

Odour-conditioned anemotaxis of apterous aphids (*Cryptomyzus korschelti*) in response to host plants

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ABSTRACT. Orientation responses of adult apterous virginoparae of *Cryptomyzus korschelti* Börner were recorded using a locomotion-compensator in front of a wind tunnel. Individual aphids were tested under four consecutive treatments: without wind; clean wind; and wind carrying odour of the host plant *Stachys sylvatica* or odour of a non-host plant *Solanum tuberosum*. The walking tracks were tortuous in all treatments except when the odour of host plants was used. Host plant odour induced upwind orientation of aphids (odour-conditioned positive anemotaxis). Track variables such as vector length, straightness, upwind time and upwind length, increased when the aphids moved upwind. Walking speeds were not affected. The simultaneous stimulation by wind and host plant odour caused aphids to walk upwind for more than 1 m in 10 min. These findings suggest that olfactory attraction of aphids is involved in host plant selection.

Key words. *Cryptomyzus korschelti*, *Stachys sylvatica*, Aphididae, chemo-attraction, insect-plant relationships, odour-conditioned anemotaxis, olfactory orientation, olfaction, kairomones, plant odour.

Introduction

In several records of host plant selection by aphids the conclusion was reached that chemo-attraction towards host plants does not occur (Kennedy *et al.*, 1959a, b; Müller, 1958, 1962; Niku, 1972). Some authors have not excluded the possibility, though they had no evidence for olfactory attraction (e.g. Moericke, 1955). On the other hand, thanks to Moericke's elegant

investigations, it is accepted that the visual orientation responses of aphids contribute to their selection of host plants (Moericke, 1955, 1969).

The studies of Pettersson (1970, 1973) on olfactory responses of *Rhopalosiphum padi* to its winter host, *Prunus padus*, and of *Brevicoryne brassicae* to rape plants, have often been overlooked. These laboratory results, however, were not confirmed in field experiments: the variation between single trap catches was too large (Pettersson, 1979). The first statistical proof that an odorous plant compound attracted aphids towards field traps was given by Chapman *et al.* (1981); yellow water traps containing carvone, collected large numbers of *Cavariella aegopodii*. Besides these observations, electro-

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physiological recordings of antennal receptors revealed clear responses to plant volatile components in *Sitobion avenae* (Yan & Visser, 1982), and in *Nasonovia ribis-nigri* (Bromley & Anderson, 1982).

Kennedy (1986) has recently raised the question again as to whether aphids are olfactorily attracted towards their host plants. This question should be reconsidered because for other phytophagous insects there is increasing evidence of such attraction (Visser, 1986). Therefore the present investigation was undertaken to test whether aphids are attracted by host plant odour, and to elucidate the behavioural mechanisms involved.

Experience from studies of the olfactory orientation of Colorado potato beetles (Thiery & Visser, 1986; Visser & Thiery, 1985, 1987) was exploited in developing methods for assessing aphid olfactory orientation. The oligophagous aphid *Cryptomyzus korschelti* Börner is common in Europe, and uses *Ribes alpinum* L. as primary host and *Stachys sylvatica* L. as a secondary host (Hille Ris Lambers, 1953). The orientation responses of the apterous virginoparae of this aphid to *S. sylvatica* odour were analysed.

Material and Methods

A stock culture of *C. korschelti* was maintained on the secondary host *S. sylvatica*, at 20°C and a photoperiod of 16 h. Adult apterous virginoparae were isolated, and reared in clip-on cages on *S. sylvatica* under the same conditions. On the second day of their reproduction these aphids were used in the experiments. The plants used were hedge woundwort, *Stachys sylvatica*, and potato, *Solanum tuberosum*, reared in glasshouses.

Recording of behaviour

Locomotory responses were recorded on the locomotion-compensator that was used previously for studies on the olfactory orientation of Colorado potato beetles (Thiery & Visser, 1986). The anemotactic responses of gypsy moths have been recorded on a similar instrument (Preiss & Kramer, 1986) which was designed originally by E. Kramer and P. Heinecke (Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, F.R.G.;

Kramer, 1976; Weber *et al.*, 1981). To outline the present methods of recording aphid behaviour, the locomotion-compensator is briefly described. Full technical details of the equipment are presented elsewhere (Visser & Thiery, 1987).

A piece of adhesive reflective sheeting (high-gain type 7610, 3M Company) is affixed on the back of an aphid. The size of the reflector is approximately 0.4 mm², and this load does not hinder an aphid's locomotion. The aphid is placed on top of a large sphere and allowed to walk freely. The sphere diameter is 50 cm and the surface is painted with black suede coating. A position-detector is suspended from the ceiling of the observation room, and projects a beam of visible light onto the aphid. The light reflected by the 'mirror' on the aphid's back is received by the position-detector which continuously evaluates deviations of the aphid's position from the origin. Deviations are automatically compensated by two motors rolling the sphere in the opposite direction: the aphid therefore stays in the same place on top of the sphere while walking. The rotations of the sphere are recorded by two pulse generators in two coordinates (resolution 0.25 mm), and are analysed by computer.

The locomotion-compensator was positioned in front of the wind tunnel described by Visser (1976). The insect test section of the original tunnel was removed, and the airflow leaving the outlet of the tunnel contraction (cross-section 30×30 cm) passed over the aphid on top of the sphere. Airflow velocities were measured at the contraction outlet. The top of the sphere was illuminated solely by the cylindrical beam of light (diameter on the sphere 3 cm) of the position-detector. This produced a light intensity of 200 lux. The room temperature was kept at 22°C.

Experiments

Individual aphids were removed gently from clip-on cages on *S. sylvatica*. Recordings were started 30 min after placing an aphid on the locomotion-compensator. The experiments consisted of four consecutive treatments of 10 min each: a control treatment, without stimulation by wind or plant odour; clean airflow at 40 cm/s; and the same airflow carrying *Stachys sylvatica* odour or *Solanum tuberosum* odour. The plant

odours were introduced by placing six pots of fully-grown plants in the dark upwind section of the wind tunnel. Between odour treatments, a clean airflow was maintained for 30 min.

As aphids walk slowly, their positions were recorded every 5 s. A treatment of 10 min thus generated 120 successive 'positions' as X-Y coordinates per aphid. These data were analysed by calculating five variables: walking speed, as the mean of 119 instantaneous speeds per individual; vector length, as the net displacement from the origin after 10 min; straightness, as the quotient of the vector length and the total length of the track; time walking upwind, as the proportion of angle observations with deviations of less than 60° from the due upwind direction; and upwind length, as the net upwind displacement after 10 min. Each treatment was repeated with twenty-two aphids. Variables calculated for individual aphids were compared between treatments using non-parametric statistics (Siegel, 1956): the Sign test and Wilcoxon test.

Results

Walking tracks

Representative examples of walking tracks are shown in Fig. 1. The same aphid walks more or less similarly under three of the four treatments. Tracks are tortuous in control conditions, clean wind and wind carrying the odour of the non-host plant *S. tuberosum*. But the tracks in wind carrying odour of the host plant *S. sylvatica* differ remarkably from the other tracks. Host odour stimulation releases upwind orientation in the aphid, whereas non-host plant odour does not.

This interpretation is verified by the statistical analysis of variables in a group of aphids under

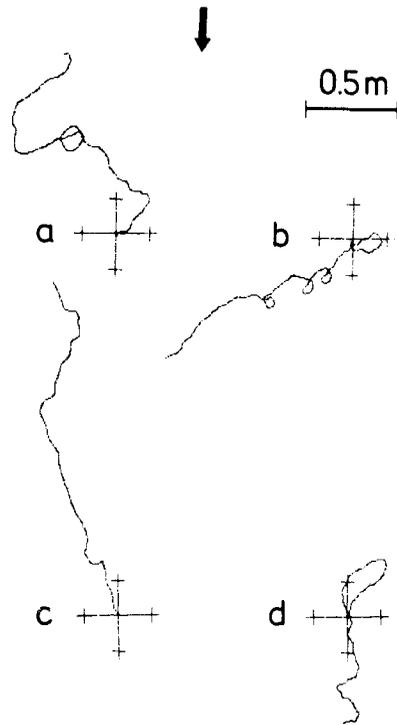


FIG. 1. Ten-minute walking tracks of an apterous aphid *Cryptomyzus korschelti* in four consecutive treatments: (a) control; (b) clean wind; (c) wind carrying odour of host plants *Stachys sylvatica*; and (d) wind carrying odour of non-host plants *Solanum tuberosum*. Arrow indicates wind direction.

the four treatments (Table 1). The upwind tracks of aphids in response to wind-borne host plant odour are characterized by an increase in the straightness of tracks and in the time the aphids spent walking upwind. As a result, vector length and upwind length are substantially increased in comparison with the values obtained under the other treatments. Mean

TABLE 1. Responses of twenty-two apterous virginoparae of *Cryptomyzus korschelti* to odours of host plants, *Stachys sylvatica*, and non-host plants, *Solanum tuberosum*.*

Stimuli	Walking speed (mm/s)	Vector length (mm)	Straightness	% Time walking upwind	Upwind length (mm)
Control	3.4±0.3 ^{a†}	574±140 ^a	0.30±0.08 ^a	34±6 ^a	14±202 ^a
Wind alone	3.6±0.3 ^a	719±152 ^a	0.35±0.07 ^a	40±7 ^a	275±220 ^a
Wind with <i>S. sylvatica</i> odour	3.6±0.3 ^a	1325±201 ^b	0.65±0.11 ^b	72±9 ^b	1184±205 ^b
Wind with <i>S. tuberosum</i> odour	3.2±0.3 ^a	720±186 ^a	0.37±0.08 ^a	31±8 ^a	-59±281 ^a

*Data represent means ±95% confidence intervals (two-tailed).

†Different letters in a column indicate statistical differences between treatments at $P \leq 0.004$ (two-tailed).

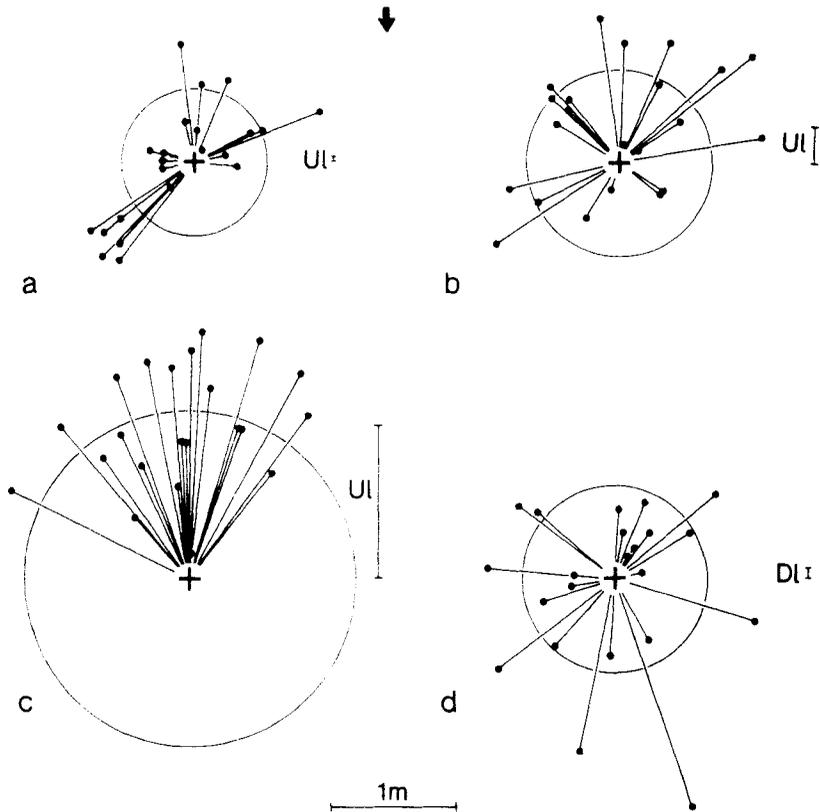


FIG. 2. Circular distribution of twenty-two apterous virginoparae of *Cryptomyzus korschelti* in four consecutive treatments: (a) control; (b) clean wind; (c) wind carrying odour of host plants *Stachys sylvatica*; and (d) wind carrying odour of non-host plants *Solanum tuberosum*. Each line represents the vector of displacement of one aphid after 10 min of walking. The mean vector length in each treatment is shown as the radius of the circle. Ul is the mean upwind and Dl is the mean downwind displacement. Arrow indicates wind direction.

walking speeds did not differ between treatments. Thus the increased vector length and upwind length were not produced by an acceleration of walking. Host plant odour stimulates apterous aphids to walk upwind for more than 1 m in 10 min (Table 1). The release of upwind orientation in *C. korschelti* is, at least to some extent, host-odour specific since non-host plant odour did not affect the behavioural responses of the aphids.

The circular distributions of vectors which were obtained under the four treatments, further support these observations (Fig. 2). In wind carrying host plant odour all the aphids showed an upwind displacement: they responded with an odour-conditioned positive anemotaxis. In the other treatments the vectors of aphid displacement reflect little or no upwind bias (Fig. 2).

Discussion

Walking speed

While walking on the locomotion-compensator, aphids frequently interrupted their locomotion, and remained stationary for varying numbers of 5 s intervals; aphids did not move an average of 65 s out of the 10 min observation period. The number of 5 s intervals without locomotion did not differ statistically between treatments. The mean walking speeds of 3.2–3.6 mm/s, shown in Table 1, were therefore calculated including these time intervals.

Binns (1977) reported that the walking speeds of alate virginoparae of *Aphis fabae* were affected by the surface structure of a treadmill. The aphids walked faster on a 'catwalk' than on a smooth surface, and faster on a smooth surface than on velvet. Mean walking speeds ranged

from 3.6 to 2.6 mm/s respectively. Light direction contributed to the regulation of locomotion in these aphids (Binns, 1978). With dorsal light, walking speeds were 3.0–3.7 mm/s.

When dislodged from their host plant, adult apterae of *Acyrtosiphon pisum* showed two types of walking behaviour: 'running' and 'searching' (Niku, 1975). Phelan *et al.* (1976) measured the walking speeds of apterous adults of three aphid species. Their data allow to discriminate between the two locomotory modes. *Acyrtosiphon pisum* 'ran' at 4.9 mm/s, *Hyadaphis erysimi* at 2.3–2.7 mm/s, and *Macrosiphum euphorbiae* at 5.8–6.2 mm/s. When 'searching', the aphids slowed down: *A. pisum* walking at 1.2 mm/s, *H. erysimi* at 0.9 mm/s and *M. euphorbiae* at 2.5–3.4 mm/s. According to Niku (1975), 'running' turned into 'searching' after c. 50 s. In our experiments the recordings of behaviour started after 30 min had elapsed. The present locomotory behaviour of *C. korschelti* is therefore thought to be 'searching' in Niku's sense, and to be within the normal range of aphid walking speeds.

Odour-conditioned anemotaxis

The upwind response to wind-borne host plant odour is considered an odour-conditioned positive anemotaxis. This consists in steering upwind on reception of an odour. Alternatives to anemotaxis, namely chemotaxis or chemokinesis in response to odour gradients, could not have been involved in the present experiments because: the aphids were kept within a small area on top of the sphere; odours were well dispersed over the cross-section of the wind tunnel (this is an intrinsic quality of the tunnel design; Visser, 1976); and the outlet of the tunnel contraction measured 30×30 cm (see for further details Visser & Thiery, 1987).

The present combination of locomotion-compensator with wind tunnel was used previously for studies on the olfactory orientation of Colorado potato beetles towards host plants (Thiery & Visser, 1986; Visser & Thiery, 1985, 1987). The intensity of the odour-conditioned anemotaxis in the Colorado potato beetle is regulated by a combination of idiothetic and allothetic control (Visser & Thiery, 1985, 1987). Circling is considered idiothetic using solely internal information (including proprioceptive feedback). The control of keeping direction is

allothetic using a control pattern which reduces the asymmetry of input from an external stimulus. Behaviour-descriptive variables fall into two groups which represent idiothetic or allothetic control.

The walking tracks of apterous *C. korschelti* and Colorado potato beetles differ in the displacement from the origin, and in the diameter of circles under control conditions. On close inspection, however, these differences are related to the contrast between the insects in size and walking speed. The behavioural responses of *C. korschelti* are based upon the same principle of combined idiothetic and allothetic control. This principle was statistically verified, for the beetles as well as the aphids, by calculating correlation coefficients between variables (Visser & Thiery, 1987). An analogous description was followed by Preiss & Kramer (1986) for the anemotactic orientation of gypsy moth males towards a source of sex pheromone.

Olfactory responses of aphids

The general conclusion that plant odours are not important for host plant selection in aphids, arose mainly from field observations of aphid landings. *Myzus persicae*, *Aphis fabae* and *Brevicoryne brassicae* alighted in more or less the same numbers on host and on non-host plants (Kennedy *et al.*, 1959a, b; Müller, 1962). The difference in resistance between two bean varieties for *A. fabae* was attributed solely to the larger percentage of landers leaving again from the more resistant cultivar (Müller, 1958).

Kennedy *et al.* (1959a) mentioned that they failed to show olfactory attraction of alate virginoparae of *A. fabae* to its host in laboratory experiments including 'screen tests' (see for method of screen test Chin, 1950). We initially carried out screen tests with alate virginoparae of *C. korschelti* reared on *Stachys sylvatica*. They spent more time in the half of the arena with *S. sylvatica* odour than in the half containing the odour of its primary host *Ribes alpinum* (χ^2 one-sample test, Siegel, 1956: $0.05 > P > 0.02$, one-tailed; Taanman & Visser, unpublished).

Walking apterous *A. fabae* were arrested by aphid odour (Kay, 1976), and also on encountering a black vertical stripe. The visual response was stronger than the olfactory one, although aphid odour did enhance the visual response.

We noticed in preliminary studies that the

orientation of both alate and apterous *C. korschelti* was strongly affected by visual cues such as light distribution and surrounding colours. To exclude visual input from the orientation studies on the locomotion-compensator, the cylindrical beam of light of the position-detector alone was used for illumination. Under these visually symmetrical conditions upwind orientation in response to host plant odour was clear. Failure to demonstrate olfactory attraction, as frequently reported for aphids in the literature, might have been due to visual cues that obscured the olfactory orientation responses.

Pettersson (1970, 1973) investigated the olfactory responses of *Rhopalosiphum padi* and *Brevicoryne brassicae* to host plant odours in a four-armed exposure chamber. His data, which represent final positions of aphids released as a group, suggest olfactory attraction. The Pettersson olfactometer was re-introduced by Vet *et al.* (1983) to measure the responses of hymenopterous parasitoids. In this apparatus, odour stimuli affect the insect's orientation in two ways: chemo-orientation responses to the sharp boundaries that exist between the test odour fields; and an odour-conditioned anemotaxis, which is uncontrolled and varies with the insect's position in the chamber. In addition, when an insect comes into contact with the walls, this is expected to act as strong guiding stimulus. These points illustrate that the behavioural mechanisms underlying insect responses cannot be analysed in such olfactometers (Kennedy, 1977).

Because most aphids of *Cavariella aegopodii* were caught on the downwind side of traps, Chapman *et al.* (1981) argued that an odour-conditioned anemotaxis might have been involved. Their experiments did not exclude odour-induced visual orientation, but the present study clearly proves the phenomenon of odour-conditioned anemotaxis in aphids. Müller & Unger (1951) observed swarms of *A. fabae* on the downwind side of bean plants in the field. Large numbers of the swarming aphids alighted on the plants. Also, these aphids alighted on the ground. They then took off again, or started to walk upwind in the direction of plants over distances of up to 25 cm. Downwind flights were never observed. When a plant was screened off by a glass cylinder, the aphid swarm broke up in a few seconds (Müller, 1951). Müller therefore attributed the swarming behaviour of aphids to

olfaction, and called it chemophobotaxis. Later, Müller changed his ideas, when he found that aphids alighted in more or less the same numbers on susceptible and resistant bean cultivars (Müller, 1958). The observed swarming of aphids downwind of plants was considered as visual station-keeping behaviour by Kennedy & Thomas (1974). An aphid flying upwind regulates its airspeed according to the wind speed, so keeping station. Nevertheless, it is not excluded that the swarming of aphids downwind of a plant is induced or enhanced by the perception of odour.

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