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ORIGINAL PAPER

Modification of tree architecture by a gall-forming aphid

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Abstract Herbivory may substantially alter the architectural structure of plants. Among insects, gall-formers that substantially manipulate host traits may have a profound effect on the plants even at low densities. The aphid, *Baizongia pistaciae* induces banana-like large galls on the terminal buds of *Pistacia palaestina*. We hypothesized that these large galls are associated with the shape of the plant which may grow as a tree or a bush. In the natural Mediterranean forest, we monitored the effects of the galls on infested branches. In the year of gall formation, usually (∼95%) there is neither elongation nor branching beyond the position of the gall. However, in the following years, galled branches produced more lateral branches (branching) than ungalled branches. This effect persists for at least 2 years. Consequently, galled branches carried more leaves and tended to gain more biomass than ungalled branches. Galling did not affect fruit yield. We suggest that repeated galling by *B. pistaciae* may promote bush-like architecture in *P. palaestina*.

Keywords Apical dominance · Branching · Compensation · Herbivory · Long-term effect

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Introduction

Most of the reports on the effect of herbivores on the architecture of plants are associated with browsing and grazing mammals (e.g., Danell et al. 1994; Fornara and Du Toit 2007). Reports of pronounced effect of insects on the architecture of trees are relatively scarce (e.g., Weis 1984; Whitham and Mopper 1985). Gall-formers have intimate physiological interactions with their host, and may trigger variable and complex responses in the plants. The effect of galls on the plant differs in many aspects from other types of damage (e.g., Fay and Throop 2005; Martinez and Wool 2003). Gallers may change the architecture of the infested plants at the attacked point as well as the whole organ or plant levels (Mani 1964; Silva et al. 1996). Some gall-formers can considerably reduce seed production or reproductive performance of the plants, and therefore may serve as biological control agents (Fernandes et al. 2007; Harris and Shorthouse 1996; Sopow et al. 2003). On the other hand, gall-formers may enhance assimilation activity (Dorchin et al. 2006) and compensatory growth of the host. For example, the gall-forming sawfly, *Euura lasiolepis* promotes vigorous vegetative growth of willows (Craig et al. 1990).

Pistacia palaestina (Anacardiaceae) is a deciduous dominant plant in the Mediterranean forest. The plant may look like a tree (tree shape) with a main trunk and few lateral branches, or like a bush (bush shape) with several trunks and high level of branching. *P. palaestina*, is the exclusive host of several species of gall-forming aphids of the subfamily Fordinae (Wool 2004). Each aphid species makes a typical gall; most of them are small (few cm long) leaf-galls. The life cycle of the Fordinae is complex and involves different reproductive strategies and various morphological stages (Inbar et al. 2004; Wool 2004; Wool

2005). In the spring, the aphid *Baizongia pistaciae* induces remarkable, banana-like galls (which may be 25 cm long or larger). The incipient galls are induced on the primordial leaflets, but eventually take over the entire apex of the branch. The gall serves as an incubator for thousands of aphids which feed on the phloem sap for nearly 8 months (spring-fall).

These large galls appear to have a profound effect not only on the galled branch, but also on the surrounding branches from which nutrients and assimilates are diverted (Burstein et al. 1994). In a previous study, Katz (1991) reported that in the year of gall formation, the elongation of branches galled by *B. pistaciae* is significantly reduced (approximately by 1/3) compared to ungalled branches. In most cases (~95%), there is neither elongation nor branching beyond the position of the gall, during that year (personal observation). Katz (1991) also found that in about 1\3 of the branches, the gall totally eliminates any further development in the following years. In preliminary observations, however, we could occasionally find in the year after gall formation extensive lateral branching on previously galled branches. In this study, we examined the possible association between the presence of galls and the shape (tree vs. bush) of *P. palaestina* and quantified the effect of *B. pistaciae* galls on the growth pattern, and fruit yield of their host plant, in the years following gall formation.

Materials and methods

Study site

The study was performed on a natural population of *P. palaestina* located near the village of Aminadav in the Judean hills (elevation ~800 m), near Jerusalem, Israel. A dense population of *P. palaestina* of variable ages and sizes exist at the site. The abundance of *B. pistaciae* galls at the site varied among trees.

Effect of galls on branch growth 1 and 2 years after gall formation

We selected branches with galls that were formed in the year 2000. The effects of the galls on the plant were examined 1 year (2001) and 2 years (2002) later. In early summer (2001), we selected eight trees (half of them females), which carried old, dry galls from the previous season (Usually the galls or gall parts of *B. pistaciae* remain attached to the branch in the following year). On each tree, five pairs of branches were labeled, each pair originating from the same primary branch. One branch of the pair was gall-free (control) and the other carried a dry gall from previous year (Fig. 1). At the end of the summer, we recorded the number of lateral branches that grew from each marked branch, their length, and number of leaves (Fig. 1). In addition, we collected and dry weighed (oven-dried at 70°C for 48 h) a sample of leaves (2 leaves in 2001 & 10 in 2002) from each marked branch. From these data, we estimated the total dry biomass of the leaves per branch that was galled in the year 2000. The same branches were re-examined in 2002. However, only 28 pairs of the 40 pairs labeled in 2001 were re-found in the second year.

Effect of the galls on the fruit yield 2 years after gall formation

Fruits in *Pistacia* originate from reproductive buds on 1-year-old segment of the branch. We examined the effect of galls on fruits that grew in 2002 on the branch segments of 2001(see Fig. 1). In the end of July 2002, when the fruits matured, we sampled three female trees (of the eight previously marked trees). On each tree, all fruits were collected from four pairs of galled and gall-free branches. The fruits were dry weighed (oven-dried at 70°C for 24 h) and the total number of fruits per branch was estimated from the average weight of three random samples of 100 fruits.

Statistical analyses

The occurrence of lateral branching is described as a binary (presence–absence) variable. To test for the association of lateral branching with gall presence, we used χ^2 tests for independence. We used mixed model, two-way ANOVA to evaluate the effect of galls on growth and yield in different

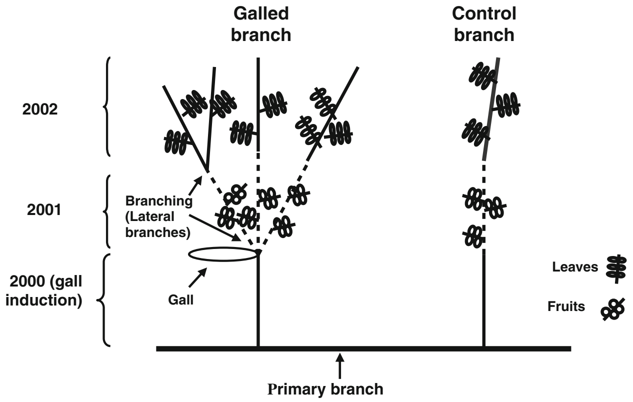

Fig. 1 Schematic representation of the experiment testing the effects of the galls produced by the aphid *B. pistaciae* on *P. palaestina* architecture and yield. The galls were formed in the year 2000 and their effect was examined in the two following years (years are indicated on the *left*). Thus, all data relates to branches that were initially galled (or not) in the year 2000

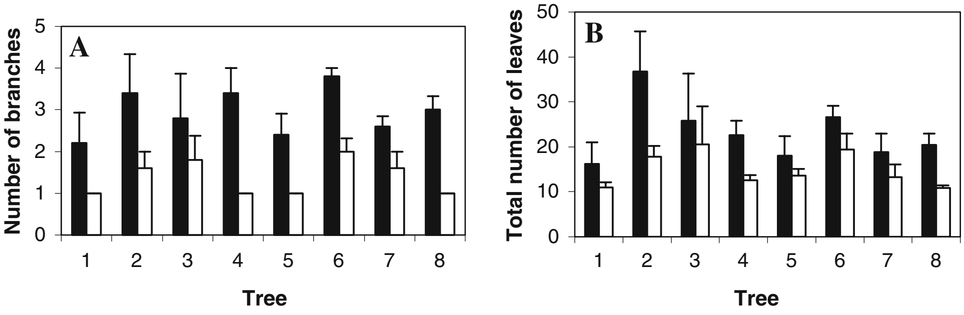

Fig. 2 The impact of *B. pistaciae* on tree growth variables 1 year after gall formation (2001). Means (±SE) of the number of branches (**a**) and total number of leaves (**b**) per branch of year 2000 in galled branches (*black*) and ungalled branches (*white*). Statistics are shown in Table 4

Table 1 The frequency of branching in galled and ungalled branches 1 and 2 years after gall formation

	1 year after gall formation ($n = 40$)		2 years after gall formation ($n = 28$)	
	Galled	Ungalled	Galled	Ungalled
Branching	35	10	17	7
No branching	5	30	11	21
	$\chi^2 = 31.75$, df = 1, $P \ll 0.001$		$\chi^2 = 7.29$, df = 1, $P < 0.01$	

trees. Since the trees were chosen randomly and pairs of galled and gall-free branches were examined in each tree, we defined the trees as a random factor (blocks) and gall presence ("treatment") as a fixed factor. The interaction between these factors was tested as well. The data of the discrete variables were tested after square root transformation.

Results

Effect of galls on tree architecture

Galled branches produced lateral branches significantly more often than ungalled branches in the first (2001) as well as in the second (2002) year after gall formation (Table 1). Lateral branching in the first year tended to be followed by further branching of the same branch in the following year (Table 2). The galls of *B. pistaciae* thus had a persistent effect on the architecture of the tree.

Although few ungalled branches did produce lateral branches in the first year, the number of lateral branches, their total length, and the total number and biomass of leaves were significantly higher in galled branches both in the first and in the second years after gall formation (Tables 3, 4). Although individual trees varied quantitatively in their response, they all exhibited the same trend (Fig. 2, the same trend was recorded for the growth variables in both years). Differences between trees were significant in some cases, especially 1 year after gall formation (Table 4). The effects of the galls on the growth of the branches were not tree-dependent.

Table 2 The relation between branching 1 year (2001) and branching 2 years (2002) after gall formation

		Branching (2002)			
		Galled branches		Ungalled branches	
Branching (2001)		Yes	No	Yes	No
	Yes	17	9	2	5
	No	0	2	5	16

Note that not all branches were found in 2002 and therefore were not re-examined

Effect of the galls on the fruit yield

In contrast to the consistently higher vegetative growth rates in the galled branches, fruit yield was much more variable (and not significant), among trees 2 years after gall formation (data not shown). The number of fruits and their dry biomass were not significantly affected by the presence of the galls (Fig. 3).

Discussion

It is not surprising that the gall of *B. pistaciae* disrupts the normal growth of the branch. The gall is a response to the attack of the tiny fundatrix, a true parasite, which draws the resources for maintaining its offspring from the photosynthetic products of the host plant (Burstein et al. 1994; Inbar et al. 1995; Wool et al. 1999). The amount of damage to the host increases with the size of the gall, which may exceed that of a banana. Since the number of galls per tree may be very high (Wool 2002), even a large *P. palaestina*

Table 3 Means (±SE's) of different growth measures on galled and ungalled branches in 1 year (2001) and 2 years (2002) after gall formation

Measure	2001		2002	
	Galled	Ungalled	Galled	Ungalled
Number of branches	2.95 ± 0.195	1.38 ± 0.149	5.01 ± 0.432	2.21 ± 0.653
Total length of branches (cm)	32.95 ± 4.906	18.64 ± 3.129	61.74 ± 11.853	22.74 ± 2.310
Total number of leaves	23.15 ± 2.341	14.88 ± 1.356	47.1 ± 7.576	19.75 ± 3.382
Total biomass of leaves (gr)	16.34 ± 3.718	11.05 ± 2.046	24.45 ± 6.063	9.08 ± 2.148

For each measure we show the mean of means (per branch of year 2000) of all trees. Measurements were taken on individual trees. Statistics is shown in Table 4

Table 4 Mixed model two-way ANOVA results for the effect of galls on growth measures of the branches, in different trees, 1 year (2001) and 2 years (2002) years after gall formation

Measure	Source	2001				2002			
		df	MS	*F*	*P*	df	MS	*F*	*P*
Number of branches	Treatment	1	5.56	73.97	***	1	7.27	18.37	**
	Tree	7	0.20	1.78	NS	6	0.32	0.93	NS
	Interaction	7	0.08	0.65	NS	6	0.40	1.16	NS
	Error	64	0.12			42	0.34		
Total length of branches	Treatment	1	4096.95	16.73	**	1	19284.16	14.17	**
	Tree	7	1109.23	3.18	**	6	2060.51	1.92	NS
	Interaction	7	244.92	0.70	NS	6	1387.02	1.29	NS
	Error	64	348.43			42	1075.58		
Total number of leaves	Treatment	1	15.53	33.60	***	1	65.21	29.32	***
	Tree	7	2.45	2.14	NS	6	4.39	1.44	NS
	Interaction	7	0.46	0.40	NS	6	2.15	0.71	NS
	Error	64	1.15			42	3.04		
Total biomass of leaves	Treatment	1	561.09	7.77	*	1	2995.94	11.34	*
	Tree	7	648.22	9.44	***	6	674.19	4.04	**
	Interaction	7	72.23	1.05	NS	6	273.12	1.64	NS
	Error	64	68.70			42	166.84		

"Treatment" is a fixed factor which refers to the state of branch (galled/ungalled). "Tree" is a random factor. The data of the discrete variables were tested after square root transformation.* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

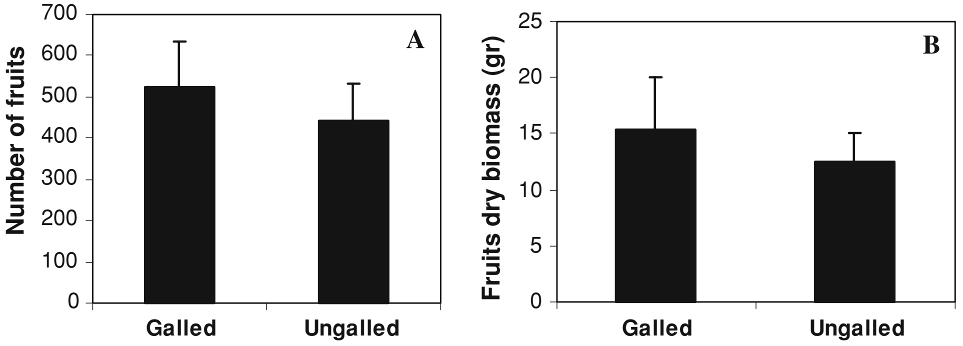

Fig. 3 The impact of *B. pistaciae* galls on the fruit yield of *P. palaestina* 2 years after gall formation. Number of fruits per branch (**a**) and their dry biomass (**b**) in galled and control ungalled branches. For each measure we show the mean of means (per branch of year 2000) of three trees. Measurements were taken on individual trees. (ANOVA results: Fruits number, $F_{1,2} = 9 \times 10^{-5}$, NS; Fruits biomass, $F_{1,2} = 0.44$, NS)

Fig. 4 The effects *of B. pistaciae* galls on the architecture of *P. palaestina* branching of lateral branches as a result of gall formation. *Arrow* indicates the remains of an old gall that released lateral branching in the following growing seasons

host may suffer reduced growth in the year of gall formation. *B. pistaciae* causes an additional unusual damage to its host: it attacks the terminal buds of new emerging branches which eventually encourage growth of axillary buds (Fig. 4). The growing branch tips are sources of development signals (especially auxin) which have systemic effects on other organs (Sachs 2005). Removal of the branch tip disrupts signal transports and destroys apical dominance (Sachs et al. 1993). The impact of the galls on the tree is not limited to the year of gall formation and may continue in the following years (see also Price and Louw 1996; Sacchi and Connor 1999).

Galling, especially in a very young plant, may thus cause a permanent and important transformation in the architecture of the host—changing it from tree to bush shape. Indeed, observations of *P. palaestina* trees in the natural Mediterranean forest of Israel confirm that small trees are very often bush-like, and are heavily infested with *B. pistaciae* galls—sometimes hundreds of galls per tree (Wool and Inbar, unpublished observation). It most likely, therefore, that the bush shapes of *P. palaestina* in nature is also a result of years of infestation by the *B. pistaciae*.

In the year of gall formation, live galls inhibit the elongation of the branch (Katz 1991). In a way, these galls replace the apical bud and impose apical dominance as long as they are live inducing changes in tissue differentiation in the branch below (Aloni et al. 1989). Weis (1984) described a similar phenomenon in midges that induce galls on apical buds of willows. However, in the autumn, the galls die along with apex bud on which it grew. This release lateral branching in the following season.

Modification of plant architecture may have variable ecological implications. The arrangement of the leaves on the plant, and consequently light absorption, depends primarily on the architecture of the branches. The level of branching has a physiological influence on the water potential in the plant. Branching intersections, as well as the formation of many thin branches, reduce water potential in the growing branches and leaves (Wilson 2000). Modifications in tree architecture may also alter subsequent colonization by other herbivores (Den Herder et al. 2004). Interestingly, in a field survey, Martinez and Wool (2003) found that on con-generic *P. atlantica* trees, aphids induced more galls on branches that were earlier browsed by cows: following browsing, more lateral branches were formed and were available for colonization by the aphids. Because of the profound effect of the *B. pistaciae* galls on *P. palaestina*, it will be interesting to examine their impact on other aphid species that form galls on the leaves of the same host (Inbar and Wool 1995).

Pistacia palaestina is a "resprouter" plant (Wool and Inbar 1998), like many other Mediterranean woody species, which are adapted to fire and browsing (Bond and Midgley 2001). In the case of *B. pistaciae* galls, the vigorous vegetative growth has been achieved by the activation of dormant buds. Modification of plant architecture by gall-formers can also reduce seed set (Silva et al. 1996). We did not find a significant effect of gall presence on fruit yield at the branch level. Obviously, it is hard to estimate the effect of the galls, on the growth and yield of the entire tree.

In conclusion, we note that *B. pistaciae* galls are abundant in *P. palaestina* trees in the Mediterranean forest of Israel, although abundance may vary between trees and years (Wool 2002). These galls dramatically impact the growth pattern of the branch for several years (at least two). Thus, it likely that in a density-dependent manner, the aphids may alter *P. palaestina* trees into a bushy shape. Our results demonstrate that the effect of gall-formers on the plant may be long lasting and therefore, require long term examination.

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