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SENSORY AND BEHAVIORAL EFFECTS OF GOSSYPLURE ALCOHOL ON SEX PHEROMONE RESPONSE OF MALE PINK BOLLWORM MOTHS, *Pectinophora gossypiella*

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Abstract—(Z,Z)- and (Z,E)-7,11-hexadecadienol, reported to be pheromone precursors, interfere with the normal sequence of behavioral response of male *Pectinophora gossypiella* to sex pheromone. The magnitude of the interference can be diminished with higher release rates of the sex pheromone. (Z,Z)-7,11-Hexadecadienol is more effective than its Z,E isomer in eliciting the reduction in the behavioral response. Electroantennographic evidence suggests that each alcohol may be interfering more with receptor sites for the conformationally similar pheromone acetate than with receptor sites for the other pheromone isomer. Defining behavioral and physiological effects of pheromone analogs such as the alcohols of gossyplure may help to determine their potential for behavioral manipulations.

Key Words—Lepidoptera, Gelechiidae, *Pectinophora gossypiella*, pink bollworm, (Z,Z)-7,11-hexadecadienyl acetate, (Z,E)-7,11-hexadecadienyl acetate, (Z,Z)-7,11-hexadecadienol, (Z,E)-7,11-hexadecadienol, pheromone analog, behavior, electroantennogram.

INTRODUCTION

The pheromonally mediated behavioral responses of many species of moths have been found to be adversely affected by compounds that are related in structure to the pheromone components (Beevor and Campion, 1979; Cardé, 1976;

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Roelofs and Cardé, 1977). Some of these compounds have been synthesized and tested in part because of their structural similarity to the naturally occurring sex pheromone (e.g., Beevor and Campion, 1979). Other chemicals have been identified from extracts of sex pheromone glands and subsequently were found to interfere with the normal sequence of male responses to sex pheromone (e.g., Cardé et al., 1973). These latter compounds may not be emitted by the female and often are likely candidates to be pheromone precursors.

The sex pheromone of the pink bollworm, *Pectinophora gossypiella* (Saunders), has been identified as a 1:1 blend of (*Z*,*Z*)-7,11-hexadecadienyl acetate [(*Z*,*Z*)-7,11-16:Ac] and (*Z*,*E*)-7,11-hexadecadienyl acetate, [(*Z*,*E*)-7,11-16:Ac] (Hummel et al., 1973; this blend was called gossyplure). When Bierl et al. (1974) confirmed the identity of this sex pheromone, they also determined that (*Z*,*Z*)-7,11-hexadecadienol [(*Z*,*Z*)-7,11-16:OH] and (*Z*,*E*)-7,11-hexadecadienol [(*Z*,*E*)-7,11-16:OH] were present in gland extracts of female moths and they assumed that these alcohols were precursors of the sex pheromone. Zhu et al. (1983) detected the same two alcohols only in mated female *P. gossypiella*. In addition they determined that ca. a 1:1 blend of these alcohols (gossyplure OH) reduced captures of male *P. gossypiella* in traps in the field. We felt that it was important to gain a better understanding of the mode of action of this communicative interference at the sensory and behavioral levels in order to determine the potential for mating disruption using these compounds.

METHODS AND MATERIALS

Insects. *P. gossypiella* larvae were reared in half-gallon cartons containing shredded wheat-germ diet modified from the diet described by Adkisson et al. (1960). Pupae were segregated by sex, and male moths were aged daily and held in 25 × 25 × 30-cm screen cages. Larvae and adults were maintained at ca. 28°C on a 14:10 light–dark cycle (lights on at noon). Adult males had access to an 8% sucrose solution. Individual 2- to 4-day-old male moths were transferred to cylindrical screen cages (3.5 × 3.3 cm diam) during the photophase and were tested during the seventh through ninth hour of the next scotophase.

Chemicals. (*Z*,*Z*)-7,11-16:Ac and (*Z*,*E*)-7,11-16:Ac were purchased from Pest-Select (Buckeye, Arizona), and we determined that they were greater than 93% free of other sex pheromone-like volatiles by a GC analysis using a 3-m column packed with 4.2 g of 10% Silar 10C (N_2 flow rate 30 ml/min; temperature 180°C; OD 4 mm). (*Z*,*Z*)-7,11-16:Ac contained as much as 4% (*Z*,*E*)-7,11-16:Ac and no detectable (*Z*,*Z*)- or (*Z*,*E*)-7,11-16:OH. (*Z*,*E*)-7,11-16:Ac contained as much as 3% (*Z*,*Z*)-7,11-16:Ac and no detectable (*Z*,*Z*)- or (*Z*,*E*)-7,11-16:OH. (*Z*)-7-16:Ac was obtained from Farchan (Wil-

loughby, Ohio), and was greater than 96% free of other sex pheromone-like volatiles. (*Z,Z*)-7,11-16:OH, (*Z,E*)-7,11-16:OH, and (*Z*)-7-16:OH were derived from the acetates by base hydrolysis (as in Bjostad et al., 1984). (*Z,E*)-7,11-16:OH contained as much as 3% (*Z,Z*)-7,11-16:OH and no detectable 7,11-16:Ac. (*Z,Z*)-7,11-16:OH used in behavioral tests contained as much as 4% (*Z,E*)-7,11-16:OH and 5% (*Z,Z*)-7,11-16:Ac. The presence of up to 5% (*Z,Z*)-7,11-16:Ac in the solution of (*Z,Z*)-7,11-16:OH did not pose a problem for behavioral tests since this alcohol was always incorporated into a blend of (*Z,Z*)-7,11-16:Ac and (*Z,E*)-7,11-16:Ac. The blend ratio of the pheromone would only be shifted by at most 1.2%. However, in the electroantennogram (EAG) study, it was important that the alcohols contained no acetates. The alcohols were rederived from the acetates, and this time we could detect no evidence of acetate contaminants in our alcohol solutions. Solutions of the compounds to be used in behavioral and EAG tests were made in hexane.

Behavioral Tests. Male *P. gossypiella* in individual screen cages were transferred to the room housing the flight tunnel at least 0.5 hr prior to the beginning of observations, in order to acclimate the moths to wind-tunnel conditions (0.3 lux from incandescent white lights; supplemental incandescent red lighting; temperature ca. 26°C; wind speed 0.5 m/sec). The wind tunnel was similar to that described by Miller and Roelofs (1978). Cotton dental rolls (1 × 1 cm diam) were loaded with 10-μl hexane solutions containing the indicated amount of compounds about 10 min before the start of a test. Treatments within an experimental series were drawn in random order for each day's test. At the beginning of a trial, a cotton wick treated with the test compounds was placed at the center of a piece of sheet metal (15 × 15 cm) situated 15 cm above the tunnel floor on a sheet-metal platform that was 50 cm from the upwind end of the tunnel and equidistant from the walls of the tunnel. Each male was released 1.4 m directly downwind of the source by placing a cage, open end up, on a metal platform. Cages and platforms were washed with acetone daily after use. The behavioral responses of males were noted in the following categories: wing fanning in the release cage (WF); taking flight (F); upwind flight in the pheromone plume (UFW); making contact with the source (SC); and the time from introduction of the moth into the flight tunnel to initiation of flight. Ryan's (1960) multiple-comparison test for proportions was used to evaluate differences between probabilities of displaying a behavior, and Duncan's multiple-range test following an analysis of variance was used to separate mean latencies.

Electroantennogram. Aspects of our EAG studies followed procedures previously described by Baker and Roelofs (1976), Payne and Dickens (1976) and Roelofs (1977). A 2- to 4-day-old male was captured and its head was removed. The base of the head was placed into saline solution (9.0 g/liter NaCl, 0.2 g/liter KCl, 1.0 g/liter BES (buffer), 4.0 g/liter sucrose, 0.2 g/liter $CaCl_2$) on a wedge of clay that was partially submerged. One antenna was teased up and the terminal two or three segments were removed. A capillary input elec-

trode (containing saline solution and silver chloride-coated silver wire) was moved into position so that it contacted the cut end of the antenna. A chloridized silver wire submerged in the saline solution served as the ground electrode. The EAG response was preamplified with a gain of 100 and frequency range of DC 5 kHz. The signal was displayed on a Tektronic 5113 storage oscilloscope with 1 vertical division equal to 1 mV and 1 horizontal division equal to 1 sec. The EAG responses were recorded to the nearest 0.1 mV.

The first electroantennogram study involved exposing the antenna of a male *P. gossypiella* to one of three adapting stimuli: (1) solvent blank (10 μl of hexane); (2) 10 μg of (*Z*,*Z*)-7,11–16:Ac in 10 μl hexane; and (3) 10 μg (*Z*,*E*)-7,11–16:Ac in 10 μl hexane. Adapting stimuli were loaded onto a 1 × 2-cm piece of fluted filter paper (Z-fold) and, following solvent evaporation, were placed into the proximal end of elbow-shaped glass cartridges (each arm of an elbow was 4 cm long and 1 cm ID). Each cartridge was connected to a laboratory airstream flowing at 2 liters/min after passing through an activated charcoal filter. Test stimuli were the following: (1) solvent blank (10 μl of hexane); (2) 10 μg of (*Z*,*Z*)-7,11–16:Ac in 10 μl of hexane; and (3) 10μg (*Z*,*E*)-7,11–16:Ac in 10 μl of hexane, each on a 1 × 2-cm fluted filter paper. The filter paper was inserted following solvent evaporation into the lumen of a disposable Pasteur-type glass pipet (14.5 cm long). During the first 3 min of exposure to each adapting stimulus, a test stimulus was puffed into the airstream using 2 ml of air forced from a 10-ml glass syringe connected by a rubber septum to the test cartridge. Adapting stimuli and test stimuli were presented in random order within each block of treatments. Each antenna was exposed to one adapting stimulus, and all of the test stimuli. In order to examine antennal recovery following removal of adapting stimuli, test stimuli were again puffed onto the antennae after 2 min in clean air.

The second EAG experiment was designed to examine the effect of the alcohols of gossyplure on the response to (*Z*,*Z*)-7,11–16:Ac and (*Z*,*E*)-7,11–16:Ac. In this experiment the adapting stimuli were 30 μg of the alcohols loaded in 30 μl hexane onto separate pieces of fluted filter paper. The solvent blank adapting stimulus was 30 μl of hexane. Test stimuli were the same as in the previous experiment and were puffed the same way into the adapting airstream as above.

RESULTS

Effects of Gossyplure Alcohol on Behavioral Responses to Gossyplure. As the total quantity of a 1:1 blend of (*Z*,*Z*)-7,11–16:OH and (*Z*,*E*)-7,11–16:OH (this blend will henceforth be referred to as gossyplure OH) was increased, there were several effects on the behavioral responses of males to 1000 ng of gossyplure (Table 1). The addition of 100 ng of gossyplure OH resulted in a sig-

TABLE 1. EFFECTS OF VARIOUS DOSES OF GOSSYPLURE OH ON BEHAVIORAL RESPONSES OF MALE *Pectinophora gossypiella* TO 1000 ng OF GOSSYPLURE (INITIAL SAMPLE SIZE FOR EACH TREATMENT WAS 100 MALES)

Treatment		Conditional probability of transition[a]					Mean latency of taking flight[b] (sec + SD)
Gossyplure (ng)	Gossyplure OH (ng)	S to WF	S to F	F to UWF	UWF to SC	S to SC[c]	
1000	0	0.69a	0.99a	0.47a	1.00a	0.47a	3.5 ± 2.3c
1000	10	0.53a	0.95ab	0.34ab	0.97a	0.31b	3.8 ± 3.2c
1000	100	0.17b	0.88b	0.19b	0.76b	0.13c	5.9 ± 5.2b
1000	1000	0.01c	0.29c	0.00c		0.00d	10.0 ± 8.5a

[a] Proportions in the same column are significantly different if they do not share a letter in common ($P < 0.05$; Ryan's multiple-comparison test for proportions. S = stationary; WF = wing fanning; F = flight; UWF = upwind flight in pheromone plume; SC = source contact.

[b] Time from introduction of the moth into the wind tunnel to initiation of flight. Mean latencies in the same column are significantly different if they do not share a letter in common ($P < 0.05$; analysis of variance followed by Duncan's multiple-range test).

[c] Probability of completing the entire behavioral sequence from stationary to contacting the source of pheromone.

nificant decrease in the probability that males would initiate wing fanning (S to WF) and flight (S to F). In addition, this quantity of gossyplure OH resulted in a significant decrease in the conditional probabilities of the transition from flight to upwind flight (F to UWF) and upwind flight to source contact (UWF to SC). A significant decrease in the overall behavioral sequence was noted even when only 10 ng of the alcohols were added to 1000 ng of gossyplure. When equal amounts of gossyplure and gossyplure OH were present on the cotton wick, no males completed the sequence of behaviors involved in location of a pheromone source. In addition to these effects on the behavioral transitions of mate location, the gossyplure OH affected the mean latency of taking flight; a significant increase in the latency was found at the 100-ng dose.

A constant amount of gossyplure OH (100 ng) added to wicks loaded with various quantities of gossyplure (1, 10, and 100 μg) resulted in a significant reduction in males landing at the source (SC) only at the lowest ratio of gossyplure to gossyplure OH (10:1) (Table 2). When the ratio was 100:1, the percentage of males contacting the pheromone source was reduced slightly, but not significantly.

Effect of (Z,Z)- *and* (Z,E)-*7,11-16:OH on Behavioral Responses to Gossyplure.* Gossyplure OH (100 ng) and one of its component isomers, (*Z,Z*)-7,11-16:OH (100 ng), were similarly effective in reducing the percentage of landing at the pheromone source in the wind tunnel. In contrast, (*Z*)-7-16:OH and (*Z,E*)-7,11-16:OH had no effect on this response at the same amount (Table 3). However, in another experiment, increasing the amount of (*Z,E*)-7,11-16:OH to 1000 ng resulted in a significant decrease in the percentage of males reaching the source (reduced from 46.7% to 13.3%; $N = 30$; $P < 0.05$). No males contacted the source when 1000 ng of (*Z,Z*)-7,11-16:OH was present (0%, not significantly different from 13.3%).

TABLE 2. EFFECT OF 100 ng OF GOSSYPLURE OH ON PERCENTAGE OF MALE *Pectinophora gossypiella* CONTACTING PHEROMONE SOURCE[a]

Gossyplure (μg)	Gossyplure OH (ng)	S to SC (%)[b]	Reduction (%)
1	0	58.8a	
1	100	35.0b	40.5
10	0	68.8a	
10	100	58.8a	14.5
100	0	76.3a	
100	100	75.0a	1.7

[a] 80 males/treatment. Percentages in the same column are significantly different if they do not share a letter in common [$P < 0.05$; Ryan's (1960) multiple-comparison test].
[b] Percentage of males that completed the entire behavioral sequence from stationary to contacting the source of pheromone.

TABLE 3. EFFECT OF (Z)-7-16:OH, (Z,E)-7,11-16:OH, (Z,Z)-7,11-16:OH, AND GOSSYPLURE OH ON PERCENTAGE OF MALE *Pectinophora gossypiella* CONTACTING A SOURCE OF PHEROMONE[a]

Gossyplure (ng)	16-Carbon alcohols	S to SC (%)[b]	Reduction (%)
1000		42.4a	
1000	(Z)-7-16:OH (100 ng)	41.2a	2.8
1000	(Z,E)-7,11-16:OH (100 ng)	43.5a	−2.6
1000	(Z,Z)-7,11-16:OH (100 ng)	21.2b	50.0
1000	Gossyplure OH (100 ng)	22.4b	47.2

[a] 85 males/treatment. Percentages in the same column are significantly different if they do not share a letter in common [$P < 0.05$; Ryan's (1960) multiple-comparison test].
[b] Percentage of males that completed the entire behavioral sequence from stationary to contacting the source of pheromone.

Effect of (Z,Z)-*7,11-16:OH and* (Z,E)-*7,11-16:OH on Behavioral Response to Blend Ratios of Pheromone.* The addition of 10 ng of (*Z,E*)-7,11-16:OH to a 30:70 blend of (*Z,Z*)-7,11-16:Ac and (*Z,E*)-7,11-16:Ac (1000 ng) resulted in a significant increase in the number of males contacting the pheromone source (Figure 1). The same quantity of (*Z,E*)-7,11-16:OH resulted in a significant decrease in the response to an 80:20 blend of (*Z,Z*)-7,11-16:Ac and (*Z,E*)-7,11-16:Ac and had no effect on the response to a 60:40 blend ratio. (*Z,Z*)-7,11-16:OH (at a 10-ng dose) did not significantly affect the response to any of the blend ratios of (*Z,Z*)-7,11-16:Ac and (*Z,E*)-7,11-16:Ac. The percentage of males contacting the pheromone source was significantly attenuated by 100 ng of (*Z,Z*)-7,11-16:OH at the 60:40 and 80:20 blend ratios of pheromone (Figure 1).

Electroantennogram. The adapting stimuli (*Z,Z*)-7,11-16:Ac or (*Z,E*)-7,11-16:Ac reduced the EAG amplitudes to puffs of either of these same isomers (Figure 2A). However, (*Z,Z*)-7,11-16:Ac diminished response to (*Z,Z*)-7,11-16:Ac more than it diminished the response to (*Z,E*)-7,11-16:Ac, as illustrated by the significant differences in the ratio of antennal response (*Z,Z*:*Z,E*). Similarly, the (*Z,E*)-7,11-16:Ac adapting stimulus diminished EAG responses to superimposed puffs of (*Z,E*)-7,11-16:Ac more than it reduced responses to puffs of (*Z,Z*)-7,11-16:Ac. This bias in the ratio of response was still significant 2 min after the adapting stimulus was turned off (Figure 2A).

When (*Z,Z*)-7,11-16:OH or (*Z,E*)-7,11-16:OH were used as adapting stimuli, the response to the acetate isomers was significantly diminished (Figure 2B). Again there seemed to be some specificity to this adaptation as evidenced by significant differences between the ratio of response to the acetates during

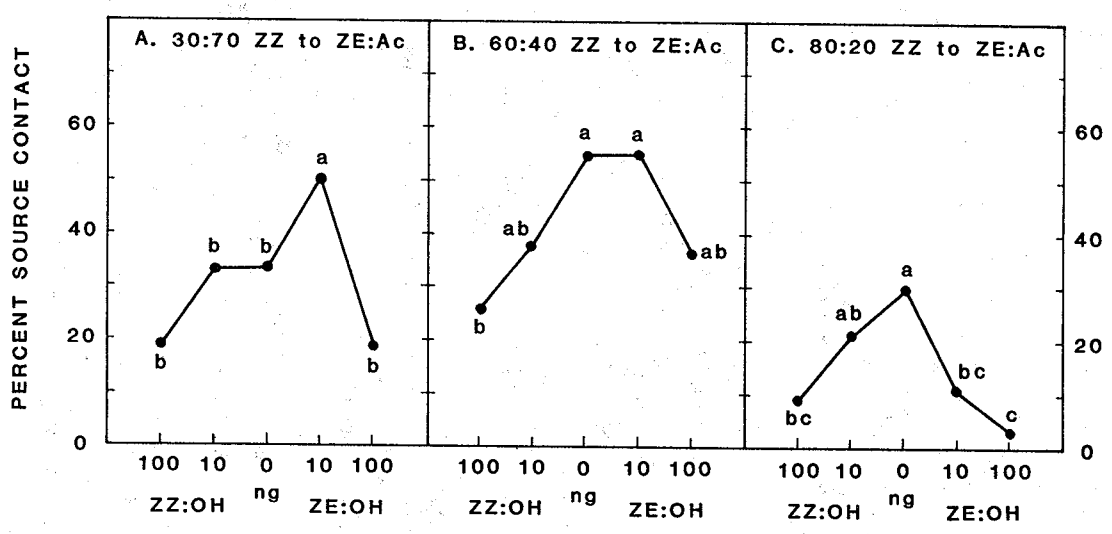

FIG. 1. Percentages of male *Pectinophora gossypiella* contacting a source (cotton dental wick) of three different blends of (*Z*,*Z*)-7,11–16:Ac (*Z*,*Z*:Ac) and (*Z*,*E*)-7,11–16:Ac (*Z*,*E*:Ac) (total 1 μg) when either (*Z*,*Z*)-7,11–16:OH (*Z*,*Z*:OH) or (*Z*,*E*)-7,11–16:OH (*Z*,*E*:OH) is added to the source. Percentages are significantly different if they do not share a letter in common [Ryan's (1960) multiple-comparison test].

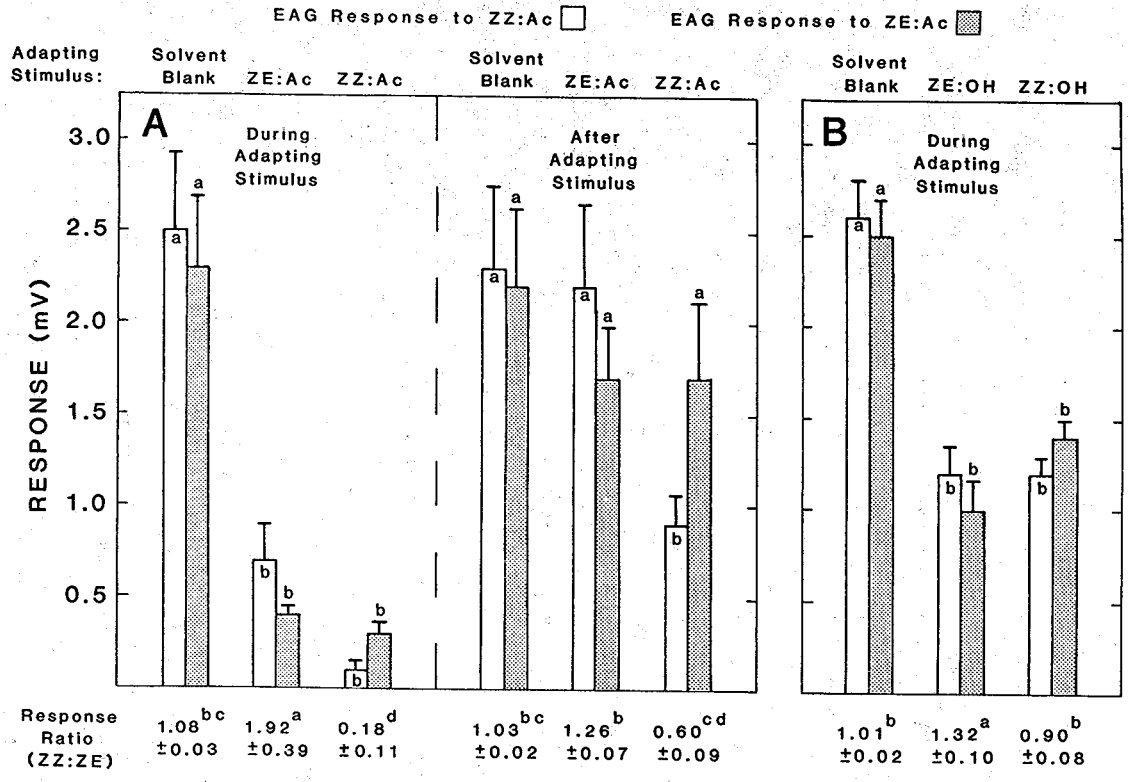

FIG. 2 (A) The electroantennogram responses of male *Pectinophora gossypiella* to (*Z*,*Z*)-7,11-16:Ac (*Z*,*Z*:Ac), and (*Z*,*E*)-7,11-16:Ac (*Z*,*E*:Ac) puffed concurrently (left) or after (right) a continuous adapting airstream containing either solvent blank, *Z*,*E*:Ac, or *Z*,*Z*:Ac. (B) Electroantennogram responses to *Z*,*Z*:Ac, and *Z*,*E*:Ac puffed concurrently with a continuous adapting airstream containing either solvent blank, (*Z*,*E*)-7,11-16:OH (*Z*,*E*:OH) or (*Z*,*Z*)-7,11-16:OH (*Z*,*Z*:OH). Vertical lines above bars indicate standard errors. Mean response ratios are shown ±SE. Mean EAG responses to the same puffed stimulus and mean response ratios within an experiment are significantly different if they do not share a letter in common ($P \leq 0.05$; Duncan's new multiple range test following ANOVA).

the (*Z*,*Z*)-7,11-16:OH adapting stimulus versus the (*Z*,*E*)-7,11-16:OH adapting stimulus.

DISCUSSION

Gossyplure OH effectively interferes with the normal sequence of behavioral responses observed when male *P. gossypiella* are stimulated by sex pheromone (Table 1). The negative effects are significant at each step in the sequence including the transition of upwind flight to source contact. This contrasts with reduced responses to off-ratios of the two acetate isomers, which most severely diminish the transition from flight to upwind flight without reducing the probability of the upwind flight to source contact transition (Linn and Roelofs, unpublished data). The cumulative effects of gossyplure OH on the behavioral responses at all stages account for the observations of Zhu et al (1983), who found that this alcohol blend interferes with the effectiveness of pheromone-baited traps. They observed that 2.5 μg of these alcohols in 30 μg of gossyplure resulted in a 97.6% reduction in trap catch of male *P. gossypiella* (0.5 μg of gossyplure OH reduced trap catch by 81.0%).

In other insects, "inhibitors" have been documented to have effects at specific stages in the behavioral sequence. For instance, (*Z*)-7-dodecenol, which decreases trap catch dramatically, does not eliminate upwind flight to pheromone in *Trichoplusia ni* (McLaughlin et al., 1974). In the gypsy moth, *Lymantria dispar*, the putative pheromone precursor found in the pheromone glands (2-methyl-*cis*-7-octadecene) actually stimulates "searching" behavior by males when it is dispersed in the environment, but reduces pheromone trap catch when volatilizing from a point source releasing disparlure (Cardé et al., 1973, 1975). Clearly the type of behavioral effect elicited by so-called inhibitors varies from species to species and from one compound to another.

The absolute amount of gossyplure OH is not as critical as its amount relative to gossyplure in determining the potential for behavioral interference. A large amount of gossyplure can overcome the negative effect of gossyplure OH. In addition, (*Z*,*Z*)-7,11-16:OH (*Z*,*Z*:OH) was more effective than (*Z*,*E*)-7,11-16:OH (*Z*,*Z*:OH) in interfering with the ability of male moths to locate a pheromone source in the wind tunnel, suggesting that the antagonistic effect of gossyplure OH may be largely due to *Z*,*Z*:OH. To explain these two findings, we propose that there are independent receptors for the two pheromone isomers, (*Z*,*Z*)-7,11-16:Ac (*Z*,*Z*:Ac) and (*Z*,*E*)-7,11-16:Ac (*Z*,*E*:Ac). Second, we suggest that *Z*,*Z*:OH and *Z*,*E*:OH interact more with receptor sites for their corresponding acetate isomers than with sites for the "opposite" isomers. Third, the interaction of alcohol molecules with acetate receptor sites interferes with the ability of those sites to produce optimal responses in the presence of the acetate isomers.

Our data provide much support for these hypotheses. If they are correct, then there should be a suboptimal blend of acetate isomers that is actually *improved* by the addition of a low dose of one of the alcohol isomers, because it interferes with the activity of the corresponding acetate. This increased response to an off-ratio should be eliminated at higher doses of that alcohol isomer. We observed precisely this pattern in response to a 30:70 blend of Z,Z and Z,E:Ac. The addition of 10 ng of Z,E:OH improved the overall response to this blend, and the improvement was eliminated at a higher dose of the alcohol. [The natural blend of Z,Z:Z,E:Ac is 61:39 according to Haynes et al. (1984), and Linn and Roelofs (unpublished data) have found the peak response of males is centered about a 60:40 and 65:35 blend ratio of Z,Z to Z,E:Ac.] Furthermore, as we expected, the addition of 10 ng of Z,E:OH to an 80:20 blend of Z,Z and Z,E:Ac resulted in a significant reduction in the response. However, we did not find a dose of Z,Z:OH that improved the response to 80:20 blend, so our hypotheses were only partially supported by the behavioral data.

The EAG results were consistent with the existence of functionally different receptor sites for each acetate isomer. In our experiments, during adaptation, the EAG response was greater in response to a puff of the acetate isomer that was not used as the adapting stimulus. Tang et al. (1980) have also postulated the presence of independent receptor sites based on an EAG study. Since both alcohols have a detrimental effect on the EAG response to both acetates, it is possible that their observed negative effect on behavior is a general, not a specific one. However, behavioral results (Figure 1) indicate that there is some independent activity of the two alcohol isomers. This independence is also seen at the receptor site level in the small but significant differences in the ratio of acetate response amplitude during adaptation with alcohols. Thus it appears plausible that the negative behavioral effects of the gossyplure alcohols are caused by an interaction of the alcohols with the acetate receptor sites, thereby reducing optimal binding with the acetates.

There are many reports of pheromone-related compounds that can interfere with the behavioral responses of male moths to sex pheromone (see references in Beevor and Campion, 1979; Cardé, 1976; Roelofs and Cardé, 1977). Unfortunately, most of the time we must infer the types of behavioral effects that these pheromone analogs elicit, since usually their effectiveness has been documented only by measuring a reduction in the number of males caught in traps. Compounds that reduce attraction are often closely related in structure to a pheromone component, suggesting that they may be interacting (suboptimally) with the same receptor sites as the pheromone component (Arn et al., 1974; Cardé et al., 1973; Roelofs and Comeau, 1971). In contrast, some evidence suggests there may be independent receptor sites for some pheromone components and "inhibitors" (McLaughlin et al., 1974; Miller et al. 1977; O'Connell et al., 1983; Schneider et al., 1974, 1977). The putative presence of independent receptors for the pheromone and "inhibitors" suggests a functional rationale for

the behavioral inhibition, such as detection of pheromone components of other species (and thus reproductive isolation could be ensured, as suggested by Roelofs and Cardé, 1977) or elimination of behavioral responses to mated females. The latter hypothesis was tested and was not supported by Cardé et al. (1973) for disparlure's olefin precursor which interrupts the response of male gypsy moths to pheromone traps.

Our behavioral and EAG studies suggest that gossyplure OH has some potential as a behavioral disruptant, but this potential is limited relative to the synthetic pheromone. Bartell (1982) suggested several mechanisms which could explain communication disruption using synthetic pheromone, including: (1) adaptation or habituation; (2) "false trail following;" (3) inability of insects to distinguish pheromone plumes from an odor background; and (4) an "imbalance in the pattern of sensory input." Bartell (1982) included an additional category which broadly covered communication disruption with nonpheromone compounds. Clearly this latter category includes compounds that could operate through one or more of the four mechanisms mentioned above. In *P. gossypiella*, gossyplure OH reduces both activation and long-range orientation to sources of pheromone, and thus may have an advantage over some "inhibitors" of other species that only affect close-range orientation [e.g., (*Z*)-7-dodecenol for *T. ni*]. However, communication disruption with gossyplure OH may be limited because sensory adaptation to *Z,Z* or *Z,E*:OH was not as severe as adaptation to *Z,Z* or *Z,E*:Ac, suggesting that one of the mechanisms hypothesized to work in mating disruption (Bartell, 1982) may not be as effective with the alcohols as with the acetates. In addition, gossyplure OH could not serve as a "false trail," and thus another hypothetical mode of action of communication disruption would be limited.

Presumably, one could use just *Z,Z*:OH and stimulate an "imbalance in the pattern of sensory input" when male *P. gossypiella* perceived the pheromone blend released by a female and this alcohol simultaneously. However, because of the greater impact of the acetates on the EAG response, it would seem that using a single acetate to disrupt mating would be more effective in this respect if one's objective is this sensory imbalance. Flint and Merkle (1983, 1984) have already documented the potential for this "sensory imbalance" using just *Z,Z*:Ac to disrupt mating. In addition to the aforementioned limitation, gossyplure OH could not be used in "attracticide" or "bioirritant" approaches, since the "attracticide" formulation relies on responders contacting the odor source (which includes insecticide), and the "bioirritant" approach relies on increased movements of the target insect in fields sprayed with the volatile chemical and an insecticide, thus presumably increasing the probability that a male will pick up a lethal dose.

We are left with two major questions that can only be addressed through field tests: (1) Does the effectiveness of gossyplure OH in interfering with ori-

entation to a point source extend to the very different situation of mating disruption? (2) How effective is mating disruption with gossyplure OH (or only a single alcohol isomer) relative to mating disruption with gossyplure (or a single acetate isomer)? The practicality and biological potential for mating disruption with gossyplure OH rests on economic considerations and the answers to these questions.

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