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Insecticide Resistance Study in *Plutella xylostella* L.

IX. The selective metabolism of insecticides[1]

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Abstract : The genetic dilution of resistance and the selective metabolism of insecticides were investigated in the diamondback moth (DBM), *Plutella xylostella* L. The resistance to mevinphos, diethquinalphion, carbofuran and fenvalerate reduced differently which indicated that the resistance mechanisms for these insecticides were independent from each other. The crossbreeding progenies of a resistant and a susceptible DBMs showed higher tolerance to cartap which may attribute to the stronger total esterase activity as the broad-spectrum esterases may attack the thio-ester bond of cartap. So far, no resistance of DBM to the two registered benzoylarylureas i.e., teflubenzuron and chlorfluazuron has been recorded in Taiwan. The susceptible DBM possesses natural MFO activity which can degrade diflubenzuron, triflumuron and ethofenprox, while with only minimum effect on teflubenzuron, chlorfluazuron and fenvalerate. With the synergist piperonyl butoxide (pb), teflubenzuron and chlorfluazuron still exert better effect on the DBM than diflubenzuron and triflumuron. This may attribute to the fitness of insecticidal structure to the receptor of their toxic action. With the action of pb, ethofenprox performed better than fenvalerate in killing the DBM, which leads to the conclusion that the ether-bond structure in ethofenprox does not make it undesirable to the action receptor of the ester-bond synthetic pyrethroid.

Introduction

For the diamondback moth (DBM), *Plutella xylostella* L., the resistance and cross resistance to different insecticides were partially sorted out in several previous reports [6,7,8,9]. Some unsolved problems and newly reported IGR resistance [12] still need to be answered. In the study of both carbamates and synthetic pyrethroids resistance, the selectivity of oxidative metabolism had been been clearly demonstrated in DBM larvae [8].

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Other than the fitness of structure of an insecticide to its target site, the metabolic degradation before the insecticide reaching the receptor is obviously another important matter to be examined for it may contribute to either the tolerance or the resistance.

In this study, several potential but rarely investigated DBM control insecticides including cartap, benzoylarylurea IGRs [2,11,13,16] and an ether-linked synthetic pyrethroid analogue, ethofenprox, were examined for their selective metabolism in the DBM larvae.

Materials and methods

Insect materials

Susceptible strain: A native I-lan (IL) strain was used, which was collected from Tou-chen (TC) of I-lan County in 1984 and has been kept in this laboratory ever since for its high sensitivity to most traditional insecticides.

Field (resistant) strains: Resistant DBM samples were collected in 1987 from Ben-chau (BC), Hsi-hu (HH), Lu-chu (LC), Hua-lien (HL), Lo-tung (LT), and Tai-tung (TT), areas that were known for their DBM resistance problem [5,7]. Especially for the Hsi-hu area, where vegetables were grown year round, the resistant DBM was collected as the highly multiple resistant sample for testing.

Insecticides

All insecticides used were commercially formulated, and they were :

Cartap, 50% SP
Chlorfluazuron, 5% EC
Teflubenzuron, 5% EC
Diflubenzuron, 25% WP
Triflumuron, 25% WP
Fenvalerate, 10% EC
Ethofenprox, 10% EC
Carbofuran, 40.64% F
Mevinphos, 25% EC
Diethquinalphion, 25%EC

Insecticides were diluted in distilled water to proper testing concentrations for spraying.

Synergist

Piperonyl butoxide (pb) was obtained from Tokyo Kasei, and formulated with insecticides in 5 to 1 ratio whenever it was used in the test.

Testing procedures

1. The crossbreeding of resistant and susceptible strains of DBM: The highly resistant HH-strain (R) was chosen to crossbreed with the susceptible IL-strain (S). The experiment had been repeated twice, hence the 3rd and the 5th generations of HH-strain were bred with the 45th and 46th generations of IL-strain. The matured larvae of both strains had been sexed before pupation, and in each experiment, the male-R was paired with the female-S as well as the female-R paired with the male-S. The offsprings of two pairing treatments were separately tested to observe the possible difference.

2. The isoelectric focusing (IEF) electrophoresis of esterases of DBM larvae: 100 4th instar DBM larvae from the same origin of crossbreeding were gathered as one sample and homogenated in 3.5ml of 0.01M KH_2PO_4 buffer (pH 7.0). For each strain, three to four replicates were prepared separately. The supernatant from one centrifugation at 5,200 rpm for 10min. in Angle Rotor RPR20—3 of Hitachi 20PR-520 centrifuge was used for the IEF study.

The apparatuses for the IEF are:

Pharmacia® Constant Power Supply ECPS 3000/150

Pharmacia® Volthour Integrator VH-1

Pharmacia® FBE-3000 Base Unit with IEF lid/cooling plate

The ultra-thin layer of polyacrylamide gel was casted on glass plate[10]. The pre-focusing condition was set at: power=4 watts, voltage=2,000 volts, and current=50mA. The focusing condition was set at: power=8 watts, voltage=3,000 volts, and current=50 mA.

All samples were focusing on a ultra-thin layer of polyacrylamide gel made from Pharmalyte® buffer, pH ranged 3—10. The plate was pre-run for 1,000 volthours before loading the samples, then 20μl of sample was loaded on each paper applicator. After focusing for another 1,000 volthours, the paper applicators were taken out, and the gel plate was focusing for another 7,000 volthours before staining.

The esterases stain used were alpha-naphathyl acetate and Fast Grant GBC in 0.1M Na_2HPO_4 buffer (pH7.0).

3. Selection of benzoylarylurea resistance in the DBM: the IL-strain DBM was used in chlorfluazuron resistance selection, and only one selection treatment was made for each generation. Usually, 2,000—3,000 3rd instar DBM larvae were treated while the selection pressure was kept within 70—90% killing level.

4. Insecticide treatments: for the spraying operation, 1 ml of insecticide solution was pipetted into the holding tube of Burkard Potter Spray Tower. When the control was switched on, the solution was sucked into a reverse U-shaped stainless steel tubing and sprayed from nozzle, then, waited for 10 seconds before lowering the stage and took out the treated leaf disc. After air-dried, the leaf disc was inverted and loaded with 20 DBM larvae, and subjected to the second spray with another 1 ml of same insecticide solution. Hence, the DBM larvae and both sides of the leaf had received the same treatment. The treated specimen was transferred into a petri dish and covered with a slightly oversized cheesecloth before putting on the lid. Total of 60 3rd instar larvae in 3 replicates were treated with each insecticide concentration. For the LC_{50} determination, 6—7 concentrations within 10—99% mortality were tested. The post-treatment holding condition was controlled at 25±1°C and 85±10% relative humidity.

For the benzoylarylureas, the mortality was counted at 96 hours after the treatment. The 24 hours mortality was used for the treatments of carbofuran, mevinphos, fenvalerate and ethofenprox. For cartap treatment, the 48 hours result was applied. All the mortality/dosage correlation were analyzed by probits.

Results

1. The genetic dilution of resistance

Generally, the crosses between susceptible (S) and resistant (R) insects led to great resistance reduction in F_1 offsprings (Table 1) with the only exception of cartap. Since the male-S was crossed with female-R while the female-S was crossed with male-R, two F_1 progenies were obtained. The test results showed no sign of difference between these two F_1 progenies, while both progenies showed the same changes in resistance to a particular insecticide. The greatest reduction was for fenvalerate, and followed by carbofuran, diethquinalphion and mevinphos. A unexpected result was happened to cartap that both progenies showed higher tolerance to cartap than the parental insects, therefore, the second cross experiment between H5 and S46 was carried out in the same way as that of H3 and S45 to verify the fact. Two progenies obtained from the second crossbreeding treatment again were less susceptible to cartap than the parental insects, while with similar resistance reduction to the first test for other insecticides.

Table 1. Susceptibility to five insecticides in resistant (H)[a] and susceptible (S)[b] strains and two crossbreeding offsprings of *P. xylostella* (in two generations)

Insecticide	LC_{50} (in ppm)			
1st experiment	H_3	H♀×S♂	S♀×H♂	S_{45}
Mevinphos	688	508	428	379
Diethquinalphion	5,568	2,758	2,968	1,224
Carbofuran	>10,000	3,086	6,654	143
Fenvalerate	>10,000	616	439	170
Cartap	1,065	1,586	1,012	916
2nd experiment	H_5	H♀×S♂	S♀×H♂	S_{46}
Mevinphos	584	529	466	254
Diethquinalphion	8,421	2,348	3,280	1,382
Carbofuran	>10,000	3,532	4,082	155
Fenvalerate	4,081	597	695	359
Cartap	883	1,394	1,489	605

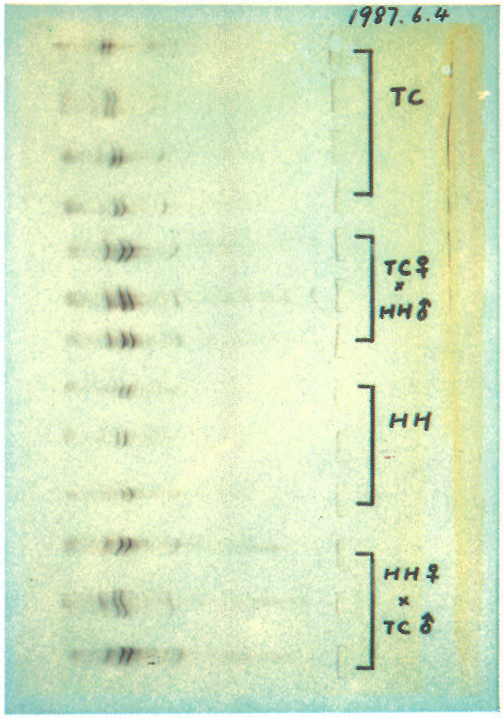
[a]H : resistant strain. [b]S : susceptible strain.

2. The study of esterases of R-, S-, and R-× S- insects by IEF

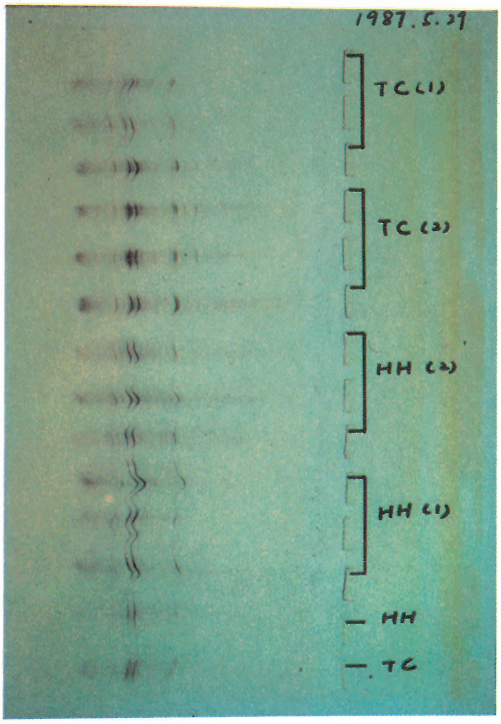
The results were presented in Figure 1a-c. The zymograms of TC-and HH- DBM strains differed from each other as can be recognized in figure 1a. All preparations of F_1 progenies showed stronger esterase activity as well as possessed both parentals' isozymes compared to R- and S- parental strains.

3. The basic susceptibilities of several native DBM strains to benzoylarylureas

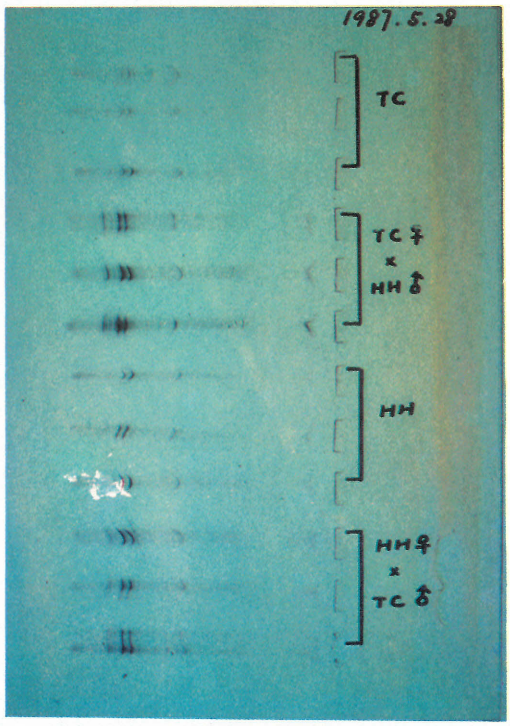
Seven DBM strains from both east and west coasts of Taiwan were highly sus-



(b)



(a)



(c)

Fig. 1. IEF of *P. xylostella* larval esterases
(a) Patterns of parental strains' esterases. (TC=susceptible IL-strain, HH=resistant HH-strain)
(b) & (c) Repeated runs of IEF patterns of esterases of two parental strains and two F_1 progenies (TC우×HH숭 and HH우×TC숭)

ceptible and showed no sensitivity difference to the two registered benzoylarylureas i.e., teflubenzuron and chlorfluazuron (Table 2), and the collected locations were marked in Figure 2.

Table 2. The basic sensitivity of 7 *P. xylostella* strains to benzoylarylurea insecticides (96 hour mortality)

Insecticide	LC_{50} in ppm/Slope						
	IL	LT	BC	HH	LC	HL	TT
Chlorfluazuron	8.8/0.53	5.0/0.55	8.1/0.58	14.2/0.42	5.2/1.03	9.6/0.34	7.9/0.56
Teflubenzuron	4.6/0.37	5.1/0.35	9.0/0.52	4.6/0.55	3.9/0.65	3.5/0.55	5.8/0.59

4. Laboratory selection of benzoylarylurea resistance

The susceptible IL-strain was continuously selected by chlorfluazuron for 11 out of 14 generations and no sign of resistance development can be noticed (Table 3).

5. The selective metabolism of benzoylarylureas

Since neither field resistant strains nor laboratory selected strains can be obtained for testing the benzoylarylureas resistance, an indirect approach was adopted by testing the tolerance difference of 4 benzoylarylureas in the DBM. In Table 4, two DBM strains separately collected from east and west coasts of Taiwan showed similar sensitivity response to 4 benzoylarylureas. Chlorfluazuron and teflubenzuron were very effective for DBM as the LC_{50}s were between 5 to 9ppm, while triflumuron and diflubenzuron were rather ineffective as the LC_{50}s were about 2,000ppm and 20,000ppm, respectively. The addition of synergist, piperonyl butoxide (pb), did not alter the susceptibility of DBM to either chlorfluazuron or teflubenzuron, while the treatment certainly enhanced the effectiveness of both triflumuron and diflubenzuron.

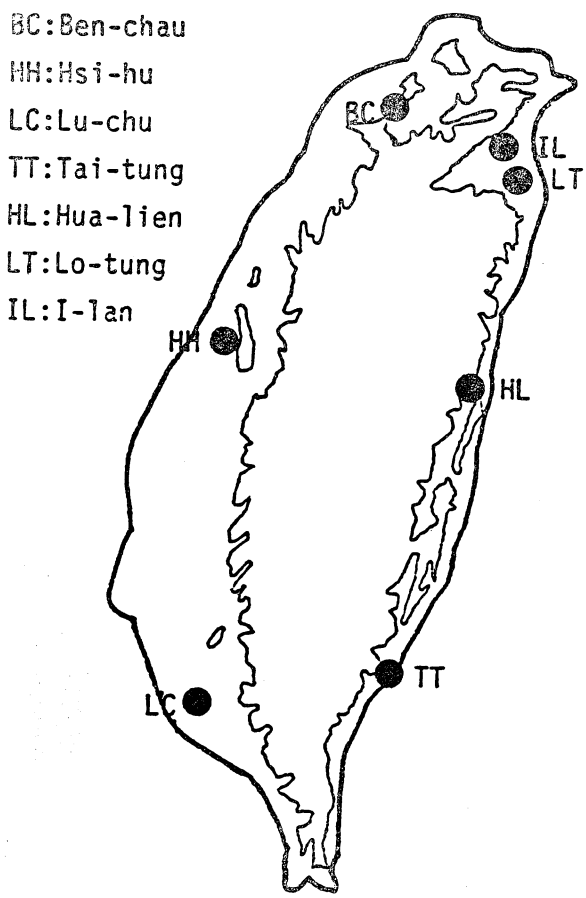


Fig. 2. Map showing locations where field resistant *Plutella xylostella* were collected.

Table 3. The laboratory selection of chlorfluazuron-resistant *P. xylostella*.

Generation	Sele. conc. of chlorfluazuron	Total larvae treated	% pupation	%failed to pupate	Date of treatment
1st	7 ppm	3,176	29.2	70.8	1986. 7.16
2nd		Not selected			
3rd	3 ppm	3,102	13.9	86.1	1986. 9.23
4th	10 ppm	2,305	22.9	77.1	1986.11.13
5th	10 ppm	2,848	10.6	89.4	1986.12.06
6th	10 ppm	2,508	8.9	91.1	1987. 1.10
7th	15 ppm	2,802	9.3	90.7	1987. 2.22
8th	15 ppm	2,493	15.1	84.9	1987. 4.02
9th		Not selected			
10th		Not selected			
11th	15 ppm	2,790	12.1	87.9	1987. 7.08
12th	15 ppm	2,341	7.8	92.2	1987. 8.10
13th	15 ppm	2,664	16.2	83.8	1987. 9.05
14th	12 ppm	3,356	6.4	93.6	1987.10.03

Table 4. The synergistic effect of four benzoylarylurea insecticides on two *P. xylostella* strains (LC_{50} in ppm and slopes).

Insecticide	LC strain			TT strain		
	Alone	+pb	S. R.	Alone	+pb	S. R.
Chlorfluazuron	5.0	7.9	0.63	8.1	5.3	1.53
Teflubenzuron	5.1	4.2	1.21	9.0	10.6	0.85
Triflumuron	2,176.4	900.2	2.42	2,312.9	818.3	2.83
Diflubenzuron	18,572.8	1,167.5	15.91	43,283.8	687.9	62.92
	(Slopes)	(Slopes)		(Slopes)	(Slopes)	
Chlorfluazuron	0.55	0.57		0.58	0.62	
Teflubenzuron	0.35	0.51		0.48	0.90	
Triflumuron	0.49	0.71		0.32	0.25	
Diflubenzuron	0.45	1.10		0.50	0.56	

6. The selective metabolism of ethofenprox vs. fenvalerate

The selective metabolism of ethofenprox and fenvalerate were tested in both the susceptible and the resistant DBMs (Table 5). The ether-bond ethofenprox [17] was less effective for controlling DBM than the ester-bond fenvalerate in both strains. After adding the synergist pb, ethofenprox became equal or even better than fenvalerate in

killing both the resistant and susceptible DBMs. The synergistic ratio is 8.88 for ethofenprox compared to only 1.99 for fenvalerate in the S-strain, and the ratio is 19.05 vs. 8.84 in the R-strain test. Obviously, the MFO of S-strain can metabolize ethofenprox more efficient than fenvalerate. With the help of synergist which rendered the activity of MFO, ethofenprox became as effective as fenvalerate which indicated the molecular fitness to a common receptor is equal in ethofenprox and fenvalerate despite the unorthodox ether-bond in a supposed ester-bond synthetic pyrethroid molecule.

Table 5. The comparison of fenvalerate and ethofenprox in their toxicities to the susceptible IL and resistant HH strains of *P. xylostella* with or without piperonyl butoxide (LC_{50} in ppm)

Insecticide	R-strain			R-strain		
	Alone	+pb	S. R.	Alone	+pb	S. R.
Fenvalerate	137.4	69.2	1.99	2,314.7	279.4	8.84
Ethofenprox	399.7	45.0	8.88	6,261.5	324.2	19.05

Discussion

The insecticide resistance in the DBM is obviously a genetic-born evolutional phenomenon since the crossbreeding of R- and S-DBMs resulted in resistance reduction in 4 out of 5 insecticides, and the reduction of resistance level differed greatly from one insecticide to another indicated there were multiple origins for resistance. By crossing the R- to S- DBMs, the resultant mevinphos susceptibility is almost equal to the mathematical average of two parental strains. The reduction is greater than the mathematical average in both diethquinalphion and carbofuran, and is even more drastic in fenvalerate. On the contrary, the crossbreeding offsprings became tolerant to cartap than both parental strains, which has usually been reported with only mild resistance to cartap [6].

The isoelectric focusing study of esterases in the DBM was intended to establish the biochemical identification for different DBM strains and their crossbreeding offsprings. The esterases activities became more intensive and combinative in the offsprings compared to two parental strains. This multiple and high esterases activity may attack the thio-este bonding structure of cartap more easily and raised the speculation that the broad spectrum esterase activity may contribute to greater hydrolysis of cartap, hence resulted in higher tolerance. Since tolerance is not necessarily to be the source of resistance, the esterase-cartap resistance hypothesis needs to be investigated further.

All field collected DBMs in Taiwan were similarly susceptible to teflubenzuron and chlorfluazuron indicated that the effectiveness of IGRs was not hindered by the cross effect from traditional insecticides. Therefore, it is very proper to monitor the possible development of IGR resistance in the DBM from now on. In our result, the DBM dose response curves for benzoylarylureas were rather flat, which was similar to the conclusions

of Becher et al.[1] and Sagenmueller and Rose[16], but differed greatly from the report of Perng and Sun[14], nevertheless, different testing methods were adopted by the above authors. There is no need to conclude which method is better since a method that is most suitable for the testing purpose will be adequate. The unsuccessful try in selecting chlorfluazuron resistance does not imply that this resistance will not develope in field DBM population, rather, it is an indication that either the selection method was not proper or the selection had not been carried out long enough. Another possibility is that the gene pool in a laboratory strain is not great enough compared to the field DBM population.

Despite the unavailability of a resistant strain, the specificity of different IGRs related to the metabolism and toxicity in the DBM still are worthwhile for investigation. The toxicity difference of 4 benzoylarylureas to the DBM and the metabolic activity related to the synergistic action of pb were observed. Both chlorfluazuron and teflubenzuron exerted excellent insecticidal action as their LC_{50}s are only 5—9ppm. Diflubenzuron showed the poorest toxicity against the DBM as its LC_{50} reached 20,000—40,000ppm, almost 4,000 times less effective than chlorfluazuron and teflubenzuron. Triflumuron is less active than teflubenzuron and chlorfluazuron but is better than diflubenzuron. The addition of pb did not alter the sensitivities of DBM to chlorfluazuron and teflubenzuron, while definitely synergized triflumuron and diflubenzuron as the synergistic ratios were 2.83 and 62.92 respectively. Similar oxidative response was reported for diflubenzuron in the housefly, *Musca domestica* L., by Pimprikar and Georghiou[15]. When diflubenzuron and triflumuron were synergized by pb, the effectiveness still are not comparable to chlorfluazuron and teflubenzuron. Since the DBM in Taiwan had never been pressed by these IGRs before, great difference in the oxidative detoxification toward four different IGRs can only be attributed to the selectivity of inherent enzymatic metabolism.

The basic requirements for an insecticide are (1) the minimum degradation from penetration to receptor site and (2) the desirability of its molecular structure to bind the receptor. Teflubenzuron and chlorfluazuron have fulfilled both requirements, while triflumuron and diflubenzuron are definitely vulnerable to the metabolic degradation. With the assistance of pb, difference between triflumuron and diflubenzuron was eliminated as their LC_{50}s were similar, but there is still 80 fold sensitivity difference when compared to teflubenzuron and chlorfluazuron. The difference may attribute from the structural fitness, or the undesirability of molecular structure in diflubenzuron and triflumuron to their action site in the DBM.

Similar selective metabolism was recorded between fenvalerate and ethofenprox. The ether-linked ethofenprox is less effective than the ester-linked fenvalerate in the susceptible DBM, hence makes the ethofenprox a undesirable choice for DBM control. By adding pb, ethofenprox became equal to or better than fenvalerate. Since the induced synthetic pyrethroid degradation enzymes were not presented in this susceptible strain, the oxidative activity toward both test compounds was presumably from the inherent MFO activity. In other word, ethofenprox was the preferred substrate for the natural

MFO in the DBM, while fenvalerate was not. Once the natural MFO degradation was prevented by pb, the performance of ethofenprox indicated that its molecular structure fitness for the receptor is equivalent to or better than fenvalerate. Unfortunately, the structure of ethofenprox made it more vulnerable to the natual enzymatic oxidation in DBM, hence the overall action of fenvalerate is better than ethofenprox. Similar phenomenon was demonstrated in a parallel test performed on the resistant DBM strain. With the presence of synthetic pyrethroid degradation enzymes, ethofenprox is almost three times less effective than fenvalerate. But when pb prevented both insecticides from the oxidative degradation, the effectiveness between ethofenprox and fenvalerate was similar as the LC_{50}s were around 300ppm. The result indicated that ethofenprox is also subjected to the pyrethroid-specific MFO degradation, just like fenvalerate i. e., the synthetic pyrethroid resistance that crossed to ethofenprox in the DBM.

The role of inherent enzymatic oxidation is as important as the degradation activity induced by selection except one was termed tolerance and other resistance. Brattsen and Metcalf had provided the biochemical evidence that the natural tolerance of an insect to insecticides is due to the inherent metabolic capability [3,4]. The same phenomenon was recognized in the DBM, which can distinguish the natural tolerance from induced resistance as carbaryl, propoxur, and methomyl can be metabolized easily by the inherent MFO activity in the DBM [8]. In this report, more evidences have been obtained, which indicate the tolerance to cartap, the selective toxicities of different analogues of benzoylarylurea and the newly introduced ether-bond synthetic pyrethroid may result from the selectivity of inherent enzymatic metabolism as well as the individual fitness of insecticidal structural design to its receptor.

Aknowledgement

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小菜蛾抗藥性之研究

Ⅸ.幼蟲體內對不同殺蟲劑之選擇代謝

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摘　要

經由抗性與感性品系小菜蛾（*Plutella xylostella* L.）雜交之子代（F_1）對殺蟲劑的抗性明顯下降，而以對芬化利之抗性下降幅度最大，其次爲加保扶，拜裕松及美文松。降幅不同之原因，可能係其抗性遺傳控制機制來源不同所致，但有一反常之現象即對培丹之抗性反而上昇。由於 F_1 子代酯酶之種類及活性均較原抗性及感性品系多且高，可導致酯酶水解培丹的能力提高，促進培丹之代謝分解，因而提高了小菜蛾之耐力。此外，感性小菜蛾天生俱有之多功能氧化酶，可代謝分解 diflubenzuron, triflumuron 及 ethofenprox，却不能代謝 teflubenzuron, chlorfluazuron 及芬化利。經以協力劑 pb 抑制多功能氧化酶之作用後發現，diflubenzuron 及 triflumuron 兩者對小菜蛾致死濃度趨於一致，但仍較 teflubenzuron 及 chlorfluazuron 爲差，因此此一毒性之差別不是由於代謝分解所造成的，可能源於前二者之分子結構不適合與小菜蛾體內作用點之結合有關。經由協力劑 pb 之作用，ethofenprox 之功效反而與芬化利相當或更佳，由此可知，係由於 ethofenprox 容易被代謝分解，以致其致死能力不如芬化利，而與其分子結構無關，即 ethofenprox 結構中之醚鍵並未對其與小菜蛾體內之毒理作用點之親和性造成差別。對於幾乎全以酯鍵爲結構之合成除蟲菊精類而言，上述結果在毒理上爲一突破性之發現，即對除蟲菊分子之毒性而言，酯鍵的存在並非一定是必要的。

1.臺灣省農業試驗所　研究報告第 1424 號。本計畫承國科會及農委會補助〔計畫編號NSC-76-0409-B055-08以及77農建—7.1—19(1)〕；簡淑貝，盧燕鈴協助工作，僅此一併致謝。

2.本所應用動物系研究員、計畫助理、計畫助理及助理。臺灣省　臺中縣　霧峰鄉。