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CROSS AND MULTIPLE RESISTANCE AND SELECTION FOR RESPONSE TO INSECTICIDES BY BEET ARMYWORM STRAINS FROM MEXICO AND GUATEMALA

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Abstract

A selection regime was conducted with 14 insecticides against strains of the beet armyworm from Rio Bravo and Estacion Cuauhtemoc, Tamaulipas, Mexico, and Tiquisate, Guatemala for four to six generations from 1991 to 1992. Four classes of insecticides were tested, pyrethroids, organophosphorus, a carbamate and a pyrrole. The LD_{50s} value for resistance threshold to each insecticide was established at 20 µg/larva. For the Rio Bravo, Tiquisate and Estacion Cuauhtemoc strains resistance was indicated by 82%, 77% and 59% of the LD_{50s} values, respectively. Cross resistance was shown by the strain from Estacion Cuauhtemoc to fenvalerate and cypermethrin. Multiple resistance by the three strains was shown for the pyrethroids and anticholinesterase insecticides in 58% of the generations. The strains were susceptible to the cyclopropane pyrethroid bifenthrin, the organophosphorus insecticide profenofos and the pyrrole, chlorfenapyr.

Introduction

The beet armyworm, *Spodoptera exigua* (Hubner), is a pest of cotton and vegetable crops in Tamaulipas, Mexico and western Guatemala. No information has been found on response by any strain of this insect from Guatemala to insecticides tested here. In Mexico, there was both resistance and susceptibility to insecticides in 1991 and from 1993 to 1995 [Teran-Vargas et al. 1997, Teran-Vargas 1997 and Wolfenbarger et al. 1997). Avila and Lagunes-Tejada (1976) showed variation in toxicity of methyl parathion to the beet armyworm from different locations in Mexico. Toxicity of chlorfenapyr, a pyrrole, to this insect was shown in the subtropical Lower Rio Grande Valley of Tamaulipas, Mexico in 1995 [Sparks et al. 1996).

Resistance to fenvalerate, methomyl, methyl parathion and permethrin has been documented for all strains tested in FL, GA and Mexico (Wolfenbarger and Brewer 1993, Wolfenbarger et al. 1997 and Wolfenbarger and Wolfenbarger 2001). Neither resistance nor susceptibility has been exhibited in Guatemala. Biochemical and non-biochemical mechanisms have not been elucidated from insects in any of the locations shown here. Marketability of vegetable crops and cotton (no damage to foliage of crucifers and fruit of cotton, pepper and tomato) is adversely affected if resistance is present in the beet armyworm populations.

The objective of this experiment in the laboratory was to select for resistance to fenvalerate, esfenvalerate, permethrin, methomyl and methyl parathion, in four to six generations, in three strains from tropical and subtropical environments in Mexico and Guatemala. Selection could be used as a predictive tool if results were consistent. These insecticides are standard insecticides against lepidopteran pests of cotton and vegetables. Different insecticides were tested each generation. Resistance to an insecticide is indicated in the first generation. Larvae were assumed to be in a different field of one of the crops in the same area where each insecticide was applied. Selection regime described here is the treatment of available progeny emphasizing treatment of standard insecticides and other insecticides used for control of the beet armyworm and other insect pests. Each insecticide would indicate resistance or susceptibility which is indicated by the threshold LD_{50s} of 20 µg/larva. This value was arbitrarily selected for the insecticides of the four classes tested because the larval populations present each generation would be difficult to control if they exceeded the resistance threshold. Reversion to susceptibility by these insecticides was also determined. Multiple resistance is shown when there is resistance to insecticides in different classes. Cross resistance is shown when there is resistance to insecticides of the same class.

Materials and Methods

Technical fenvalerate, esfenvalerate and methomyl were obtained from DuPont, Inc., Wilmington, DE; chlorpyrifos from DOW, Inc., Midland, MI; fenpropathrin from Valent, Inc., Richmond, CA; methyl parathion from Cheminova, Agro., Lemvig, Denmark; bifenthrin, cypermethrin and permethrin from FMC, Inc., Princeton, NJ; chlofenapyr from American Cyanamid, Inc., Princeton, NJ; cyfluthrin from Bayer, Inc., Kansas City, KS; deltamethrin from Aventis, Inc., Research Triangle, NC; profenofos and *lambda* cyhalothrin from Syngenta, Inc., Richmond, CA. Classes of insecticides include pyrethroids, organophosphorus, a carbamate and a pyrrole.

At the three locations larvae (20 - 80/collection) of each strain were collected from cotton. In the laboratory in Weslaco larvae were maintained and reared to pupae on the same artificial diet each generation (Shaver and Raulston 1974). Diet was prepared within one to two d prior to placement of larvae.

Larval survivors of all doses of the insecticides tested each generation were combined for the next generation. In each generation15 to 30 female and male moths of each strain were placed in a 3.78 l plastic lined cardboard container and held for oviposition (Wolfenbarger and Brewer 1993). There were three to six egg hatches of each strain each generation. A generation is about 30 d. All moths of each strain were paired each generation as brothers-sisters. A 5% sucrose solution was included as food for the moths during their 6 to 18 day lifetime.

A neonate larva was placed in a 30 ml plastic cup containing 12 to 15 ml artificial diet. Larvae weighing 15 ± 6 mg were treated with insecticides formulated in 1 µl acetone. All insecticides were serially diluted (50%) from the greatest to lowest dose. Doses, as µg/larva, of chlorpyrifos (0.03875 to 25), chlorfenapyr (0.0975 to 2), bifenthrin, cyfluthrin, cypermethrin, deltamethrin and *lambda* cyhalothrin (0.00625 to 10), esfenvalerate and methomyl (0.195 to 100) fenpropathrin and fenvalerate (0.39 to 200), methyl parathion (0.01 to 100), permethrin (0.00775 to 200) and profenofos (0.0975 to 25) were used. All larvae of desired size of each strain were treated each generation. Untreated larvae were not used to correct for natural mortalities (nuclear and cytoplasmic polyhedrosis viruses). Low doses of an insecticide which killed <2% of the larvae were tested against each generation of each strain. This allowed us to maintain the selection regime.

Strains were tested for four to six generations/strain from February, 1991, to June, 1992. Resistance can be determined for any insecticide in four to six generations. Strains were collected from cotton grown in a field selected at random about five to 10 km from Estacion Cuauhtemoc, Tamaulipas, Mexico and Tiquisate, Guatemala which are tropical environments. Insects were collected from a field within 2 km of Rio Bravo, Tamaulipas, Mexico, a subtropical environment. One collection of 20 to 60 larvae of all sizes was made at each location.

Mortalities were determined after 72 h. Only larvae with no movement following probing were counted as dead. LD50 and 95% confidence interval (CI), as µg/larva, slope ± standard error (SE) and the total number of larvae treated with each insecticide were determined by probit analysis of SAS (1988). LD_{50s} for each strain determined each generation were ranked from greatest to lowest. Significant differences between LD_{50s} were indicated by non-overlapping confidence intervals. When the confidence interval was infinity their LD_{50s} overlapped confidence intervals of all other LD_{50s} of that strain that generation. Slopes < 1 are considered to be flat so heterozygosity or polygenic factors predominate in response to most of the insecticides. Where slope/SE ratios were < 1.96 the regression was not significantly different from zero. Non-significant regressions are shown because they represent a response to that insecticide in that generation. Mortalities are shown for the greatest dose tested. If doses exceeded the resistance threshold and mortalities were < 50% the strain was resistant.

Results

Rio Bravo, Tamaulipas

The strain from the subtropical area was selected for six generations from August to January, 1992 (Table 1); 23 regressions of pyrethroids and anticholinesterase insecticides were determined. Methomyl, bifenthrin, permethrin and permethrin were the most toxic in generations one - three and five. The strain showed resistance to methomyl and permethrin in generations one and three. The strain was resistant to methomyl in generation six. Selection for resistance was not indicated with any insecticide.

In generations one - three and five permethrin, fenvalerate, methyl parathion and fenvalerate were the least toxic, respectively. In all generations this strain was resistant to both methomyl and fenvalerate. Multiple resistance for the pyrethroids and anticholinesterase insecticides was shown in generations one and five.

Non-significant regressions were determined for fenvalerate (0.92 ± 0.51 for 30 larvae) and permethrin (0.43 ± 0.22 for 249 larvae) in generation three, methyl parathion (1.68 ± 0.94 for 25 larvae) in generation five and 0.99 ± 0.55 for 46 larvae, 0.8 ± 0.45 for 49 larvae and 0.57 ± 0.34 for 48 larvae by fenvalerate, permethrin and methyl parathion in generation six, respectively. At the greatest doses tested mortalities were 18%, 21%, 7%, 3%, 28% and 11% for fenvalerate, permethrin, methyl parathion, fenvalerate, permethrin and methyl parathion, respectively. The greatest dose tested was 200 µg/larva for fenvalerate and methyl parathion and 100 µg/larva for permethrin. The strain was resistant to these insecticides.

In generation one the strain was resistant to permethrin, but in generation five it was susceptible. This is reversion to susceptibility. The six generations of treating allowed us to determine the direction of response to an insecticide.

In generation two only one (14%) insecticide was resistant. With the threshold the most toxic insecticides were resistant in generations one and three. In generation six 75% of insecticides indicated a non-significant regression as was the single insecticide with a significant regression.

Slope values of all regressions ranged from 0.4 to 1.68. Most (57%) showed values < 1 which are flat regressions. The remainder ranged from 1-2.

In 1995, another strain from Rio Bravo showed resistance to methomyl, but showed susceptibility to chlorpyrifos (Sparks et al. 1996). With 2 μg chlorfenapyr/larva 35% of larvae of the Rio Bravo strain were killed. The strain was susceptible to chlorfenapyr because the maximum dose tested was less than the dose for the resistance threshold. In 1996 another strain from Rio Bravo showed only susceptibility (LD_{50}s < 20 μg/larva) to chlorpyrifos, cypermethrin, deltamethrin, methomyl, methyl parathion, permethrin and profenofos (Teran-Vargas et al. 1997). This is a reversal of the LD_{50}s shown here (Table 1).

Estacion Cuauhtemoc, Tamaulipas

The tropical strain was selected for four generations from March to June, 1992 (Table 2); 23 regressions were determined. Generations one through four were susceptible to methomyl, methomyl, chlorfenapyr and chlorfenapyr, respectively. These insecticides were the most toxic,. Selection for resistance was not indicated for any of the most toxic insecticides. LD LD_{50}s of methomyl steadily increased from generation one to three, but reverted to susceptibility in generation four. This response probably involves a polygenic mechanism. The LD LD_{50}s for chlorfenapyr in generations three and four were significantly lower than LD_{50}s for all the other insecticides.

Fenvalerate, fenvalerate, methomyl and fenvalerate were the least toxic, respectively, in generations one through four. No selection for resistance was indicted. Beet armyworms from this southern Tamaulipas, Mexico area were resistant to methomyl in generation three, but not in generations one, two and four. Resistance to fenvalerate was shown in generations two and four, but not generations one and three. Results indicate great variation, but confirm polygenic response to insecticides tested. Cross resistance to fenvalerate and cypermethrin was shown in generation four.

Non-significant regressions were determined for fenvalerate (0.72 ± 0.41 for 30 larvae) in generation one, bifenthrin (1.1 ± 0.66 for 88 larvae) in generation three and deltamethrin (0.3 ± 0.24 for 65 larvae) and fenpropathrin (-0.12 ± 0.29 for 69 larvae) in generation four. At the greatest dose tested mortalities were 29%, 52%, 37% and 13% for fenvalerate, bifenthrin, deltamethrin and fenpropathrin, respectively, in the generations above. Greatest doses tested were 200 μg/larvae for fenvalerate and fenpropathrin and 10 μg/larva for bifenthrin and deltamethrin. The strain was resistant to fenvalerate, deltamethrin and fenpropathern. The maximum dose of bifenthrin was less than the threshold. The mortalities were > 50% , so the strain was susceptible.

Slopes for all significant and non-significant regressions < 1, 1-2 and 2-3 were 52%, 39% and 9%, respectively. Most of the slopes were flat.

Strains of beet armyworm larvae from Estacion Cuauhtemoc in 1991, 1993 - 1995 were susceptible to chlorpyrifos, cypermethrin, deltamethrin, methomyl, methyl parathion, permethrin and profenofos (Teran-Vargas 1997 and Wolfenbarger et al. 1997). In 1993 the strain was resistant to azinphosmethyl and sulprofos. In 1992 [Table 1] the strain only showed resistance to methomyl in Rio Bravo in northern Tamaulipas [Table 1], while the strain showed both resistance and susceptibility in southern Tamaulipas [Table 2]. Susceptibility was shown in 75% of the generations.

Tiquisate, Guatemala

This location was the second tropical area (Table 3); 18 regressions were determined for four generations from February to June, 1992.

The strain showed resistance to an insecticide in each generation. This is the first report from Guatemala of resistance to an insecticide. In generations one through three methomyl, methomyl and chlorfenapyr were susceptible and the most toxic, respectively. LD_{50}s of methomyl nine, 12, and 53 μg/larva in generations one through three, which indicate selection for resistance. In generation four the strain was resistant to fenvalerate. Selection for resistance was not shown for the most toxic insecticides. Chlorfenapyr showed LD_{50}s < 1 against strains from southern Tamaulipas and Guatemala.

In generations one through four methyl parathion, methyl parathion, fenvalerate and fenvalerate were the least toxic insecticides, respectively. The strain was resistant to fenvalerate in generation three and four. Reversion by the strain to susceptibility to methyl parathion was shown. Multiple resistance among the two to three pyrethroid and anticholinesterase insecticides was shown in generations one and three.

Two non-significant regressions were determined; fenvalerate (0.067 ± 0.11 for 133 larvae) in generation one and *lambda* cyhalothrin (0.24 ± 0.17 for 132 larvae) in generation three. At 200 and 10 μg/larva, the greatest dose tested, mortalities were 29% and 41% for fenvalerate and *lambda* cyhalothrin, respectively, in indicated generations. The strain was resistant to fenvalerate, but was susceptible to *lambda* cyhalothrin.

Slopes for all significant and non-significant regressions for the Tiquisate strain were 76% and 24%, for those < 1 and 1-2, respectively. Most of the slopes were flat.

DOW-Zeneca Laboratory Reference Strain. This strain is considered to be susceptible to all insecticides. Sparks, et al. (1996), Wolfenbarger et al. (1997), Teran-Vargas (1997) and Wolfenbarger and Wolfenbarger (2001) showed LD_{50}s for bifenthrin, chlorpyrifos, chlorfenapyr, cyfluthrin, cypermethrin, deltamethrin, fenvalerate, *lambda* cyhalothrin, methomyl, methyl parathion, permethrin and profenofos of 0.0013, 0.48 and 0.00002, 0.0044, 0.18, 0.013 and 0.0021, 0.0034, 0.037, 0.0091, 0.00097 and < 5, 0.12 and < 5, 0.0086 and 0.00025 and 0.00029 µg/larva, respectively. All LD_{50}s were < 0.05 for pyrethroids and the pyrrole and < 1 for anticholinesterase insecticides against this susceptible strain except those shown by Sparks et al. (1996). None of the LD_{50}s for the field collected strains were less than any LD_{50}s shown for the reference strain.

Discussion

The Rio Bravo strain was resistant to fenvalerate, permethrin, methyl parathion and methomyl in generation one. The Estacion Cuauhtemoc strain was susceptible to fenvalerate and methomyl in generation one. The Tiquisate strain was resistant to methyl parathion and permethrin in generation one. The non-significant regressions shown here generally indicate resistance. Most of the slopes were flat; those < 1 ranged from 52% to 76% for 64 regressions. . Standard error of slope followed no trend for steep or flat slopes.

The flatness of the slopes indicate many factors are involved in response to these insecticides. Steepness of slope would probably be the best indicator of homozygosity.

Factors for resistance to the insecticides indicate they have to be polygenic. There may be two or more mechanisms which cause resistance to the different insecticides each generation. The next generation these mechanisms change because alleles for resistance are enhanced or lost. These changes were present in all three locations where the strains were collected. Cross and multiple resistance and susceptibility to these pyrethroid and anticholinesterase insecticides show the vagaries of resistance by these strains.

Differences in response to the seven cyclopropane pyrethroid insecticides by the three field-collected strains were extremely variable. Four or more were tested once and twice on the Rio Bravo, Estacion Cuauhtemoc and Tiquisate strains. All strains were susceptible to bifenthrin.

For the two non-cyclopropane pyrethroids it would be expected that the fully resolved isomer esfenvalerate would be more toxic than the mixed isomer fenvalerate, but this was not always shown by the three strains. In generation two of the Rio Bravo strain and generation four of the Estacion Cuauhtemoc strain LD_{50}s for esfenvalerate indicated susceptibility and were significantly less than shown for fenvalerate which was always resistant. In generation three the Tiquisate strain was resistant to both non-cyclopropane pyrethroids, but LD_{50}s of esfenvalerate were significantly less than shown for fenvalerate.

Differences in response to the four anticholinesterase insecticides were as variable as those for the pyrethroids.. Both resistance and susceptibility were shown for all the organophosphorus insecticides, except profenofos, in one or more generations among the three strains. All generations were susceptible to profenofos.

Comparison of response to any class of insecticide by the three field-collected strains and the susceptible strain was difficult because the LD_{50}s were so variable. LD_{50}s of the susceptible strain showed hundreds - fold difference to certain insecticides. Without the resistance threshold comparisons of the field collected strains would have been impossible.

The strain from Rio Bravo showed that 0%, 86%, 33%. 0%, 33% and 0%, were susceptible to all insecticides in generations one through six, respectively,. The strain from Estacion Cuauhtemoc showed that 100%. 0%, 86% and 75% were susceptible to all insecticides in generations one through four, respectively. The strain from Tiquisate showed that 33%, 50%, 50% and 0% were susceptible to all insecticides in generations one through four, respectively. All three strains were susceptible to one cyclopropane pyrethroid or one organophosphorus insecticide in most generations. Results show the extreme variation of response to these three classes of insecticides. It would not be possible to predict which insecticide would be toxic to any of the three strains in any generation.

Numbers of larvae treated by insecticides each generation were as variable as the LD_{50}s determined. In generation one of Rio Bravo, Estacion Cuauhtemoc and Tiquisate strains 725, 105 and 863 larvae were treated, respectively. These progeny were from adults reared from a single collection of larvae from the field. In the last generation of the same strains 233, 1448 and 417 larvae were treated, respectively. The brother-sister matings show reduced numbers of larvae in the last generation in 80% of the Rio Bravo and Tiquisate strains. The Estacion Cuauhtemoc strain showed more larvae in the last generation than in the first. Authors conclude that totals of larvae are the best estimate of fitness when insecticides are applied.

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Table 1. Toxicity of insecticides against beet armyworm for four generations, Rio Bravo, Tamaulipas, Mexico.

Insecticide	Number treated	Slope ± SE	LD_{50s} [µg/larva]	95% Confidence Interval
		Generation 1 -August 1991		
Permethrin	259	0.64 ± 0.16	99.86	36.54-1453.0
Methyl Parathion	206	0.98 ± 0.17	53.8	34.48-101.66
Methomyl	260	1.16 ± 0.24	32.93	16.47-97.2
		Generation 2-September 1991		
Fenvalerate	136	0.67 ± 0.26	172.06	77.53-8204
Lambda Cyhalothrin	144	0.91 ± 0.39	12.89	∞-∞
Esfenvalerate	250	0.7 ± 0.16	12.56	5.58-41.51
Chlorpyrifos	278	1.56 ± 0.38	10.01	4.47-25.45
Cypermethrin	340	0.84 ± 0.2	8.08	2.49-20.13
Profenofos	252	1.4 ± 0.18	7.24	5.4-9.95
Bifenthrin	139	0.89 ± 0.24	1.98	0.88-3.52
		Generation 3.-October, 1991		
Methyl parathion	72	1.02 ± 0.32	68.38	32.21-534.47
Methomyl	154	0.62 ± 0.17	32.16	14.4-187.34
		Generation 4-November 1991		
Fenvalerate	89	0.4 ± 0.18	291.92	∞-∞
		Generation 5 -December 1991		
Fenvalerate	122	0.54 ± 0.2	388.0	$115.86\text{-}1.06 \times 10^5$
Methomyl	100	0.9 ± 0.22	59.05	27.27-269.21
Permethrin	194	1.34 ± 0.24	5.1	2.21-9.67
		Generation 6 -January, 1992		
Methomyl	58	0.96 ± 0.34	55.25	20.61-3055.0

Table 2. Toxicity of insecticides against the beet armyworm for 4 generations, Estacion Cuauhtemoc, Tamaulipas, Mexico.

Insecticide	Number treated	Slope ± SE	LD_{50s} [μg/larva]	95% Confidence Interval
Generation 1 -March 1992				
Fenvalerate	39	0.72 ± 0.32	2.96	0.0054-13.3
Methomyl	36	0.76 ± 0.33	2.59	0.0089-6.65
Generation 2 -April, 1992				
Fenvalerate	75	2.36 ± 0.7	26.14	8.93-147.72
Methomyl	103	0.63 ± 0.2	15.77	5.95-260.25
Generation 3 -May, 1992				
Methomyl	207	0.89 ± 0.15	51.64	29.48-121.66
Profenofos	84	1.06 ± 0.29	9.05	4.27-56.66
Fenvalerate	132	1.74 ± 0.29	8.1	5.75-11.38
Methyl parathion	181	1.24 ± 0.29	6.85	3.1-20.39
Permethrin	216	0.96 ± 0.13	1.64	0.9-2.62
Cypermethrin	120	0.97 ± 0.15	1.23	0.58-2.35
Chlorfenapyr	141	1.91 ± 0.28	0.3	0.22-0.41
Generation 4 -June, 1992				
Fenvalerate	115	0.97 ± 0.35	59.11	33.19-436.31
Cypermethrin	78	0.59 ± 0.27	23.44	∞-∞
Methyl parathion	312	0.84 ± 0.19	17.26	7.45-91.6
Esfenvalerate	88	1.63 ± 0.36	15.4	9.84-26.71
Methomyl	196	1.07 ± 0.16	5.94	3.9-9.77
Permethrin	193	1.09 ± 0.19	0.98	0.43-1.91
Bifenthrin	77	1.67 ± 0.52	0.34	0.088-3.41
Chlorfenapyr	255	2.07 ± 0.39	0.17	0.083-0.26

Table 3. Toxicity of insecticides against beet armyworm larvae after four generations, Tiquisate, Guatemala.

Insecticide	Number treated	Slope ± SE	LD_{50s} [μg/larva]	95% Confidence Interval
Generation 1 -February, 1992				
Methyl parathion	158	0.64 ± 0.15	59.9	23-511.3
Permethrin	355	0.51 ± 0.16	50.6	17.3-1089.0
Methomyl	217	0.9 ± 0.15	8.9	4.9-14.1
Generation 2 -March, 1992				
Methyl parathion	158	0.54 ± 0.27	484.47	∞-∞
Methomyl	120	0.91 ± 0.17	11.69	6.24-25.15
Generation 3 -April, 1992				
Fenvalerate	183	0.7 ± 0.2	461.05	131-24744.0
Methomyl	285	0.52 ± 0.17	53.88	13.65-26866.0
Deltamethrin	203	0.45 ± 0.12	27.55	7-1291.0
Permethrin	287	1.32 ± 0.15	26.15	19.13-37.36
Esfenvalerate	119	1.44 ± 0.31	24.29	15.69-42.11
Methyl parathion	196	0.97 ± 0.2	17.48	8.1-61.1
Cypermethrin	83	0.59 ± 0.27	11.61	∞-∞
Bifenthrin	286	1.03 ± 0.14	2.98	2.02-4.88
Profenofos	96	1.41 ± 0.42	2.63	0.68-12.74
Chlorfenapyr	242	1.82 ± 0.2	0.31	0.24-0.39
Generation 4 -June, 1992				
Fenvalerate	121	0.94 ± 0.38	489.13	$143.86\text{-}3.4\times10^6$