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Chapter 10

Behavioral Responses of the Colorado Potato Beetle to Stimulation by Wind and Plant Odors

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Plant odors act as chemical signals for phytophagous insects that walk or fly in search of host plants. The attraction of the Colorado potato beetle, *Leptinotarsa decemlineata* Say, towards the odor of potato foliage was demonstrated by McIndoo (1926) using a Y-tube olfactometer. These experiments were confirmed by Schanz (1953). Additionally, she identified the sensory organs to be located in the top five segments of the antennae. In a slightly modified olfactometer Jermy (1958) obtained negative results, and concluded that the beetle's perception of plant odor was not essential for host-plant selection. In wind tunnel experiments de Wilde et al. (1969) found upwind locomotory responses of Colorado potato beetles to odor from potato foliage. Since then, these experiments have been repeated (Visser 1976), and extended to the odors of other plant species (Visser and Nielsen 1977), the chemical composition of the odor of potato foliage (Visser et al. 1979, Visser 1979a, 1983), and the beetle's perception of plant volatiles (Ma and Visser 1978, Visser and Avé 1978, Visser 1979b, 1983).

To describe the insect response to plant odors or to other chemical signals like sex pheromones in terms of attraction is doubtful, as attraction refers solely to the experimental methods used, e.g., counting the number of insects in the arm of an olfactometer or the number of insects in trap catches (Kennedy 1978). In this way, the behavioral responses of insects as released by a set of stimuli remain obscure, and therefore information is lacking on the conditions under which attraction occurs. For this reason, Kennedy (1978) proposed focusing on the

orientation mechanisms used by insects. The old classification of kinesis and taxis, with its various subdivisions, is still valuable (see Fraenkel and Gunn 1961, Kennedy 1977). The conditions releasing several types of orientation mechanisms are defined by, in the case of olfactory stimulation: (a) responses to steep odor gradients occurring close to the source (klinokinesis, orthokinesis and osmotropotaxis) or at the edge of an odor plume (longitudinal klinotaxis), and (b) the odor releasing a response to wind (odor-conditioned positive anemotaxis), at a low odor concentration far away from the source (Kennedy 1977, 1983).

This terminology, however, still ignores the insect's perception. An insect walking or flying controls two variables, i.e. speed and direction. The behavioral response can be considered as the steering of these two variables by an internal program (idiothetic control), without external stimulation other than the animal itself, based on proprioceptive information, or by external stimulation (allothetic control), or by the mixture of the two (see Mittelstaedt et al. 1979, Bell and Tobin 1982). The time course in steering causes the insect to walk or fly along a particular track. An individual insect does not foresee the track, but just modulates its control of speed and direction in the course of time. This kind of approach is more satisfactory, as it describes behavior in terms of steering, changing speed and being variable. The present study gives examples of such an approach for the olfactory orientation of the Colorado potato beetle.

MATERIALS AND METHODS

Locomotory responses of Colorado potato beetles were measured automatically using a locomotion-compensator. This instrument was constructed with the help of the designers E. Kramer and P. Heinecke (Max - Planck Institut für Verhaltensphysiologie, Seewiesen, FRG). A full description of the equipment is presented elsewhere (Visser, in preparation). The locomotion-compensator has been used in several studies on insect orientation (see Kramer 1976, Weber et al. 1981). This instrument operates as follows. A tiny piece of reflective material is affixed to the back of a beetle. The beetle is placed on top of a sphere (diameter 50 cm) and observed by a camera. The camera projects a beam of visible or infra-red light onto the insect, which is reflected by means of the 'mirror' on the beetle's back, thereby the position of the beetle is constantly monitored. As soon as the beetle starts to walk, its positional change is monitored by the camera, which engages the

two motors and rotates the sphere in the opposite direction at the same speed as the insect is walking, hence keeping the beetle in a fixed position relative to cardinal points. Pulse generators, which make contact with the sphere, quantify the beetle's movements, and in combination with a computer, walking speed and direction are calculated.

The locomotion-compensator was positioned at the outlet of the wind tunnel described by Visser (1976). For these experiments, the insect test section of the tunnel was removed, and the air flow leaving the apparatus passed over the beetle on top of the sphere. This wind tunnel offered several advantages: a low turbulent air flow, and an upwind section large enough to place a number of pots with fully grown potato plants (80 cm high). By means of two high-frequency illumination units (220 V, 2500 Hz), each containing six day-light fluorescent lamps, the illumination was set at 1750 lux on top of the sphere. A number of precautions were taken to reduce the beetle's visual response to the background surrounding the sphere. Full details are presented elsewhere (Visser, in preparation).

The experiments consisted of three successive treatments. After a beetle was placed on top of the sphere, locomotory responses were recorded for a ten minute period in each treatment: (1) without wind, (2) with an air flow of 80 cm/s (measured at the outlet of the wind tunnel) and (3) with an air flow of 80 cm/s carrying the odor of potato foliage; six pots with fully grown potato plants were positioned in the upwind section of the wind tunnel. Female Colorado potato beetles were used in the experiments; the beetles were obtained from the laboratory stock culture after emergence and fed for two hours on potato foliage and then starved for at least another twelve hours prior to the experiments. The potato plants, Solanum tuberosum L. (cv 'Eigenheimer'), were grown in the greenhouse.

RESULTS AND DISCUSSION

In Figures 1, 2 and 3 representative walking tracks of nine female beetles are shown in response to the three experimental conditions, i.e. control, wind, and wind plus the potato foliage odor. The same lettering indicates the same individual. The tracks were obtained by plotting the position of the beetle every second. At the same time, speed and direction were calculated and stored on floppy disks. Computer programs were designed to sort the data (600 observations in a 10 minute period), and to calculate parameters defining the ultimate walking path, and the beetle's control of speed, direction and change in direction.

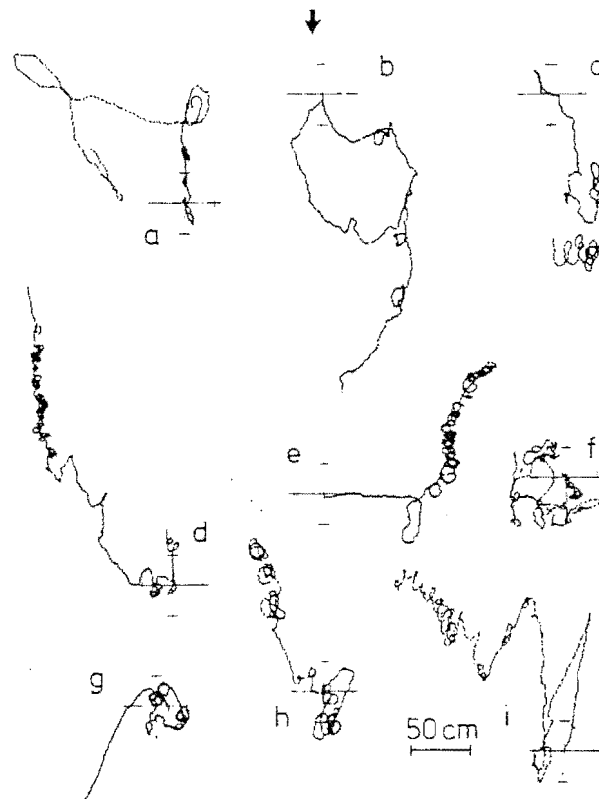


Fig. 1. Walking tracks of nine female Colorado potato beetles in control situations. Arrow indicates the position of the wind tunnel. At reaching the edge of the paper, the plotter was reset to the starting point.

Track descriptive parameters - The resultant walking paths are described by the mean angle, the displacement from the origin, and the straightness of the track, that being the length of displacement divided by the length of the walking path. In control conditions, the angles of the walking tracks were scattered, in wind a slight preference for upwind angles was observed, while in wind with the odor of potato plants the beetles showed more definitive upwind responses. The displacement from the origin, after ten minutes of walking, was on the average, 154 cm in the control, 294 cm in wind and 988 cm in wind carrying potato odor. The straightness of the tracks was, on the average, small in the control (0.19), medium in the wind (0.31) and high in the wind plus odor (0.90). A considerable variation exists between individual beetles. The extremes in the length of displacement were, in the control, beetle f (45 cm) and beetle b (338 cm, see Fig. 1), in the wind, beetle i' (8 cm) and beetle e'

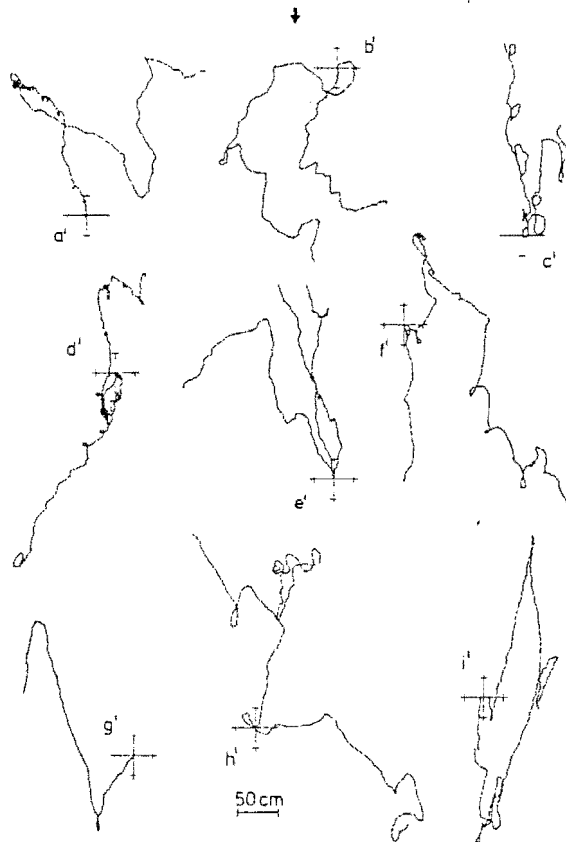


Fig. 2. Walking tracks of nine female Colorado potato beetles stimulated by wind.

(678 cm, see Fig. 2), and in the wind carrying potato odor, beetle g'' (531 cm) and beetle f'' (1346 cm, see Fig. 3). This variation was due to the varying persistence in maintaining direction in the control and wind treatments. In the control, the straightness ranged from 0.05 (beetle f) to 0.46 (beetle b) and in the wind, from 0.01 (beetle i') to 0.68 (beetle e'). In the case of wind carrying potato foliage odor, the variation between beetles in the displacement from the starting point was due to variations in mean walking speeds (beetle g'' 9.4 mm/s, beetle f'' 22.9 mm/s).

Beetle's steering - In comparing walking paths in the control and wind treatments, it was striking that beetles walked much straighter and turned less in the wind treatment. This feature can be demonstrated by using a parameter like straightness; however, this particular parameter does not completely account for the beetle's response to the set of stimuli presented. In Fig. 2, beetle i' walked rather straight,

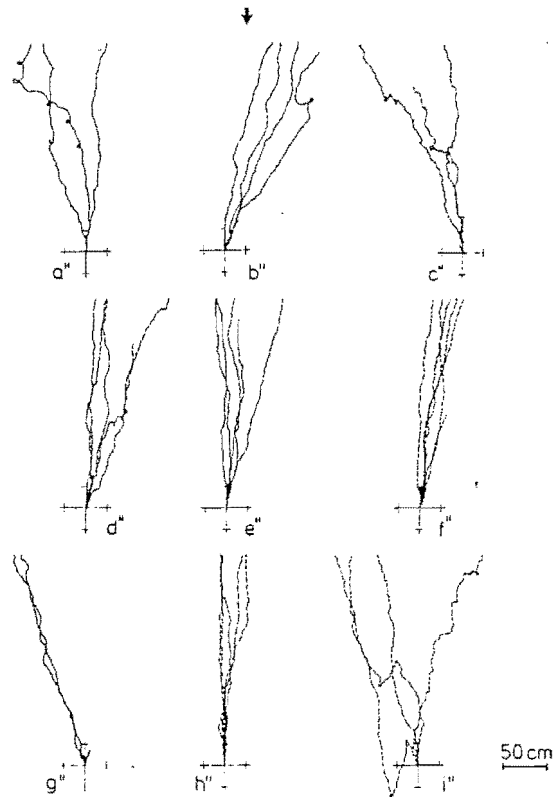


Fig. 3. Walking tracks of nine female Colorado potato beetle stimulated by wind carrying potato plant odor.

but the few turns brought the beetle close to the starting point by accident. During the experiments, stimulation was kept constant for a ten minute period; even so, the beetles frequently turned. This turning response was not due to a change in external stimulation, but internally controlled.

The tracks presented clearly show that an increase in stimulation by wind and odor reduced the frequency of turning when compared to the control treatment. From the distributions of angle deviations (changes in direction), the percentage of time spent by the beetle on making turns and full circles was estimated. This circling time was an expression of the amount of idiothetic control, and ranged on the average from 48% in the control, 21% in the wind, to 6% in the wind and odor treatments. Because of an increasing amount of stimulation, idiothetic control was suppressed, and allothetic control became more important in regulating activity. The balance between these two types of control, as affected by stimulation, determined the

resultant walking path. Walking speed was affected in a similar way by external stimulation. In the control treatment, the walking speed was on the average 13.6 mm/s, and in the wind and in the wind plus plant odor it was 17.4 mm/s. Walking speed is better controlled by the beetle in wind together with odor as concluded from the standard deviations of the mean speeds in each individual, which were lower than in wind without plant odor.

The responses of insects to wind have been described as anemomenotaxis (Linsenmair 1969), i.e., an insect maintains direction at a particular angle to the wind. The tracks in Fig. 2 show that the beetles walked straighter because of wind stimulation; however, the persistence in maintaining direction was small compared to the responses to wind carrying odor. The percentage of time spent by the beetle on moving upwind (upwind being defined as angles at a deviation $\leq 60^\circ$ from the wind direction) was, on the average, in the three treatments: control 45%, wind 50%, and wind plus odor 96%. In addition to the suppression of idiothetic control, potato plant odor induced a strong angle preference in the locomotory responses of the beetles.

Olfactory orientation and host-plant selection - The first step in host-plant selection is the orientation of an insect while walking or flying. It cannot be denied that olfactory cues from plants affect the orientation patterns of insects. Under field conditions insects experience a complex of stimuli important in locating host plants. Besides chemical stimuli, uneven light intensity and distribution, and visual background, together with mechanical barriers, form the ultimate track along which the insect travels. Because of the turbulent nature of wind, plant odors are mixed, thus distorting the chemical message. The effects of plant odors on host-plant selection should not be studied solely in terms of attraction, as an existing or non-existing phenomenon, but should be regarded as being variable and modifiable. An analysis of insect behavioral responses being steered by both internal as well as external control mechanisms will give more reliable clues for the manipulation of insect olfactory orientation. Presently, experiments are being conducted in our department to evaluate confusion methods by mixing host- and nonhost-plant odors.

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