Beet Armyworm (Lepidoptera: Noctuidae) Adult and Larval Susceptibility to Three Insecticides in Managed Habitats and Relationship to Laboratory Selection for Resistance

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ABSTRACT A field bioassay that measures adult male susceptibility was used to document resistance to fenvalerate, permethrin, and methomyl in beet armyworm, *Spodoptera exigua* (Hübner), in California, Baja California Norte (Mexico), and Sinaloa (Mexico). At the LC_{50}, the highest levels of resistance (R) were typically found at sites in Monterey County, Calif. (resistance [R] ratio of 11 and 29 for fenvalerate and methomyl, respectively); Kern County, Calif. (R ratio of 10 and 19 for fenvalerate and methomyl, respectively), and the Del Fuerte and Guasave valleys of Sinaloa (R ratio of 22, 7, and 16 for fenvalerate, permethrin, and methomyl, respectively). Geographic and temporal variability in resistance followed this trend: overall variation among regions > variation among sampling dates at the same site within a region ≥ variation among sites in a region within three consecutive days. Concurrent with field bioassays, larval susceptibility was measured with topical application bioassays in the laboratory. Resistance was detected in larvae. Larval and adult susceptibility were significantly correlated for fenvalerate and methomyl ($r = -0.84$ and -0.78, respectively). Selection experiments with fenvalerate and methomyl on larvae confirmed potential for increases in resistance. For fenvalerate, adult susceptibility was similar to larval susceptibility in selection experiments, agreeing with the above adult–larval correlations. This correspondence was not apparent for methomyl.

KEY WORDS Insecta, *Spodoptera exigua*, pyrethroids, carbamate

VARIABLE RESPONSES of beet armyworm, *Spodoptera exigua* (Hübner), to insecticides occur in managed habitats. Although the variation could not be related to patterns of insecticide use in the field, Meinke & Ware (1978) detected variation in susceptibility to methomyl in three beet armyworm strains collected on cotton in Arizona in 1975. Yoshida & Parrella (1987) detected resistance to methomyl in beet armyworm collected from floricultural crops in Florida. They reported that the industry discontinued use of this insecticide because of control failures. Brewer & Trumble (1989) detected resistance to methomyl in beet armyworm collected from tomato in Orange County, Calif., in fall 1986; resistance levels declined fourfold by the following spring. Resistance to several pyrethroid insecticides also has been documented. Chaufaux & Ferron (1986) detected pyrethroid resistance in a Guatemalan strain. Use of fenvalerate as well as methomyl for control of beet armyworm in tomato in the Del Fuerte and Guasave valleys of Sinaloa, Mexico, has not been satisfactory (B.A.-R., unpublished data).

The pattern and potential for increases of resistance to commonly used carbamate and pyrethroid insecticides need to be clarified. In our study, a field bioassay that measures adult male susceptibility (Brewer & Trumble 1989) was used to document resistance to fenvalerate, permethrin, and methomyl in beet armyworm in California, Baja California Norte (Mexico), and Sinaloa (Mexico). Response to selection of the larval stage was measured to determine potential for increased resistance. Larval as well as adult susceptibility was measured during the field study and selection experiments because the expression of resistance mechanisms may differ in adults and larvae of Lepidoptera (Dittrich et al. 1980). Correlation of larval and adult susceptibility is needed to determine if use of an adult susceptibility test is applicable when the principal target of control is larvae. The field study sites were selected to reflect a wide range of use patterns of these insecticides; the laboratory studies were done to assess the resistance more critically.

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Materials and Methods

Field Monitoring of Adult Susceptibility. Beet armyworms were monitored for resistance to two pyrethroids—permethrin (94.3%; FMC Corporation, Philadelphia) and fenvalerate (94%; E.I. du Pont de Nemours & Company, Wilmington, Del.)—and a carbamate, methomyl (98%; Du Pont). Susceptibility of adult males to these insecticides was monitored in the field with technical insecticide mixed into the adhesive of pheromone traps (described by Brewer & Trumble [1989]). Serial dilutions of the pyrethroids in 9:1 hexane/ethanol and serial dilutions of methomyl in acetone were mixed separately into insect adhesive (Tanglefoot Company, Grand Rapids, Mich.). Addition of 1 ml of the appropriate dilutions per 100 g of adhesive yielded concentrations of 0, 10, 40, 80, 160, 320, 500, 1,000, and 4,000 μg (AI)/g of adhesive. Pyrethroid concentrations of 8,000 and 16,000 μg (AI)/g of adhesive were made by adding the insecticide directly to the adhesive and heating the mixture at 37°C for 10 min. Treated adhesive (5.5 g) was spread evenly onto pressed cardboard inserts (325 cm^2) coated with wax and cut to fit into the base of a pheromone trap (Pherocon 1C; Trece, Salinas, Calif.). The traps were baited with beet armyworm pheromone lure (Trece, Salinas, Calif.). At least seven concentrations of each insecticide, including a control (solvent only), were used in the pheromone traps for field bioassays. Each concentration was replicated with at least four traps.

Field bioassays were conducted as described by Brewer & Trumble (1989) in crops with different histories of insecticide use (Table 1). The pheromone traps were placed ≥20 m apart in a randomized complete block. All concentrations of an insecticide were represented within each block. Traps were placed in the field in the late afternoon; they were retrieved the next morning before the temperature increased above 21°C. The inserts were removed from the traps and held at 21 ± 2°C and ≥95% RH. If <90 insects were captured or the pooled number of moths from traps of a concentration was <20 for three or more concentrations, additional traps were placed in the field the following afternoon. However, traps were not set out for >3 consecutive days. Mortality data were collected 38–40 h after sunset on the day the traps were placed in the field. Therefore, moths were inspected between 0800 and 1100 hours (PST) the day after trap inserts were removed from the field. A moth was considered dead if no movement of wings, legs, or head occurred after one wing was lifted from the adhesive. Histories of insecticide use were provided by pest control advisors and growers. No inferences were made on the selection of insecticides. This monitoring study was intended to provide empirical data on resistance diversity in field populations.

Resistance of beet armyworm was monitored in nine regions (seven counties of central and southern California and two states in Mexico). Listed from north to south, the locations were three sites in Monterey, San Luis Obispo, Kern, and Ventura counties; one site in Riverside County; two sites in Orange County; one site in Imperial County and Colonia Guerrero, Baja California Norte (Mexico); and four sites in the Del Fuerte and Guasave valleys of Sinaloa (Mexico) (Fig. 1). Multiple sites within a region were separated by at least 5 km.

Mortality data from each concentration were pooled for probit analysis (POLO-PC; LeOra Software 1987). A field bioassay was omitted from analysis if control mortality was >15%, the number of insects caught was <90, or the pooled number of moths from traps of a concentration was <20 for three or more concentrations. Because field populations might be heterogenous in resistance, probit analysis would tend to yield low slopes (Hoskins 1960). Resultant LCs at the extreme end of the probit line (e.g., at LC_{90} or higher) would not adequately represent the resistant part of the population. Brent (1986) recommended reporting LC_{50}'s when monitoring for resistance in field populations. The value is a good measure that is widely understood and it can be measured relatively accurately compared with higher LCs. Any higher levels of resistance could be detected after isolation of the most resistance insects in the population (see *Selection Tests*). Therefore, LC_{50}'s (the best estimate on the probit line) were reported. Resistance (R) ratios were calculated as LC_{50} field population ÷ LC_{50} males of a laboratory reference (CA) strain. The CA strain has been maintained continuously in the laboratory without insecticide pressure since establishment from collections made at Orange County, Calif., in 1982. The susceptibility of this colony corresponded closely with that of a laboratory colony from the Western Cotton Research Laboratory (USDA–ARS, Phoenix, Ariz.) that had been continuously reared for 25 yr (Brewer & Trumble 1989).

Likelihood ratio tests for equality of response (LeOra Software 1987) were used to compare beet armyworm susceptibility with these insecticides among field bioassays. The comparisons for each insecticide were (1) all field bioassays among regions, (2) field bioassays among sampling dates in a region at the same site, and (3) field bioassays among sites in a region within three consecutive days.

Comparison of Adult and Larval Susceptibility. Strains were established in the laboratory to obtain larvae of uniform age for determining larval susceptibility. Field collections of egg masses and larvae were made on seven occasions at the same location of a field bioassay when collection and transportation to our laboratory were possible. At these times, at least 20 egg masses, 50 larvae, or both were collected at the field site. Eggs were surface sterilized with 10% formaldehyde for 5 min, rinsed with tap water for 10 min, and dried at room temperature. The rearing procedure de-

Table 1. Average frequency of fenvalerate, permethrin, and methomyl use at field monitoring sites during survey[a]

Region	Sites	Crops	Plantings per year	Insecticide	Applications per crop
Monterey	3	P, L, Ar	1, 2, yr	fen	0.5, 0.5, 3.5
				per	0.5, 3.5, 2.5
				met	0.5, 2.5, 2.5
San Luis Obispo	3	P, P, P	1, 1, 1	met	0.5, 0.5, 0.5
Kern	3	T, L, L	1, 1, 1	per	1, 0, 0
				met	1.5, 1, 1
				met + per	0, 7, 7
Ventura	3	T, T, T	1, 1, 1	met	3.5, 3.5, 3.5
Riverside	1	A	yr	none used	
Orange	2	T, T	1, 1	fen	5, 5
				fen + Bt	2, 2
Imperial[b]	1	T	1		
Baja California Norte	1	T	2	met	5, 5
				met + fen	7, 7
Sinaloa[c]	4	T, T, T, T	3, 3, 3, 3	fen	3, 3, 4, 3.5
				per	7, 13, 7, 19.5
				met	3, 5, 4, 3.5

a All applications were within label specifications. Sites, number of sites monitored. Crops: A, alfalfa; Ar, artichoke; L, lettuce; P, pepper; T, tomato. Plantings, yr indicates year round planting. Insecticide: fen, fenvalerate; per, permethrin; met, methomyl; Bt, *Bacillus thuringiensis* var. *kurstaki* (Berliner); insecticides separated by + indicate their use as a mixture. Applications, average number of applications of insecticide per crop. Commas in the Crops, Plantings, and Applications separate information for the different sites in respective sequence, A through D.

[b] Insecticide use reports were not obtained.

[c] Mixtures of two or three insecticides (carbamates, organophosphates, and pyrethroids) were used ≈65% of the time but were recorded as separate applications. Amount of insecticide per application was the same if used alone or in mixture.

scribed by Brewer & Trumble (1989) was used to establish the parent generation in this and subsequent tests.

To determine differences in larval susceptibility between field strains, 30 F_1 larvae were treated with the concentration of each insecticide that was estimated to give 50% kill. A Burkard microapplicator (Burkard, Rickmansworth, Herts, England) was used to deliver 0.5 μl to the thoracic dorsum of each third instar for this and subsequent topical bioassays. Larval weights were 3–5 ± 0.02 mg. The insecticides were diluted in acetone. Fifteen larvae from the CA strain were tested with the same concentration concurrent with each bioassay of a field strain. The concentrations were 0.1 μg of fenvalerate per insect, 0.025 μg of permethrin per insect, and 2.0 μg of methomyl per insect. These concentrations were average LC_{50}'s from probit analyses of earlier bioassays of field-collected larvae from Orange County in 1986 (M.J.B., unpublished data). After treatment, larvae were held individually in 30-ml plastic cups (filled with diet) at 27 ± 1°C and a photoperiod of 16:8 (L:D). Mortality was recorded 24 h after application. A larva was considered dead if it remained immobile for 15 s after being turned on its dorsum.

Comparisons of proportion of larvae killed with each insecticide for the field and CA strains were made with Ryan's (1960) multiple comparison test for proportions. The linear correlation coefficient, r, between these data and the LC_{50}'s of the corresponding field bioassay was calculated after arcsine square root transformation of the proportion data and logarithmic transformation of the LC_{50}'s.

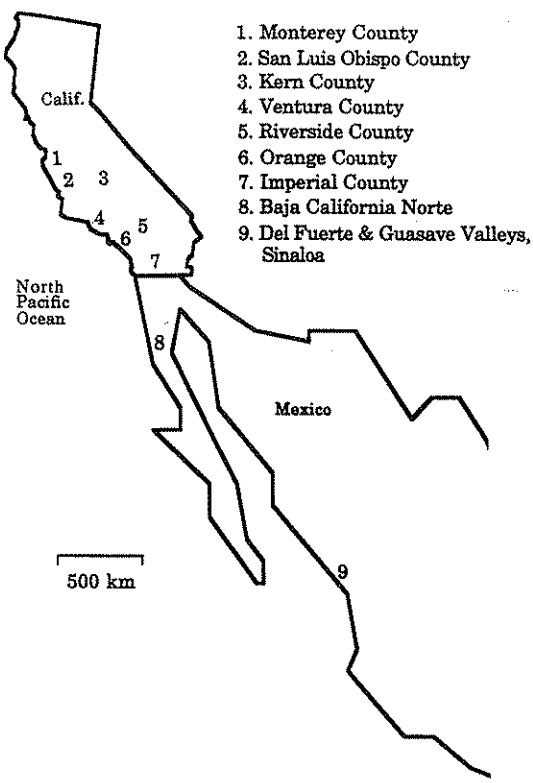

Fig. 1. Sampling regions for field monitoring for beet armyworm susceptibility to fenvalerate, permethrin, and methomyl.

A t test was used to determine if the correlations differed from $r = 0$ (Steel & Torrie 1980).

Selection Tests. Laboratory strains originating from the September 1987 Baja California Norte (BJ) and August 1987 Kern County (KN) collections were selected for enhanced levels of resistance. Fenvalerate and methomyl were used as the selective agents for the BJ and KN strains, respectively. The highest levels of resistance to these insecticides were detected in 1987 at these locations. For each strain, the total number of eggs from the parental strain was randomly divided into two subcolonies. Each T (treated) subcolony was selected with insecticide topically applied to third instars as described in the previous section. Survivors were reared to establish the next generation. The other subcolony was reared without selection and was labeled the C (control) strain. The colonies reared were fenvalerate-selected and unselected BJ larvae (BJ-T and BJ-C subcolonies, respectively) and methomyl-selected and unselected KN larvae (KN-T and KN-C subcolonies, respectively).

Selection concentrations were chosen from probit regressions from topical bioassays of ≥20 F_1 larvae per each of seven concentrations. These bioassays were done concurrently with the larval tests described in the previous section. The remaining F_1 larvae of the T strains were treated with the LC_{50} estimated by probit analysis. The concentration applied to larvae was increased in increments (listed below) through generation 19. At least 660 larvae were treated per selection. Selections were not done at generations 6, 11, 12, 15, and 16. The selection concentrations of fenvalerate on the BJ-T strain were 0.10 μg per F_1 larvae (LC_{50}); 0.16 μg per F_2 larvae (LC_{60}); 0.24 μg per F_3 larvae (LC_{70}); 0.38 μg per F_4 larvae (LC_{80}); 0.64 μg per F_5 and F_7 larvae (LC_{90}); 1.08 μg per F_8 and F_9 larvae (LC_{95}); 1.64 μg per F_{10}, F_{13}, and F_{14} larvae (LC_{97}); and 3.20 μg per F_{17}, F_{18}, and F_{19} larvae (LC_{99}). The selection concentrations of methomyl on the KN-T strain were 4.0 μg per F_1 larvae (LC_{50}); 4.88 μg per F_2 larvae (LC_{60}); 5.96 μg per F_3 larvae (LC_{70}); 7.29 μg per F_4 larvae (LC_{80}); 9.20 μg per F_5 larvae (LC_{90}); 11.62 μg per F_7 larvae (LC_{95}); 15.17 μg per F_8 larvae (LC_{98}); 22.34 μg per F_9 larvae ($LC_{99.5}$); 28.4 μg per F_{10}, F_{13}, F_{14}, F_{17}, and F_{18} larvae (LC_{99} times 1.5); and 37.8 μg per F_{19} larvae (LC_{99} times 2).

Progeny were tested for response to the selection regime with a topical application bioassay (larvae and 3-d-old males) and field bioassay (3-d-old males). Bioassays were done at generations 6, 11, 15, and 20; however, field bioassays at generation 15 and topical application and field bioassays with methomyl on males at generation 11 were not done. Topical application to males was done as described for larvae except 1.0 μl was applied on the thorax. Adult weights were 30–50 mg. For the field bioassay, males were attached to the adhesive by hand (Brewer & Trumble 1989). Six to nine concentrations that caused mortality between 5 and 95% were used in each bioassay. Each bioassay was replicated three times with at least 20 insects tested per concentration. Toxicity to larvae and males was determined with topical application bioassays for direct comparison of larval and adult susceptibility on a body weight basis (μg toxicant per g body weight). Toxicity to males also was determined in the field bioassay and compared with field data.

Results and Discussion

Field Monitoring of Adult Susceptibility. Ten field bioassays were omitted from analysis because control mortality was >15%. On six of these dates, hot, dry winds prevailed and traps were placed in young plantings, affording no protection from the dry wind. Placement of traps just within the plant canopy resulted in ≤10% control mortality in 73% of field bioassays analyzed. An average of 427 insects (range, 93–1,800) were analyzed per bioassay, with 82% of the bioassays consisting of >200 insects. The probit model adequately fit the data for the field bioassays in 71 of 85 tests (see χ^2 test results [Table 2]).

When the CA strain was compared with the field strains at the LC_{50}, the field strains were 2.4–22.5, 0.8–7.4, and 4.4–28.8 times less susceptible to fenvalerate, permethrin, and methomyl, respectively (Table 2). Comparing probit regression lines for each insecticide by the likelihood ratio test for equality (LeOra Software 1987), we detected significant variation among bioassays from all regions and dates ($\chi^2 = 380$, df = 56, $P < 0.001$ for bioassays with fenvalerate; $\chi^2 = 697$, df = 50, $P < 0.001$ for bioassays with permethrin; and $\chi^2 = 712$, df = 58, $P < 0.001$ for bioassays with methomyl). The R ratios typically were highest at sites in Monterey (fenvalerate and methomyl) and Kern counties (fenvalerate and methomyl), and Sinaloa (all three insecticides).

Variation within regions also was detected at many of the regions sampled (Table 3). Because multiple comparisons were made, the hypothesis of equality was rejected at $P \leq 0.01$ to ensure an overall rejection probability of about 0.05. Variation among sampling dates in a region (separated by ≥3 mo at site A) was detected in 11 of 20 comparisons (Table 3). Variation among these sampling dates was greater for resistance to fenvalerate (1.0–3.8-fold difference between the lowest and highest LC_{50}) than to methomyl (1.1–2.6-fold) or permethrin (1.1–2.4-fold). There was probably less variation in resistance among sites in a region (tested within 3 consecutive days of one another); variation was detected in 6 of 14 comparisons (Table 3). Variation among these sites did not differ between insecticides: fenvalerate (1.2–2.1-fold difference between the lowest and highest LC_{50}), permethrin (1.2–1.8-fold), and methomyl (1.1–2.0-fold). In summary, variability in resistance followed this trend: overall variation among regions > variation among sampling dates at site A within a region ≥

variation among sites in a region tested within 3 consecutive days.

Less variation would have been detected if paired comparisons of fiducial limits were made (two populations would be judged different in susceptibility if 95% FLs did not overlap), but the same trend in variation among regions, dates, and sites would be seen. The likelihood ratio test appears to be a more sensitive test. Savin et al. (1977) have documented its use in determining if populations of insects differ in susceptibility to an insecticide.

Comparison of Adult and Larval Susceptibility. Analyses of larval data showed that the CA strain was more susceptible ($P < 0.05$) than most field collections and arithmetically more susceptible in all cases (Table 4). Mortality of the field strains was 37–100%, 7–87%, and 9–52% lower than mortality of the CA strain treated with fenvalerate, permethrin, or methomyl, respectively.

After treatment with fenvalerate and methomyl, larval mortality was negatively correlated with LC_{50}'s of adults (Fig. 2). These correlations differed from $r = 0$ ($t = 4.49$ and 3.56; df = 6 and 5; $P < 0.01$ and 0.05 for fenvalerate and methomyl correlations, respectively). The significant correlations between larvae and adults for fenvalerate and methomyl supported use of the field bioassay as an indicator of resistance in larvae as well as adults. The correlation between larval and adult susceptibility to permethrin ($r = -0.20$) did not differ significantly from 0 ($t = 2.28$, df = 5, $P > 0.05$). This result was expected because a wide range of permethrin resistance was not detected in the field (Table 2). The only resistance level that differed greatly from the rest was not used in the permethrin correlation analysis because field bioassay data (Sinaloa, May 1988) were not analyzed because of high control mortality. If a broader range of resistance to permethrin is detected in the future, we expect the correlation of larvae and adult susceptibility to be similar to that found for the other pyrethroid, fenvalerate.

Selection Tests. When topical bioassays with fenvalerate were compared, larval and adult responses were similar after 20 generations for the BJ subcolonies (Fig. 3, top left). At the LD_{50}, resistance in BJ-C declined in larvae (3.3-fold from F_1 to F_{20}) and adults (2.8-fold from F_6 to F_{20}) (male susceptibility between generation 1 and 20 was not compared because bioassays were not done at generation 1). Resistance in larvae increased 8.3-fold from generation 1 to 20 for the selected subcolony; most shifts occurred within the first six generations. At generation 20, resistance of BJ-T larvae was 27.3 times higher than BJ-C larval resistance, and resistance of BJ-T males was 30.7 times higher than BJ-C male resistance. These resistance levels corresponded with R ratios of 64.2 and 52.8 for larvae and males, respectively, based on a comparison with the CA strain (Fig. 3). When field bioassays were compared, resistance of BJ-C males declined 1.3-fold from F_1 to F_{20}, whereas resistance of BJ-T males increased 2.9-fold from F_1 to F_{20} (Fig. 3). At generation 20, the R ratio of the BJ-T subcolony was 33.9 (Fig. 3). The highest R ratio detected in wild populations was 22.5 (Table 2).

These data suggest that resistance could increase if fenvalerate use is increased. The data also demonstrated that resistance to fenvalerate in males was associated with the pattern seen in larvae, even when selection pressure occurred in the larval stage. This pattern of expression in larvae and adults probably explains the success of our field bioassay with fenvalerate. Similarly, other tests that measure susceptibility of adult Lepidoptera to pyrethroids (e.g., Haynes et al. 1987, Plapp et al. 1987, Roush & Luttrell 1989) have successfully detected resistance.

Resistance of larvae to methomyl increased under selection pressure, but adults did not become more resistant. When topical bioassays with methomyl were compared, larval and adult responses differed after 20 generations for the KN subcolonies (Fig. 3, bottom left). At the LD_{50}, resistance in KN-C was stable in larvae (Fig. 3) and declined slightly in adult males (2.3-fold from F_6 to F_{20}) (male susceptibility between generation 1 and 20 was not compared because bioassays were not done at generation 1). Resistance in larvae increased 5.4-fold from generation 1 to 20 for the selected subcolony and actually declined slightly (1.2-fold from F_6 to F_{20}) for KN-T males. At generation 20, resistance of KN-T larvae was 4.0 times higher than KN-C larval resistance, but resistance of KN-T males differed little from KN-C male resistance. These resistance levels corresponded with R ratios of 22.7 and 1.1 for larvae and males, respectively, based on comparison with the CA strain (Fig. 3). Results of the field bioassay indicated that resistance of KN-C males declined 103.5-fold from F_1 to F_{20}, and resistance of KN-T males declined 64.7-fold from F_1 to F_{20} despite selection pressure on the larvae (Fig. 3). At generation 20, the susceptibility level of the KN-T subcolony was similar to that of the CA strain (R = 1.0) (Fig. 3).

These data suggest that selection of methomyl resistance in adults and larvae differed. Increased resistance was seen only in larvae in laboratory selections. When wild populations were tested (Fig. 2), adult and larval susceptibility to methomyl was correlated ($r = -0.78$). For this carbamate insecticide, resistance selected in larvae may not express itself in adults. But selection pressure on larvae and adults, such as may occur in agricultural fields, may lead to larval and adult resistance. Palazzo (1978) reported LD_{50}'s for methomyl between 200 and 280 μg/g body weight for *Trichoplusia ni* (Hübner) larvae and adults recently established in the laboratory. These LD_{50}'s were 26- and 50-fold greater than LD_{50}'s for adults and larvae, respectively, of a Louisiana State University laboratory culture. The data suggest adult resistance in *T. ni* increased under field selection although at a slower rate than larval resistance.

Table 2. Probit analysis of bioassays testing beet armyworm susceptibility to fenvalerate, permethrin, and methomyl

Region Site	Date	Fenvalerate				Permethrin				Methomyl			
		n	Slope ± SE	LC_{50} (95% FL)[b]	R[a]	*n*	Slope ± SE	LC_{50} (95% FL)[b]	R[a]	*n*	Slope ± SE	LC_{50} (95% FL)[b]	R[a]
Laboratory													
CA strain[a]		360	1.83 ± 0.30	95.6[c] (45–173)	—	339	2.39 ± 0.31	142.1[c] (113–173)	—	360	3.55 ± 0.92	11.5[c] (7–15)	—
Monterey													
A	Oct. 1988	533	1.76 ± 0.19	576[c] (268–1,093)	6.0	517	2.10 ± 0.25	258[c] (185–329)	1.8	—	—	—	—
B	Oct. 1988	217	0.97 ± 0.16	1,044[c] (430–8,599)	10.9	219	1.99 ± 0.22	311[c] (180–498)	2.2	199	1.54 ± 0.25	246[c] (91–434)	21.4
C	Oct. 1988	166	2.07 ± 0.48	696[c] (444–1,074)	7.3	202	1.97 ± 0.30	235[c] (96–422)	1.6	190	2.74 ± 0.70	331[cd]	28.8
San Luis Obispo													
A	Aug. 1987	284	1.59 ± 0.24	604[c] (297–964)	6.3	257	2.33 ± 0.24	275[c] (338–744)	1.9	295	2.11 ± 0.21	90[c] (52–137)	7.8
A	Aug. 1988	221	1.73 ± 0.23	479[c] (297–719)	5.0	243	3.46 ± 0.47	145[c] (119–172)	1.0	493	2.35 ± 0.21	119[c] (90–152)	10.4
B	Aug. 1988	—	—	—	—	281	2.65 ± 0.28	197 (93–374)	1.4	401	2.30 ± 0.20	105[c] (66–151)	9.1
C	Aug. 1988	—	—	—	—	135	2.03 ± 0.35	119[c] (67–196)	0.8	116	1.74 ± 0.38	51[c] (21–81)	4.4
Kern													
A	Aug. 1987	1,152	1.20 ± 0.97	577[c] (452–722)	6.0	1,006	2.81 ± 0.28	399 (191–568)	2.8	909	3.45 ± 0.29	219[c] (179–256)	19.0
A	Nov. 1987	264	0.92 ± 0.26	983[c] (266–2,514)	10.3	—	—	—	—	—	—	—	—
A	Nov. 1988	197	1.49 ± 0.23	259[d]	2.7	172	2.50 ± 0.54	212[c] (130–287)	1.5	155	2.51 ± 0.40	123[c] (37–225)	10.7
B	Nov. 1988	245	1.49 ± 0.16	547[c] (132–1,555)	5.7	202	3.43 ± 0.64	255[c] (195–316)	1.8	258	2.27 ± 0.32	126[c] (80–173)	11.0
C	Nov. 1988	604	1.28 ± 0.14	339 (90–689)	3.6	657	2.44 ± 0.26	232[c] (143–315)	1.6	531	1.79 ± 0.16	153[c] (99–212)	13.3
Ventura													
A	May 1987	281	1.37 ± 0.18	522[c] (282–851)	5.5	396	4.74 ± 1.74	322[cd]	2.3	257	1.92 ± 0.42	56[c] (23–88)	4.9
A	Sept. 1987	496	2.00 ± 0.27	691[c] (402–1,014)	7.2	590	3.18 ± 0.39	283[c] (210–352)	2.0	296	2.12 ± 0.33	51[c] (34–67)	4.4
A	Sept. 1988	577	1.43 ± 0.15	732 (204–1,694)	7.7	—	—	—	—	334	3.97 ± 0.74	87[c] (61–108)	7.6
B	Sept. 1988	447	1.56 ± 0.19	761[c] (438–1,289)	8.0	552	1.77 ± 0.17	209 (73–390)	1.5	431	2.58 ± 0.29	130[d]	11.3
C	Sept. 1988	548	1.62 ± 0.16	387[c] (236–589)	4.0	—	—	—	—	424	2.86 ± 0.49	67[c] (31–93)	5.8

Table 2. Continued

Region Site	Date	Fenvalerate				Permethrin				Methomyl			
		n	Slope ± SE	LC_{50} (95% FL)[b]	R[a]	*n*	Slope ± SE	LC_{50} (95% FL)[b]	R[a]	*n*	Slope ± SE	LC_{50} (95% FL)[b]	R[a]
Riverside													
A	May 1987	550	1.68 ± 0.12	292[c] (246–349)	3.0	396	2.84 ± 0.23	251[c] (220–289)	1.8	704	2.49 ± 0.25	55[c] (43–66)	4.8
A	Aug. 1987	391	1.14 ± 0.14	430[c] (284–612)	4.5	396	3.13 ± 0.50	282[c] (219–339)	2.0	265	2.80 ± 0.50	61[c] (42–78)	5.3
A	May 1988	165	1.22 ± 0.20	232[c] (82–459)	2.4	—	—	—	—	157	2.53 ± 0.37	57[c] (25–107)	5.0
Orange													
A	April 1987	351	1.63 ± 0.17	700 (402–1,239)	7.3	287	4.05 ± 0.63	351[c] (287–410)	2.5	252	2.85 ± 0.29	90[c] (75–107)	7.8
A	July 1987	225	1.43 ± 0.20	711[c] (334–1,272)	7.4	230	3.78 ± 0.42	534[c] (456–642)	3.8	247	2.64 ± 0.42	107[c] (38–168)	9.3
A	Oct. 1987	258	1.76 ± 0.35	719[c] (504–1,064)	7.5	227	2.09 ± 0.33	412[c] (295–552)	2.9	114	3.20 ± 0.61	118[c] (87–160)	10.3
A	April 1988	146	1.55 ± 0.23	352[c] (235–502)	3.7	—	—	—	—	93	2.10 ± 0.37	70[c] (26–130)	6.1
B	April 1988	232	1.29 ± 0.19	303[c] (189–446)	3.2	—	—	—	—	121	1.75 ± 0.34	65[cd]	5.6
Imperial													
A	June 1987	787	1.14 ± 0.21	505[c] (89–975)	5.3	747	1.67 ± 0.19	288 (90–497)	2.0	—	—	—	—
A	Oct. 1987	588	1.33 ± 0.14	495[c] (352–664)	5.2	564	2.88 ± 0.34	439[c] (355–520)	3.1	522	1.89 ± 0.19	60[c] (45–76)	5.2
Baja California Norte													
A	April 1987	1,800	2.10 ± 0.13	674[c] (607–746)	7.1	1,584	3.58 ± 0.22	380 (323–436)	2.7	1,528	2.96 ± 0.18	97 (78–117)	8.4
A	Sept. 1987	668	1.45 ± 0.18	1,129[c] (828–1,472)	11.8	1,051	2.28 ± 0.18	336[c] (284–389)	2.4	934	2.25 ± 0.24	64[c] (48–78)	5.6
Sinaloa													
A	May 1988	118	1.30 ± 0.22	2,147 (747–33,019)	22.5	—	—	—	—	158	2.23 ± 0.40	183[c]	15.9
B	March 1989	197	1.45 ± 0.28	863[c] (387–1,416)	9.0	276	1.59 ± 0.27	593[c] (353–880)	4.2	255	1.97 ± 0.38	116[c] (66–165)	10.1
C	March 1989	—	—	—	—	220	2.11 ± 0.78	1,051[cd]	7.4	232	1.78 ± 0.31	105 (11–261)	9.1
D	March 1989	—	—	—	—	515	2.25 ± 0.30	832[d]	5.9	849	2.22 ± 0.22	136 (52–222)	11.8

[a] Laboratory CA strain used as baseline susceptibility data; resistance ratios (R) = LC_{50} of test strain ÷ LC_{50} of laboratory CA strain.
[b] 95% fiducial limits of the LC_{50}.
[c] $P \geq 0.05$, χ^2 test of the hypothesis that the data do not differ from the probit model.
[d] Fiducial limits not reported because $g \geq 0.50$ (LeOra Software 1987).

Table 3. Likelihood ratio test for equality of response to fenvalerate, permethrin, and methomyl used to compare differences in bioassays among site and dates in a region

Region	Comparisons[a] sites(s); dates(s)	Fenvalerate		Permethrin		Methomyl	
		df	*P*	df	*P*	df	*P*
Monterey	all; Oct. 1988	4	0.00[b]	4	0.61	2	0.04
San Luis Obispo	A; all	2	0.38	2	0.00[b]	2	0.22
	all; Aug. 1988		—[c]	4	0.00[b]	4	0.01[b]
Kern	A; all	4	0.00[b]	2	0.00[b]	2	0.00[b]
	all; Nov. 1988	4	0.02	4	0.42	4	0.02
Ventura	A; all	4	0.04	2	0.53	4	0.00[b]
	all; Sept. 1988	4	0.00[b]		—[c]	4	0.00[b]
Riverside	A; all	4	0.00[b]	2	0.54	4	0.96
Orange	A; all	6	0.02	4	0.00[b]	6	0.02
	all; April 1988	2	0.62		—[c]	2	0.77
Imperial	A; all	2	0.51	2	0.00[b]		—[c]
Baja California Norte	A; all	2	0.00[b]	2	0.00[b]	2	0.00[b]
Sinaloa	all; March 1989		—[c]	4	0.01[b]	4	0.66

[a] The sites and dates specify the bioassays compared; all refers to all bioassays done at the specified site or date.
[b] Hypothesis of equality rejected, $P \leq 0.01$.
[c] Comparison not done because results of only one field bioassay were reported.

These results may be interpreted by proposing that expression of resistance in adults and larvae may differ between types of resistance (resistance mechanisms) (e.g., Dittrich et al. 1980, Plapp et al. 1987). Dittrich et al. (1980) reported that the major component of *Spodoptera littoralis* (Boisduval) resistance to monocrotophos was metabolic resistance (monooxygenases) in the larvae. Metabolic resistance was greatly reduced or absent in adults. They suggested that this characteristic may be a generalized trait of Lepidoptera. The poor correspondence of adult and larval resistance in our selection experiment was consistent with this report if methomyl selected for metabolic resistance in the larvae but not the adult. The correlation of adult and larval resistance seen in the field populations may be the result of nonmetabolic resistance in the adults and larvae. Once brought into the laboratory, this resistance may have regressed. These possibilities need to be substantiated with studies on the expression of known resistance mechanisms in different life stages. In our study, we relied on laboratory and field comparisons of larval and adult susceptibility to determine if an adult susceptibility test was appropriate for use when larvae were the target of control.

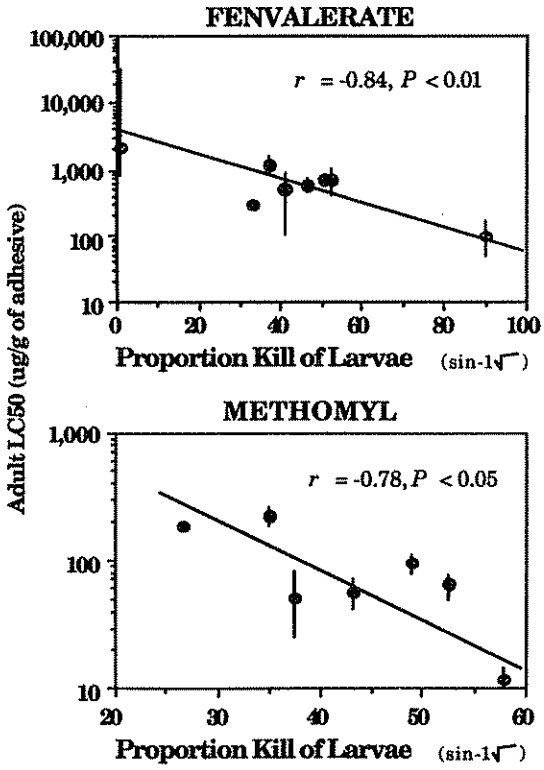

Fig. 2. Correlation of adult and larval susceptibility. Susceptibility estimated by LC_{50}'s from adult field bioassays (Table 2) and proportion kill of larvae (Table 4). Vertical bars are 95% FL of the LC_{50}. Data transformed by the logarithm (LC_{50}'s) and arcsine square root (proportion kill).

The field bioassay on beet armyworm adults appears adequate for detecting fenvalerate resistance. In contrast, we cannot ignore the possibility that the bioassay may underestimate methomyl resistance in larvae. To detect methomyl resistance, the larval susceptibility test is apparently more desirable than the field bioassay. If the necessary resources are unavailable to test larvae, we suggest that the field bioassay on adults is useful if a follow-up larval susceptibility test is done yearly or when any increase in resistance is detected. It should not be assumed that adult susceptibility tests can be universally adopted to detect resistance if larvae are the intended target of control.

Correspondence with Field Conditions. Variation among regions did not follow a directional (compass) trend (comparing data in Table 2 with location [Fig. 1]). Also, no apparent relationship

Table 4. Larval susceptibility of selected field strains and a laboratory reference (CA) strain of beet armyworm to fenvalerate, permethrin, and methomyl

Region	Site	Date	Proportion killed[a]		
			Fenvalerate	Permethrin	Methomyl
Kern	A	Aug. 1987	0.53bc	0.40bc	0.33ab
Ventura	A	Sept. 1987	0.63c	0.27bc	0.37abc
Riverside	A	May 1987	0.30b	0.20b	0.47abc
Imperial	A	June 1987	0.43bc	0.33bc	0.47abc
Baja California Norte	A	April 1987	0.60bc	0.80de	0.57abc
Baja California Norte	A	Sept. 1987	0.37bc	0.57cd	0.63bc
Sinaloa	—[b]	May 1988	0.00a	0.00a	0.20a
CA strain			1.00d	0.87e	0.72c

[a] Proportions in same column followed by same letter are not significantly different ($P > 0.05$; Ryan's [1960] multiple comparison test for proportions), based on 30 larvae per insecticide for each strain and 105 larvae for the CA strain. Concentration, 0.1 μg per insect for fenvalerate; 0.025 μg per insect for permethrin; and 2.0 μg per insect for methomyl.

[b] Insects collected near site C.

was detected between the crop grown and resistance (comparing data in Tables 1 and 2). However, insecticide use did correspond with resistance. Areas with the highest levels of resistance detected (Monterey and Kern counties and Sinaloa) had the heaviest amount of use of insecticides (Table 1). This relationship appeared to overshadow any migration or host plant effect.

Because resistance levels appeared to be mainly a consequence of insecticide use, comparisons of resistance levels and insect control among locations are valuable. In Sinaloa, an R ratio reported in 1988

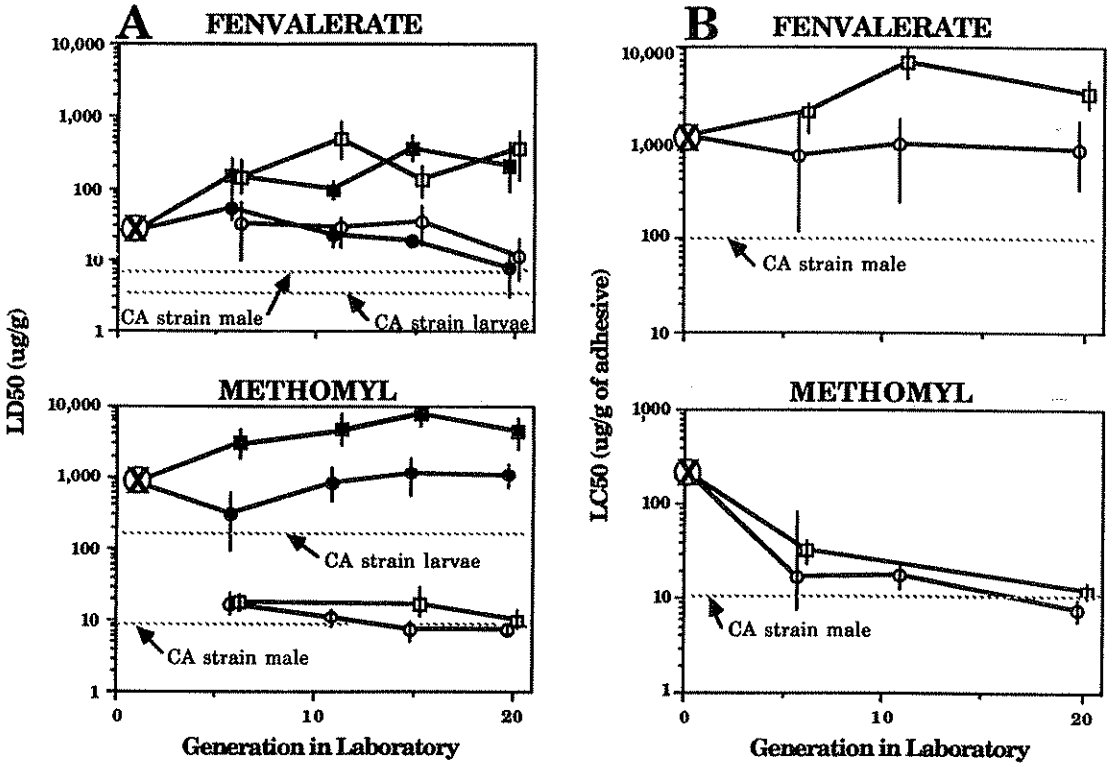

Fig. 3. Response of selected and nonselected strains as measured by topical bioassay (A) with larvae (—■—, selected strain and —●—, nonselected strain) and males (—□—, selected strain and —○—, nonselected strain) and by field bioassay (B) with males in the laboratory (—□—, selected strain and —○—, nonselected strain) over 20 generations. Separate selected and nonselected strains were maintained for fenvalerate (top graphs) and methomyl (bottom graphs) tests. The symbol ⊗ is the LD_{50} of F_1 larvae before the first selection (A) or the LC_{50}'s of males caught in pheromone traps in the field (B). LD_{50}'s, LC_{50}'s, and 95% FL (vertical bars) are offset slightly on the x-axis to allow discrimination between data. Dashed horizontal lines refer to larval or male susceptibility of a laboratory reference (CA) strain.

for methomyl (15.9) corresponded with known lack of control (B.A.-R., unpublished data) and high use rates (Table 1). Resistance to methomyl in Monterey (R ratios, 21.4–28.8) and Kern counties (R ratios, 10.7–19.0) should be of concern because the resistance levels are at or above those detected in Sinaloa.

For fenvalerate, an R ratio of 22.5 in 1988 in Sinaloa corresponded with lack of control with this insecticide (B.A.-R., unpublished data). Before 1987, fenvalerate was used about as frequently as permethrin. Currently, permethrin use predominates (Table 1). In Sinaloa, R ratios for permethrin were higher than in any other region in our study, and resistance to permethrin may reach levels similar to that of fenvalerate if this use pattern is continued. We do not recommend use of either pyrethroid at the current use rate of permethrin in Sinaloa. Resistance was substantially lower in other regions.

The geographic and temporal variation of beet armyworm resistance to these insecticides suggests that their use can be managed to avoid levels of resistance that result in economic crop loss. Adoption or continuation of resistance management strategies (Georghiou 1983) at Monterey and Kern counties, and Sinaloa should be considered to increase the possibility that these insecticides can be conserved (in Monterey and Kern counties) or reclaimed (in Sinaloa) as control agents. Moderation of the use of fenvalerate, permethrin, and methomyl (as is occurring in many of our monitoring sites [Table 1] through well-timed applications) appears to forestall development of higher degrees of resistance. Use of mixtures appear to prevent control failure in some areas of higher beet armyworm resistance (e.g., Monterey and Kern counties). In Sinaloa, where high resistance levels to multiple insecticides were detected, use of mixtures ≈65% of the time (Table 1) was not a successful strategy. Alternative insect pest and resistance management tactics are warranted in this region.

Our laboratory studies also suggest that resistance levels may become higher than those found in our field study if selection pressure with a single insecticide is increased. We recommend continued resistance monitoring in the regions where high resistance has been detected to determine if resistance decreases as alternative use patterns are practiced.

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