

ASSESSING THE ATTRACTIVENESS OF VOLATILE PLANT COMPOUNDS TO WESTERN FLOWER THRIPS *Frankliniella occidentalis*

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Abstract—The responses of walking adult female western flower thrips, *Frankliniella occidentalis*, to plant volatiles at several concentrations were investigated in a Y-shaped glass tube olfactometer. The simple experimental design allowed comparing the effect of numerous volatiles and differentiated clearly between attractive and repellent compounds. Western flower thrips were attracted by the benzenoids benzaldehyde and *p*- and *o*-anisaldehyde; the monoterpenes geraniol, nerol, linalool, and (+)-citronellol; the sesquiterpene (*E*)- β -farnesene, eugenol, and 3-phenylpropionaldehyde; two phenylpropanoids; and the nonfloral odor ethyl nicotinate. *p*-Anisaldehyde, nerol, ethyl nicotinate, and (*E*)- β -farnesene elicited positive responses at several concentrations; all other volatiles were attractive at a specific concentration. Salicylaldehyde, a benzenoid, elicited negative responses at two concentrations. Experimental series with several other volatiles belonging to the above mentioned chemical groups and the essential oils from rose and geranium did not result in either clearly positive or negative responses by tested thrips.

Key Words—*Frankliniella occidentalis*, western flower thrips, Thysanoptera, Thripidae, attraction, olfactometer, semiochemicals, plant volatiles, kairomones.

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INTRODUCTION

During recent decades, thrips (Thysanoptera; Thripidae) have become key insect pests in many cultivated crops in the field and in greenhouses (Berlinger et al., 1993; Brødsgaard, 1995; Brownbridge, 1995; Mateus and Mexia, 1995; Parrella and Murphy, 1996). Especially *Frankliniella occidentalis* (Pergande), the western flower thrips, causes serious damage to vegetable and ornamental crops, and its potential for transmitting the tomato spotted wilt virus lowers economic thresholds (Riduavets, 1995). To control thrips pest outbreaks, growers are very often forced to apply chemical treatments intensively (Brownbridge, 1995; Parrella and Murphy, 1996). For monitoring thrips populations, colored sticky traps commonly are used (Brødsgaard, 1990; Teulon and Ramakers, 1990; Vernon and Gillespie, 1990; Heinz et al., 1992) in order to detect the initial presence of thrips and to predict outbreaks (Teulon and Ramakers, 1990; Frey et al., 1994).

Several attempts have been made to improve trapping of *F. occidentalis* by using plant odors (Brødsgaard, 1990; Teulon and Ramakers, 1990; Frey et al., 1994). It has been shown that western flower thrips, being mainly a flower-inhabiting species, responds not only to a specific odor, but also to a number of odors commonly found in floral fragrances (Teulon et al., 1993b). The effects of various olfactory attractants such as *p*-anisaldehyde (Brødsgaard, 1990; Teulon and Ramakers, 1990; Baranowski and Gorski, 1993; Teulon et al., 1993a,b; Hollister et al., 1995), geraniol, eugenol, myrcene (Holtmann, 1963; Kirk, 1985; Frey et al., 1994), benzaldehyde (Morgan and Crumb, 1928; Baranowski and Gorski, 1993; Teulon et al., 1993b) and nonfloral volatile chemicals such as ethyl nicotinate (Penman et al., 1982; Teulon et al., 1993b) have been tested on several flower thrips species and to a lesser extent on cereal thrips. Divergent results of experiments examining the responses of thrips to volatile chemicals may be due to different methods and/or different behavioral aspects of the host plant selection process of thrips, which comprises long- and short-range host cues (Terry, 1997). To evaluate behavioral responses at short distance, bioassays in the laboratory were conducted with the Petterson olfactometer (Pow et al., 1999), a V-shaped olfactometer tube (Gerin, 1994), and a Y-tube olfactometer (Holtmann, 1963; Gaum et al., 1994) for investigation of responses of walking thrips. Different kinds of flight chamber olfactometers (Teulon et al., 1993b; Frey et al., 1994; Hollister et al., 1995) were used for flying thrips. For observations of long-distance responses of flying thrips, most greenhouse and field trials are simple bioassays comparing trap catches from paired colored or noncolored water or sticky traps, (Morgan and Crumb, 1928; Penman et al., 1982; Kirk, 1985; Brødsgaard, 1990; Baranowski and Gorski, 1993; Teulon et al., 1993a,b; Frey et al., 1994; Roditakis and Lykouressis, 1996). Because the distance between traps often is too small, volatiles from baited traps may affect the catches from nearby nonbaited traps (Teulon et al., 1993b). Although optimal concentrations

of floral volatiles may be critical for attraction (Terry, 1997), most of these studies neglect the role of concentration of volatile compounds in attracting western flower thrips. In conclusion, reports on the attractiveness of volatiles to western flower thrips often are not comparable and sometimes contradictory.

The objective of the present study was, therefore, to adapt and enhance methods to evaluate the short-distance attractiveness to western flower thrips of volatile plant compounds belonging to different chemical groups and at several concentrations. Volatile components that frequently occur in flower odors and some that have been reported to elicit responses of other phytophagous insect species have been selected in order to compare their attractiveness with already well-known attractants for *F. occidentalis*.

METHODS AND MATERIALS

Rearing of Western Flower Thrips. A culture of *F. occidentalis* was maintained on potted, flowering plants of the susceptible chrysanthemum cultivar Sunny Cassa in a greenhouse at 25°C and 70% relative humidity. Female adult western flower thrips of different age were randomly collected with a small aspirator and confined in Perspex ring cages (Murai, 1990) at room temperature without food but with water for at least 14 hr prior to the experiments.

Olfactometer. Studies of olfactory behavior of thrips towards flower odors and various volatile chemicals were conducted with a Y-shaped glass tube olfactometer (Figure 1), modified from Holtmann (1963) and Sabelis and Van de Baan (1983). The apparatus was placed in a dark, air-conditioned room (22°C). A tripod in the center of a black box (36 × 38 × 57 cm), covered inside with black paper and cloth in order to avoid visual effects, held the Y tube (inner diameter 0.5 cm) in an inclining position (acute angle of 25° between the Y tube and horizontal plane). Light coming from a halogen lamp attached to the ceiling of the box illuminated the Y junction of the olfactometer with about 160 lux light intensity. The end tubes of the glass Y were connected to two Wheaton Micro Kit adapters made of glass, having attached 4-ml glass vials, each containing a piece of filter paper 1 cm². One microliter of the volatile component diluted in paraffin oil (Uvasol, Merck) or the pure solvent were applied to the filter paper pieces 30 min before the first thrips was released. This time period allowed the diluted odor to reach constant release rates. Preliminary assays have shown that paraffin oil used as control was not attractive for western flower thrips. The airflow was first purified by passage through a wash bottle filled with charcoal pellets and then led into the vials containing the solvent and the odor loaded solvent. At the base of the Y tube the air was sucked off by means of a membrane pump, producing an airflow of 5 cm/sec and 10 cm/sec in the Y tubes and the base tube, respectively. A smoke test showed that at the Y junction the

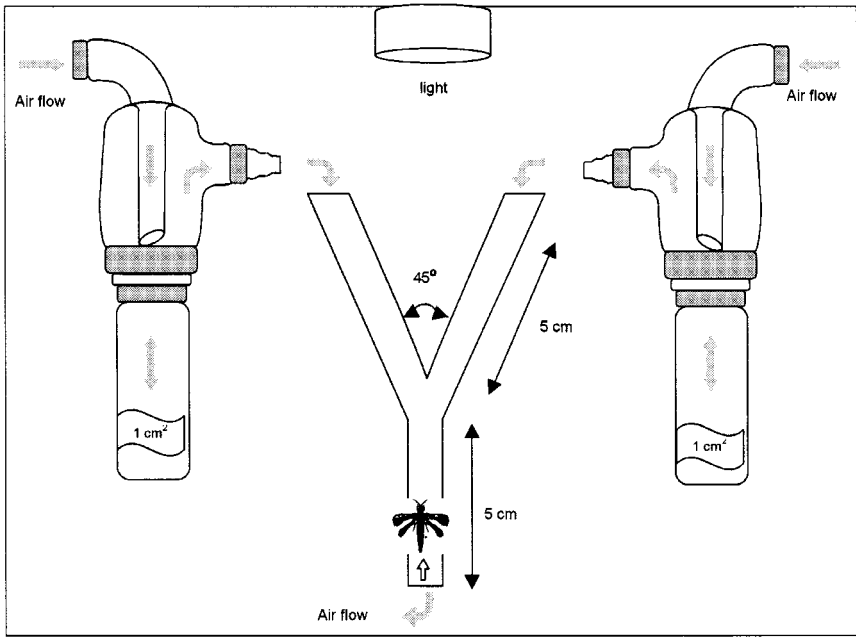


FIG. 1. Diagram of Y-shaped glass tube olfactometer for recording the responses of western flower thrips to plant odor components.

air of the odor arm did not mix with that of the control arm. Tubing removed the odor-loaded air from the room. All connections between different parts of the set-up consisted of silicone tubing.

Bioassay Procedure. Individual western flower thrips females were released within the first centimeter of the base tube of the Y olfactometer from a small aspirator. The 5-mm inner diameter of the glass-Y prevented thrips from flying within the tube. Activated by the odor-loaded airflow and additionally motivated by the light, they walked upwards in the tube. The experimental time was recorded from the time the air suction tube was connected to the glass Y. Upon reaching the Y junction in the glass tube, a thrips chose between the clean airflow and the airflow loaded with odor. When the thrips reached the far end of one arm, the choice was scored and the thrips was removed from the Y tube. When case a thrips made no choice within 3 min, a zero was recorded. Because only the scores for one or the other Y arm, i.e., test compound or control, can be compared with each other, one experiment was completed after 25 scores, disregarding the number of zeros recorded. After testing five insects, the entire set-up, i.e., all parts shown in Figure 1, were rotated 180° to avoid position effects. The

TABLE 1. SOURCE AND PURITY/DENSITY OF TESTED VOLATILE PLANT COMPOUNDS^a

Component	Source	Purity/density
Benzenoids		
Benzaldehyde	Fluka	99%
<i>o</i> -Anisaldehyde (2-methoxybenzaldehyde)	Aldrich	98%
<i>m</i> -Anisaldehyde (3-methoxybenzaldehyde)	Aldrich	99%
<i>p</i> -Anisaldehyde (4-methoxybenzaldehyde)	Fluka	98%
Salicylaldehyde (2-hydroxybenzaldehyde)	Roth	99%
Monoterpene isoprenoids		
Geraniol	Fluka	99%
Nerol	Aldrich	97%
Linalool	Fluka	97%
1,8-Cineole (eucalyptol)	Roth	99%
(<i>E</i>)- β -Ocimene	Fluka	97%
(+)-Citronellal	Fluka	97%
(+)-Citronellol	Roth	97%
Myrcene	Roth	91%
(+)-Limonene	Roth	99%
Sabinene	Roth	96%
Sesquiterpene isoprenoids		
(-)-(<i>E</i>)-Caryophyllene	Fluka	99%
(<i>E</i>)- β -Farnesene	IACR-Rothamsted	97.5%
(-)- α -Bisabolol	Roth	96%
Phenylpropanoids		
Eugenol	Roth	99%
(<i>E</i>)-Cinnamic aldehyde	Roth	97.5%
3-Phenylpropionaldehyde	Fluka	92%
Nicotinate		
Ethyl nicotinate	Fluka	98%
Essential oils		
Geranium oil	Roth	density = 0.95
Rose oil	Roth	density = 0.85

^aChemical groups are according to Knudsen et al. (1993).

average duration of an experiment was 45 min. After each experiment all parts of the set-up were cleaned with acetone.

Each experiment was replicated at least three times, i.e., the responses of at least 3×25 thrips towards each volatile component at the respective concentration were recorded.

Volatiles. All volatile plant chemicals used for the olfactometer bioassays, their source, and purity/density are listed in Table 1.

Statistical Analysis. The data were analyzed based on the null hypothesis that the probability of scores for the test compound or the control is equal to 50% (Sachs, 1997).

RESULTS

Series of olfactometer experiments were carried out in order to evaluate the responses of western flower thrips to volatile plant components belonging to five chemical groups at several doses. All results of the olfactometer bioassays are presented in Table 2.

Attractive volatile components for *F. occidentalis* were found among the monoterpenes. High percentages of female thrips were attracted by 10% of geraniol, linalool, and (+)-citronellol dissolved in a total volume of 1 μ l paraffin oil, with 82.7%, 76.0%, and 65.3% of tested thrips attracted, respectively. Nerol was attractive at 10% and 1% concentrations. The responses to 10% or 1% concentrations of 1,8-cineole, (*E*)- β -ocimene, (+)-citronellal, myrcene, (+)-limonene, and sabinene indicated no preferences.

(*E*)- β -Farnesene, a sesquiterpene, attracted 64% and 65.3% of western flower thrips at 10% and 1% concentrations, respectively, but at higher and lower concentrations, no attraction was observed. Neither (–)-(*E*)-caryophyllene nor (–)- α -bisabolol and none of the essential oils from geranium or roses provoked clearly positive or negative reactions.

Within the group of phenylpropanoids, two floral compounds were attractive to *F. occidentalis*. Eugenol and 3-phenylpropionaldehyde were preferred at 1% concentration. At the higher 10% concentration and the lower 0.1% concentration, both were shown to be neutral to thrips. A slightly positive reaction to (*E*)-cinnamic aldehyde was observed with 60% (at 1% concentration) and 61.3% (at 10%) thrips responding.

Three of five tested benzenoids were attractive to western flower thrips. Adult females responded positively to odor concentrations from 0.001% to 10% *p*-anisaldehyde. Except for 0.01% *p*-anisaldehyde, where no significant response was found, the component was preferred by 62.7% (at 0.001%) to 74.7% (at 10%) of the thrips tested. When 98% pure *p*-anisaldehyde was tested, 61.3% thrips chose the clean airflow. *O*-Anisaldehyde and benzaldehyde elicited positive response in 80% and 66.7% of thrips, respectively, at a 10% concentration. No significant attraction occurred to application of 10% and 1% *m*-anisaldehyde. Repellent effects were observed with salicylaldehyde. Application of 99% pure salicylaldehyde resulted in 76.8% thrips choosing the clean airflow. A negative response to salicylaldehyde was also found at 1% dilution.

The nonfloral odor ethyl nicotinate attracted thrips over a range of four different concentrations from 0.01% to 10%. A solution of 10% ethyl nicotinate resulted in 69.3% choices for the sample side. Even at a 1000-fold lower concentration, a positive reaction was observed with 62.7% tested insects responding.

TABLE 2. ATTRACTIVENESS OR REPELLENCY OF VOLATILE COMPONENTS AND ESSENTIAL OILS TO *Frankliniella occidentalis* (ADULT FEMALES) IN Y OLFACTOMETER BIOASSAY^a

Component	Adult females <i>F. occidentalis</i> choosing odor arm (%)					
	Undiluted	10%	1%	0.1%	0.01%	0.001%
Benzenoids						
Benzaldehyde		66.7**	60.0			
<i>o</i> -Anisaldehyde (2-methoxybenzaldehyde)		80.0***	60.0			
<i>m</i> -Anisaldehyde (3-methoxybenzaldehyde)		57.3	61.3			
<i>p</i> -Anisaldehyde (4-methoxybenzaldehyde)	38.7	74.7***	64.0*	67.0***	45.6	62.7*
Salicylaldehyde (2-hydroxybenzaldehyde)	21.4***	48.0	36.0*	53.3	48.0	
Monoterpenes isoprenoids						
Geraniol		82.7***	48.0			
Nerol		65.3**	70.7***	49.3		
Linalool		76.0***	56.0			
1,8-Cineole (eucalyptol)		53.3	41.3			
<i>trans</i> - β -Ocimene		46.0	41.0			
(+)-Citronellal		49.3	54.7			
(+)-Citronellol		65.3**	50.7			
Myrcene		50.7	56.0			
(+)-Limonene		60.0	50.7			
Sabinene		38.7	60.0			
Sesquiterpene isoprenoids						
(-)-(<i>E</i>)-Caryophyllene		50.7	56.0			
(<i>E</i>)- β -Farnesene	53.3	64.0*	65.3**	61.3		
(-)- α -Bisabolol		49.3	40.0			
Phenylpropanoids						
Eugenol		56.0	65.3**	54.7		
(<i>E</i>)-Cinnamic aldehyde		61.3	60.0			
3-Phenylpropionaldehyde		56.0	61.0*	49.3		
Nicotinate						
Ethyl nicotinate		69.3***	63.0*	68.0***	62.7*	56.0
Essential oils						
Geranium oil		50.7	45.3			
Rose oil		53.3	60.0			

^a All substances are applied in 1 μ l paraffin oil and diluted at concentrations from 10% to 0.0001%. Significance levels are based on average choices of 75 or 125 individual thrips. Significance levels for *P* ($H_0: P = 50\%$) are ≤ 0.05 (*), ≤ 0.01 (**), and ≤ 0.001 (***). Numbers in italics (salicylaldehyde) indicate significant repellent responses.

DISCUSSION

The simple and easy to handle experimental design of the Y-tube olfactometer used in the present study allowed assessment of the attractiveness or repellency of plant volatiles at different concentrations to *F. occidentalis*. It was possible to examine the response of 25 individuals in less than 1 hr and to repeat each experiment between three and five times to achieve statistically valid results within a reasonable time period.

In the literature, several mechanisms have been suggested to explain the behavior of thrips in the presence of volatile attractants. Shipp (1995) pointed out the need for laboratory and field investigations to determine if the behavioral response of flying western flower thrips to floral scents such as *p*-anisaldehyde at long distances is chemokinesis, anemotaxis, odor-induced visual response, or chemotaxis. Teulon et al. (1993b) showed that thrips respond to chemical volatiles in windy conditions in the field as well as in relatively calm air conditions in the greenhouse. Under natural conditions, anemotactic response seems unlikely because adult thrips are weak flyers (Teulon et al., 1993b; Hollister et al., 1995). Hollister et al. (1995) found evidence that olfactory stimuli in the absence of an additional color stimulus are important for host finding in western flower thrips. Their observations in the glasshouse suggested a chemokinetic response because captures in chemically baited black traps were higher than in nonbaited black traps.

Our observations on short-distance behavioral reactions of walking thrips in the Y tube olfactometer provide evidence for an oriented movement directed towards the odor source, probably involving the distinction of concentration differences between the left and the right arm, although anemotactic responses cannot be excluded. The definition of repellents as chemicals that cause insects to move away from their source (Dethier et al., 1960) is only valid for oriented movements at a short distance from the source (Visser, 1986). Although the olfactometer used in the present study is not suitable for general behavioral studies, it was possible to observe thrips at the Y junction of the olfactometer where they had to decide to move towards the clean airflow or the airflow loaded with odor. When the odor was attractive, thrips continued walking upwind towards the odor source. In contrast, thrips evaded a repellent odor by choosing the unscented airflow, even if they had already run into the scented arm and had to walk back. Holtmann (1963) observed similar reactions of *Limothrips cerealium* (Haliday) and *Haplothrips aculeatus* (Fabricius), two thrips species on cereals, to different diluted organic acids.

For this study volatiles were selected based on the fact that the floral scent components found in the greatest number of plant taxa are mainly distributed within the chemical groups of benzenoids and isoprenoids (Knudsen et al., 1993). Aldehydes such as cinnamic aldehyde, salicylaldehyde, anisaldehyde, and benzaldehyde were shown earlier to attract thrips (Morgan and Crumb, 1928).

Generally, the results of the olfactory bioassays demonstrate that the benzenoid *p*-anisaldehyde is attractive to *F. occidentalis*. This is in agreement with results of Brødsgaard (1990), Baranowski and Gorski (1993), Teulon et al. (1993a,b), Frey et al., (1994), Hollister et al., (1995), and Roditakis and Lykouressis (1996), who found that addition of *p*-anisaldehyde to yellow or blue water or sticky traps increased thrips catch results by a factor between 1.6 and 10 compared to unscented traps. These studies do not consider that western flower thrips may respond differently to different odor concentrations, although a dose-dependent attraction may explain these variable findings. Also in the present study *p*-anisaldehyde elicited positive reactions over a range of five concentrations from 10% to 0.001% except for 0.01% *p*-anisaldehyde, where no significant response was found. Western flower thrips is considered to be a polyphagous species (Brødsgaard, 1989). Kirk (1985) and Teulon et al. (1993b) showed that many flower-inhabiting thrips species react positively to *p*-anisaldehyde, a common component of flower odors of many of their hosts. Because of their similar chemical structures we expected positive reactions also to *o*-anisaldehyde and *m*-anisaldehyde. Clear attraction was recorded only at a 10% concentration of *o*-anisaldehyde. Our results support observations that components that attract insects exert repellancy at high concentrations (Visser, 1986). In the Y tube, air-flow loaded with 980 μg pure *p*-anisaldehyde clearly repelled western flower thrips. A similar, negative reaction was elicited not only by pure salicylaldehyde, but also at lower concentrations of this compound. Conversely, Roditakis and Lykouressis (1996) found in the field that salicylaldehyde in a mixture with ethanol (50%) attracted 40.0% more adult western flower thrips than the control. Morgan and Crumb (1928) reported two cereal thrips species reacting positively to salicylaldehyde.

In our experiments, thrips females preferred benzaldehyde, which is the most common benzenoid (Knudsen et al., 1993), at a 10% concentration. In the field, traps with benzaldehyde were shown also to be attractive to western flower thrips (Teulon et al., 1993b), some other flower thrips species (Baranowski and Gorski, 1993; Teulon et al., 1993b), and cereal thrips (Morgan and Crumb, 1928).

Myrcene, linalool, limonene, ocimene, and 1,8-cineole are the most common monoterpenes found in floral fragrances. Of these, only linalool appeared to be attractive to western flower thrips. In our experiments less common monoterpenes provoked significant responses. Geraniol at a 10% concentration attracted slightly more western flower thrips females than linalool. Geraniol was previously shown to elicit positive responses by *F. occidentalis* (Frey et al., 1994), several other flower-inhabiting thrips species (Kirk, 1985), and two cereal thrips species (Holtmann, 1963). In the present study, nerol, the isomer of geraniol, and (+)-citronellol have been tested on western flower thrips for the first time. Both compounds were attractive to western flower thrips. Series of olfactometer experiments with myrcene did not result in either clearly positive or negative

responses of thrips. Kirk (1985) found in the field that undiluted myrcene applied on dental roll wicks attached over water traps reduced the catch of four different flower-inhabiting thrips species, but he suggested that catches might increase at lower concentrations.

Among the group of sesquiterpenes, caryophyllene and farnesene commonly occur in both floral scents and the scent from green plant parts (Knudsen et al., 1993). In our bioassays western flower thrips did not show any preference for caryophyllene and bisabolol. With (*E*)- β -farnesene we achieved a dose-dependent positive reaction at two concentrations, which is in agreement with results of Pow et al. (1999) and Manjunatha et al. (1998). They demonstrated that (*E*)- β -farnesene was attractive to western flower thrips in a Petterson olfactometer bioassay. However, attraction was only detected at intermediate concentrations and not at higher or lower concentrations. This dose-dependent attraction was also supported in glasshouse trials.

Phenylpropanoids are a large structurally distinct chemical group, which comprises common substances such as eugenol and cinnamic acid derivatives (Knudsen et al., 1993). We recorded positive responses to 3-phenylpropionaldehyde and eugenol, both at a specific (1%) concentration. In glasshouse experiments, Baranowski and Gorski (1993) caught high numbers of western flower thrips on blue sticky traps with 3-phenylpropionaldehyde. Eugenol has been tested for attractiveness to cereal thrips species (Holtmann, 1963; Kirk, 1985), and some flower-inhabiting thrips (Kirk, 1985), but only Holtmann (1963) found a concentration that elicited a positive response. Morgan and Crumb (1928) found that *L. cerealium* and *F. tritici* (Fitch) were attracted by cinnamic aldehyde in simple water traps, whereas our experiments demonstrated this compound to be neutral for western flower thrips females.

The significance of ethyl nicotinate, a compound that is not found in floral fragrances, for host finding of flower-inhabiting thrips species is not clear (Teulon et al., 1993b). Two hypotheses are suggested by Teulon et al. (1993b). Either ethyl nicotinate might be found in small quantities in host plants or it is very rare and not normally encountered by thrips but elicits a strong response when detected by thrips' olfactory receptors. We observed a positive reaction of *F. occidentalis* to ethyl nicotinate at concentrations ranging from 10% to 0.01%. These results are consistent with observations by Teulon et al. (1993b) and Frey et al. (1994). In field trials, Penman et al. (1982) increased the efficiency of sticky traps by adding ethyl nicotinate for *Thrips obscuratus* (Crawford), an indigenous species of New Zealand that is strongly attracted to ripe peaches.

We expected to achieve clear attraction with diluted essential oils of geranium and rose, both preferred host plants of western flower thrips, but no positive response was recorded. Similar results were found by Gaum et al. (1994), also in Y-tube olfactometer tests. Floral volatiles of several rose cultivars being tested did not attract western flower thrips, but rather repelled them. An expla-

nation for this phenomenon could be that the presence of other odor compounds in the essential oils suppressed the effects of the attractants in these oils. An example of such a masking effect was reported by Yamasaki et al. (1997), who showed that the cerambycid beetle *Monochamus alternatus* (Hope) was attracted by oxygenated terpenes separated from *Pinus densiflora* wood. In combination with (–)-germacrene D, a compound isolated from the same plant species, the attractiveness of the terpenes was inhibited. Thus, (–)-germacrene D functioned as a masking substance.

In general, our results provide evidence that *F. occidentalis*, a polyphagous flower-inhabiting thrips species, is mainly attracted by common flower odors within the chemical class of benzenoids and monoterpenes. We found compounds such as anisaldehyde and ethyl nicotinate elicit positive responses over a wide range of concentrations, while others such as eugenol or benzaldehyde are only attractive at a specific concentration. Bioassays in flight cages and in the greenhouse to evaluate responses of flying western flower thrips to different odor concentrations are needed to further evaluate the attractiveness of the compounds tested in our present study.

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