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POTENTIAL FOR EVOLUTION OF RESISTANCE TO PHEROMONES: Interindividual and Interpopulational Variation in Chemical Communication System of Pink Bollworm Moth[1]

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Abstract—After an extensive examination of the release rates and blend ratios of pheromonal components emitted by field-collected female *Pectinophora gossypiella* (Saunders), we find no evidence of resistance to pheromones applied to cotton fields to disrupt mating. Females from fields with 3–5 years of exposure to disruptant pheromones as well as those from fields with only minimal exposure to disruptant pheromones emitted (*Z,Z*)-7,11-hexadecadienyl acetate at a rate of ca. 0.1 ng/min and (*Z,E*)-7,11-hexadecadienyl acetate at ca. 0.06 ng/min. The ratio of pheromonal components was much less variable than the measured emission rate and was centered about a 61:39 *Z,Z* to *Z,E* ratio. In contrast to the blend ratio emitted by females, the composition of the pheromonal blend used in monitoring populations and disrupting mating is centered about 50:50 *Z,Z* to *Z,E*. In general there was a remarkable consistency in the release rate and blend ratio among populations of females throughout southern California and those from a laboratory colony. It would appear that, although resistance to the *P. gossypiella* pheromone is still a very real possibility when it is used heavily in pest management as a mating disruptant, there are current agricultural practices and conditions which would hinder its development.

Key Words—Resistance, mating disruption, sex pheromone, (*Z,Z*)-7,11-hexadecadienyl acetate, (*Z,E*)-7,11-hexadecadienyl acetate, Lepidoptera, Gelechiidae, pink bollworm, *Pectinophora gossypiella*, cotton, pheromone collection.

[1] *Pectinophora gossypiella* (Saunders), Lepidoptera: Gelechiidae

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INTRODUCTION

Several years after the identification of the sex pheromone of the pink bollworm moth *Pectinophora gossypiella* (Saunders) as a 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; Bierl et al., 1974), a 1:1 blend of these isomers (gossyplure) became commercially available to cotton growers in the United States for mating disruption (Brooks et al., 1979). The efficacy of mating disruption using gossyplure to control of *P. gossypiella* was established by Gaston et al. (1977) and, on a larger scale, by Brooks et al. (1979). After the Environmental Protection Agency registered the pink bollworm mating disruptant, many growers in Arizona and California began using it for early-season control of this pest. Use of the disruptant grew, and now yearly over 100,000 acres receive at least one application of pheromone (C.C. Doane, personal communication). At this early stage in the use of disruptant pheromones it is important to establish the potential for evolution of resistance to synthetic pheromones.

Since there is a limited understanding of the mechanism(s) by which mating disruption works, it is difficult to anticipate all of the potential means for the development of resistance of pheromones. However, evolution of resistance to pheromones could include selection for an increase in the rate of pheromone emission and/or selection for a shift in the ratio of pheromone components with a concomitant "fine-tuning" of the response of males to the blend released by females. Interindividual variation in release rate or blend ratio may partly determine the potential for resistance to pheromones, since selection would operate on such variation. The development of an efficient system for quantifying the release rate and blend ratio of pheromonal components by Baker et al. (1981) allowed us to measure the interindividual and interpopulational variation in these aspects of chemical communication in *P. gossypiella*, a species that has been subject to commercial control with disruptant pheromones longer than any other species.

METHODS AND MATERIALS

Collection and Handling of Insects. Cotton bolls were collected during August, September, and October, 1982, from selected cotton fields in the three major cotton-producing valleys in southern California: Palo Verde, Imperial, and Coachella valleys. There was at least 100 km separating our sampling sites between these three valleys, and the valleys are separated by deserts and/or mountains. In each valley, fields were selected according to their history of use of mating disruptants. One group of fields had had no exposure or one year of exposure to disruptant pheromones (henceforth

called insecticide-treated fields). The other group had had 3–5 years of treatment with disruptant pheromones (henceforth called pheromone-treated fields). Only in Imperial Valley was it necessary to select insecticide-treated fields with one year of exposure to mating disruptants, since an abatement program requiring the application of disruptant pheromones in 1982 had been enacted by the growers.

Between 1000 and 3000 bolls were collected in each field (the actual number of bolls collected depended on estimates of the infestation level), and then bolls were transported back to Riverside, California, where they were stored in screened cages in a lathhouse. The screened cages consisted of stacks (two to five) of 76 × 122-cm hardware cloth trays (1.25 cm mesh) with 5-cm rims. Last-instar larvae dropped from the bolls onto a fine-mesh nylon screen attached 5 cm below each tray, and the larvae pupated in several layers of cheesecloth. Screening was wrapped around each stack of trays, ensuring isolation of populations from the various fields. Pupae were collected from these cages semiweekly and brought into the laboratory where they were separated according to sex. Female pupae from each field were placed in one-pint paper cartons with nylon screen lids and housed in an environmental cabinet (15:9 light–dark and temperature 25°C). Adult females were transferred daily to one-pint cartons and had access to 8% sugar water.

Laboratory *P. gossypiella* were reared in half-gallon cartons of shredded wheat germ diet described by Adkisson et al. (1960). The procedure for handling the laboratory-reared pupae and adults was identical to that followed for field-collected insects. The laboratory population orignated from insects collected before 1976 from fields in Coachella Valley.

Collection and Quantification of Pheromone. Pheromone was collected from individual female *P. gossypiella* following the procedures first described by Baker et al. (1981) and modified by Haynes et al. (1983). A 2- to 4-day-old female was cold-anesthetized between five and nine hours after the start of the scotophase which is the normal period of calling behavior under the specified laboratory conditions (Haynes, unpublished observations). The female's wings were folded back over her head and she was inserted abdomen-first into a 2.0-mm ID glass tube with a 0.5-mm (diam.) hole at the distal end. This hole was large enough to allow only the ovipositor and associated pheromone gland to emerge when a light pressure was applied to the female's head with a pipe cleaner. The glass tube was then inserted through a Teflon-coated GLC septum into the collector as described by Haynes et al. (1983). Volatiles emitted from the gland's surface were collected for 10 min (at ca. 25°C) onto ca. 10 mg of glass wool. An internal standard [either 3.0 ng of (*Z*)-7-hexadecenyl acetate or 5-hexadecynyl acetate] was added to the glass wool before the inside of the collector was rinsed with ca. 200 μl of CS_2. This volume of CS_2 was then reduced to ca. 6 μl under a nitrogen stream before it was pulled up into a 10-μl Hamilton syringe for injection onto the GLC column.

Analyses were made on a Varian 3700 gas chromatograph equipped with a hydrogen flame detector, a Hewlett-Packard 3380A integrator, a Honeywell Electronik 196 chart recorder, and a Silar 10C packed column (4 g of 10% Silar 10C on acid-washed 100–120 mesh Chromosorb W; glass column 3 m × 4 mm (OD); oven temperature 175°C; N_2 flow rate 30 ml/min). The heights of peaks corresponding to the internal standard and the two pheromone isomers were measured. The amount of each isomer was calculated from a standard curve relating peak heights to mass. These values were then corrected for recovery efficiency by standardizing the measurement relative to the internal standard (recovery efficiency averaged ca. 85%). Recovery efficiency includes loss of compounds at all steps of the work-up, including concentrating the sample under nitrogen. The collection efficiency of the device (adsorption and desorption of pheromone) is ca. 100% (Baker et al., 1981). The lower analytical limit of this system was ca. 0.1 ng (0.01 ng/min); less than 5% of all values fell below this limit (these were discarded from blend ratio data and averaged as 0 ng/min for release rate data).

RESULTS

Pheromone-Treated Vs. Insecticide-Treated Fields. There was no significant difference between the mean emission rate of pheromone by females from fields with different histories of exposure to disruptant pheromone. Females from pheromone-treated fields released (*Z,Z*)-7,11-16:Ac at a rate of 0.095 ± 0.0557 (SD) ng/min ($N = 252$), while those from insecticide-treated fields released 0.102 ± 0.0535 (SD) ng/min ($N = 156$) (Figure 1; no significant difference; $P > 0.05$; two-way analysis of variance). The mean emission rate of (*Z,E*)-7,11-16:Ac was consistently lower than that of (*Z,Z*)-7,11-16:Ac. There was also no significant difference in the emission rate of this *Z,E* isomer in a comparison between females from pheromone-treated fields [0.060 ± 0.0350 (SD) ng/min; $N = 238$] and those from insecticide-treated fields [0.063 ± 0.0338 (SD) ng/min; $N = 145$]. Thus, we could detect no evidence of resistance to pheromones involving a shift in the emission rate of pheromone.

The ratio of the two pheromonal components was not found to be significantly different ($P > 0.05$) in a comparison of females from pheromone-treated and insecticide-treated fields. Females from pheromone-treated fields released 61.7 ± 4.22 (SD) % (*Z,Z*)-7,11-16:Ac ($N = 218$), while females from insecticide-treated fields released 61.9 ± 5.02 % (*Z,Z*)-7,11-16:Ac ($N = 137$) [Figure 2; two-way analysis of variance was run on data transformed by arcsin $\sqrt{p}$, where p is the proportion of (*Z,Z*)-7,11-16:Ac in the two component blend]. Apparently, the use of disruptant pheromones had not resulted in a local evolutionary shift in the blend ratio.

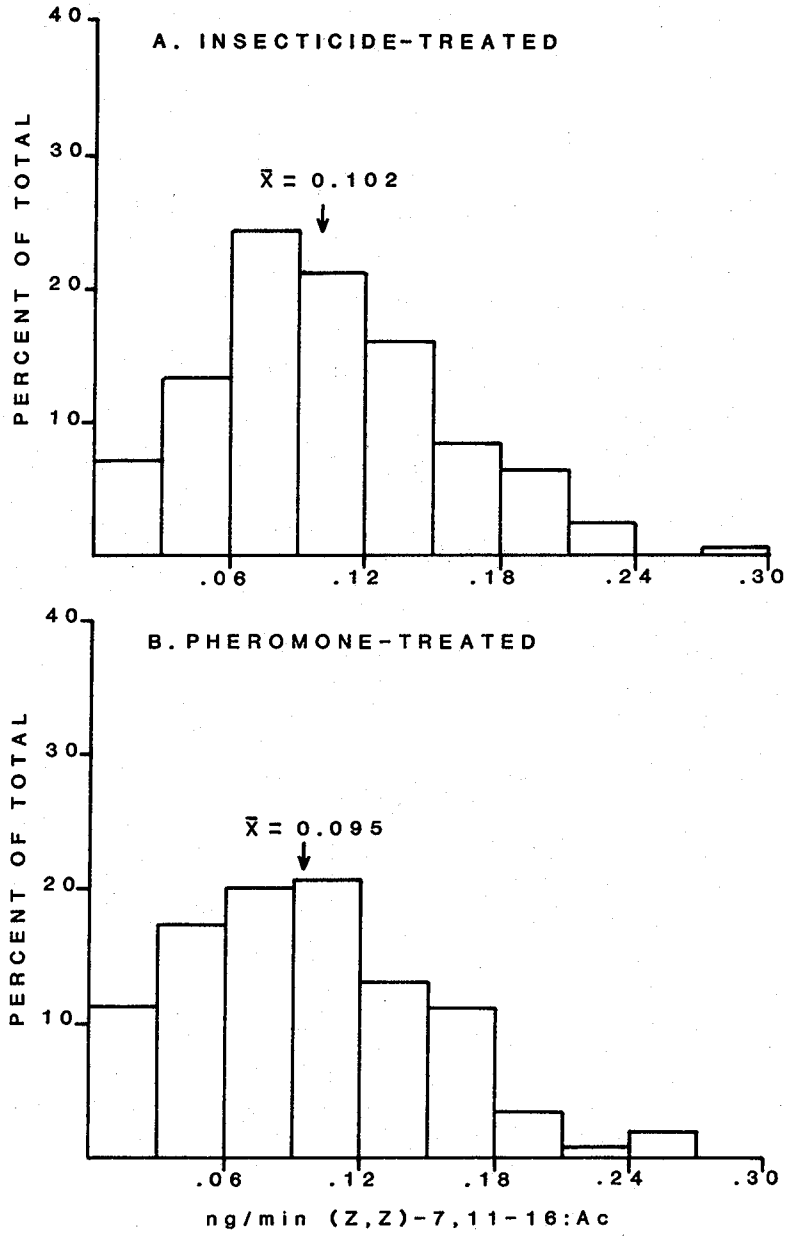

FIG. 1. Variation in emission rates of (*Z*,*Z*)-7,11-16:Ac from female *Pectinophora gossypiella* collected in cotton fields during 1982. (A) Females from insecticide-treated fields (1 year or less of disruptant pheromone treatments) had an average emission rate of 0.102 ± 0.0535 (SD) ng/min ($N = 156$). (B) Females from pheromone-treated fields (3–5 years of disruptant pheromone treatments) released 0.095 ± 0.0557 (SD) ng/min ($N = 252$). There was no significant difference between these samples ($P > 0.05$).

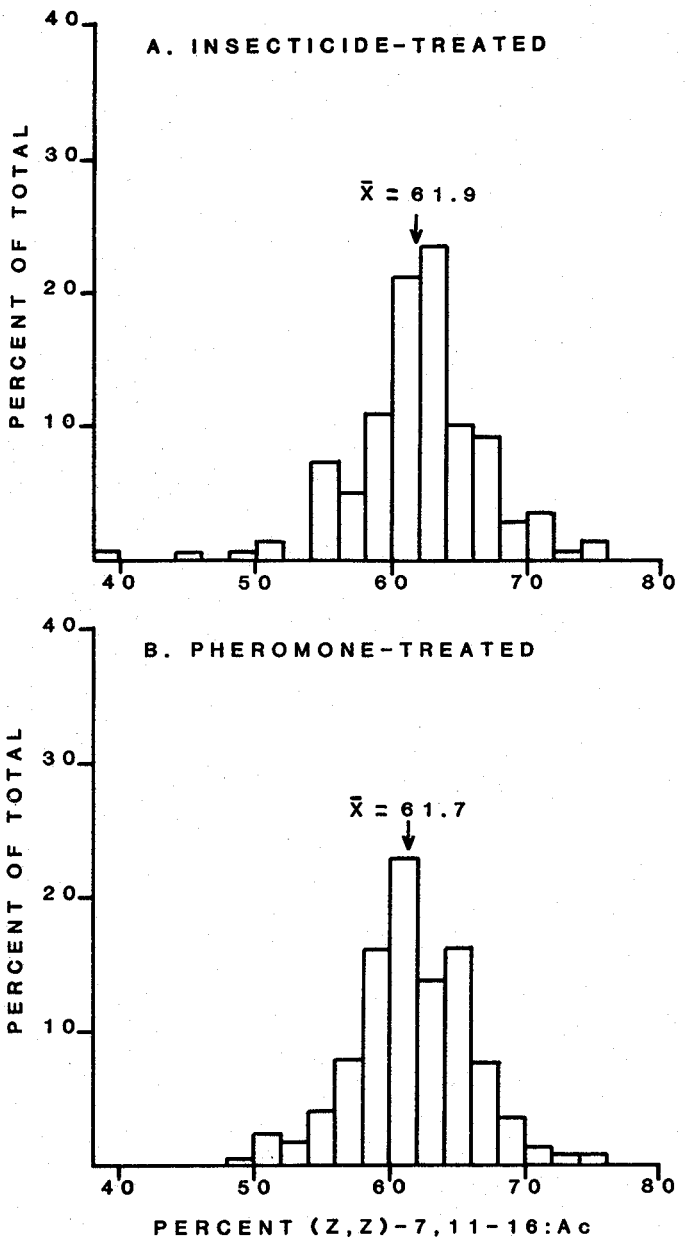

FIG. 2. Variation in the emitted blend ratios from female *Pectinophora gossypiella* collected in cotton fields during 1982. (A) Females from insecticide-treated fields (1 year or less of disruptant pheromone treatments) emitted 61.9 ± 5.02 (SD)% (*Z*,*Z*)-7,11-16:Ac ($N = 137$), while those from pheromone-treated fields (3–5 years of disruptant pheromone treatments) released 61.7 ± 4.22% (*Z*,*Z*)-7,11-16:Ac ($N = 218$). There was no significant difference between these samples ($P > 0.05$).

The similarities of pheromone emission rates and blend ratios by females from fields with different exposures to disruptant pheromones and from a laboratory colony are graphically illustrated in Figure 3. These plots of release rate of (*Z*,*E*)-7,11-16:Ac vs. (*Z*,*Z*)-7,11-16:Ac demonstrate that not only is there very little variation in the ratio of the two isomers, but also that the ratio is independent of release rate. The release rate of the two isomers is relatively more variable, but graphically the distribution of these values is similar in females from pheromone-treated and insecticide-treated fields, as well as in females from our laboratory colony. The similarity of the regression parameters quantifying the relationship between the emission rate of the two isomers demonstrates the consistency of these aspects of chemical communication in these three population samples of females (pheromone-treated fields: $y = 1.53x + 0.0050$, $r = 0.961$, $P < 0.001$; insecticide-treated fields: $y = 1.49x + 0.0092$, $r = 0.941$, $P < 0.001$; laboratory colony, $y = 1.59x - 0.0010$, $r = 0.975$, $P < 0.001$).

Comparison of Populations from Three California Valleys and Laboratory. The consistency of the emission rate of (*Z*,*Z*)-7,11-16:Ac between females from pheromone-treated and insecticide-treated fields was also found in a comparison between populations from the three cotton-producing valleys of southern California and our laboratory colony (Figure 4). There were no significant differences between females from these populations in the release rate of (*Z*,*E*)-7,11-16:Ac [one-way analysis of variance, $P > 0.05$; Palo Verde Valley, 0.062 ± 0.0352 (SD) ($N = 209$); Imperial Valley, 0.062 ± 0.0351 (SD) ($N = 127$); Coachella Valley, 0.056 ± 0.0303 (SD) ($N = 47$); and laboratory, 0.059 ± 0.0298 ng/min (SD) ($N = 51$)]. The percent of (*Z*,*Z*)-7,11-16:Ac in the pheromone blend was significantly different between females from Coachella [60.1 ± 4.17 (SD) ($N = 45$)] and those from Imperial [62.1 ± 5.41 (SD) ($N = 118$)] or Palo Verde Valleys [61.9 ± 3.95 (SD) ($N = 92$)], but there were no other differences (Figure 5; one-way analysis of variance on arcsine $\sqrt{p}$ transformed data; means separated by Duncan's multiple range test). The blend ratio released by females from our laboratory colony [60.7 ± 3.76 (SD)% ($N = 51$)] was not significantly different from that emitted by females from any of the valleys.

DISCUSSION

Selection for an increase in the emission rate of pheromone by females would be perhaps the most straightforward route to resistance in *P. gossypiella*, since it would not necessarily involve a concomitant shift in the males' behavioral threshold. Doane and Brooks (1981), in an experiment designed to test the effect of increasing release rates of pheromone from a hollow-fiber delivery system in pheromone-treated and untreated fields, demonstrated that in pheromone-treated fields such an increase resulted in the cap-

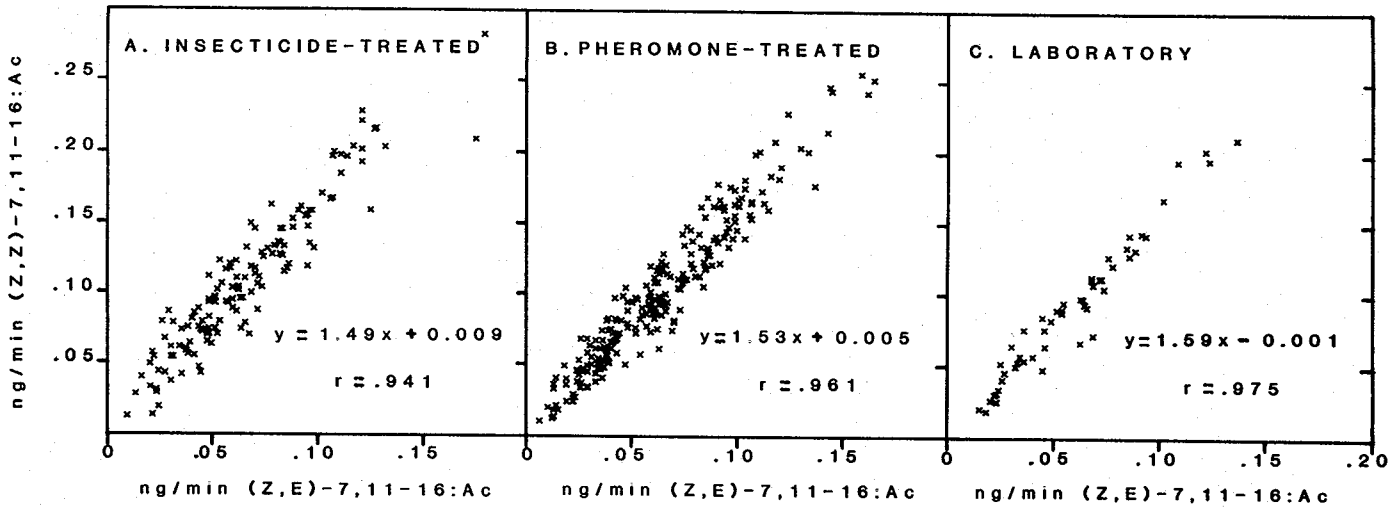

FIG. 3. Emission rate of (*Z*,*E*)-7,11-16:Ac vs. (*Z*,*Z*)-7,11-16:Ac from three samples of female *Pectinophora gossypiella:* (A) insecticide-treated field ($N = 137$), (B) pheromone-treated fields ($N = 218$), and (C) a laboratory colony ($N = 51$). These graphs illustrate the consistency of the emission rate and blend ratio in these three samples of females. The highly significant ($P < 0.001$) correlation coefficients (r) illustrate the tight control over the emitted blend ratio in this species.

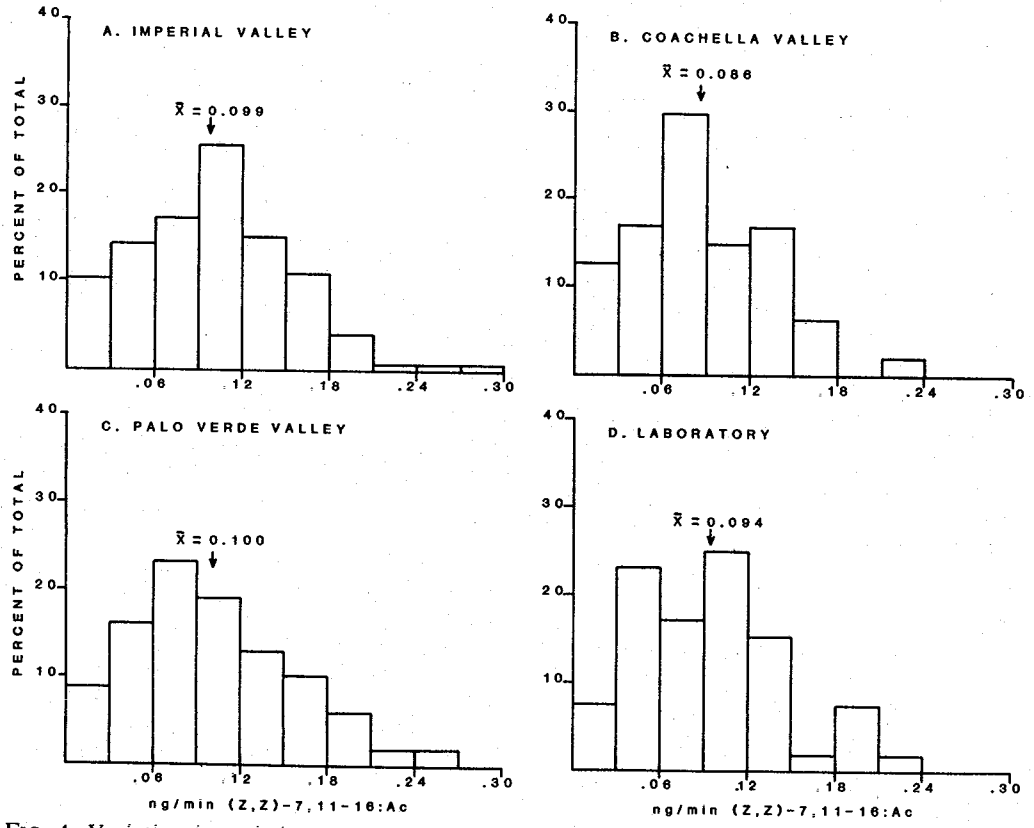

FIG. 4. Variation in emission rates of (*Z*,*Z*)-7,11-16:Ac by female *Pectinophora gossypiella* from the three cotton-growing valleys of southern California and from a laboratory colony. The mean emission rates for these four populations was: (A) Imperial Valley, 0.099 ± 0.0544 (SD), $N = 145$; (B) Coachella Valley, 0.086 ± 0.0498 (SD), $N = 47$; (C) Palo Verde Valley, 0.100 ± 0.0562 (SD), $N = 216$; and (D) laboratory colony, 0.094 ± 0.0498 (SD), $n = 52$. There were no significant differences between any of these means ($P > 0.05$).

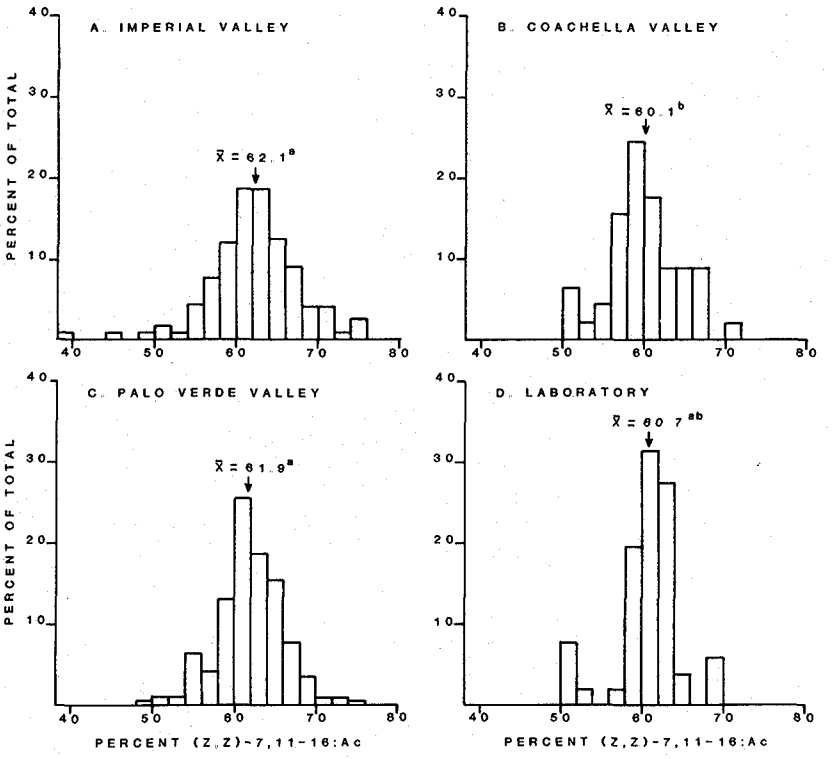

FIG. 5. Variation in the emitted blend ratio from female *Pectinophora gossypiella* from the three cotton-growing valleys of southern California and from a laboratory colony. The mean percent (*Z*,*Z*)-7,11-16:Ac for these four populations was: (A) Imperial Valley, 62.1 ± 5.41 (SD), $N = 118$; (B) Coachella Valley, 60.1 ± 4.17 (SD), $N = 45$; (C) Palo Verde Valley, 61.9 ± 3.95 (SD), $N = 192$; and (D) laboratory colony, 60.7 ± 3.76 (SD), $N = 51$. Means followed by the same letter are not significantly different ($P > 0.05$).

ture of more males in traps. In untreated fields, trap catch did not increase over the entire range of release rates tested, but an upper threshold, above which trap catches would drop off, was not reached. Thus it is clear that males are already capable of responding to a very high emission rate of pheromone and that, within pheromone-treated fields, there would be a selective advantage for females to release more pheromone.

Relatively good analogies to resistance to pheromones are found in examples of reproductive isolation between species. In these cases selection may have favored divergence of communication systems once two related species have come into geographical contact (Dobzhansky, 1970). One hy-

pothesis is that the release rate of pheromone may play a critical role in reproductive isolation between certain species. In *Autographa californica* (Speyer) (the alfalfa looper) and *Trichoplusia ni* (Hübner) (the cabbage looper), there appears to be a difference in how they respond to concentration of the same pheromone component, (*Z*)-7-dodecenyl acetate. *A. californica* preferentially responds to a lower emission rate of pheromone than does *T. ni* (Kaae et al., 1973). It is possible that selection for differences in emission rate and response has minimized reproductive encounters between individuals of these two species. However, recent studies have shown that additional pheromonal components are involved in the communication system of *T. ni* (Bjostad et al., 1980) and additional components are implicated in the pheromonal blend of *A. californica* (Steck et al., 1979), so blend components may play a primary or contributory role to reproductive isolation.

The hypothesis that the blend ratio of pheromonal components may be involved in reproductive isolation of many species of moths suggests that evolutionary shifts in blend ratio may be an effective route to resistance to pheromones. Perhaps the most thorough study concerning the species specificity of pheromonal blends comes from the guild of tortricid moths that feeds on apples in New York (Cardé et al., 1977). In this case, closely related species are reproductively isolated from one another by their blends of pheromonal components. For instance, the pheromone of the fruit-tree leaf roller moth (*Archips argyrospilus*) is a blend of four chemical components: (*Z*)- and (*E*)-11-tetradecenyl acetate, (*Z*)-9-tetradecenyl acetate, and dodecyl acetate (Cardé et al., 1977). A sympatric species, *A. mortuanus*, is maximally attracted to the same four compounds, but only when the compounds are emitted in a different ratio. Roelofs and Brown (1982) cite many examples where the specificity of the sex pheromone blend of closely related tortricid moths involves different combinations or ratios of a restricted number of components. Analogously, the specificity of the communication channel in *P. gossypiella* could be ensured by selection for females that emit a blend ratio different from the disruptant pheromone and a parallel shift in the behavioral specificity of males.

Roelofs et al. (1984) have documented that it is possible to select for a change in the blend ratio of the redbanded leafroller moth, *Argyrotaenia velutinana* (Walker), in two ways. First, offspring of females with high blend ratios of (*E*)-11-tetradecenyl acetate to (*Z*)-11-tetradecenyl acetate tended to have higher than average *E* to *Z* blend ratios. Second, selecting males for mating that were attracted to an abnormally high percentage of (*E*)-11-tetradecenyl acetate generally resulted in female offspring with higher amounts of (*E*)-11-tetradecenyl acetate than their mothers. This pattern suggests genetic coupling or common genes involved in pheromonal perception in males and pheromonal release by females, a phenomenon which has been

found in the pheromone system of another moth, the European corn borer (*Ostrinia nubilalis* (Hübner) (Klun and Maini, 1979). A similar genetic coupling has been documented in acoustical communication of crickets (Hoy and Paul, 1973; Hoy et al., 1977). Involvement of genetic coupling in the control of the emitted pheromone blend and response specificity would make evolution of resistance to disruptant pheromones easier, since selection imposed on one sex could show immediate results in both sexes, and thus resistance would not involve a more complex two-step process.

Selection operates on the existing interindividual phenotypic variation and leads to a change in frequency of genotypes in subsequent generations. Thus, an understanding of the potential for evolution of resistance requires quantification of existing variation. Miller and Roelofs (1980), using glands rinsed with solvent, quantified the interindividual variation in the pheromonal blend of *A. velutinana*, the redbanded leafroller moth. Their report was the first published account of variation in the blend ratio between individual females and between laboratory and field populations. Our comparison between *P. gossypiella* populations from pheromone-treated fields and insecticide-treated fields revealed no difference between these populations of females in either mean emission rate of pheromone or mean ratio of pheromonal components. However, variation in these two aspects of chemical communication was documented. The percent (*Z*,*Z*)-7,11-16:Ac in all populations ranged from 39.4 to 74.7, and the release rate of (*Z*,*Z*)-7,11-16:Ac ranged from 0 to 0.283 ng/min. From our data, we cannot determine the genetic contribution to the measured variation, but such variability would be necessary to rapidly select for resistant phenotypes.

The data presented here suggest an alternative route to resistance to pheromones. Since the blend ratio released by females is centered about a 61:39 ratio of (*Z*,*Z*)- to (*Z*,*E*)-7,11-16:Ac and the blend ratio released by the commercially available disruptant pheromones is approximately 50:50, then resistance may be possible simply by selection for males with a fine-tuned response to the blend released by females. Flint et al. (1979) have documented that populations of males have a relatively broad response spectrum to blends of the *Z*,*Z* and *Z*,*E* isomers. This finding is supported by data collected by Linn (personal communication) and Haynes (unpublished data) in flight tunnels. However, as Cardé et al. (1976) pointed out for another species, populational variation in response could reflect both variation within and between individuals. If response phenotypes exist narrowly centered about the blend released by females, then use of disruptant pheromones of a different blend could rapidly lead to selection for this phenotype. Thus it is important to document the phenotypic variation in the response of males to determine the potential for resistance to disruptant pheromones.

There is some evidence from other species that indicates that small dif-

ferences in the ratio of pheromonal components, such as that between the females' release ratio and the release ratio from disruptant pheromone sources, can be sufficient to aid in reproductive isolation between species. For instance, Roelofs and Brown (1982) cite examples of sympatric leafroller moths that use well-defined blend ratios of (*Z*)-11-tetradecenyl acetate and (*E*)-11-tetradecenyl acetate including 97:3, 91:9, 60:40, 50:50, 33:67, 24:76, 15:85, and 12:88. However, additional components are used by some of these species.

The intensity, continuity, and "homogeneity" of selection pressure are important factors in determining the rate and potential for the development of resistance (Georghiou, 1983). Brooks et al. (1979) showed that gossyplure applied in a disruptant formulation decreased mating in *P. gossypiella* by 97% relative to control fields. The selection pressure on the chemical communication system would seem to be intense. However, cotton growers generally do not apply the disruptant pheromone throughout the growing season. In fact pheromone applications usually end in July in California, leaving two or three generations per year that are not exposed to disruptant pheromones. In addition, the use of disruptant pheromones has not been universally adopted by cotton growers or their pest-control advisors, and as a result, the use of these mating disruptants is patchy in the three cotton-growing valleys of southern California. (One exception was Imperial Valley in 1982, when a program requiring cotton growers to put on at least four applications of gossyplure was in effect.) The patchy nature of pheromone use allows gene flow between untreated and treated fields which could swamp the effect of the locally intense selection pressure. Both long- and short-range dispersal have been documented in this species by several authors (Bariola et al., 1973; Flint and Merkle, 1981; Stern, 1979). However, the relative contribution of this potential gene flow has not been documented. It appears that the disruptant pheromone of the pink bollworm moth is generally being used in a way that makes the evolution of resistance less likely.

The present study has focused on shifts in blend ratios and release rates as potential avenues to resistance to pheromone in *P. gossypiella*. However, there are a number of alternative means to resistance that have not been examined at this point. First, resistance could evolve through selection for males that spend less time in contact with each point source of pheromone, thereby increasing the probability that they will contact females. Second, an increase of flight activity in females between calling bouts could increase the probability of attracting a mate in fields with a high background level of pheromone. Third, there could be selection for females and males that disperse out of the cotton field to mate, with the females returning to oviposit (a behavior which has been observed in the European corn borer on corn by Showers et al., 1976). These hypotheses and a continued investigation of

shifts in emission rate and blend ratio from field-collected females are the central focus of our ongoing investigation into the potential for evolution of resistance to pheromone in the pink bollworm moth.

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