Labeyrie, V., Fabres, G., Lachaiṣe, D. (eds) Insects – Plants 129
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PLANT ODOUR PERCEPTION IN THE COLORADO POTATO BEETLE: CHEMOATTRACTION TOWARDS HOST PLANTS

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Host selection behaviour of phytophagous insects is divided in (1) searching for host plants, and (2) host plant recognition. In these two phases insects are exposed to very different stimulus conditions. In host plant recognition, the insect's conclusion to accept or reject a plant for feeding or oviposition, is reached upon the perception of a number of stimuli being associated with the one plant under inspection. When searching for host plants, insects walk of fly around, and, at a first glance, their movements seem to be at random. There is an increasing evidence, however, that insects direct their movements towards host plant patches as they perceive olfactory and visual plant characteristics from a distance (Visser, 1986). In this respect the term attraction is often used.

Chemoattraction

We have previously reported on the chemoattraction of the Colorado potato beetle, **Leptinotarsa decemlineata** Say, to its host plant potato, **Solanum tuberosum** L.. Wind-borne potato plant odour elicits a positive anemotactic response in the beetle (Visser, 1976). The perception of both odour and wind is indispensable for the release of the odour-conditioned anemotaxis.

The next step was to isolate the host plant odour by steam distillation and direct vapour sampling techniques. GC-MS analyses of these samples identified, among other components, cis-3-hexen-1-ol, cis-3-hexenyl acetate, trans-2-hexenal, trans-2-hexen-1-ol, and 1-hexanol (Visser et al., 1979; Visser, 1983).

In addition, we conducted studies on the olfactory receptors. The identified C6 components, their isomers, and members of other classes of plant volatile compounds were screened for EAG activity (Visser, 1979). The data led us to conclude that the antennal receptor system of the Colorado potato beetle is sensitively tuned to the reception of the C6 components which are present in potato leaf odour. Furthermore, we recorded receptor activities of single olfactory sensilla when stimulated by individual C6 components (Ma & Visser, 1978; Visser, 1983). The receptor cells respond differentially to the class of C6 components, and, in this way, they may discriminate between individual components.

Additional support for the idea that the C6 components are involved in the chemoattraction of Colorado potato beetles, was obtained through wind tunnel studies (Visser & Ave, 1978). None of the individual C6 components elicit odour-conditioned positive anemotaxes in the beetles. When individual components are artificially mixed with the odour of potato plants, however, its prevents the beetle's upwind orientation. The induced change in concentration ratios between components in the leaf odour blend eliminates the attractiveness of the host plant odour. Thus, chemoattraction of the Colorado potato beetle depends on the ratios between C6 components.

The C6 components which were identified in potato leaf odour, are present in all green leaves, and their concentrations differ between plant species (Visser et al., 1979). A relatively large number of phytophagous insects have now been tested on their antennal sensitivities for these components (Visser, 1983, 1986). All leaf feeding insects respond to the C6 components, and one might call this class of chemicals the green odour. The specificity of the green odour (the tint of green) is set by the concentration ratios between constituents.

Biological factors affecting the range of chemoattraction

Our recent research focusses on the searching efficiency of the Colorado potato beetle. In a more precise sense, we are interested in the biological factors affecting the range of the insect's olfactory orientation. We restrict ourselves to biological factors, and will not discuss the impact of physical factors on the range of chemoattraction, such as odour release and dispersion (Visser, 1986). In brief, biological factors include: (1) the intensity of the odour-conditioned anemotaxis, (2) the integrity of the chemical message, and (3) the insect's responsiveness to host plant odour. In order to recognize the significance of these factors we use the Colorado potato beetle as a model to study the chain of stimuli - receptors - central nervous system - behavioural patterns.

1. Intensity of the odour-conditioned anemotaxis

We realized that further behavioural analyses ought to contain precise information on (a) the intensity of the odour-conditioned anemotaxis, and (b) the steering mechanisms involved in orientation. For these reasons a locomotion-compensator was constructed in our department, with the help of the original designers E. Kramer and P. Heinecke (Max-Planck Institut fuer Verhaltensphysiologie, Seewiesen, FRG). A full description of the equipment will be presented elsewhere (Visser & Thiery, in prep; see Thiery & Visser, 1986a). For the present discussion it is sufficient to report that this instrument automatically compensates all movements of an insect freely walking on a large sphere. At the same time pulses are generated, and analysed by a microprocessor in order to quantify the beetle's orientation. The locomotion-compensator is positioned at the outlet of the contraction of the wind tunnel described by Visser (1976).

Experiments were carried out with starved females as to assess their behaviour under (a) control conditions, (b) at wind stimulation (80 cm/s), and (c) stimulation by wind-borne host plant odour. Under all conditions the light intensity on top of the sphere was set at 1750 Lux by means of two high-frequency illumination units which were suspended at the ceiling of the observation room.

In every second angle and speed were calculated; representative distributions are shown in Figures 1 and 2.

Under control conditions angles are evenly distributed, at wind stimulation downwind classes dominate, and in the combination with host plant odour the angle of movement is restricted to upwind directions (Fig. 1). Wind stimulates the beetle to walk faster (Fig. 2). When a beetle is simultaneously stimulated by wind and host plant odour the variation in mean walking speed, that is the standard deviation, is reduced (Fig. 2). This second effect of odour stimulation is related to the straightness of the track since minor angle deviations will cause only small reductions in walking speeds (Visser & Thiery, in prep).

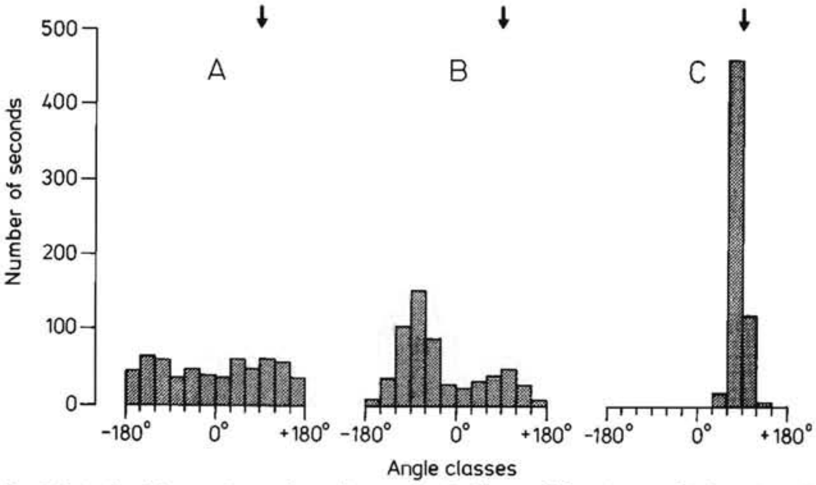

Figure 1. Distribution of angle classes of three 10-min. walking tracks of one Colorado potato beetle. A: control conditions; B: stimulated by wind; C: stimulated by wind carrying potato plant odour. Arrows: position of wind tunnel.

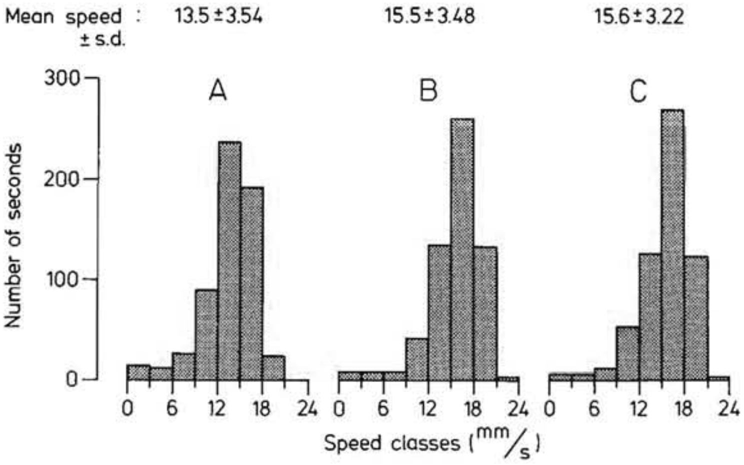

Figure 2. Distribution of speed classes. See legend of Fig. 1.

A large number of walking tracks were analysed by defining descriptive measures like: vector length, vector angle, upwind length, total straightness, walking speed, mean straightness, circling time, angle preference, and upwind time (Visser & Thiery, 1985, in prep.; Thiery & Visser, 1986a, 1986b).

The first striking feature of tracks is the amount of circling. In control conditions beetles walk in circles for long periods. The time spent on circling is reduced by wind stimulation, and circling behaviour is nearly absent in wind carrying host plant odour. The second characteristic of tracks is the angle preference which is defined as the angle preference during straight walks (corrected for circling). In control conditions the angle preference is small. Wind releases anemotactic orientation at angles that are, about every 2 minutes, changed in a new direction. Wind in combination with host plant odour elicits a constant upwind angle preference.

Under all conditions, that is included of controls, descriptive measures fall into two groups denoted by the motor patterns: (1) walking circular or (2) keeping direction. Variations in orientation betwee individuals, and the variations within one individual during prolonged testing, are explained by the varying proportions of the motor patterns walking circular and keeping direction. Two types of steering mechanisms control these motor patterns. Idiothetic control or walking circular is considered as an internal programme. Allothetic control of keeping direction is a programme which reduces the asymmetrical input of an external stimulus. Thus, the intensity of the odour-conditioned anemotaxis is regulated by the combined actions of idiothetic and allothetic control (Visser & Thiery, 1985, in prep.)

2. Integrity of the chemical message

In diverse vegetations or mixed croppings wind turbulence will blend volatiles from host and nonhost plants. The integrity of the chemical message, therefore, may by changed or even lost. We tested this hypothesis by combining potato plants with wild tomatoes, **Lycopersicon hirsutum** f. **glabratum** C.H. Mull, or cabbage, **Brassica oleracea** L. var. **gemmifera** D.C., in the upwind compartment of the wind tunnel (Thiery & Visser, 1986a, 1986b). In these odour blends Colorado potato beetle do not show odour-conditioned anemotaxes, their responses are identical with those in pure wind. The attractiveness of host plant odour is neutralized by blending with nonhost plant odours.

It is noteworthy that these behavioural observations confirm our conclusions on the perception of plant odour blends. Intracellular recordings of deutocerebral neurones revealed two reaction groups for (a) the detection of C6 components, and (b) the detection of incorrect ratios (De Jong & Visser, this volume).

3. Insect's responsiveness

The insect's responsiveness is changed as a result of feeding experience (Visser & Thiery, 1986). We compared two groups of beetles. One group of newly-emerged females was starved, while another group of females was fed for 2 h on potato leaves, and then starved. Experienced beetles show a significant increase of upwind responses compared with non-experienced beetles.

We illustrated in the present paper that the range of the insect's chemoattraction is not solely affected by physical factors. The elucidation of biological factors implicates detailed analyses of the insect's behaviour in the laboratory. Further field experiments are needed as to appreciate the chemoattraction of insects, and to proceed with the development of intelligent methods of insect pest control.

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