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Cross-resistance and Inheritance of Resistance in Laboratory-selected Strains of the Brown Planthopper (*Nilaparvata lugens* Stål)

벼멸구의 저항성 유발, 교차저항성 및 저항성 유전에 관한 연구

朴 亨 萬[1] · 崔 承 允[2]
Hyung Man Park[1] and Seung Yoon Choi[2]

ABSTRACT Cross-resistance and inheritance of resistance in laboratory-selected strains of the brown planthopper to various types of the insecticides were investigated. The fenobucarb-selected (R_f), carbofuran-selected(R_c), and diazinon-selected(R_d) strains were 50.3, 49.2 and 5.8 times less sensitive to the corresponding insecticides than the susceptible strain. Both R_f and R_c strains were highly resistant to the other carbamate insecticides, and moderately resistant to cypermethrin and deltamethrin, but nearly not resistant to fenvalerate and the organophosphorus insecticides except malathion and phenthoate. Moderate resistance to malathion and phenthoate in the R_f and R_c strains was obtained at the rate of 13.0-12.0 and 8.5-7.5 times, respectively. The R_d strain showed low levels of resistance to the carbamate, organophosphorus and pyrethroid insecticides, but negatively correlated cross-resistance to fenvalerate. Resistance of the brown planthopper to all the test insecticides was inherited by partially dominant autosomal factor(s).

KEY WORDS Brown planthopper, resistance, fenobucarb(BPMC), carbofuran, diazinon, cross-resistance, inheritance of resistance

초 록 벼멸구를 fenobucarb, carbofuran 및 diazinon 등 3종의 살충제로 누대선발하여 얻어진 저항성 벼멸구를 대상으로 저항성 유발, 교차저항성 및 저항성 유전에 대해서 조사한 결과를 보고하고자 한다. Fenobucarb, carbofuran으로 18세대, diazinon으로 14세대 누대선발한 결과 각 선발 계통의 반수치사약량은 50.3배, 49.2배 및 5.8배씩 증가하였다. Fenobucarb 및 carbofuran 선발계통은 carbamate계 살충제에 각각 17.7-45.2배, 19.4-40.8배의 높은 교차저항성을 보였고, 분자구조 중 carboxyl ester bond를 가지고 있는 malathion, phenthoate에 대해서도 13.0-12.0배, 8.5-7.5배로 다른 유기인계 살충제에 비하여 높은 교차저항성을 나타내었으며, cypermethrin및 deltamethrin에도 diazinon선발계통에 비하여 3-7배 정도 높은 교차저항성을 보였다. diazinon선발계통은 유기인계 살충제(평균 5.0배) 및 카바메이트계 살충제(평균 7.0배)에서 diazinon수준(5.8배)의 교차저항성을 보였다. Fenvalerate에 대한 교차 저항성은 fenobucarb 및 carbofuran 선발 계통에서 낮았으며 diazinon 선발계통에서는 역상관 교차저항성으로 나타났다. 벼멸구의 살충제 저항성은 교잡종(F_1)의 우성도가 암컷에서 0.54-0.70, 수컷에서 0.45-0.80으로 나타나 상염색체상의 불완전우성 유전자에 의해 유전되는 것으로 판단된다.

검 색 어 벼멸구, 저항성, fenobucarb(BPMC), carbofuran, diazinon, 교차저항성, 저항성 유전

The brown planthopper (*N. lugens* Stål) has become a serious insect pest in Southeast Asia where the high-yielding rice varieties have been grown since the early 1970s. Because of its severe damage

1 Agricultural Chemicals Research Institute, Rural Development Administration, Suweon 441-707, Korea(농촌진흥청 농약연구소)
2 Late Professor, Dept. of Agricultural Biology, College of Agriculture, Seoul Natl. University(故 최승윤 교수, 서울대학교 농과대학 농생물학과)

on the rice yield, large amount of the various insecticides have been inputted to suppress the brown planthopper (BPH) population, which might result consequently in resistance to the insecticides.

Since Nagata and Moriya recognized first the scanty lethal activity of γ-BHC(Lindane®)on the BPH in 1969, several scientists reported the insecticide resistance of this insect. According to IRRI report (1971) and Heinrichs (1979), LD_{50} values of diazinon and carbofuran against field strains of the BPH had increased 3-7 times. Chung et al.(1982) also found that field strain of the BPH in Taiwan possessed about 300 times and 10-18 times resistance to malathion and isoprocarb, respectively. In Japanese strains of the BPH, resistance to the organophosphorus insecticides had developed initially during 1967-1969, increased slowly during 1969-1972, and enlarged sharply after 1975(Nagata et al. 1979, Ozaki & Kassai 1982, Hosoda 1983), whereas resistance to the carbamate insecticides had gradually accelerated after 1979.

We have surveyed resistnace strains of the BPH collected from several localities in Korea during 1982-1983 and 1986-1987. The BPH strains showed only 2-7 times and 2-5 times resistance to the carbamate and organophosphorus insecticides, respectively, compared to the susceptible laboratory strain. Besides, resistance level was not abruptly changed throughout test periods.

We cannot, however, be at ease, because the BPH migrates from the south part of Mainland China annually, and is unable to overwinter in Korea. In other words, it is impossible for us to control resistance level of the BPH in original habitat. Furthermore, resistance level of the BPH may increase according to enlargement of insecticide use in China. For that reason, we should make preparations against sudden incidence of the BPH resistance.

In this paper, we report cross-resistance patterns and inheritance of resistance to the insecticides of the carbamate and organophosphorus insecticide-selected BPH.

MATERIALS AND METHODS

Brown planthopper strains

The brown planthopper tested was reared on the 7-15 day old rice seedling (Chucheong-byeo) with plastic cage (26 × 30 × 20 cm) at 25 ± 3℃. The insectary was illuminated for 16 hours in summer and for 24 hours in winter.

The susceptible BPH strain had been maintained for 6 years without exposure to any insecticide in our laboratory. R_f, R_c and R_d strains were derived by selecting the susceptible strain with fenobucarb (50 % EC), carbofuran (10 % WP) and diazinon(34 % EC) for 14-18 generations at a selection pressure of 30-70 % mortality. Selections were performed on the 4-5th instar nymphs by spray method. The treated hoppers were held for 24 hours at room temperature to determine the percentage mortality, and surviving hoppers were collected and utilized for the production of the next generation.

Female of the each selected strain was coupled with male of the susceptible strain and vice versa to obtain reciprocal F_1 hybrids.

Chemicals

As shown in Table 1, 18 insecticides were tested to investigate resistance and cross-resistance. These chemicals were supplied by pesticide formulators.

Toxicity test

The BPH adult, within 5 days after emergence, was asphyxiated with CO_2 gas for 5 to 10 seconds. Each dosage of tested insecticides in 0.2 and 0.1 μl of acetone was topically treated to the dorsal thorax of the female and male, respectively. Mortality was checked after 24 hours of application, and probit analysis was also carried out to compute the LD_{50}

Table 1. Insecticides used in the present study

Types/Common name	Chemical name	Chemical purity(%)
Carbamate insecticides		
Fenobucarb(BPMC)	2-sec-butylphenyl methylcarbamate	98.2
Carbofuran	2,3-dihydro-2,2-dimethylbenzofuran-7-yl methylcarbamate	75.8
Isoprocarb(MIPC)	2-isopropylphenyl methylcarbamate	98.5
Carbaryl(NAC)	1-naphthyl methylcarbamate	99.0
Metolcarb(MTMC)	m-tolyl methylcarbamate	98.2
Organophosphorus insecticides		
Acephate	O, S-dimethyl acetylphosphoramidothioate	85.2
Chlorpyrifos	O, O-diethyl O-3, 5, 6-trichloro-2-pyridyl phosphorothioate	94.0
Pyridaphenthion	O,O-diethyl 2, 2-dihydro-3-oxo-2-phenyl= -6-pyridazinyl phosphorothioate	98.2
Fenitrothion	O, O-dimethyl O-4-nitro-m-tolyl phosphorothioate	96.0
Malathion	S-1, 2-bis(ethoxycarbonyl)ethyl O, O-dimethyl phosphorodithioate	90.9
Phenthoate	S-α-ethoxycarbonylbenzyl O, O-dimethyl phosphorodithioate	91.5
Diazinon	O,O-diethyl O-2-isopropyl-6-methyl pyrimidin-4-yl phosphorothioate	98.7
Monocrotophos	Dimethyl(E)-1-methyl-2-(methylcarbamoyl) vinylphosphate	71.1
Pyrethroid insecticides		
Cypermethrin	(RS)-α-cyano-3-phenoxybenzyl (1RS, 3RS ; 1RS,= 3SR)-3-(2,2-dichlorovinyl)-2,2-dimethyl= cyclopropanecarboxylate	76.4
Deltamethrin	(S)-α-cyano-3-phenoxybenzyl (1R, 3R)-3-= (2, 2-dibromovinyl)-2, 2-dimethylcyclo= propanecarboxylate	99.2
Fenvalerate	(RS)-α-cyano-2-phenoxybenzyl (RS)-2-(4-= chlorophenyl)-3-methylbutyrate	96.0
Organochloride insecticides		
Endosulfan	(1, 4, 5, 6, 7, 7-hexachloro-8, 9, 10-trinorborn-= 5- en-2, 3-ylenebismethylene)sulphite	96.9
Other		
Cartap	S, S'-(2-dimethylaminotrimethylene)bis= (thiocarbamate)	91.0

with computer (VAX 11/785).

Degree of dominance

The degrees of dominance(D) in hybrids between the susceptible and selected hoppers were calculated by the method of Stone (1968) as follows;

$$D = \frac{2X_2 - (X_1 + X_3)}{X_1 - X_3}$$

whereas,

X_1 = logarithmic value of median lethal dose of the resistant strain

Table 2. Changes in the LD_{50} value($\mu g/g$) of the resistant brown planthopper strains along the number of selection[a]

Strains	Generation				
	0	5	10	14	18
R_f	1.21	17.49	44.08	51.20	60.82
R_c	0.34	2.60	6.28	13.58	16.72
R_d	12.59	34.89	60.82	72.39	–

[a] The brown planthopper was selected once for each generation and each strain was tested with the same insecticide used for the selection.

Table 3. The LD_{50} value($\mu g/g$) of resistant and susceptible female brown planthopper strains[a] to carbamate insecticides

Insecticides	R_f	R_c	R_d	S
Fenobucarb	60.82 (38.5)[b]	61.69 (39.0)	9.02 (5.7)	1.58
Carbofuran	18.52 (45.2)	16.72 (40.8)	2.13 (5.2)	0.41
Isoprocarb	53.71 (44.4)	46.52 (38.4)	5.73 (4.7)	1.21
Carbaryl	40.69 (17.7)	44.61 (19.4)	7.20 (3.1)	2.30
Metolcarb	41.59 (33.3)	29.62 (23.7)	7.59 (6.1)	1.25

[a] This experiment was carried out with 18th to 19th generation of R_f and R_c, and 14th to 15th generation of R_d.
[b] The figures in parentheses are resistance ratios.
(LD_{50} of resistant strain/LD_{50} of susceptible strain)

Table 4. The LD_{50} value($\mu g/g$) of resistant and susceptible female brown planthopper strains[a] to organophosphorus insecticides

Insecticides	R_f	R_c	R_d	S
Phosphoramidothioate				
Acephate	18.53 (5.2)[b]	12.73 (3.6)	8.42 (2.4)	3.56
Phosphorothioate				
Chlorpyrifos	24.41 (1.7)	42.62 (3.0)	38.47 (2.7)	14.11
Pyridaphenthion	16.35 (3.5)	17.16 (3.7)	26.78 (5.7)	4.67
Diazinon	31.66 (2.5)	44.01 (3.5)	72.39 (5.8)	12.48
Fenitrothion	85.97 (3.1)	82.45 (3.0)	113.86 (4.1)	27.73
Phosphorodithioate				
Malathion	337.84 (13.0)	220.74 (8.5)	275.80 (10.6)	25.92
Phenthoate	238.24 (12.0)	148.57 (7.5)	384.03 (19.3)	19.93
Phosphate				
Monocrotophos	5.03 (2.7)	9.55 (5.2)	8.17 (4.4)	1.84

[a] This experiment was carried out with 18th to 19th generation of R_f and R_c, and 14th to 15th generation of R_d.
[b] The figures in parentheses are resistance ratios.
(LD_{50} of resistant strain/LD_{50} of susceptible strain)

X_2 = logarithmic value of median lethal dose of the hybrid strain

X_3 = logarithmic value of median lethal dose of the susceptible strain

The degree of dominance was categorized as follows;

$D = 1$	perfect dominance
$0 < D < 1$	partially dominance
$D = 0$	intermediate
$-1 < D < 0$	partially recessiveness
$D = -1$	perfect recessiveness

RESULTS AND DISCUSSION

Cross-resistance

The LD_{50} values of the laboratory-selected BPH strains to the carbamate and organophosphorus insecticides over the succeeded generation are given in Table 2. After 18 generations of selection, the R_f and R_c strains were highly resistant to fenobucarb (50.3 fold) and to carbofuran(49.2 fold), respectively. Resistance level in the R_d strain, however, was not significantly increased (5.8 fold).

The increased rate of LD_{50} values in the R_f strain was extremely steep during the first five generations, but was sharply diminished during the next five generations. After that, the rate was dully increased. Similar resistance pattern in the R_c strain was also obtained. The R_d strain did not reveal typical change because of low resistance level.

Several investigators (Lin et al. 1979, Chung et al. 1982, Miyata et al. 1983, Kassai & Ozaki 1984, Ozaki & Kassai 1984b) reported that resistance development in the BPH varied with types of the test insecticides, which could not allow to presume resistance level in the BPH. Based upon our data, high frequency of use of fenobucarb and carbofuran in the field might develope resistance more stable and faster in the BPH, although this mechanism could not be explained exactly.

The LD_{50} values of the four BPH strains to several carbamate insecticides are shown in Table 3. The R_f and R_c strains exhibited high resistance level to all the carbamate insecticides, but the R_d strain showed a relatively low resistance level to those. It has been well known that cross-resistance is readily acquired in those chemicals with same categories of molecular structure (Lin et al. 1979, Miyata et al. 1983). The present result also revealed that resistance might be easily obtained within the insecticides having similar molecular structure.

The LD_{50} values of the selected BPH strains to some organophosphorus insecticides are given in Table 4. All the resistant strains showed relatively low resistance level to the organophosphorus insecticides except phosphorodithioates like malathion and phenthoate. It is of interest that the R_f and R_c strain showed a relatively high resistance to malathion and phenthoate among the organophosphosphorus insecticides. It has been reported that resistance mechanism of the BPH was different according to types of the insecticides. Resistance to the organophorus and carbamate insecticides were due to increase of esterase activity and acetylcholinesterase insensitivity (Chung & Sun 1983, Hama & Hosoda 1983, Miyata et al, 1983), respectively, but not owing to mixed function oxidase and/or glutathione S-transferase. Dai & Sun (1984) reported that resistance to the pyrethroid insectciides was mainly due to esterase, and subsidiarily mixed function oxidase. According to our experiments (going to report), however, the R_f and R_c strains showed 6-8 fold increase of esterase activity. And, Miyata et al.(1983) suggested that hydrolysis by carboxyl esterase was one of the resistance mechanism in the malathion-resistant BPH. To consider that carboxyl ester bond is coincident in the molecule of the test carbamate insecticides, malathion and phenthoate, it is presumed that carboxyl esterase might have a significant role in moderate level of cross-resistance of the R_f and R_c strain to malathion and phenthoate.

The LD_{50} valuse of the selected strains to nerve poisons are given in Table 5. Only a slight or no decrease in susceptibility to the pyrethroid insecticides, endosulfan and cartap was observed in all three resistant BPH strains, except resistance level of the carbamate insecticide-selected strains to cypermethrin and deltamethrin. The negatively correlated cross-resistance was shown in R_d strain to fenvalerate, and also reported in the BPH and green

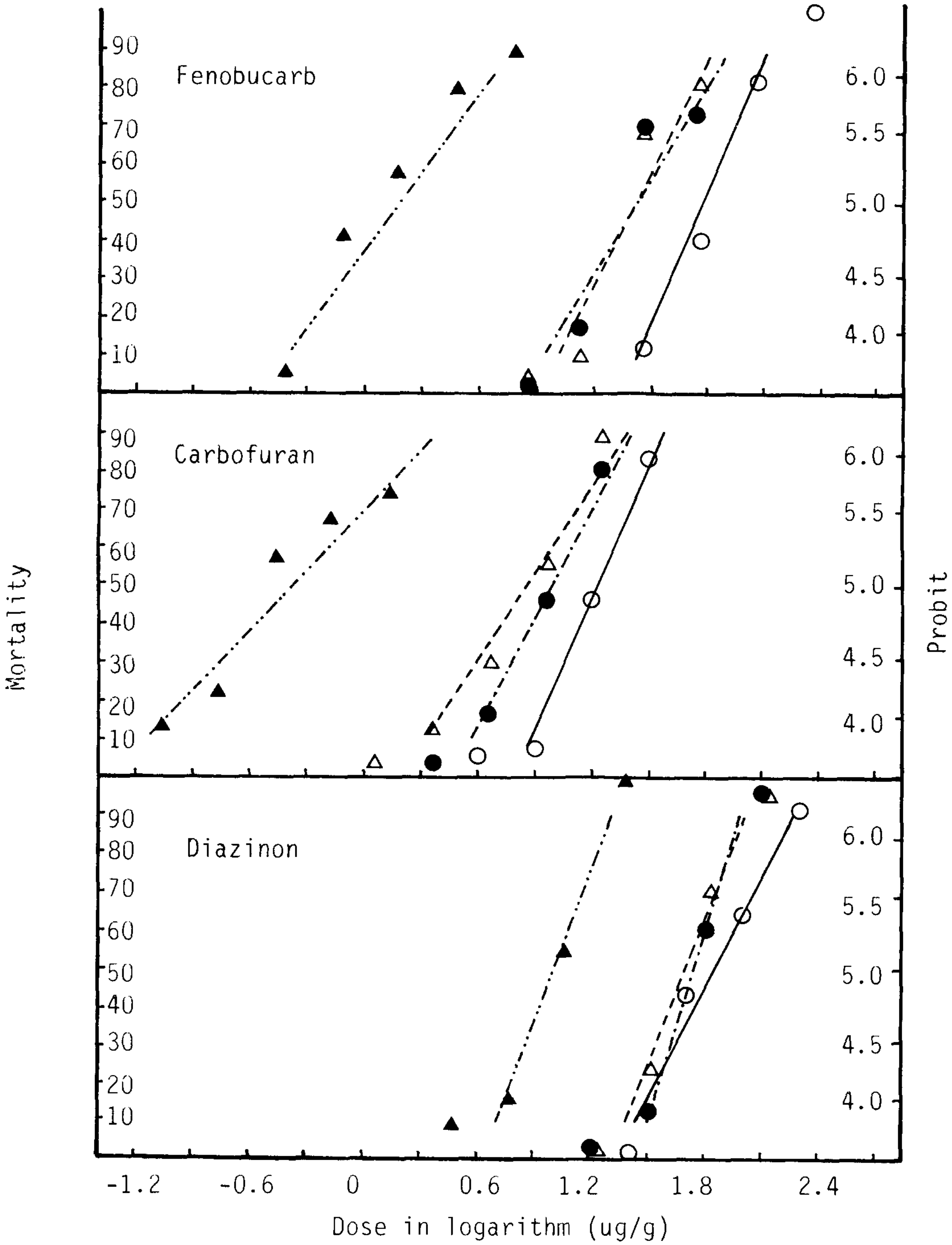

Fig. 1. Log-dose mortality lines of resistant and hybrid (F) female brown planthopper strains against three insecticides.
○——○ : Resistant strain ▲-··-▲ : Susceptible strain
△·······△ : F (resistant female × susceptible male)
●-·-● : F (resistant male × susceptible female)

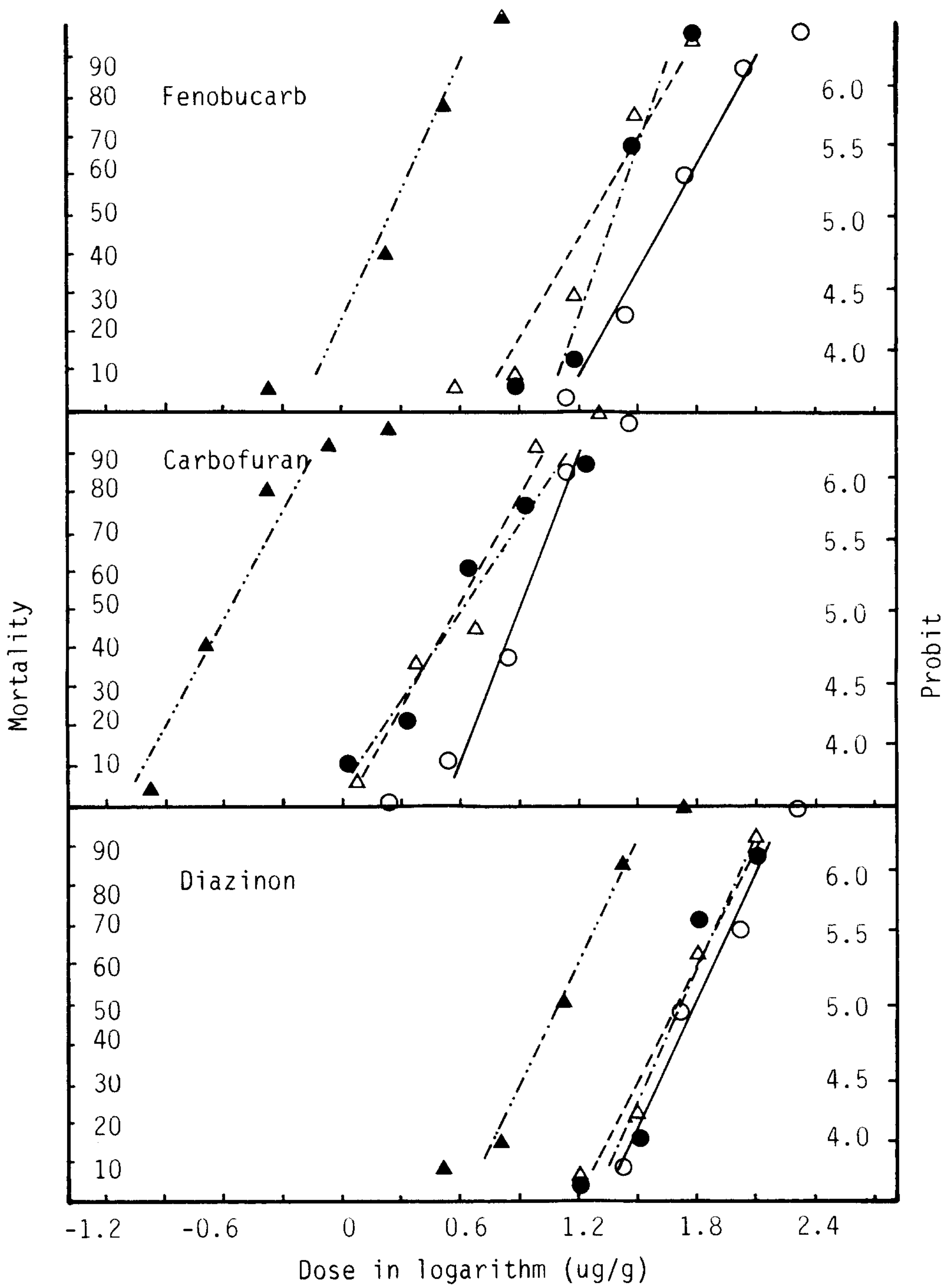

Fig. 2. Log-dose mortality lines of resistant and hybrid (F) male brown planthopper strains against three insecticides.
○——○ : Resistant strain ▲—··—▲ : Susceptible strain
△······△ : F (resistant female × susceptible male)
●—·—● : F (resistant male × susceptible female)

Table 5. The LD_{50} value($\mu g/g$) of resistant and susceptible female brown planthopper strains[a] to pyrethroid and organochlorine insecticides

Insecticides	R_f	R_c	R_d	S
Cypermethrin	25.03 (11.3)	10.56 (4.8)	3.37 (1.5)	2.22
Deltamethrin	37.75 (6.3)	43.15 (7.2)	12.67 (2.1)	5.98
Fenvalerate	19.16 (2.9)	9.34 (0.9)	2.71 (0.3)	9.85
Endosulfan	9.15 (1.7)	8.74 (1.6)	4.19 (0.8)	5.45
Cartap	215.58 (1.1)	180.58 (0.9)	237.16 (1.2)	192.47

[a] This experiment was carried out with 18th to 19th generation of R_f and R_c, and 14th to 15th generation of R_d.
[b] The figures in parentheses are resistance ratios.
(LD_{50} of resistant strain/LD_{50} of susceptible strain)

Table 6. The LD_{50} value($\mu g/g$) of the female hybrid(F) progenies between the resistant and susceptible brown planthopper strains

Strains	Fenobucarb	D[a]	Carbofuran	D	Diazinon	D
R_f	60.82 (38.5)	–	18.52 (45.2)	–	31.66 (2.5)	–
$F(R_{f.f} \times S_m)$	26.89 (17.0)	0.55	4.47 (10.9)	0.25	21.96 (1.8)	0.21
$F(R_{f.m} \times S_f)$	27.14 (17.2)	0.56	5.42 (13.2)	0.35	21.28 (1.7)	0.15
R_c	61.69 (39.0)	–	16.72 (40.8)	–	44.01 (3.5)	–
$F(R_{c.f} \times S_m)$	25.39 (16.1)	0.52	7.14 (17.4)	0.54	29.33 (2.4)	0.35
$F(R_{c.m} \times S_f)$	16.93 (10.7)	0.29	9.45 (23.0)	0.69	28.24 (2.3)	0.30
R_d	9.02 (5.7)	–	2.13 (5.2)	–	72.39 (5.8)	–
$F(R_{d.f} \times S_m)$	8.92 (5.6)	0.99	1.50 (3.7)	0.57	50.59 (4.1)	0.59
$F(R_{d.m} \times S_f)$	7.14 (4.5)	0.73	1.19 (2.9)	0.30	55.58 (4.5)	0.70
S	1.58	–	0.41	–	12.48	–

[a] Degree of dominance : calculated by the formula of Stone (1968)
[b] The figures in parentheses are resistance ratios.
(LD_{50} of resistant strain/LD_{50} of susceptible strain)
[c] f : female, m : male

rice leafhopper by Ozaki et al. (1984) and Ozaki & Kassai (1984a).

There were some differences in cross-resistance pattern between carbamate- and diazinon-selected BPH against 3 categories of test insecticides, suggesting the discrepancy in resistance mechanism between the carbamate- and organophosphorus-resistant BPH, as implied by Chung & Sun (1983), Hama & Hosoda (1983) and Miyata et al.(1983).

Inheritance of resistance

Log-dose mortality lines of the susceptible, F_1 hybrid and resistant strains are illustrated in Figure 1 and 2. The lines of the hybrid progenies of all the strains were close to those of the resistant strains regardless of the sex. It is proven that resistance gene(s) locate(s) on the somatic chromosome.

The degree of dominance, calculated by Stone's formula, were 0.54-0.70 in female and 0.45-0.80 in male (Table 6 and 7). It was coincided with the report of Chung & Sun (1983), that the degree of dominance of the organophosphorus insecticide-resistant BPH was 0.39-0.48 in the female and 0.34-0.44 in the male. It means that inheritance of resistance of the BPH is partially dominance. But, they said that inheritance of resistance might be controlled more than one factor. Therefore, the number of gene(s) which relate(s) to resistance mechanism is not clear. So, further investigations is needed on the resistance mechanisms and exact mode of action

Table 7. The LD_{50} value($\mu g/g$) of the male hybrid(F) progenies between the resistant and susceptible brown planthopper strains

Strains	LD_{50}	D[a]
	for Fenobucarb	
R_f	45.24 (25.4)	–
$F(R_{f.f} \times S_m)$	18.62 (10.5)	0.45
$F(R_{f.m} \times S_f)$	23.35 (13.1)	0.59
S	1.78	–
	for Carbofuran	
R_c	8.00 (29.6)	–
$F(R_{c.f} \times S_m)$	3.91 (14.5)	0.58
$F(R_{c.m} \times S_f)$	4.06 (15.0)	0.60
S	0.27	–
	for Diazinon	
R_d	61.66 (4.9)	–
$F(R_{d.f} \times S_m)$	50.27 (4.0)	0.74
$F(R_{d.m} \times S_f)$	52.66 (4.2)	0.80
S	12.54	–

[a] Degree of dominance : calculated by the formula of Stone (1968).
[b] The figures in parentheses are resistance ratios. (LD_{50} of resistant strain/LD_{50} of susceptible strain)
[c] f : female, m : male.

of action of inheritance at the molecular and biochemical levels.

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