

# Interactions between Biotypes of the Brown Planthopper and Rice Varieties<sup>1</sup>

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**Abstract** : Behaviors of four biotypes of the brown planthopper on rice varieties with different resistance genes were investigated. Results showed that the behavioral and physiological responses of a biotype to rice varieties having the same resistance gene on which the biotype was developed, in general, resemble the response to susceptible varieties. The biotypes developed from the varieties with a stronger antibiotic factor to the insect showed more virulent to different varieties than those from a weaker one. Histological studies of the feeding sites in the tissues of resistant varieties revealed that no mechanical barrier to the insect's feeding involved. However, any biotype put on unsuitable host plants showed restless and changed their feeding sites frequently, and fed less from resistant varieties.

Genetic studies on the ability of biotypes to survive on resistant varieties showed that the virulence of biotype was controlled by polygenes, and dominance effects were the most important factor in determining the inability of biotype to survive on resistant varieties. A simulated study indicated that rotation and mixed planting of plants with different resistance genes will be effective in lowering the rate of development of virulent biotypes.

(Key words : Brown planthopper, Resistant variety, Biotype)

## Introduction

The brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae) has been the most destructive insect pest of rice in Taiwan since 1960 (Tao, 1963; Ho and Liu, 1969; Chou, 1970; Cheng, 1977). For control of the pest, three to six applications of insecticides per crop season were usually practised (Yen and Chen, 1977). In order to develop the brown planthopper-resistant varieties, a research program has been initiated in Taiwan since 1969 (Cheng and Chang, 1979). So far, twelve resistant varieties have been developed and released for commercial cultivation.

Since the resistance of most newly-developed varieties are governed by major genes,

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and a plant resistance controlled by major or "vertical genes" generally is more vulnerable to a build-up of new biotypes than that of polygenic resistance (Pathak, 1970), it is important to understand the possibility of the development of new virulent biotypes of brown planthopper through the selection pressures imposed by the host, and the biological characteristics of the biotypes before the resistant varieties have been grown extensively in a wide area.

The majority of the planthopper populations collected from different localities in Taiwan belongs to the so-call biotype 1 (Cheng, 1975). But for the sake of comparative studies, four biotypes of brown planthopper have been developed in my laboratory through rearing the hoppers continuously on respective varieties having different resistance genes (Cheng, 1975). Thus, the original population which is unable to overcome any resistance gene is called biotype I. And the population which is able to overcome the resistance of Mudgo (with *Bph-1*), H 105 (with *bph-2*) and both Rathuheenati (with *Bph-3*) and H 105 is biotype II, III and IV, respectively.

The study is aimed to investigate the biological and genetic nature of the biotypes of the brown planthopper and to observe the effectiveness of rotation and mixed planting of varieties with different resistance genes in lowering the evolution of virulent biotypes.

### Materials and Methods

#### 1. Host preference of each biotype and its damage to rice varieties

A total of 10 rice varieties with two varieties representing each resistant gene were chosen for this study. Ten germinated seeds of each variety were sown in a row in clay plates. Seven days after seeding, the seedlings were infested separately with about 500 third-instar nymphs of the four biotypes, each with 3 replications. The number of the insects on each seedling and the damage of seedling were recorded on the 3rd and 10th days after infestation, respectively.

In order to learn whether or not differences in reactions occur between seedlings and developed plants, 60-day-old potted plants of tested varieties with one pot for each were placed together in a nylon-mesh cage. Sixty pairs of adults were released in each cage. There were 6 replications for each biotype. The number of insects on each plant and the damage of each variety were recorded on the 6th and 30th days after infestation, respectively.

#### 2. Survival and development of nymphs and population growth of each biotype

Thirty newly hatched nymphs of each biotype were individually reared on 10-day-old seedlings of tested varieties. Single seedling of each variety was grown in a glass tube. After inoculation, the seedlings were renewed every other day. The molting and mortality of nymphs were recorded daily.

The population growth of each biotype on the tested varieties was measured by caging 2 pairs of newly emerged adults on 40-day old potted plants for a period of 30 days. The number of nymphs produced in each potted-plant was counted 30 days after infestation.

#### 3. Feeding of each biotype on tested rice varieties

The feeding behavior of biotypes on varieties having different resistance genes were observed by measuring the feeding punctures, feeding site, and the amount of honeydew excretion of the insects. The feeding punctures were measured by using the method described by Naito and Makaki (1967). Feeding sites were determined by making cross-sections of the infested leaf-sheaths according to a method described by Jenson (1962), and the amount honeydew excreted by an insect was measured by following Sogawa's technique (1973).

#### 4. Genetics of the ability of different biotypes to survive on the tested rice varieties

The biotypes maintained as inbred population in the laboratory without further purification were used as the materials in this study. Reciprocal mating was made between biotypes I and II, biotypes II and III, and biotypes I and III. Each crossing was made in a group of 10 females of one biotype and 10 males of another biotype. The mated females of reciprocal crosses,  $F_1$  hybrids and back-crosses were allowed to oviposit on TN 1, and the hatched nymphs were used for measuring their ability to survive and feed on the differential varieties. Mudgo was used as the differential variety for the crosses between biotypes I and II, and biotypes II and III; and H 105 was used as the differential variety for the cross between I and III.

The same test procedures were used for the  $F_1$ ,  $F_2$ , and backcross progenies. For testing the ability of hybrid progenies to survive on differential varieties, ten-day-old seedlings were grown in test tubes (5×18cm), each with two seedlings. Ten first-instar nymphs were released in each tube. There were 10 replications per cross. The seedlings in test tubes were renewed at 3-day intervals, and the mortality of the nymphs was recorded daily. When the nymphs became adults, they were moved out and the duration of nymphal stage was recorded. Once the nymphs which could overcome the host resistance became adults, the nymphs of the avirulent biotypes and the progenies of the crosses smaller than the fifth instar were considered as incapable of survival.

#### 5. Effects of rotation and mixed planting of resistant varieties on the survival of each biotype a simulated study

Three varieties, Mudgo (with *Bph-1*), H 105 (with *bph-2*) and TN 1 (susceptible) were selected for this study. Each variety was planted separately in clay pots (12×10cm) with 5 seedlings per pot. Thirty days after planting, the plants were used for feeding the hoppers.

The treatment was divided into three groups: (1) the insects collected from the field were reared on a single variety separately for 12 generations. (2) The collected insects were reared on the above three varieties in rotation with one variety for 4 generations (equal to the generations propagating during a crop season), (3) The collected hoppers were reared on a mixture of the three varieties for 12 generations. The insects used were collected from the experimental farm of the Chiayi Agricultural Experiment Station. One hundred females were reared on TN 1 for oviposition. A group of 50 first-instar nymphs taken from the stock culture was separately released on potted plants of different varieties place randomly in wooden rearing cages (50×50×100cm). There were six plots in each cage, and four cages (replications) for each treat-

ment. When nymphs of the next generation appeared, 50 nymphs were collected from each cage and were transferred to new plants (varieties depending on the treatment). The survival rate of nymphs from each colony on TN 1, Mudgo and H 105 was determined every 2 generations as described in the second experiment.

## Results

### 1. Host preference of each biotype and its damage to rice varieties

Seedlings and developed rice plants had significant effect in causing the difference in number of insects and damages caused by different biotypes (Table 1). The suscep-

**Table 1.** Host preference and plant damage of four biotypes of brown planthopper on seedlings and adult plants of rice varieties with different resistance genes

Rice varieties	15-day-old seedling				60-day-old plant			
	No. insects/pt. on biotype							
	I	II	III	IV	I	II	III	IV
TN 1 (S)	5.9 a	6.3 a	4.3 ab	9.2 a	22.3 a	17.3 a	11.8 b	13.5 a
Tainung 67 (S)	4.2 b	4.7 bc	3.6 ab	6.8 b	11.0 bc	14.3 ab	9.0 b	14.3 a
Mudgo (Bph-1)	1.5 c	4.2 cd	0.7 c	4.0 d	4.0 d	11.4 b	3.0 c	0.5 e
IR 26 (Bph-1)	1.2 c	4.4 c	1.3 c	4.7 cd	0.5 e	7.0 b	1.0 cd	0.5 e
H 105 (bph-2)	4.7 ab	2.9 de	4.7 a	5.8 bc	5.8 cd	2.5 c	20.5 a	5.3 bc
ASD 7 (bph-2)	3.7 b	5.0 b	4.4 ab	6.2 bc	12.5 b	3.3 c	13.3 ab	9.8 ab
Rathuheenati (Bph-3)	0.6 c	1.8 ef	1.1 c	3.7 d	0.3 e	0.3 c	0.3 d	3.8 cd
Muthumanikan (Bph-3)	0.5 c	1.4 f	0.4 c	3.6 d	0.3 e	0.3 c	0.3 d	7.3 b
Babawee (bph-4)	0.8 c	1.0 f	0.3 c	3.2 d	0.2 e	0.4 c	0.3 d	0.3 e
Thirissa (bph-4)	—	—	—	—	4.8 d	0.2 c	2.0 c	4.0 bc
Damage grading <sup>1)</sup>								
TN 1 (S)	9	9	9	9	9	9	9	9
Tainung 67 (S)	9	9	9	9	9	9	9	9
Mudgo (Bph-1)	2	9	2	3	2	9	1	0
IR 26 (Bph-1)	2	9	2	3	2	9	1	2
H 105 (bph-2)	6	7	9	9	4	4	9	6
ASD 7 (bph-2)	6	8	9	9	5	4	9	5
Rathuheenati (Bph-3)	2	3	2	9	0	0	0	4
Muthumanikan (Bph-3)	2	3	2	9	0	0	0	4
Babawee (bph-4)	2	3	1	2	0	2	0	0
Thirissae (bph-4)	—	—	—	—	0	3	2	2

1) Damage grading: 0: no visual damage; 9: plant killed completely.  
a, b, c etc. show ranks differing at 5% level of significance.

tible varieties TN 1 and Tainung 67 were preferred by all biotypes, and the seedlings were killed by any of them within 10 days after infestation. When test varieties were infested with biotype II, all seedlings with *Bph-1* were killed and the varieties with *bph-2* genes were also damaged severely. In contrast, when biotype III was used, varieties having *bph-2* attracted more insects resulting in a significant difference in plant damage between the varieties with *Bph-1* and *bph-2* genes. All seedlings with *bph-2* were killed within 10 days after infestation, while the damage on the seedlings with *Bph-1* was slight. Varieties with *Bph-3* and *bph-4* were not preferred by biotypes I, II and III, and the damage caused by them was negligible. Biotype IV had the ability to infest plants with *bph-2* and *Bph-3*, but was unable to infest varieties with *Bph-1* and *bph-4*. It is shown in Table 1 that the insects of biotype IV preferred varieties with *Bph-1*, and *bph-2* to those with *Bph-3*. Therefore, it took a longer time to kill the seedlings with *Bph-3* than those with *bph-2*.

The test of 60-day-old plants for host preference of the biotypes revealed that the varieties preferred by a biotype at the seedling stage were also preferred at more mature stages. Adult insects on the preferred plants had more offsprings and caused more severe damage to the plants. However, varieties with *bph-2*, when matured, seemed more tolerant to the damage by biotypes II and IV than those at the seedling stage. Similar phenomena were also observed in varieties Rathuheenati and Muthumanikan (both with *Bph-3*) to the damage caused by biotype IV.

## 2. Survival and development of nymphs and population growth of each biotype

There were no significant differences in the survival of first-instar nymphs of different biotypes feeding on varieties having different resistance genes (Table 2). The survival of late-instar nymphs of different biotypes on Rathuheenati and Babawee was very low, indicating that those varieties possess a strong antibiotic factor to older nymphs. A more gradual reduction in the survival of successive instars was found on Mudgo with biotypes I, III and IV. Variety H 105 imposed a relatively low mortality rate on nymphs of all the biotypes, indicating that this variety had a weak antibiotic factor.

The brown planthopper nymphs undergo 5 nymphal instars to become adults. The

**Table 2.** Survival rate and duration of the nymphs of four biotypes of brown planthopper on seedling of rice varieties with different resistance genes

Rice varieties	Survival rate (%) of biotype				Nymphal period (days) of biotype			
	I	II	III	IV	I	II	III	IV
TN 1	97a	80a	87a	90a	14.3c	16.0b	15.4b	13.8c
Mudgo (Bph-1)	30c	83a	17b	27d	16.8b	16.3b	18.5ab	18.2bc
H 105 (bph-2)	73b	70b	83a	73b	16.5b	16.8b	16.9b	17.4c
Sathuheenati (Bph-3)	7d	3c	7c	43c	19.2a	16.7b	19.8a	19.4b
Babawee (bph-4)	0	3c	0	10e	—	20.9a	—	26.7a

a, b, c etc. show ranks differing at 5% level of significance.

duration of each instar was generally longer on resistant varieties than on susceptible ones. The difference becomes more pronounced when the total nymphal period on resistant and susceptible varieties is considered. The duration of the nymphal period on resistant varieties was about 2 to 10 days longer than that on susceptible varieties. Nymphs suffering from a high mortality rate on a resistant variety also had a longer duration of nymphal development.

The test of population growth of different biotypes on rice varieties with different resistance genes indicated that the biotypes differed significantly in the number of progenies produced by a female on the test varieties (Table 3). In general, the number of progenies produced correlated with the longevity of females of all biotypes survived on the susceptible TN 1, while the survival of females on varieties with different resistance genes varied according to the adaptability of a biotype. Varieties Babawee (with *bph-4*) and Ptb 33 (with dominant and recessive resistant genes, unidentified) were not suitable for all the biotypes tested, and the number of progenies produced on them was the lowest. On the other hand, biotypes II, III and IV could survive on Mudgo, H 105 and Rathuheenati, respectively. The number of progenies produced by biotype II on Mudgo, biotype III on H 105, and biotype IV on Rathuheenati was higher than those on resistant varieties with other different resistance genes.

**Table 3.** Population development of biotypes of brown planthopper on rice varieties with different resistance genes

Rice varieties <sup>1)</sup>		♀♀ survival (%) of biotype				No. progenies/♀ of biotype			
		I	II	III	IV	I	II	III	IV
TN 1	(S)	90	100	90	80	241.0a	182.6a	225.0a	202.0a
Mudgo	(Bph-1)	30	90	40	50	59.0bc	184.0a	91.0b	31.0cd
H 105	(bph-2)	40	100	100	100	89.0b	103.0b	181.0a	117.0b
Rathuheenati	(Bph-3)	20	30	20	60	19.0c	7.6c	19.2c	67.6bc
Babawee	(bph-4)	0	30	50	30	3.4d	23.2c	8.8c	6.2d
Ptb 33	(?)	20	10	40	40	9.2c	10.2c	8.6c	2.4d

1) Two-pair of newly emerged adults were caged on 40-day-old plants for a period of 30 days, average for 5 replications  
a, b, c etc. show ranks differing at 5% level of significance.

### 3. Feeding of each biotype on the tested varieties

It was observed that the feeding punctures made by female adults of different biotypes differed significantly among test varieties (Table 4). The number of feeding punctures on TN 1 made by any biotype was the least. But the feeding punctures on resistant varieties made by an insect varied according to biotype. Biotypes II and III made the least feeding punctures on Mudgo (with *Bph-1*) and ASD 7 (with *bph-2*), respectively. And biotype IV made the least feeding punctures on Rathuheenati (with *Bph-3*). Feeding punctures on Babawee (with *bph-4*) made by any of the biotypes were significantly higher than those on susceptible ones. ASD 7 was slightly resistant to

**Table 4.** Feeding punctures made by biotypes of brown planthopper on rice varieties with different resistance genes at 30°C

Rice varieties <sup>1)</sup>	No. of feeding punctures/female/24 hrs by biotype			
	I	II	III	IV
TN 1 (S)	28.7b	30.2c	28.6b	27.4b
Mudgo (Bph-1)	53.7a	32.2bc	67.9a	56.0a
ASD 7 (bph-2)	32.6b	34.6bc	28.5b	31.1b
Rathuheenati (Bph-3)	56.2a	65.3a	71.2a	43.2ab
Babawee (bph-4)	51.2a	48.4ab	53.2a	56.8a

1) 15-day-old seedlings.

a, b, etc. show ranks differing at 5% level of significance.

biotypes II and IV, it had less number of feeding punctures than highly resistant varieties. Thus, evidently hoppers on an unfavorable host plant were restless, and they

**Table 5.** Feeding sites observed in four biotypes of brown planthopper on resistant and susceptible varieties

Rice varieties	No. stylet sheath obd.	No. branches/sheath	Branched sheath (%)	Place of termination	
				Phloem <sup>1)</sup> (%)	Vascular <sup>2)</sup> bundle (%)
Biotype I					
TN 1 (S)	21	1.3 a	21.3 a	59.4 b	95.4 c
Mudgo (R)	38	2.2 c	57.9 b	23.8 a	73.7 b
ASD 7 (MR)	36	1.4 a	22.2 a	46.2 b	83.3 bc
Rathuheenati (R)	23	1.8 b	56.5 b	19.0 a	47.8 a
Babawee (R)	24	2.3 c	79.2 c	12.5 a	79.2 b
Biotype II					
TN 1 (S)	21	1.2 a	23.4 a	53.6 c	83.4 c
Mudgo (S)	30	1.6 a	26.6 a	36.4 b	53.3 a
ASD 7 (MR)	34	1.4 a	32.4 ab	40.2 bc	56.3 a
Rathuheenati (R)	34	3.9 c	85.3 d	16.1 a	67.6 ab
Babawee (R)	37	2.0 b	52.6 c	20.1 a	70.2 bc
Biotype III					
TN 1 (S)	17	1.4 a	19.4 a	49.3 b	82.8 b
Mudgo (R)	26	1.9 b	61.5 c	37.5 b	100.0 c
ASD 7 (S)	24	1.6 a	33.3 b	50.0 b	83.3 b
Rathuheenati (R)	38	2.6 c	57.9 c	21.4 a	57.9 a
Babawee (R)	20	1.5 a	40.0 b	10.0 a	90.0 bc
Biotype IV					
TN 1 (S)	24	1.2 a	23.2 a	62.1 c	92.6 c
Mudgo (R)	34	1.8 ab	52.9 b	26.6 a	73.5 b
ASD 7 (MS)	34	1.5 a	29.4 a	44.2 b	91.2 c
Rathuheenati (MS)	46	2.4 c	58.7 b	21.8 b	69.6 b
Babawee (R)	32	2.4 c	81.3 c	13.1 a	50.0 a

1) Based on the termination of each branch of stylet sheath.

2) Based on each feeding puncture.

changed their feeding sites more frequently, resulted in more punctures on resistant varieties than on non-resistant varieties.

Anatomical examination of feeding sites of the hopper showed that on both resistant and susceptible varieties, the stylet sheaths of the hopper of different biotypes reached vascular bundles more than reaching non-vascular tissues (Table 5). This indicates that nomenclature barrier to feeding existed in any resistant variety. But the stylet sheath recorded in the tissues of resistant varieties tended to have a higher percentage of branching, and more branches per sheath were observed. It is possible that resistant varieties could possess some substance which was not preferable or even repellent to insect feeding.

The amount of honeydew excreted by a sucking insect is generally correlated with the amount of food intake from the plant (Sogawa, 1973). The results of the study showed that any of the biotypes was able to intake food from plants with different resistance genes because significant amount of honeydew was excreted by an insect as compared to that fed only on water (Fig. 1). However, the amount of honeydew excreted differed significantly, depending upon the biotype and the variety. Less amount

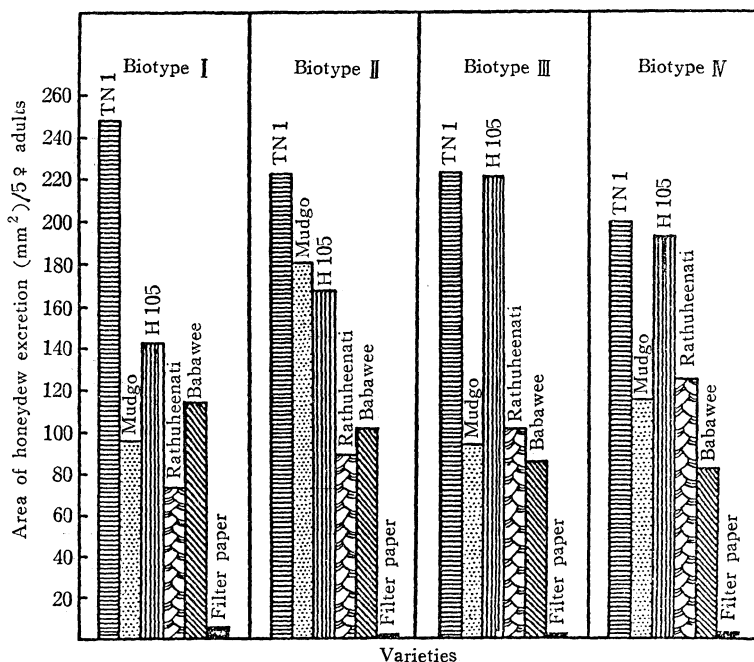


Fig. 1. Honeydew excretion of female adults of different biotypes on rice varieties with different resistance genes

of honeydew was excreted by insects feeding on resistant plants than by those on susceptible plants. It is evident that although the insects could take food from resistant varieties, they did not like to feed on them. Certain antibiotic substances produced by resistant varieties might play an important role in regulating the feeding activity and survival of hoppers.



## 4. Genetics of the ability of different biotypes to survive on the tested rice varieties

The mean survival rates of progenies from crosses between biotypes I and II, and biotypes II and III reared on Mudgo, and biotypes I and III on H 105 are present in Table 6. Since the differences between reciprocal crosses were minor, data for the two

**Table 6.** Mean survival rate of brown planthopper progenies from reciprocal crosses between biotypes I, II and III, reared on Mudgo (I × II and II × III) or H 105 (I × III)

crosses	Generation	No. of replicates	% survival ( $\bar{x} \pm s. e.$ )
I × II	P <sub>1</sub>	10	14.0 ± 5.4
	P <sub>2</sub>	10	89.0 ± 2.8
	F <sub>1</sub>	20	18.0 ± 3.9
	F <sub>2</sub>	40	41.3 ± 4.1
	BC <sub>1</sub>	40	23.0 ± 3.6
	BC <sub>2</sub>	40	40.0 ± 4.0
II × III	P <sub>1</sub>	10	82.0 ± 3.3
	P <sub>2</sub>	10	27.0 ± 5.7
	F <sub>1</sub>	20	23.0 ± 3.9
	F <sub>2</sub>	40	65.3 ± 3.7
	BC <sub>1</sub>	40	47.8 ± 3.6
	BC <sub>2</sub>	40	52.5 ± 4.1
I × III	P <sub>1</sub>	10	42.0 ± 2.8
	P <sub>2</sub>	10	95.0 ± 2.2
	F <sub>1</sub>	20	60.5 ± 3.0
	F <sub>2</sub>	40	59.0 ± 1.0
	BC <sub>1</sub>	40	52.0 ± 1.7
	BC <sub>2</sub>	40	58.8 ± 2.0

Data from reciprocal crosses were pooled since they differed only slightly.

crosses are pooled in the table. The survival rate of F<sub>1</sub> indicated that biotype II was recessive to biotype I and III in the ability to survive on Mudgo, as the F<sub>1</sub> survival rates of the I × II and II × III crosses were quite close to the parental avirulent biotypes I and III, respectively. The F<sub>1</sub> survival rate of I × III reared on H 105 was higher than that of avirulent biotype I, indicating that biotype I was partly dominant to biotype III in its ability to survive on H 105. The lack of reciprocal difference suggests that the inheritance of differences between biotypes is not sex-linked.

The variations observed in F<sub>2</sub> and backcross populations were continuous and inappropriate for testing Mendelian segregation. The virulence of biotypes could be controlled by multiple genes. Therefore, the model of polygenic inheritance was adopted

to the data. On the basis of the mean survival rates of the parents and  $F_1$  on resistant varieties, the degree of dominance was estimated by Mather and Jink's (1971) formulae as follows: for the cross between biotypes I and II, the mid-parental value,  $m = (\bar{P}_1 + \bar{P}_2)/2 = 51.5$ ;  $da = \bar{P}_1$  (or  $\bar{P}_2$ )  $- m = 37.5$ ;  $ha = \bar{F}_1 - m = 33.5$ . Then,  $ha/da = 0.89$ . The  $ha/da$  value (less than 1) indicates that the avirulence of biotype I to Mudgo was partly dominant to the virulence of biotype II. Likewise,  $ha/da$  value for the cross between biotype I and III showed partial dominance of biotype I to biotype III;  $ha/da$  value for the cross between biotype II and III was 1.15, indicating the overdominance of biotype III over biotype II.

The data of mean survival rate obtained in  $F_2$  and backcross were analysed by using Hayman and Mather (1955) equations to estimate gene effects with 6 parameters. The results are given in Table 7, which showed that the dominance effect ( $d$ ) was most important in controlling the avirulence to resistant varieties in all the three

**Table 7.** Estimation of gene effects on percent survival of brown planthopper progenies, in reciprocal crosses between biotypes I, and III, by Hayman and Mather (1955) equations

crosses	m	a	d	aa	ad	dd
I × II and II × I (on Mudgo)	4.14**±0.41	2.01**±0.54	-6.66**±2.03	-3.31 ±1.97	1.75**±0.62	4.02* ±2.89
II × III and III × II (on Mudgo)	6.33**±0.37	0.48 ±0.55	-9.20**±1.92	-6.05**±1.86	-3.23**±0.64	1.50 ±2.84
I × III and III × I (on H105)	5.90**±0.11	0.68 ±0.26	-2.24**±0.78	-1.44* ±0.69	1.97**±0.32	5.08**±1.33

m:  $F_2$  mean, a: additive gene effects, d: dominance effects, aa: interaction between additive effects, ad: interaction between additive and dominance effects, dd: interaction between dominance effects.

\*, \*\* Significant at 5% and 1% levels, respectively.

crosses (minus signs for all ( $d$ ) estimates). Simple additive effects ( $a$ ) were insignificant in all crosses. The estimates of epistasis ( $aa$ ,  $ad$ , and  $dd$ ) indicated that the interaction between additive and dominance effects ( $ad$ ) was significant in all crosses, while the interaction between additive effects ( $aa$ ) was significant in crosses II×III and I×III and that between dominance effects ( $dd$ ) was significant in I×II and I×III. The nonallelic interaction between additive effects ( $aa$ ) tended toward avirulence (minus sign), while that between dominance effects ( $dd$ ) tended toward virulence (plus sign). The interaction between additive and dominance effects ( $ad$ ) had different signs according to the crosses. Thus, the genic effects in crosses of the biotypes may be considered as complex.

#### 5. Effects of rotation and mixed planting of resistant varieties on the survival of each biotype—a simulated study

When field-collected insects were reared continuously either on Mudgo (with *Bph-1*) or H 105 (with *bph-2*), the respective survival rate of nymphs in the first generation was 10.1 and 32.4 percent, 55.6 and 51.1 percent in the fourth generation, and 88.9

and 71.1 percent in the sixth generation (Fig. 2). By the sixth generation, the survival rate of the nymphs on the resistant variety was near to that on susceptible varieties.

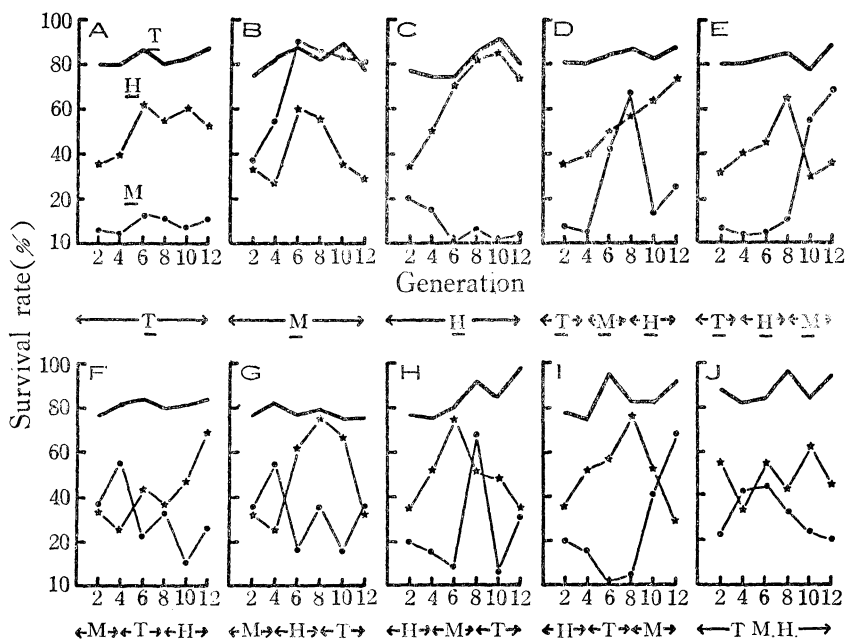


Fig. 2. Survival rate of brown planthopper on resistant varieties (Mudgo, abr. as M; and H 105, abr. as H) and susceptible TN 1 (abr. as T) when they were reared on a variety continuously (Fig. A-C), on varieties having different resistance genes in rotation with one variety for four generations (D-I), or on a mixture of resistant and susceptible varieties (J).

On the other hand, when the collected insects were rotatively reared on varieties having different resistance genes for every four generation on a variety, the survival rate on Mudgo and H 105 varied greatly, depending on the variety used for feeding. In general, when the hoppers were transferred from a resistant variety to another, the survival rate on the new host was low in the first and second generation, and tended to increase in the third and fourth generation. However, the survival rate decreased again when they were transferred to another variety.

When the collected insects were reared on a mixture of varieties having different resistant genes, the survival rate of nymphs on Mudgo and H 105 varied from generation to generation, but it showed no steady increase with the lapse of generations.

The results obtained suggest that the field-collected insects were apt to shift their ability to survive on a resistant variety when they were forced to feed on the variety for 6 generations. However, when the resistant varieties with different resistance genes grown in rotation or in mixture, the survival on a particular resistant variety was evidently lower than that which was forced to feed on a particular resistant variety continuously. This indicates that rotative or mixed cultivation of resistant varieties having different resistance genes can slow down the development of new biotypes.

## Discussion

Biological race have been defined as noninterbreeding sympatric populations, which differ in biology but not, or scarcely, in morphology; presumably prevented from interbreeding by preference for different food plants or other hosts (Mayr, 1976). In general, biotypes or biological races of an insect species have been referred to an insect populations possessing different physiological reactions, but no morphological distinction (Painter, 1951). It is believed by a majority of biologists that the Neo-Darwinian hypothesis of evolution involving the three steps: genetic variation, natural selection and isolation is the best theory yet advanced to explain the origin of species, as well as new biotypes (Smith, 1941).

In nature, wild populations of an insect species consist of individuals genetically diverse in their ability to survive on different plant varieties, and are limited by some inherent handicap (Smith, 1941; Painter, 1951; Pathak and Saxena, 1976). When a resistant variety is planted over a large area continuously imposing a pressure of selection on the insect population, individuals that survive better on resistant varieties contribute more offsprings to following generations and finally develop a new biotype adapted to the resistant variety (Painter, 1951; Pathak and Khush, 1979).

In the present study, the biological nature of four biotypes of the brown planthopper were comparatively investigated in the laboratory. In general, the behavioral and physiological responses of a biotype to rice varieties having the same resistant gene on which the biotype was developed resemble the responses to susceptible varieties. For instance, biotype II was able to feed, develop, and reproduce on varieties with *Bph-1* as well as on susceptible varieties. However, it is worthy to note that biotypes II and IV were more virulent to different varieties than biotypes I and III. Biotypes II and IV were not only capable of causing severe damage on varieties with *Bph-1* and *Bph-3*, respectively, but also capable of doing moderate to severe damage on varieties with *bph-2*. Biotype III was capable of infesting varieties with *bph-2* and susceptible varieties only. Varieties with *bph-2* imposed a relatively low mortality on all biotypes, indicating that this group of varieties had a weak antibiotic factor, while the varieties with *Bph-1*, *Bph-3* and *bph-4* allowed low survival for respective biotypes feeding on them. This indicates that the varieties with those resistant genes possess a strong antibiotic agent to the insect.

Three biotypes of the brown planthopper were also developed in the Philippines and Japan (IRRI, 1976; Ito and Kisimoto, 1981). The reactions of biotype I and III developed in Taiwan to resistant varieties were similar to those of the Philippines and Japan. But biotype II developed in Taiwan caused more severe damage to varieties with *bph-2* than those of the Philippines although both the Taiwanese and Philippines biotypes were developed similarly from the resistant variety, Mudgo. A colony collected from Victoria, the Philippines where a resistant variety IR 26 (with *Bph-1*) was extensively grown, could survive on varieties with *Bph-1* and those with *bph-2* (IRRI, 1976). The reaction of this colony to resistant varieties was more similar to those of biotype

II of Taiwan than those biotype 2 maintained at IRRI. The higher virulence of the biotype II of Taiwan than that of biotype 2 of the Philippines is probably due to the more virulence genes carried by the Taiwanese strain than by the Philippines strain.

Studies on the feeding behavior of biotypes on varieties with different resistance genes indicated that the insects put on unsuitable host plants were restless and they changed their feeding site frequently. An anatomical examination of the feeding sites indicated that no mechanical barrier was involved in the resistance. However, any biotype fed less from resistant varieties. This strongly suggested that differences in the response of biotypes to different resistance genes was likely to be due to different gustatory responses of the insect to some substance in the phloem. Observing the feeding behavior of brown planthopper on Mudgo, Sogawa (1973) suggested that the parenchymal fluid might contain some feeding inhibitory substance which play a role in determining the process of stylet insertion, and the concentration of amino acids and sucrose in vascular tissues plays an important role as phago-stimulants in determining the sustained feeding of the insects. The gustatory threshold is genetically controlled and differs according to species (Dethier, 1947). Therefore, the responses of different biotypes to different resistance genes is likely to be due to different gustatory thresholds of the biotypes to the concentration of feeding inhibitory or stimulating factors controlled by resistance genes.

The genetic studies on the ability of biotypes I, II and III to survive on resistant varieties Mudgo and H 105 showed that virulence of the brown planthopper would not be controlled simply by major genes, as was accounted for by models of polygenic inheritance. The degree of dominance as estimated by Mather and Jinks (1971) formula indicated that the inability of biotype I to survive on Mudgo was partly dominant to the ability of biotype II, while the inability of biotype III was overdominant to the ability of biotype II; the inability of biotype I to survive on H 105 was partly dominant over the ability of biotype III. These trends are in agreement with the results of studies at IRRI (IRRI, 1978; Sogawa, 1981). On the other hand, analysis of the data of mean survival rate of the insect progenies by Hayam and Mather (1955) equations showed that the virulence of biotype was controlled by many genes, and supported the postulation of Claridge (1979).

Since the biotypes are differentiated by polygenic changes, field populations must be heterogeneous and variable, and the initial low virulence of a population to a resistant variety may rapidly be improved by gene recombination. This was actually observed in IR 26 (with *Bph-1*) in the Philippines, Indonesia, Solomon Islands and Vietnam, only two to three years after this variety was released (Feuer, 1976; Varca and Feuer, 1976; Mochida et al., 1977; Oka, 1977, Stapley, 1979). To cope with the evolution of new virulent biotypes, four strategies have been suggested by Khush (1979), i. e., 1) sequential release of cultivars with different resistance genes, 2) accumulation of the vertical resistance genes, 3) breeding of multiline for resistance, and 4) improvement of horizontal resistance.

The present proved that rotation and mixed planting of plants with different

resistance genes were effective in lowering the rate of evolution of virulent biotypes. This suggests that to increase genetic diversity in the field is an effective means and the breeding of multiline varieties will be most useful. Since virulent biotypes are generally recessive genetically, they may not persist in nature unless they are selected continuously. As discussed by Cheng (1977) and Sogawa (1982), avoidance of a monoculture of a single variety is strongly recommended.

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## 褐飛蝨生物小種與抗蟲稻種之相互作用<sup>1</sup>

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### 摘 要

褐飛蝨為本省水稻重要害蟲，栽植抗蟲品種為一經濟而有效抑制本害蟲的方法。然而當一種抗蟲品種被連續大面積地栽培，可能引起有害生物小種之產生，而危害抗蟲品種。本研究在觀察於室內培育而成之褐飛蝨的四種生物小種在含有不同抗蟲遺傳因子稻種上的行為反應，遺傳以及尋求可能抑制生物小種演化之有效途徑。結果顯示，由一種抗蟲品種汰選而得之生物小種在與該抗蟲品種含有相同抗蟲遺傳因子之所有品種上的行為或生理反應，如同其存活於感蟲品種。由含有抗性較強之抗蟲品種所汰選而得之生物小種，其危害性亦較由抗性較弱者汰選所得之生物小種為強。切片檢查各生物小種在各抗蟲品種之取食部位，顯示各種水稻並無明顯的機械障礙可阻止各生物小種由維管束取食。然而若將各生物小種強迫於其不適當的稻種上取食，則顯不安並經常更換取食部位，且減少其取食量，進而影響其存活與繁殖。

探討有害生物小種可存活於抗蟲品種的遺傳行為，顯示係受數量因子所支配，顯性因子效應為控制生物小種不能在抗蟲品種存活之主要因素。本研究亦證明使用輪植或混植含有不同抗蟲因子之稻種可有效地減緩有害生物小種之演化。

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