance of the gall-inducing aphid *Baizongia pistaciae* from a continuous sequence of 20 years of observation. I was convinced at the start that weather, and in particular rainfall, should affect gall abundance. It is disappointing that no significant correlation was discovered between weather variables and gall abundance at the three sites. This may be indicative of a real difficulty in detecting the regulating variables of a complex system in nature.

It is very likely that weather variables do affect the aphids at some stages in their 2-year life cycle, directly as well as indirectly, mediated by weather effects on the growth of both the primary and secondary host plants. However, these effects may not be expressed in gall abundance. Processes acting on the gall stage and on the root generations may not work in the same direction (Yukawa 2000), and chance may obscure any patterns during the two migratory phases in the life cycle.

Quantitative data on populations of the Fordini on the roots of secondary hosts in the field are unavailable. We have reared *B. pistaciae* for several generations in soil-free root cages in the laboratory (Wool 1998). In laboratory cages, *B. pistaciae* tends to form dense, wax-covered colonies, and newborn nymphs tend to settle near their mothers. We have no information on their behavior in the field. Density at the root stage may affect the numbers of

Table 8. Peaks in gall abundance in wet and dry years. Carmel data are shown in detail, followed by summaries of the other sites

Year	No. of peaks	RainFall	RainWinter	RainSpring	RainTotal
1980		W	W	W	W
1981	4	D	W	D	W
1982	–	D	D	D	D
1983	9	W	W	D	W
1984	–	D	D	W	D
1985	1	D	D	W	D
1986	–	D	D	W	D
1987	2	W	D	D	W
1988	–	W	W	D	W
1989	3	D	D	D	D
1990	6	W	W	W	W
1991	1	D	W	W	D
1992	–	W	W	D	W
1993	–	W	D	D	W
1994	2	D	W	D	D
1995	4	W	D	D	W
1996	4	D	W	W	D
1997	1	D	W	D	W
1998	–				
Peaks in W		21	27	12	26
Peaks in D		16	10	25	11
χ^2		2.27 ns	4.55 $P < 0.05$	0.65 ns	6.08 $P < 0.01$
Beit Guvrin					
Peaks in W		8	15	15	14
Peaks in D		25	18	18	19
χ^2		1.23 ns	0.27 ns	0.27 ns	0.75 ns
Tel Aviv					
Peaks in W		17	17		18
Peaks in D		24	24		23
χ^2		1.12 ns	1.12 ns		0.61 ns

D, rainfall below average; W, rainfall above average

sexuparae arriving at the trees, and hence gall abundance in the following year, but these effects may be obscured by variation in mating of their sexual offspring, and by differential survival of the fertilized eggs.

My failure to detect significant self-regulation (density-dependence) in *B. pistaciae* gall abundance may be due to the complexity of the life cycle. The tendency of K to decrease with increasing N_t may imply some self-regulation, but the wide scatter of points on most trees indicates that if present, it is only a minor regulator of abundance. Loman (2001) searched for density effects in a field experiment with populations of a frog, *Rana arvalis*. Like many amphibia, this organism has two phases in its life cycle: an aquatic (tadpole) stage and a terrestrial phase. The effects of input egg density on tadpole performance were comparatively minor (Loman 2001). Needless to say, the life-cycle complexity of the galling aphids is far greater than in the amphibia.

In population ecology, mean numbers of individuals are often used to describe and predict temporal trends. Although criticisms and alternative approaches have been suggested, the “demographic paradigm” (Hengeveld and Walter 1999) has contributed much to the understanding of natural processes, and, because a similar paradigm is used in population genetics, has enabled ecological genetics and evolutionary thinking about natural phenomena.

My null hypothesis was that climatic variables should synchronize peaks or troughs in gall abundance. The results do not support this hypothesis. Single weather factors do not have overriding effects on abundance, since peaks and troughs on different trees were only rarely synchronized. Trees varied individually both in the amplitude and the timing of peaks in gall abundance. A whole range of possible causes of this individual variation could be postulated. (1) A preference by sexuparae for some trees and not others (Moran and Whitham 1990; Hamilton and Brown 2001). (2) The varying distance of trees from the source of sexuparae. (3) The random (or wind-affected) drifting of the weak-flying sexuparae during the spring migration. (4) The differences in tree age (aphids prefer older to younger trees), bud-break times, and shoot growth among trees, or genetic differences in resistance to galling. Therefore, I resorted to the alternative, “autecological” paradigm (Hengeveld and Walter 1999) and analyzed the pattern on each individual tree as a distinct unit.

However, asynchrony among trees was not the reason for the absence of significant correlations of gall abundance with weather. Synchrony between the four trees at BG (see Fig. 4) was achieved because they resprouted simultaneously after being burned in 1982, but no significant correlations with weather variables were obtained.

Two-year periodicity

The 2-year periodicity in gall abundance on individual trees reported in the first 10 years of the study was less obvious when the study was extended to 20 years. On most trees, the pattern of fluctuations was not significantly different from random. It is interesting to note that at CAR, the more central site in the distribution of the host tree, about half the trees did show negative autocorrelations with a lag of 1 year.

Sequeira and Dixon (1997) used time-series analysis of the log-abundance of a free-living aphid, *Myzocallis boernerii*, on two oak trees during 17 years. They detected biannual fluctuations in the first 8 years, and the numbers remained stable after that. These authors interpreted this pattern as reflecting regular density-dependent changes in within-year abundance. This explanation cannot hold for *B. pistaciae*, where the numbers of galls, which are induced in early spring, either remain stable or decrease within 1 year. Although galls do compete for resources when they occur on the same shoot or leaf (Inbar et al. 1995), I found no evidence for density-dependence in *B. pistaciae*.

Redfern and Cameron (1998) described biannual fluctuations in the abundance of the yew gall midge *Taxomyia taxi*. On two of three trees, the biannual pattern persisted only in the first 10–12 years of a 28-year study. On the third tree, no pattern was observed for 18 years, and then abundance started to fluctuate biannually. The authors attributed these patterns to the life cycle of the midge and its parasitoids. No parasitoids were discovered in galls of *B. pistaciae* in 20 years of research. The only parasitoid known from aphid galls, *Monoctonia pistaciaecola* Stary (Wool and Burstein 1991), is apparently unable to penetrate sealed galls like those of *B. pistaciae*. One species of predator, the larva of the pyralid moth *Alophia combustella* (Bodenheimer and Swirski 1957), was observed in the galls, but its quantitative impact on gall abundance is unknown.

I suggest that the tree stress/resource depletion mechanism postulated in 1990 to explain the 2-year periodicity in the abundance of *B. pistaciae* may be effective only in times of high aphid population size. High gall abundance may then drain tree resources and lower the probability of galling success in the following year. This explanation does not hold where the gall load on most trees is rather small, as at BG and TAU. I tend to explain the pattern at TAU by the biannual life cycle of the aphids. Since this site is man-made, it is possible that only one of the two cohorts (even-years or odd-years) colonized the site (this explanation was considered in 1990, but the tree-stress hypothesis was then preferred).

The regular alternation of K on many trees may also suggest cohort alternation in odd- and even-numbered years. For example, troughs in K on BG tree 16 occurred in odd-numbered years (years 5, 7, 9, 11, and 13 after the start of the observations, followed by peaks in even-numbered years; see Fig. 5B, where year 1 was 1979). However, this hypothesis requires support from genetic (or perhaps molecular genetic) studies which so far have not been carried out.

Correlation with weather variables

Gall abundance on individual trees was not significantly correlated with weather variables (e.g., Table 4). Climatic variables may affect gall abundance with a time lag: a rainy winter may facilitate tree (or grass) growth, and aphid success will be improved 1 year later. Nevertheless, correlations with climatic variables did not increase with a lag of 1 or 2 years.

I expected to find significant correlations of gall abundance with rainfall at BG in particular. Because this site is near the southern limit of the distribution of the host trees, I expected that precipitation would be a limiting factor. However, rainfall was not significantly correlated with *gallmean* at this site. The reason may be that the trees are located along a road and receive runoff water from the asphalt. This creates a favorable environment for the trees as well as for aphid colonization (Martinez and Wool 1999), making them less dependent on direct precipitation.

Autecological analysis

A tree is a stable resource for aphids: it is perennial, and its growth is supported by an extensive root system and by reserves accumulated over many years. It seems that most of the time, the environmental conditions are sufficient for new shoot growth and aphid colonization, allowing some level of gall abundance on each tree, and the fluctuations are not much affected by changes in temperature or precipitation. It may not matter to the aphids if the tree received 300 or 600 mm rainfall in a particular year, so long as it was able to produce new shoots and support induced galls.

It is possible that the effect on gall abundance is detectable only when weather conditions depart very considerably from normal, whether it is favorably or unfavorably for the aphids. Strong (1984), in his discussion of density-dependence in insect populations, introduced the concept of “density-vague ecology,” i.e., populations may be regulated by density only at very low or very high densities. At intermediate densities, the variance in measured population parameters due to other factors precludes the detection of density-dependence (if it exists). I extend this idea of vagueness to the analysis of the effect of weather, in particular in the galling aphids. Gall abundance on a tree depends not only on insect characteristics, but also on the individual properties of the host trees. The interactions of *B. pistaciae* with its host plants during the complex, 2-year holocycle can add to the “vagueness.” Also, gall abundance in year N depends, at least in part, on the reproductive success in year $N-2$ (mature aphids per gall), which was not measured in the present study.

The significant preponderance of peak abundance in wet years at CAR (see Table 8) shows that rainfall does affect gall abundance in some years. Winter rain affects both the primary and the secondary hosts, but the peak abundance occurred *in the same year as the recorded rainfall*. This suggests that rainfall affected abundance positively through the primary host plant, and not through the subterranean

aphids on the secondary hosts. Positive effects on growth of grasses would cause an increase in the numbers of sexuparae produced, but gall abundance would only be affected 1 year later.

Concluding remarks

The patient study of the gall abundance of *B. pistaciae* over 20 years has provided little evidence that a single key weather factor, such as precipitation, can explain fluctuations in abundance. The population in each locality, and even on each tree, seems to respond differently. Perhaps events affecting abundance in the 2 years of the life cycle may cancel each other out, or dampen the oscillations to such an extent that the net result is an apparent absence of pattern. Also, to the extent that abundance reflects the genetic properties of the aphids (e.g., genotypic differences in reproductive capacity), the gene pool in odd- and even-numbered years may not be the same. If there is selection for galling success in aphids, it must be intermittent (once in 2 years) in *B. pistaciae* and hence ineffective (as suggested by Kurosu and Aoki 1991).

Finally, there is always the possibility that I have not measured the relevant variables. I would prefer to apply Laplace's principle of ignorance (Lewontin 1966): events seem to be governed by chance because the complexity of the universe makes it impossible to know all the relevant facts.

Acknowledgments I am grateful to Prof. Peter W. Price (Northern Arizona University) for fruitful discussions about the approach to the analysis of long-term studies, and to reviewers of earlier drafts of the manuscript, who suggested further analyses and thus contributed to the value of the present paper. Dr. Moshe Inbar (Haifa University) made useful comments on the earliest draft manuscript. Several of my former graduate students deserve thanks for their help in the field work over the years. Thanks are due to the Israel Meteorological Service for the weather data.

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