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Do anthocorid predators respond to synomones from *Psylla*-infested pear trees under field conditions?

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Abstract

Because Y-tube olfactometer experiments in the laboratory showed a response of anthocorid bugs to odour from *Psylla*-infested leaves, it was of interest to assess its relevance under field circumstances. This was done by measuring the density of predatory bugs on pear trees adjacent to *Psylla*-infested or control trees that were covered with fine mesh gauze-screens. In this way odours from these caged trees could spread through the screen, while contact with the *Psylla* prey in the cage was prevented. The density of anthocorid predators around cages with heavily infested trees was significantly higher than around uncaged control trees and around cages containing uninfested or little infested trees. Covering a cage with *Psylla*-infested trees by an airtight plastic sheet led to an immediate drop in the density of anthocorid predators, whereas removal of the sheet led to predator aggregation again. The results of these field experiments strongly support the hypothesis that anthocorid predators respond to volatile chemicals emanating from *Psylla*-infested pear trees.

Introduction

Responses of arthropod predators to volatile chemicals emanating from plants infested by their prey (synomones *sensu* Dicke & Sabelis, 1988) have been convincingly demonstrated in several laboratory experiments with olfactometers and windtunnels and with different predator-herbivore-plant systems: predatory mites respond to odours from bean plants infested by spider mites (Dicke *et al.*, 1990a, b) and parasitoids respond to odours from corn plants infested by *Heliothis* caterpillars (Turlings *et al.*, 1990). Such evidence has also been obtained for two anthocorid predators, *Anthocoris nemorum* (L.) and *A. nemoralis* (Fabricius), responding to odours from pear leaves infested by psyllids, *Psylla pyri* L. and *P. pyricola* Forster (Drukker & Sabelis, 1990). Moreover, recent GC-MS analyses of volatiles in the headspace of infested and uninfested pear trees show that *Psylla* attack on pear trees triggers the production of volatile chemicals, such as methyl-salicylate, (E,E)- α -farnesene

and 4,8-dimethyl-1,3(E),7-nonatriene (Scutareanu c.s., unpubl.). As these volatile compounds are likely of plant origin, it is reasonable to hypothesize that the herbivore triggers the plant to produce them (but note that a microbial origin cannot yet be excluded). All these laboratory experiments and analyses demonstrate that olfaction is implicated in prey-searching. What they do not show, is how the chemical information is used to find the prey (Sabelis *et al.*, 1984; Sabelis & Dicke, 1985; Sabelis & van der Weel, 1993) and to what extent orientation responses can be manifested in the field. In this paper, we deal with the latter question by studying responses of anthocorid predators to *Psylla*-infested trees in a pear orchard.

This predator-prey-tree system is very suitable for studying the role of volatiles in searching behaviour in the field because the predators have to migrate each year into pear orchards to find their psyllid prey and because it seems reasonable to hypothesize that the migrating predators will use chemical signals related to the presence of psyllids on the pear trees. In April/June

anthocorid predators forage predominantly for aphids on trees outside pear orchards, so that they have to migrate into the pear orchards in July/August, when *Psylla* populations expand and become a profitable food source (Solomon *et al.*, 1989). It is also reasonable to hypothesize that natural selection will promote pear trees releasing volatiles upon infestation by psyllids as they will incur severe damage when *Psylla* populations grow unchecked (Atger, 1982; Blom *et al.*, 1985; Bouyjou *et al.*, 1984; Booij, 1990; Fuog, 1983; Herard & Chen, 1985; Hodgson & Mustafa, 1984; Solomon *et al.*, 1989; Stäubli & Anthonin, 1984; Trapman & Blommers, 1992; C. J. Booij, pers. comm.). Especially when outbreaks of psyllids are severe, a timely influx of predatory bugs from outside the pear orchard plays a crucial role in pest suppression (Booij, 1990). Immigration of anthocorid predators probably depends on the density of psyllid prey in the pear orchard (Balkhoven & Jansen, 1988; Stäubli *et al.*, 1992) and therefore it is reasonable to hypothesize that *Psylla*-induced production of plant volatiles has an influence on predator migration.

Preliminary experiments showed that it is possible to intercept migrating anthocorids before they arrive at the *Psylla*-infested tree (Drukker *et al.*, 1992). This was done by putting a cage of gauze screen over infested pear trees. The interception was manifested by arrestment of predatory bugs on trees surrounding the cages with infested trees. In this paper we discuss the results of a similar type of experiments (1) to measure the population growth of psyllids throughout the summer season on selected pear trees in cages and on the trees surrounding the cages, (2) to simultaneously assess the response of migrating anthocorids to odours from these cages containing pear trees with various levels of *Psylla*-infestation, and (3) to study how the response of the predatory bugs is changed immediately after stopping the odour emission from the cages.

Materials and methods

Experimental site. The field experiments were carried out at the experimental orchard 'De Schuilenburg' in Kesteren, The Netherlands. Here, a total area of c. 7000 m² was planted with 9 rows of pear trees (c.v. Conference) in 1988 and was made available for our preliminary experiments in 1991 (Drukker *et al.*, 1992) and the experiments in 1992, the results of which are the subject of this paper. This pear orchard was bordered by a hedgerow at three sides: the south-

ern hedgerow consisting of willow trees, the western hedgerow consisting of alder trees, the eastern hedgerow consisting of a mixture of trees and shrubs (thus no hedgerow at the northern side). Throughout the growing season all hedgerows contained anthocorids and several homopteran prey species in large numbers (especially *Psylla alni* (L.) on alder), but no pear psyllids (Scutareanu *et al.*, 1993).

Caging the pear trees. To prevent the predatory bugs from contacting their prey and to allow them to respond only to prey-related signals that transfer information over some distance away from the tree (sound, odour) some selected pear trees were covered by a cage of 2 × 2 × 2.4 m, made of gauze screen with a mesh width of 1 mm. Throughout this paper we will assume that the signal consists of volatile chemicals emanating from the infested tree and not of sounds (see also discussion).

Apart from fencing off the predators the cages around the infested trees also served to prevent the pear psyllids from escaping and moving to neighbouring trees. To create high levels of *Psylla*-infestation the trees inside the cage were first sprayed with a broad spectrum insecticide for predator extermination and then (once per week during 5 weeks) provided with pear tree branches infested mainly by *Psylla pyricola*, taken from an orchard in the Watergraafsmeerpolder, Amsterdam. By using permethrin (Ambush, 15 mg/l, 1.5 l/tree) it was ensured that the natural enemies (including anthocorids) were wiped out while leaving a large part of the pear psyllids unharmed as they are resistant to this pyrethroid (Stäubli & Anthonin, 1984; Oomen & Romeyn, 1984). To prevent ground-dwelling predators (ants, earwigs, carabids) from invading the trees and affecting *Psylla* population growth on the caged tree, Tanglefoot was applied as a sticky barrier on the trunk of the pear tree. Regular checks during the year demonstrated that the pyrethroid treatment and the Tanglefoot barrier ensured that the predators were virtually absent in the cages. To create very low *Psylla*-infestation levels pear trees inside cages were sprayed four times at two-week intervals with amitraz (2 ml/l, 3 l/tree). This insecticide has the advantage of being effective against pear psyllids while leaving the anthocorids virtually unharmed (Hassan *et al.*, 1987).

Design of field experiments. Four treatments were applied: (1) severe *Psylla*-infestation on caged trees, (2) little or no infestation on caged trees, (3) low (nat-

Fig. 1. Spatial arrangement of pear trees under the following treatments: ▨ – caged tree with high density of pear psyllids □ – caged tree with little or no pear psyllids + – open 'control' tree at 30 m from caged trees * – open 'control' tree at 65–90 m from caged trees

ural) infestation on pear trees that were not in cages and c. 30 m away from treatment 1, (4) idem as treatment 3 but now c. 65 to 90 m away from trees under treatment 1. The latter three treatments could be considered as three types of control experiments for treatment 1. Each of the four treatments was replicated three times with each replicate in a separate row of pear trees, i.e. in row 2, 6 and 9. The trees selected for treatment were at least 30 m apart, i.e. 14 pear trees in between selected trees. Treatment 1 and 2 were applied to trees in the northern part of the pear orchard and treatment 3 in the middle, whereas treatment 4 was applied in the southern part. Thus, comparing the treatments can only be done under the assumption that there are no systematic effects of spatial position in the pear orchard. This set-up was chosen because a randomized design has a higher probability of possible interactions between effects of treatments, since it is not known over how long a distance the attraction is effectuated. An overview of the spatial arrangement is given in Fig. 1.

Sampling procedure. Two methods of sampling were simultaneously used with a frequency of once every one or two weeks. To estimate the density of immature psyllids (eggs and larvae), samples of 30 leaves were taken from the tree crown and brought to the laboratory where they were inspected under a binocular microscope. This method was applied to pear trees inside the cages and adjacent to the cages in the same row. To estimate the density of adult psyllids and both juvenile and adult anthocorids, samples were collected in nets kept under a branch that was beaten three times using a club to dislodge the insects from the branch. This

method was applied to a total of 30 branches from the two pear trees at both sides of each cage and also to the pear trees surrounding preselected control trees without cages. As a check on the population size of adult psyllids inside the cages beating net samples were also collected at the very end of the field experiment.

Experimental interruption of odour emission from cage. During the field experiments in 1992 the odour emission from one of the three severely infested, caged trees was interrupted by putting an airtight plastic sheet over the cage. The plastic (polyethene) sheet (thickness: 1.5 mm) was transparent and assumed not to release repellent/attractive substances. This experiment was started on the 12th of August, when the influx of anthocorids was at its peak. The density of predatory bugs in the trees surrounding the cage was assessed before and after positioning of the sheets. After two weeks the sheet was removed and the effect of removal on the density of predatory bugs on surrounding trees was measured again.

Results and conclusions

Effect of treatments on *Psylla* densities: caged and uncaged trees. To evaluate the effect of the treatments on *Psylla* densities leaf samples were taken from trees selected for the field experiment. The results in Fig. 2a show that (1) compared to all three types of control trees the density of psyllid nymphs is much higher on caged trees that were provided with branches infested with *P. pyricola* and that (2) the density of psyllid nymphs is lower on the caged trees treated with Amirtaz than on open, untreated control trees at 30–90 m distance from the caged trees. In all these cases data ranges did not overlap between treatments, making statistical testing superfluous.

Effect of treatments on *Psylla* densities: trees adjacent to caged and uncaged trees. On trees adjacent to the caged, infested trees (Fig. 2b, c and d) *Psylla* densities (all stages) were much lower than within the cage, but compared with trees adjacent to the caged or uncaged control trees there appeared to be a somewhat higher density level. This difference was significant according to a Mann-Whitney test when applied to the annual totals of per-tree densities of *Psylla* nymphs ($w=6$, $P<0.05$), as well as *Psylla* eggs ($w=6$, $P<0.05$), but the same test repeated for each sampling date showed significant differences on three sampling dates in July,

(a)

(b)

Fig. 2. The abundance of pear *Psylla* nymphs (number per leaf) on pear trees selected for the various treatments (2a), and the abundance of *Psylla* eggs (2b), nymphs (2c) (number per leaf) and *Psylla* adults (number per branch beaten 3 times) (2d) on trees adjacent to these selected trees. Bold type lines: caged trees with high *Psylla* infestation ($n=3$); Thin lines: caged trees with little or no psyllids ($n=3$); Dashed lines: open 'control' trees at a distance of 30–90 m from the caged trees ($n=6$). Points indicate means and bars indicate standard deviations. Note that Fig. 2a has a logarithmic scale on the y-axis, whereas Fig. 2b, c, d have a linear y-axis.

(c)

(d)

Fig. 2. Continued.

but starting from July 30 until September 9 the densities in all replicates dropped and no statistical differences were observed for both eggs and nymphs. With respect to *Psylla* adults a Mann-Whitney test applied to the annual totals of per-tree densities also showed significant differences ($w = 6$, $P < 0.05$), but the same test repeated to each sampling date showed that the difference was consistently significant in July, but after July the differences were much more variable. Inspection of Fig. 2b, c and d shows that the numbers of *Psylla* eggs, nymphs and adults on adjacent trees steeply decline at the end of July and early August.

These results suggest that the cages were not completely 'Psylla-proof' or that the in-and-out movement of samplers via the cage doors enabled some *Psylla* adults to escape (leaving aside the theoretical possibility of pheromonal attraction). However, the effects of leakage seem less important after July.

Effect of treatments on anthocorid bugs. Based on beating net sampling of trees adjacent to the trees selected for treatments it was found that the numbers of nymphs in July and August as well as the numbers of adult anthocorids in August are higher around the caged and severely infested trees, than around any of the control trees. With respect to the annual totals for the two treatments with caged trees (Fig. 3) the data ranges for the adult anthocorids do not overlap (18–20 adults vs 1–7 adults; 8–15 nymphs vs 2–3 nymphs), making statistical testing superfluous. Mann-Whitney tests repeated for each sampling date show that in the second half of July and the whole month of August the trees adjacent to the severely infested pear trees harbour a significantly larger number of adult anthocorid bugs than the caged, control trees ($w = 6$ in all cases; thus, $P < 0.05$). The three types of control experiments do not significantly differ from each other. Thus, there are good reasons to conclude that *Psylla* infestation has an effect on the density of anthocorid bugs on adjacent trees.

Identification of the anthocorids collected by beating net sampling revealed that several species of anthocorids were attracted to the infested pear trees. Figure 4 shows the generic composition; it appears that *Anthocoris* spp. have a large share in the population of anthocorids attracted, but *Orius* spp. are at least as abundant. In order of their abundance (in ratio of 5:3:2:1:1) the following species were identified in a subsample of all specimens collected: *Anthocoris nemorum*, *Orius vicinus* *O. minutus*, *O. majusculus* and *A. nemoralis*.

In all samples we discriminated between the *Anthocoris nemorum*, *A. nemoralis* and the genus *Orius* and did not take the effort to discriminate between the various *Orius* spp (except for the subsample mentioned above), as the discriminating characters of *Orius* spp. are less conspicuous. Taking the data only as far as they were collected in August, the densities of each of these three groups of anthocorids differed significantly (according to Mann-Whitney tests) between treatment (high prey density on caged tree) and control (low prey density on caged tree) (Table 1). This is remarkable because the total numbers of individual anthocorids was not high and after splitting them into three categories they became low. Despite this reduction in sample yield per category the significant difference between treatment and control was maintained.

Interruption of odour emission. Covering one of the three severely infested, caged trees with airtight plastic had a marked effect on the densities of anthocorids on the adjacent pear trees (Fig. 5). Before the 12th of August 1992 adult anthocorids were observed in densities of c. 1 per 10 branches on all trees adjacent to the caged trees, but two days after covering one of the caged trees with airtight plastic not a single predatory bug was found on the adjacent trees, whereas the trees adjacent to the other two caged, infested trees continued to harbour anthocorid bugs in densities of 4 or 7 adult anthocorids per 30 branches. This drop to zero density is unlikely to be a coincidence as – in the period from mid July through August – none of the trees surrounding the caged trees had anthocorid densities equal to zero except when the cage was covered with airtight plastic. Two weeks after plastic sheet treatment (26th August), one day after the airtight sheet was removed, adult anthocorids were found again on the adjacent trees in densities of more than 2 per 30 branches, which was in the same order of magnitude as the densities found on trees adjacent to the other two caged trees. That a sudden interruption of odour emission has such an immediate effect on the observed predator densities, is a strong indication that the predatory bugs respond to odours; they are arrested when the odours are present and they actively resume search when these odours disappear.

Discussion

Interpretation of treatment effects. There are three hypotheses on the cues that stimulated the anthocorid

Fig. 3. The abundance of anthocorid nymphs (3a) and adults (3b) (number per branch beaten 3 times) on trees adjacent to trees selected for treatments. Bold type lines: caged trees with high *Psylla* infestation (n=3); Thin lines: caged trees with little or no psyllids (n=3); Dashed lines: open 'control' trees at a distance of 30–90 m from the caged trees (n=6). Points indicate means and bars indicate standard deviations.

Table 1. Total catches in August, carried out separately pertaining for the most abundant taxa: (1) *Anthocoris nemorum* and (2) *Orius* spp.

Treatments	<i>Anthocoris nemorum</i>			<i>A. nemoralis</i>			<i>Orius</i> spp.		
	Replicate no.			Replicate no.			Replicate no.		
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
Caged trees with high <i>Psylla</i> density	6	3	3	0	2	1	4	8	7
Caged trees with low <i>Psylla</i> density	1	2	2	0	0	0	0	0	1

Fig. 4. Composition of anthocorid fauna on trees adjacent to the caged trees with high *Psylla*-infestation throughout the year 1992. Black columns: *Anthocoris nemorum* and *A. nemoralis*; White columns: *Orius majusculus*, *O. vicinus* and *O. minutus*. The total number of anthocorids found at each sampling date are given above each column.

Fig. 5. Anthocorid adults on trees adjacent to three caged trees with high *Psylla*-infestation, one of which was temporarily wrapped in an airtight plastic sheet to interrupt odour emission. The black columns relate to the anthocorids observed on the trees adjacent to the sheet-covered cage, whereas the other two columns relate to the trees adjacent to the other two caged trees, that were not covered by a sheet.

predators to aggregate close to the cages with infested trees. First, the predators may respond to odour produced by the pear trees within the cages and induced in the pear leaves by *Psylla* feeding (the plant synomone hypothesis). Second, they may respond to pheromone production by female psyllids on the infested trees within cages (the prey pheromone hypothesis). Third, they may respond to the *Psylla* prey on trees adjacent to the (caged) infested trees, which are present at slightly elevated densities as a result of inadvertent leakage of psyllids from the cage.

The third hypothesis seems unlikely because the densities of *Psylla* prey around the caged, infested trees are very low in an absolute sense (on average 0.3 nymph per leaf with a range of 0–1.3 nymph per leaf) and because they are in the same range as (and do not differ significantly from) densities on the uncaged, control trees (on average 0.2 nymph per leaf with a range of 0–1.2 nymph per leaf). Moreover, this prey resource on the trees adjacent to the caged trees seems to be of little value to the predators because the prey stages vulnerable to predation by adult anthocorids, i.e. the *Psylla* eggs and nymphs (Lauenstein, 1980), are scarce just in the period when the aggregation of anthocorids is most pronounced; after July 23 the most crucial effects on the anthocorid aggregation were observed and just in that period there were no significant differences in densities of *Psylla* nymphs between the caged trees with and without *Psylla* infestation. It should be stressed that anthocorid adults are not likely to seize *Psylla* adults due to the prey's ability to escape by jumping away. Hence, the occasionally higher densities of *Psylla* adults around the infested trees are of little or no relevance with respect to the aggregation of anthocorid adults.

More specifically the mean egg densities in August, 1992, were between 0.05 and 0.8 per leaf, and psyllid nymph densities were even lower than those of psyllid eggs (maximally 7 per 30 leaves; thus on average less than 0.25 per leaf). This represents a total prey density (eggs and nymphs) that certainly does not suffice for anthocorids to complete juvenile development and that certainly does not meet the daily food demands of anthocorid adults. According to laboratory studies by Brunner & Burts (1975) anthocorids cannot develop to maturity at densities of 5 nymphs or eggs per leaf per day and anthocorid adults require more than 30 psyllid nymphs/eggs per day for normal egg production, which corresponds to a prey density of 30 to 200 psyllid nymphs per leaf. For these reasons we do not think that the egg and nymph supply on trees adjacent to the caged trees can explain the observed increase in aggregation of anthocorids on these trees.

Odour seems much more likely to be the cue triggering the aggregative response. The strongest support comes from the experiment where a cage with an infested pear tree was covered with plastic. This treatment caused the anthocorids to stop aggregating, whereas cover removal caused them to aggregate again. This is convincing evidence for a role of odour, but whether the odour originates directly from the psyllids (the prey pheromone hypothesis) or indirectly – after feeding by the psyllids – from the plant (the plant synomone hypothesis), remains to be investigated. Based on what is currently known, the prey pheromone hypothesis has little support because no sex pheromones or other types of pheromones have been shown to play a role in psyllids and if a sex pheromone would be involved, one would expect a preponderance of *Psylla* males on the trees adjacent to the infested trees. This appeared clearly not the case, as the female/male ratios on the trees adjacent to the infested tree and the control tree did not differ (1.03 vs 1.17 female/male). In addition, the volatile compounds that have been identified in the headspace of infested pear trees, can in principle all be produced by the plant (Dicke *et al.*, 1990a; Turlings *et al.*, 1990) and are therefore not likely to be produced *de novo* by the phytophagous insect. Hence, the available evidence points to a major role of plant produced synomones in attracting or arresting anthocorid predators to infested pear trees.

That olfaction is implicated in the searching behaviour of anthocorid predators, seems quite likely. Our olfactometer experiments in the laboratory (Drukker & Sabelis, 1990) have demonstrated behavioural responses of *A. nemoralis* and *A. nemorum*

to odours from uninfested plants and odours from pear leaves infested by *P. pyricola*. Similarly, Mpakagiannis (1982) and Dwumfour (1992) showed that *A. nemorum* responds to odour from bean leaves infested by two-spotted spider mites. In all these olfactometer experiments in the laboratory orientation on visual stimuli can be ruled out as a possibility, but an influence of sound, as demonstrated for sexual attraction in other Homoptera (Claridge, 1985; Winter & Rollenhagen, 1990) cannot be excluded. However, auditory signals in related Homoptera of similar size are thought to be effectively transmitted through the leaf substrate, not through air. Thus, the response to infested leaves in the olfactometers is likely to be triggered exclusively by the perception of odour.

Prospects. Our next step will be to isolate and identify the volatile chemicals emanating from uninfested and infested pear trees. These chemicals can then be released in the field to elucidate their effect on attracting anthocorids by comparison with the attractivity of infested pear trees. Most likely, the odours originate from the plant after being attacked by the pear psyllids. Another possibility is that the plant chemicals pass the digestive system of the psyllids and volatilize from their excretions, such as faeces or honeydew. However, proof that the producer is not the psyllid itself, is still needed. It seems not plausible from a selectionist's point of view that psyllids betray themselves to their predators by releasing odours, but if the odours serve other vital functions, the benefits may outweigh the costs in terms of increased predation risk. A major question left unanswered by the field experiments is why the anthocorid predators were found arrested on trees adjacent to the caged, infested ones (It is possible that such arrestment also occurred on the gauze screens of the cages, but these have not been inspected). There are several alternative, but not mutually exclusive explanations. First, it may still be profitable to forage on the adjacent trees because some leakage of psyllid adults resulted in a somewhat higher prey density. Second, the higher density may be a byproduct of the absence of some other (e.g. visual) stimuli that would normally help to home in on the odour source. Third, it may be part of the predator's searching strategy not to continue investing in energy-consuming flight upon perception of a signal that tells them their prey is nearby. It may be more economic to respond by landing and continue by ambulatory search on the trees. As this mode of searching takes more time than flight, the result is a higher density of predatory bugs on adjacent

trees. Fourth, the adjacent trees may have become contaminated with the volatile chemicals from the infested trees and release them at a slower rate with the consequence that some predators are arrested. Or these trees may actively respond to odours from the infested tree by releasing volatile chemicals themselves. In this way the adjacent pear trees would misguide flying predatory bugs by luring them away from the predator flux to the infested trees and thereby exploit them for their own protection. Phenomena pointing at this possibility have been found in studies of predatory mites and their response to clean bean and cotton plants previously exposed to odour from spider-mite infested plants (Bruin *et al.*, 1992).

As a final important question with particular reference to biological control of the pear psyllids one may ask where the anthocorid bugs came from that aggregated around the caged pear trees with high *Psylla*-infestation. One possibility is that the aggregation is no more than a regrouping of predators within the pear orchard. The other possibility is that they migrated from the hedgerows (or from trees elsewhere) into the pear orchard. Support for the latter hypothesis is presented in Drukker *et al.* (1992) and Scutareanu *et al.* (1993) who showed that the peak of adult anthocorids in the pear orchard is not preceded by a corresponding peak in immature anthocorids, whereas precedence of the immature peak was found in the hedgerows bordering the pear orchard. Future studies with marked individuals should provide more definite proof of the anthocorid predators migrating from other trees into the orchard when psyllid densities increase. If this hypothesis holds, it would be a unique case demonstrating the importance of migratory flight and synomones for biological control.

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