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DOI

[10.1007/BF00058895](https://doi.org/10.1007/BF00058895)

Publication date

1993

Published in

Experimental and Applied Acarology

[Link to publication](#)

Citation for published version (APA):

Sabelis, M. W., & van der Weel, J. J. (1993). Anemotactic responses of the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, and their role in prey finding. *Experimental and Applied Acarology*, 17, 521-529. <https://doi.org/10.1007/BF00058895>

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Anemotactic responses of the predatory mite, *Phytoseiulus persimilis* Athias–Henriot, and their role in prey finding

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(Accepted 3 May 1993)

ABSTRACT

Sabelis, M.W. and van der Weel, J.J. 1993. Anemotactic responses of the predatory mite, *Phytoseiulus persimilis* Athias–Henriot, and their role in prey finding. Exp. Appl. Acarol. 17: 521–529

Although it is well established that the predatory mite *Phytoseiulus persimilis* Athias–Henriot responds to odour emanating from leaves infested by its phytophagous prey, the two-spotted spider mite *Tetranychus urticae* Koch. little is known of the behavioural mechanisms elicited by odour perception and how they contribute to finding the prey. In this paper the influence of prey-related odour on orientation to wind direction is discussed. It was analysed by observing the predator's walking paths in still air and in an air stream uniformly permeated either with or without prey-related odour stimuli. The results show that well-fed predator females move upwind in presence of these stimuli, but downwind otherwise. Starved predators always move upwind. The anemotactic responses observed are therefore both odour-conditioned and (feeding) state-dependent.

In an attempt to explain these responses it is argued that the anemotactic responses of well-fed predators may contribute to arrestment within the area marked by a cluster of prey-colonized leaves. The anemotactic responses of starved predators may help them to find clusters of spider mite colonies located upwind. Why predatory mites also move upwind in absence of prey-related odour stimuli, is a question that remains to be answered.

INTRODUCTION

That predatory mites (Acari: Phytoseiidae) can respond to volatile chemicals (synomones) released by plants after being infested by spider mites (Acari: Tetranychidae), has been convincingly shown by use of Y-tube olfactometers (Sabelis and Van der Baan, 1983; Sabelis *et al.*, 1984a,b; Sabelis and Dicke, 1985; Dicke *et al.*, 1986; Dicke and Groeneveld, 1986; Dong and Chant, 1986; Dicke, 1988; Dicke *et al.*, 1988; Bruin *et al.*, 1992) and chemical analyses (Dicke *et al.*, 1990ab). These olfactory responses may well promote the likelihood of finding prey, but in view of the complexity of their natural environment it is as yet unclear to what extent the predator really benefits. Predatory mites are small and they search by walking

on the surface of plants or soil, which comprises so many hurdles, deviating routes, dead-end streets and dangers, that it is not at all obvious whether they will always find their prey after perceiving the odours.

Yet, even if a predatory mite will stand a very low chance to reach the odour source anyway, natural selection will favour a more elaborate and effective repertoire of responses to synomones. To see this, consider a randomly searching predator that may reach the spider-mite infested plant with probability 1 out of a million times. Suppose its ability to respond to the synomones increases this probability to 2 out of a million, then the chances for this predator are still very low in an absolute sense, but they increased twofold when compared to the randomly searching predator. Note that for the same reason the production of synomones by the plant is favoured by natural selection. The important lesson to be drawn from this simple example is that low rates of arrival at the odour source should not lead one to think that the underlying searching mechanisms are probably primitive and irrelevant. On the contrary, it should be taken as a good reason to expect strong selection for ever more effective searching behaviour of predatory mites.

Rather than investigating the effect of all possible complexities on arrival rates, we studied the searching behaviour in an environment that is simple, yet much more complex than a Y-tube in that: (1) the environment is larger, and (2) consists of a grid of wire positioned in an air stream with or without synomone. In this paper, we describe experiments with the predatory mite *Phytoseiulus persimilis* Athias-Henriot in an air stream that was permeated (1) with volatile kairomones emanating from Lima bean plants infested by two-spotted spider mites, *Tetranychus urticae* Koch, or (2) with volatiles emanating from uninfested Lima bean plants, or (3) without any of the odours present in (1) and (2).

MATERIALS AND METHODS

Experimental conditions

All experiments were carried out in a large room ($9 \times 6 \times 3.2$ m) with its windows covered by luxaflex and some additional black plastic taping. The light was produced by a series of daylight fluorescent tubes at the ceiling. It was made diffuse by hanging a thin white cloth under the lamps near the position of the experimental set-up. Temperature ranged between 20 °C and 26 °C and relative humidity varied from 35% to 70%.

Experimental set-up

In the middle of the room ($8.7 \times 5.7 \times 3.2$ m) a few tables supported the experimental set-up shown in Figure 1. At one side of the tables there was a row of six equidistant ITHO-(20W) wind fans, followed by one or two rows of Lima bean plants and then a right-angled grid of iron wire supported at five positions by legs of wire (20 cm) to lift it from the substrate. The grid had a rather large mesh width (10 cm) to simplify observation and recording of behaviour. It was constructed by

slightly bending the transverse wires near the points where they were fused with the six longitudinal wires. In a series of preliminary experiments it was found that care should be taken to make one-level crossings by squeezing the crossing wires with a pair of pincers. Otherwise, the mites tend to move preferentially lengthwise once they are on the longitudinal wire.

Further dimensions of the grid and its distance from the plant row(s) and wind fans are shown in Fig. 1.

Standardization of wind speed distribution

Before each experiment wind speed was standardized to $\sim 7 \text{ m s}^{-1}$ at various points on the grid. This was done (1) by measuring wind speed near the grid using a hot-wire anemometer, (2) by controlling rotation of the fans using a voltage regulator, (3) by changing position of fans and (4) by changing position of plants. It appeared to be quite possible to keep wind speed close to 0.7 m s^{-1} , but there was a slight gradient in longitudinal direction (from 0.8 at the windward side to 0.55 at the leeward side).

Standardization of odour concentration distribution

To obtain a uniform distribution of odour concentration over the grid the row of windfans and plants was made 1.5 times longer than the width of the grid. Plants were selected that were in an approximately equal state of infestation by spider mites. To check how the odour concentration was distributed over the grid, we simulated an odour plume by releasing a tracer gas, SF_6 at six positions just behind the plant row. The rate of release was $30.8 \mu\text{g s}^{-1}$. The tracer gas was collected via tubes with their opening positioned near the grid. These tubes were connected to bottles that were initially waterfilled, but gradually lost water via a valve at the underside of the bottle. In this way the bottles loose 300 mL water in 1.5 min, which is equivalent to the amount of air that enters the bottle. The amount of tracer gas that entered the bottles was then determined by use of a gas chromatograph. Repeated measurements at various times showed that the odour concentration did not show a

Fig. 1. Schematic representation of the experimental set-up, including a row of wind fans, one row of Lima bean plants (usually two rows were used) and a grid of $1.2 \times 0.6 \text{ m}$ with the center positioned at 1.2 m from the plant row.

gradient going from the windward side to the leeward side. The concentrations of SF_6 ranged from 140–170 $\mu\text{g m}^{-3}$ with an average of 156 $\mu\text{g m}^{-3}$. An additional measurement at 2 m distance from the grid also showed that the background concentrations drastically change just after the start of releasing the tracer, but that it reaches an equilibrium within one hour. For this reason experiments were not started until 1 hour after the plants were put in position and the windfans started rotation.

Standardization of the (infested) plants

The plants used for the experiments were Lima bean plants that were in a growth stage with 3–4 leaves, *i.e.* two large single leaves and 1 or 2 compound leaves. The total leaf surface per plant was 500–600 cm^2 and, if infested by two-spotted spider mites, there were 400–600 adult females and their eggs (but few other stages). Plants were placed in two rows of seven plants (except in the one case of but four plants in one row).

Standardization of predatory mites

All predatory mites used for the experiments were adult females of *P. persimilis*. They were 4–8 days old since their last moult and in the oviposition phase. All predators had been reared under conditions of ample prey supply (25°C, 75% RH) and they were either directly transferred from the rearing unit to the centre of the grid (and thus in a well fed condition) or they were first starved for 1 day in a small vial closed by a piece of parafilm and then transferred to the grid.

Treatments

Each treatment was replicated 50 times with different predator individuals. Observations per predator lasted a maximum of 20 min, but were stopped earlier when the predators reached the windward or the leeward side of the grid. Per day 10 replicates were obtained. The results of five of such series were pooled.

RESULTS AND CONCLUSIONS

The results are shown in Table 1 (well-fed predators) and Table 2 (starved predators). In still air the majority of predators did not reach the windward side nor the leeward side of the grid within 20 minutes after release in the centre of the grid. Walking paths were very tortuous resulting in final positions not very far from where the predators had been released. A unidirectional wind current, however, elicited a pronounced response with many more predators reaching the sides of the grid. Starved predators most frequently reached the windward side, whereas well-fed predators ended up at the leeward side.

Very similar results were obtained when uninfested Lima bean plants were placed in front of the windfans. Again, the starved predators moved upwind and the well-fed predators downwind. Thus, permeating the air with odour from clean plants

TABLE 1

Response of young, **well-fed** females of *P. persimilis* to various combinations of wind and odour emanating from either clean Lima bean plants or plants that were infested by two-spotted spider mites.

Treatment Wind ¹	Odour ²	Number of predators that reached ³			Significance level (α) ⁴
		Windward side	Leeward side	Neither side	
0	0	0	4	46	-
+	0	0	29	21	< 10 ⁻⁶
+	+P	1	27	22	< 10 ⁻⁶
+	+PS	21	26	3	0.56
+	+PSS	39	5	6	< 10 ⁻⁶

¹ 0 = wind speed less than 0.1 m s⁻¹

+ = wind speed of 0.5 - 0.9 m s⁻¹

² 0 = no odour of Lima bean plants

+P = odour from 14 clean (=uninfested) Lima bean plants

+PS = odour from 4 Lima bean plants infested by two-spotted spider mites

+PSS = as +PS, but from 14 plants

³ Within 20 minutes after release at centre of grid

⁴ Two-sided binomial test with $p = \frac{n(\text{windward})}{n}$, $n = n(\text{windward}) + n(\text{leeward})$ and level of significance $\alpha = P(k(n,p) \geq n(\text{windward}) | H_0)$.

TABLE 2

Response of young, **starved** females of *P. persimilis* to various combinations of wind and odour emanating from either clean Lima bean plants or plants that were infested by two-spotted spider mites.

Treatment Wind ¹	Odour ²	Number of predators that reached ^{3,4}			Significance level (α) ⁵
		Windward side	Leeward side	Neither side	
0	0	6	5	39	>0.95
+	0	29	8	13	0.0008
+	+P	33(28)	6(1)	11(21)	< 10 ⁻⁵ (< 10 ⁻⁶)
+	+PSS	37(33)	5(2)	8(15)	< 10 ⁻⁶ (< 10 ⁻⁶)

^{1,2,3,4} See Table 1

⁵ Between brackets: results of similar experiments but with grid turned 90°.

evidently did not modify the responses of both the starved and the well-fed predators. Using infested Lima bean plants instead, the response of the starved predators was not significantly changed, but it had a strong effect on the well-fed predators. Permeating the air stream with odour from bean plants infested by two-spotted spider mites completely reversed the response of the well-fed predators; they now moved upwind rather than downwind (especially when 14 rather than four infested plants were used). The starved predators also moved upwind, but they did equally so when 'clean' bean plants were used or no plants at all. If the intensity of the

response would be higher in reality, then a statistical test would reveal it only after a very high number of replicates.

It is reasonable to interpret the orientational responses as being of an anemotactic nature because the air was close to being uniformly permeated by odour and the time-average concentrations of odour showed only a small longitudinal decline. Nevertheless, the experimental set-up did not completely exclude the possibility of longitudinal gradients of odour concentrations. However, air movement was very turbulent preventing such gradients to assume a permanent spatial position and direction. Even if such gradients would have been present, then they do not provide information to the predators as to whether they move upwind or downwind. Hence, an anemotactic response is required to understand the differential responses recorded.

In conclusion starved predators respond to unidirectional wind by *positive anemotaxis* and there is little reason to believe that this response is modified by the presence of odour from uninfested bean plants or odour from bean plants infested by two-spotted spider mites. Well-fed predators, however, respond to unidirectional wind by negative anemotaxis and this response is reversed into a positive anemotaxis when air is permeated with odour from infested bean plants. The anemotactic response is therefore both *odour-conditioned* and *state-dependent*.

DISCUSSION

It is one thing to measure differential anemotactic responses, but it is another to explain why the starved and well-fed predators respond so differently. The anemotactic responses recorded in our experiments do not have an immediate intuitive appeal. Below we will provide an hypothesis that may explain why well-fed phytoseiid predators show both positive and negative anemotactic responses depending on whether the odour comes from infested bean plants or not.

Before doing so, it should be realized first that any interpretation strongly depends on the spatial scale under consideration. One way to distinguish different hierarchical levels in space is to consider the distribution of their prey, the two-spotted spider mite. Adult females and offspring of this prey form colonies in webs that they lay down on the underside of leaves of the host plant. When the female offspring reach adulthood, they mate and then disperse before laying their eggs, founding new colonies on leaves in close vicinity. We refer to the resulting cluster of colonized leaves as a spider-mite patch. Now imagine a well-fed predatory mite walking from prey colony to prey colony within a spider mite patch. In doing so, it passes plant areas without any prey, such as stems, petioles and leaves. Thus, it may easily move out of the area within which the prey colonies are located, unless this area is somehow marked. Such border marks may arise from gradients of the odour emanating from leaves infested by spider mites. These odour gradients may be a reliable mark in still air, but what will happen when turbulent air movements tend to make the borders more diffuse? Clearly, predatory mites run the risk of

moving out of the target area, referred to as a spider mite patch. Would a well-fed predator move out at the windward side of the patch, then it enters the upwind area without kairomones and negative anemotaxis would enable the predator to return to the spider mite patch. Conversely, would the predator move out at the downwind side, then clearly a positive anemotaxis is exactly what is needed to bring it back into the spider mite patch area. Thus the odour-conditioned switch in the anemotactic response of well-fed predatory mites may be considered as a behavioural mechanism underlying arrestment in a spider mite patch. If valid, this hypothesis sheds new light on results of population experiments and model simulations (Sabelis and Van der Meer, 1986). Simulations did not at all match the measured fluctuations in predator and prey number when the predators were allowed to move out of the spider mite patch at a fraction of the dispersal rates measured in laboratory experiments. Simulation results were satisfactory only when the model was based on the assumption that predators would not leave before having exterminated the prey population. The odour-conditioned anemotaxis in well-fed predatory mites may well be part of the underlying mechanisms.

The anemotactic switch in response to presence/absence of odour in the air stream was only observed in well-fed predators. Starved predators always tend to move upwind. Such behaviour is clearly adaptive when they happen to move into a plume of odour emanating from plants infested by spider mites. However, why they also move upwind in absence of prey related stimuli and not downwind nor cross-wind, remains an open question.

What these experiments on the grid have shown, is that one should be cautious in interpreting results obtained from Y-tube olfactometry. Although the Y-tube experiments are useful in demonstrating a response to odours, it does not suffice as a tool to analyse the importance of the responses in various phases of the searching process. For example, in many of these experiments satiated females of *P. persimilis* have been used for reasons that were intuitively obvious: the more satiated, the more selective. Takabayashi and Dicke (1992) found a very weak, but clearly significant response of satiated females of *P. persimilis* towards uninfested Lima bean plants. They conclude that the response observed is significantly positive, whereas our experiments on the grid show that the response is *not* positive, but negative; in the experiments with clean Lima bean plants satiated predators actually move downwind, and thus away from the uninfested Lima bean plants. Thus, positive results in the Y-tube olfactometer do not necessarily always imply positive responses in another experimental set-up, such as the grid. Clearly, a downwind response cannot be determined by using a Y-tube, as the predators are released at the downwind end; only upwind responses or absence of responses were recorded, thereby obscuring possibilities for a downwind orientation. It remains to be investigated why the predatory mites exhibited a weak, but significantly positive response to uninfested Lima bean leaves in the Y-tube experiments of Takabayashi and Dicke (1992) and what the relevance of this response is under field conditions. Evidently, satiated females of *P. persimilis* do not use this cue for locating their

host plant (they moved away from the host plant in downwind direction). Whether hungry females make more intensive use of host-plant odours during their upwind excursions, is a question for future studies.

As stressed in the introduction, environmental complexity is likely to impose serious problems for predatory mites in finding the odour source. Experiments in simple olfactometers, such as the Y-tube, are an important first step in analysing behavioural responses, but they should not be the last (Kennedy, 1977, 1978). Entirely different results may be obtained in other experimental set-ups aiming at analysing orientation behaviour that manifests itself at other spatial scales. In addition, there may be new, hitherto overlooked problems, associated with larger spatial scales. For example, it may be questioned how a predator will respond when it happens to enter a dead-end branch while moving upwind towards an odour source. It may either move backwards and try another road, or it may drop itself to a lower part of the vegetation where it may continue in upwind direction. Both responses will obscure the interpretation of the results of a Y-tube experiment, even when the innate response of the predator is positive. Another example is the question how a predator will respond when it moves upwind to an odour source, but upon approaching its target loses contact with the odour plume because the source is located higher up in the vegetation. It may be that geotactic movements are manifested after a trial-and-error phase in which retrieval of the plume is decisive for the type of geotaxis that arises. These examples serve to illustrate that searching behaviour of predatory mites is an exciting, new topic for future research.

ACKNOWLEDGEMENTS

We wish to thank H.H. Harssema and H. Wegh (Department of Air Pollution, Agricultural University of Wageningen) for detailed advice regarding the experimental set-up and for the gas chromatographic assessments of tracer gas concentrations. Jan Bruin provided useful comments on the manuscript. The assistance of Tine Dijkman in text processing was greatly appreciated.

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