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BEHAVIORAL RESPONSES OF MALE Heliothis zea¹ MOTHS IN SUSTAINED-FLIGHT TUNNEL TO COMBINATIONS OF 4 COMPOUNDS IDENTIFIED FROM FEMALE SEX PHEROMONE GLAND

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Abstract—Each of the four compounds that have been identified from sex pheromone glands of *Heliothis zea* female moths was examined for its ability to elicit sexual responses from male moths in a flight tunnel. Males flew upwind to (Z)-11-hexadecenal alone, but greater levels of behavioral activity were evoked with the addition of (Z)-9-hexadecenal to the treatment Addition of hexadecanal or (Z)-7-hexadecenal to the initial two components had no effect in raising the behavioral response of the males in the flight tunnel whether added singularly at both the normal gland-emission ratio or at varying ratios or in combination at the normal ratio. Live, calling females elicited levels of sexual activity from males not significantly different from that elicited by the mixture of (Z)-11- and (Z)-9-hexadecenal on cotton wicks.

Key Words—Corn earworm, *Heliothis zea*, Lepidoptera, Noctuidae, flight tunnel, sex pheromone, moth behavior.

INTRODUCTION

Klun et al. (1980) identified four compounds from the sex pheromone gland of the female corn earworm moth, *Heliothis zea* (Boddie): (Z)-11-hexadecenal (Z11-16:Ald), hexadecanal (16:Ald), (Z)-9-hexadecenal (Z9-16:Ald), and (Z)-7-hexadecenal (Z7-16:Ald) in approximately a 92:5:2:1 ratio. The combination of Z11-16:Ald and Z9-16:Ald captured as many males as did all four compounds when evaporated from cotton wicks in some field tests (Sparks et al., 1979; Hartstack et al., 1980; Klun et al., 1980) and in addition,

¹Lepidoptera: Noctuidae

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the two-compound mixture occasionally caught as many or more males than traps baited with live females (Hartstack et al., 1980; Klun et al., 1980). However, in other studies, traps baited with females caught significantly more males than did the best pheromone treatment (Sparks et al., 1979), although there was variability of catch dependent upon style of trap used. In addition, number of males captured was dependent upon the type of pheromone dispenser used, of which cotton dental wicks were the most attractive (Hartstack et al., 1980; Lopez et al., 1981). We undertook a flight tunnel study to complement the work that has been done in the field and to determine the role, if any, that each of the four compounds plays in sexual communication in H, zea.

METHODS AND MATERIALS

Rearing. H. zea larvae were raised on a modified pinto bean diet (Shorey and Hale, 1965) at the UC Riverside campus or on a casein-wheat germ diet at Agresearch, Inc. (Los Angeles, California). The two colonies were kept separate throughout the experiment to detect any differences that might exist. Pupae were segregated by sex; moths were segregated by age and the sexes kept in separate chambers after emergence. Larvae and adults were maintained at $24 \pm 2^{\circ}$ C on a 14:10 light-dark photoperiod. Adults always had access to an 8% sucrose solution.

Chemicals. All compounds were obtained from the Controlled Release Division of Albany International Corporation. Purity, as a percentage of total volatiles measurable by gas-liquid chromatography, was determined on a 30-m \times 0.24-mm SP2330 column using a Varian 3700 GC run isothermally at 135°C. Purities for the compounds were as follows: Z11-16: Ald, Z9-16:Ald, 16:Ald (all >99%), and Z7-16:Ald (95%). Each compound contained no detectable quantities of the other three compounds. The hexane solutions used in the experiments were formulated prior to each series of tests and were stored at $<-20^{\circ}$ C. Emission rates were measured from the cotton wicks to be used in the behavioral tests in a device modified from Baker et al. (1981). The 15-mm-diam dental wicks (#3, Johnson & Johnson) were cut down to ca. 10-mm lengths and impregnated with $10 \,\mu l$ of solution containing varying amounts of Z11-16: Ald. The emission rate of 3000 ng of Z11-16: Ald, 0.73 ng/min, was approximately that emitted by a forcibly extruded sex pheromone gland of a H. zea female, 0.42 ng/min (Pope et al., 1983). In the first experiments (Tables 1-3), the other three compounds (Z9-16:Ald, 16: Ald, and Z7-16: Ald) were loaded in relation to Z11-16: Ald at ratios similar to those found in gland extracts (Klun et al., 1980): 30, 150, and 30 ng, respectively. In later experiments (Tables 4 and 5), a series of loadings of these three compounds were varied as binary mixtures of each compound to 3000 ng of Z11-16: Ald.

H. zea male responses to female compounds

Compound Mixtures on Cotton Wicks. Male moths were tested during the 5th through 8th hr of their 4th, 5th, or 6th scotophase in a clear plastic flight tunnel (1 m wide at the floor, 0.9 m high, 3.65 m long) modified after Miller and Roelofs (1978). Moths were acclimated to flight tunnel conditions (0.5 m/sec wind velocity, $24 \pm 3^{\circ}$ C, 0.3 lux light level) ca. 30 min prior to testing and transferred to individual release cages ca. 15 min prior to testing.

Cotton wicks, in lots of 50, were cut down to 10-mm lengths, soaked in distilled acetone for 30 min, and oven-dried at 120°C overnight to remove potential contaminants. Wicks were loaded with 10 μ l of pheromone solution in hexane 15-20 min before testing. Treatments within an experimental series were drawn in random order for each daily testing in a complete block design. At the beginning of a trial, the loaded wick was placed in the center of a 2-mmthick metal ring washer (30 mm OD, 13 mm ID) which was then placed at the center of a 15×15 -cm piece of sheet metal situated 15 cm above the tunnel floor on a sheet-metal platform. The ring washer prevented the males from knocking the wick off the platform. Each male was placed in the middle of the pheromone plume (predetermined by a TiCL smoke source) ca. 3 m downwind of the wick and was given 1 min to take flight out of the cage. If found to be incapable of sustained flight (due to damage, etc) after attempting to fly, the male was not scored and then replaced with a new moth. Males that were capable of flight were observed until they left the pheromone plume and contacted the flight tunnel ceiling or flew out the back of the flight tunnel. Those males capable of sustained flight were scored for the following behaviors: UpW-Moth flies upwind in the pheromone plume from the release point; Pl-moth flies within 10 cm of platform edge; S-moth lands on source; Hp-after landing on the source, moth everts his hairpencils; and C-after landing on the source, moth exhibits the copulatory response (i.e., full hairpencil eversion, curling of the abdomen).

For each behavioral category, no male contributed more than 1 data point and the number reported for each category in each table is the percentage of flight-capable males that exhibited at least that level of behavior (i.e., a male that exhibited a Hp response added 1 positive response to each of the first four categories but not the last). Observations of hairpencil extrusions near the source were aided with a flashlight that had several layers of red cellophane pasted over the lens and whose light beam was shielded slightly by the observer's fingers. The light did not appear to affect the moths' behaviors.

All approaches by males were recorded, although most moths made only one approach and then flew up and out of the plume toward the top of the flight tunnel. Males were used once and then discarded from further testing; no more than 8 males were flown to one treatment per day. If moths from both colonies were used in the same series, equal numbers of flights for each colony were recorded for each treatment to eliminate potential bias. Each

trial (i.e., the amount of time the wick was in the flight tunnel airstream) lasted no more than 15 min.

All statistical analysis was performed using a $\chi^2 2 \times 2$ test of independence with Yates' correction at the 0.05 level of significance.

Female vs. Wick. Cotton wicks impregnated with the two-component mixture (3000 ng Z11-16: Ald-30 ng Z9-16: Ald) were tested against live, calling H. zea females that were in the 2nd through 6th hr of their 4th scotophase. Pretrial acclimation and handling are described previously (Vetter and Baker, 1983). Data were recorded from males that flew upwind in the plume for >0.25 m or hovered in the plume for >2 sec. If a male flew out of the release cage but did not fly upwind in the plume, no data were recorded since it was not known if he had stopped responding to the pheromone or if the female had stopped calling and no pheromone was present. The calling female was contained on the platform by an inverted release cage. When the wick was tested, it was pinned to the top on the inside of the cage (loaded end down) to mimic the female's calling position. Upon landing on the cage containing either the wick or female, the male was observed for 10 sec and removed. [This should not have biased the results since male H_{zea} exhibit their most intense response on the first approach (97%, N = 406).] This removal was necessary to prevent the male from disturbing the female, whereupon she might cease calling. No more than eight males were allowed to fly to a single female, and most trials with a female lasted 10 min, none more than 20 min.

RESULTS

One-Compound Treatments. When each compound was tested singularly, only Z11-16: Ald elicited significant levels of upwind flight, but these levels were significantly lower than the control, the four-compound mixture (Table 1). No significant differences were noted in subsequent behavioral levels among the four individual compounds; all elicited significantly fewer responses than the four-compound mixture, although Z11-16: Ald did evoke slight activity in each category.

Two-Compound Mixtures. All six possible combinations of binary mixtures from four compounds were tested. Those treatments containing Z11-16: Ald again elicited small percentages of upwind flight while those lacking it were inactive (Table 2). As in Table 1, the greatest attrition in behavior occurred between UpW and Pl levels of activity. Only one two-compound mixture, the combination of Z11-16: Ald and Z9-16: Ald, evoked response levels not significantly different from the four-compound mixture in all categories of behavior. Hereafter, this blend will be referred to as the two-component mixture.

Three-Compound Mixtures. To determine if either 16: Ald or Z7-16:

H. zea male responses to female compounds

% behavioral response ^a (32 flights/treatment)							
Compound	UpW ^b	Pl	S	Hp	С		
Z11-16:Ald	25b	6b	6b	3b	.3b		
Z9-16: Ald	0c	0b	0Ъ	0b	0b		
16:Ald	0c	0b	0Ъ	0Ъ	0b		
27-16: Ald	0c	06	0Ь	0Ъ	0Ъ		
Four-compound mixture	72a	44a	28a	28a	25a		

TABLE 1. RESPONSE OF MALES TO ONE-COMPOUND TREATMENTS

^aUpW—moth flies upwind in plume from release point; Pl—moth flies < 10 cm from platform edge; S-moth lands on source; Hp-after landing, moth everts hairpencils; and C-after landing, moth exhibits copulatory response.

^bPercentages in the same column having no letters in common are significantly different according to a $\chi^2 2 \times 2$ test of independence with Yates' correction (P < 0.05).

Ald play a communicatory role in the sexual behavior of H. zea, each compound was admixed to the two-component mixture and then the response of males to these blends was compared to the two-component and fourcompound mixtures. Addition of either 16: Ald or Z7-16: Ald to the twocomponent mixture caused no increase of response over that of the twocomponent mixture (Table 3). Also, the four-compound mixture did not significantly increase behavioral activity over that of the two components.

Varying Ratios of 16: Ald. Since the addition of 16: Ald (1:20 ratio to Z11-16: Ald) to the two-component blend evoked no significant increase of

	Treatme	nts ^a		% () behavi 28 fligh	oral res ts/treat	ponse ^b ment)	
Z11-16:Ald	Z9-16:Ald	16:Ald	Z7-16:Ald	UpW	Pl	S	Hp	С
+	+			71a	36a	25a	25a	25a
+		+		11bc	0Ь	0b	0b	0b
+			+	29b	0Ъ	0b	0b	0Ь
	+	+	,	0c	0b	0b	0Ъ	0Ь
	+		+	0c	0Ь	0b	0b	0Ь
		+	+	0c	0b	0b	0b	0Ъ
+	+	+	+	82a	29a	25a	25a	21a

TABLE 2. RESPONSE OF MALES 10 TWO-COMPOUND MIXTURES

^aA "+" in the column indicates the presence of this compound in the treatment. ^bAbbreviations for the behavioral responses as described in Table 1

'Percentages in the same column having no letters in common are significantly different according to a $\chi^2 2 \times 2$ test of independence with Yates' correction (P < 0.05).

		% behavioral response ^a (100 flights/treatment)				se ^a (t)
Treatments	Additional compound	Up W ^b	Pl	S	Hp	p C
	16:Ald	88a	43a	38a	35a	24a
Z11-16:Ald + Z9-16:Ald	Z7-16: Ald	89a	34a	28a	28a	9b
	None	84a	40a	32a	30a	21a
	16: Ald + Z7 - 16: Ald	81a	43a	35a	28a	21a

TABLE 3. RESPONSE OF MALES 10 THREE-COMPOUND MIXIURES

^aAbbreviations for the behavioral responses as described in Table 1 ^bPercentages in the same column having no letters in common are significantly different according to a χ^2 2 × 2 test of independence with Yates' correction (P < 0.05)

A mount (ng) loo dod on wisk	% behavioral response ^b (50 flights/treatment)					
(ratio to $Z11-16$: Ald) ^{<i>a</i>}	UpW	Pl	S	Hp	С	
16: Ald	· · ·					
0	76ab	46a	38ab	24a	12a	
$150(1:20)^d$	82ab	54a	46ab	42a	20a	
300 (1:10)	92a	48a	38ab	30a	16a	
900 (1:3.3)	68b	36a	26b	22a	12a	
3000 (1:1)	86ab	54a	48a	38a	22a	
Z7-16: Ald						
0	78a	46a	38a	32a	28a	
$30(1:100)^d$	84a	50a	48a	46a	36a	
100 (1:30)	78a	48a	46a	44a	34a	
1000 (1:3)	70a	40a	34a	32a	24a	
3000 (1:1)	82a	46a	40a	34a	28a	

TABLE 4. RESPONSE OF MALES 10 3-COMPOUND DOSAGE SERIES INVOLVING 16: ALD AND Z7-16: ALD AS VARIABLE COMPOUND

"The amount (ratio) of Z11-16: Ald to Z9-16: Ald loaded onto the wick was 3000 ng and 30 ng,

respectively (100:1). ^bAbbreviations for the behavioral responses as described in Table 1. ^cPercentages in the same column having no letters in common are significantly different accord-

ing to a $\chi^2 2 \times 2$ test of independence with Yates' correction (P < 0.05). The natural loading in approximate ratio of compounds as found in gland extracts (Klun et al, 1980) and volatile collections (Pope et al., 1984).

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the sexual response of *H. zea* males in comparison to the two-component mixture (Table 3), a series of treatments was run with a variable loading of 16: Ald to examine whether it might be active at some higher ratio. Addition of 16: Ald to the two-component mixture in ratios to Z11-16: Ald of 1:20 [the natural gland-emission ratio (Klun et al., 1980; Pope et al., 1984)], 1:10, 1:3.3, and 1:1 neither elevated nor depressed the behavior of the males compared to the two component mixture (Table 4).

Varying Ratios of Z7-16: Ald. Similar to the previous experiment, a wide range of ratios of Z7-16: Ald were added to the two-component blend to determine if it would affect behavioral responses. As with 16: Ald, addition of Z7-16: Ald to the two-component mixture in ratio to Z11-16: Ald of 1:100 (the natural gland-emission ratio), 1:30, 1:3, and 1:1 had no effect on any of the behaviors in comparison to the two-component mixture (Table 4).

Two-Component Dosages and Ratios. A series of two experiments was run using the two-component mixture; the first one varied the ratio of Z9-16: Ald while holding the amount of Z11-16: Ald constant and the second was a serial dilution of the two components held at a constant ratio to one another. Z9-16: Ald was admixed with Z11-16: Ald in ratios of 1:100 (the natural

TABLE 5. RESPONSE OF MALES 10 2-COMPONENT DOSAGE SERIES INVOLVING
Z9-16: Ald as Variable Compound (Z11-16: Ald Loading Held Consiani)
AND RATIO OF Z11-16: ALD HELD CONSTANT IN A SERIAL DILUTION

	% behavioral response ^a (50 flights/treatr		atment)		
Amount loaded on wick	UpW ^b	Pl	S	Hp	С
Z9-16:Ald (ratio to Z11-16:Ald)					
0 ng	24c	0c	0b	0b	0b
$30 \text{ ng} (1:100)^{\circ}$	86a	46a	42a	38a	34a
100 ng (1:30)	76ab	48a	40a	38a	32a
1000 ng (1:3)	68ab	32ab	28a	26a	22a
3000 ng (1:1)	62b	20b	10ь	4b	2ь
Z11-16: Ald (100:1 ration to Z9-16: Ald)					
0.3 µg	70a	28a	26a	24a	14b
$3 \mu g^c$	84a	26a	24a	22a	18ab
$30 \ \mu g$	86a	42a	42a	36a	.36a
300 µg	78a	40a	26a	24a	20ab
3000 µg	80a	38a	32a	28a	24ab

^aAbbreviations for the behavioral responses as described in Table 1.

^bPercentages in the same column having no letters in common are significantly different according to a $\chi^2 2 \times 2$ test of independence with Yates' correction (P < 0.05).

The natural loading resulting in an emission rate similar to maximally emitting females (Pope et al., 1984).

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TABLE 6. RESPONSES OF MALES TO 2-COMPONENT MIXTURE VS. LIVE, CALLING FEMALES

Treatments	% beha	vioral resp	onse ^a (50 fl	ights/treat	ment)
	UpW ^b	Pl	S	Hp	С
Calling female	98a	62a	60a	48a	22a
2-component mixture	98a	54a	50a	42a	32a

^aAbbreviations for the behavioral responses as described in Table 1.

^bPercentages in the same column with no letters in common are significantly different according to a $\chi^2 2 \times 2$ test of independence with a Yates' correction (P < 0.05).

Cotton wick loaded with 3000 ng Z11-16: Ald and 30 ng Z9-16: Ald

gland-emission ratio), 1:30, 1:3, and 1:1 as well as a treatment consisting of Z11-16:Ald alone. There were no significant differences in the behavioral responses when the 1:30 and 1:3 ratio treatments were compared to the natural ratio treatment, although there was a slight decrease in response with increasing amounts of Z9-16:Ald (Table 5). At the 1:1 mixture, the responses decreased significantly from those to lower ratios, although 10% of the males still landed on the wick. Consistent with the previous experiments, Z11-16:Ald alone elicited upwind flight but addition of 1% Z9-16:Ald increased activity significantly.

In the serial dilution series, Z11-16: Ald + 1% Z9-16: Ald was diluted in tenfold steps and $10 \ \mu$ l were loaded in tenfold decrements from 3000 to 0.3 mg onto the cotton wicks. There were no significant differences among the five treatments, except the 0.3- μ g loading which elicited fewer copulatory attempts than the 30- μ g treatment (Table 5).

Wick vs. Live Female. There were no statistical differences between the responses of males to live, calling females and the two-component mixture on cotton wicks (Table 6). The overall percentages of males responding were higher than in earlier experiments since males that flew straight up and out of the plume from the release cage were discarded from the data whereas previously they were included.

DISCUSSION

In our flight tunnel, the initiation of upwind flight and subsequent closerange sexual behaviors in male H. zea were mediated by the two pheromone components, Z11-16: Ald and Z9-16: Ald. Although Z11-16: Ald alone was capable of eliciting upwind flight and, once, copulatory behavior (Tables 1, 2, and 5), all sexual behaviors were increased significantly with addition of 1% Z9-16: Ald (Tables 2 and 5).

Activity of Z11-16: Ald alone is consistent with earlier findings in activa-

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tion bioassay chambers (Roelofs et al., 1974; Klun et al., 1980). All of the above was also consistent with the findings of Carpenter and Sparks (1982a) in a field-flight-tunnel study. However, they tested treatments simultaneously in a transverse array that allowed for the mixing of up to as many as five different pheromone plumes, thereby making the isolated effect of single treatments difficult to observe.

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Although 16: Ald and Z7-16: Ald were also found in the sex pheromone glands of *H* zea females (Klun et al., 1980), in our flight tunnel, they were inert in regard to H. zea sexual communication. These compounds have also been found to be emitted by H. zea females (Pope et al., 1984) in ratios similar to those reported by Klun et al. (1980). However, there was no effect of either compound on altering the response of males in comparison to the two components when admixed as singular additions to the two-component mixture in natural ratios (Table 3) or added together to form a four-compound mixture (Tables 2 and 3). These data are consistent with field trapping experiments (Sparks et al., 1979; Hartstack et al., 1980; Klun et al., 1980). Furthermore, in our study, when each compound was tested in a dosage series where the load varied from natural to 1:1 ratios (to Z11-16: Ald), the presence of either 16: Ald or Z7-16: Ald caused no significant changes in male response when compared to those elicited by the two-component mixture (Table 4). Despite the fact that both compounds are present in female gland and volatile emissions, we could find no evidence that 16: Ald or Z7-16: Ald plays any behavioral role in pheromone communication in this species.

In the flight tunnel, male *H. zea* responded to a wide range of ratios and loadings. First, although the ratio of emission of the two components is ca. 100:1, males responded equally well even when Z9-16: Ald accounted for 25% of the treatment (Table 5). A decrease in the response was observed only when the 1:1 ratio was tested. In field trapping, Klun et al. (1982) observed some decrease in trap catch of male *H. zea* when 93:7 Z11-16: Ald-Z9-16: Ald was tested (as compared to 96:4), significant decrease at 87:13, and almost no trap catch at 76:24. Flight-tunnel assays may be less discriminating than field trapping tests because they lack long-distance flight, but significant reduction of response was eventually observed at the highest level of Z9-16: Ald tested.

Responses to the two-component mixture and to live, calling females were not significantly different even at close range (Table 6). This was a somewhat surprising result because male *H. zea* use vision at close range (<12 cm) once they have been attracted from greater distances (Carpenter and Sparks, 1982b). However, in our study, all females were contained in an inverted wire release cage, and some may have been only partially visible as they called from the upwind portion of the cage. Also, although only females that could elicit upwind flight in males were used, there happened to be greater sameday variation among the male's response to calling females than to pheromone

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evaporated from cotton wicks; some females were much better than wicks, some much worse. This may be the reason for some of the variation in field trapping (Sparks et al., 1979; Klun et al., 1980) when live females were compared with pheromone components on cotton wicks.

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