

**THE DESIGN OF A LOW-SPEED WIND TUNNEL AS AN
INSTRUMENT FOR THE STUDY OF OLFACTORY
ORIENTATION IN THE COLORADO BEETLE
(*LEPTINOTARSA DECEMLINEATA*)**

BY

J. H. VISSER

Department of Entomology, Agricultural University, Binnenhaven 7, Wageningen, The Netherlands

Aerodynamic phenomena relevant to the olfactory orientation of walking adult Colorado beetles are discussed and a low-speed wind tunnel suitable for the study of olfactory orientation is described. It is concluded that in this wind tunnel the beetles respond to attractive plant volatiles by odour-conditioned anemotaxis. The presence of potted potato plants in the air stream of the wind tunnel causes positive anemotactic responses of male and female Colorado beetles. The maximum positive anemotactic response of the male beetles is obtained after 6 hours of starvation. Fully grown potato plants are more attractive to male beetles than young plants.

Two approaches are available for studying the responses of insects to olfactory stimuli. One involves presenting the odour in still air, limiting the range of the signal to very short distances. In still air the larvae of the Colorado beetle, *Leptinotarsa decemlineata* Say perceive olfactory stimuli of their host plant effectively at a distance of up to a few millimetres (Chin, 1950). The second approach makes use of wind-borne odours, which can be perceived at longer distances (Bossert & Wilson, 1963; Bossert, 1968).

In the past, tests with wind-borne volatiles in Y-tube olfactometers have shown olfactory attraction of Colorado beetles to their host plant potato (McIndoo, 1926; Schanz, 1953; Jermy, 1958). In experiments of this type negative results can be misleading because the two air streams mix at the junction, interfering with the insects' discrimination between them. Moreover, there is little room for the animal to behave normally.

Low-speed "wind tunnels" have therefore been employed in the study of olfactory orientation to plant volatiles (Haskell *et al.*, 1962; Kennedy & Moorhouse, 1969; de Wilde *et al.*, 1969; de Wilde, 1974; Coaker & Hawkes, 1974), pheromones (Farkas & Shorey, 1972; Mayer, 1973; Kennedy & Marsh, 1974) and host vapours (Gatehouse & Lewis, 1973).

It is generally held that long-range olfactory orientation in insects is brought about by an anemotactic response (Grubb, 1973). In this way, the wind acts not only as the dispersal medium of volatiles, but also guides the insects to the source of the stimulus. Hence the reliability of data on olfactory orientation depends on a

number of aerodynamic phenomena of the air flow. This paper describes these phenomena which are important in designing a wind tunnel for olfactory orientation of Colorado beetles to host plant vapours.

Wind Tunnel Theory

The turbulent components of air flow are usually important (Bradshaw, 1971). Outdoors, a high degree of turbulence tends to distribute the vapours more uniformly through the atmosphere (Bossert & Wilson, 1963) and is likely to interfere with directional cues for the searching insect.

The flow of air in a tunnel may be turbulent or laminar, depending on the diameter of the tunnel and the air velocity under a given set of conditions. In the main stream of a wind tunnel, the transition of laminar to turbulent flow occurs at a critical air flow velocity U_{crit} given by the following formula (Schlichting, 1955; Ower & Pankhurst, 1966):

$$U_{\text{crit}} = \frac{2300 \cdot \nu}{D_H}$$

2300 being the critical Reynolds number; ν is usually termed the kinematic coefficient of viscosity of the medium; D_H is named the hydraulic diameter, $D_H = 4A/C$; A denotes the cross-sectional area and C denotes the perimeter of the wind tunnel. The relationship between the critical velocity U_{crit} of the main stream in a wind tunnel and its hydraulic diameter D_H is illustrated in Fig. 1. Obstructions in the air stream, e.g. plants, other odour sources, air filters and the ventilator of the wind tunnel, increase the amount of turbulence, which declines with the distance. Low turbulence can be obtained in the following manners: (1) by increasing the distance between the obstructions and the test section of the tunnel ("setting region") and (2) by keeping the initial section of the tunnel, containing the obstructions, wider than the terminal test section (Pankhurst & Holder, 1952; Pope, 1954); in such a low velocity compartment of the wind tunnel, obstructions will give rise to little turbulence, and (3) damping screens will reduce its intensity. By the action (4) of a tunnel contraction, the turbulent velocity components of the air stream, passing through this contraction into the narrower test section, decrease mainly in the longitudinal direction.

In a thin layer near the wall the air velocity, u , is lower than in the main stream, U , as shown in Fig. 2. The thickness of this boundary layer δ is defined as the distance from the wall where $u/U = 0.99$ (Schlichting, 1955), and increases along the plate in a downstream direction. The boundary layer near the leading edge of the plate is laminar and becomes turbulent further downstream. In case of a flat plate with a sharp upwind edge the transition of laminar to turbulent flow occurs at a distance from the leading edge, the region of transition x_t , given by the following formula:

$$R_{\text{crit}} = \frac{U \cdot x_t}{\nu} = 3.2 \cdot 10^5 \text{ to } 5 \cdot 10^5$$

$3.2 \cdot 10^5$ to $5 \cdot 10^5$ being the critical Reynolds number, depending on the intensity of

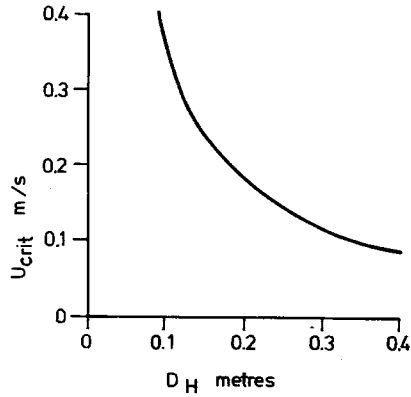


Fig. 1. The relationship between the critical velocity U_{crit} of the main stream in a wind tunnel and its hydraulic diameter D_H at 25° and 760 mm Hg ($\nu = 0.1544 \cdot 10^{-4} \text{ m}^2/\text{s}$). Exceeding the critical velocity implies that the air flow will be turbulent.

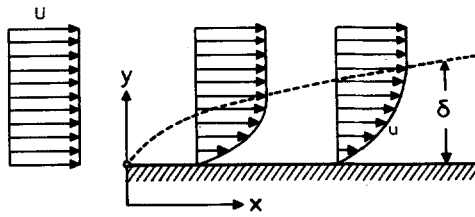


Fig. 2. Sketch of boundary layer on a flat plate in parallel flow. It is shown that there is a thin layer near the wall in which the air velocity u is smaller than in the main stream, U . The thickness of this boundary layer δ increases along the plate in a downstream direction.

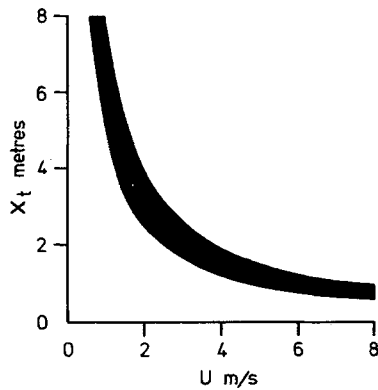


Fig. 3. The transition from a laminar to a turbulent boundary layer on a flat plate occurs at regions x_t from the leading edge, depending on the air velocity in the free stream, U ($\nu = 0.1544 \cdot 10^{-4} \text{ m}^2/\text{s}$).

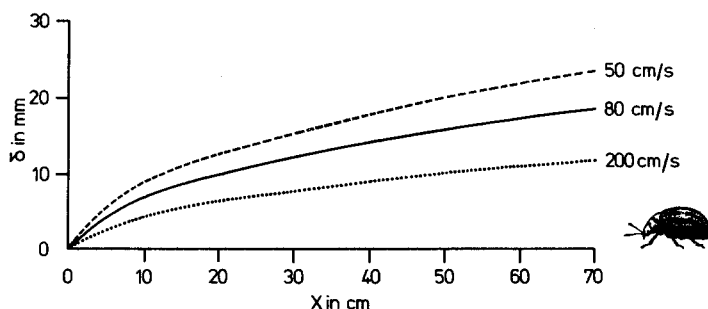


Fig. 4. The thickness of the laminar boundary layer δ along a flat plate at several distances x from the upwind edge and with different velocities of the main stream (at 25° and 760 mm Hg). For comparison, a Colorado beetle in real size is shown.

the turbulence in the free stream. The relationship between the main stream velocity U and the region of transition x_t is shown in Fig. 3. The thickness of the laminar boundary layer can be calculated, as in Fig. 4, by applying the formula given by Blasius (Schlichting, 1955):

$$\delta = 5 \sqrt{\frac{\nu x}{U}}$$

where x denotes the distance from the leading edge. The thickness of the boundary layer might have important effects on the olfactory orientation of walking insects. As small walking insects move in the boundary layer, the possibility of their detecting the air flow and its direction can be limited by the thickness of the boundary layer.

Wind Tunnel Design

Diagrams of the low-speed wind tunnel are given in Figs. 5 and 6. A centrifugal ventilator (Fischbach D770/E650-4; c.v.) sucks air through two air filters (A.A.F. Amer-glass Blue and Varicel 60 PS; a.f.l.-a.f.2.). The resistances of a 80 mesh screen (s.) and the activated charcoal filter (a.c.f.) raise the air pressure in the pressure section (pr. s.), allowing pressure equilibration. The air leaves the filter at a more uniform flow rate across the cross-section, leaving most unwanted volatiles behind. The activated charcoal filter consists of folded perforated metal plates, spaced 17 mm apart and filled with activated charcoal pellets. In experiments on olfactory orientation undamaged potted plants are placed in the next section (pl.s.) through a door (d.) at one side of the wind tunnel. Four 18 mesh damping screens 0.34 mm wire (d.s.1-d.s.4), the setting region (s.r.) and the contraction (t.c.) decrease the turbulence intensity of the air flowing into the narrower insect test section (i.t.s.). By the contraction, the air velocity is raised ten times in the insect test section as compared with the preceding region of low velocity in the wind tunnel. The wind speed can be set by the power control of the ventilator. The test section is enclosed by walls ("closed throat" type), equipped with several glass windows (g.w.) which can be opened. A glass walking plate (w.p.) 70 cm long, 23.5

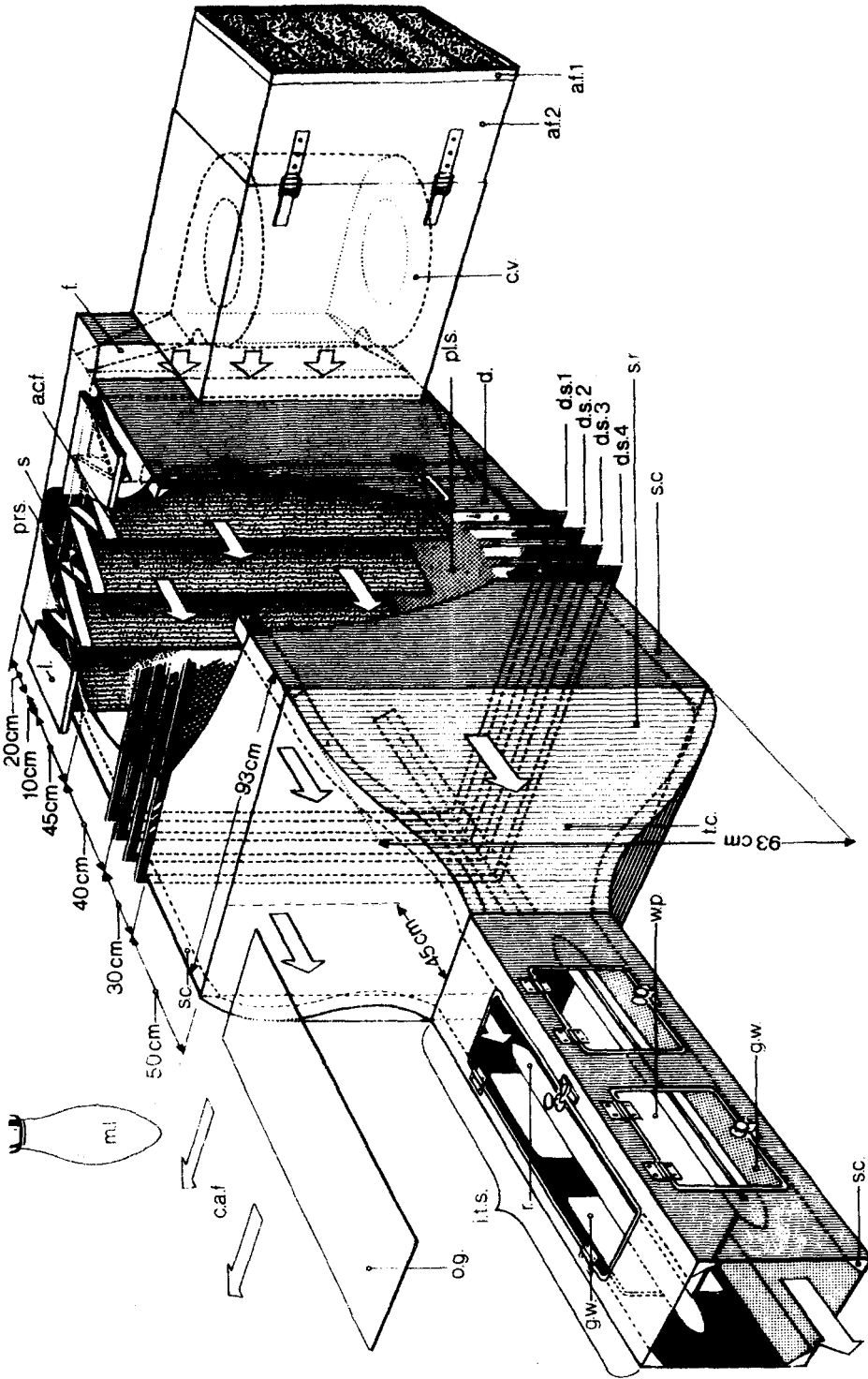


Fig. 5. Diagram of the low-speed wind tunnel. a.c.f.: activated charcoal filter; af.1.-af.2.: air filters; c.v.: cooling air flow; c.v.: centrifugal ventilator; d.: door; d.s.1.-d.s.4.: four damping screens; f.: funnel; g.w.: glass windows sealed with silicone tubing; i.t.s.: insect test section; l.: lid of activated charcoal filter sealed with Ethafoam; m.l.: high-pressure mercury bulb; o.g. opaline glass; pl.s.: plant section; pr.s.: pressure section; r.: streamlined rails; s.: screen; s.c.: streamlined corners; s.r.: setting region; t.c.: tunnel contraction; w.p.: walking plate. Arrows indicate the direction of the air flow.

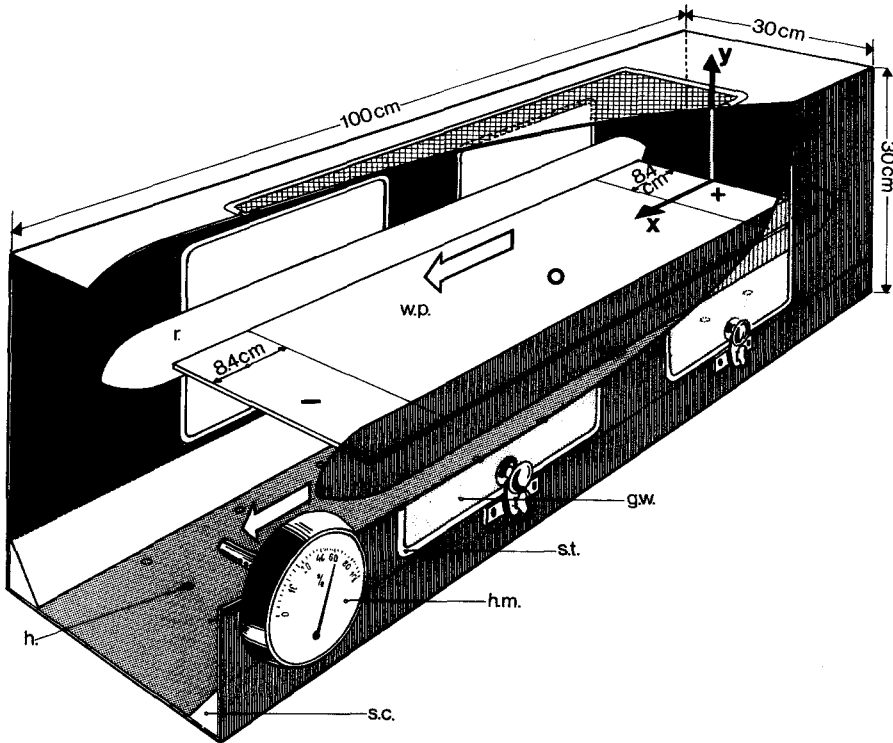


Fig. 6. Detailed diagram of the insect test section. h.: holes; h.m.: hygrometer; s.t.: silicone tubing; x,y: ordinates; + : positive, 0 : indifferent and — : negative regions of the walking plate. Arrows indicate the direction of the air flow. See Fig. 5 for further explanations.

cm wide and 3 mm thick, scoured with Carborundum, is fixed at half height in the test section with streamlined rails (r.). The side glass windows are darkened with black paper on the outsides and the walking plate is illuminated from above by a high-pressure mercury bulb (Philips HPL 400W; m.l.), cooled by outside air (c.a.f.). In the bottom of the insect test section 36 holes (h.) are available for the introduction of hot-wire probes of the anemometer, normally these holes are closed. The wind tunnel is housed in a controlled environment room; at least 90% of the total air volume of this room is replaced by fresh air every 30 minutes. Air is taken from the room and returned again by this "open circuit" tunnel. Contamination problems like those described by Browne *et al.* (1974), have been avoided by using clean air and "non-emitting" materials in the construction of the wind tunnel; mainly zinc, but also brass, iron, glass, silicone tubing and Ethafoam (Dow Chemical).

MATERIAL AND METHODS

The measurement of air flow

A hot-wire anemometer (Disa 55D05) with temperature-compensated hot-wire probes (Disa 55P81) was used in the measurements of air flow velocities in the

boundary layer of the rough glass walking plate in the insect test section. In combination with an r.m.s. voltmeter (Disa 55D35), a Digitest voltmeter and an oscilloscope (Tektronix 502A), the intensity of turbulence of the main stream was defined in the insect test section. The measurements were performed at 20°.

The olfactory orientation of Colorado beetles

After emergence the male and female Colorado beetles of the laboratory stock culture were separated and reared on greenhouse-grown potato plants (cultivar Eigenheimer) at an 18 hour photoperiod at 25° and 60% relative humidity. Before the experiments, individual beetles were isolated in vials and starved for several hours. In the insect test section of the wind tunnel the responses of these individuals to a "control air stream" were examined, pots with wetted soil and sticks standing in the plant section, and also their responses to the air stream plus potato plant volatiles by the introduction of four greenhouse-grown potted potato plants (cultivar Eigenheimer) into the plant section. Care was taken not to bruise the leaves and stems. Small potato plants were raised, so that the foliage was positioned at half height in the plant section. The streamlined rails on both sides of the walking plate were painted with Fluon (Polytetrafluoro-ethylene dispersion, Imperial Chemical Industries) to prevent beetles from climbing up. The upwind and downwind edges were also painted with Fluon, thus causing beetles reaching these edges to fall off.

In each experiment, one beetle was placed carefully in the centre of the walking plate and was allowed to walk around. Five minutes after it started locomotion, the position of this individual on the walking plate was recorded. The response was noted as positive when the beetle fell off the upwind edge or was situated within 8.4 cm from the upwind edge, and as negative when the animal fell off the downwind edge or was situated within 8.4 cm from the downwind edge. Otherwise the response was noted as indifferent (see also Fig. 6). The results were analysed statistically by the χ^2 test (Siegel, 1956), positive choices versus combined negative and indifferent choices.

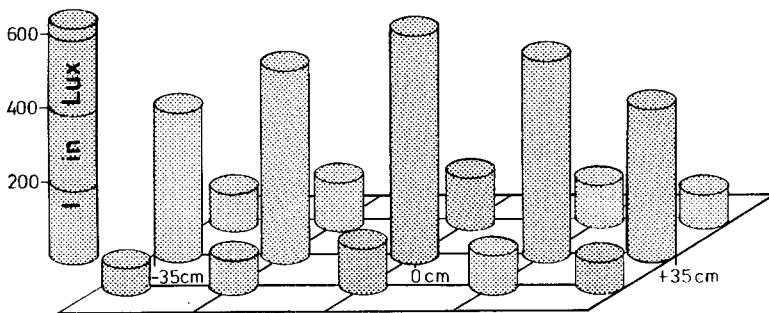


Fig. 7. The distribution of light intensities over the walking plate in the insect test section. Ordinate: intensity. Abscissa: +35 cm = upwind edge, 0 cm = centre and -35 cm = downwind edge of the walking plate.

The velocity of the main stream was set at 80 cm/s in the insect test section. The wind tunnel was housed in a controlled environment room at 25° and 60% R.H. The four damping screens in the low velocity compartment of the wind tunnel were removed. At the in- and outstream ends of the insect test section 18 mesh screens were fixed in order to obtain a more uniform light distribution over the walking plate. This light intensity distribution was measured by a Hartmann & Braun EBLXI photometer, fitted with a circular detector of 66 mm diameter, and is shown in Fig. 7.

RESULTS AND DISCUSSION

The measurement of air flow

The hydraulic diameter of the insect test section is 0.3 m, and as a consequence, wind exceeding a speed of 12 cm/s will be turbulent in the main stream of the test section (Fig. 1). The percentage of turbulence, an indication the amount of turbulence, can be defined (Schlichting, 1955) as:

$$\% T = 100 \cdot \frac{\sqrt{\bar{u}^2}}{U}$$

where $\sqrt{\bar{u}^2}$ denotes the mean velocity fluctuations of the air flow and U is the mean air flow rate. Without damping screens in the low velocity compartment of the wind tunnel, the percentage of turbulence in the main stream of the insect test section is 3% at a wind speed of 1 m/s. With the four damping screens installed,

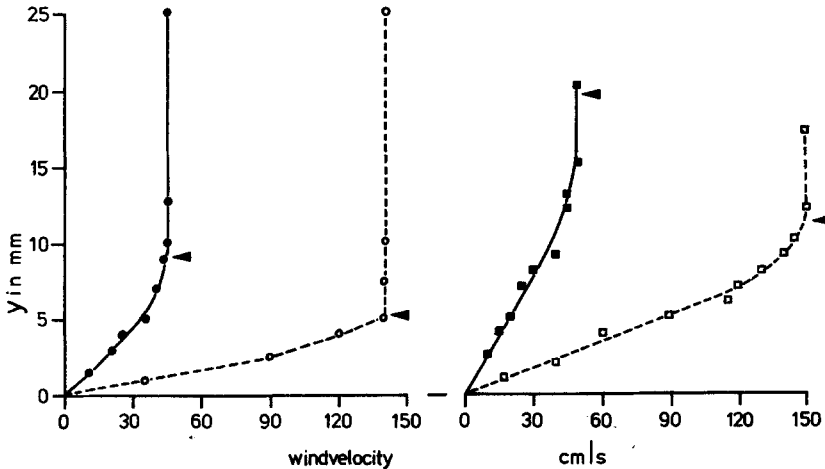


Fig. 8. Measurements of the wind speeds at several heights y above the walking plate and with different main stream velocities U in the insect test section. 10 cm downwind the leading edge: $U = 45$ cm/s: (●—●) and $U = 140$ cm/s (○---○); 50 cm downwind the leading edge: $U = 50$ cm/s (■—■) and $U = 150$ cm/s (□---□). Arrows indicate the laminar boundary layer thickness, calculated by applying the formula of Blasius (at 20° and 760 mm Hg, $\nu = 0.1499 \cdot 10^{-4}$ m²/s).

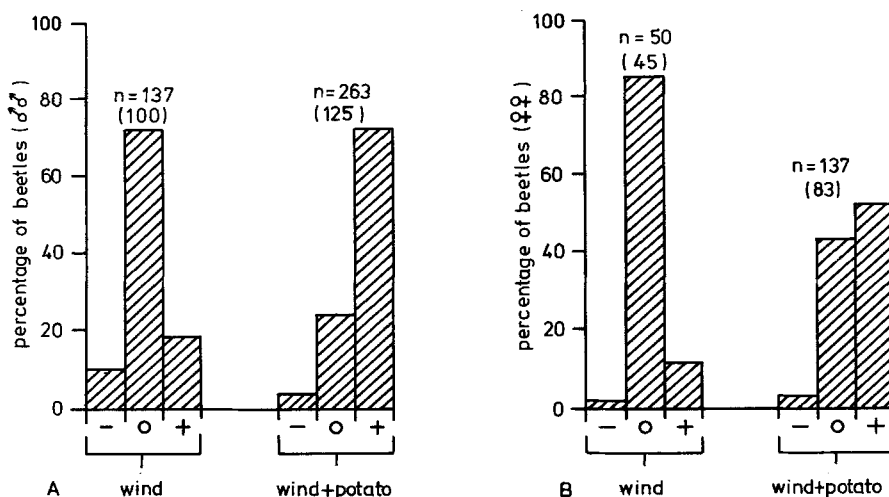


Fig. 9. The responses of Colorado beetles to wind and to wind plus potato plant volatiles. Undamaged potted potato plants 2–8 weeks old were used. Abscissa: — = negative, 0 = indifferent and + = positive choices. A. male beetles 0–4 weeks after emergence and starved for 1–17 h. B. female beetles 0–2 weeks after emergence and starved for 1–19 h. In parentheses the number of individuals; n is the number of tests.

measurements revealed that this percentage of turbulence was reduced to 1% at a wind speed of 1 m/s. Because the amount of turbulence in the test section proved to be limited, the damping screens were omitted in the olfactory orientation studies. Air flow measurements and the introduction of smoke behind the activated charcoal filter showed many eddies, a high degree of turbulence originating from the folded perforated metal plates of the filter. This turbulence appeared to decrease in the setting region and in the tunnel contraction. Volatiles of plants placed directly behind the activated charcoal filter, are thus distributed over the total cross-sectional area of the wind tunnel, resulting in a uniform vapour concentration in the insect test section. Therefore, in this wind tunnel, while it is not possible for the beetles to react to concentration gradients (e.g. osmotropotaxis, see Haskell *et al.*, 1962), they will respond to attractive plant volatiles by an odour-conditioned anemotaxis. The main stream of the test section exhibited a uniform air flow rate.

The total boundary layer of the walking plate will be laminar, when the main stream does not exceed 7.1 m/s in the insect test section (Fig. 3). At several positions on the walking plate and at different free stream velocities, air flow measurements in the boundary layer, as shown in Fig. 8, revealed values in good agreement with the formula of Blasius. In the olfactory orientation studies the main stream velocity was set at 80 cm/s in the insect test section, the resulting laminar boundary layer over the walking plate being illustrated in Fig. 4.

The olfactory orientation of Colorado beetles

The responses of walking individual male and female Colorado beetles to wind and to wind plus potato plant volatiles were examined, as shown in Fig. 9.

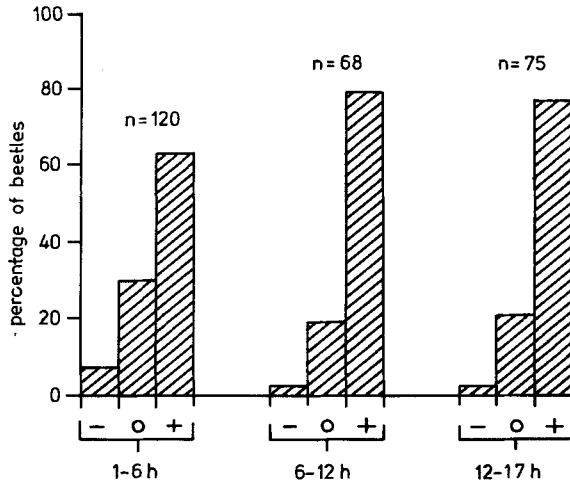


Fig. 10. The effects of prolonged starvation on the responses of male Colorado beetles to wind plus potato plant volatiles. Abscissa: — = negative, 0 = indifferent and + = positive choices. The male beetles were starved for periods of 1-6 h, 6-12 h and 12-17 h; n is the number of tests.

Subsequently the figures obtained in these tests with male Colorado beetles were re-arranged in order to differentiate between various starvation periods (Fig. 10) and various potato plant ages (Fig. 11). Confusing the effects of these last-mentioned conditions was thereby avoided. As preliminary experiments with groups of Colorado beetles showed that the individuals affected one another's behaviour, it was decided to use single individuals.

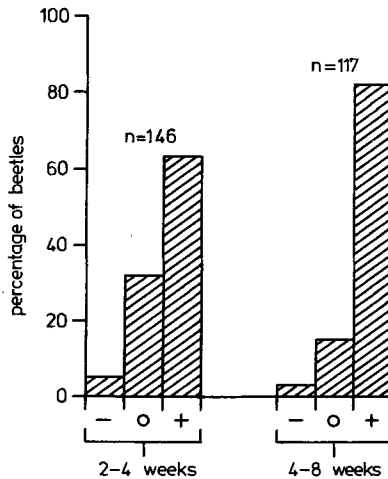


Fig. 11. The effects of the age of potato plants on the responses of male Colorado beetles to wind plus potato plant vapours. Abscissa: — = negative, 0 = indifferent and + = positive choices. Undamaged potted plants 2-4 weeks and 4-8 weeks old were used; n is the number of tests.

Without potato plant vapours, starved beetles tended to move slightly upwind (Fig. 9). This probably does not result from the distribution of light intensity over the walking plate (see Fig. 7). The responses to wind were not altered by different starvation periods. The introduction of potato plants into the air stream caused substantial positive anemotactic responses of male and female beetles ($p < 0.001$). The nature of the responses did not change remarkably with the age of the beetles. The maximum positive anemotactic responses of male beetles to potato plant volatiles were obtained after 6 hours of starvation (Fig. 10); 1-6 h compared with 6-12 h: $p < 0.02$. Moorhouse (1969) showed that, in locusts, this response was maximal after they had been starved for 4 hours or longer. Potato plants grown for 4-8 weeks, 60-100 cm high, were more attractive to male beetles than 2-4 weeks old plants, 20-60 cm high (Fig. 11, $p < 0.001$). This is probably caused by a lower amount of attractive volatiles being emitted by the young plants.

In long-range olfactory orientation of insects, the wind dispersing the volatile sign-stimuli through the atmosphere directs the insects to the source of the stimulus. Bossert & Wilson (1963) have demonstrated the effect of wind speed on the distribution of the signal. In the atmosphere the amount of turbulence is increased at higher wind velocities, "diluting" the attractant in the air flow.

Turbulence is also likely to interfere with anemotactic orientation of insects in another way. The scale of turbulence, the magnitude of turbulent eddies may affect the ability of insects to detect the main direction of the air flowing downwind from the odour source. The size of an insect is small compared to the big eddies which arise from obstructions in the air flow, like the vegetation. Walking insects are faced with a second obscuring factor; the boundary layer in which the air velocities are less than in the free stream. Linsenmair (1969, 1970, 1973) showed that several walking coleopterous species not subjected to attractants are able to use pure anemomenotactic orientation. In these experiments, the lowest wind velocities which will evoke anemomenotactic orientation were about 0.15 m/s for *Geotrupes* and 0.4 m/s for *Pimelia* species. In the field, the size of the boundary layer over the ground will be much larger than the laminar one over the walking plate in the test section. It is therefore likely that the low air velocities in the boundary layer will impair the anemotactic responses of walking insects. Vogel (1969) has discussed the design of low-speed wind tunnels for biological investigations and he, too, did not mention the boundary layer phenomena. Outdoors, it is observed that Colorado beetles searching for potato plants frequently climb tiny hills obviously thus "escaping" the boundary layer.

In view of this it is likely that the statement of Jermy (1958), that the olfactory responses of Colorado beetles to potato plants are limited to a range of a few dm, is not in conflict with the results obtained by McIndoo (1926), Schanz (1953), de Wilde *et al.* (1969) and de Wilde (1974). Furthermore, the age of the potato plants may have affected the outcomes of his field experiments.

Linsenmair (1969) observed preference for upwind angles in the anemomenotaxis of *Pimelia*, *Tenebrio* and *Geotrupes* species. In addition, the mentioned (1973) anemomenotactic orientation of *Leptinotarsa decemlineata*.

We observed that in a clean air flow the Colorado beetles spent much time on the sides of the walking plate; the positive anemotaxis of the beetles in wind without potato plants, distinct in the experiments of de Wilde *et al.* (1969) and de Wilde (1974), and less marked in the present investigation, seems to be a transformed anemomenotaxis. The findings of de Wilde *et al.* (1969) and de Wilde (1974) that starvation enhances the anemotactic response in "pure" air contradict with my own observations and the results of Linsenmair (1969, 1973) with other coleopterous species. It is advantageous for walking insects searching for food to move by an anemomenotactic orientation (Linsenmair, 1969). Wind-borne attractants will then shift the angle of their orientation to the upwind direction, guiding the insects to the source of the stimulus.

In 1926 McIndoo showed that Colorado beetles can be attracted by emanations from their living host plants. In the experiments of Schanz (1953) humidity was excluded as a causal factor in the attraction of Colorado beetles. Jermy (1958) did not believe that low concentrations of potato plant volatiles were sufficient to play a rôle in host plant finding from large distances. He concluded that contact chemoreception is the principal factor in host plant selection by Colorado beetles.

Our present observations reveal that unbruised potato plants can also attract Colorado beetles at a longer range, by inducing positive anemotactic responses. More extended experiments, using the actual tracks of the beetles showing that these responses were not caused by a kinetic effect, will be published in a subsequent paper.

I wish to acknowledge the valuable advice on the design of the wind tunnel given by Prof. W. Draijer and Ir. A. Kortleven, and to thank Ir. C. Keizer for his help. I am indebted to our technicians Mr. G. van Surksun, Mr. G. van den Brink, Mr. O. van Geffen, Mr. G. G. Schuurman and Mr. B. Tollenaar for constructing the wind tunnel, and to Mr. W. C. Th. Middelplaats and Mr. F. J. J. von Planta for drawing the figures. I am grateful to Prof. Dr. J. de Wilde and Prof. Dr. L. M. Schoonhoven for criticizing the manuscript, and I thank Prof. Dr. K. N. Saxena for reading the manuscript.

ZUSAMMENFASSUNG

BESCHREIBUNG EINES WINDTUNNELS FÜR GERINGE WINDGESCHWINDIGKEIT ALS GERÄT ZUM STUDIUM DER GERUCHSORIENTIERUNG DES KARTOFFELKÄFERS (LEPTINOTARSA DECEMLINEATA)

Aerodynamische Phänomene werden diskutiert, die für die geruchliche Orientierung der adulten Kartoffelkäfer von Bedeutung sind, nämlich der Übergang von wirbelfreier zu turbulenter Strömung im freien Strom; die Grenzschicht; der Übergang von wirbelfreier zu turbulenter Strömung in der Grenzschicht und die Dicke der wirbelfreien Grenzschicht. Ein Windtunnel für niedrige Windgeschwindigkeit wird beschrieben, der sich für das Studium der geruchlichen Orientierung des Kartoffelkäfers als günstig erwies. Messungen der Windströmung in diesem Tunnel zeigten, daß der Prozentsatz von Turbulenz im Hauptstrom der Insektenprüfkammer niedrig ist und daß eine einheitliche Lockstoffkonzentration in dieser Kammer vorliegt. Es wird geschlossen, daß die Käfer auf

pflanzliche Duftstoffe mit Geruch-induzierter Anemotaxis reagieren. Die Dicke der wirbelfreien Grenzschicht über der Laufplatte in der Prüfkammer wurde ermittelt.

Die Einführung von getopften Kartoffelpflanzen in den Luftstrom des Windtunnels löst positive anemotaktische Reaktionen bei Männchen und Weibchen des Kartoffelkäfers aus. Die stärkste positive anemotaktische Reaktion der Männchen wird nach sechs Stunden Hunger erzielt. Ausgewachsene Kartoffelpflanzen sind attraktiver für Männchen als junge.

In der Diskussion wird vermutet, daß die Größe der Turbulenz und die Dicke der Grenzschicht unter Freilandbedingungen die geruchlich induzierte anemotaktische Reaktion der Insekten beeinträchtigt.

REFERENCES

- BOSSERT, W. H. (1968). Temporal patterning in olfactory communication. *J. Theoret. Biol.* **18**: 157—170.
- BOSSERT, W. H. & WILSON, E. O. (1963). The analysis of olfactory communication among animals. *J. Theoret. Biol.* **5**: 443—469.
- BRADSHAW, P. (1971). *An introduction to turbulence and its measurement*. Pergamon Press, New York.
- BROWNE, L. E., BIRCH, M. C. & WOOD, D. L. (1974). Novel trapping and delivery systems for airborne insect pheromones. *J. Ins. Physiol.* **20**: 183—193.
- CHIN, C. T. (1950). Studies on the physiological relations between the larvae of *Leptinotarsa decemlineata* Say and some solanaceous plants. *Tijdschr. Pl. ziekte.* **56**: 1—88.
- COAKER, T. H. & HAWKES, C. (1974). Behavioural response to host-plant odours in adult cabbage root fly. In: *The host plant in relation to insect behaviour and reproduction*. Symposium Tihany, Hungary, in press.
- FARKAS, S. R. & SHOREY, H. H. (1972). Chemical trail- following by flying insects: a mechanism for orientation to a distant odor source. *Science* **178**: 67—68.
- GATEHOUSE, A. G. & LEWIS, C. T. (1973). Host location behaviour of *Stomoxys calcitrans*. *Ent. exp. & appl.* **16**: 275—290.
- GRUBB, Jr. T. C. (1973). Odor-following and anemotaxis. *Science* **180**: 1302.
- HASKELL, P. T., PASKIN, M. W. J. & MOORHOUSE, J. E. (1962). Laboratory observations on factors affecting the movements of hoppers of the desert locust. *J. Ins. Physiol.* **8**: 53—78.
- JERMY, T. (1958). Untersuchungen über Auffinden und Wahl der Nahrung beim Kartoffelkäfer (*Leptinotarsa decemlineata* Say). *Ent. exp. & appl.* **1**: 197—208.
- KENNEDY, J. S. & MARSH, D. (1974). Pheromone-regulated anemotaxis in flying moths. *Science* **184**: 999—1001.
- KENNEDY, J. S. & MOORHOUSE, J. E. (1969). Laboratory observations on locust responses to wind-borne grass odour. *Ent. exp. & appl.* **12**: 487—503.
- LINSENMAYER, K. E. (1969). Anemomenotaktische Orientierung bei Tenebrioniden und Mistkäfern (*Insecta, Coleoptera*). *Z. vergl. Physiol.* **64**: 154—211.
- (1970). Die Interaktion der paarigen antennalen Sinnesorgane bei der Windorientierung laufender Mist- und Schwarzkäfer (*Insecta, Coleoptera*). *Z. vergl. Physiol.* **70**: 247—277.
- (1973). Die Windorientierung laufender Insekten. *Fortschr. Zool.* **21**: 59—79.
- MAYER, M. S. (1973). Attraction studies of male *Trichoplusia ni* (*Lepidoptera: Noctuidae*) with new combination of olfactometer and pheromone dispenser. *Ann. ent. Soc. Amer.* **66**: 1191—1196.
- MCINDOO, N. E. (1926). An insect olfactometer. *J. econ. Ent.* **19**: 545—571.
- MOORHOUSE, J. E. (1971). Experimental analysis of the locomotor behaviour of *Schistocerca gregaria* induced by odour. *J. Ins. Physiol.* **17**: 913—920.
- OWER, E. & PANKHURST, R. C. (1966). *The measurements of air flow*. Pergamon Press, Oxford-London.
- PANKHURST, R. C. & HOLDER, D. W. (1952). *Wind-tunnel technique*. Pitman and Sons, London.
- POPE, A. (1954). *Wind-tunnel testing*. Chapman and Hall, London.
- SCHANZ, M. (1953). Der Geruchssinn des Kartoffelkäfers (*Leptinotarsa decemlineata* Say). *Z. vergl. Physiol.* **35**: 353—379.

- SCHLICHTING, H. (1955). *Boundary layer theory*. Pergamon Press, London.
- SIEGEL, S. (1956). *Nonparametric statistics for the behavioral sciences*, 104—111. McGraw-Hill Kogakusha, Tokyo.
- VOGEL, S. (1969). Low speed wind tunnels for biological investigations. In: G. A. KERKUT (ed), *Experiments in physiology and biochemistry* 2 : 295—325. Academic Press, London.
- WILDE, J. DE (1974). The olfactory component in host plant selection in the adult Colorado beetle (*Leptinotarsa decemlineata* Say). In: *The host plant in relation to insect behaviour and reproduction*, Symposium Tihany, Hungary, in press.
- WILDE, J. DE, HILLE RIS LAMBERS-SUVERKROPP, K. & TOL, A. VAN (1969). Responses to air flow and airborne plant odour in the Colorado beetle. *Neth. J. Pl. Path.* 75 : 53—57.