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Genetic Analysis of Brown Planthopper Resistance in Twenty Varieties of Rice, *Oryza sativa* L.

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Summary. The inheritance of resistance to brown planthopper, *Nilaparvata lugens* (Stol.), of 20 rice cultivars was studied. Single dominant genes that are allelic to *Bph 3* condition the resistance in cultivars 'Ptb 19', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarwala', 'Mudu Kiriyal' and 'Muthumanikam'. Single recessive genes that are allelic to *bph 4* govern the resistance in cultivars 'Gambada Samba', 'Heenhoranamawee', 'Hotel Samba', 'Kahata Samba', 'Kalukuruwee', 'Lekam Samba', 'Senawee', 'Sulai', 'Thirissa' and 'Vellai Illankali'. The resistance in 'Ptb 33', 'Sudu Hondarwala', and 'Sinna Sivappu' is governed by one dominant and one recessive gene which segregate independently of each other. The dominant resistance genes in these cultivars appear allelic to either *Bph 1* or *Bph 3*. Similarly, the recessive genes in these cultivars seem allelic to either *bph 2* or *bph 4*. Further investigations are needed to conclusively determine the allelic relationships of resistance genes in 'Ptb 33', 'Sudu Hondarwala' and 'Sinna Sivappu'.

Key words: *Nilaparvata lugens* (Stol.) – Dominant gene – Recessive gene – Inhibitory gene – Germ plasm

Introduction

The brown planthopper, *Nilaparvata lugens* (Stol.), is one of the most serious rice insect pests. Heavy infestations of the brown planthopper result in complete drying and death of the crop. Because chemical control of the insect is expensive and not very practical emphasis is on the development of improved germ plasm with resistance to this insect.

Several hundred rice cultivars resistant to the brown planthopper have been identified (Pathak and Khush, in press). Genetics of resistance was first investigated by Athwal et al. (1971). A single dominant gene designated *Bph 1* was found to confer resistance in cultivars 'Mudgo', 'MTU 15' and 'Co 22' and a single recessive gene called *bph 2* conveys resistance in 'ASD 7'. *Bph 1* and *bph 2* are closely linked (Athwal and Pathak 1972).

Our earlier investigations revealed that 'TKM 6' is homozygous for *Bph 1* as well as for an inhibitory gene *I-Bph 1*, which inhibits *Bph 1* (Martinez and Khush 1974). Lakshminarayana and Khush (1977) investigated the inheritance of resistance in 28 rice cultivars. Nine of them were found to have *Bph 1* for resistance whereas 16 had *bph 2*. The resistance in 'Ptb 21' was found to be conditioned by one dominant and one recessive gene. The resistance in 'Rathu Heenati' is conferred by a single dominant gene that segregates independently of *Bph 1*. This gene was designated *Bph 3*. Similarly, the resistance in 'Babawee' is governed by a single recessive gene that segregates independently of *bph 2*. This gene was designated as *bph 4*. Our unpublished results show that *Bph 3* and *bph 4* are closely linked.

Two genes for resistance, *Bph 1* and *bph 2*, have been incorporated into improved varieties. Those resistant varieties are now planted on more than 8 million hectares of rice land in Asia (Khush, in press). *Bph 3* and *bph 4* are now being incorporated into improved germ plasm. This study sought additional genes for resistance.

Materials and Methods

Twenty rice cultivars investigated in this study are listed in Table 1. These cultivars were not a random sample of resistant germ plasm. Rather, only those that showed resistance to three known biotypes of brown planthopper at the International Rice Research Institute (IRRI) were included.

Those cultivars were crossed with 'Taichung Native 1' (TN1), a dwarf cultivar with high susceptibility to the brown planthopper. The F_1, F_2, and F_3 progenies from the crosses of 'TN1' were studied to determine the mode of inheritance of resistance. The cultivars with recessive resistance genes were crossed with 'IR1154-

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Table 1. Brown planthopper resistant rice cultivars studied

Cultivar	IRRI Acc. No.	Country of Origin
Ptb 19	6107	India
Ptb 33	19325	India
Gambada Samba	15406	Sri Lanka
Gangala	7733	Sri Lanka
Gangala	15207	Sri Lanka
Heenhoranamawee	15286	Sri Lanka
Horana Mawee	15332	Sri Lanka
Hotel Samba	15206	Sri Lanka
Kahata Samba	15297	Sri Lanka
Kalukuruwee	15279	Sri Lanka
Kuruhondarawala	7731	Sri Lanka
Lekam Samba	15389	Sri Lanka
Mudu Kiriyal	15489	Sri Lanka
Muthumanikam	8960	Sri Lanka
Senawee	15281	Sri Lanka
Sinna Sivappu	15444	Sri Lanka
Sudu Hondarawala	15541	Sri Lanka
Sulai	15421	Sri Lanka
Thirissa	7734	Sri Lanka
Vellai Illankali	15233	Sri Lanka

243', a dwarf selection homozygous for recessive gene *bph 2* for resistance (Martinez and Khush 1974) and 'Babawee' a tall cultivar homozygous for recessive gene *bph 4* for resistance (Lakshminarayana and Khush 1977). Only the F_1 progenies from the crosses of 'IR1154-243' were studied. However, the F_1, F_2, and F_3 progenies from the crosses of 'Babawee' were investigated to determine the allelic relationships of recessive resistance genes to *bph 4*.

The cultivars with dominant resistance genes were crossed with 'IR1539-823', a dwarf selection homozygous for the dominant resistance gene *Bph 1* (IRRI 1973), and 'Rathu Heenati', a tall cultivar homozygous for dominant resistance gene *Bph 3* (Lakshminarayana and Khush 1977). The F_1, F_2, and F_3 progenies from the crosses of 'IR1539-823' and 'Rathu Heenati' with resistant cultivars were investigated to determine the allelic relationships of dominant resistance genes to *Bph 1* and *Bph 3*.

The bulk seedling test (Athwal et al. 1971) was used to evaluate the hybrid materials for brown planthopper resistance. The method consists of planting the test materials in rows about 5 cm apart in 60 × 45 × 10 cm flats. To test the F_3 materials, the 45-cm rows were divided in the middle, thus obtaining 24 subrows per flat. 'IR26' was used as the resistant check and 'TN1' as the susceptible check. A single flat thus had 22 test rows with about 30 seedlings each of the test materials and two rows of checks. One row was planted with a single F_3 family for testing the reaction of F_3 populations.

The seedlings were infested at the one leaf stage with second or third-instar nymphs of the common biotype (biotype 1) reared on 'TN1'. The insects were evenly distributed throughout the flats, with six to seven insects per seedling.

Reactions were recorded when seedlings of the susceptible check had been killed, generally 7 to 8 days after infestation. At this stage resistant seedlings exhibited little or no feeding damage. The F_1 populations were scored on a row basis. Each F_2 seedling was classified as resistant or susceptible. The F_3 lines were classified as either homozygous resistant, segregating or homozygous susceptible.

Results

Inheritance of Resistance

The reactions of F_1, F_2 and F_3 progenies from the crosses of 'TN1' with resistant cultivars are presented in Table 2. The F_1 progenies from the crosses of 'TN1' with 'Ptb 19', 'Ptb 33', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarwala', 'Mudu Kiriyal', 'Muthumanikam', 'Sinna Sivappu' and 'Sudu Hondarwala' were resistant, thereby indicating the dominant nature of resistance in these varieties. The F_2 populations from the crosses of 'TN1' with 'Ptb 19', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarawala', 'Mudu Kiriyal' and 'Muthumanikam' segregated in the ratios of three resistant to one susceptible seedlings, indicating thereby that single dominant genes condition resistance in these cultivars. The conclusions about the monogenic control of resistance in these varieties were confirmed by the reactions of F_3 lines from their crosses. The F_3 families from these crosses segregated in the ratio of 1 resistant: 2 segregating: 1 susceptible expected for monogenic control of resistance. Thus, resistance in each of those seven varieties is conferred by a single dominant gene.

The proportion of resistant and susceptible seedlings in the F_2 populations of 'TN1' × 'Ptb 33' and 'TN1' × 'Sinna Sivappu' agreed closely to the 13:3 ratio expected for independent segregation of one dominant and one recessive gene. The F_3 families from these crosses segregated in the ratio of 7 resistant: 8 segregating: 1 susceptible, thereby confirming the two gene control of resistance in these two varieties. Although the proportion of resistant and susceptible seedlings in the cross 'TN1' × 'Sudu Hondarwala' agreed with the 3:1 ratio expected for monogenic control of resistance ($X^2 = 0.56$), the F_3 population segregated into 7 resistant: 8 segregating: 1 susceptible families. It appears that like 'Ptb 33' and 'Sinna Sivappu', resistance of 'Sudu Hondarwala' is also governed by two independently segregating genes. The F_2 data of this cross fit the 13:3 ratio better than 15:1 ratio. Thus, it appears that one gene is dominant and the other recessive.

The F_1 progenies from the crosses of 'TN1' with 'Gambada Samba', 'Heenhoranamawee', 'Hotel Samba', 'Kahata Samba', 'Kalukuruwee', 'Lekam Samba', 'Senawee', 'Sulai', 'Thirissa' and 'Vellai Illankali' were susceptible (Table 2). The F_2 populations from these crosses segregated in the ratio of 1 resistant to 3 susceptible, thereby indicating that resistance in these cultivars is conferred by single recessive genes. The F_3 families from the crosses of 'TN1' with these cultivars segregated in the ratio of 1 resistant: 2 segregating: 1 susceptible, thus confirming the conclusion about the monogenic recessive control of resistance in these cultivars.

Table 2. Reactions to brown planthopper of F_1 and F_2 populations and F_3 lines from crosses of 'TN1' with resistant cultivars

Cross	F_1 React.	F_2 seedlings			F_3 lines			
		Resist. (no.)	Susc. (no.)	x^2 3:1	Resist. (no.)	Segr. (no.)	Susc. (no.)	x^2 1:2:1
TN1 X Ptb 19	Resist.	373	112	0.93	48	73	30	4.46
TN1 X Ptb 33	Resist.	318	88	2.39[a]	131	130	15	1.68[c]
TN1 X Gambada Samba	Suscep.	103	326	0.22[b]	42	71	39	0.78
TN1 X Gangala (Acc. 7733)	Resist.	246	95	1.49	45	79	27	4.62
TN1 X Gangala (Acc. 15207)	Resist.	417	109	5.13	37	72	41	0.44
TN1 X Heenhoranamawee	Suscep.	103	264	1.83[b]	40	81	29	2.57
TN1 X Horana Mawee	Resist.	271	97	0.36	41	75	33	0.87
TN1 X Hotel Samba	Suscep.	103	420	7.85[b]	30	80	40	2.00
TN1 X Kahata Samba	Suscep.	115	288	2.69[b]	40	74	36	0.24
TN1 X Kalukuruwee	Suscep.	86	295	1.20[b]	35	71	41	0.66
TN1 X Kuruhondarawala	Resist.	300	116	1.84	41	73	30	2.04
TN1 X Lekam Samba	Suscep.	82	308	3.28[b]	38	71	40	0.72
TN1 X Mudu Kiriyal	Resist.	392	152	1.83	46	76	29	3.83
TN1 X Muthumanikam	Resist.	235	96	2.83	37	83	32	1.60
TN1 X Senawee	Suscep.	95	260	0.59[b]	31	77	42	1.92
TN1 X Sinna Sivappu	Resist.	281	58	0.60[a]	60	77	15	3.83[c]
TN1 X Sudu Hondarawala	Resist.	318	115	0.56	73	66	11	2.19[c]
TN1 X Sulai	Suscep.	115	310	0.96[b]	30	86	33	3.61
TN1 X Thirissa	Suscep.	95	249	1.25[b]	41	81	29	2.71
TN1 X Vellai Illankali	Suscep.	80	273	1.03[b]	44	72	34	1.58

[a] = x^2 for 13:3 expected ratio, [b] = x^2 for 1:3 expected ratio, [c] = x^2 for 7:8:1 expected ratio

Table 3. Reactions to brown planthopper of F_2 populations and F_3 lines from crosses of 'IR1539-823' with cultivars having a dominant gene for resistance

Cross	F_2 seedlings			F_3 lines			
	Resist. (no.)	Susc. (no.)	x^2 15:1	Resist. (no.)	Segr. (no.)	Susc. (no.)	x^2 7:8:1
IR1539-823 X Ptb 19	460	37	1.22	70	73	7	0.94
IR1539-823 X Ptb 33	480	6	–	149	2	0	–
IR1539-823 X Gangala (Acc. 7733)	425	30	0.09	72	75	7	0.96
IR1539-823 X Gangala (Acc. 15207)	430	40	4.10	80	60	9	6.29
IR1539-823 X Horana Mawee	410	30	0.24	71	64	14	4.34
IR1539-823 X Kuruhondarawala	450	40	3.06	68	69	11	0.83
IR1539-823 X Mudu Kiriyal	461	25	1.58	65	70	15	3.70
IR1539-823 X Muthumanikam	432	35	1.24	66	71	11	0.47
IR1539-823 X Sinna Sivappu	430	18	–	134	15	2	–
IR1538-823 X Sudu Hondarawala	455	5	–	151	0	0	–

Allele Tests

The F_1, F_2 and F_3 populations from the crosses of 'IR1539-823' (homozygous for *Bph 1*) with 10 cultivars with dominant genes for resistance were studied. As expected, all the F_1 progenies were resistant. The F_2 populations from the crosses of 'IR1539-823' with 'Ptb 19', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarwala', 'Mudu Kiriyal' and 'Mathumanikam' segregated in the ratio of 15 resistant: 1 susceptible seedlings (Table 3) expected on the basis of independent segregation of two dominant genes. The F_3 populations from these crosses segregated in the ratio of 7 resistant: 8 segregating: 1 susceptible families (Table 3) and confirmed the conclusion drawn from the F_2 data that the two dominant genes segregated independently of each other in these populations. Thus, the results presented in Table 3 show that resistance in 'Ptb 19', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarwala', 'Mudu Kiriyal' and 'Muthumanikam' is conferred by single dominant genes that segregate independently of *Bph 1*.

In the F_2 populations of 'IR1539-823' × 'Ptb 33', 'IR1539-823' × 'Sudu Hondarwala', and 'IR1539-823' × 'Sinna Sivappu', 1.25 percent, 1.08 percent and 4.02 percent seedlings, respectively, were classified as susceptible (Table 3). Among 151 F_3 families of 'IR1539-823' × 'Ptb 33', none was susceptible and only two were classified as segregating. In the F_3 population of 'IR1539-823'× 'Sudu Hondarwala', all 151 families were resistant. In the F_3 population of 'IR1539-823' × 'Sinna Sivappu', there were 134 resistant, 15 segregating and 2 susceptible families. The presence of a few susceptible seedlings in the F_2 populations from crosses of resistant cultivars does not necessarily indicate genetic segregation for susceptibility as a small proportion of seedlings of resistant parents are also killed. It therefore appears that no segregation for susceptibility occurred in the crosses 'IR1539-823' × 'Ptb 33' and 'IR1539-823' × 'Sudu Hondarwala'. These observations indicate that one of the two genes in 'Ptb 33' and 'Sudu Hondarwala' is allelic to, or is very closely linked with, *Bph 1*. If the latter, it could be allelic to *bph 2*. Because genetic recombination between *Bph 1* and *bph 2* is rare, allele tests with *Bph 1* cannot clearly reveal whether one of the two genes in 'Ptb 33' and 'Sudu Hondarwala' is *Bph 1* or *bph 2*.

In the F_3 population of 'IR1539-823' × 'Sinna Sivappu', on the other hand, there were two susceptible and 15 segregating families. In the F_2 population of this cross 4.02% susceptible seedlings were recorded. These data indicate genetic segregation for susceptibility in this cross. Thus none of the two genes in 'Sinna Sivappu' may be allelic to *Bph 1* or *bph 2*.

The F_1, F_2 and F_3 populations from the crosses of 'Rathu Heenati' with 10 cultivars, having dominant genes for resistance, were studied to determine the allelic relationships of dominant genes with *Bph 3*. As expected, the F_1 progenies were resistant. No susceptible seedlings were observed in the F_2 populations of 'Rathu Heenati' × 'Ptb 33' and 'Rathu Heenati' × 'Sudu Hondarwala' (Table 4). The F_2 populations of all other crosses exhibited a few susceptible seedlings. However, in the F_3 populations all

Table 4. Reactions to brown planthopper of F_2 populations and F_3 lines from the crosses of 'Rathu Heenati' with cultivars having a dominant gene for resistance

Cross	F_2 seedlings		F_3 lines		
	Resist. (no.)	Susc. (no.)	Resist. (no.)	Segr. (no.)	Susc. (no.)
Rathu Heenati X Ptb 19	433	1	150	0	0
Rathu Heenati X Ptb 33	450	0	147	0	0
Rathy Heenati X Gangala (Acc. 7733)	480	2	150	0	0
Rathy Heenati X Gangala (Acc. 15207)	450	8	150	0	0
Rathu Heenati X Horana Mawee	513	3	147	0	0
Rathu Heenati X Kuruhondarawala	661	1	150	0	0
Rathu Heenati X Mudu Kiriyal	545	3	152	0	0
Rathu Heenati X Muthumanikam	405	10	151	0	0
Rathu Heenati X Sinna Sivappu	448	12	151	0	0
Rathu Heenati X Sudu Hondarawala	520	0	150	0	0

Table 5. Reactions to brown planthopper of F_1 and F_2 populations and F_3 lines from the crosses of 'Babawee' with cultivars having a recessive gene for resistance

Cross	F_1 React.	F_2 seedlings		F_3 lines		
		Resist. (no.)	Susc. (no.)	Resist. (no.)	Segr. (no.)	Susc. (no.)
Babawee X Gambada Samba	Resist.	500	16	148	0	0
Babawee X Heenhoianamawee	Resist.	480	20	150	0	0
Babawee X Hotel Samba	Resist.	480	15	152	0	0
Babawee X Kahata Samba	Resist.	720	15	149	0	0
Babawee X Kalukuruwee	Resist.	580	7	150	0	0
Babawee X Lekam Samba	Resist.	633	25	150	0	0
Babawee X Senawee	Resist.	530	15	147	0	0
Babawee X Sulai	Resist.	468	12	149	0	0
Babawee X Thirissa	Resist.	456	10	150	0	0
Babawee X Vellai Illankali	Resist.	495	5	150	0	0

the families were resistant. These results indicate that dominant genes for resistance in 'Ptb 19', 'Gangala' (Acc. 7733), 'Gangala' (Acc. 15207), 'Horana Mawee', 'Kuruhondarwala', 'Mudu Kiriyal' and 'Muthumanikam' are allelic to *Bph 3*. Because 'Ptb 33', 'Sudu Hondarwala' and 'Sinna Sivappu' each has one dominant and one recessive gene and because *Bph 3* and *bph 4* are closely linked, one of the two genes in these cultivars is allelic either to *Bph 3* or *bph 4*. Because of the tight linkage between *Bph 3* and *bph 4*, allele tests with either do not conclusively reveal whether 'Ptb 33', 'Sudu Hondarwala' and 'Sinna Sivappu' have *Bph 3* or *bph 4*.

The F_1 progenies from the crosses of 'IR1154-243' (homozygous for *bph 2*) with 10 varieties found to have recessive genes for resistance were susceptible, thereby showing that the recessive genes for resistance in these varieties are nonallelic to *bph 2*. However, the F_1 progenies from the crosses of these cultivars with 'Babawee' were resistant (Table 5). In the F_2 populations of these crosses only a few susceptible seedlings were observed. In the F_3 populations of these crosses no segregation for susceptibility was observed and all the F_3 families were resistant. These data indicate that recessive genes for resistance in 10 cultivars, namely 'Gambada Samba', 'Heenhoranamawee', 'Hotel Samba', 'Kahata Samba', 'Kalukuruwee', 'Lekam Samba', 'Senawee', 'Sulai', 'Thirissa' and 'Vellai Illankali', are allelic to *bph 4*.

Discussion

The results of our study show that of the 20 cultivars analyzed, 7 have *Bph 3*, 10 have *bph 4* and 3 have two genes for resistance. 'Ptb 33' and 'Sudu Hondarwala' appear to have a combination of two already known genes, one of which is dominant and the other recessive. However, from the available information it is difficult to conclude whether they have a *Bph 1* and *bph 4*, or a *bph 2* and *Bph 3* combination. One of the two genes in 'Sinna Sivappu' is either *Bph 3* or *bph 4*. The second gene may be different from *Bph 1* and *bph 2*.

More information is needed to confirm these preliminary findings. Thus all the cultivars analyzed in this study have either *Bph 3* or *bph 4*. With the possible exception of a second gene of 'Sinna Sivappu', no new gene for resistance was found.

In addition to these 20 cultivars, 40 were analyzed earlier (Athwal et al. 1971; Athwal and Pathak 1972; Martinez and Khush 1974; Chang 1975; Lakshminarayana and Khush 1977). Thus, of the 60 cultivars analyzed to date, 14 have *Bph 1*, 23 have *bph 2*, 8 have *Bph 3*, 11 have *bph 4* and 4 have two genes for resistance.

More than 200 resistant cultivars are now known. Several of them are being analyzed genetically and hopefully new genes will be found which can be utilized in developing resistant germ plasm.

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