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RESPONSE TO INSECTICIDES BY FOUR CROSSES OF BEET ARMYWORM (LEPIDOPTERA: NOCTUIDAE) STRAINS FROM NORTH AMERICA

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Abstract

Larvae from four crosses of three field collected strains of beet armyworm (*Spodoptera exigua* (Hubner)) (BAW) from FL and TX, United States of America (USA) and northern Tamaulipas, Mexico were treated with 14 insecticides for one, two and 10 generations. An LD_{50s} of 20 µg/larva was used as a resistance threshold to separate resistance from susceptibility. Cypermethrin showed selection for resistance in the cross of the three strains, while the other crosses and the three strain cross showed cross and multiple resistance and reversion to susceptibility. Susceptibility was shown to bifenthrin, chlorpyrifos, deltamethrin, zeta cypermethrin, fenpropathrin, *lambda* cyhalothrin and chlorphenapyr by the Alva x Donna and the Alva x Donna x Rio Bravo crosses. Crosses of strains of the BAW can be resistant to one insecticide one generation yet be susceptible to the same insecticide the next. Factors for resistance and susceptibility of these crosses have to be polygenic.

Introduction

Thousands of fields of cotton and vegetables are planted in the USA and Mexico each year. BAW can be a major pest in any of these fields any year. Populations were often difficult to control with the anticholinesterase insecticides, i.e. methomyl and methyl parathion, which are often used in these fields. Most of the populations in FL and GA, USA, were resistant, while populations in CA, USA, were susceptible [Wolfenbarger and Brewer 1993). Information on toxicity and efficacy of insecticides against this insect in Mexico was not extensive. Strains of the BAW were collected from flowers at Alva, FL (Wolfenbarger and Wolfenbarger 2001) and from peppers near Donna, TX, in the Lower Rio Grande Valley (LRGV) and from cotton near Rio Bravo, Tamaulipas, Mexico (Wolfenbarger and Wolfenbarger 2003).

The major objective was to determine selection for resistance and reversion to susceptibility to 15 insecticides of four classes by progeny of crosses of two and three strains. Four of these insecticides were used as standards in all the crosses. The crosses were selected with the same insecticides tested against the parental strains. The strains were crossed and maintained for one, two and 10 generations. Another objective was to determine cross and multiple resistance to the insecticides by each cross each generation. LD_{50s} of the crosses in the one and the two generations were compared to LD_{50s} of each parental strain to determine if the crosses were more, less or equally resistant to the strains. Slopes of each cross were evaluated for homozygosity and heterozygosity.

Materials and Methods

Technical of all insecticides was obtained from sources listed by Wolfenbarger and Brewer (1993) and Wolfenbarger and Wolfenbarger (2001). Insecticides were three organophosphorus, one carbamate, eight cyclopropane pyrethroids, two non-cyclopropane pyrethroids and a pyrrole. They were selected for various reasons. Bifenthrin, cyfluthrin, *lambda* cyhalothrin, zeta cypermethrin and profenofos were selected because no information has been found on their toxicity to larvae of this pest. Cypermethrin, chlorpyrifos, deltamethrin, esfenvalerate, fenvalerate, fenpropathrin and methyl parathion were selected because they are used on cotton and vegetable crops for control of this pest and other pests in the USA and Mexico. Chlorfenapyr was selected because it was shown to be toxic to this pest in the laboratory (Elzen 1996) and the field (Sparks et al. 1996).

The crosses tested were Alva x Donna, Alva x Rio Bravo, Donna x Rio Bravo and Alva x Donna x Rio Bravo. In the same month the LD_{50} of the cross was determined LD_{50s} of the parent strains were also determined. About 50% of available moths from strains were combined for generation one. The remaining 50% were used to maintain the selection regime of each strain. LD_{50s} for the three strain cross were compared to LD_{50s} of strains for the first four generations. All moths of the strains were included in the cross of the three strains by generation five.

Moths (16 to 30) were placed in a 3.78 L oviposition chamber with 5% sugar water for their six to 18 d lifetime. If more moths were available another chamber was used. The first cross was made July, 1991 and the last larvae of the three strain cross were treated January, 1994. Each generation, from egg to egg, was about 30 d.

There were three to eight hatches of various number of egg masses/generation of each cross. The egg masses, on plastic sheets on the top and sides of each oviposition chamber, were removed daily or every other d and held for larval eclosion. Egg masses from all chambers of each cross each generation were held in a container to insure that the progeny were only from the population of each cross. Hatches were held separately for each cross. Larvae were removed from each hatch daily and placed individually on larval diet (Shaver and Raulston 1974) in 30 ml plastic cups with cardboard caps [Wolfenbarger and Wolfenbarger 2001].

Larvae were selected by weight and treated. The desired weight for treating larvae is 15 ± 6 mg. All available larvae were treated every generation. This information indicates population sizes and fecundity of all females in the cross each generation. It is useful in evaluating the capability of females and the populations they produce as well as the males which mate with them. An untreated check was not used to estimate natural mortality each generation. Instead, a low dose of a different insecticide was used in certain generations of each cross to estimate natural mortalities (Wolfenbarger and Wolfenbarger 2001).

Larvae were treated with one µl of acetone containing a dose of insecticide (Wolfenbarger and Brewer 1993 and Wolfenbarger and Wolfenbarger 2001). Doses of all insecticides, from low to high as µg/larva, were applied to the dorsum of the thorax with bifenthrin lambda cyhalothrin, zeta cypermethrin and cyfluthrin (0.00775 to 100), chlorfenapyr (0.000775 to 2), cypermethrin (0.0775 to 800), deltamethrin (0.01 to 10), esfenvalerate and methomyl (0.195 to 100), fenvalerate (0.39 to 200), methyl parathion, chlorpyrifos and fenpropathrin (0.01 to 100), permethrin (0.00775 to 200) and profenofos (0.0975 to 25).

Mortalities were determined after 72 h. Probit analysis (SAS 1988) of dead and total treated larvae for each dose each generation was determined (Wolfenbarger and Brewer 1993 and Wolfenbarger and Wolfenbarger 2001). LD_{50}s, 95% confidence intervals (CI), as µg/larva, slope ± standard error (SE) and total larvae treated were determined. Equal LD_{50}s showed overlapping CIs. Non-overlapping CIs indicate significant differences between LD_{50}s. Regressions are not significant when the ratios of slope/SE is <1.96 because t_∞ at 0.05=1.96. They are offered because they represent a response by that insecticide. LD_{50}s were ranked from greatest to lowest each generation.

Slopes were also used to indicate homozygosity or heterozygosity of the indicated response. Slopes of all regressions <1 were considered to be flat and heterozygous. Flat slopes indicate multiple factors for the response to each insecticide. Fewer factors for resistance are expressed by homozygous strains or crosses. Slope values of > 3.0 are considered to be steep and therefore express homozygosity for response of each insecticide. Slope values of > 3.0 were arbitrarily selected to indicate homozygosity of that insecticide against that cross. All survivors of treated larvae of each generation were combined for the next generation.

The percentage of insecticides used on each cross that was susceptible each generation was determined by those with significant regression (shown by LD_{50}s of insecticides) and those with significant regression plus those with non-significant regressions. Resistance for a non-significant regression of each insecticide is shown by percentage mortality < 50% at doses >20 µg/larva.

An LD_{50}s >20 µg/larva for each insecticide was selected as a resistance threshold and used to separate resistance from susceptibility each generation (Wolfenbarger and Wolfenbarger 2001). The insect would be difficult to control in the field with applications of insecticides if LD_{50}s exceeded this threshold. Multiple resistance is indicated when insecticides of different classes had LD_{50}s which exceeded the threshold value the same generation.

Fitness of the crosses was estimated by the counts of larvae treated each generation. Results reflect the sum of all the factors that are involved in the size of the population of each cross in each generation.

Results and Discussion

Alva x Donna

The cross was maintained for two generations in July and August, 1991. In generations one and two methomyl and bifenthrin were the most toxic and methyl parathion and fenvalerate were the least toxic, respectively (Table 1). LD_{50}s of methyl parathion showed resistance in generation one and susceptibility in generation two. Methyl parathion and fenvalerate showed LD_{50}s >20 µg/larva both generations, thus the population exhibited multiple resistance. Cross resistance to fenvalerate and cypermethrin was also shown in generation two.

A non-significant regression was determined for *lambda* cyhalothrin in generation two; slope ± SE was 0.47 ± 0.36 for 63 larvae. The population was susceptible because the lowest dose tested (0.00775 µg/larva) killed 83% of the larvae.

Susceptibility was determined for 66% and 70% of insecticides tested in generations one and two, respectively, based on the LD_{50}s with significant regression and the resistance threshold. Susceptibility was indicated when LD_{50}s with significant regression and the non-significant regression were 66% and 73% in generations one and two, respectively. No difference in susceptibility was shown with this cross.

LD_{50}s of methyl parathion were equal in generation one of this cross and generation six of the Alva strain. Fenvalerate, methyl parathion, methomyl and permethrin were tested on generation two of the cross and generation three of the Donna strain; LD_{50s} of the strain and cross were equal or significantly less. LD_{50s} of fenvalerate and permethrin for the Alva strain in generation seven were significantly less than the LD_{50s} for the Alva x Donna cross in generation two. The cross combined genes for two or more mechanisms of resistance by the parents.

In generation two, cross resistance was shown for cypermethrin and fenvalerate, but the cross was susceptible to the pyrethroids bifenthrin, cyfluthrin and permethrin. Multiple resistance was shown for profenofos and fenvalerate. The cross was resistant to methyl parathion in generation one, but it was susceptible in generation two. These results indicate a polygenic mode of inheritance. Different modes of action which confer resistance to the different insecticides are present in different larvae. In generation one and two 278 and 1,031 larvae were treated, respectively. This five fold difference in number of progeny is indicative of the variation in fitness for a cross of BAW.

There are differences in cross resistance to pyrethroids with the cyclopropane moiety vs. those with the non-cyclopropane moiety. In generation two the Alva x Donna cross was resistant to the cyclopropane pyrethroid cypermethrin and the non-cyclopropane pyrethroid fenvalerate, yet the LD_{50s} of the cyclopropane pyrethroids bifenthrin, permethrin, *lambda* cyhalothrin, cyfluthrin and the non-cyclopropane esfenvalerate indicated susceptibility.

Slope values for significant and non-significant regressions ranged from 0.39 to 2.75 both generations. Fifty percent were < l, 43% ranged from 1 - 2 and 7% were > 2, respectively. None of the slopes were homozygous for response to these insecticides.

Alva x Rio Bravo and Donna x Rio Bravo

LD_{50s} exceed resistance threshold of both crosses indicating resistance to methomyl and permethrin in generation one (October 1991) (Table 2). Both Alva x Rio Bravo and Donna x Rio Bravo crosses showed a non-significant regression to fenvalerate; slope ± SE and number treated were 0.97 ± 0.66 for 65 larvae and -0.014 ± 0.35 for 67 larvae, respectively. Mortalities at 200 µg fenvalerate/larva were 37% and 28% in the Donna x Rio Bravo and Alva x Rio Bravo crosses, respectively. Both crosses were resistant. A review of LD_{50s} from the Alva strain (Wolfenbarger and Wolfenbarger 2001), Donna strain (Wolfenbarger 2002) and Rio Bravo strain (Wolfenbarger and Wolfenbarger In Press) suggests that most resistant factors were from the Rio Bravo parent. The results show there was no susceptibility to any insecticide in the single generation of either cross.

Both crosses were treated at the same time as generation 10 of the Alva strain, generation five of the Donna strain and generation three of the Rio Bravo strain. LD_{50s} of methomyl and permethrin were equal in the Alva x Rio Bravo cross and the Rio Bravo strain. LD_{50s} of permethrin for both crosses were equal to the LD_{50s} of permethrin for the Alva strain. LD_{50s} of methomyl were equal and resistant in both crosses with the Rio Bravo strain.

In generation one slopes of significant and non-significant regressions were 67% <1 and 33% 1-2, respectively, for the three regressions of Donna x Rio Bravo. Slopes were 33% < 1 and 67% 1-2, respectively, for the three regressions of Alva x Rio Bravo. Slopes only exhibited degrees of heterozygosity. In the Donna x Rio Bravo and Alva x Rio Bravo crosses 224 and 433 larvae were tested, respectively. Fitness of the two crosses is about equal.

Alva x Donna x Rio Bravo

The triple cross was treated for 10 generations from October, 1991 to July, 1992. In generations one through 10 methyl parathion, permethrin, methomyl, methomyl, not determined, methyl parathion, chlorfenapyr, chlorfenapyr, bifenthrin and chlorfenapyr, respectively, were the most toxic [Table 3]. Larvae were resistant to all insecticides in generation one. In generation 10 fenpropathrin and bifenthrin were susceptible and equally toxic. In this generation zeta cypermethrin was toxic to the cross and was significantly more toxic than the racemic mixture cypermethrin. This is the first example of equal toxicity by these pyrethroids. In generation five there were not enough larvae to treat with even one insecticide. In generations one through 10 methomyl, fenvalerate, methyl parathion, methyl parathion, not determined, permethrin, methomyl, methyl parathion, methomyl and fenvalerate were the least toxic, respectively. Anticholinesterase insecticides (methyl parathion and methomyl) comprised 70% of the least toxic insecticides.

The only example of selection for resistance was shown by cypermethrin. The cross was susceptible in generations one and eight, but resistant in generation 10. Cross resistance by fenvalerate, cypermethrin and cyfluthrin was shown in generation 10. Examples of multiple resistance were shown by methomyl, permethrin and methyl parathion in generation one, fenvalerate and methomyl in generation two and cypermethrin, cyfluthrin and methomyl in generation 10. These results clearly show that multiple factors which cause resistance to each insecticide are present in larvae in each generation.

Eight non significant regressions of this cross were determined for esfenvalerate (1.52 ± 0.8 for 61 larvae) and fenvalerate (0.47 ± 0.57 for 66 larvae) in generation one, methyl parathion (0.47 ± 0.25 for 67 larvae) in generation two, permethrin (0.47 ± 0.26 for 145 larvae) in generation three, fenvalerate (0.6 ± 0.58 for 49 larvae) in generation four, fenvalerate (0.59 ± 0.33 for 47 larvae) in generation seven and permethrin (0.61 ± 0.4 for 102 larvae) and fenvalerate (0.92 ± 0.54 for 82 larvae) in generation nine. Six (86%) of the non-significant regressions were determined for fenvalerate and permethrin. The same insecticides which showed non-significant regressions for the Alva, Donna and Rio Bravo strains showed the same for this cross. Mortalities did not exceed 43% at the greatest doses tested (100, 200, 200, 100 µg/larva) for esfenvalerate, fenvalerate, methyl parathion and permethrin, respectively. This three strain cross was resistant to all these insecticides that showed a non-significant regression. Cross also showed resistance and equal toxicity to the resolved isomer (esfenvalerate) and its racemic mixture insecticide (fenvalerate).

The cross was resistant to methomyl in generations one and two, susceptible in generations three and four, resistant in generation seven, then susceptible in generations eight, nine and 10. This result with methomyl clearly indicates the polygenic inheritance of resistance mechanism in this triple cross.

Slopes for 44 significant and non-significant regressions showed that 57% were <1 which is considered to be flat. Slope values of <2 and >2 were 41%, and 2%, respectively. None of the slopes showed homozygosity.

In generations one through 10 the number of larvae treated was 384, 391, 535, 233, 18, 124, 277, 91, 607 and 2,470, respectively. Populations of larvae increased about 6 fold from the first to last generation, but in generation five there was about a 19 fold reduction in population from generation one. There is no known reason(s) why these population sizes rise and fall. Author suggests that inherit genetic differences in moths and their ability to produce progeny of this cross are the cause of this variation in fitness.

Insecticides with LD_{50s} showed 25%, 33%, 50%, 67%, not determined,100%, 50% 88%, 67% and 84% susceptibility in generations one through 10, respectively. The cross showed great variation in susceptibility. Insecticides with significant plus non-significant regression showed 17%, 25%, 33%, 50%, not determined, 100%, 40% 8%, 40% and 84% in generations one through 10, respectively. Resistance steadily increased from generation one through six. Then there was a reversion to susceptibility from seven through 10 generations and this is why the experiment was discontinued. Non-significant regressions In generations two, three, seven and nine indicated resistance because mortalities were <50% and/or dose tested was greater than 20 µg /larva.

LD_{50s} of methomyl were equal for generation one of this cross, generation three of the Rio Bravo strain and generation 10 of the Alva strain. LD_{50s} of methyl parathion were equal in generation 10 of the cross and generation three of the Rio Bravo strain, generation five of Donna strain and generation 10 of Alva strain. The LD_{50s} of permethrin for the cross in generation one was equal to the LD_{50s} in generation three of the Rio Bravo strain and generation five of the Donna strain.

Generation two of the cross and generations 11, six and four of the Alva, Donna and Rio Bravo strains, respectively. were treated with fenvalerate, methomyl and permethrin. The LD_{50s} of fenvalerate for the triple cross was significantly less than the LD_{50s} for the Alva strain. The LD_{50s} of fenvalerate, methomyl and permethrin in this cross were equal to those determined for the Rio Bravo strain. The LD_{50s} for the cross and Donna strain was equal for permethrin.

In generation three of this cross LD_{50s} of methomyl were equal to those for the Donna and Rio Bravo strains in generations seven and five, respectively. In generation four of the cross LD_{50s} of fenvalerate, methomyl and permethrin were equal to LD_{50s} for Alva, Donna and Rio Bravo strains treated in generations 13, eight and six, respectively. Again, the LD_{50s} for the crosses showed no increased toxicity compared to the strains.

Minimal larval mortality was obtained with the lowest dose of cypermethrin, methomyl and methyl parathion which was 0.0775, 0.195, and 0.01 µg/larva, respectively. In generation one methomyl was tested on the Alva x Donna, Alva x Rio Bravo and Donna x Rio Bravo crosses. Cypermethrin was tested on the cross of three strain in generation eight and with methyl parathion in generation nine. Zero to nine percent larval mortality was determined at the indicated doses against each cross.

Females can and do mate with one or more males during their lifetime. Males produce the spermatophores and diversity of production can cause a poor structure. Mixing of the sperm in the spermatheca from the multiple matings is likely. This makes it difficult to determine which male fertilized which egg in each egg mass. It is unknown if the sperm of the later matings is more important in fertilizing each egg than the sperm of the earlier matings. This instability of resistance factors each generation has to involve 'spontaneous' genetic factors as suggested by Muggleton [1984].

In conclusion, resistance or susceptibility for each insecticide by crosses tested was separated by a resistance threshold of 20 µg/larva. Crosses were susceptible to bifenthrin and chlorfenapyr in all generations. Selection for resistance, reversion to susceptibility and cross and multiple resistance of the two and three strain crosses to the insecticides were shown during 13 generations. Reversion to susceptibility was shown more often than selection for resistance. Fifty to 69% of the slopes of the crosses were flat [<1] and none of the slopes indicated homozygosity. The LD_{50s} for all crosses were equal or lower than the LD_{50s} for the strains. LD_{50s} were so variable that many factors have to be involved in the responses for the same insecticide by the crosses from generation to generation.

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Table 1. Toxicity of insecticides against larvae of the Alva x Donna cross of beet armyworms for two generations.

Insecticide	Number treated	Slope ± SE	LD50s [µg/larva]	95% Confidence Interval
Generation 1 - July, 1991				
Methyl parathion	80	1.17 ± 0.38	23.56	10.93-339.4
Permethrin	103	1.21 ± 0.21	11.51	6.54-22.58
Methomyl	95	1.05 ± 0.22	9.62	4.87-18.46
Generation 2 - August, 1991				
Fenvalerate	94	0.71 ± 0.24	71.36	27.68-2377.0
Profenofos	90	0.6 ± 0.26	69.63	13.88-1.93x10^9
Cypermethrin	125	0.39 ± 0.13	36.33	8.14-5181.0
Permethrin	97	1.03 ± 0.24	19.36	10.39-41.54
Methyl parathion	57	1.34 ± 0.44	11.82	6.38-58.95
Cyfluthrin	92	0.76 ± 0.24	10.37	3.78-300.36
Methomyl	99	1.38 ± 0.26	9.2	5.36-14.76
Esfenvalerate	137	0.94 ± 0.17	2.39	1.35-4.81
Chlorpyrifos	115	2.57 ± 0.42	1.58	1.22-2.14
Bifenthrin	62	0.61 ± 0.27	0.045	1.99x10^{11}-0.24

Table 2. Toxicity of insecticides against larvae of Alva x Rio Bravo and Donna x Rio Bravo crosses of beet armyworm for one generation.

Insecticide	Number treated	Slope ± SE	LD_{50s} [µg/larva]	95% Confidence Interval
		Alva x Rio Bravo		
		Generation 1 - October, 1991		
Methomyl	137	1.04 ± 0.44	106.57	∞-∞
Permethrin	164	1.71 ± 0.23	34.35	25.08-47.53
		Donna x Rio Bravo		
		Generation 1 - October, 1991		
Methomyl	81	0.9 ± 0.33	128.71	50.18-1.03x10^4
Permethrin	143	1.33 ± 0.43	30.38	5.77-4023.0

Table 3. Toxicity of insecticides against larvae of Alva x Donna x Rio Bravo cross of beet armyworm for 10 generations.

Insecticide	Number treated	Slope ± SE	LD_{50s} [µg/larva]	95% Confidence Interval
		Generation 1 - October, 1991		
Methomyl	85	0.68 ± 0.34	551.88	94.63-9.4x10^{53}
Permethrin	84	2.2 ± 0.84	39.58	∞-∞
Methyl parathion	69	1.15 ± 0.34	26.6	13.97-127.87
		Generation 2 - November, 1991		
Fenvalerate	78	1.28 ± 0.39	67.15	36.04-161.98
Methomyl	79	0.46 ± 0.19	58.68	11.92-1.92x10^6
Permethrin	167	0.65 ± 0.16	3.53	0.71-28.46
		Generation 3 - December, 1991		
Methyl parathion	91	1.25 ± 0.3	43.37	24.05-117.93
Methomyl	199	0.85 ± 0.23	18.11	6.1-120.37
		Generation 4 - January, 1992		
Methyl parathion	69	0.96 ± 0.36	24.45	9.76-2490.00
Permethrin	59	1.2 ± 0.42	13.84	5.54-27.15
Methomyl	56	1.05 ± 0.33	11.21	4.67-34.44
		Generation 6 - March, 1992		
Permethrin	77	1.26 ± 0.35	7.02	2.28-12.4
Methyl parathion	47	0.97 ± 0.29	3.15	0.5-8.22
		Generation 7 - April, 1992		
Methomyl	60	0.57 ± 0.27	94.14	18.74-9.6x10^{19}
Methyl parathion	61	0.96 ± 0.31	38.5	15.44-550.34
Permethrin	47	1.54 ± 0.38	2.75	1.17-5.59
Chlorfenapyr	62	1.86 ±0.43	0.31	0.17-0.5
		Generation 8 - May, 1992		
Methyl parathion	72	1.29 ± 0.36	52.62	28.85-179.44
Methomyl	241	0.75 ± 0.11	14.87	8.66-29.4
Fenvalerate	176	1.13 ± 0.14	8.19	5.1-13.19
Permethrin	192	1.05 ± 0.18	1.07	0.45-2.27
Lambda cyhalothrin	60	1.08 ± 0.29	0.96	0.39-2.3
Cypermethrin	84	1.11 ± 0.3	0.87	0.098-5.55
Deltamethrin	72	0.43 ± 0.17	0.35	0.0055-2.18
Chlorfenapyr	84	1.94 ± 0.55	0.22	0.049-0.59
		Generation 9 - June, 1992		
Methomyl	101	0.72 ± 0.18	30.17	12.53-154.8
Methyl parathion	236	0.89 ± 0.21	10.62	4.63-42.79
Chlorfenapyr	86	1.99 ± 0.38	0.21	0.14-0.32
		Generation 10 - July, 1992		
Fenvalerate	432	0.21 ± 0.093	332,481.0	4,919.0-2.15x10^{43}
Methomyl	331	0.45 ± 0.1	284.54	86.45-4,490.0
Cypermethrin	274	0.93 ± 0.23	44.72	18.4-191.8
Cyfluthrin	107	0.63 ± 0.25	38.89	8.11-9.6x10^5
Methyl parathion	338	0.67 ± 0.17	16.29	6.48-263.2
Permethrin	372	0.66 ± 0.077	11.7	7.09-21.63
Zeta cypermethrin	177	0.98 0.26	6.54	2.69-81.21
Profenofos	88	1.67 ± 0.28	2.54	1.58-4.04
Fenpropathrin	99	0.6 ± 0.17	0.61	0.2-9.53
Bifenthrin	102	1.61 ± 0.3	0.41	0.22-0.63