

Electroantennogram responses of the carrot fly, *Psila rosae*, to volatile plant components

P. M. GUERIN* and J. H. VISSER Department of Entomology, Agricultural University, Wageningen, The Netherlands

ABSTRACT. Electroantennogram (EAG) responses of male and female carrot flies, *Psila rosae* F. (Diptera: Psilidae), were recorded to thirty-six volatile plant constituents. The most distinct EAG responses were obtained to: (1) the general green leaf volatiles 1-hexanol, trans-2-hexen-1-ol and cis-3-hexen-1-ol, their isomers cis-2-hexen-1-ol and trans-3-hexen-1-ol, the alcohol 1-heptanol, the ester cis-3-hexenyl acetate and the leaf aldehydes hexanal and trans-2-hexenal, and (2) from four compounds associated with the umbelliferous host plants of this insect, namely trans-methyl-iso-eugenol, β -caryophyllene, linalool and trans-2-nonenal. Higher responses were elicited by the leaf aldehydes than by the corresponding alcohols. Although the absolute amplitude of the female response was over twice that of the male, there were no differences between the relative responses to the compounds tested in both sexes, with the exception of a much higher response to the leaf aldehydes in the male. The shape of the EAG evoked by the various compounds was consistently different, with the slowest recovery being recorded for trans-methyl-iso-eugenol. While the antennal olfactory receptors of the carrot fly are sensitive to the closely related general green leaf volatiles, they are most specifically tuned to the aldehyde component of this green odour complex. In addition, the ability of this insect to discriminate between different plants may be augmented by the perception of a group of more host specific volatiles. The conformity of the responses of males and females to the compounds tested may indicate that host plant volatiles plays an additional role as an aggregation cue for both sexes.

Introduction

The carrot fly, *Psila rosae* F. (Diptera: Psilidae), is oligophagous since females have been reported to oviposit in the ground surrounding plants of the Umbelliferae and the larvae tunnel in their roots (Van't Sant, 1961; Städler, 1972). On emergence, carrot flies move to dense vegetation, especially head-

lands bordering on host crops; mature females move out from these situations to seek a host plant for the oviposition act, while males move little from the protective vegetation (Wakerley, 1964; Städler, 1972). After initial contact with the host plant leaves, females run over the surface followed by an uninterrupted run down the leaf stem to the soil, where oviposition occurs (Bohlen, 1967; Städler, 1977).

Three volatile oviposition stimulants for the carrot fly have been identified: trans-methyl-iso-eugenol isolated from carrot leaves (Berüter & Städler, 1971); p-allylanisole and

* Present address: Swiss Federal Research Station, CH-8820, Wädenswil, Switzerland.

Correspondence: Dr J. H. Visser, Department of Entomology, Agricultural University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands.

anisaldehyde from leaves of both celery and fennel (see Städler, 1972). As activity by oviposition stimulants does not necessarily entail an initial attraction over longer distances, the role of these three volatiles in attraction of carrot flies has yet to be demonstrated.

To establish the potential of volatiles in olfactory stimulation, the electroantennogram (EAG) is commonly used. It represents the summed receptor potentials of many olfactory receptor cells in the antenna as elicited by odours (Boeckh *et al.*, 1965). This indicates the qualitative spectrum of the main olfactory sense system of an insect and it records the intensity of responses of a large number of receptor cells, thus indicating the sensitivity of the olfactory system. In the present study the EAG was used as a bioassay to determine the responses of the carrot fly to a range of volatile plant constituents.

Materials and Methods

Carrot flies were collected as pupae at Noordwijk, The Netherlands. After emergence, flies

were kept in rearing cages under conditions described by Städler (1971). In preparation for EAG recordings, the test insect was momentarily anaesthetized with CO₂ and its head was removed. EAGs were recorded with electrolyte-filled (0.1 M KCl) glass capillary electrodes; the reference electrode was placed in the pedicellus and the recording electrode was pierced through the ventral tip of the funiculus (Fig. 1A). To observe the insertion of the reference electrode, its tip was painted black. A space was made inside the head from the occipital opening to the base of the antenna making use of an insect pin. The reference electrode was inserted into the opening and through the scapus into the pedicellus. With this preparation movement artefacts were eliminated and desiccation was prevented. It had an effective life-span of 1–2 h. The tip diameter of the recording electrode was 5–10 μm and the reference electrode 10–20 μm. The preparation was connected via Ag–AgCl wires in the glass capillary electrodes to recording instruments.

The odour delivery system and response evaluation method were essentially the same as that of Visser (1979a); in essence this

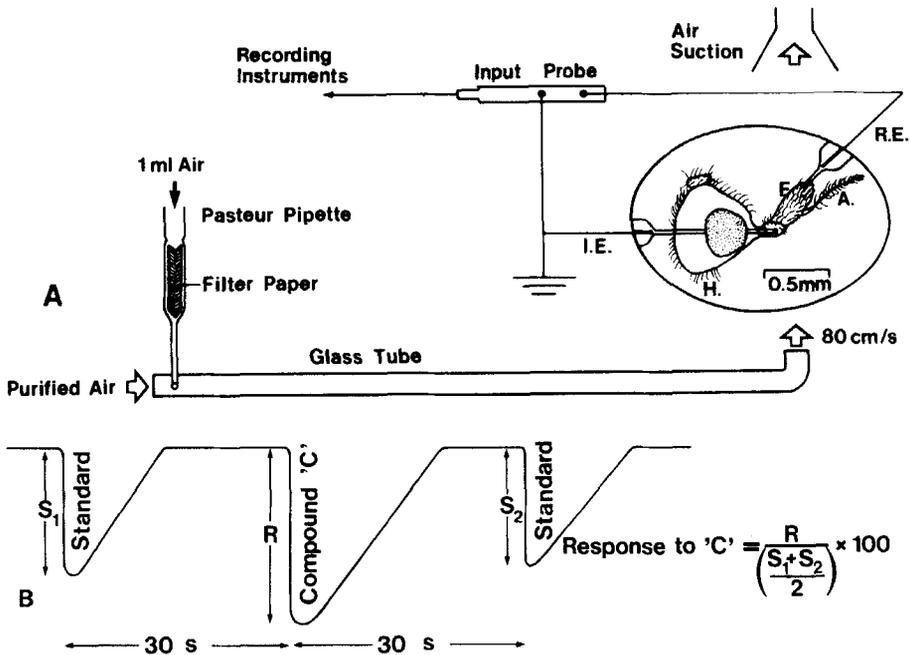


FIG. 1. EAG recording technique. (A) Preparation: A., arista; F., funiculus; H., insect head; I.E., indifferent electrode; R.E., recording electrode. (B) Response evaluation method. For further explanation see text.

involved the following. Charcoal filtered air from a central supply passed continuously over the preparation at a flow rate of 80 cm/s from a glass tube, which terminated within 5 mm of the fixed preparation, as illustrated in Fig. 1A. Test chemicals were dissolved in paraffin oil (Merck Uvasol); 25 μ l of each solution had been pipetted onto a piece of filter paper which was placed in a pasteur pipette and attached to a syringe. The tip of the pipette was inserted through a hole in the glass tube and the syringe plunger was quickly depressed to pass 1 ml of air through the pipette into the air stream.

For convenience, concentrations of test compounds refer to the dilution (volume/volume) in paraffin oil of the chemical inside the pasteur pipette. Using female antennae, compounds eliciting consistent EAG responses at 10^{-1} , 10^{-2} and 10^{-3} were tested at successively lower concentrations until no response was recorded. Male antennae were tested at 10^{-1} and 10^{-3} concentrations of the thirty compounds which gave clear EAG responses

in the female at the same concentrations. Compounds were tested randomly on antennae of six different animals at each concentration.

To correct for changes in the antennal responses during the experimental period, the antenna was stimulated alternatively every 30 s by the test chemical or the standard, cis-3-hexen-1-ol 10^{-2} . The amplitude of the response to the test compound is expressed as a percentage of the mean of the two adjacent standard response amplitudes (Fig. 1B). Differences in volatility between test compounds were not corrected for and accordingly comparisons between the responses elicited are relative.

The choice of test compounds was based on their distribution in member species of the Umbelliferae (Table 1) and their presence in the green leaf volatile complex (Visser *et al.*, 1979). Chemically related compounds and isomeric forms were included. Compounds were $\geq 98\%$ pure except for α -pinene and β -ionone (97%), α -phellandrene and Δ^3 -carene (95%), camphene (92%) and myrcene (90%).

TABLE 1. Distribution of the volatile compounds screened for EAG responses of carrot flies, in five umbelliferous species

<i>Daucus carota</i> , carrot	
seeds:	Myrcene ^a , Linalool ^a , Limonene ^{a,b} , γ -Terpinene ^a , α -Terpineol ^a , α -Pinene ^{a,b} , β -Pinene ^{a,b} , Camphene ^a , Bornylacetate ^a , β -Caryophyllene ^{a,b}
roots:	trans-2-Nonenal ^{c,d,e} , trans, trans-2,4-Decadienal ^c , Myrcene ^{c,d,e,f} , Linalool ^d , β -Ionone ^{d,e} , 2,4-Dimethylstyrene ^{e,f} , Biphenyl ^{c,d,e} , Limonene ^{c,d,e,f} , Terpinolene ^{c,d,e,f} , α -Terpinene ^{c,d,e} , γ -Terpinene ^{c,d,e,f} , α -Phellandrene ^f , α -Terpineol ^{c,d} , trans-Methyl-iso-eugenol ^e , α -Pinene ^{c,d,e,f} , β -Pinene ^{c,d,e,f} , Camphene ^{c,d,e,f} , Bornylacetate ^{c,d,e,f} , γ -Bisabolene ^{c,d,e} , β -Caryophyllene ^{c,d,e,f}
stems:	Myrcene ^c
leaves:	trans-Methyl-iso-eugenol ^f
<i>Petroselinum crispum</i> , parsley	
seeds ^h :	Myrcene, Limonene, γ -Terpinene, α -Phellandrene, Δ^3 -Carene, α -Pinene, β -Pinene, Camphene
leaves:	cis-3-hexen-1-ol ⁱ , cis-3-Hexenyl acetate ⁱ , trans-2-Hexenal ^j , n-Tridecane ^j , Myrcene ^{i,j} , Naphthalene ^j , Terpinolene ^{i,j} , γ -Terpinene ^j , α -Phellandrene ^{i,j} , α -Pinene ^{i,j} , β -Pinene ^{i,j} , Camphene ^j , β -Caryophyllene ^j
<i>Apium graveolens</i> , celery	
seeds ^h :	Myrcene, Limonene, β -Pinene
stems:	1-Hexanol ^k , 1-Heptanol ^k , trans-2-Hexen-1-ol ^l , cis-3-Hexen-1-ol ^l , cis-3-Hexenyl acetate ^m , Hexanal ^k , Myrcene ^{k,n} , Limonene ^{k,n} , γ -Terpinene ⁿ , α -Terpineol ^l , Carvone ^{k,m} , α -Pinene ⁿ , β -Pinene ⁿ , β -Caryophyllene ⁿ
leaves ^o :	p-Allylanisole, Anisaldehyde
<i>Foeniculum vulgare</i> , fennel	
leaves ^o :	p-Allylanisole, Anisaldehyde
<i>Carum carvi</i> , caraway	
seeds:	Myrcene ^p , Limonene ^{h,p} , Terpinolene ^p , α -Terpinene ^p , γ -Terpinene ^p , α -Phellandrene ^{h,p} , Δ^3 -Carene ^{h,p} , α -Pinene ^{h,p} , β -Pinene ^{h,p} , Camphene ^p

^a Seifert *et al.*, 1968; ^b Zalkow *et al.*, 1963; ^c Buttery *et al.*, 1968; ^d Alabran *et al.*, 1975; ^e Guerin, 1978; Heatherbell *et al.*, 1971; ^f Berüter & Städler, 1971; ^h Ikeda *et al.*, 1962; ⁱ Freeman *et al.*, 1975; ^j Kasting *et al.*, 1972; ^k Gold & Wilson, 1963; ^l Wilson, 1969b; ^m Wilson, 1970; ⁿ Wilson, 1969a; ^o Städler, 1972; ^p Salvesson & Baerheim Svendsen, 1976.

TABLE 2. Mean EAG responses of female carrot flies to volatile plant constituents expressed as a percentage of the response to *cis*-3-hexen-1-ol 10^{-2} (\pm 95% confidence intervals; $n = 6$ in each case)

Compound	Concentration		Compound	Concentration	
	10^{-3}	10^{-1}		10^{-3}	10^{-1}
1-Hexanol	40 \pm 13	159 \pm 18	d-Limonene	0	98 \pm 18
1-Heptanol	32 \pm 14	141 \pm 20	Terpinolene	3 \pm 8	123 \pm 29
<i>trans</i> -2-Hexen-1-ol	47 \pm 11	176 \pm 26	α -Terpinene	2 \pm 3	128 \pm 13
<i>cis</i> -2-Hexen-1-ol	22 \pm 9	198 \pm 86	γ -Terpinene	1 \pm 4	106 \pm 27
<i>trans</i> -3-Hexen-1-ol	34 \pm 10	181 \pm 39	α -Phellandrene	6 \pm 10	138 \pm 29
<i>cis</i> -3-Hexen-1-ol	42 \pm 12	165 \pm 27	α -Terpineol	8 \pm 9	106 \pm 36
<i>cis</i> -3-Hexenyl acetate	32 \pm 14	214 \pm 67	Carvone	1 \pm 4	179 \pm 30
Hexanal	32 \pm 22*	383 \pm 134	Eugenol	4 \pm 10	88 \pm 52
<i>Trans</i> -2-Hexenal	48 \pm 40	404 \pm 133	<i>trans</i> -Methyl-iso-eugenol	70 \pm 42	279 \pm 77
<i>trans</i> -2-Nonenal	44 \pm 25	169 \pm 31	<i>p</i> -Allylanisole	0	118 \pm 30
<i>trans, trans</i> -2,4-Decadienal	4 \pm 5	152 \pm 40	Anisaldehyde	2 \pm 5	74 \pm 18
<i>n</i> -Tridecane	1 \pm 3	17 \pm 30	Δ^3 -Carene	0	82 \pm 29
Myrcene	2 \pm 6	109 \pm 13	α -Pinene	0	61 \pm 12
Linalool	41 \pm 14	187 \pm 43	β -Pinene	0	59 \pm 9
β -Ionone	3 \pm 3	51 \pm 19	Camphene	0	47 \pm 12
2,4-Dimethylstyrene	2 \pm 4	66 \pm 13	Bornylacetate	0	71 \pm 17
Biphenyl	0	50 \pm 24	γ -Bisabolene	9 \pm 12	98 \pm 48
Naphthalene	20 \pm 21	93 \pm 27	β -Caryophyllene	24 \pm 8	110 \pm 33
			Paraffin oil		0

Concentration of the compound in paraffin oil expressed as volume/volume.

* EAG response of male: 110 \pm 32 ($P < 0.001$; *t*-test).

Results

The EAG responses of female carrot flies to thirty-six compounds at two concentrations are shown in Table 2. Although all compounds elicited a response at 10^{-1} , the number of compounds responded to was markedly reduced at 10^{-3} . At both concentrations distinct EAG responses were obtained to the following compounds: (1) saturated and unsaturated leaf alcohols namely 1-hexanol, *trans*-2-hexen-1-ol and *cis*-3-hexen-1-ol, their isomers *cis*-2-hexen-1-ol and *trans*-3-hexen-1-ol, the ester *cis*-3-hexenyl acetate and the alcohol 1-heptanol; (2) the saturated and unsaturated leaf aldehydes hexanal and *trans*-2-hexenal; (3) the aliphatic aldehyde *trans*-2-nonenal; (4) the acyclic unsaturated alcohol linalool; (5) the methoxy phenyl compound *trans*-methyl-iso-eugenol; and (6) the sesquiterpene β -caryophyllene. The response elicited by *trans*-methyl-iso-eugenol was much higher than that of the structurally related compounds eugenol, *p*-allylanisole and anisaldehyde.

Among the benzene derivatives the bicyclic aromatic naphthalene, was more stimulating than 2,4-dimethylstyrene and biphenyl. The solvent itself, paraffin oil, did not elicit a measurable response.

Although the absolute amplitude of the responses obtained from female antennae was over twice that for male antennae, there were no differences between the relative responses to the compounds tested in both sexes, with the exception of that to the leaf aldehydes. At the lower concentration (10^{-3}), the EAG responses of males to *trans*-2-hexenal (91%) and hexanal (110%) were much higher than that of females (see Table 2).

Addition of increasing amounts of *cis*-3-hexen-1-ol to the air flowing over the antennae resulted in EAGs of increasing amplitude as shown in Fig. 2A. Representative EAG recordings for *cis*-3-hexenyl acetate, linalool and *trans*-methyl-iso-eugenol are presented in Fig. 2B. It was observed that the shape of the EAG evoked by the various compounds was consistently different; the fastest recovery

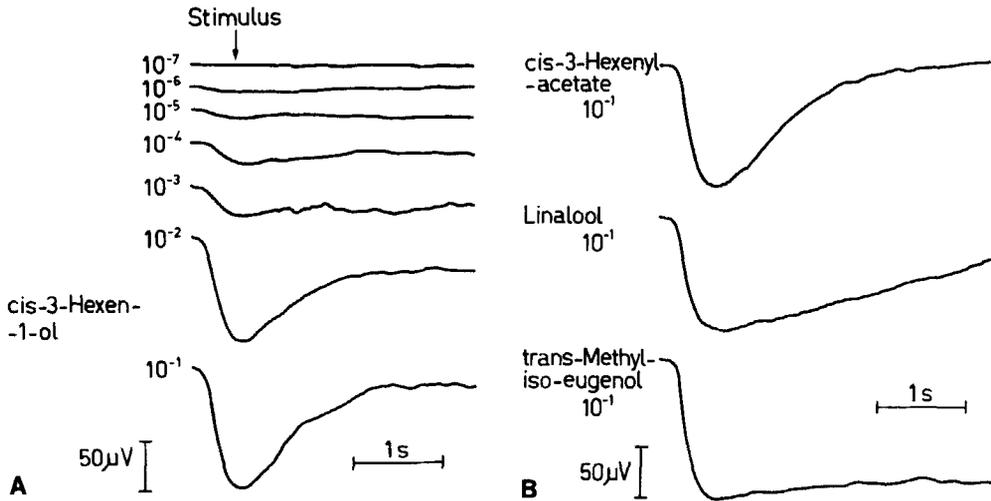


FIG. 2. EAGs of female carrot flies. A, to a range of concentrations of cis-3-hexen-1-ol. B, responses of different shapes. Concentrations refer to dilution in paraffin oil (v/v).

after maximum depolarization was recorded for 1-hexanol, trans- and cis-2-hexen-1-ol, trans- and cis-3-hexen-1-ol and cis-3-hexenyl acetate; an intermediate type of recovery was observed in the case of 1-heptanol, hexanal, trans-2-hexenal, trans-2-nonenal, linalool and β -caryophyllene, and the slowest recovery was for trans-methyl-iso-eugenol.

Dose-response curves for trans-2-hexenal, trans-2-hexen-1-ol, hexanal, 1-hexanol, cis-3-hexen-1-ol, cis-3-hexenyl acetate, trans-methyl-iso-eugenol and trans-2-nonenal are presented in Fig. 3. These curves indicate the sensitivity of the antenna and show that higher responses are elicited by leaf aldehydes than by the corresponding alcohols (Fig. 3). Following the leaf aldehydes, trans-methyl-iso-eugenol is the most effective compound. Responses were recorded to 1-hexanol, trans-methyl-iso-eugenol and cis-3-hexen-1-ol at levels as low as 1 ppm in paraffin oil. The wide confidence intervals attached to hexanal, trans-2-hexenal, and to trans-methyl-iso-eugenol (Fig. 3), resulted from consistent differences in the dose-response curves of individual carrot fly antennae at higher test concentrations (Fig. 4), and were therefore not due to any variations in stimulus strength. (Using the same odour delivery system, Visser (1979a) reported small confidence intervals for EAGs of Colorado beetles stimulated with trans-2-hexenal.)

Discussion

Plant odour perception in the carrot fly involves the reception of the general green leaf volatiles and in particular the leaf aldehydes hexanal and trans-2-hexenal. These compounds are found in the foliage of numerous plant species and contribute to the 'green odour' of leaves (Visser *et al.*, 1979). Green leaf volatiles are present in Umbelliferae as indicated by analyses of the foliar parts of parsley and celery: cis-3-hexen-1-ol, cis-3-hexenyl acetate and trans-2-hexenal have been isolated from leaves and petioles of parsley (Freeman *et al.*, 1975; Kasting *et al.*, 1972), and 1-hexanol, trans-2-hexen-1-ol, cis-3-hexen-1-ol, cis-3-hexenyl acetate and hexanal from celery stems (Gold & Wilson, 1963; Wilson, 1969b, 1970), see Table 1.

EAG responses of the Colorado beetle, *Leptinotarsa decemlineata*, to plant volatiles indicate that the antennal olfactory receptors are sensitively tuned to the perception of a group of closely related general green leaf volatiles (Visser, 1979a), and evidence from both behavioural and electrophysiological experiments indicate that the 'green odour' complex plays a role in host selection by a range of phytophagous insects (see Visser & Avé, 1978; Visser, 1979a). It could be assumed that this complex also acts in the olfactory orientation of the carrot fly as judged by the

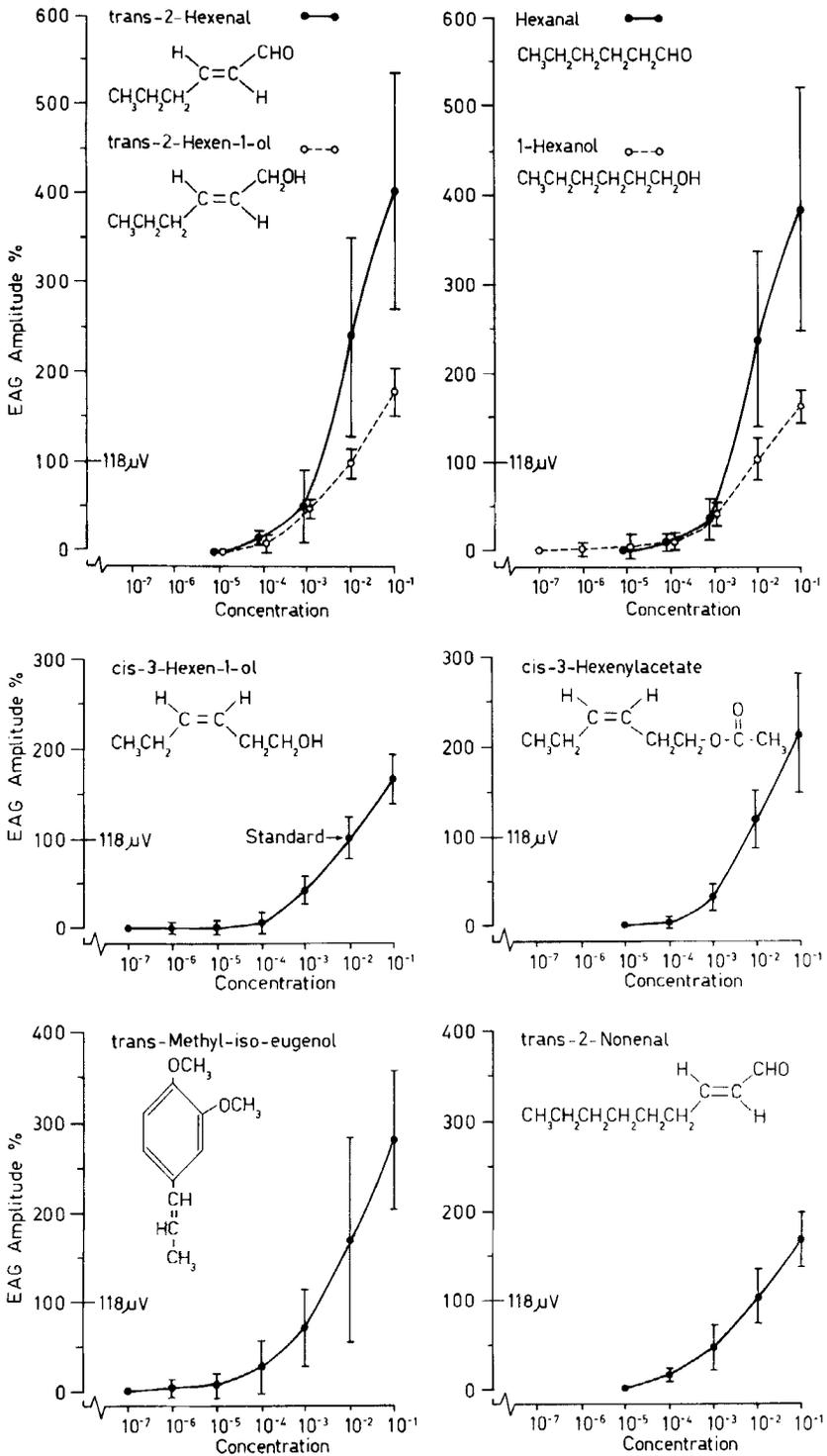


FIG. 3. Mean EAG responses of female carrot flies responding to a range of concentrations of eight plant volatiles. Concentrations refer to dilution in paraffin oil (v/v). Vertical lines indicate 95% confidence intervals (*n* = 6 flies).

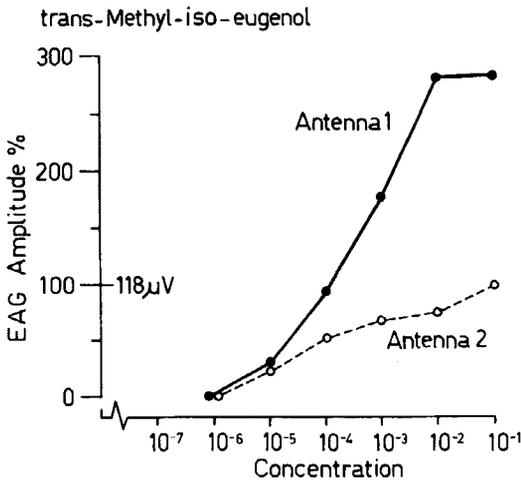


FIG. 4. Dose-response curves of EAGs of two female carrot fly antennae to trans-methyl-iso-eugenol (one antenna from each of two flies). Concentrations refer to dilution in paraffin oil (v/v). Each point represents one stimulation.

sensitivity of the olfactory system to green leaf volatiles. The relative proportions of the constituents composing this complex varies in and over different plant species. (Visser *et al.*, 1979). The ability of an insect to discriminate between plants would accordingly be augmented by being tuned to the particular quality of this complex emanating from its host plant. The highest EAG responses of the Colorado beetle are evoked by leaf alcohols, which are present in potato leaf odour (Visser, 1979a, b). By contrast, the olfactory system of the carrot fly is more sensitive to leaf aldehydes than to alcohols.

Trans-methyl-iso-eugenol is the most stimulating aromatic compound tested. Besides being a chemo-contact oviposition stimulant for the carrot fly (Berüter & Städler, 1971), it is suggested that it may also be an attractant as the number of flies caught in coloured traps is doubled by incorporation of trans-methyl-iso-eugenol dispensers (Städler, personal communication). On the other hand, the weak EAG responses evoked by the oviposition stimulants p-allylanisole and anisaldehyde may indicate that their perception is restricted to close-range.

The remaining compounds which elicit strong EAGs, namely β -caryophyllene, linalool and trans-2-nonenal, are all associated with the Umbelliferae: β -caryophyllene has been

found in the foliar parts of celery (Wilson, 1969a) and parsley (Kasting *et al.*, 1972), and is also present in the headspace over carrot root (Guerin, 1978); in addition, β -caryophyllene, linalool and trans-2-nonenal are present in carrot root oil (Buttery *et al.*, 1968; Alabran *et al.*, 1975; Guerin, 1978; Heatherbell *et al.*, 1971), and the former two components are also present in carrot seed oil (Seifert *et al.*, 1968; Zalkow *et al.*, 1963), see Table 1. Thus the olfactory sense of the carrot fly is tuned not only to specific qualities of the 'green odour' complex, but also to more host specific volatiles such as trans-methyl-iso-eugenol, β -caryophyllene, linalool and trans-2-nonenal. Behavioural experiments demonstrate also that volatile constituents of the root oil and headspace vapour of carrot roots are strongly attractive to carrot fly larvae (Ryan & Guerin, 1980).

The capacity of quality discrimination as indicated by the response spectra of single olfactory receptors in the antenna of the Colorado beetle, revealed two groups of receptors, one group reacting differentially to the green leaf volatiles and their isomers, and another group being responsive to an aromatic volatile (Ma & Visser, 1978). Single unit recordings from receptors in the antenna of the carrot fly may reveal a similar type of response patterning.

The amplitude of the EAG evoked by cis-3-hexen-1-ol 10^{-2} in the carrot fly is 65% that of the Colorado beetle, and for this reason the concentration of standard used here was 10 times higher than that used by Visser (1979a), in order to reduce response variations. Accordingly, the recorded response threshold of the carrot fly to green leaf volatiles is higher than that of the Colorado beetle, being in the order of 10 times greater for cis-3-hexen-1-ol and 100 times greater for trans-2-hexen-1-ol (see Visser, 1979a). Naphthalene is a known repellent for the carrot fly (Dethier, 1947), but it elicits a relatively weak EAG response, with a threshold of approximately 100 ppm in paraffin oil, indicating that its effective range is short.

With the exception of the higher response in males to hexanal and trans-2-hexenal, there are no differences between the sexes in the responses to the odorous compounds tested. By contrast, only gravid female cabbage root

flies, *Delia brassicae*, show a marked increase in activity to host leaf vapours (Traynier, 1967), and EAG responses to apple odours were recorded only in the female summerfruit tortrix moth, *Adoxophyes orana* (Den Otter *et al.*, 1978). In the carrot fly, it is possible that host plant volatiles may have an additional role as an aggregation cue for both sexes.

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References

- Alabran, D.M., Moskowitz, H.R. & Mabrouk, A.F. (1975) Carrot root oil components and their dimensional characterization of aroma. *Journal of Agricultural and Food Chemistry*, **23**, 229–232.
- Berüter, J. & Städler, E. (1971) An oviposition stimulant for the carrot rust fly from carrot leaves. *Zeitschrift für Naturforschung*, **26B**, 339–340.
- Boeckh, J., Kaissling, K.E. & Schneider, D. (1965) Insect olfactory receptors. *Cold Spring Harbor Symposia on Quantitative Biology*, **30**, 263–280.
- Bohlen, E. (1967) Untersuchungen zum Verhalten der Möhrenfliege, *Psila rosae* Fab. (Dipt. Psilidae) im Eiablagefunktionskreis. *Zeitschrift für Angewandte Entomologie*, **59**, 325–360.
- Buttery, R.G., Seifert, R.M., Guadagni, D.G., Black, D.R. & Ling, L.C. (1968) Characterization of some volatile constituents of carrot. *Journal of Agricultural and Food Chemistry*, **16**, 1009–1015.
- Dethier, V.G. (1947) *Insect Attractants and Repellents*, p. 225. Blakiston, Philadelphia.
- Freeman, G.G., Whenham, R.J., Self, R. & Eagles, J. (1975) Volatile flavour components of parsley leaves (*Petroselinum crispum* (Mill.) Nyman). *Journal of the Science of Food and Agriculture*, **26**, 465–570.
- Gold, H.J. & Wilson, C.W. (1963) The volatile flavor substances of celery. *Journal of Food Science*, **28**, 484–488.
- Guerin, P.M. (1978) The chemical ecology of the carrot fly, *Psila rosae* (F.), in relation to its host plant *Daucus carota* (L.). Part I, Behavioural responses of the carrot fly larva to carrot root volatiles, pp. 1–71. Ph.D. thesis, The National University of Ireland, Dublin.
- Heatherbell, D.A., Wrolstad, R.E. & Libbey, L.M. (1971) Carrot volatiles. I. Characterization and effects of canning and freeze drying. *Journal of Food Science*, **36**, 219–224.
- Ikeda, R.M., Stanley, W.L., Vannier, S.H. & Spitler, E.M. (1962) The monoterpene hydrocarbon composition of some essential oils. *Journal of Food Science*, **27**, 455–458.
- Kasting, R., Andersson, J. & Von Sydow, E. (1972) Volatile constituents of leaves of parsley. *Phytochemistry*, **11**, 2277–2282.
- Ma, Wei-Chun & Visser, J.H. (1978) Single unit analysis of odour quality coding by the antennal olfactory receptor system of the Colorado beetle. *Entomologia Experimentalis et Applicata*, **24**, 520–533.
- Otter, C.J. den, Schuil, H.A. & Sander-van Oosten, A. (1978) Reception of host plant odours and female sex pheromone in *Adoxophyes orana* (Lepidoptera: Tortricidae): electrophysiology and morphology. *Entomologia Experimentalis et Applicata*, **24**, 570–578.
- Ryan, M.F. & Guerin, P.M. (1980) Responses of the carrot fly larva, *Psila rosae*, to chemical constituents of its host. *Physiological Entomology*, in press.
- Salveson, A. & Baerheim Svendsen, A. (1976) Gas liquid chromatographic separation and identification of the constituents of caraway seed oil. *Planta Medica*, **30**, 93–96.
- Sant, L.E. van't (1961) Levenswijze en bestrijding van de wortelvlug (*Psilae rosae* F.) in Nederland. *Verslagen van Landbouwkundige Onderzoekingen*, **67-1**, 131 pp.
- Seifert, R.M., Buttery, R.G. & Ling, L.C. (1968) Identification of some constituents of carrot seed oil. *Journal of the Science of Food and Agriculture*, **19**, 383–385.
- Städler, E. (1971) An improved mass-rearing method of the carrot rust fly, *Psila rosae* (Diptera: Psilidae). *Canadian Entomologist*, **103**, 1033–1038.
- Städler, E. (1972) Über die Orientierung und das Wirtswahlverhalten der Möhrenfliege, *Psila rosae* F. (Diptera: Psilidae). II. Imagines. *Zeitschrift für Angewandte Entomologie*, **70**, 29–61.
- Städler, E. (1977) Host selection and chemoreception in the carrot rust fly (*Psila rosae* F., Dipt. Psilidae): extraction and isolation of oviposition stimulants and their perception by the female. *Comportement des Insectes et Milieu Trophique* (ed. by V. Labeyrie), pp. 357–372. Colloques Internationaux du C.N.R.S., no. 265.
- Traynier, R.M.M. (1967) Effect of host plant odour on the behaviour of the adult cabbage root fly, *Eriosechia brassicae*, *Entomologia Experimentalis et Applicata*, **10**, 321–328.
- Visser, J.H. (1979a) Electroantennogram responses of the Colorado beetle, *Leptinotarsa decemlineata*, to plant volatiles. *Entomologia Experimentalis et Applicata*, **25**, 86–97.
- Visser, J.H. (1979b) Olfaction in the Colorado beetle at the onset of host plant selection. Thesis, Agricultural University, Wageningen, The Netherlands.
- Visser, J.H. & Avé, D.A. (1978) General green leaf

- volatiles in the olfactory orientation of the Colorado beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, **24**, 738–749.
- Visser, J.H., Straten, S. van & Maarse, H. (1979) Isolation and identification of volatiles in the foliage of potato, *Solanum tuberosum*, a host plant of the Colorado beetle, *Leptinotarsa decemlineata*. *Journal of Chemical Ecology*, **5**, 13–25.
- Wakerley, S.B. (1964) The sensory behaviour of the carrot fly (*Psila rosae*, Fab., Dipt., Psilidae). *Entomologia Experimentalis et Applicata*, **7**, 167–178.
- Wilson, C.W. (1969a) Terpene and sesquiterpene hydrocarbons in the essential oil from fresh celery. *Journal of Food Science*, **34**, 521–523.
- Wilson, C.W. (1969b) Identification and quantitative estimation of alcohols in celery essential oil. *Journal of Food Science*, **34**, 535–537.
- Wilson, C.W. (1970) Relative recovery and identification of carbonyl compounds from celery essential oil. *Journal of Food Science*, **35**, 766–768.
- Zalkow, L.H., Park, M.K. & Ellis, J.W. (1963) A vapour phase chromatographic analysis of carrot seed oil. *Perfumery and Essential Oil Record*, **54**, 507–509.

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