Ent. exp. & appl. **30** (1981) 269—279 *Ned. Entomol. Ver. Amsterdam*

SEX PHEROMONE DOSAGE AND BLEND SPECIFICITY OF RESPONSE BY ORIENTAL FRUIT MOTH MALES

THOMAS C. BAKER[1], WENDY MEYER and WENDELL L. ROELOFS

Department of Entomology, New York State Agricultural Experiment Station, Geneva, N.Y. 14456, U.S.A.

The sex pheromone-mediated responses of male oriental fruit moths, *Grapholitha molesta* (Busck), to an array of blends and dosages of Z8-12Ac and E8-12:Ac, were analyzed. Males exhibited sustained upwind flight resulting in source location only to intermediate blends and dosages. This optimal range of treatments appeared to be bounded by dosages too low or too high to result in significant attraction (net within-plume displacement toward the source), the higher concentrations causing arrestment (no net within-plume displacement) at some distance from the source. Similar results were obtained in field-trapping studies with the same treatments, except that the optimal dosages were moved up about 10-fold. Increased turning and decreased linear velocity could account for arrestment with increasing amounts of the (*E*) isomer in high dosages and high (*E*)/(*Z*) ratio blends.

KEY WORDS: *Grapholitha molesta*; oriental fruit moth; sex pheromone-mediated behavior; attraction; arrestment; (*Z*)-8-dodecenyl acetate; (*E*)-8-dodecenyl acetate; (*Z*)-8-dodecenyl alcohol.

Many lepidopteran species have been found to use specific pheromone component blends of geometrical or positional isomers (Roelofs, 1980). Male moths respond to a range of ratios and release rates approximating those occurring naturally, but the specificity of these ranges generally is not known. It has been suggested (Roelofs, 1978) that the sequence of behavioural responses resulting in attraction will be elicited by ratios bounded by a lower concentration threshold for flight activation and by an upper concentration threshold for alteration of in-flight behaviour (disorientation). The shape of these threshold curves would determine the attraction response specificity of the ♂♂ involved. Although field-trapping data have provided some information on the specificity of blends affecting trap catch, they do not reveal which male behaviours are affected by changes in the concentration and quality of the odor source.

The mechanisms by which a male moth arrives at a sex pheromome source are still unknown. There is much evidence for the use of odor-conditioned, optomotor anemotaxis (Kennedy, 1977) by flying ♂♂, yet this mechanism for steering cannot, by itself, result in movement toward a pheromone source. A kinetic component is necessary to propel the moth at a particular rate through the air and over the ground so that a new displacement toward the source can result. The magnitude and speed of this displacement will naturally result from the underlying movement reactions and should depend on, among other things, the concentration and quality of the odor to which the male is exposed.

In order to describe such behavioural changes more precisely, we analyzed the behavioural sequences of male oriental fruit moths, *Grapholitha molesta* in a laboratory wind tunnel as they responded to a large array of blends and dosages. Attempts were made to correlate changes in movement behaviour, measured as attraction (net within-plume displacement toward the source), and arrestment (no net within-plume displacement) with blends and concentrations. We also initiated investigations on the underlying mechanisms determining the outcome of these displacements. The same array of lures was also used in a field-trapping experiment to compare trap catch with flight-tunnel behavioural responses.

MATERIALS AND METHODS

Rearing. *G. molesta* males were reared on small green thinning apples on a 16:8 light: dark photoperiod regime at 25° and variable

[1] Present address: Department of Entomology, University of California, Riverside, California 92521, U.S.A.

humidity. Light: dark lighting intensities were 1400 and less than 0.3 lux, respectively. Male pupae were segregated daily and adults were held at 25° in a 16:8 photoperiod regime in 33 × 27 × 31 cm screen cages in rearing rooms devoid of ♀♀. They were divided into two groups for which scotophase (dark phase) commenced at 1500 and 1700 hr, respectively. This photoperiod shift allowed for testing of the complete series of treatments on two separate groups of ♂♂ during each group's period of optimum responsiveness (each lasting ca. 2.5 hr), rather than over 5 hr for a pooled group, which would result in poor responsiveness for part of the testing period.

Chemicals. (*Z*)-8-dodecenyl acetate (*Z*8-12:Ac) (Roelofs *et al.*, 1969) was purchased from Farchan Corporation and found to contain over 3% of the (*E*) isomer (E8-12:Ac) as checked on a 10% XF-1150 (50% cyanoethyl, methylsilicone on 100—120 mesh Chromosorb W-AW DMCS) 2 mm × 2 m ID glass GLC (gas-liquid chromatography) column in a Packard model 7300 series gas chromatograph. We purified the Z8-12:Ac by high performance liquid chromatography (HPLC) using a 2.5-cm ID glass column packed with 46 cm of 20% $AgNO_3$ on Silica Gel H (30—70 mesh) using a 95:5 Skellysolve-B: ethyl acetate solvent system flowing at 5 ml/min. The resulting purified Z8-12:Ac contained 0.04% of the (*E*) isomer, determined by GLC analysis on XF-1150 (using peak height retention times) no detectable (*Z*)-8-dodecen-1-ol (Z8-12:OH), and less than 0.1% other volatile impurities. The E8-12:Ac (Cardé *et al.*, 1979; Biwer *et al.*, 1979) obtained from Farchan Corp., also was purified on the 20% $AgNO_3$ HPLC column. The resulting E8-12:Ac contained no detectable (*Z*) isomer or Z8-12:OH, and less than 0.5% other volatile impurities. The Z8-12:OH (Cardé *et al.*, 1979; Biwer *et al.*, 1979), made by base hydrolysis of the above-purified Z8-12:Ac, contained 0.1% Z8-12:Ac, 0.04% E8-12:OH, no detectable E8-12:Ac, and less than 0.2% other volatile impurities as checked on XF-1150. From these three purified compounds, 6 blends were formulated at a concentration of 100 µg Z8-12:Ac per µl hexane. As checked on XF-1150, the blends were: 1) pure Z8-12:Ac + 3.6% Z8-12:OH; 2) Z8-12:Ac + 1.7% E8-12:Ac + 3.7% Z8-12:OH; 3) Z8-12:Ac + 5.9% E8-12:Ac + 3.8% Z8-12:OH; 4) Z8-12:Ac + 10.2% E8-12:Ac + 3.5% Z8-12:OH; 5) Z8-12:Ac + 20.4% E8-12:Ac + 3.4% Z8-12:OH; 6) Z8-12:Ac + 36.3% E8-12:Ac + 4.0% Z8-12:OH. The E8-12:Ac and Z8-12:OH percentages are expressed relative to Z8-12:Ac. From the 100 µg/µl solutions a 30 µg/µl dilution was made for each blend, and then 10-fold serial dilutions were made from each of these two starting concentrations, resulting in concentrations of 100, 30, 10, 3, 1, 0.3, 0.1 and 0.03 µg/µl.

Trapping experiment. An orchard block of semi-dwarf apple trees on the Experiment Station grounds was used to test male capture to traps containing a range of component ratios and dosages. The six ratios described above were pipetted in 10 µl of solution onto rubber septum dispensers (Arthur Thomas No. 8753-022, sleeve type). The dosages, expressed as amount of Z8-12:Ac, were 0.3, 1, 3, 10, 30, 100, 300 and 1000 µg. The septa were placed in Pherocon 2 sticky traps with restricted entrances, and the traps suspended, one per tree, at ca. 1.8 m height on the outer tree branches nearest an aisle. Distance between traps in a row was ca. 6.2 m and between rows, 12.4 m. Three replicates were set out in the orchard in a randomized, complete-block design, a total of 49 treatments (48 plus solvent blank) per replicate. Re-randomization was performed twice during each daily capture period to minimize corner and edge effects. When appreciable capture had occurred, all traps in a block were placed on the ground within 5 min to prevent further capture, the ♂♂ were counted, and the traps randomly replaced on the trees. Capture then continued uninterrupted to the end of the evening when the ♂♂ were counted and removed, and the traps re-randomized within blocks again for the next day's capture period. Data were subjected to a 2-way analysis of variance and differences between means were tested for significance by Waller & Duncan's BSD test.

Flight observations. The same 49 treatments used in trapping plus six more (adding a 0.1 µg dosage) were used to observe and compare behaviours elicited in a 2.0 × 0.89 × 0.96 m laboratory wind tunnel (Miller & Roelofs, 1978). Treatments were tested on individual 4—5-day-old males during their period of optimal responsiveness beginning 2.5 hr before lights-off, using a randomized, complete-block design. Because testing one-half of the treat-

ments usually took over 2 hr, and the period of optimal response was only ca. 2.5 hr (Baker & Cardé, 1979a), another group of ♂♂ having their photoperiodic regime delayed by 2 hr was used for the remaining treatments each day. Wind tunnel conditions were 21—22°, 50—70% RH, light intensity 700 lux, and a wind velocity of 0.3 m/sec. N = 48 for each of the 55 treatments.

From their holding cage, ♂♂ were transferred ca. 10 min before each testing period to individual steel screen cones, 8 cm high × 10 cm basal diam, open at the base. Only males that remained sitting until testing time were used. A randomly chosen treatment septum was placed, wide end downwind, at the centre of a 15 × 15 × 15 cm high galvanized steel platform located 0.2 m from the upwind end of the wind tunnel. Then a screen cone containing a male was placed, wide end upwind, on a 15-cm high cylindrical screen platform 1.5 m downwind of the septum. Cones and platforms were replaced between treatments, and washed thoroughly with acetone before their next use.

Using a 10-channel strip-chart event recorder, the following behaviours were monitored: sitting, walking, wing fanning while walking in release cone, flight, stationary flight, upwind flight, wing fanning while walking on upwind platform, and hairpencil display at septum (Baker & Cardé, 1979b). Upwind flight was defined as apparent within-plume flight with simultaneous forward displacement of at least 20 cm toward the pheromone source. In stationary flight the male's track exhibited no net forward or backward displacement with respect to the source. Stationary flight often occurred as an initial flight behaviour immediately following take-off, when it was characterized by large, sweeping side-to-side track reversals with little or no plume contact. However, it also occurred later following upwind flight, and here the track reversals were very narrow, the majority of the movement apparently confined to within the (time-averaged) plume boundaries. Flight comprised all flight, including upwind and stationary flight, as well as apparently random flight trajectories toward the ceiling, out the back of the tunnel, or into the exhaust tube. When ♂♂ touched the tunnel's sides or flew out the back, observation of that male was terminated. Observations ended for ♂♂ remaining sitting in the cone after 30 sec. If after that time moving ♂♂ had not left the cone, observations were continued until the male either flew from cage or was quiescent for 10 consecutive sec, whereupon observations ended. Percentages of ♂♂ responding to the various blends and dosages were compared within each behavior according to a method of adjusted significance levels for multiple comparisons (Ryan, 1960). Males were used once and discarded.

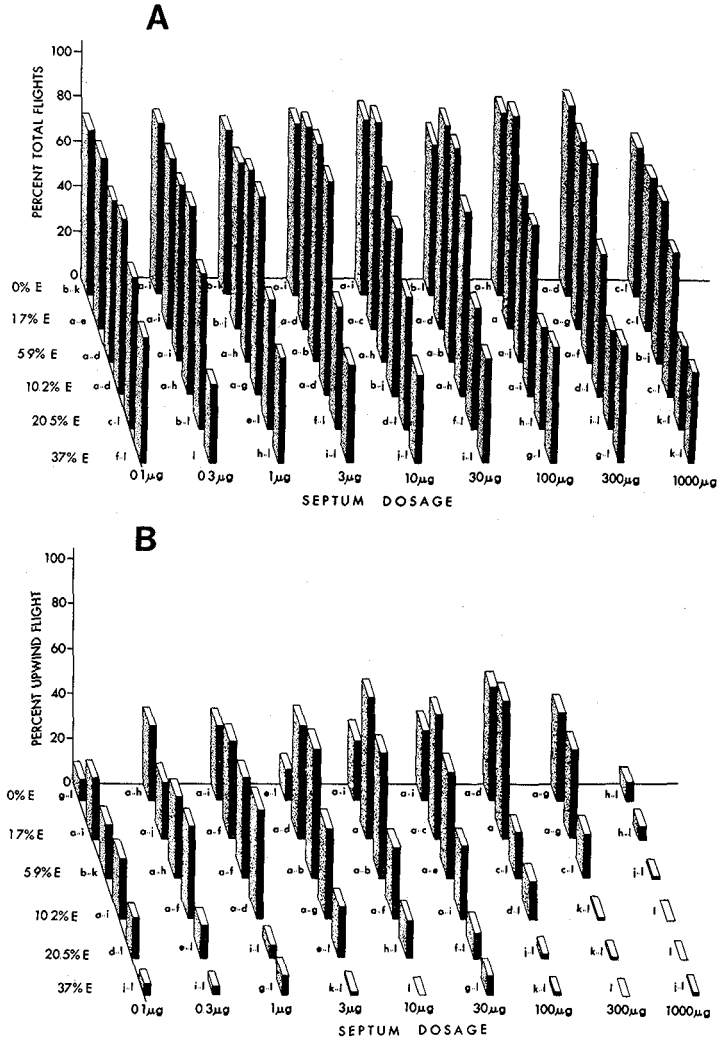
Wing fanning while walking observations. To observe effects of varying concentration upon orientation to the pheromone source while in the wing fanning while walking state, the tunnel was cooled to 18—19° to favor wing fanning rather than flight (Baker & Roelofs, 1981). Fifteen cm from the floor a 50 cm × 15 cm galvanized steel platform was erected and placed longitudinally down the tunnel's center, the downwind end being the point of male release in the previous flight experiments, 0.3 cm from the tunnel's end. A septum containing either 0.1, 1, 10 or 100 μg of the 5.9% and 1.7% (*E*) ratios was placed at the platform's center, 7 cm from its upwind end. Wind velocity was 0.3 m/sec. Males were released individually onto the ramp's downwind end from screen cones held in the pheromone plume. Their tracks made by wing fanning while walking toward the source were recorded on a Sanyo model VTC 7100 videorecorder and GE model 4TE44B5A117 video camera positioned above the platform outside the tunnel. Tracks were later traced onto clear plastic film from the monitor during slow motion playback, and a mark was made every 1 sec elapsed time. Velocity of movement during each 1 sec interval was measured by placing narrow mesh graph paper beneath each track and counting the total number of squares through which the track passed between marks. An index of track straightness was calculated each sec by dividing upwind movement by the sum of total left-right plus upwind-downwind movement, again using graph paper divisions. A track straightness value of 1.0, therefore, would be a perfectly straight track directly upwind, and similarly, -1 value indicates direct downwind movement with no turning. Frequency (number of turns per sec) and severity (radians per turn) of turning were calculated by drawing tangents to each track at the end of each turn and measuring the degrees with a protractor. A turn was defined as any change in clockwise to anticlockwise direction, or vice versa, great-

er than 10°. To avoid unduly weighting the sample in favor of the tortuous, long-duration tracks of arrested moths, only the first 10 sec of each track were analyzed. The initial 3 sec or so of nearly all tracks were straight upwind, and this, plus the fact that many extremely convoluted tracks were unmeasurable, probably created a bias against finding turning changes.

In another experiment, a permeated airstream was used to minimize the unknown effects of the plume boundaries on degree of turning. Seven identically loaded septa were lined up across the platform 2 cm apart using the same 4 concentrations of 5.9% (*E*) used in the single septum experiment. All other experimental conditions and procedures were as described above for the single septum experiment.

RESULTS

Flight observations. In the wind tunnel, changes in behaviour corresponding to both dosage and blend alterations were observed (Fig. 1). With the exception of the 37% (*E*) blend, most moths took flight in response to the entire range of treatments (Fig. 1A). Fewer flew upwind in the plume for at least 20 cm, however, and to a narrower range of treatments (Fig. 1B) than for flight. Despite the at-



traction (upwind flight) of some ♂♂ to these blends, fewer made it to the next behavioural step of wing fanning near the source (Fig. 1C) and fewer still to the hairpencil display (Fig. 1D), their range of blends narrowing even further. Termination of upwind flight occurred most frequently among ♂♂ attracted to high dosages of all blends and to moderate dosages of blends containing high amounts of (*E*) (Fig. 2). The termination of upwind flight before reaching the platform by ♂♂ attracted to high (*E*) ratios and high dosages of all ratios appeared to be characterized by an apparent within-plume decrease in net forward ground speed to zero with narrow lateral and vertical oscillations. This momentary arrestment within the plume, one of the forms of stationary flight, often lasted several sec and was followed by upward flight out of the plume, the male usually ending up at the downwind end or on the ceiling of the tunnel.

To the lowest dosages and (*E*) ratio, however, termination of upwind flight (Fig. 2) or failure to initiate such flight once airborne (Fig. 1A, 1B) appeared more often to be due to rapid erratic flight out of the plume followed by a failure to relocate it during subsequent wide-oscillation stationary flight. Hence, it appears that sources were successfully located (Fig. 1c) and displayed at (Fig. 1D) when these contained intermediate blends and dosages above the threshold needed for significant attraction,

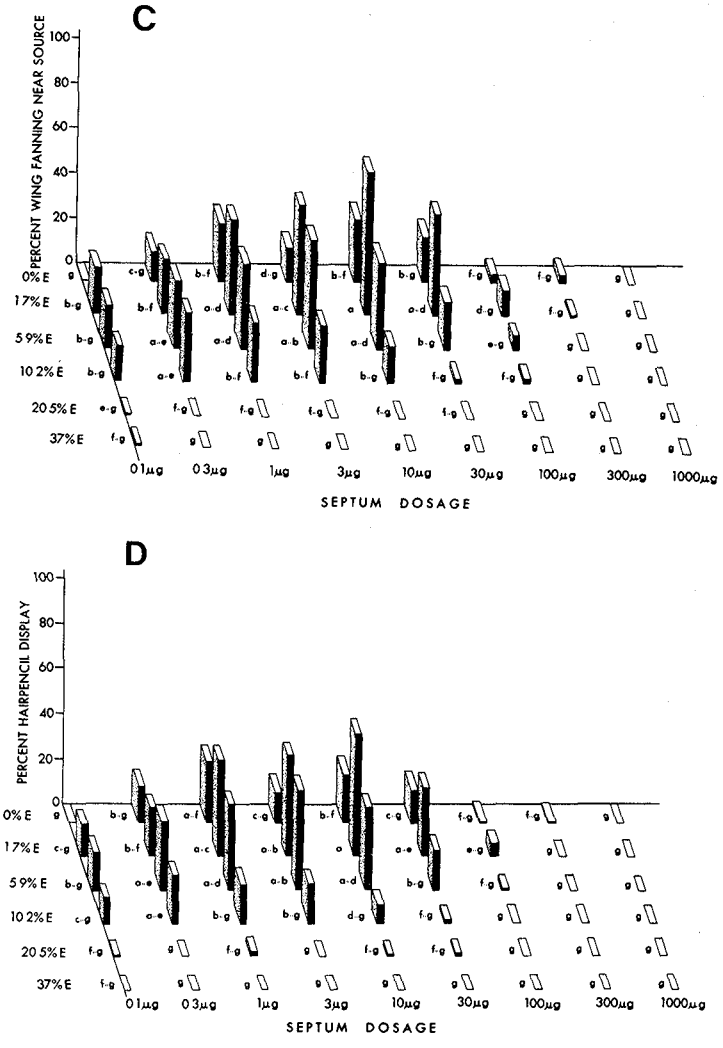


Fig. 1. % ♂♂ exhibiting indicated behaviours in laboratory wind tunnel in response to various blends and dosages. Dosages expressed as amount of Z8-12:Ac on rubber septum dispenser. E8-12:Ac is as a % of Z8-12:Ac and all blends also contained ca. 3% Z8-12:OH. Treatments having no letters in common are significantly different according to a method of adjusted significance levels for multiple comparisons (Ryan, 1960) ($P < 0.05$). N = 48 for each treatment. A—D: see text.

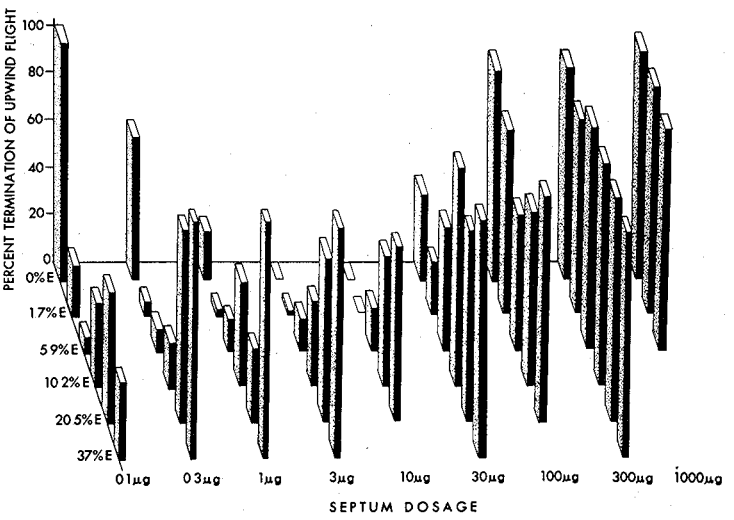
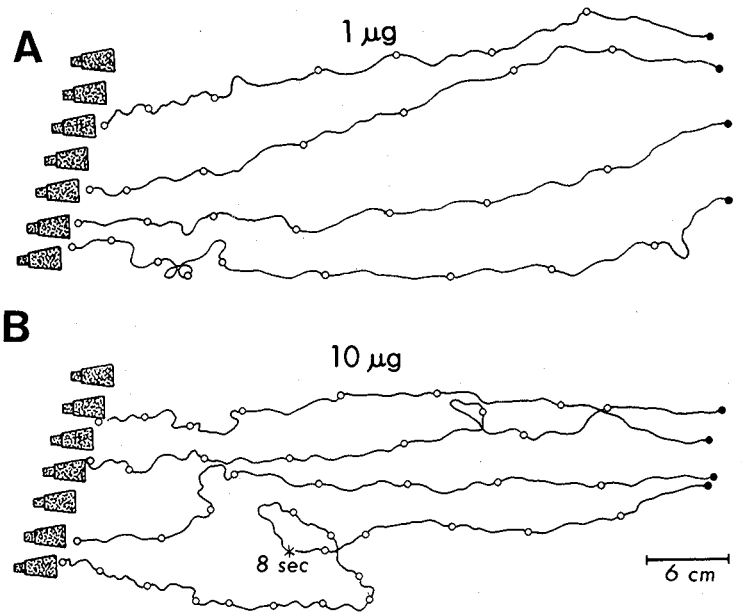


Fig. 2. % ♂♂ terminating upwind flight before reaching platform supporting pheromone source. Upwind flight termination at high dosages and (*E*) % appeared to be due to arrestment.

but below that for arrestment. The lowest dosages and (*E*) ratios barely produced the above-threshold concentrations for upwind flight at the release platform 1.5 m away, and there was a high likelihood at this distance of a male removing himself from the upwind flight active space (Baker & Roelofs, 1981) and not relocating it. Conversely, at the highest dosages, little upwind flight occurred, probably because the release platform was subjected to concentrations already exceeding the arrestment threshold, and if it could have been moved several meters farther downwind, more attraction, albeit of short duration, might have been observed.

Wing fanning while walking observations. Two major features of males' orientation movements changed during fanning while walking with exposure to increasing concentrations of either 1.7% or 5.9% (*E*). Linear veloc-



ity decreased (Table I), as did track straightness. It can be seen in a more detailed analysis of turning changes that straightness diminished not as a result of greater turning frequency (which actually declined with concentration), but rather of greater turning severity (Table II). The number of radians per turn increased with dosage, and the fewer turns that were made at the highest dosage were more severe than those at lower dosages. These concurrent reactions, seen in the extreme to 100 μg, caused ♂♂ to stop net progress toward the septa (Fig. 3C). Also, the inverse orthokinetic response to higher concentrations caused greater duration of sitting (Table I) which may be considered the extreme manifestation of arrestment on the ground. The decreased orthokinesis and increased turning with dosage occurred in a permeated airstream as well (Fig. 3, Tables I & II). Therefore, these changes in movement were not due to effects of the pheromone plume-air gradient, but to true effects of the chemicals themselves. Cessation of progress toward the source (Fig. 3C), arrestment,

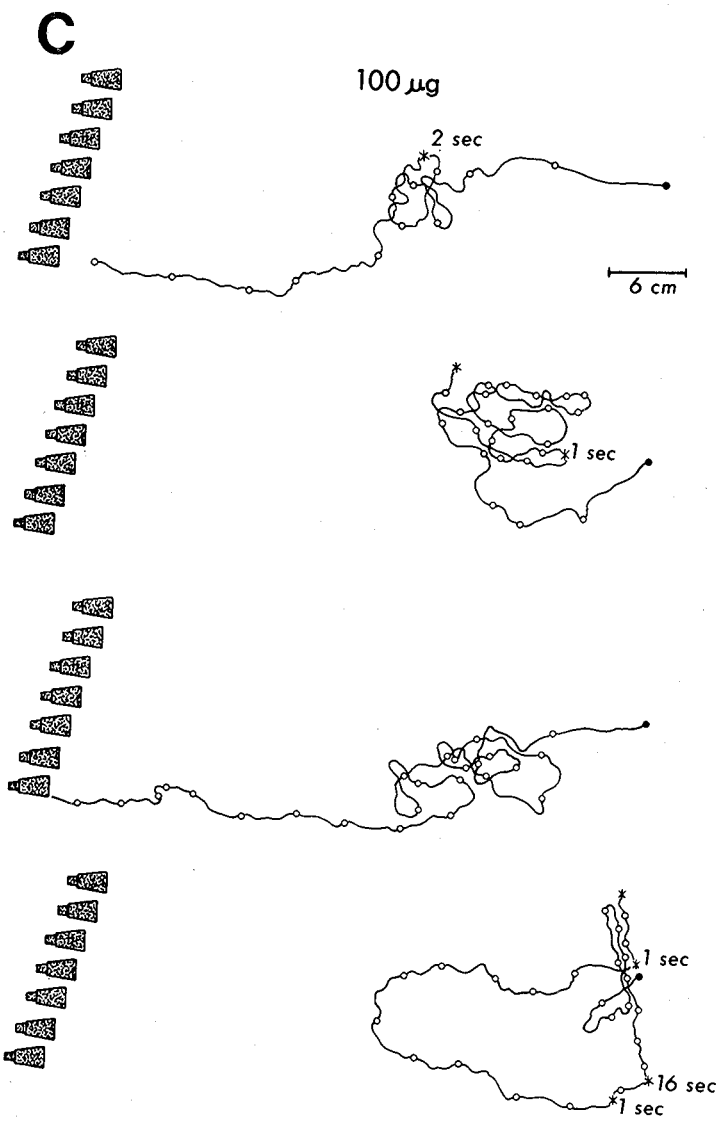


Fig. 3. Sample tracks of % ♂♂ wing fanning while walking in response to airstream permeated with 5.9% (*E*). Wind blowing from left at 0.3 m/sec. Males released individually onto platform containing septa from right where they began wing fanning while walking. Time elapsed between each open circle 1 sec. Distance from septa to ♂ release point 43 cm. Asterisks denote periods of sitting. Four ♂♂ responding to (A) 1 μg (B) to 10 μg, (C) to 100 μg on each of seven septa.

TABLE I

Changes in speed of movement and straightness of video-recorded movement tracks of males wing fanning while walking on a platform to different dosages of 1.7% and 5.9% (E)

Treatment (N)	% ♂♂ Responding[1]	Of Responders, % ♂♂ Locating source[1]	X̄ Linear velocity (cm/sec ± SD)[2]	X̄ Track straightness[2,3]	X̄ Time (sec) sitting per ♂ (± SD)[2,4]
Single septum					
0.1 µg 1.7% (*E*)	39 a	80 a	8.5 ± 1.5 a	0.70 ± 0.13 a	0.0 ± 0.0 b
(13)	(5)	(4)			
1 µg 1.7% (*E*)	54 a	87 a	8.1 ± 1.4 a	0.70 ± 0.18 a	0.0 ± 0.0 b
(28)	(15)	(13)			
10 µg 1.7% (*E*)	75 a	91 a	5.3 ± 1.1 b	0.68 ± 0.13 a	0.0 ± 0.0 b
(28)	(21)	(19)			
100 µg 1.7% (*E*)	73 a	21 b	4.4 ± 1.1 c	0.32 ± 0.27 b	2.8 ± 4.5 a
(33)	(24)	(5)			
0.1 µg 5.9% (*E*)	31 b	80 a	10.0 ± 2.4 a	0.63 ± 0.24 ab	0 ± 0 b
(16)	(5)	(4)			
1 µg 5.9% (*E*)	41 b	92 a	9.4 ± 1.3 a	0.75 ± 0.10 a	0 ± 0 b
(32)	(13)	(12)			
10 µg 5.9% (*E*)	62 ab	69 a	6.0 ± 1.3 b	0.50 ± 0.26 b	1.3 ± 3.3 b
(26)	(16)	(11)			
100 µg 5.9% (*E*)	77 a	21 b	5.5 ± 1.8 b	0.32 ± 0.31 b	5.4 ± 6.8 a
(44)	(34)	(7)			
Permeated airstream					
1 µg 5.9% (*E*)	77 a	84 a	7.3 ± 1.6 a	0.73 ± 0.30 a	0 ± 0 a
(17)	(13)	(11)			
10 µg 5.9% (*E*)	86 a	75 ab	6.4 ± 1.5 ab	0.60 ± 0.32 ab	0 ± 0 a
(14)	(12)	(9)			
100 µg 5.9% (*E*)	79 a	36 b	5.8 ± 1.2 b	0.43 ± 0.31 b	1.1 ± 2.0 a
(14)	(11)	(4)			

[1] % in same column having no letters in common significantly different according to χ^2 2 × 2 test of independence with Yates' correction ($P < 0.05$).

[2] Means in same column having no letters in common significantly different according to T-test ($P < 0.05$).

[3] A 1.0 value would be perfectly straight track directly toward source, and -1.0 would be straight track directly away from the source.

[4] Sitting time included only those occurrences where sitting was interspersed with wing fanning while walking and does not include long bouts of sitting at end of each moth's trial, especially to 100µg dosage.

may be only one extreme of turning-to-velocity ratios that at lower concentrations results in attraction.

Field trapping tests. The same set of lures used for behavioural observations in the flight tunnel was used in traps in the field. Males were captured in significantly greater numbers in traps containing 10—100 µg of 5.9% (*E*), the naturally occurring ratio, than to any other treatment (Fig. 4). The poor trap catches with blends containing 20.5% (*E*) or more were in accord with the reduced behavioural responses elicited by these blends in the flight-tunnel tests.

DISCUSSION

Three pheromone components (Z8-12:Ac, E8-12:Ac and Z8-12:OH) previously (Baker & Cardé, 1979c) have been shown to act together to influence all stages of a sequence of traditional bioassay response forms, such as flight, walking, wing fanning, etc. These behaviours have been analyzed now using a range of dosages and (*Z*):(*E*)-acetate mixes (the Z8-12:OH was held constant at 3—4% for all treatments). Fig. 1 shows the pattern of response obtained during exposure to the treatments for four consecutive behaviours: flight, upwind flight, wing fanning near the source, and hairpencilling. Male moths were activated to take flight to

TABLE II

Changes in turning frequency and severity in tracks of video-recorded wing fanning while walking males (same as in Table I) to different dosages of 5.9% (E)

Treatment (N)	$\bar{X}$ turn frequency (Turns/sec ± SD)[1]	$\bar{X}$ turn severity (Radians/turn ± SD)[1]	$\bar{X}$ turning: velocity ratio (Radians/cm ± SD)[1]
Single septum			
0.1 µg 5.9% (*E*)	4.99 ± 1.44 a	1.34 ± 0.56 a	0.66 ± 0.29 b
1 µg 5.9% (*E*)	4.93 ± 1.28 a	1.16 ± 0.21 b	0.63 ± 0.08 b
10 µg 5.9% (*E*)	2.74 ± 0.88 b	1.75 ± 0.56 a	0.80 ± 0.22 ab
100 µg 5.9% (*E*)	3.21 ± 0.69 b	1.75 ± 0.39 a	1.05 ± 0.29 a
Permeated airstream			
1 µg 5.9% (*E*)	4.52 ± 1.00 a	1.11 ± 0.25 b	0.77 ± 0.26 b
10 µg 5.9% (*E*)	3.72 ± 0.83 a	1.34 ± 0.30 ab	0.92 ± 0.27 ab
100 µg 5.9% (*E*)	3.90 ± 0.82 a	1.59 ± 0.20 a	1.13 ± 0.31 a

[1] Means in same column having no letters in common significantly different according to a T-test ($P < 0.05$)

most of the treatments, but during movement toward the source (monitored by each successive behaviour recorded), their behaviour was modulated by the concentration and blend presented. The complete sequence, ending with hairpencilling at the source was only elicited by a narrowly defined range of pheromone concentrations and (*E*):(*Z*) ratios.

It also is apparent that much of the variability in response was related to arrestment, induced by treatments containing increasing amounts of (*E*)-isomer, whether this was by higher (*E*):(*Z*) ratios or by increasing dosages of any blend. An increase in turning by a flying moth in response to an increase in the amount of (*E*)-isomer could account for the arrestment observed in these experiments, and to the changes in movement tracks of walking while fanning moths (Fig. 3, Tables I & II). However, the idea of a "turning" component interacting in the right ratio and dosage with an "orthokinetic" component, Z8-12:Ac, to modulate anemotactically guided movement to the source needs further investigation, since these movement changes could have been caused by an increase in total concentration of both components. Also, the influence of varying ratios of Z8-12:OH on turning and speed of movement still needs to be investigated.

The amount of arrestment observed in the

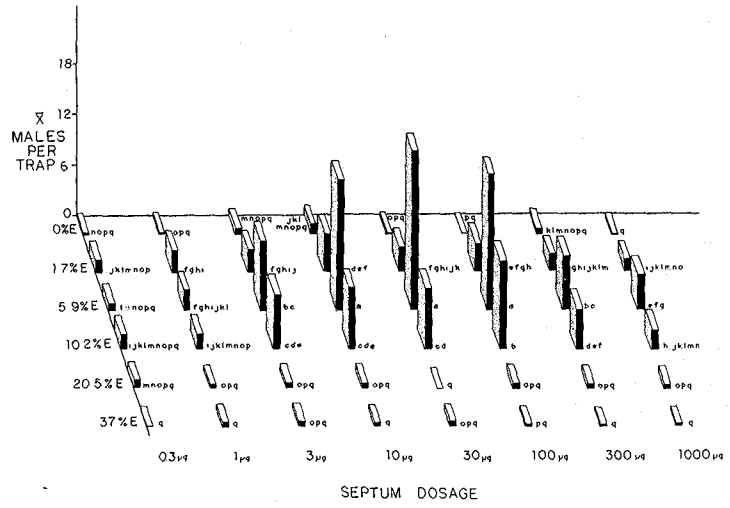


Fig. 4. Captures of ♂ oriental fruit moths in field to indicated blends and dosages. Means having no letters in common significantly different according to Waller & Duncan's BSD test ($P < 0.05$). Blank traps in all replicates captured zero ♂♂ and should be followed by letter *q*.

flight tunnel is depicted in Fig. 5 by overlaying a drawing of the arrestment threshold (>50%) (from Fig. 2) on a horizontal slice through the 50% level of the upwind flight response "mountain" (1B) that includes all the best response treatments. The area outlined below the arrestment threshold would correlate to the "attraction area" of the threshold hypothesis (Roelofs, 1978), which was bounded by a "flight activation" threshold and a "disorientation" threshold. The "active" area depicted in Fig. 5 outlines treatments for successful source

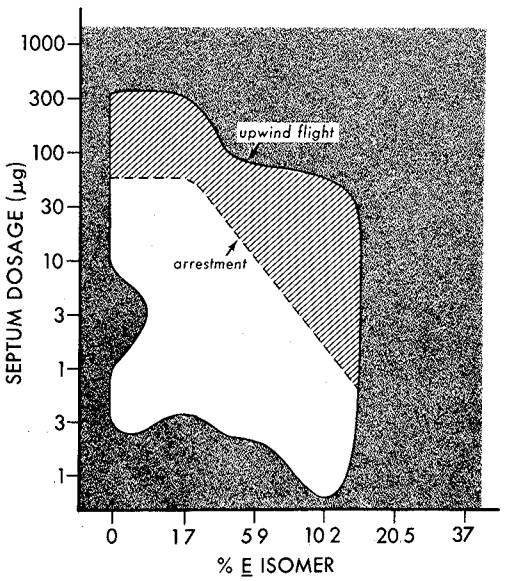


Fig. 5. An "active" area produced by drawing 50% arrestment threshold from Fig. 2 on a slice through 50% level of upwind flight profile (1B) to include best response treatments.

location by *G. molesta*, which occurs when the (instantaneous) pheromone plume is sufficiently concentrated 1.5 m downwind to elicit movement reactions sustaining attraction and sufficiently dilute near the source so as not to result in arrestment prematurely. This "active" area is similar to the field-trapping pattern (Fig. 4), which is characterized by reduced captures at extremes of ratio and dosage and by good catches in the area between upwind flight initiation (lower threshold) and flight termination (upper threshold).

However, the lower and upper thresholds in the field test appear to have shifted up ca. 10-fold compared to the flight-tunnel responses. A reduction in the level of response to the low release rates in the field when compared to the flight tunnel might be expected with all the possible dilution effects in the field environment, while the apparent raising of the arrestment threshold could result from several factors. Turbulence-induced dispersion of plumes from the traps could reduce the effective concentration of material to which the flying moth is actually exposed for each load rate and thus result in arrestment at higher release rates in the field, but another salient factor could be changes in the arrestment threshold as male moths fly in and out of an odor plume (possibly more than one plume) in a much longer-distance flight to the source (Bartell, 1977).

Wind tunnel data does not adequately represent the distance over which an array of blends and dosages can elicit upwind flight, but it can be used to determine the specificity of male behavioural responses to various blend ratios and dosages. It also must be realized that just one behaviour is occurring in the zone of blends and dosages between the threshold boundaries in Fig. 5: upwind flight to the source from 1.5 m away. A truer depiction of blend and dosage interactions resulting in trap catch must take into account the entire flight active distance (Baker & Roelofs, 1981) for every ratio and dosage combination. Our wind tunnel restricted distance measurements because above-threshold concentrations needed to occur only 1.5 m from the source and what occurred beyond that distance could not be measured. However, for 4 dosages of 5.9% (*E*) (Baker & Roelofs, 1981) it was found that the active distances for upwind flight initiation and termination occurred farther from the source as dosage increased. At the highest dosage, 1000 µg, upwind flight was initiated at an average of ca. 80 m away and ended with arrestment at 1.5 m, whereas to 10 µg the values were 12 and 0 m, respectively.

Further research will be conducted on environmental stimuli that can modify the male's behavioural response thresholds, and on the movement changes in behaviour caused by altering the concentrations of individual components in a blend.

We thank Dr. L. Bjostad for interest and help, Dr. D. Barnard for help with computer-generated response surfaces, Dr. C. Linn and the late Dr. A. Hill for discussion, F. Wadhams, K. Pool and B. Carney for rearing, and

R. McMillan and B. Aldwinckle for preparation of Figs 1, 2 and 3.

ZUSAMMENFASSUNG

Der Einfluss von Dosierung und Mischungsverhältnis der Pheromonkomponenten auf das Verhalten männlicher Pfirsichtriebwickler

Das Sexualverhalten männlicher Falter des Pfirsichtriebwicklers, *Grapholitha molesta* (Busck), gegenüber verschiedenen Dosierungen und Mischungen von (*Z*)-8- und (*E*)-8-Dodecenylacetat wurde untersucht. Ein stetiger Aufwindflug, der zum Auffinden der Duftquelle führte, konnte nur im mittleren Dosierungs- und Mischungsbereich beobachtet werden. Ausserhalb dieses Optimums war die Dosierung offenbar entweder zu hoch oder zu niedrig, um eine deutliche Anlockung, d.h. einen gerichteten Flug innerhalb der Duftfahne zu bewirken; bei hoher Konzentration näherten sich die Tiere der Quelle nur auf bestimmte Distanz (arrestment). Freilandversuche mit Fallen führten zu ähnlichen Ergebnissen, nur dass dort das Dosierungsoptimum bei ca. zehnmal höheren Werten lag als in den Versuchen im Windkanal. Der bei hohen Mengen an *E*-Isomer (hohe Dosis oder hohes *E*/*Z*-verhältnis) beobachtete Arrestment-Effekt könnte auf Erhöhung der Drehbewegungen oder Verringerung der Fluggeschwindigkeit zurückzuführen sein.

REFERENCES

Baker, T. C. & Cardé, R. T. (1979a). Endogenous and exogenous factors affecting periodicities of female calling and male sex pheromone response in *Grapholitha molesta* (Busck). *J. Ins. Physiol.* **25** : 943—950.

Baker, T. C. & Cardé, R. T. (1979b). Courtship behavior of the oriental fruit moth: experimental analysis and consideration of the role of sexual selection in evolution of courtship pheromones in the Lepidoptera. *Ann. Entomol. Soc. Am.* **72** : 173—188.

Baker, T. C. & Cardé, R. T. (1979c). Analysis of pheromone-mediated behavior in male *Grapholitha molesta*, the oriental fruit moth (Lepidoptera: Tortricidae). *Environ. Entomol.* **8** : 956—968.

Baker, T. C. & Roelofs, W. L. (1981). Initiation and termination of oriental fruit moth male response to pheromone concentrations in the field. *Environ. Entomol.* **10** : 211—218.

Bartell, R. J. (1977). Behavioral responses of Lepidoptera to pheromones. In: *Chemical Control of Insects Behavior: Theory and Application*, eds.: H. H. Shorey and J. J. McKelvey, Jr., New York, John Wiley & Sons, pp. 201—213.

Biwer, G. C., Descoins, C. & Gallois, M. (1979). Étude des constituants volatils présents dans la glande productrice de phéromone de la femelle vierge de *Grapholitha molesta* Busck, Lépidoptère Tortricidae (Olethreutinae). *C. R. Acad. Sc. Paris*, t. **288** : 413—416.

Cardé, A. M., Baker, T. C. & Cardé, R. T. (1979). Identification of a four-component sex pheromone of the female oriental fruit moth, *Grapholitha molesta* (Lepidoptera: Tortricidae). *J. Chem. Ecol.* **5** : 423—427.

Kennedy, J. S. (1977). Olfactory responses to distant plants and other odor sources. In: *Chemical Control of Insect Behavior: Theory and Application*, eds.: H. H. Shorey and J. J. McKelvey, Jr., New York, John Wiley & Sons, pp. 67—91.

Miller, J. R. & Roelofs, W. L. (1978). Sustained-flight tunnel for measuring insect responses to wind-borne sex pheromones. *J. Chem. Ecol.* **4** : 187—198.

Roelofs, W. L. (1978). Threshold hypothesis for pheromone perception. *J. Chem. Ecol.* **4** : 685—699.

Roelofs, W. L. (1980). Pheromones and their chemistry. In: *Insect Biology In The Future*, eds.: M. Locke and D. S. Smith, New York, Academic Press.

Roelofs, W. L., Comeau, A. & Selle, R. (1969). Sex pheromone of the oriental fruit moth. *Nature* **244** : 723.

Ryan, J. A. (1960). Significance tests for multiple comparison of proportions, variances, and other statistics. *Psychol. Bull.* **57** : 318—328.

Accepted: May 30, 1981