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IDENTIFICATION AND BIOACTIVITY OF ALARM PHEROMONE IN THE WESTERN FLOWER THRIPS, *Frankliniella occidentalis*

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Abstract—Analysis by gas chromatography (GC) and GC-mass spectroscopy disclosed that droplets of anal fluid produced by second-instar western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), contain a two-component alarm pheromone, comprised of decyl acetate and dodecyl acetate, in a molar ratio of approximately 1.5:1. Both nymphs and adults responded to the pheromone by walking away from the source. The synthetic pheromone was active at a concentration of 1.0 ng, and the proportions of insects responding to the pheromone, but not the distances moved, increased with increasing dose. Each component was active alone, although at low doses, the response to decyl acetate was less than to either dodecyl acetate or the blend. The pheromone also induced some second instars to drop from leaves and reduced oviposition by adult females in both two-choice and no-choice experiments. Because the response of western flower thrips to the alarm pheromone is relatively weak, the potential for its use in pest management is limited, unless it is used in conjunction with other control measures.

Key Words—*Frankliniella occidentalis*, western flower thrips, Thysanoptera, Thripidae, alarm pheromone, decyl acetate, dodecyl acetate, pest management.

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INTRODUCTION

Although alarm pheromones are most commonly found in eusocial insects (Blum, 1969, 1985), they do occur in some presocial or gregarious species. Alarm pheromones have been found in several Homoptera, particularly treehoppers (Membracidae) and aphids (Aphididae). Aggregations of treehoppers disperse in response to alarm pheromones (Nault et al., 1974; Wood, 1976), and aphids also disperse by walking away or dropping from their feeding sites when exposed to alarm pheromone (Bowers et al., 1972; Montgomery and Nault, 1977; Calabrese and Sorensen, 1978; Wholers, 1981b). Nymphs of a pyrrhocorid (Calam and Youdeowei, 1968) and both nymphs and adults of some Pentatomidae (Ishiwatari, 1974; Lockwood and Story, 1987) disperse from aggregations and often drop from feeding sites in response to their alarm pheromones. Alarm pheromones also cause dispersal behavior in species of Cimicidae (Levinson and Bar Ilan, 1971; Levinson et al., 1974), Tingidae (Kearns and Yamamoto, 1981), and Acanthosomidae (Maschwitz and Gutmann, 1979).

The only thysanopteran known to produce an alarm pheromone, perillene, is the gregarious tubuliferan thrips, *Varshneyia pasaniae* Mukaigawa (Suzuki et al., 1988). Western flower thrips, *Frankliniella occidentalis* (Pergande), are not highly gregarious, but do exhibit a tendency toward clumped distributions (Peterson, 1990). Therefore, utilization of an alarm pheromone would be an adaptive trait in this species. Our preliminary observations suggested that this thrips produces an alarm pheromone that is released in droplets of anal fluid.

Herein, we verify the presence of an alarm pheromone in the western flower thrips and report on its isolation and identification and on some behavioral responses of thrips to the pheromone.

METHODS AND MATERIALS

Maintenance of Thrips Colony. Western flower thrips were obtained from colonies at the Agriculture Canada Research Station, Agassiz, British Columbia. A stock colony of thrips was reared in 1-liter glass canning jars. Each jar contained a 2 to 3-cm-deep layer of damp peat moss on the bottom to provide pupation sites. The metal lid of the jar was replaced with filter paper held in place by the screwtop ring. Each jar held a small, water-filled plastic container with a hole in the lid. Thrips were reared on pinto beans, *Phaseolus vulgaris* L., with the severed stems, usually bearing two leaves, extending through the hole in the lid into the water. Leaves were replaced as they wilted or sustained severe feeding damage.

Large quantities of even-aged nymphs were obtained by placing 20–30 adult thrips of both sexes on each of several leaves, as above. Adults were removed from the leaves every one to two days, and the leaves replaced. Adult

thrips were added to the jars as numbers declined. Leaves with eggs were removed from the jars and placed on styrofoam trays floating in water, with the petioles of the leaves extending through holes in the styrofoam into the water. The age of the thrips developing on each leaf was therefore known within a range of one to two days.

Demonstration of Alarm Response. Thirteen adult thrips, 20 second-instar, and 37 first-instar thrips were tested for response to the secretions of second instars. Experiments were conducted in a laboratory at approximately 25°C and with light intensity varying from 600 to 21500 lx. Single thrips of the three stages were isolated on pinto bean leaves (area approximately 25 cm^2) floating adaxial (upper) surface up in 2–3 mm of water in a 10-cm-diameter Petri dish. The thrips were allowed to settle for at least 2 hr.

To collect thrips secretions, second-instar thrips were picked up at the thorax with forceps. A triangular, filter-paper wick (base = 2 mm, sides = 7 mm) was held in a second pair of forceps and the point rubbed gently over the abdomen of the thrips. Any anal droplet produced was absorbed. Secretions of five thrips were collected on one filter-paper wick, after which it was immediately held 2–3 mm above a stationary thrips isolated on a leaf. A new wick was used for each insect tested.

Each thrips was observed for 1 min. Any thrips moving ≥ 2 mm was considered to have responded to the stimulus. The net distance moved from the starting point in 1 min was recorded for each thrips. The control treatment was a clean wick presented to similar numbers of thrips in the same way.

A crude extract was made by crushing second-instar thrips in distilled pentane at −78.5°C. The supernatant was removed and concentrated under a stream of nitrogen to 2 nymph equivalents (NE) per microliter. The extract was stored at −5°C until used. Second-instar and adult thrips were isolated on leaves as above and tested for response to the extract. Five nymph equivalents of extract in 2.5 μl of pentane were placed on a wick and held above a stationary thrips. Numbers responding and distance moved were recorded. The control stimulus was a wick treated with 2.5 μl of pentane.

A chi-square test for comparing two proportions (Zar, 1984) was used to compare the proportion of thrips responding in control and experimental treatments. Mean distances moved were calculated for responding individuals and compared by one-tailed t tests.

Sensitivity of second-instar thrips to the extract of second instars was tested at doses of 0.001, 0.01, 0.025, 0.05, 0.1, 0.5, 1.0, and 5.0 NE. A 2.5-μl aliquot of solvent was used as a control treatment. A linear model for categorical data (Grizzle et al., 1969) with modified Bonferroni t tests (Myers, 1979) was used to compare the proportions of insects responding. Tukey's test (Zar, 1984) was used to compare a logarithmic transformation of distances moved by responding insects. Doses at which only one insect responded were excluded from the analysis.

Pheromone Chemistry. A Hewlett-Packard 5830 gas chromatograph equipped with a capillary inlet system and flame-ionization detector was employed for analyses by gas–liquid partition chromatography (GC). A glass column (30 m × 0.5 mm ID) coated with SP-1000 (Supelco Canada Ltd., Oakville, Ontario) was used. The injection port and detector temperatures were 260 and 270°C, respectively. A Hewlett-Packard 5895B GC/MS/DS was employed for coupled gas chromatography–mass spectroscopy (GC-MS). A fused silica column (0.32 mm ID) coated with DB-1 (30 m) (J & W Scientific, Inc., Folsom, California) was coupled directly into the ion source. The injection port, transfer line, and ion source were 260, 250, and 200°C, respectively. Helium was the carrier gas for GC and GC-MS.

In a cold room, first- or second-instar thrips of mixed sex, or adults of each sex, were transferred directly from the host into a pentane-containing vial set in Dry Ice. The frozen thrips were finely crushed. Any sample not immediately processed and analyzed was stored at −27°C. After removal from Dry Ice, the sample was allowed to warm to room temperature, and the supernatant was transferred to a clean vial. After concentration to approximately 100 μl under a stream of nitrogen at 0°C, the extract was placed on glass wool in a small glass chamber to which was attached an analytical Porapak Q trap (6 mm OD packed with approximately a 30-mm length of absorbent). The volatiles were transferred from the glass wool to the Porapak Q with nitrogen (130 ml/min for 2 hr) and recovered by eluting the Porapak Q trap with 2 ml pentane. The eluent was concentrated under a stream of nitrogen to 300 μl, and then analyzed by GC and GC-MS. Volatiles recovered from the Porapak Q trap were tested against second-instar western flower thrips nymphs. Anal droplets were collected from second instars with very fine micropipets, stored in hexane, and analyzed in the same way.

Decyl acetate (99.2%) was prepared by reaction of decyl alcohol with acetic anhydride in pyridine, isolated by extractive work-up in the usual way, and purified by distillation at reduced pressure. Dodecyl acetate (97%) was purchased from the Aldrich Chemical Co., Milwaukee, Wisconsin.

Bioactivity of Synthetic Pheromone. The bioassy used to test the nymph extract was used to test the bioactivity of the synthetic pheromone. Second-instar thrips were used since they were abundant and easy to handle. Because the response of thrips to the nymph extract had seemed to vary with weather-driven changes in the laboratory, two experiments were conducted to test the hypothesis that low levels of light reduce the response of thrips to their alarm pheromone. These experiments demonstrated that the number of second instars responding to the synthetic pheromone increased significantly (χ^2 test, $P < 0.05$) from 33.3% to 83.3% ($N = 12$) when bioassays were done at 7490 lx and 25°C in a controlled-environment chamber compared to 588 lx and 25°C in the laboratory. Within the chamber, responses increased significantly (χ^2 test,

$P < 0.05$) from 58.3% to 91.7% ($N = 12$) when light intensity was increased from 1712 to 7490 lx. Therefore, all bioassays with synthetic pheromone were conducted in the controlled-environment chamber at 25°C and 7490 lx.

The candidate, two-component alarm pheromone (decyl acetate and dodecyl acetate), in the naturally occurring molar ratio of 1.5:1, and each component alone were tested against second-instar thrips at doses of 0.1, 1.0, 10, 100, 1000, and 10000 ng. Pentane (2 μl) and 1 NE of crude extract served as negative and positive control treatments, respectively. The proportions of thrips responding were analyzed with a linear model for categorical data (Grizzle et al., 1969), with modified Bonferroni t tests (Myers, 1979) used to compare proportional data >0%. The Fisher exact test (Zar, 1984) with modified Bonferroni t tests was used to test for differences between responses of 0% and the next 1–3 higher responses. Tukey's test was used to compare a logarithmic transformation of distances moved. Doses at which only one insect responded were excluded from the analysis.

Effects of Pheromone on Nymphal Dropping. Four experiments were conducted to test the hypothesis that the alarm pheromone causes nymphs to drop from the leaves on which they are feeding. Populations of 50–225 second instars were either knocked onto a bean leaf from an aspirator and allowed to settle for 24 hr, or adults were allowed to oviposit on a bean leaf for 24 hr, and the resulting offspring were used when they became second instars. A cardboard trap coated with Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan) was placed around the stem of each leaf to trap any thrips dropping from the leaf.

In the first experiment, the synthetic pheromone (decyl acetate–dodecyl acetate, molar ratio 1.5:1) in 10 μl of pentane, was placed on a 1.27-cm-diameter filter-paper disk pierced by a stainless steel pin. When the solvent had evaporated, disks were placed on both the upper and lower surfaces of each leaf by penetrating the leaf with the pins until the paper disks touched the leaf surface. One to four populations of second instars were exposed to each treatment at doses of 0.1, 1.0, and 10 μg of pheromone, divided equally between the upper and lower disk. Pentane was used as a control treatment. The second experiment was similar to the first, but after the disks had been pinned to the leaves, the petiole of each leaf was lightly tapped five times with a pencil.

In the third experiment, the pheromone was sprayed directly on leaves containing thrips. The synthetic pheromone was dissolved in 66.7% ethanol at 10 μg/ml and was dispensed at 5 μg of pheromone per spray from a 15-ml perfume atomizer. A similar atomizer containing 66.7% ethanol was used for control treatments. Each leaf was sprayed with approximately 4–5 μg of pheromone on each surface.

In the fourth experiment, a leaf with thrips was placed in a 140-ml closed chamber. In each chamber, a 1-cm-diameter filter-paper disk treated with 10 μg

of pheromone was placed 1–2 cm from the leaf. The leaves on which the thrips were located were not touched or disturbed during the experiment.

In each experiment, the thrips were observed for 30 min, after which the numbers of nymphs on the sticky traps and the numbers remaining on the leaves were counted. In each experiment, the numbers within treatments were pooled, and the percent dropping calculated. The data were analyzed using a linear model for categorical data (Grizzle et al., 1969).

Effects of Pheromone on Oviposition. In the first of two experiments on oviposition, thrips were allowed to choose between an oviposition substrate treated with the alarm pheromone and one treated with solvent. Bean pod segments, 5 cm long, were used as oviposition substrates. The cut ends of the beans were coated with melted paraffin to prevent thrips from entering the interior of the pods. The synthetic pheromone was dissolved in 66.7% ethanol and applied from a 15-ml perfume atomizer. A similar atomizer containing 66.7% ethanol was used for control treatments. Twelve bean segments were each sprayed with 1–2 μg of pheromone and 12 with 70 μl of solvent. When the solvent had evaporated, a pheromone-treated and a control bean were placed with 20 adult females in a 1-liter canning jar covered with filter paper.

After 24 hr the females were removed and each bean was placed in a separate plastic vial covered with 203 PeCap mesh (B & SH Thompson, Scarborough, Ontario). Six days later, the numbers of nymphs on each bean were recorded. Because western flower thrips eggs are very small and difficult to find, nymphs rather than eggs, were counted. The data were analyzed using a paired sample t test.

In a second, no-choice experiment, single bean segments, treated with either the pheromone or ethanol as above, were confined in mesh-covered plastic vials with 20 adult females for 24 hr (10 replicates) or 48 hr (six replicates). Six days after removal of the females, the numbers of nymphs on each bean were counted. A one-tailed t test was used to compare the mean numbers of nymphs produced per 24 hr.

RESULTS

Demonstration of Alarm Response. The typical response by thrips of all three life stages to both the natural secretions and extract of second instars was to walk away from the stimulus source, usually in a fairly straight line. Turns of $>90°$ were uncommon unless the thrips encountered a large vein or the edge of a leaf. Before moving, a thrips often would twitch its abdomen from side to side. This action was also seen when several thrips were in close proximity to each other. When a second instar was unable to move in response to the alarm stimulus (possibly because its proboscis was stuck in the leaf tissue), a droplet

of anal fluid was often produced. The same response was seen in second instars touched or seized by predators. When a thrips was free to move away from the stimulus, the production of an anal droplet was never observed.

A greater proportion of first- and second-instar thrips responded to second-instar secretions than to control treatments (Table 1). Of the insects that responded, only second instars moved a significantly greater distance in response to the secretions than to the control wick. There was no significant difference between the proportions of adults responding to the two treatments or in the distances moved. Adult thrips are more mobile than nymphs and, during testing, often moved in response to any disturbance or movement in their vicinity.

Second instars and adults responded in greater numbers to the extract of second instar thrips than to the solvent control (Table 2). Thus, the high but not significant response by adults to the anal fluid (Table 1) was apparently real. In no case was the distance moved by thrips responding to the extract significantly greater than for those responding to the control stimulus.

The response of second instars to the nymphal extract increased with increasing dose (Figure 1), the greatest response occurring at 1 NE. The distance moved by responding insects exposed to 0.01 NE was significantly less than the distances moved at doses of 0.05–1.0 NE (Figure 2).

Pheromone Identification. Analysis of second-instar volatiles by GC revealed the presence of only two compounds (Figure 3) in a ratio of approximately 2:1. In another sample the ratio was 1.5:1. The mass spectra of the unknowns were readily obtained by analysis of the volatiles by GC-MS, and each exhibited a base peak at m/z 43, suggesting that the compounds were

TABLE 1. ALARM RESPONSE OF *F. occidentalis* TO SECRETIONS OF FIVE SECOND INSTARS PRESENTED ON FILTER-PAPER WICKS TO STATIONARY THRIPS

Developmental stage of test insect	Treatment	Number tested	Percent response[a]	Distance (mm) moved by responding insects (mean ± SE)[b]
First instar	control	20	25.0a	5.8 ± 2.3a
	secretions of 5 nymphs	20	85.0b	9.5 ± 1.7a
Second instar	control	37	24.3a	5.1 ± 1.7a
	secretions of 5 nymphs	37	67.6b	17.1 ± 2.3b
Adult	control	13	23.1a	10.3 ± 1.9a
	secretions of 5 nymphs	13	46.2a	9.8 ± 3.0a

[a] Paired percents followed by the same letter are not significantly different, χ^2 test, $P < 0.05$.
[b] Paired means followed by the same letter are not significantly different, t test, $P < 0.05$.

TABLE 2. ALARM RESPONSE OF *F. occidentalis* TO CRUDE PENTANE EXTRACT OF SECOND INSTARS PRESENTED ON FILTER-PAPER WICKS TO STATIONARY THRIPS

Developmental stage of test insect	Treatment	Number tested	Percent response[a]	Distance (mm) moved by responding insects (mean ± SE)[b]
Second instar	control	29	20.7a	8.7 ± 2.8a
	extract of 5 nymphs	29	75.9b	12.3 ± 1.6a
Adult	control	20	35.0a	5.7 ± 1.0a
	extract of 5 nymphs	20	65.0b	9.5 ± 1.7a

[a] Paired percents followed by the same letter are not significantly different, χ^2 test, $P < 0.05$.
[b] Paired means followed by the same letter are not significantly different, t test, $P < 0.05$.

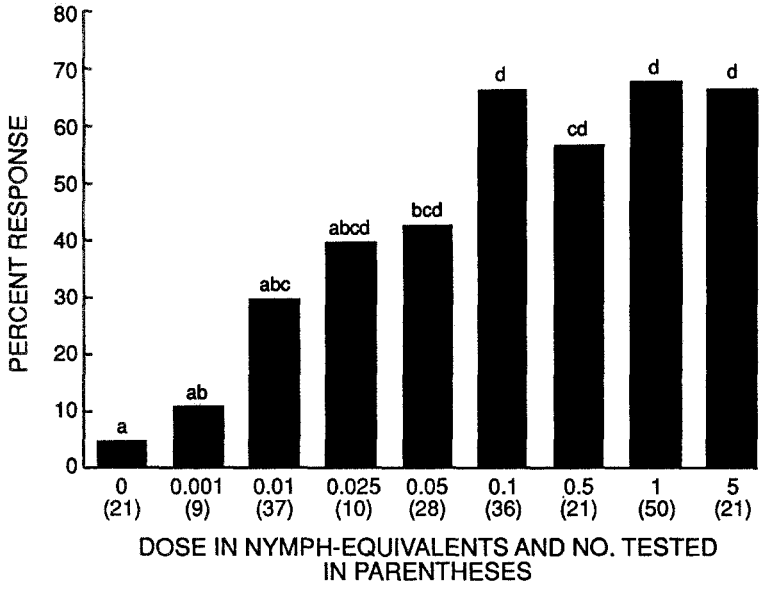

FIG. 1. Percent responses by second-instar *F. occidentalis* exposed to crude pentane extract of second-instar nymphs presented on a filter-paper wick to stationary thrips. Bars topped by the same letter are not significantly different, linear model for categorical data with Bonferroni t tests, $P > 0.05$.

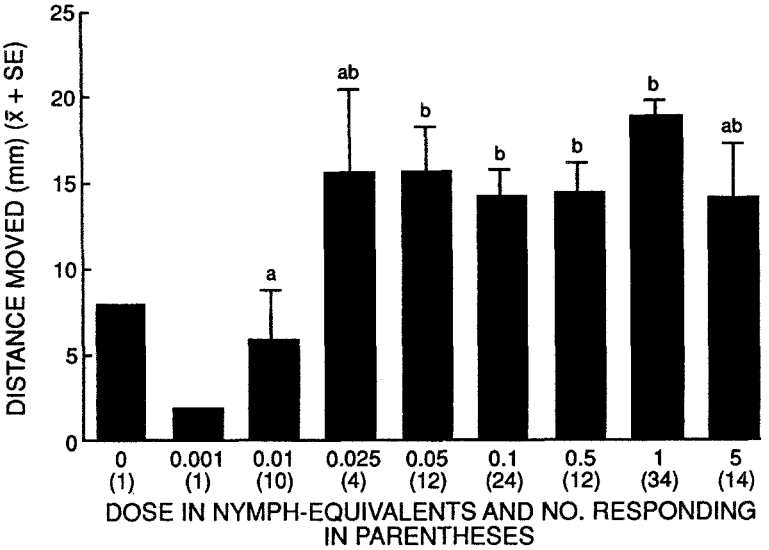

FIG. 2. Distances moved by second-instar *F. occidentalis* exposed to crude pentane extract of second-instar nymphs presented on a filter-paper wick to stationary thrips. Bars topped by the same letter are not significantly different, Tukey's test, $P > 0.05$.

probably acetate esters. The highest observed ions in mass spectra of the unknowns were, in order of elution, *m/z* 140 and 168, respectively, indicating the compounds were homologs differing by two methylene units. Since an acetate ester readily loses acetic acid (mol wt = 60), the fragment ions at *m/z* 140 and 168 were most likely derived from compounds with molecular weights of 200 and 228, respectively. Search of reference spectra revealed that mass spectra of the two unknown compounds matched those of decyl and dodecyl acetate, respectively. The identity of the unknowns was confirmed by comparison of their mass spectra and GC retention times to those of authentic samples. Decyl acetate and dodecyl acetate were also present in first instars and in the anal droplet produced by second instars. Only trace amounts of dodecyl acetate were found in adults of both sexes.

Bioactivity of Synthetic Pheromone. The synthetic pheromone and each component alone were biologically active. The percent responses to each increased significantly with increasing concentration (Figure 4). The response to decyl acetate plus dodecyl acetate (molar ratio 1.5:1) peaked at 10 and 100 ng, and the responses to decyl acetate and to dodecyl acetate peaked at 1000 ng. Responses to the two-component blend were significantly greater than to decyl acetate at doses of 1.0, 10, and 100 ng (linear model for categorical data, $P < 0.05$), but responses to the two-component blend and to dodecyl acetate

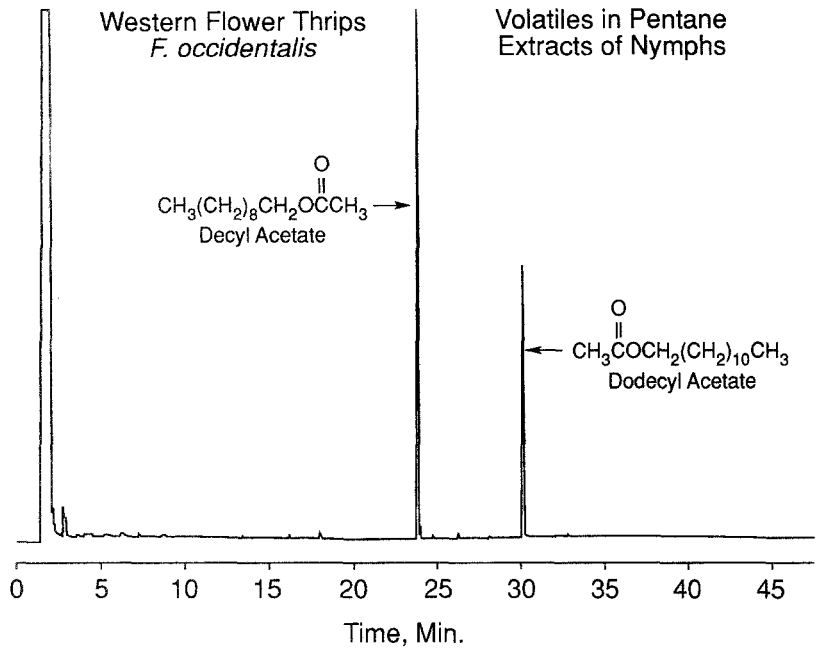

FIG. 3. Gas chromatogram of volatiles from whole crushed second-instar *F. occidentalis*. Column: glass capillary (30 m × 0.5 mm ID) coated with SP-1000. Temperature program: 70°C (2 min), 4°/min to 180°C (20 min).

were never different. The distance moved in response to 0.1 ng of the blend was significantly less than the distances moved at 10 ng and 1.0 NE of extract (Figure 5). The distance moved at 1.0 ng of dodecyl acetate was less than the distances moved at all other doses. There was no significant trend in the distances moved in response to decyl acetate (Figure 5).

Effects on Nymphal Dropping. Treatment with the alarm pheromone caused nymphs to drop from leaves at low rates (Table 3). When the pheromone source was pinned to a leaf, the rate of dropping was significantly greater at 1.0 and 10 μg than in control treatments. A similar result was obtained when the pheromone was diffused through a closed chamber. When the pheromone was sprayed on the leaf, the rate of dropping was not significantly different from that in the control, probably because the thrips became entrapped in the liquid on the leaf and were unable to move. Movement (tapping) of leaves with the pheromone source pinned on them approximately tripled the rate of dropping, compared to when the leaf was not tapped.

Effects on Oviposition. When female thrips were allowed a choice of oviposition sites, fewer than half the number of eggs were laid per 24 hr on phero-

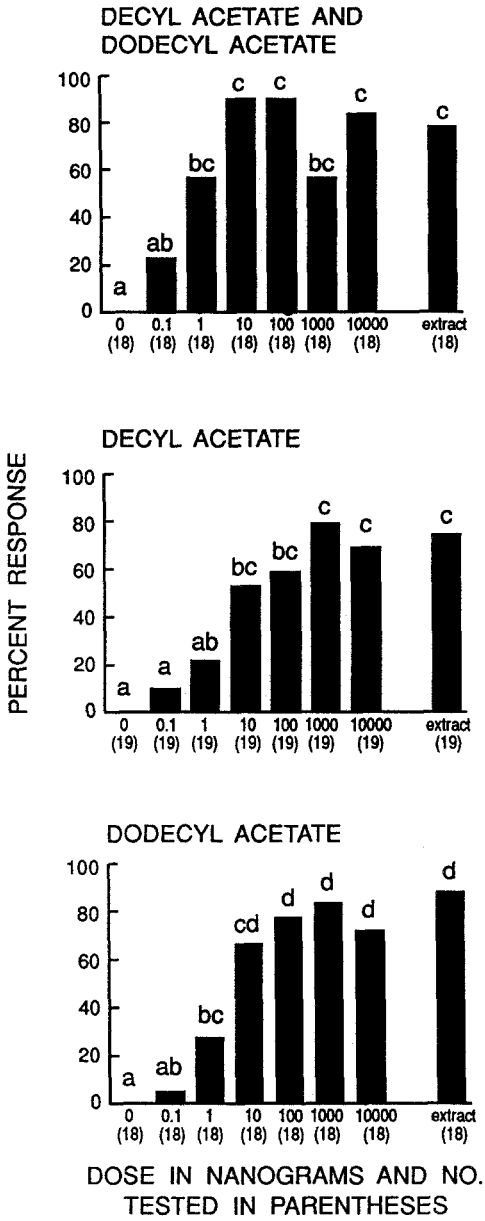

FIG. 4. Percent responses of second-instar *F. occidentalis* to synthetic alarm pheromone components presented on a filter-paper wick to stationary thrips. Bars topped by the same letter are not significantly different, linear model for categorical data and Fisher exact test with Bonferroni t tests, $P > 0.05$.

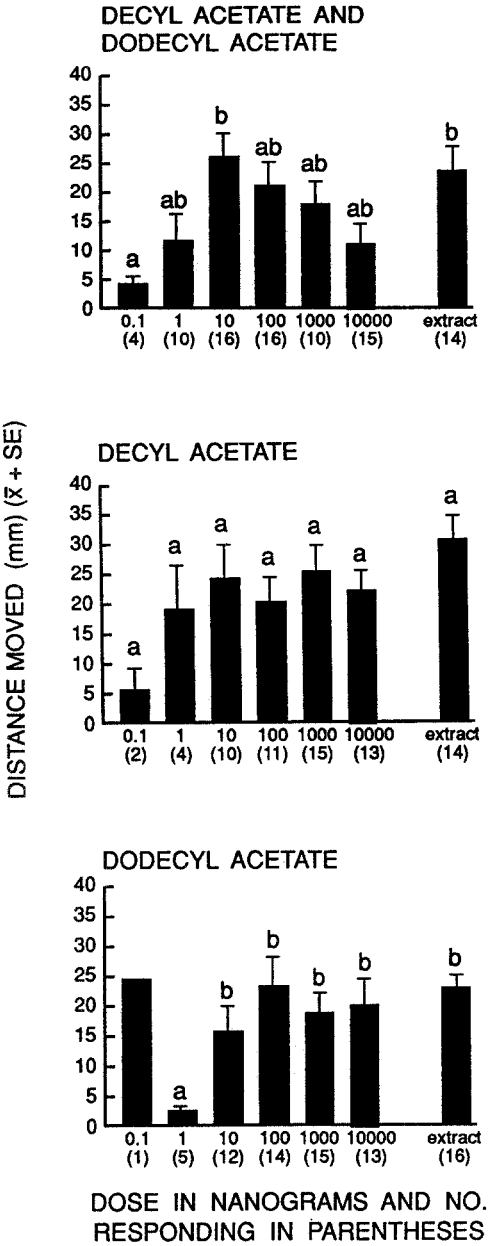

FIG. 5. Distances moved by second-instar *F. occidentalis* exposed to synthetic alarm pheromone components presented on a filter paper wick to stationary thrips. Bars topped by the same letter are not significantly different, Tukey's test, $P > 0.05$.

TABLE 3. PERCENT SECOND INSTAR *F. occidentalis* DROPPING FROM LEAVES IN RESPONSE TO SYNTHETIC ALARM PHEROMONE

		Pheromone source pinned to leaf, leaf not tapped		Pheromone source pinned to leaf, leaf tapped		Pheromone sprayed on leaf		Pheromone diffused in a closed chamber	
Treatment	Dose	Number tested[a]	% drop[b]	Number tested[a]	% drop[b]	Number tested[a]	% drop[b]	Number tested[a]	% drop[b]
Solvent	10 μl	380(4)	0.79a	140(2)	1.43a	185(2)	2.81a	150(3)	0.67a
Pheromone	0.1 μg	80(1)	2.50ab	90(1)	1.11a				
Pheromone	1 μg	320(4)	5.63b	90(2)	14.44b				
Pheromone	10 μg	270(3)	5.56b	60(1)	15.00b	450(2)	6.00a	150(3)	3.33b

[a] Number of populations in parentheses

[b] Percents in a column followed by the same letter are not significantly different, linear model for categorical data, $P < 0.05$.

mone-treated than on control substrates (Figure 6). In the no-choice experiment, significantly fewer eggs were laid per 24 hr on the pheromone-treated beans, but the difference was much less than in the two-choice experiment (Figure 6).

DISCUSSION

The results of these experiments demonstrate the existence of an alarm pheromone in western flower thrips. The only other pheromone identified in a thysanopteran is the monoterpene, perillene, which functions as an alarm pheromone in the gall-inhabiting *V. pasaniae* (Suzuki et al., 1988). Perillene has also been isolated from two other species of gall-inhabiting thrips (Suzuki et al., 1986, 1988). The chemistry of defensive secretions has also been investigated in several species of tubuliferans. γ-Decalactone is the major allomone in *Bagnalliella yuccae* (Hinds) (Howard et al., 1983), and pentadecane and hexadecyl acetate are the primary components of the defensive secretion of *Gynaikothrips ficorum* (Marchal) (Howard et al., 1987). Methylbutyric acid is a very minor, but active component in the defensive allomone of *V. pasaniae* (Suzuki et al., 1988). A number of acetates are found in the secretions of several tubuliferan species, although their functions are not known (Suzuki et al., 1988, 1989). The alarm pheromone of western flower thrips apparently does not have a defensive function. Although the droplet of anal fluid produced by second instars physically deters some predators, decyl acetate and dodecyl acetate act as a kairomone for two thrips predators (Teerling et al., 1993).

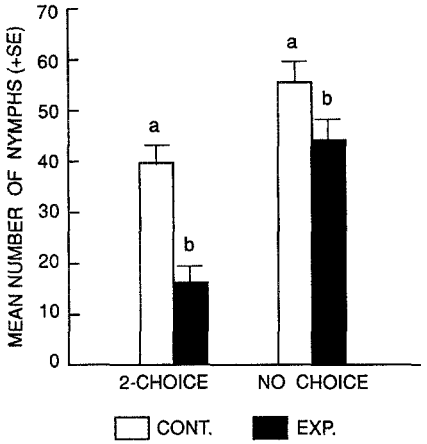

FIG. 6. Numbers of nymphs produced in choice and no-choice experiments by 40 female *F. occidentalis* in 24 hr on alarm pheromone-treated and solvent-treated substrates. Paired bars topped by the same letter are not significantly different, t test, $P > 0.05$.

Although both compounds in the western flower thrips alarm pheromone are independently active (Figure 4), they are not additive or synergistic. As in some attractive pheromone systems (Linn et al., 1984; Borden et al., 1990), such redundancy could serve as a fail-safe method of ensuring perception of and response to a critical stimulus. Alternatively, each component may elicit a slightly different behavior in the several alarm responses (negative taxis, dropping from the host, reduced oviposition) or in aggressive bouts between individual thrips (Crespi, 1986a,b; Terry and Gardner, 1990).

The responses of western flower thrips to their alarm pheromone are quite weak. The distance moved in response to the pheromone is small, but it may be sufficient to remove the thrips from the immediate area where a nymph is under attack. Anthocorids encountering a point source of thrips pheromone seemed to confine their most intensive searches to within 5 mm of the source (Teerling et al., 1993), so thrips moving >5 mm (Tables 1, 2; Figures 2, 5) would reduce their chance of being located by a predator.

The rate of dropping in response to alarm pheromone (Table 3) was much lower in western flower thrips nymphs than in many aphid species (Bowers et al., 1972; Montgomery and Nault, 1977; Calabrese and Sorensen, 1978; Wholers, 1981b). Because thrips are smaller than aphids, the risks of dropping from a feeding site are likely greater. Dropping to the ground involves risk of predation by ground-dwelling predators, and the chance of not regaining a suitable host. For western flower thrips, the benefits of remaining on a leaf, which is a proven source of food, thus seem to outweigh the risks of leaving it. Similarly, adult females may have risked oviposition on a substrate contaminated with alarm pheromone, rather than laying no eggs. Alternatively, females may have adapted or habituated to the pheromone within the 24-hr period, or the pheromone may not have persisted for 24 hr.

Because the responses of thrips to their alarm pheromone are so weak, there is no great potential for direct application of the pheromone in pest management. For example, there is little benefit in inducing dropping from leaves to reduce populations of thrips nymphs already on a crop unless use of the pheromone is integrated with that of some other control agent. Even at the high rates of dropping seen in several aphid species (Bowers et al., 1972; Montgomery and Nault, 1977; Calabrese and Sorensen, 1978; Wholers, 1981b), there is almost no prospect of economically reducing populations already on a plant, since disturbed aphids can return to the host plant within an hour (Montgomery and Nault, 1977; Calabrese and Sorensen, 1978). In addition, aphids rapidly habituate to the pheromone, and climb treated plants (Wholers, 1981a,b).

The alarm pheromone reduced oviposition by female thrips, especially when some oviposition sites were left untreated (Figure 6). Therefore, continuous pheromone release might provide protection for high-value plants, such as floral crops, if some plants or parts of plants were left untreated. Since the alarm

pheromone reduces oviposition, adults may tend to avoid landing and settling on treated plants if given the choice of leaving. Alate aphids avoid landing on plants treated with alarm pheromone, and treatment of plants in a greenhouse reduced colonization (Wholers, 1981a; Dawson et al., 1982). Thus, treatment of a crop with western flower thrips alarm pheromone might reduce adult immigration into the crop from surrounding fields.

Perhaps the most promising use of aphid alarm pheromone in pest management is as a bioirritant. The efficacies of insecticides can be significantly increased by applying a pheromone as a vapor before application of a contact insecticide or by formulating it with an insecticide (Griffiths and Pickett, 1980; Griffiths et al., 1983). Because the synthetic alarm pheromone induces western flower thrips to move, contact with either chemical or microbial insecticide deposits would be increased, possibly to the extent that mortality would be enhanced.

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