

Inheritance of Bacterial Blight Resistance in Rice

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ABSTRACT

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We studied the inheritance and allelic relationships of the genes for resistance to bacterial blight in three rice breeding lines IR1330-3-2, IR944-102, IR1698-241, and in three cultivars, Pelita I/1, Kele, and Chinsurah Boro II. The study of F₁, F₂, F₃, and reciprocal backcross populations of crosses between resistant parents and the susceptible cultivar Taichung Native 1 (TN-1) revealed that resistance in these rices is under monogenic control. The resistance of IR1330-3-2 and Pelita I/1 is incompletely dominant, whereas that of

Kele and Chinsurah Boro II is recessive. The genes that govern resistance in IR944-102 and IR1698-241 show recessive gene action with the method of inoculation used in this study. Evidence from allele tests with known genes for resistance indicates that *Xa4* governs resistance in IR1330-3-2 and Pelita I/1, and *xa5* in Kele and Chinsurah Boro II. Rice breeding lines IR944-102 and IR1698-241 have the same gene for resistance which is closely linked to *Xa4*.

Additional key words: *Oryza sativa*, *Xanthomonas oryzae*, allelic relationships.

Bacterial blight of rice [which is caused by *Xanthomonas oryzae* (Uyeda and Ishiyama) Dowson] causes serious damage to that crop throughout Asia (16). The disease has been identified in Japan since the latter 19th century. In tropical Asia, however, it has been noted only during the last 25 yr. Bacterial blight incidence has increased recently owing to the use of intensive agronomic practices that favor the development of the disease, such as high rates of nitrogenous fertilizers, close spacing, and continuous cropping with susceptible cultivars. Chemical control has not been effective (17). The control of the disease through cultivar resistance is now emphasized in most areas (7).

Numerous rice cultivars that are resistant to Japanese isolates of the bacterium have been identified (1, 2, 4, 10, 11, 21). Three loci for resistance have been identified in several of these cultivars (3, 12, 15, 20, 22); *Xa1* and *Xa2* loci are closely linked, whereas *Xa3*, formerly known as *Xaw*, segregates independently.

Many cultivars that are resistant to Philippine isolates of the bacterium also have been identified (5, 18); these are used in the breeding program at the International Rice Research Institute (9) and elsewhere, and several improved resistant cultivars have been released. Two loci for resistance to Philippine isolates of the bacterium have been identified (6, 13, 14, 19). A dominant gene at the *Xa4* locus conveys resistance in Sigadis, TKM 6, IR20, and IR22; a recessive gene at *xa5* locus controls resistance in BJ 1 and DZ 192. Genes *Xa4* and *xa5* segregate independently of each other (19).

This study was undertaken to investigate the mode of inheritance and the allelic relationships of resistance genes in three breeding lines and three cultivars of rice.

MATERIALS AND METHODS

Table 1 lists the rice cultivars and selections used in this study. For inheritance studies, Taichung Native 1 (TN1), a semidwarf cultivar from Taiwan that is highly susceptible to Philippine isolates of the bacterium, was used as a susceptible parent in crosses with resistant cultivars or lines. Rice line IR20, with resistance derived from TKM 6, is homozygous for *Xa4* and was used in crosses for allelism tests with *Xa4*. Line IR1545-339, which was derived from DZ 192, is homozygous for *xa5* and has improved plant type. It was used in crosses for allelism tests with *xa5*. The remaining six cultivars and selections listed in Table 1 were subjected to genetic analysis.

Selection IR1330-3-2 has an improved plant type and is used extensively in IRRRI's breeding program. It derives its resistance to bacterial blight from W1263. The tall cultivar from India, W1263, derives its resistance from MTU 15. It is derived from the cross MTU 15 × Eswarakorra. Pelita I/1 is a popular, high-yielding cultivar from Indonesia that derives its resistance from Syntha. An improved breeding line, IR944-102, derives its resistance from the Philippine cultivar Malagkit Sungsong. Selection IR1698-241 is an improved type that derives its resistance from Zenith. Selections IR944-102 and IR1698-241, like their resistant parents Malagkit Sungsong and Zenith, respectively, show susceptible reactions at seedling and maximum tillering stages, but they are resistant when inoculated at the booting stage or at 70 or more days of age. Kele and Chinsurah Boro II are tall, traditional cultivars from India that are highly resistant to bacterial blight.

The six cultivars and selections were crossed with TN 1; we investigated segregation for resistance in the F₁, F₂, and F₃ populations, and reciprocal backcross

populations from most of the crosses. The cultivars that showed dominant gene action for bacterial blight resistance were crossed with IR20, and those that showed recessive gene action were crossed with IR1545-339. We studied F₁ and F₂ populations from these crosses to determine the allelic relationships of the resistance genes.

The hybrid populations were inoculated with the PXo 25 strain of the bacterial blight pathogen from The Philippines, most at maximum tillering stage (45-50 days old). The hybrid populations from the crosses involving IR944-102 and IR1698-241 however, were inoculated at the booting stage or 70-75 days after seeding. Cultivar TN1 and the resistant parents were grown along with hybrid populations as checks. Plants were inoculated by the clipping technique (8), which consists of clipping off the leaf tips with scissors, or special inoculation clippers, dipped in a suspension of the bacterial blight organism containing 10⁹ cells/ml. The bacterial pathogen was cultured on the Wakimoto medium.

Disease scores were taken 2 wk after inoculation following the standard system of Kauffman et al. (8). In the F₁, F₂, and backcross populations the disease score was taken on an individual plant basis. Individual plants of the F₃ lines also were scored and each family was classified as homozygous resistant, segregating, or homozygous susceptible.

RESULTS

Inheritance studies.—The F₁ hybrids of the cross IR1330-3-2 × TN1 and of Pelita I/1 × TN1 were moderately resistant, indicating that resistance in IR1330-3-2 and Pelita I/1 is incompletely dominant. The F₁ hybrids of crosses of TN1 with Kele, Chinsurah Boro II, IR944-102, and IR1698-241 were susceptible, showing that these rice lines have recessive resistance. The backcross populations of (IR1330-3-2) × TN1 and (Pelita I/1 × TN1) × TN1 segregated in a resistant:susceptible ratio of 1:1 (Table 2). Their reciprocal backcross progenies were resistant. These results show that resistance in IR1330-3-2 and Pelita I/1 is controlled by a single dominant gene. The backcross progenies of (Kele × TN1) × TN1, (IR944-102 × TN1) × TN1, and (IR1698-241 × TN1) × TN1 were susceptible. But the progenies of their reciprocal backcrosses segregated in a resistant:susceptible ratio of 1:1 (Table 2), thereby showing that resistance is controlled by a single recessive gene in Kele, IR944-102, and IR1698-241.

The reactions of F₂ populations from the crosses of resistant parents with TN1 were determined (Table 3). The F₂ populations of IR1330-3-2 × TN1 and Pelita I/1 × TN1 segregated in a ratio of 3 resistant to 1 susceptible, thus confirming that resistance in IR1330-3-2 and Pelita

TABLE 1. Rice cultivars and selections used in this study and their reactions to bacterial blight, which is caused by *Xanthomonas oryzae*

Cultivar/Selection	Origin	Parents	Reaction
Taichung Native 1	Taiwan	DGWG ^a × Ts'ai-yuan-chung	Susceptible
IR20	IRRI	(Peta/3 × TN 1 ^b) × TKM6	Resistant
IR1545-339	IRRI	IR24 × DZ 192	Resistant
IR1330-3-2	IRRI	(IR8 × Leuang Tawng) × W1263	Resistant
Pelita I/1	Indonesia	IR5 × Syntha	Resistant
IR944-102	IRRI	(TN1 × Malagkit Sungsong) × IR8	Resistant ^c
IR1698-241	IRRI	IR8/4 × Zenith	Resistant ^c
Kele	India		Resistant
Chinsurah Boro II	India		Resistant

^aCoding DGWG stands for Dee-Geo-Woo-Gen.

^bCoding TN 1 stands for susceptible cultivar Taichung Native 1.

^cSusceptible at seedling stage but resistant at booting and postflowering stages.

TABLE 2. Classification of rice plants from reciprocal backcrosses for resistance to bacterial blight, which is caused by *Xanthomonas oryzae*

Cross	Plants (no.)			χ ² (1:1)	P-value (1:1)
	Resistant	Susceptible	Total		
(IR1330-3-2 × TN 1) × TN 1 ^a	44	48	92	0.17	0.50-0.75
(Pelita I/1 × TN 1) × TN 1	39	42	81	0.11	0.50-0.75
(Kele × TN1) × TN-1	...	84	84
(IR944-102 × TN 1) × TN 1	...	79	79
(IR1698-241 × TN 1) × TN 1	...	56	56
(IR1330-3-2 × TN-1) × IR1330-3-2	70	...	70
(Pelita I/1 × TN 1) × Pelita I/1	68	...	68
(Kele × TN 1) X× Kele	46	47	93	0.01	0.90-0.95
(IR944-102 × TN 1) × IR944-102	41	36	77	0.32	0.50-0.75
(IR1698-241 × TN 1) × IR1698-241	45	42	87	0.10	0.50-0.75

^aCoding TN 1 stands for susceptible cultivar Taichung Native 1.

I/1 is controlled by a single dominant gene. On the other hand, the F₂ populations of Kele × TN1, IR944-102 × TN1, and IR1698-241 × TN1 crosses segregated in a ratio of 1 resistant to 3 susceptible, thus confirming that single recessive genes govern the resistance in Kele, IR944-102, and IR1698-241. Analysis of the F₃ confirmed the hypothesis regarding monogenic control of resistance in IR1330-3-2, Pelita I/1, IR944-102, and IR1698-241. The proportion of resistant, segregating, and susceptible F₃ families in each cross closely approximates the 1:2:1 ratio expected for monogenic control of resistance (Table 4).

Allele tests.—The F₁ progenies of the crosses IR1330-3-2 × IR20 and Pelita I/1 × IR20 were resistant. All the plants of the F₂ populations of these two crosses also were resistant (Table 5) which showed that IR1330-3-2 and Pelita I/1 possess *Xa4* for resistance. The F₁ hybrids of Kele × IR1545-339 and Kele × Chinsurah Boro II were also resistant, and the F₂ populations did not segregate for susceptibility (Table 5). Therefore, it appears that Kele and Chinsurah Boro II possess the same recessive gene, *xa5*, for resistance. The F₁ progenies of IR1698-241 × IR1545-339 were susceptible, indicating that these two selections have non-allelic genes. The F₁ progenies of

IR1698-241 × IR20 were resistant and 1.3 percent of the F₂ plants of this cross were susceptible (Table 5), which showed that the recessive gene for resistance in IR1698-241 is closely linked with *Xa4*. The F₁ progenies of IR1698-241 × IR944-102 were resistant and all the F₂ plants of this cross also were resistant (Table 5), thereby showing that these two selections possess the same recessive gene for resistance.

In the F₂ population of Kele × IR22, 19.8% susceptible plants were observed (Table 5). This proportion agrees well with the 18.7 percent expected for two independently segregating genes. These results confirm the conclusions of Petpisit et al. (19) regarding independence of *Xa4* and *xa5*.

DISCUSSION

The results of this study suggest that IR1330-3-2 and Pelita I/1, which derive their resistance from MTU 15 and Syntha, respectively, have gene *Xa4* for resistance. The same gene confers resistance in TKM6, Sigadis, and IR22 (19). The resistance in Kele and Chinsurah Boro II is governed by the recessive gene *xa5*, which also confers resistance in DZ192 and BJI (19). The four cultivars with

TABLE 3. Classification of F₂ plants for bacterial blight resistance from crosses of resistant parents with the susceptible cultivar Taichung Native 1^a

Cross	Plants (no.)			χ^2 (3:1/1:3)	P-value (3:1/1:3)
	Resistant	Susceptible	Total		
IR1330-3-2 × TN 1	911	310	1,221	0.04	0.75-0.90
Pelita I/1 × TN 1	589	223	812	2.62	0.10-0.25
IR944-102 × TN 1	344	914	1,258	3.68	0.05-0.10
IR1698-241 × TN 1	202	558	760	1.01	0.25-0.50
Kele × TN 1	553	1,772	2,325	1.83	0.10-0.25

^aDesignated TN 1 in the indicated crosses.

TABLE 4. Classification of F₃ families for bacterial blight resistance from crosses of resistant parents with the susceptible cultivar Taichung Native 1^a

Cross	Families (no.)			χ^2 (1:2:1)	P-value (1:2:1)
	Homozygous-resistant	Segregating	Homozygous-susceptible		
IR1330-3-2 × TN 1	31	67	28	0.65	0.50-0.75
Pelita I/1 × TN 1	35	63	29	0.57	0.50-0.75
IR944-102 × TN 1	29	58	31	0.10	0.95-0.97
IR1698-241 × TN 1	28	66	29	0.67	0.50-0.75

^aDesignated TN 1 in the indicated crosses.

TABLE 5. Classification of F₂ rice plants for bacterial blight resistance from crosses between resistant parents

Cross	Plants (no.)			Susceptible (%)
	Resistant	Susceptible	Total	
IR1330-3-2 × IR20	1,431	0	1,431	...
Pelita I/1 × IR20	1,475	0	1,475	...
Kele × IR1545-339	750	0	750	...
Kele × Chinsurah Boro II	1,492	0	1,492	...
IR1698-241 × IR20	735	10	745	1.3
IR1698-241 × IR944-102	500	0	500	...
Kele × IR22	897	222	1,119	19.84

recessive genes for resistance are from Bangladesh and the adjoining Indian state of West Bengal.

Selections IR944-102 and IR1698-241 probably have the same gene for resistance, which is non-allelic to *Xa4* and *xa5*. However, it appears closely linked to *Xa4*. Similar observations were made by Murty et al. (14) who found only a few susceptible plants in the F₂ population of Zenith × Sigadis. Because IR1698-241 derives its resistance from Zenith, and because Sigadis was shown to possess *Xa4* for resistance (19), the third locus for resistance to the Philippine isolates of the bacterium is firmly established. This source of resistance is being used in our breeding program.

The gene for resistance in IR944-102 and IR1698-241 appears to be recessive when the segregating populations are inoculated at the booting stage or at about 70-75 days after sowing, but there is some evidence that the pattern of segregation is monogenic dominant when plants are inoculated after flowering or at about 90-95 days after sowing. Plants that are heterozygous for the resistance gene seem to show a susceptible reaction at the booting stage, but they have a resistant reaction at post-flowering stages. Thus, an F₂ population that is inoculated at booting stage would segregate 3 susceptible:1 resistant, as in this study, but the same F₂ population would segregate 1 susceptible:3 resistant if inoculated after flowering. The gene symbol to this locus will be assigned after this problem is thoroughly investigated.

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