

Sources and Inheritance of Resistance to Brown Planthopper in Some Breeding Lines of Rice¹

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ABSTRACT

The inheritance of resistance to the brown planthopper (*Nilaparvata lugens* Stal.) in three breeding lines of rice (*Oryza sativa* L.), IR747B2-6, IR1154-243, and IR4-93, was studied. Seven-day-old seedlings were infested with second- and third-instar nymphs of brown planthopper and seedling injury was recorded 7 to 8 days after infestation.

The resistance of IR747B2-6 was conditioned by a single dominant gene which was allelic to the dominant gene of the variety 'Mudgo' (*Bph 1*). The resistance of IR1154-243 and of IR4-93 was governed by the same recessive gene which was also allelic to the recessive gene conditioning the resistance of 'ASD 7' (*bph 2*). IR4-93 inherited its resistance from 'H-105.' But both parents of IR747B2-6 and of IR1154-243 were susceptible. We concluded that 'TKM 6,' one of the parents of IR747B2-6, is homozygous for *Bph 1* but is also homozygous for a gene, *I-Bph-1*, which inhibits *Bph 1*. 'Zenith,' one of the parents of IR1154-243, may also have a similar inhibitor gene.

Additional index words: Insect resistance, *Nilaparvata lugens*, Inhibitor gene, Hopper burn, Grassy stunt virus.

THE brown planthopper (*Nilaparvata lugens* Stal.) is one of the most serious insect pests of rice (*Oryza sativa* L.) throughout Asia. Light infestations of planthoppers reduce tillering, plant height, number of productive tillers per plant, and general vigor of the crop and increase the number of unfilled grains. Heavy infestations can destroy the crop completely, a condition known as "hopperburn" (10). The brown planthopper also transmits the grassy stunt virus (11) which causes serious damage to rice in some areas. Improved cultural practices (heavy application of nitrogen fertilizer, for example) which are used with high-yielding, high-tillering cultivars have favored

the build-up of brown planthopper populations. Because chemical control of high insect populations for prolonged periods is expensive, the development of insect-resistant cultivars is receiving increased attention at International Rice Research Institute (IRRI), Los Baños, Philippines (5) and elsewhere.

Several tall tropical cultivars which are highly resistant to the brown planthopper have been identified (10). These cultivars, however, have poor plant type and low yielding ability. The inheritance of resistance in cultivars 'Mudgo,' 'CO 22,' 'MTU 15,' 'ASD 7,' and 'PTB 18' has been investigated by Athwal et al. (2) and by Athwal and Pathak (1), and in Mudgo by Chen and Chang (3). The resistance to brown planthopper in Mudgo, 'MGL 2,' CO 22, and MTU 15 is governed by dominant alleles at the same locus (*Bph 1*), whereas recessive alleles at *bph 2* locus convey resistance in ASD 7 and PTB 18. *Bph 1* and *bph 2* are either allelic or are very closely linked and no recombination between these two genes has been observed.

In 1969, severe outbreaks of brown planthoppers occurred at the IRRI farm. A yield trial of 55 early-maturing selections with improved plant type was severely attacked and all but two selections suffered hopperburn. These two selections, IR747B2-6 and IR1154-243, suffered little damage in all replications (7). When tested in the greenhouse, they were found again to be resistant to the brown planthopper. Surprisingly, none of the parents of these two selections were resistant to the brown planthopper.

Since IR747B2-6 and IR1154-243 have improved plant type and other desirable agronomic traits, they are used as parents in the IRRI breeding program. Another dwarf selection, IR4-93, which has improved plant type and is resistant to brown planthopper, is also being used in the breeding program. It inherited its resistance from H-105.

The objectives of the studies reported herein were: 1) to determine the mode of inheritance of resistance

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Table 1. Rice cultivars and selections and their reactions to brown planthoppers.

Selection or variety	Parents	IRRI Acc. no.	Origin	Reaction*
IR4-93	H-105 × Dee-geo-woo-gen	10922	IRRI	R
IR747B2-6	TKM-6/2 × TN1	19908	IRRI	R
IR1154-243	IR8/2 × Zenith	19909	IRRI	R
Taichung Native 1	Dee-geo-woo-gen × Tsal-yuan-chung wan	105	Tai-	S
IR8	Peta × Dee-geo-woo-gen	10320	IRRI	S
IR5	Peta × Tangkai Rotan	9926	IRRI	S
IR20	(Peta/3 × TN1) × TKM 6	11355	IRRI	S
IR22	IR8 × Tadukan	11356	IRRI	S
IR24	IR8 × (CP 231 - SLO 17 × Slgadis)	19907	IRRI	S
Mudgo		6663	India	R
ASD 7	Sel. from Karsamba Red	6303	India	R
TKM 6	CO 18 × GEB 24	237	India	S

* R = resistant; S = susceptible.

to the brown planthopper in IR747B2-6, IR1154-243, and IR4-93; 2) to determine the allelic relationships of the genes for resistance in these selections and in Mudgo and ASD 7; and 3) to find out the origin of resistance in IR747B2-6 and IR1154-243.

MATERIALS AND METHODS

Twelve rice cultivars and selections were studied at the International Rice Research Institute, which is located at 14°N latitude and 39 m above sea level. These cultivars and their reactions to the brown planthopper are listed in Table 1.

The three resistant selections, IR4-93, IR747B2-6, and IR1154-243, were crossed with 'Taichung Native 1' (TN1), a dwarf, high-yielding cultivar from Taiwan, which is highly susceptible to the brown planthopper. The F₁, F₂, and F₃ populations of the crosses were tested to determine the mode of inheritance of resistance to the brown planthopper.

A diallel cross was made with the three resistant selections and the cultivar Mudgo, which has the dominant gene (*Bph 1*) for resistance, as parents. Since our studies showed that IR1154-243 and IR4-93 have a recessive gene for resistance, the former was crossed with ASD 7 which has a recessive gene (*bph 1*) for resistance.

The F₂ and F₃ progenies of the crosses were grown to determine the allelic relationships in the crosses involving one or both parents possessing dominant genes for resistance. The F₂ and F₃ progenies of IR4-93 × IR1154-243 and of IR1154-243 × ASD 7 were also studied to verify the conclusions drawn from the study of F₁ progenies.

Since IR747B2-6 originated from a cross between two susceptible varieties, TKM 6 and TN1, the cross was repeated to study the mode of origin of its resistance. TKM 6 was also crossed with several other susceptible cultivars and F₁ and F₂ populations from the crosses were screened for resistance to the brown planthopper.



Fig. 1. Bulk seedling test for resistance to brown planthopper. Susceptible rows have been killed by the insect feeding; resistant rows have suffered no visible damage.

Table 2. Segregation for resistance to brown planthopper in the F₂ generation of crosses between resistant and susceptible parents.

Cross	Seedlings, #			X ² , 3:1/1:3	P, 3:1/1:3
	Resistant	Susceptible	Total		
TN1 × IR747B2-6	1582	575	2157	3.06	0.1-0.05
IR1154-243 × TN1	904	2802	3706	0.70	0.5-0.30
IR4-93 × TN1	727	2090	2817	0.93	0.5-0.30

Table 3. Classification of F₃ families of crosses between resistant selections and TN1 for their reaction to the brown planthopper.

Cross	Families, #			X ² , 1:2:1	P value, 1:2:1
	Homozygous resistant	Segregating	Homozygous susceptible		
IR747B2-6 × TN1	57	109	54	220	0.08
IR1154-243 × TN1	53	108	59	220	0.39

The bulk seedling test (2) was used for testing the parental cultivars and hybrid material. We planted the test material in rows about 5 cm apart in 60 × 45 × 10 cm wooden flats. One row each of the resistant and susceptible checks was planted in each flat. At the one-leaf stage the seedlings were infested with second- and third-instar nymphs of brown planthopper. The insects were distributed evenly with six to seven insects per seedling. We recorded the reaction of the test material when the seedlings of the susceptible check had been killed, generally about 7 to 8 days after infestation. At this stage resistant seedlings had little injury from the insects (Fig. 1).

RESULTS

Inheritance of Resistance. Reciprocal F₁ hybrids from crosses between IR747B2-6 and TN1 were resistant, indicating that the resistance of IR747B2-6 was dominant. Reciprocal F₁ plants from crosses between IR1154-243 and TN1 and from crosses between IR4-93 and TN1 were susceptible, revealing that the resistance in IR1154-243 and IR4-93 was recessive. The absence of differences in the reciprocal crosses rules out the possibility of cytoplasmic inheritance.

The F₂ population of TN1 × IR747B2-6 segregated in a ratio of 3 resistant:1 susceptible (Table 2), indicating that a single dominant gene governed resistance in IR747B2-6. On the other hand, F₂ populations of IR1154-243 × TN1 and of IR4-93 × TN1 segregated into 1 resistant: 3 susceptible, thereby confirming that the resistance in IR1154-243 and IR4-93 was conferred by a single recessive gene.

The F₂ results were verified for crosses IR747B2-6 × TN1 and IR1154-243 × TN1 by classifying F₃ lines as homozygous resistant, segregating, or homozygous susceptible (Table 3). The F₃ breeding behavior agreed with the expected 1:2:1 ratio in both crosses, thus confirming the monogenic control of resistance.

Allele Tests. Information on allelic relationships of resistance genes was obtained from the reaction of F₁, F₂, and F₃ progenies. The F₁ progenies of all cross combinations among resistant parents were resistant and the reciprocal crosses showed no differences. Since IR1154-243, IR4-93, and ASD 7 had recessive genes and the F₁ progenies of IR1154-243 × IR4-93 and IR1154-243 × ASD 7 were resistant, these three lines must have the same recessive gene for resistance.

The data on these F₂ segregations are presented in Table 4. A few seedlings died and were classified as susceptible in all F₂ populations, but fewer seedlings died than expected on the basis of independent assortment of resistance genes. In the Mudgo × IR747B2-6 cross, 1.51% of the seedlings were killed.

Table 4. Resistance to brown planthopper in the F₂ generation of crosses between resistant lines.

Parent or hybrid	Number of plants			Dead seedlings, %
	Total	Live	Dead	
IR747B2-6	631	597	34	5.89
IR1154-243	787	740	47	5.97
IR4-93	618	590	28	4.53
Mudgo	615	608	7	0.01
ASD 7	355	350	5	0.01
Mudgo × IR747B2-6	4032	3971	61	1.51
IR1154-243 × IR747B2-6	3381	3251	130	3.85
IR4-93 × IR747B2-6	4156	4115	41	0.99
IR1154-243 × Mudgo	4863	4842	21	0.43
Mudgo × IR4-93	4411	4355	56	1.27
IR4-93 × IR1154-243	3986	3857	129	3.24
IR1154-243 × ASD 7	2721	2704	17	0.62

From these data it is difficult to determine whether the dead seedlings represented the susceptible class that resulted from the recombination of nonallelic genes or whether these seedlings died due to lack of penetrance of the gene for brown planthopper resistance in some individuals. Since a similar proportion of the seedlings of the resistant parents also died, the latter possibility seems more plausible. Therefore, the dominant genes for resistance in Mudgo and IR747B2-6 were apparently allelic. This conclusion was confirmed in a study of 219F₃ lines of this cross, all of which were homozygous resistant (Table 5).

Similar results were obtained from the study of F₂ and F₃ populations of other crosses between resistant varieties (Tables 4 and 5). A small proportion of seedlings were killed in the F₂ populations of all cross combinations but all F₃ lines were homozygous resistant except one line of the IR1154-243 × IR747B2-6 cross. This line must have resulted from a contaminant seed, since the product of a rare recombination would be heterozygous. Thus, we found no evidence of genetic recombination between the dominant gene for resistance in Mudgo and IR747B2-6 and the recessive gene for resistance in IR4-93, IR1154-243, and ASD 7.

Crosses Between Susceptible Parents. All F₁ seedlings of TKM 6 crossed with several other susceptible varieties were susceptible. However, a few resistant seedlings were obtained from these cross combinations in F₂ (Table 6). No resistant seedlings appeared in the IR20 × TKM 6 cross although resistant seedlings were obtained from this cross in another study (8). F₃ progeny tests verified the resistance of the seedlings in this study, except for resistant seedlings from TNI × TKM 6 and IR22 × TKM 6 crosses, which were infected by the grassy stunt virus and produced no seed for the progeny tests. Resistant seedlings from other crosses proved to be heterozygous for resistance since they produced segregating progenies. Therefore, they must all have had dominant genes for resistance. Although allele tests between these resistant seedlings and IR747B2-6 or Mudgo have not been made, we suspect that they all have the *Bph 1* gene.

Since IR1154-243 was obtained from a cross of IR8 and Zenith, we have repeated this cross and have crossed Zenith with several other susceptible varieties. The F₂ and F₃ progenies are under study.

DISCUSSION

When the resistance of IR747B2-6 and IR1154-243 to brown planthoppers was first detected, it was suspected to have originated through complementary

Table 5. Classification of F₃ families of crosses between resistant varieties and selections for reaction to brown planthopper.

Cross	Families, #		
	Homozygous resistant	Segregating	Homozygous susceptible
IR747B2-6 × Mudgo	219	0	0
IR1154-243 × IR747B2-6	209	0	1
IR4-93 × IR747B2-6	220	0	0
IR1154-243 × Mudgo	220	0	0
Mudgo × IR4-93	220	0	0
IR4-93 × IR1154-243	220	0	0
ASD 7 × IR1154-243	217	0	0

gene action. If one susceptible parent was homozygous for one gene of the complementary system and the other susceptible parent homozygous for the second gene, resistant plants should be obtained at a predictable frequency in the F₂ generation. However, the F₂ populations of crosses between TKM 6 and several other susceptible varieties did not yield resistant plants at the expected frequency on the basis of combination of two complementary genes from two parents. Moreover, the resistance in both selections is under monogenic control, not under complementary gene action. Therefore, the origin of resistance in these two selections cannot be explained on the basis of combination of complementary genes.

The possibility that resistance in these selections originated through mutation was also considered, but resistant seedlings appear in many crosses involving TKM 6 at frequencies too high for random mutational events. The logical explanation which the available data permit is that TKM 6 is homozygous for *Bph 1* gene as well as for a gene which inhibits *Bph 1*. Since F₁ seedlings of TKM 6 crossed with other susceptible varieties, like IR8 and TNI, were found susceptible, the inhibitor of *Bph 1* must be dominant. Following the recommended procedures for gene symbolization in rice (6), this inhibitor is designated *I-Bph 1*. The genotype of TKM 6 thus would be *I-Bph 1 I-Bph 1, Bph 1 Bph 1* and that of TNI, *i-bph 1, i-bph 1, bph 1, bph 1*. An independent assortment of *I-Bph 1* and *Bph 1* from crosses of TKM 6 and other susceptible varieties like TNI should yield 18.75% resistant seedlings, but the proportion of resistant seedlings in such crosses is much lower. It therefore appears that *I-Bph 1* and *Bph 1* are closely linked. Only the recombinant gametes with *i-bph 1, Bph 1* alleles yield the resistant seedlings.

The discovery of *Bph 1* in TKM 6 is significant for rice breeders because the variety is resistant to several other diseases and insects and it yields progenies with good plant type when crossed with dwarf varieties. Crossing it with IR24 has resulted in progenies resistant to brown planthopper which have improved plant type; high yield potential; resistance to tungro, bacterial leaf blight, bacterial leaf streak, and green leafhopper; and moderate levels of resistance to stem borers and blast. Two such lines with multiple disease

Table 6. Reaction of F₂ seedlings from the crosses of TKM 6 and other varieties susceptible to brown planthopper.

Cross	Seedlings, #		Resistant seedlings, %
	Susceptible	Resistant	
TNI × TKM 6	4926	1	0.02
IR5 × TKM 6	1672	3	0.18
IR8 × TKM 6	1872	4	0.21
IR20 × TKM 6	2111	0	0.00
IR22 × TKM 6	1997	2	0.10
IR24 × TKM 6	230	2	0.86



Fig. 2. Field reaction of resistant and susceptible selections to the brown planthopper. Susceptible varieties IR8 and IR20 have been killed; resistant selection IR1541-76-3-65 has suffered no visible damage.

and insect resistance were widely tested in various national and international yield trials. One of them was recently named IR26 and released for general cultivation. Such cultivars should help suppress the brown planthopper populations which have been increasing alarmingly in recent years. These cultivars are so resistant that they hardly suffer any damage under population pressures high enough to kill susceptible cultivars (Fig. 2). Since brown planthoppers cannot multiply on resistant cultivars, large-scale cultivation of such cultivars would be the most logical and cheapest way to control this serious pest of rice.

Although brown planthopper is a major pest of rice throughout Asia, 25 resistant cultivars identified to date (9) and TKM 6, come from either South India or Sri Lanka. All of these cultivars belong to the indica group. No Japonica cultivar with resistance to this pest is known, although Kaneda (4) has developed resistant lines with japonica traits from crosses of Mudgo and japonica cultivars.

Numerous lines with improved plant type having either *Bph 1* or *bph 2* have been developed at IIRRI and distributed to breeders and entomologists throughout Asia. Several breeding programs in Asia are now trying to incorporate these resistance genes into their future cultivars. Several resistant selections with either *Bph 1* or *bph 2* were tested for resistance to local biotypes of brown planthopper in Korea, Taiwan, Vietnam, Sri Lanka, British Solomon Islands, and Fiji by local scientists and were found to be resistant. Thus, no evidence for biotype variation in the natural insect populations has yet been found in Asia, al-

though a laboratory biotype to which *Bph 1 Bph 1* genotypes were susceptible was isolated at IIRRI (1). Selections of *bph 2 bph 2* genotype, however, were resistant to this biotype.

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