New Genes for Resistance to the Brown Planthopper in Rice[1]

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ABSTRACT

The inheritance of resistance to brown planthoppers (*Nilaparvata lugens* Stal.) was studied in 28 rice (*Oryza sativa* L.) cultivars in the greenhouse. Seven-day-old seedlings were infested with second and third-instar nymphs of brown planthoppers and seedling injury was recorded at 7 to 8 days after infestation.

Single dominant genes that are allelic to *Bph 1* condition the resistance in 'Balamawee', 'CO 10', 'Heenukkulama', 'MTU 9', 'Sinnakayam', 'SLO 12', 'Sudhubalawee', 'Sudurvi 305', and 'Tibiriwewa'. Single recessive genes that are allelic to *bph 2* govern resistance in the cultivars 'Anbaw C7', 'ASD 9', 'Dikwee 328', 'Hathiel', 'Kosatawee', 'Madayal', 'Mahadikwee', 'Malkora', 'M.I. 329', 'Murungakayan 302', 'Ovarkaruppan', 'Palasithari 601', 'PK-1', 'Seruvellai', 'Sinna Karuppan', and 'Vellailangayan'. A single dominant gene also conveys resistance in 'Rathu Heenati', but it segregates independently of *Bph 1* and is designated as *Bph 3*. Similarly, a single recessive gene conveys resistance in 'Babawee' but it segregates independently of *bph 2* and is designated as *bph 4*. The resistance in 'Ptb 21' is controlled by one dominant and one recessive gene. The allelic relationships of these two genes to other genes are not known.

Additional index words: Oryza sativa L., *Nilaparvata lugens* (Stal.), Grassy stunt virus, Insect resistance, Inheritance of resistance, Allelic relationships, Hopperburn.

THE brown planthopper *Nilaparvata lugens* (Stal.) is one of the most serious insect pests of rice (*Oryza sativa* L.) throughout Asia. Light infestations of the insect reduce plant height, crop vigor, number of productive tillers per plant, and number of filled grains per panicle. Heavy infestations cause "hopperburn" – the complete drying and death of the crop. The brown planthopper also transmits grassy stunt virus disease which may seriously damage the rice crop (8).

Populations of planthoppers have generally increased in recent years and severe outbreaks of hopperburn have been reported from several countries. This increased hopper incidence often is attributed to the large-scale cultivation of short-statured and high-tillering rice cultivars and the greater use of N fertilizers. Chemical control of high insect populations for pro-

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Table 1. Brown planthopper resistant cultivars used as parents.

Cultivar	IRRI acc. no.	Country of origin
Anbaw C7	6069	Burma
ASD 9	6380	India
Babawee	8978	Sri Lanka
Balamawee	7752	Sri Lanka
CO 10	3691	India
Dikwee 328	12087	Sri Lanka
Hathiel	7730	Sri Lanka
Heenukkulama	11978	Sri Lanka
Kosatawee	11677	Sri Lanka
Madayal	12001	Sri Lanka
Mahadikwee	11956	Sri Lanka
Malkora	11716	Sri Lanka
M.I. 329	12089	Sri Lanka
Murungakayan 302	11097	Sri Lanka
MTU 9	7919	India
Ovarkaruppan	11963	Sri Lanka
Palasithari 601	12069	Sri Lanka
PK-1	11703	Sri Lanka
Ptb 21	6113	India
Rathu Heenati	11730	Sri Lanka
Seruvellai	8990	Sri Lanka
Sinnakayam	11687	Sri Lanka
Sinna Karuppan	11731	Sri Lanka
SLO 12	6300	India
Sudhubalawee	8900	Sri Lanka
Sudurvi 305	3475	Sri Lanka
Tibiriwewa	11969	Sri Lanka
Vellailangayan	8956	Sri Lanka

longed periods is too expensive for most Asian farmers in the monsoon tropics, where insect generations overlap throughout the year. Further, constant insecticide use aggravates environmental pollution. The most logical and economical way to control this pest therefore appears to be through varietal resistance. Several tall tropical cultivars have been identified that are highly resistant to the brown planthopper (9, 10). Some of these cultivars are being used as sources of resistance in breeding programs at IRRI and elsewhere (6).

Inheritance of resistance to the brown planthopper in six cultivars was investigated by Athwal et al. (2), Athwal and Pathak (1) and Chen and Chang (3). These studies revealed that a dominant gene, *Bph 1,* governs resistance in 'Mudgo', 'MTU 15', 'CO 22,' and 'MGL 2', while a single recessive gene, *bph 2,* conveys resistance in 'ASD 7' and Ptb 18'. *Bph 1* and *bph 2* loci are closely linked and the susceptible cultivars are of *bph1 bph1 Bph2 Bph2* genotype. No recombination has been observed between these two genes. Studies with different biotypes have shown that *Bph1* and *bph2* are two different genes. The resistance of 'H 105' was shown to be due to *bph 2* (7). The first semidwarf cultivar with resistance to the brown planthopper, 'IR26', was released by IRRI in 1973. Its source of resistance is from 'TKM 6' which itself is susceptible. Martinez and Khush (7) showed that TKM 6 is homozygous for *Bph 1* as well as an inhibitor gene *I-Bph 1,* which inhibits *Bph 1.* When TKM 6 is crossed with other susceptible cultivars, a small proportion of segregating progeny are resistant to the brown planthopper as they inherit the *Bph 1* gene but not the *I-Bph 1.*

We have incorporated the two genes for brown planthopper resistance into rices of improved plant type; numerous IRRI breeding lines have either *Bph 1* or *bph 2* for resistance. Of the brown planthopper-resistant cultivars released by IRRI, IR26, 'IR28', 'IR29', 'IR30', and 'IR34' have *Bph 1,* while 'IR32' has *bph 2.* Thus, the breeding program for resistance to brown planthopper is based on two genes. We undertook the present study to identify new genes for resistance to this insect.

MATERIALS AND METHODS

Twenty-eight rice cultivars that IRRI entomologists (9) identified as resistant to brown planthopper were studied (Table 1). All were crossed with 'TN1', which is highly susceptible to the brown planthopper; the F_1 and F_2 progenies were studied to determine the mode of inheritance. We also studied F_3 lines of those cross combinations that did not show clear cut segregation in the F_2.

Cultivars which produced susceptible F_1 hybrids when crossed with TN1 were crossed with IR1154-243, a selection with the recessive gene, *bph 2* for resistance (7). Cultivars, whose F_1 hybrids with TN1 were resistant, were crossed with IR1539-823, a dwarf selection that is homozygous for the dominant gene, *Bph 1* for resistance (5).

To determine the allelic relationships of the genes for resistance, we tested the F_1, F_2, and F_3 generations of crosses with IR1154-243 and with IR1539-823.

The bulk seedling test (2, 7) was used to test the hybrid material for brown planthopper resistance. The method consists of planting the test material in rows about 5 cm apart in 60- × 45- × 10-cm wooden flats. To test the F_3 materials, the 45-cm rows were divided in the middle, thus obtaining 24 sub-rows 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 test materials and two rows of checks. One row was planted to a single F_3 family for testing the F_3 populations.

The seedlings were infested at the one-leaf stage with second- to third-instar nymphs of the common brown planthopper biotype. The insects were evenly distributed throughout the flats, with six to seven insects per seedling.

We recorded the seedling reaction when the seedlings of the susceptible check had been killed, generally about 7 to 8 days after infestation. At this stage, the resistant seedlings had little visible injury from the insects. 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 F_1 hybrids of the following cultivars with TN1 were resistant, indicating that dominant genes govern their resistance: Balamawee, CO 10, Heenukkulama, MTU 9, Ptb 21, Rathu Heenati, Sinnakayam, SLO 12, Sudhubalawee, Sudurvi 305, and Tibiriwewa. The F_1 hybrids of the following cultivars with TN1 were susceptible, indicating that their resistance is recessive: Anbaw C7, ASD 9, Babawee, Dikwee 328, Hathiel, Kosatawee, Madayal, Mahadikwee, Malkora, M.I. 329, Murungakayan 302, Ovarkaruppan, Palasithari 601, PK-1, Seruvellai, Sinna Karuppan, and Vellailangayan.

The F_2 populations of the crosses of TN1 with Heenukkulama, MTU 9, Sinnakayam, SLO 12, Sudhubalawee, Sudurvi 305, and Tibiriwewa segregated as 3 resistant:1 susceptible. This confirms that their resistance is governed by single dominant genes. The χ^2 value for the 3:1 ratio in these cross combinations varied from 0.0 to 3.27 (Table 2).

The X^2 value for 3:1 segregation was significant in the F_2 populations of TN1 × Balamawee, TN1 × CO 10 and TN1 × Rathu Heenati. Therefore, we studied F_3 progenies of these three cross combinations. The F_3 population of TN1 × Ptb 21 was studied also, although F_2 analysis of this cross could not be carried out because seeds were not available.

Table 2. Segregation for resistance to the brown planthopper in the F_2 populations of crosses of TN1 with resistant cultivars.

Cross	No. of seedlings			% susceptible	χ^2 3:1/1:3	P value 3:1/1:3
	Resistant	Susceptible	Total			
TN1 X Anbaw C7	140	511	651	78.50	4.24	0.025-0.050
TN1 X ASD 9	142	471	613	76.84	1.10	0.250-0.500
TN1 X Babawee	208	640	848	75.48	0.10	0.750-0.900
TN1 X Balamawee	691	275	966	28.47	6.19	0.010-0.020
TN1 X CO 10	643	269	912	29.49	9.82	<0.005
TN1 X Dikwee 328	121	433	554	78.16	2.94	0.050-0.100
TN1 X Hathiel	243	636	879	72.35	3.28	0.050-0.100
TN1 X Heenukkulama	435	166	601	27.62	2.20	0.100-0.250
TN1 X Kosatawee	172	626	798	78.45	5.05	0.010-0.030
TN1 X Madayal	152	502	654	76.75	1.07	0.250-0.500
TN1 X Mahadikwee	140	410	550	75.64	0.06	0.750-0.900
TN1 X Malkora	172	588	760	77.37	2.27	0.100-0.250
TN1 X M.I. 329	144	514	658	78.12	3.40	0.050-0.100
TN1 X Murungakayan 302	124	453	577	78.50	3.79	0.050-0.100
TN1 X MTU 9	448	149	597	24.96	0.0	1.0
TN1 X Ovarkaruppan	86	205	291	70.44	3.21	0.050-0.100
TN1 X Palasithari 601	303	940	1,243	75.62	0.25	0.500-0.750
TN1 X PK-1	149	638	787	81.06	15.44	<0.005
TN1 X Rathu Heenati	579	238	817	29.13	7.43	0.005-0.010
TN1 X Seruvellai	118	306	424	72.17	1.81	0.100-0.250
TN1 X Sinnakayam	389	154	543	28.36	3.27	0.050-0.100
TN1 X Sinna Karuppan	55	198	253	78.26	1.43	0.100-0.250
TN1 X SLO 12	470	149	619	24.07	0.28	0.500-0.750
TN1 X Sudhubalawee	515	173	688	25.14	0.01	0.990-0.995
TN1 X Sudurvi 305	396	147	543	27.07	1.24	0.250-0.500
TN1 X Tibiriwewa	212	73	285	25.61	0.05	0.750-0.900
TN1 X Vellailangayan	160	504	664	75.90	0.28	0.500-0.750

Table 3. Classification of F_3 lines of crosses of TN1 with resistant cultivars for their reactions to the brown planthopper.

Cross	No. of families			χ^2		P value	
	Homozygous resistant	Segregating	Homozygous susceptible	1:2:1	7:8:1	1:2:1	7:8:1
TN1 X Anbaw C7	33	58	35	0.84		0.75-0.90	
TN1 X Balamawee	28	59	35	0.92		0.50-0.75	
TN1 X CO 10	38	60	29	1.65		0.25-0.50	
TN1 X Kosatawee	28	73	31	1.61		0.25-0.50	
TN1 X PK-1	34	61	35	0.50		0.25-0.50	
TN1 X Ptb 21	96	132	18	--	2.36	--	0.25-0.50
TN1 X Rathu Heenati	32	59	37	1.11		0.25-0.50	

The F_2 populations of the crosses of TN1 with the following cultivars segregated as 1 resistant:3 susceptible ($X^2 = 0.05$ to 3.79), thereby confirming that their resistance is governed by single recessive genes: ASD 9, Babawee, Dikwee 328, Hathiel, Madayal, Mahadikwee, Malkora, M.I. 329, Murungakayan 302, Ovarkaruppan, Palasithari 601, Seruvellai, Sinna Karuppan, and Vellailangayan. But the F_2 populations of the crosses of TN1 with Anbaw C7, Kosatawee, and PK-1 deviated from the expected ratio of 1 resistant:3 susceptible (Table 2). Hence, their F_3 progenies were investigated.

The deviations from the expected 3:1/1:3 ratios in the F_2 populations may be due to misclassification of a few seedlings. Even in the resistant checks, a few seedlings died. Their death could be due to:

1) attack of certain pathogens such as soil-borne fungi;

2) injury caused by an unusually high population of insects; or

3) incomplete penetrance of the genes for resistance.

Similarly, some susceptible seedlings may escape insect damage and be classified as resistant.

Table 3 shows reactions of the F_3 lines of the various crosses. All of these F_3 lines could be classified as homozygous resistant, segregating and homozygous susceptible. The segregation gave a good fit to a ratio of 1 resistant:2 segregating:1 susceptible in all crosses except TN1 × Ptb 21, thus confirming monogenic control of resistance in the cultivars Anbaw C7, Balamawee, CO 10, Kosatawee, PK-1, and Rathu Heenati. But in the F_3 of the cross TN1 × Ptb 21, 96 families were homozygous resistant, 132 segregating and 18 homozygous susceptible, which fitted the ratio 7:8:1. Apparently, two independent genes confer resistance in Ptb 21.

The segregating F_3 families of the TN1 × Ptb 21 cross were further analyzed to determine the nature of resistance genes in Ptb 21. Of 132 segregating families, 42 had an excess of susceptible seedlings approximating 1 resistant:3 susceptible in each family. Thus, one of the two genes conveying resistance in Ptb 21 is recessive. The remaining 90 segregating F_3 families had an excess of resistant seedlings approximating 3 resistant:1 susceptible in each family. This information, as well as the fact that F_1 progenies of TN1 × Ptb 21 were resistant, indicates that the second gene for resistance in Ptb 21 is dominant. Actually, the 90 segregating families with an excess of resistant seedlings were composed of those segregating only for the dominant gene (3R:1S ratio), and those segregating for the dominant as well as for the recessive gene (13R:3S ratio). The number of seedlings in these rows, however, was not large enough to discriminate between those segregating in ratios of 3:1 and 13:3. Of the 132 segregating families, 25% should segregate 3R:1S; 50%, 13R:3S; and 25% 1R:3S. In other words, the ratio of families with an excess of resistant

Table 4. Reactions to the brown planthopper of F_2 populations and F_3 lines of crosses of IR1539-823 and resistant cultivars with dominant gene for resistance.

Cross	Reactions of F_2 seedlings			Reactions of F_3 lines			
	Total	% susc.	P value 15:1	No. resis.	No. segr.	No. susc.	P value 15:1
IR1539-823 X Balamawee	351	0		110	0	0	
IR1539-823 X CO 10	302	0		128	0	0	
IR1539-823 X Heenukkulama	314	0		129	0	0	
IR1539-823 X MTU 9	356	0		130	0	0	
IR1539-823 X Ptb 21	425	1.40		132	0	0	
IR1539-823 X Rathu Heenati	404	7.42	0.25-0.50	187	99	21	0.50-0.75
IR1539-823 X Sinnakayam	349	0.85		130	0	0	
IR1539-823 X SLO 12	309	0		130	0	0	
IR1539-823 X Sudhabalawee	337	0.89		130	0	0	
IR1539-823 X Sudurvi 305	312	0		130	0	0	
IR1539-823 X Tibiriwewa	327	0.91		128	0	0	

Table 5. Reactions to the brown planthopper of F_2 populations and F_3 lines of crosses of IR1154-243 and resistant cultivars with recessive gene for resistance.

Cross	Reactions of F_2 seedlings			Reactions of F_3 lines			
	Total	% susc.	P value 7:9	No. resis.	No. segr.	No. susc.	P value 7:8:1
IR1154-243 X Anbaw C7	872	3.67		132	0	0	
IR1154-243 X ASD 9	318	2.83		128	0	0	
IR1154-243 X Babawee	1,006	57.65	0.25-0.50	49	71	12	0.10-0.25
IR1154-243 X Dikwee 328	758	0		132	0	0	
IR1154-243 X Kosatawee	686	5.68		132	0	0	
IR1154-243 X Madayal	645	3.01		132	0	0	
IR1154-243 X Mahadikwee	628	2.87		132	0	0	
IR1154-243 X Malkora	558	2.50		132	0	0	
IR1154-243 X M.I. 329	608	4.27		132	0	0	
IR1154-243 X Murungakayan 302	1,017	4.42		132	0	0	
IR1154-243 X Ovarkaruppan	835	3.11		132	0	0	
IR1154-243 X Palasithari 601	863	6.14		132	0	0	
IR1154-243 X PK-1	650	3.38		132	0	0	
IR1154-243 X Seruvellai	1,046	4.01		132	0	0	
IR1154-243 X Sinna Karuppan	704	5.25		132	0	0	
IR1154-243 X Vellailangayan	1,050	1.14		132	0	0	

seedlings (3R:1S + 13R:3S) and those segregating 1R:3S should be 3:1. The observed values of 90 for the former and 42 for the latter fit the expected values ($X^2 = 3.27$). Thus, these data clearly show that resistance in Ptb 21 is controlled by one dominant and one recessive gene, and that these genes segregate independently of each other.

Allele tests. We studied the F_1, F_2, and F_3 populations of crosses of the experimental line IR1539-823 with the 11 cultivars with dominant genes for resistance. All of the F_1 hybrids were resistant. However, the F_1 progenies of crosses in which one or both of the parents have dominant genes yield no information about the allelic relationships.

Table 4 shows that the F_2 populations of 10 crosses did not segregate for susceptibility. Three dead seedlings each were observed in the crosses of IR1539-823 with Sinnakayam, Sudhubalawee, and Tibiriwewa; 6 dead seedlings were found in the cross IR1539-823 × Ptb 21. However, such small proportions of dead seedlings were observed also in the check rows of resistant cultivars. All of the F_3 families of these four crosses, as well as the F_3 families of crosses of IR1539-823 with Balamawee, CO 10, Heenukkulama, MTU 9, SLO 12, and Sudurvi 305 were homozygous resistant (Table 4). Evidently, all these cultivars have the *Bph 1* gene for resistance with the possible exception of Ptb 21. Ptb 21 has a dominant and a recessive gene for resistance. The two genes appear to segregate independently of each other. Because none of the F_3 families from the cross IR1539-823 × Ptb 21 were susceptible, Ptb 21 obviously has either *Bph 1* or *bph 2* gene. Because *Bph 1* and *bph 2* are so closely linked, allele tests with either do not conclusively determine whether Ptb 21 has the *Bph 1* or *bph 2* gene. But this cultivar has one of these two genes, plus another independent gene.

In the F_2 population of IR1539-823 × Rathu Heenati, 7.42% of the seedlings were susceptible (Table 4). This is close to the 15:1 ratio expected ($X^2 = 0.95$) for two independently segregating dominant genes. One-sixteenth of the F_3 families were homozygous susceptible (Table 4), thus confirming that Rathu Heenati has a different dominant gene for resistance that segregates independently of *Bph 1*. The X^2 value (0.18) for 15:1 ratio is non-significant. The number of segregating families was lower than expected as some segregating families may have been misclassified as homozygous resistant.

We studied the F_1, F_2, and F_3 populations of crosses of IR1154-243 with resistant cultivars having recessive genes for resistance. All of the F_1 progenies showed resistant reactions except the F_1 progenies of IR1154-243 × Babawee which were susceptible. These results clearly show that all the cultivars except Babawee have the same recessive gene for resistance as IR1154-243. A few dead seedlings were observed in the F_2 populations of the crosses of these cultivars with IR1154-243 (Table 5) but their proportion was no higher than in the resistant check cultivars. All of the F_3 lines of these crosses, however, were homozygous resistant (Table 5), confirming the conclusion drawn from the reactions of F_1 and F_2 populations.

In the F_2 of the cross IR1154-243 × Babawee, 57.65% of the seedlings were susceptible. These data agree with the 7:9 ratio expected for two independent-

ly segregating recessive genes (Table 5). These results were confirmed by the study of F_3 progenies of this cross. Forty-nine lines were homozygous resistant, 71 were segregating, and 12 were homozygous susceptible (Table 5). These data are in agreement with the expected ratio of 7:8:1 ($X^2 = 3.39$). Among the 71 segregating families, 39 segregated in the ratio of 7 resistant:9 susceptible; the remaining 32 segregated in the ratio of 1 resistant:3 susceptible. The proportions of these families agree with the expected 1:1 ratio ($X^2 = 0.69$). These results indicate that Babawee has a different recessive gene for resistance that segregates independently of *bph 2*.

DISCUSSION

Two genes for resistance to brown planthopper were identified earlier by Athwal et al. (2). One is dominant and was designated *Bph 1*. This gene is present in Mudgo, MTU 15, MGL 2, and CO 22. The other gene is recessive and was designated *bph 2*. It is found in ASD 7, H 105, and Ptb 18. Martinez and Khush (7) showed that TKM 6 is homozygous for *Bph 1*, but possesses *I-Bph 1*, which inhibits *Bph 1*. *Bph 1* from TKM 6 and Mudgo, as well as *bph 2* from Ptb 18, have been incorporated into breeding materials at IRRI and elsewhere. IRRI has recently released six cultivars that are resistant to the brown planthopper. One of these, IR32, has *bph 2* for resistance, whereas the other five, IR26, IR28, IR29, IR30, and IR34, possess *Bph 1*. There is a real danger, however, that when resistant cultivars are grown on a large scale for several years, new biotypes of the insect will develop that can attack these cultivars. In fact, brown planthopper biotypes already exist in India and Sri Lanka to which these cultivars are susceptible.

To stay ahead of the problem, improved cultivars must be developed with different genes for resistance. The present study was undertaken to identify such genes. The results are encouraging — two new genes for resistance have been identified. Rathu Heenati has a dominant gene for resistance which is non-allelic to, and independent of, *Bph 1*. This gene is designated *Bph 3* according to the standard procedure for gene nomenclature (4). Babawee has a recessive gene for resistance which is non-allelic to, and independent of, *bph 2*. This gene is designated *bph 4*. Tests should be conducted on the independence of *Bph 3* and *bph 4*. Ptb 21 is the first known cultivar with two independent genes for resistance to the brown planthopper. One is dominant and the other recessive. One gene is allelic to either *Bph 1* or *bph 2*. The allelic relationships of the second gene to *Bph 3* and *bph 4* are not known. If the second gene is found non-allelic to either of these two genes, it would be the fifth gene for resistance. Detailed analysis of this cultivar is under way.

Because *Bph 1* and *bph 2* are closely linked, they cannot be combined into the same cultivar. However, *Bph 3* and *bph 4* are independent of *Bph 1* and *bph 2*. Now it should be possible to develop resistant cultivars that are homozygous for two resistance genes such as *Bph 1* with either *Bph 3* or *bph 4*, or *bph 2* with either *Bph 3* or *bph 4*. Programs are under way at IRRI to obtain such combinations as well as to combine the *Bph 3* and *bph 4* genes with improved plant type and resistance to other diseases and insects. National rice breeding programs are urged to use the new genes in their breeding programs.

This study is the first attempt to investigate the genetics of resistance to the brown planthopper in a large number of cultivars. As a result, we know that the following cultivars possess the same recessive gene (*bph 2*) for resistance: Anbaw C7, ASD 9, Dikwee 328, Hathiel, Kosatawee, Madayal, Mahadikwee, Malkora, M.I. 329, Murungakayan 302, Ovarkaruppan, Palasithari 601, PK-1, Seruvellai, Sinna Karuppan, and Vellailangayan. 'Dikwee' was found to be identical to Dikwee 328 in morphological traits; 'Podimawee' was found identical to Madayal. Similarly, 'Murungakayan', 'Murungakayan 3', 'Murungakayan 101', 'Murungakayan 104', 'Murungakayan 303', and 'Murungakayan 304' are all identical to Murungakayan 302 and are probably selections from the same basic stock. The F_1 hybrids of Dikwee × TN1 and Podimawee × TN1, and of the Murungakayan selections with TN1, were recessive, thus indicating that these cultivars have *bph 2* for resistance. Further genetic analysis of these cultivars was considered unnecessary.

The cultivars Balamawee, CO 10, Heenukkulama, MTU 9, Sinnakayam, SLO 12, Sudhubalawee, Sudurvee 305, and Tibiriwewa have the same dominant gene (*Bph 1*) for resistance. Pawakkulama was found identical to Heenukkulama, and Andaragahawewa is morphologically similar to Tibiriwewa. The F_1 hybrids of Pawakkulama and Andaragahawewa with TN1 were resistant. We therefore concluded that these two cultivars have *Bph 1* for resistance and discontinued further genetic analysis.

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