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The effect of *Agonoscena targionii* (Licht.) (Homoptera: Psylloidea) on seed production by *Pistacia terebinthus* L.

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Abstract This study investigated the potential negative effect that psyllids may have on the production of viable seeds in *Pistacia terebinthus,* a wild plant species with a circummediterranean distribution. Manipulative experiments, involving the application of insecticide, showed that the reduction in fruit maturation is rather low, not exceeding 10%. This is mainly due to other factors that determine seed inviability. Such factors include those intrinsic to the plant, such as parthenocarpy and seed abortion, and extrinsic to it, such as seed predation by chalcidoid wasps. There is much variation in the frequency of psyllids per plant; such variation appears uncorrelated with variables decribing plant size, fecundity, and distance to fruiting conspecifics. No consistency in the incidence of psyllids on a given individual plant was found between years.

Key words Insect herbivory · Sap-feeding insects Psyllidae · Anacardiaceae · Southeastern Spain

Introduction

Sap-feeding insects, and homopterans in particular, often have a detrimental effect on growth and reproduction of their host plants (e.g. Kennedy and Stroyan 1959; Windle and Franz 1979; Brown et al. 1987; Snow and Stanton 1988; Gange and Brown 1989). Much of the available information on the influence that these insects, especially the Aphidoidea, have on their hosts comes from cultivated plants (e.g. Barbagallo 1985, and references therein), whereas few studies deal with wild species (Brown et al. 1987; Snow and Stanton 1988; Gange and Brown 1989).

Here I examine the effect that *Agonoscena targionii* (Lichtenstein) (Homoptera: Psylloidea) has on the production of viable seeds in a wild tree/shrub, *Pistacia terebinthus* L. (Anacardiaceae). The psyllid is found feeding upon the fruit pulp of this species. The Psylloidea – which include about 1300 species in one family, Psyllidae – are closely related to the Aphidoidea, and are known to damage the fruits of various cultivated trees (e.g. Matvievskii 1976; Pfeiffer and Burts 1983).

The main objectives of the study were (1) to estimate the impact of psyllids on the production of viable seeds and (2) to determine the individual variation in the frequency of psyllid attack within a population and between two populations differing in plant density. Manipulative experiments, involving the use of an aphicide, allowed the evaluation of the effect of psyllids on seed production.

Methods

Study area

The study took place at the Parque Natural de Cazorla, Segura y Las Villas (Jaén province, southeastern Spain) during spring and summer of 1990. Additional observations were made the following year in the same seasons. Experiments were carried out at Las Navillas (about 1000 m in altitude), where *P. terebinthus* is quite common. The other population examined is in the Fresnedilla-Agracea area (1100–1200 m), where the plant is rather scarce. A brief description of these areas can be found in Traveset (1993a).

Study organisms

Agonoscena targionii (Psyllidae) has a wide distribution and has been found in North Africa as well as in southern Europe and Iran (Davatchi 1958). It has been reported to attack the leaves of several species of *Pistacia,* including *P. terebinthus* (Davatchi 1958). Damage, however, also takes place in the fruits, at least in this species. The psyllids suck the pulp of the fruits, exuding a sticky honeydew on them. *A. targionii* spends the winter on the plant, in a larval or adult stage, and can have up to five generations per year (Davatchi 1958). As in other species of the family, the first instars are practically immobile. The imagos are often less host-specific than the earlier instars, a trait that is related to their greater ability

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to fly and jump (Hodkinson 1974). By mid-September, they are no longer observed on the fruits. Ants of the genus *Camponotus* have often been seen on the attacked fruits, eating the honeydew. The natural enemies of the psyllids observed on *P. terebinthus* are *Tyreonotus bidens* (Bolivar, 1887) (Tettigoniidae) and *Coccinella* sp. (Coccinellidae). In the study area, no other species of *Pistacia* occurs which might serve as a reservoir of psyllids.

P. terebinthus is a dioecious tree/shrub (often reaching more than 3 m in height) with a circum mediterranean distribution (Zohary 1952). The fruits reach full size about a month after anthesis which takes place from April to June; they are 6.6±0.7 (SD) mm long and 5.9±0.7 mm wide (n=575), containing one seed each. As in the other species of *Pistacia,* a large proportion of fruits are parthenocarpic, i.e. come from unpollinated flowers; other fruits are the result of embryo abortions which occur at different stages of development, and others contain wasp larvae inside the seeds (Grundwag 1976; Jordano 1989; Traveset 1993a, b). Immature fruits, both viable and inviable, are red and have the same amount of pulp. The mature fruits are bluish-green and, except on rare occasions, they contain a viable seed (Traveset 1993a, b). Final-sized fruits, viable or not, are retained on the plant until late October. The mature fruits are removed by birds during the autumn (Traveset 1993a).

Experimental design and procedure

On 4 July 1990, shortly after psyllids were first observed on the fruits, I haphazardly chose a total of 20 trees of *P. terebinthus* in Las Navillas, regardless of whether they already had psyllids or not. From each tree, ten healthy (unattacked) fruit clusters were selected and marked (there was one exception, a plant with few fruits on which only six clusters were labelled). I treated half of the clusters with an aphicide, ZZ-Aphox (Pirimicarb, 2-dimethylamine 5,6-dimethylpirimidine 4-dimethyl carbamate) which worked well against psyllids, leaving the other half as controls. The aphicide was sprayed three times on each treated cluster, approximately every two weeks until no more psyllids were seen on the fruits (mid September). In order to avoid any possible effect of the aphicide on the control fruits, the control clusters were selected from branches that were not too close to the treated ones. The total number of fruits in each cluster was recorded. By the end of September-beginning of October, I checked all clusters, recording both the total number of fruits and the number of fruits that ripened from each. I also recorded, for each tree, the total number of fruits infested by psyllids, as well as the number of mature fruits in the entire crop (both numbers were estimated by counting groups of about 50 fruits per whole plant).

It must be noted that by having two different herbivory treatments on the same plant, rather than different treatments on different individuals, the impact of herbivores on seed production might either be under- or overestimated, as pointed out by Snow and Stanton (1988). If infested fruit clusters used more energy and nutrients than uninfested clusters, the effect might be underestimated, whereas if psyllid feeding caused unused resources to be allocated to uninfested clusters, the effect of psyllids would be overestimated. Unfortunately, we do not know the relative amount of resources used by psyllids and uninfested fruits. In the case of *Pistacia terebinthus,* the usually low incidence of psyllids on an individual makes it unlikely that they often deprive other parts of the plant of resources. However, in those clusters where fruits are intensely infested, the nearby leaves from the same branch dry up together with the fruits. By choosing fruit clusters well separated from each other, the effect of resource-sharing among experimental branches was probably much reduced. Furthermore, the large differences among individuals in seed inviability rendered it better to use the two treatments within the same plant.

To determine a possible association between a plant trait and the frequency of psyllids on it, I measured several variables describing plant size – plant height, maximum crown diameter – and fecundity – total number of fruits produced – and also calculated the average distance to the two nearest fruiting conspecifics.

To estimate the incidence of psyllids in the two plant populations I examined, in 1990, a total of 35 trees from Las Navillas and 15 from Fresnedilla-Agracea, recording the proportion of the crop infested by these insects. In the fruiting season of 1991, I observed a total of 77 trees from both populations, recording again crop size and proportion of fruits attacked by psyllids. To determine the consistency between the two years in psyllid occurrence on an individual plant, I re-examined 32 of the trees studied in 1990.

Statistical analysis

All analyses were performed using the SAS statistical package (SAS Institute 1987). A two-way ANOVA, including treament and tree as fixed and random effects, respectively, tested for differences in the proportion of mature fruits. Of the 20 experimental plants 6 were not attacked by psyllids and were thus excluded from the analysis. Angular transformation was used to normalize the proportions. A multiple regression analysis tested for any relationship between the plant variables measured and psyllid occurrence. Unless otherwise indicated, means are accompanied by standard deviations.

Results

Of the 20 plants used in the experiment, 14 were attacked to a greater or lesser extent by psyllids. Of the total 63 control clusters in the 14 plants (initially 68, but 5 were lost due to a storm which broke some infructescences), 25 (40%) were infested by these insects. Clusters treated with aphicide, in contrast, suffered no damage by psyllids.

The total number of fruits per cluster at the beginning of the experiment was not significantly different between control and treated clusters (65±31, n=98 vs. 63±29, n=98, respectively).

Table 1 Mean and SE of the percentage of fruits that matured in the clusters that were attacked by psyllids and in those that remained intact. Data from 1990. Numbers in parentheses are the clusters from which fruits were counted (note that they are lower in the first column because a larger number remained intact; treated and unattacked control clusters are pooled in the second column). Clusters that were partially or totally lost during the experiment are excluded

Tree #	% Fruits maturing in attacked clusters	% Fruits maturing in unattacked clusters
1	17.2±14.7 (3)	25.2±2.9 (6)
2	0 (4)	22.2±5.8 (5)
3	18.2±9.9 (2)	60.2±4.1 (8)
4	0 (1)	5.4±2.9 (9)
5	0 (2)	3.8±1.8 (4)
6	0 (1)	2.2±2.2 (3)
7	0 (2)	0 (8)
8	8.3±0 (1)	27.4±6.0 (5)
9	9.8±9.8(2)	22.1±7.9 (2)
10	21.2±0 (1)	34.2±6.2 (5)
11	0 (3)	0 (6)
12	4.2±4.2 (3)	25.5±13.2 (4)
13	23.6±0 (1)	25.4±4.6 (6)
14	1.8±0 (1)	23.7±6.8 (2)
Grand mean	6.5±2.2	20.1±2.4

Table 2 Total crop (viable + inviable seeds) and losses in viable seeds due to psyllids in the infested trees. The percentage of viable seeds that are lost due to psyllids in each tree is the percentage of the crop attacked multiplied by the result of subtracting the two columns in Table 1 (i.e. by the percentage of attacked fruits that would have reached maturity had they not been attacked)

Tree	Crop size	% Crop attacked	%Mature crop lost
1	5400	7.4	0.6
2	8750	43.4	9.6
3	17500	7.1	3.0
4	1000	15.0	0.8
5	800	75.0	2.9
6	2100	47.6	1.1
7	900	5.6	0
8	2500	28.0	5.4
9	2150	18.6	2.3
10	20000	1.8	0.2
11	2700	16.7	0
12	10000	2.5	0.5
13	15000	2.3	0.04
14	10000	4.5	1.0

A significantly lower proportion of fruits matured in the clusters that were attacked than in those that remained intact ($F_{1,13}$=16.77, P=0.001) (Table 1). A total of 36 clusters were lost (mainly because of the severing of infructescences due to a storm) during the experiment, and were not included in the analyses. The aphicide itself did not have any significant effect on fruit maturation ($F_{1,71}$=0.20, P>0.05); this was determined by comparing proportion of maturing fruits in treated clusters and unattacked control clusters.

In 44% of the attacked clusters, the psyllid infestation was so high that the insects caused complete drying of the infructescences, which became yellowish and promptly fell off the tree.

Due to the fact that some individuals of *P. terebinthus* mature only a small proportion of the fruits they produce, and since psyllids attack fruits regardless of whether they contain viable seeds or not, the net effect of these insects on viable seed production varies among trees even if they have a similar incidence of psyllid attack (Table 2).

The frequency distribution of the proportion of the crop attacked by psyllids is shown in Fig. 1. The incidence of these insects on an individual tree during 1990 varied between 0 and 75% of the fruit crop, the average being 8.0±15.1% (n=50). In 1991, this figure was 16.3±22.3, ranging from 0 to 90% (n=77). A median test showed no significant differences between the two years (χ^2=0.70, P>0.05).

Although the maximum percentage of the crop attacked was found in Las Navillas, the variance within each area was very high both years. The plant variables measured (height, crown diameter, total number of fruits and average distance to the two closest fruiting neighbours) did not have any significant effect (all P values >0.05) on the proportion of fruits attacked by psyllids, explaining less than 1% of its variance. Moreover, there was no consistency between the two years in psyllid incidence on an individual plant (r_s=0.17, P>0.05). Of the 32 individuals examined both in 1990 and 1991, 5 (16%) had no fruits attacked in either of the two years.

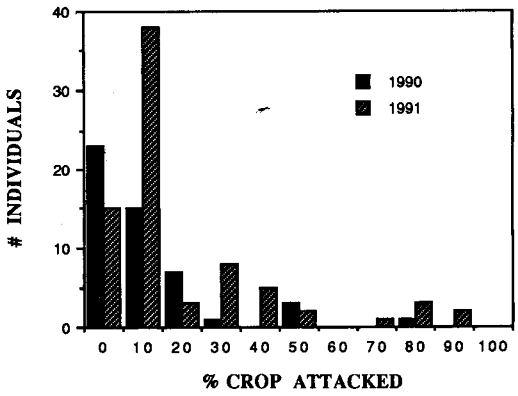

Fig. 1 Frequency distribution of the percentages of fruits attacked per crop (n=50 and n=77 for 1990 and 1991, respectively)

Discussion

Agonoscena targionii has shown to reduce, to a greater or lesser extent, the potential number of viable seeds produced. The actual damage to the plant is low, in no case representing a reduction in the number of viable seeds of more than 10%. This is mainly due to the large number of inviable fruits (parthenocarpic, aborted or damaged by wasps) produced by the plant, which are, apparently, not distinguished by the psyllids from viable ones.

A similar incidence of psyllid attack between two trees does not translate into a similar negative effect on the production of mature fruits (this is clearly observed in Table 2, comparing tree 2 and tree 6, for instance). In other individuals (e.g. trees 7 and 11), the attack by psyllids has no effect on seed viability because no fruits matured anyway for reasons intrinsic to the plant. Even in those cases where psyllid attack is intense (75–90% of the crop), the fitness reduction for the individual plant is usually much lower. This would not be the case if the viable seed production of the species attacked were less limited by other biotic and abiotic factors.

Insect herbivory has been shown to reduce the number and size of seeds produced in a variety of species (Bentley et al. 1980; Louda 1982, 1984; Kinsman and Platt 1984; Brown et al. 1987; Snow and Stanton 1988). The effect of sap-feeding insects, in particular, causes a decrease in seed weight of species such as *Vicia hirsuta* (Brown et al. 1987), and in the number of seeds in species such as *Raphanus sativus* (Snow and Stanton 1988). In the present case, the effect on reproduction is direct because the insects are feeding upon the sap of the fruit, somehow preventing the complete development of the seed in it. It is possible that the seed needs the protection given by a juicy pulp to survive high temperatures and aridity, although this remains to be demonstrated.

The incidence of psyllid attack on an individual tree was extremely variable. This variability did not respond, however, to any of the traits measured from each plant. Large differences between individual plants in susceptibility to attack have also been found for other psyllids (Journet 1980) and aphids (Snow and Stanton 1988; Akimoto 1990). Gene flow between insect populations on separate trees might be highly restricted, as found by Akimoto (1990) in aphid populations. This author finds that between-tree variations were consistent over years, suggesting that heterogeneity in host traits may have promoted the evolution of philopatry in these insects. Wool (1990), on the other hand, finds that aphid population sizes on individual trees vary considerably among years. In the present case, no consistency was observed between 1990 and 1991 in the incidence of attack; the fact that five individuals suffered no attack in either of the two years suggests that some trees are either less preferred or less encountered by the psyllids. However, it is also possible that, as found in aphids by Maddox and Capuccino (1986), resistance to psyllids is due to some environmental and/or genetic factors.

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