

## Masking of host plant odour in the olfactory orientation of the Colorado potato beetle

D. Thiery\* & J. H. Visser

Department of Entomology, Agricultural University, P.O. Box 8031, 6700 EH Wageningen, the Netherlands; \*present address: Laboratoire de Neurobiologie sensorielle de l'Insecte, Station de Recherches sur l'Abeille, Rue de la Guyonnerie, F-91440 Bures sur Yvette, France

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### Abstract

The odour of potato plants *Solanum tuberosum* L., elicits a true odour-conditioned positive anemotaxis in the Colorado potato beetle, *Leptinotarsa decemlineata* Say. Blending the odour of non-host plant species, namely wild tomatoes *Lycopersicon hirsutum* f. *glabratum* C.H. Mull or cabbage *Brassica oleracea* L. var. *gemmifera* DC., with the attractive host plant odour blocks the release of upwind responses in non-experienced as well as experienced females. The neutralization of the beetle's orientation responses is obtained without repellency. It is expected that masking of host plant odour occurs often in mixed cropping systems.

### Introduction

Extensive monocultures facilitate insect pest outbreaks (Altieri & Letourneau, 1982). The diversification of agroecosystems by means of intercropping or by maintenance of reservoirs of diverse vegetation, reduces the incidence of several phytophagous insects (Altieri & Letourneau, 1982; Cromartie, 1981; Kareiva, 1983; Risch *et al.*, 1983). These authors all suggest that the reduction of insect pest populations is caused by the interference with the searching behaviour of these herbivores. In this respect the terminology 'chemical repellency or masking' is frequently referred (see Altieri & Letourneau, 1982). The effects of plant diversity on long-distance attraction of insects, however, have not been tested.

The present study was undertaken as to see whether blending of non-host plant odour with attractive host plant odour negatively affects the long-range olfactory orientation of the Colorado potato beetle. The effects of odour blending on the odour-conditioned positive anemotaxis of the Colorado potato beetle were evaluated. This be-

havioural response is released downwind of an attractive source as soon as the odour concentration is above the threshold of detection. This orientation mechanism is thought to be effective over long distances, and differs from close-range olfactory orientation in response to steep odour gradients (Visser, 1986).

### Materials and methods

*Insects and plants.* Each day newly-emerged Colorado potato beetles were collected from the laboratory stock culture, and kept isolated in petri dishes lined with wet filter paper. Prior to the experiments, one group of females was starved for at least 12 h (non-experienced females), while the other females were fed for 2 h on small disks of potato leaves before being starved for at least 12 h (experienced females). At the time of the experiments the females were about one day old. Plants were reared in greenhouses: potatoes – *Solanum tuberosum* cultivar Eigenheimer –, wild tomatoes – *Lycopersicon hirsutum* f. *glabratum* –, and cabbage – *Brassica oleracea* var. *gemmifera* –.

**Recordings of behaviour.** Behavioural responses of the beetles to plant odours were studied using a locomotion-compensator in front of a wind tunnel (Fig. 1). This low-speed wind tunnel has previously been described (Visser, 1976), and it contains a dark upwind section where potted plants were placed, and a contraction (10:1). Incoming air was filtered by passing through activated charcoal. In the present set-up the insect test section of the original tunnel has been removed, and the flow leaving the contraction passed over the beetle on the locomotion-compensator.

The locomotion-compensator was designed by E. Kramer and P. Heinecke, and similar instruments have been used in a number of studies on insect orientation (Kramer, 1976; Weber *et al.*, 1981). It operates as follows: A tiny piece of reflective material is glued on the back of an insect. The insect is placed on top of a large sphere, and observed by a detector. The detector projects a beam of visible light onto the insect, which is reflected by means of the 'mirror' on the insect's back, thereby the position of the animal is detected. As soon as the insect starts walking its positional change is seen by the detector, which initiates that two motors rotate the sphere in the opposite direction with the same speed as the insect is walking – the insect stays on top of the sphere while walking. The rotations of the sphere are detected by two pulse generators in contact with the sphere, and pulses are recorded and analyzed by a microprocessor (Fig. 1).

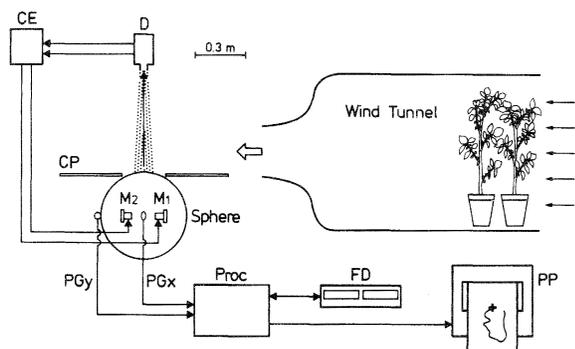


Fig. 1. Combination of wind tunnel and locomotion-compensator used for study of olfactory orientation of the Colorado potato beetle. CE – electronic circuit for compensation; CP – circular plate; D – detector; FD – floppy disk drive; M1, M2 – two motors for compensation; PGx, PGy – two pulse generators for registration of xy coordinates; PP – printer-plotter; Proc – microprocessor. Arrow: wind direction.

The beetle's position was recorded every second, and walking speed and direction were calculated. The walking track was plotted at the same time. Data stored on floppy disks were further analyzed by specially designed software. The light intensity on top of the sphere was set at 1750 Lux by means of two high-frequency illumination units (2500 Hz), which were suspended at the ceiling of the observation room. Each unit contained six day-light fluorescent lamps. Precautions were made in order to prevent that the beetles responded visually to the background surrounding the compensator: a white circular plate was installed (Fig. 1), and walls and ceiling were painted black. Full technical details of this equipment will be presented elsewhere (J.H. Visser, in litt.).

**Experiments.** Individual females were exposed for ten minutes to each of four successive treatments: (1) a clean air flow of 80 cm/s as control, and the same air flow carrying (2) non-host plant odour, (3) host plant odour, and (4) odour from a mixture of the two plant species. The experiments with non-experienced females were carried out in two sets covering all four treatments. For each individual female the time interval between successive exposures was at least one hour.

Three pots containing fully-grown plants were used for *L. hirsutum* as well as *S. tuberosum*. For *B. oleracea* six fully-grown potted plants were placed in the upwind section of the wind tunnel. The foliage of the three plant species was estimated to contain an equal volume. The air flow was measured at the outlet of the tunnel contraction. Temperature was  $24 \pm 1$  °C.

In the present study five variables are used to describe the beetle's responses: (a) walking speed is the mean of 599 instantaneous speeds per individual, (b) vector length is the resultant displacement from the origin after 600 s, (c) straightness is the quotient of the vector length and the total length of the walking track, (d) time spent walking upwind corresponds to the proportion of angle observations with deviations of less than 60° from the wind direction, and (e) upwind length is the upwind displacement after 600 s. Variables were compared between treatments using nonparametric statistics (Siegel, 1956); Sign test (var. c) and Wilcoxon's test (var. a, b, d & e). In this way the variables from the four treatments were tested as related samples

which compensates for the large variations in walking speeds between individual beetles.

## Results

*Masking by wild tomatoes.* Non-experienced female Colorado potato beetles were observed under four treatments, namely wind, potato plant odour,

odour of wild tomatoes, and odour from the mixture of potatoes and wild tomatoes (Table 1, groups A + B). Potato plant odour elicits strong positive anemotactic responses in the beetles. They spend most of their time on walking upwind, and walk straighter compared to the responses under control conditions. The lengths of the resultant vector and upwind displacement, consequently are increased relative to the clean air treatments. The odour of

Table 1. Responses of ♀ Colorado potato beetles to odours of host plants, *S. tuberosum*, non-host plants, *L. hirsutum* or *B. oleracea*, and mixtures of host and non-host plants. Means ± 95% confidence intervals (two-tailed).

	Walking speed (mm/s)	Vector length (mm)	Straightness	Time walking upwind (%)	Upwind length (mm)
A: non-exp. ♀ ♀, n = 18 <sup>1</sup>					
Wind	13.5 ± 1.0 a <sup>3</sup>	4109 ± 999 a	0.50 ± 0.11 a	57 ± 12 a	1726 ± 1887 a
<i>S. tuberosum</i> (3) <sup>2</sup>	14.1 ± 1.0 a	6439 ± 1013 b	0.77 ± 0.10 b	85 ± 7 b	5927 ± 1259 b
<i>L. hirsutum</i> (3)	13.8 ± 0.9 a	4775 ± 891 a	0.58 ± 0.10 ab	50 ± 12 a	1601 ± 1607 a
B: non-exp. ♀ ♀, n = 35					
Wind	14.4 ± 0.8 a	4354 ± 635 a	0.51 ± 0.07 a	49 ± 8 a	1317 ± 1268 a
<i>S. tuberosum</i> (3)	15.6 ± 0.7 b	7021 ± 698 b	0.74 ± 0.07 b	82 ± 5 b	6541 ± 703 b
<i>S. tuberosum</i> (3) + <i>L. hirsutum</i> (3)	13.6 ± 0.8 a	3616 ± 665 a	0.44 ± 0.07 a	50 ± 6 a	1836 ± 869 a
C: non-exp. ♀ ♀, n = 19					
Wind	14.5 ± 1.0 a	3572 ± 688 a	0.42 ± 0.08 a	54 ± 8 a	1467 ± 1093 a
<i>S. tuberosum</i> (3)	13.8 ± 0.8 a	6139 ± 1097 b	0.72 ± 0.12 b	79 ± 13 b	4909 ± 1952 b
<i>B. oleracea</i> (6)	12.4 ± 1.0 b	3259 ± 569 a	0.45 ± 0.09 a	42 ± 9 a	-119 ± 1260 a
D: non-exp. ♀ ♀, n = 31					
Wind	14.1 ± 0.9 a	3452 ± 693 a	0.41 ± 0.08 a	61 ± 5 a	2793 ± 742 a
<i>S. tuberosum</i> (3)	14.6 ± 0.9 a	6629 ± 750 b	0.75 ± 0.06 b	84 ± 4 b	6322 ± 746 b
<i>S. tuberosum</i> (3) + <i>B. oleracea</i> (6)	13.6 ± 1.0 a	4210 ± 595 a	0.52 ± 0.07 a	60 ± 7 a	2488 ± 931 a
E: exp. ♀ ♀, n = 24					
Wind	12.9 ± 1.1 a	3598 ± 748 a	0.46 ± 0.09 a	58 ± 9 a	1446 ± 1461 a
<i>B. oleracea</i> (6)	11.3 ± 0.8 b	3493 ± 690 a	0.50 ± 0.09 a	66 ± 7 a	2704 ± 946 a
<i>S. tuberosum</i> (3)	11.9 ± 0.8 ab	5178 ± 816 b	0.70 ± 0.08 b	83 ± 5 b	5033 ± 847 b
<i>S. tuberosum</i> (3) + <i>B. oleracea</i> (6)	11.4 ± 0.6 b	4188 ± 495 a	0.61 ± 0.07 ab	67 ± 9 a	2687 ± 1168 a

<sup>1</sup> No. beetles.

<sup>2</sup> No. pots with plants.

<sup>3</sup> Different letters in a column indicate statistical differences between treatments of a group at  $P \leq 0.02$  (two-tailed).

wild tomatoes does not elicit such positive anemotactic responses in the beetles: their responses are identical with those in pure wind conditions. In the blend of potatoes with wild tomatoes all variables, however, are drastically reduced to the original levels found in clean air. The addition of the odour of wild tomatoes severely distorts the attractiveness of potato plant odour.

Similar results were obtained with experienced females (D. Thiery & J. H. Visser, in litt.). In the experiments the odour of wild tomatoes alone was neither attractive nor repellent. The distributions of mean angles for both non-experienced and experienced beetles under the four treatments, are shown in Fig. 2A. It is clearly observed that the attractiveness of host plant odour is neutralized by blending with the odour of wild tomatoes. The neutralization is obtained without repellency.

**Masking by cabbage.** Two groups of females were tested: one non-experienced, the other with a previ-

ous experience of food, *i.e.* potato foliage. Representative walking tracks of one experienced beetle under the four treatments are shown in Fig. 3. In this example the beetle demonstrates a true odour-conditioned positive anemotaxis in response to potato plant odour (c), which is interrupted by blending with cabbage odour (d). Tracks illustrate that responses to cabbage odour alone (b) are fairly similar to those to clean air (a).

In both groups of beetles track variables change in the same order with type of stimulation (Table 1, groups C + D, group E). Treatments with potato plant odour increase straightness, time spent walking upwind, vector length, and upwind displacement. Additions of cabbage odour to the attractive host plant, reduces all these variables to the original measures for clean air. Cabbage odour alone is neither attractive nor repellent for non-experienced as well as experienced females as this odour elicits responses similar to those in clean air.

Mean walking speeds differ between groups, and

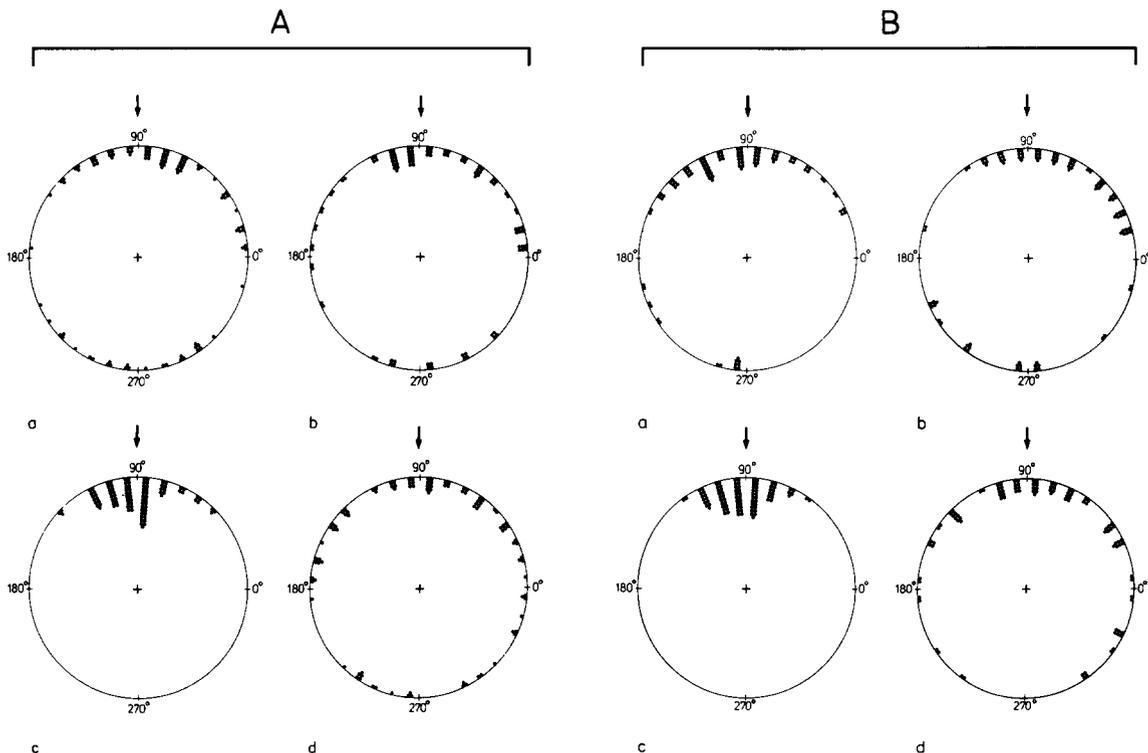


Fig. 2. Orientation of female Colorado potato beetles in response to (a) wind control, (b) non-host plant odour, (c) *S. tuberosum* odour, (d) odour blend of the two plant species. A: non-host plant is *L. hirsutum*; 49–66 beetles. B: non-host plant is *B. oleracea*; 24–55 beetles. Circular distribution of mean angles as % of non-experienced and experienced beetles. Mean angle for each individual calculated from a 10 min-period of walking. Arrows: wind direction.

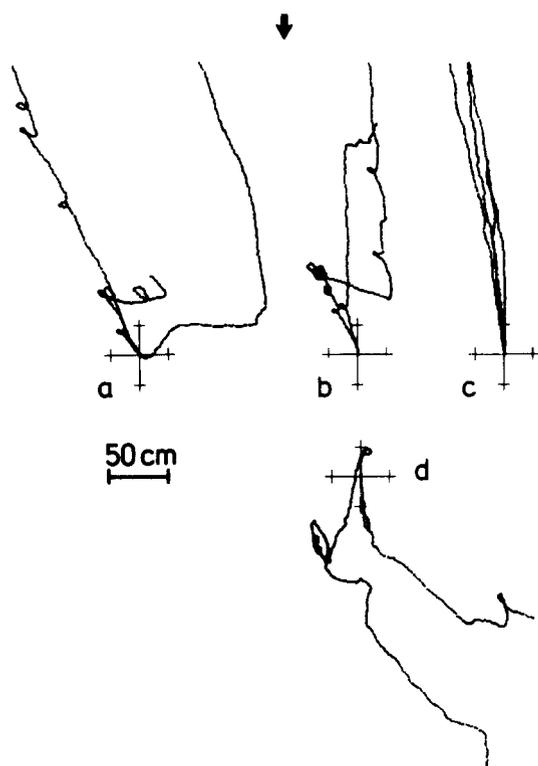


Fig. 3. Tracks of one experienced female Colorado potato beetle in 4 successive runs of 10 min each: (a) wind control, (b) *B. oleracea* odour, (c) *S. tuberosum* odour, (d) odour blend of *B. oleracea* with *S. tuberosum*. Arrow: wind direction. Plotter reset to origin automatically at reaching paper edge.

in a group between treatments. In group B non-experienced females walk faster in response to potato plant odour, while in other groups such an activation is not detectable (Table 1). Cabbage odour reduces the walking speed in two of three cases (groups C & E, Table 1).

In other experiments it was detected that wind activates the Colorado potato beetle, and together with host plant odour produce a better control of walking speed (Visser & Thiery, 1985; J. H. Visser, in litt.).

The experiments on masking by cabbage odour were examined by the distributions of mean angles of the walking tracks in the four treatments, as shown in Fig. 2B. In the odour blend of potatoes with cabbage (d), the large variance in final positions illustrates the neutralization of upwind responses.

## Discussion

In the present study beetles were exposed to a particular plant odour for 10 min. More than 1 h elapsed between the successive exposures of individual beetles. When stimulated repeatedly by host plant odour, starved beetles show positive anemotactic responses irrespective of previous exposures (Visser & Avé, 1978). For these reasons it is not likely that the succession of treatments, on itself, has affected the behavioural patterns of the beetles. The experiment on masking of the attractive host plant odour by cabbage for experienced females (Table 1, group E) was recalculated using varying time periods (Fig. 4). Upwind length increases proportionally in time, and between potato plant odour and the other treatments this variable differs already at 30 s. Although straightness decreases in time, in response to host plant odour beetles walk straighter in most of the time periods (Fig. 4B). As the other variables show the same trend, it is concluded that masking of an attractive host plant odour starts immediately on the blending with non-host plant odour, and lasts for at least 10 min. The neutralization of the beetle's responses is constant and, thus, not caused by habituation or adaptation.

*Masking of host plant odour.* Potato plant odour elicits true odour-conditioned positive anemotactic responses in Colorado potato beetles. The potato leaf odour has been analysed by steam distillation (Visser *et al.*, 1979), as well as by direct vapour sampling (Visser, 1983), and contains *cis*-3-hexen-1-ol, *cis*-3-hexenyl acetate, *trans*-2-hexenal, and *trans*-2-hexen-1-ol. 1-Hexanol is possibly present (J. H. Visser, in litt.). These compounds are generally distributed in green leaves (Visser *et al.*, 1979). The specificity of this so-called green odour is set by the ratios of its individual components. Addition of pure volatile chemicals to the odour of potatoes, which will change the ratios, interrupts the upwind movements of the beetles: the attractive host plant odour is masked (Visser & Avé, 1978).

The results of the present study demonstrate that host plant camouflage is also obtained on blending with non-host plant odour. When presented alone, both non-host plant species are neutral in their effects on the olfactory orientation of Colorado potato beetles. Therefore, it is concluded that the

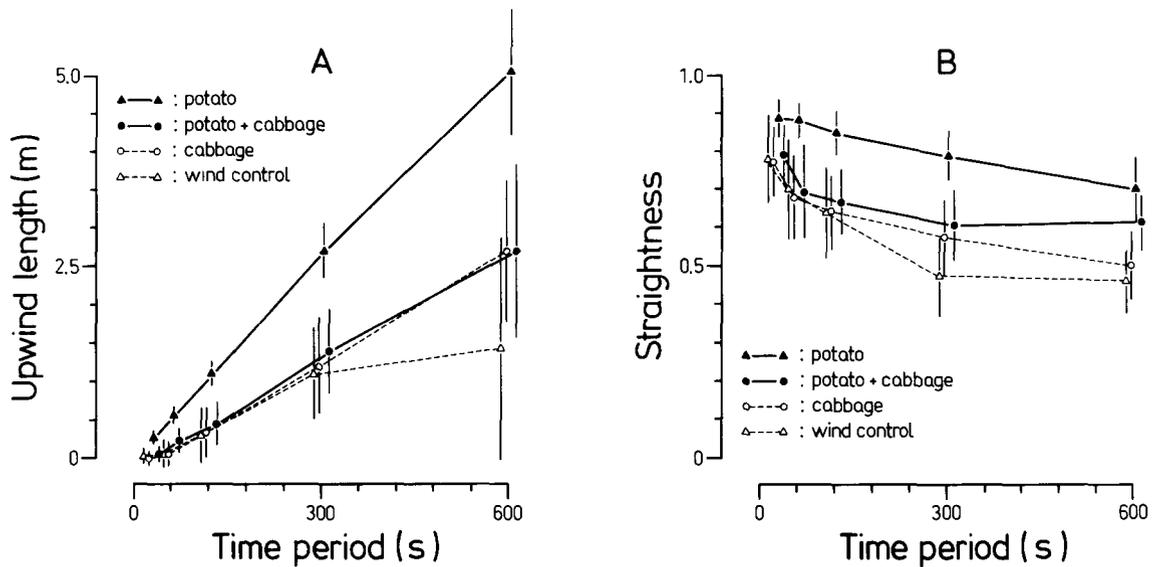


Fig. 4. Cumulative plots of (A) upwind length and (B) straightness under 4 successive treatments: (a) wind control, (b) *B. oleracea* odour, (c) *S. tuberosum* odour, (d) odour blend of *B. oleracea* with *S. tuberosum*. Means of 24 experienced ♀ Colorado potato beetles calculated over time periods of 30, 60, 120, 300 and 600 s. Vertical lines: 95% confidence intervals (two-tailed).

neutralization of responses is not caused by the negative action of repellents. Repulsion by non-host plant odours in the long-range olfactory orientation of insects is not likely to occur for two reasons. In the strict sense, repellency refers to a movement being directed away from the odour source (Dethier *et al.*, 1960), and would be directed downwind in case of anemotaxis. An insect moving downwind, however, will stay in the odour plume and would thus not escape from the repellent odour. This should be considered as a maladjusted behaviour. The movement of the Colorado potato beetle in pure wind and in neutralized host plant odour is not, however, directed specifically upwind or downwind, but shows an angle preference that is changed in a new direction every few minutes. The resultant walking track is straighter than without wind, which indicates that the beetle uses wind stimulation for an efficient exploration in all directions (Visser & Thiery, 1985). The second thought is that repellency at a long distance would require large numbers of chemoreceptors tuned to repellents as to detect the minute concentrations downwind from the source. It is hardly feasible that all kind of specific receptors would have evolved in large numbers as to cope with the extreme chemical diversity in non-host plant species (Visser, 1983,

1986). Until now, none such repellent receptors have been found on the antennae of insects (Visser, 1986).

The neutralization of orientation responses in the Colorado potato beetle on blending with non-host plant odour, may be obtained by the distortion of the particular green odour composition of the host plant. The predominant vapour component of cruciferous plants is *cis*-3-hexenyl acetate (Wallbank & Wheatley, 1976). The blend of cabbage odour, therefore, will change the original leaf odour composition of potatoes. It is expected that the odour of wild tomatoes blocks likewise the release of a positive anemotactic response in the Colorado potato beetle.

The experiments were conducted indoors, using sophisticated instruments in order to quantify the beetle's behavioural patterns in response to olfactory stimuli, and were performed under controlled conditions of temperature, light intensity distribution and visual background. This approach offers the advantage that changes in behaviour are unambiguously related to the experimental treatment. The results of these behavioural studies need to be translated into field conditions as to improve our insights of host selection by phytophagous insects. The behaviour studied here, is relevant to field con-

ditions: Colorado potato beetles walk anemotactically towards host plants in the field (de Wilde, 1976). The beetle carries anemoreceptors on its antennae that are very sensitive to air currents; responses were obtained to just a few cm/s (J.H. Visser, in litt.).

*Host plant camouflage in mixed cropping systems.* In the field wind turbulence will blend volatiles from a mixed stand of plants. Plant odours consist of specific as well as general components (Visser, 1983, 1986). For these two reasons it is likely that the insect's range of attraction to host plant odour is often reduced in mixed cropping systems. This principle may be used in order to limit the numbers of insects entering a crop. The extension of the results of the present study to field conditions necessitates a good understanding of crop architecture and consequent plume structures (Stan-ton, 1983).

Furthermore, it should be realized that specialized herbivores may also find plants by close-range orientation to other plant stimuli.

Methods of intercropping can be compared with the application of pheromones in the mating disruption of pest insects. Mating disruption can be achieved in two ways: (a) the application of high levels of synthetic sex pheromone, or (b) changing the ratio of the components by treatments with one compound only (Rothschild, 1981). There exist striking analogies between the second method of mating disruption and host plant camouflage as presented in this paper. Both methods interfere at the level of perception of an odour complex being composed of several constituents in a particular ratio.

The outbreaks of insect pests may be prevented by mixed cropping (Altieri & Letourneau, 1982). The application of these systems in insect pest control needs further substantial studies on insect behaviour in order to exploit host plant camouflage to the full extent.

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#### Résumé

##### *Masquage de l'odeur de la plante hôte lors de l'orientation à longue distance du doryphore*

Un certain nombre d'articles rapporte une diminution du nombre des insectes phytophages spécialistes comme une conséquence à la diversification des agroécosystèmes (Altieri & Letourneau, 1982; Cromartie, 1981; Kareiva, 1983; Risch *et al.*, 1983). Ainsi, il a été supposé que la présence de plantes non-hôtes pouvait interférer avec celle de plantes hôtes en modifiant la nature des informations chimiques parvenant aux insectes. Les modifications comportementales qui peuvent en résulter lors de l'attraction à distance sont toutefois encore peu claires. Les expérimentations présentées ici analysent les réponses individuelles du doryphore à diverses stimulations olfactives issues de plantes entières. Des femelles ont été ainsi étudiées un jour après l'émergence en présence d'air vierge et d'air chargé d'odeurs de *Solanum tuberosum*, *Lycopersicon hirsutum* f. *glabratum*, *Brassica oleracea* var. *gemmifera*, ainsi que des mélanges *S. tuberosum* avec *L. hirsutum* et *S. tuberosum* avec *B. oleracea*. A partir de l'enregistrement continu de l'activité locomotrice dans chaque condition (à l'aide du compensateur de locomotion), nous avons déterminé que *L. hirsutum* et *B. oleracea* masquaient l'odeur de la plante hôte *S. tuberosum* en supprimant la réponse anémotactique positive conditionnée par l'odeur de cette dernière. Les mélanges d'odeurs ainsi obtenus sont considérés comme neutres pour l'orientation à longue distance du doryphore. L'expérience préalable par le doryphore de l'ingestion de feuillage de pomme de terre ne modifie pas l'effet du camouflage obtenu. Ces résultats laissent penser qu'il est possible de limiter la découverte de la plante hôte chez les insectes, et que les méthodes de camouflages olfactives pourraient prévenir les attaques de certains ravageurs.

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