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Original Article

Development and Mechanism of Insecticide Resistance in Rice Brown Planthoppers Selected with Malathion and MTMC

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The development of insecticide resistance in rice brown planthoppers and its mechanism were studied. The susceptibility of malathion- and MTMC-selected strains to malathion decreased to 1/39 and 1/25 of the initial level after 45 selections, respectively, while that to MTMC decreased to 1/2.5 and 1/4.2. These selected strains were more susceptible to synthetic pyrethroids than the parent strain. K1 and K2 showed high synergism to the selected strains, and also inhibited the decomposition of malaoxon. Malathion resistance in the malathion- or MTMC-selected strains was suggested to be caused by high degradative activity to malathion and malaoxon. The mechanism of MTMC resistance in the MTMC-selected strain was presumed to be caused by low sensitivity of acetylcholinesterase.

INTRODUCTION

The rice brown planthopper, *Nilaparvata lugens* STÅL, is found in most part of Asia. The insect has increased in numbers since the late 1960s in Southeast Asia, being one of the serious insect pests to rice plants.[1] Chemicals have been used for control of rice brown planthoppers, and the development of insecticide resistance has been very much apprehended. Nagata & Moriya[2] reported that the insecticide resistance of rice brown planthoppers to lindane developed with the advancement of generations in 1969. Their study also showed that an immigrated generation recovered susceptibility to lindane the following year.[2] Recently the development of resistance to organophosphorus and carbamate insecticides has been reported in Japan and Taiwan.[3-8] Controlling this insect pest by chemicals has become difficult due to the development of insecticide resistance.

We conducted the selection experiment on rice brown planthoppers with malathion and MTMC, to observe a decrease in susceptibility and to clarify the mechanism of insecticide resistance.

MATERIALS AND METHODS

1. Selection with Insecticides

Rice brown planthoppers collected in Kagoshima Prefecture in 1970 were selected with malathion and MTMC. Fourth to 5th instar nymphs were put into a plastic pot ($11 \times 12 \times 18$ cm) with rice seedlings in. Emulsifiable concentrates of malathion or MTMC diluted with tap water to appropriate concentrations were sprayed to the insects and rice seedlings. When insect mortality reached about 50%, survived insects were transferred to new rice seedlings for mass rearing. Mass rearing was carried out at 25°C under 16 hr illumination per day. Approximately 500 nymphs were used for selection up to the 15th generation, and 2000 to 3000 nymphs were treated thereafter. The final survival ratio

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after pesticide application was approximately 30–50%.

2. Bioassay

2.1 In vivo test

Insecticidal test: The insects used in this experiment; a susceptible strain collected at Kagoshima in 1970 (NK) and selected with malathion (Ma) or with MTMC (MT), a strain collected in July 1981 at Chikugo (1981 Chikugo), a strain collected in October 1981 at Nagasaki (1981 Nagasaki) and a strain collected in August 1986 at Chikugo (1986 Chikugo).

A 0.05 μl droplet of acetone solution of insecticides was administered to the pronotum of female adults with microapplicator. Mortality was recorded 24 hr after treatment at 25°C. LD_{50} values were obtained through statistical analysis according to the Bliss formula.[9]

Insecticides used in this study: malathion, malaoxon, diazinon, fenitrothion, MTMC (*m*-tolyl methylcarbamate, XMC (3,5-xylyl methylcarbamate), isoprocarb, BPMC (2-*sec*-butylphenyl methylcarbamate), propoxur, carbofuran, carbaryl, deltamethrin and ethofenprox. Synergists; piperonyl butoxide (PB), triphenyl phosphate (TPP), diethyl malate (DEM), *S*-benzyl diisopropyl phosphorothiolate (IBP), *S*,*S*,*S*-tributyl thiophosphate (DEF), 2-phenyl-4*H*-1, 3, 2-benzodioxaphosphorothiolate (K1), 2-phenoxy-4*H*-1, 3, 2-benzodioxaphosphorin 2-oxide (K2), di-*n*-propyl *p*-methyl thiophenyl phosphate (PRO) and *O*-ethyl-*O*,*O*-bis(2,4-dichlorophenyl) phosphate (PDP). A synergist and an insecticide (1 : 1) were simultaneously administered to insects.

2.2 In vitro test

Preparation of Enzyme: Fifty females were homogenized at 0°C with 10 ml of 1/20 M phosphate buffer (pH 8.0) for the inhibition test of acetylcholinesterase, and 200 females were homogenized with 10 ml of 1/15 M phosphate buffer (pH 7.2) for the degradation test of insecticides. The homogenate was filtrated through nylon gauze, and then centrifuged at $700\times g$ for 20 min to remove the debris. The supernatant was used as the source of enzyme.

Degradation of insecticides by the homogenate: Ten μl of 1.0×10^{-3} M insecticide solution was added to test tubes. After the solution was air-dried, 0.5 ml of the enzyme solution was added, and 0.5 ml of phosphate buffer or 8.0×10^{-3} M glutathione solution was further added. The mixture was incubated at 28°C for 60 min.

The remaining insecticide was extracted four times with dichloromethane, and the extract was analyzed by ECD-GC using the monochloroacetylation method for MTMC,[10] and by FPD-GC for malathion.[11]

Effect of synergists on insecticide degradation: Ten μl of 1.0×10^{-3} M insecticide solution and 10 μl of 313 ppm synergist solution were added to test tubes. After the solution was air-dried, 0.5 ml of enzyme solution and phosphate buffer (1/15 M, pH 7.2) were added for the malathion and MTMC degradation tests, and 2.0 ml of enzyme solution was added for the malaoxon degradation test. Incubation was conducted at 28°C for 60 min for the malathion and MTMC degradation tests, and for 120 min for the malaoxon degradation test. The remaining insecticide was analyzed by ECD-GC[10] and FPD-GC.[11]

Inhibition of acetylcholinesterase: A series of concentrations of malaoxon or MTMC solutions was placed in test tubes, and a solvent was air-dried. Inhibition was tested by the Ellman method[12] at 28°C. Preincubation was carried out at 28°C for 15 min.

Activity of aliesterase: Activity of aliesterase was measured by the method of van Asperen,[13] using α-naphthylacetate as the substrate. The enzyme was used at a lower concentration (1/500) than for the inhibition test of acetylcholinesterase.

Activity of glutathione *S*-transferase: The activity of glutathione *S*-transferase was measured by the method of Habig *et al.*,[14] using 2,4-dinitrochlorobenzene (CDNB) as the substrate. The enzyme preparations mentioned above were again centrifuged at 105,000 $\times g$ for 60 min and 0.5 ml of the supernatant was used for activity measurement.

RESULTS AND DISCUSSION

Changes in insecticide susceptibility of rice brown planthoppers in course of selection with malathion and MTMC are shown in Fig. 1.

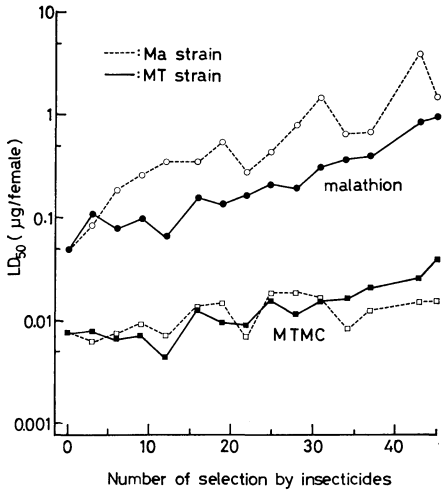

Fig. 1 Changes in insecticide susceptibility by selection.

The insecticide susceptibility of the Ma strain to malathion rapidly decreased to 1/39 up to the 45th-selection. The insecticide susceptibility to malathion decreased more slowly in the MT strain than in the Ma strain.

The susceptibility of the MT strain to MTMC slightly decreased up to the 45th selection, but that of the Ma strain remained unchanged.

The insecticide susceptibility of each strain to organophosphates, carbamates, and synthetic pyrethroids is shown in Table 1. Less resistance developed in the 1981 (Nagasaki) and 1986 (Chikugo) field strains than in the Ma-45 and MT-45 strains. This result may suggest the possibility of higher resistance development to malathion in field populations in the future. The Ma-45 and MT-45 strains were more susceptible to diazinon and fenitrothion than to malathion. There was little difference in insecticide resistance between the selected strains and the field strains collected in 1981 (Nagasaki) and 1986 (Chikugo). Ozaki & Kassai[15] observed the cross resistance to organophosphates in rice brown planthoppers selected with malathion or fenitrothion. We also recognized a cross resistance to organophosphates in the strain selected with malathion, although it was in a lesser degree.

The Ma-45 and MT-45 strains were five to seven times more resistant to isoprocarb and carbofuran than the NK strain, but their resistance to other carbamates was only 1.5 to 3.2 times higher. Such a resistance pattern was similar in the field strains (1981 Nagasaki and 1986 Chikugo).

Kassai & Ozaki[16] reported that the LD_{50} values of a malathion-selected strain of rice brown planthoppers to fenvalerate were smaller than those of the parent strain. The present study also shows that the susceptibility of the Ma-45 and MT-45 strains to deltamethrin and ethofenprox is higher than that of the NK

Table 1 Insecticide susceptibility of several rice brown planthopper strains.

Insecticide	LD_{50} (μg/♀)									
	NK	Ma-45		MT-45		1981 (Nagasaki)		1986 (Chikugo)	
Malathion	0.031	1.2	(39)	0.78	(25)	0.32	(10)	0.19	(6.1)
Diazinon	0.030	0.16	(5.3)	0.068	(2.3)	0.19	(6.3)	0.071	(2.4)
Fenitrothion	0.041	0.18	(4.4)	0.16	(3.9)	—		0.15	(3.7)
MTMC	0.0060	0.015	(2.5)	0.025	(4.2)	0.032	(5.3)	0.016	(2.7)
XMC	0.0076	0.020	(2.6)	0.021	(2.8)	0.023	(3.0)	0.022	(2.9)
Isoprocarb	0.0051	0.030	(5.9)	0.031	(6.1)	0.027	(5.3)	0.018	(3.5)
BPMC	0.0093	0.030	(3.2)	0.017	(1.8)	0.020	(2.2)	0.027	(2.9)
Propoxur	0.0052	0.0078	(1.5)	0.016	(3.1)	—		0.0063	(1.2)
Carbofuran	0.00037	0.0018	(4.9)	0.0026	(7.1)	—		0.0029	(7.8)
Cabaryl	0.0050	0.014	(2.8)	0.015	(3.0)	0.010	(2.0)	0.013	(2.6)
Deltamethrin	0.018	0.0017	(0.094)	0.0038	(0.21)	—		0.050	(2.8)
Ethofenprox	0.0018	0.00063	(0.35)	0.00076	(0.42)	—		0.0057	(3.2)

Figures in the parentheses indicate the susceptibility ratios of a tested strain to that of the NK strain.

Table 2 Effect of synergists to malathion and MTMC on several rice brown planthopper strains.

Insecticide +synergist		LD_{50} (μg/♀)					
		NK	Ma-16	Ma-45	MT-16	MT-45	1981 (Chikugo)
Malathion	alone	0.050	0.35	1.2	0.16	0.79	0.21
	+PB	0.13	1.5	2.7	0.18	2.3	0.45
	+TPP	0.040	0.24	0.091	0.16	0.11	0.078
	+DEM	0.14	0.53	1.3	0.18	1.3	0.22
	+IBP	0.018	0.041	0.027	0.031	0.023	0.035
	+DEF	0.021	0.042	0.027	0.027	0.033	0.026
	+K1	0.047	0.015	0.056	0.017	0.024	0.028
	+K2	0.034	0.0070	0.017	0.021	0.012	0.026
	+PRO	0.017	0.021	0.020	0.012	0.013	0.025
	+PDP	0.078	0.17	0.20	0.12	0.11	0.13
MTMC	alone	0.0078	0.014	0.027	0.013	0.045	0.013
	+PB	0.0094	0.0074	0.033	0.010	0.017	0.014
	+TPP	0.0081	0.011	0.0081	0.031	0.020	0.014
	+DEM	0.014	0.0094	0.018	0.0098	0.032	0.018
	+IBP	0.012	0.011	0.0087	0.0070	0.012	0.017
	+DEF	0.0068	0.011	0.019	0.0081	0.024	0.012
	+K1	0.011	0.0051	0.019	0.0093	0.022	0.011
	+K2	0.0080	0.012	0.030	0.0090	0.019	0.014
	+PRO	0.012	0.0046	0.0076	0.0070	0.013	0.011
	+PDP	0.0088	0.0079	0.011	0.0085	0.016	0.013

strain. But the susceptibility of the 1986 (Chikugo) strain to these pyrethroids was about three times lower than that of the NK strain. The LD_{50} values to pyrethroids differed between the selected strains and the 1986 (Chikugo) strain.

The effect of synergists on each strain is shown in Table 2. IBP showed synergism in the NK, Ma-16, Ma-45, MT-16, MT-45 and 1981 (Chikugo) strains. Addition of K1 and K2 was also effective, especially for the Ma-45 and MT-45 strains, but it was not effective for the NK strain. PRO, a phosphate type organophosphorus insecticide, however, did not show synergism in any strain. DEM and PB did not show any synergism, either.

The degradation of malathion and MTMC in homogenates of rice brown planthoppers is shown in Table 3. The homogenates of the Ma-45 and MT-45 strains decomposed malathion easily, while those of the NK strain did not decompose the insecticide so fast. The inhibition of malathion degradation with synergists was examined. K1 and K2 inhibited the degradation of malathion in the NK, Ma-45, and MT-45 strains. K1 and K2 showed a considerable synergistic effect on the resistant strains (Ma-16, -45, MT-16, -45, 1981 Chikugo), but not on the NK strain. PRO also strongly inhibited the degradation of malathion, but it did not show high synergism.

The effect of synergists on malaoxon degradation is shown in Table 4. The Ma-45 and MT-45 strains decomposed malaoxon more easily than the NK strain. Addition of K1 and K2 inhibited the decomposition of malaoxon in every strain.

Synergism with K2 revealed that the compound inhibits decomposition of malathion by carboxylesterase in malathion-resistant house flies and green rice leafhoppers[17] and that it inhibits decomposition of malaoxon and paraoxon by hydrolytic enzyme in organophosphate-resistant *Myzus persicae*.[18] Konno & Shishido[19] reported that K2 inhibits the degradation of fenitroxon in the organophosphate-resistant strain of rice stem borers. It is also suggested that K1 and K2 inhibit the

Table 3 Degradation of malathion and MTMC in the homogenate of rice brown planthoppers.

Insecticide+synergist	Ratio of degradation (%)		
	NK	Ma-45	Mt-45
Malathion alone	66.7, 66.9 (66.8)	82.6, 88.3 (85.5)	82.6, 87.1 (84.9)
+PB	52.4, 46.0 (49.2)	72.6, 66.4 (69.5)	72.2, 65.9 (69.1)
+TPP	18.1, 27.2 (22.7)	31.4, 44.9 (38.2)	33.3, 42.9 (38.1)
+DEM	44.0, 55.8 (49.9)	75.6, 81.9 (78.8)	61.9, 71.9 (66.9)
+IBP	23.2, 23.0 (23.1)	24.8, 21.1 (23.0)	24.3, 16.6 (20.5)
+DEF	45.0, 30.7 (37.9)	36.9, 33.8 (35.4)	39.1, 40.8 (40.0)
+K1	14.9, 12.2 (13.6)	11.9, 6.5 (9.2)	8.5, 8.4 (8.5)
+K2	17.3, 2.0 (9.7)	14.7, 12.2 (13.5)	21.2, 10.3 (15.8)
+PRO	15.5, 6.8 (11.2)	11.8, 25.2 (18.5)	20.8, 36.7 (28.8)
+PDP	15.4, 21.1 (18.3)	21.2, 28.7 (25.0)	25.4, 35.1 (30.3)
MTMC alone	10.1, 6.3 (8.2)	6.7, 8.0 (7.4)	14.3, 9.1 (11.7)
+PB	9.1, 6.1 (7.6)	12.0, 7.0 (9.5)	3.4, 6.4 (4.9)
+TPP	0, 3.2 (1.6)	12.3, 3.1 (8.2)	1.9, 8.1 (5.0)
+DEM	0, 0 (0)	4.1, 4.7 (4.4)	8.9, 1.3 (5.1)
+IBP	0, 4.8 (2.4)	8.2, 0 (4.1)	0, 3.0 (1.5)
+DEF	0.8, 0 (0.4)	10.4, 5.0 (7.7)	3.8, 8.6 (6.2)
+K1	10.9, 2.9 (6.9)	11.5, 2.0 (6.8)	2.3, 8.7 (5.5)
+K2	12.5, 5.9 (9.2)	2.0, 0.8 (1.4)	4.0, 11.8 (7.9)
+PRO	4.4, 7.0 (5.7)	9.7, 3.2 (6.5)	3.8, 0.4 (2.1)
+PDP	0, 0 (0)	4.4, 0 (2.2)	3.0, 4.8 (3.9)

Figures in parentheses indicate the mean of degradation ratios.

Table 4 Effect of synergists on malaoxon degradation in the homogenate of rice brown planthoppers.

Synergist	Ratio of residue (%)		
	NK	Ma-45	MT-45
Homogenate alone	64, 69 (67)	31, 30 (31)	33, 36 (35)
+K1	100, 96 (98)	93, 95 (94)	96, 100 (98)
+K2	96, 102 (99)	88, 93 (91)	101, 99 (100)
+PDP	74, 90 (82)	64, 62 (63)	77, 70 (74)
Phosphate buffer alone	103, 93, 96 (97)		

Figures in parentheses indicate the mean of residue ratios.

hydrolysis of oxon analogs of organophosphates in rice brown planthoppers. PB, a typical inhibitor of mfo, inhibited the degradation of malathion in the range of 16% in each strain. The results from this experiment suggested that mfo activity did not vary among the strains used. Konno & Shishido[19] reported the higher activity of a resistant strain of rice stem borers in the degradation of fenitroxon. Higher activity of malaoxon-decomposing enzyme in rice brown planthoppers might be induced as the result of selection with malathion and MTMC.

In case of MTMC, only 10% of the insecticide was decomposed in every strain (Table 3).

The result of the aliesterase activity test is shown in Table 5. The activity in the Ma-45 and MT-45 strains was 2.0, and 2.7 times higher than that of the NK strain. Furthermore, the 1981 (Nagasaki) strain also showed high aliesterase activity. The high aliesterase activity was one of the malathion resistance factors in rice brown planthoppers. This result was in good accordance with the results by

Table 5 Activity of aliesterase and glutathione *S*-transferase on several strains.

Strain	Activity (μmol/♀/min)	
	Aliesterase	Glutathione *S*-transferase
	α-Naphthylacetate[a)]	CDNB[a)]
NK	0.0770, 0.112, 0.106 (0.098)	0.0046, 0.0038 (0.0042)
Ma-28	0.165, 0.179, 0.193 (0.178)	—
Ma-45	0.237, 0.401, 0.235 (0.291)	0.0034, 0.0030 (0.0032)
MT-28	0.100, 0.152, 0.114 (0.122)	—
MT-45	0.184, 0.304, 0.245 (0.244)	0.0047, 0.0040 (0.0044)
1981 (Nagasaki)	0.216, 0.216, 0.196 (0.209)	0.0036, 0.0044 (0.0040)
1986 (Chikugo)	0.194, 0.199 (0.197)	—

[a)] Substrate.
Figures in parentheses indicate the mean of each activity.

Table 6 Degradation of malathion in the homogenate of rice brown planthoppers.

Contents	Ratio of degradation (%)		
	NK	Ma-45	MT-45
Enzyme+glutathione	69.0, 61.9 (65.4)	93.6, 89.7 (91.6)	90.4, 87.0 (88.7)
Enzyme+phosphate buffer	63.4, 65.0 (64.2)	94.3, 90.5 (92.4)	89.7, 84.1 (86.9)
Phosphate buffer+glutathione	0, 0, 0 (0)		
Phosphate buffer	0, 0.2, 3.0 (1.1)		

Figures in parentheses indicate the mean of degradation ratio.

Hama & Hosoda,[20)] Chung *et al.*[21)] and Miyata *et al.*[22)]

The activity of glutathione *S*-transferase is shown in Table 4. The activity did not differ among the strains. Hama & Hosoda,[20)] and Chung *et al.*[21)] have also presented the similar results. The degradation of malathion was not affected by addition of glutathione to the homogenate (Table 6).

The inhibition of acetylcholinesterase with malaoxon and MTMC is shown in Table 7. The I_{50} values of acetylcholinesterase of the Ma-45 and 1986 (Chikugo) strains to malaoxon were larger than that of the NK strain. In case of MTMC, The I_{50} values of the NK and Ma strains were 3.2×10^{-7} and 3.3×10^{-7} M, respectively. But the I_{50} values of the MT-45 and 1986 (Chikugo) strains were slightly larger than that of the NK strain.

Selection of rice brown planthoppers with malathion or MTMC induced high aliesterase activity. This high activity is considered to be one of the malathion-resistance factors, with higher activity of malaoxon degradation being another. Motoyama *et al.*[23)] reported that esterases in the resistant strains of green rice leafhoppers served as catalysts for hydrolysis of malathion and binding protein to oxygen analogs of organophosphorus insecticides. A similar mechanism might work in resistance of rice brown planthoppers, scavenging malaoxon by enhancing carboxylesterase through insecticide selection. Such a mechanism of rice brown planthoppers remains to be studied

Table 7 Inhibition of acetylcholinesterase with malaoxon and MTMC.

Strain	I_{50}	
	Malaoxon ($\times10^{-8}$ M)	MTMC ($\times10^{-7}$ M)
NK	6.2, 4.0 (5.1)	3.9, 2.4 (3.2)
Ma-45	9.9, 8.2 (9.1)	3.8, 2.7 (3.3)
MT-45	6.9, 6.6 (6.8)	9.1, 10.5 (9.8)
1981 (Chikugo)	8.5, 7.1 (7.8)	7.1, 5.9 (6.5)
1986 (Chikugo)	9.2, 12.3 (11)	8.8, 13.1 (11)

Figures in parentheses indicate the mean of I_{50}.

further.

Our study suggests that resistance to MTMC is due to low sensitivity of acetylcholinesterase to MTMC, and that degradation of MTMC is not involved in resistance to MTMC.

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要　　約

マラチオンおよび MTMC で淘汰したトビイロウンカの抵抗性発達とその抵抗性機構

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トビイロウンカをマラチオンおよび MTMC で淘汰し，その後の薬剤感受性変化と抵抗性機構について検討した．トビイロウンカのマラチオンに対する感受性はマラチオン，MTMC の 45 回淘汰によりそれぞれ 1/39，1/25 に低下した．しかし，MTMC に対する感受性は MTMC，マラチオンの 45 回淘汰によりそれぞれ 1/4.2，1/2.5 に低下した．両淘汰系統とも合成ピレスロイドに対する感受性は高くなった．K1，K2 は虫体ホモジネートによるマラチオン分解を非常に良く抑えたが，*in vivo* の感受性検定では薬剤淘汰系統のみに共力効果が認められた．淘汰系統の抵抗性機構としてはマラチオンに対してはマラチオン，マラオクソンの分解活性の増大によるとみられた．MTMC に対する若干の感受性低下は MTMC に対する分解活性の増大ではなく MTMC に対するアセチルコリンエステラーゼの感受性低下が主要因とみられた．