Inheritance of Resistance to Bacterial Blight in Seven Cultivars of Rice

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ABSTRACT

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The mode of inheritance and allelic relationships of resistance genes for bacterial blight (caused by *Xanthomonas campestris* pv. *oryzae*) were investigated in seven rice cultivars. Four races of the bacterial blight pathogen from the Philippines were used for studying the disease reactions of parental, F_1, and F_2 populations. The reactions of F_1 and F_2 populations from the crosses of seven cultivars with three testers (TN1, IR22, and CAS209) revealed that ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 each have *Xa-4* and *Xa-10* genes for resistance. The cultivars Arairaj, BR11, and Chhatari have only the *Xa-10* gene. These seven cultivars and CAS209 constitute a new group, distinct from the three known groups of cultivars resistant to bacterial blight. This new group is here designated group IV, or the CAS209 group.

Additional keywords: dominant, nonallelic, *Oryza sativa*, recessive

Bacterial blight of rice (*Oryza sativa* L.), caused by *Xanthomonas campestris* pv. *oryzae* (Ishiyama) Dye, is one of the most widespread diseases of rice in Asia, Africa, and Australia. Its occurrence has also been reported in South America (3). Most rice-breeding programs in Asia are endeavoring to incorporate genetic resistance to bacterial blight in improved cultivars. Rice germ plasm collections have been screened, a large number of donors for resistance selected (2), and 12 resistance genes identified (7-9, 13).

Variation in the host range of the bacterial blight pathogen has been observed (4,5). In the Philippines, four races of *X. c.* pv. *oryzae* have been characterized (6).

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Resistant cultivars have been divided into three groups, on the basis of their reaction to four races of *X. c.* pv. *oryzae* from the Philippines (8). The cultivars of group I are resistant to all four races but express resistance at the booting or flowering growth stages only. These cultivars have gene *Xa-3* for resistance. The cultivars of group II are resistant to race 1, susceptible to races 2 and 3, and moderately resistant to race 4, and they express resistance at the tillering and later stages. These cultivars have gene *Xa-4* for resistance. The cultivars of group III are resistant to races 1, 2, and 3 and moderately susceptible to race 4, and they express resistance at the seeding stage and later. These cultivars have gene *Xa-5* for resistance. Cultivar CAS209 is resistant to race 2 only and thus does not belong to any of the three groups described above. This cultivar has one dominant gene for resistance, *Xa-10* (15).

Recently, we found a few additional cultivars with resistance to race 2. This study analyzes the genetics of resistance in these cultivars.

MATERIALS AND METHODS

Seven cultivars with high levels of resistance to race 2 were included in this study. Of these, four are also resistant to race 1 (Table 1). To study the inheritance of resistance, these cultivars were crossed with TN1, which is susceptible to all four races from the Philippines. The F_1 and F_2 populations of these crosses were inoculated with each of the four races. To determine the allelic relationships, all seven cultivars were crossed with CAS209, and the F_1 and F_2 progenies were inoculated with each of the four races. Since ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 are resistant to race 1, these cultivars were also crossed with IR22, which has the *Xa-4* gene for resistance, and the F_1 and F_2 populations were inoculated with each of the four races.

The parental, F_1, and F_2 populations were grown in the greenhouse. Tillers of each plant were divided into four groups. Each group was tied with a different colored vinyl tie. Tillers with the same colored tie were inoculated with the same race. The bacterial strains PXO 61 (race 1), PXO 86 (race 2), PXO 79 (race 3), and PXO 71 (race 4) were used for inoculation. The inoculum was prepared by culturing bacteria on Wakimoto semisynthetic agar medium (14) and incubating for 3 days at 30 C. The inoculum density was adjusted to about 10^9 cells per milliliter. The plants were inoculated by the clipping method (1) at the maximum tillering stage (50 days after sowing). The upper one-third of the leaves was cut with scissors whose blades had been dipped in the inoculum.

The plants were scored for disease reaction 14 days after inoculation, as being either resistant, moderately resistant, moderately susceptible, or susceptible. The following scale was used for classification of the plants into the various categories: lesion length less than 5 cm = resistant; lesion length more than 5 cm but less than 10 cm = moderately resistant; lesion length more than 10 cm but less than 15 cm = moderately susceptible; lesion length more than 15 cm = susceptible. For genetic analysis, resistant and moderately resistant plants were grouped together and considered resistant, and moderately susceptible and susceptible plants were considered susceptible. A chi-square test was used for determining the goodness of fit to the expected genetic ratios.

RESULTS

Crosses with TN1. The reactions of the F_1 and F_2 populations from the crosses of TN1 with the seven cultivars are presented in Table 2. The F_1 progenies of the crosses with ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 were moderately resistant to race 1, indicating that the resistance to race 1 in these cultivars is conveyed by partially dominant genes. The F_1 progenies were resistant to race 2, thereby showing that resistance to race 2 in these cultivars is governed by dominant genes. All the F_1 progenies were susceptible to race 3, and those of the crosses with ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 were moderately susceptible to race 4. The F_1 progenies of Arairaj, BR11, and Chhatari were susceptible to race 4. The F_2 populations from all crosses with TN1 were entirely susceptible to race 3.

The F_2 populations from the crosses of TN1 with ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 segregated for reaction to races 1 and 2, in a ratio of 3R:1S. Therefore, single dominant genes confer resistance to races 1 and 2. The segregation for reaction to race 4 did not fit any genetic ratio (Table 2). Our previous experience shows that this race is quite unstable, and plants inoculated with it have variable reactions, depending upon the season and temperature effects. The F_2 populations from the crosses of TN1 with Arairaj, BR11, and Chhatari were susceptible to races 1, 3, and 4 but segregated for reaction to race 2 in a ratio of 3R:1S. Therefore, resistance to race 2 in each of these cultivars is governed by a single dominant gene.

Crosses with CAS209. The F_1 progenies of all crosses with CAS209 were resistant to race 2, and no segregation for susceptibility to race 2 was observed in any of the F_2 populations (Table 3). Therefore, the single dominant genes that convey resistance to race 2 in these cultivars are allelic to *Xa-10*. The F_1 progenies of crosses of CAS209 with ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 were moderately resistant to race 1 and moderately susceptible to race 4. The F_2 populations from these crosses segregated for reaction to race 1 in a ratio of 3R:1S, but segregation

Table 1. Rice cultivars used for genetic analysis for resistance to bacterial blight

Cultivar	IRRI[a] accession number	Origin	Reactions to four Philippine races[b] 1	2	3	4
ADT22	5901	India (Tamil Nadu)	R	R	S	MR
Mondba	15813	Senegal	R	R	S	MR
Hegarmanah-2	17733	Indonesia	R	R	S	MR
BR116-3B-53	39559	Bangladesh	R	R	S	MR
Arairaj	26536	Bangladesh	S	R	S	S
BR11	53458	Bangladesh	S	R	S	S
Chhatari	—	India (Madhya Pradesh)	S	R	S	S
TN1	38845	China	S	S	S	S
IR22	11356	IRRI	R	S	S	MR
CAS209	15793	Senegal	S	R	S	S

[a]International Rice Research Institute.
[b]R = resistant; MR = moderately resistant; S = susceptible.

Table 2. Reactions to four races of *Xanthomonas campestris* pv. *oryzae* of F_1 and F_2 progenies from crosses of TN1 with resistant rice cultivars

	Race	Disease reaction[a] F_1	F_2 R	S	X^2 (3:1)[b]
TN1 × ADT22	1	MR	329	97	1.01
	2	R	324	103	0.13
	3	S	0	427	—
	4	MS	347	80	8.60**
TN1 × Mondba	1	MR	207	75	0.30
	2	R	226	58	3.14
	3	S	0	284	—
	4	MS	110	172	—
TN1 × Hegarmanah-2	1	MR	241	85	0.14
	2	R	245	77	0.14
	3	S	0	322	—
	4	MS	237	85	0.26
TN1 × BR116-3B-53	1	MR	366	100	2.93
	2	R	364	110	1.12
	3	S	0	472	—
	4	MS	374	103	3.04
TN1 × Arairaj	1	S	0	467	—
	2	R	364	103	2.05
	3	S	0	467	—
	4	S	0	467	—
TN1 × BR11	1	S	0	465	—
	2	R	360	105	1.33
	3	S	0	465	—
	4	S	0	465	—
TN1 × Chhatari	1	S	0	240	—
	2	R	168	72	2.94
	3	S	0	240	—
	4	S	0	240	—

[a]R = resistant; MR = moderately resistant; MS = moderately susceptible; S = susceptible. The data for the F_2 progenies are numbers of plants with resistant or moderately resistant reactions (R) and with susceptible or moderately susceptible reactions (S).
[b]Chi-square test for goodness of fit to a 3:1 ratio. ** = Significantly different from a 3:1 ratio at $P = 0.01$.

Table 3. Reactions to four races of *Xanthomonas campestris* pv. *oryzae* of F_1 and F_2 progenies from crosses of CAS209 with resistant rice cultivars

		Disease reaction[a]			
			F_2		
	Race	F_1	R	S	X^2 (3:1)[b]
CAS209 × ADT22	1	MR	355	125	0.27
	2	R	480	0	—
	3	S	0	480	—
	4	MS	310	170	27.77**
CAS209 × Mondba	1	MR	364	116	0.17
	2	R	480	0	—
	3	S	0	480	—
	4	MS	322	158	16.04**
CAS209 × Hegarmanah-2	1	MR	346	134	1.08
	2	R	480	0	—
	3	S	0	480	—
	4	MS	336	144	6.40*
CAS209 × BR116-3B-53	1	MR	369	111	0.90
	2	R	480	0	—
	3	S	0	480	—
	4	MS	298	182	42.71**
CAS209 × Arairaj	1	S	0	480	—
	2	R	480	0	—
	3	S	0	480	—
	4	S	0	480	—
CAS209 × BR11	1	S	0	480	—
	2	R	480	0	—
	3	S	0	480	—
	4	S	0	480	—
CAS209 × Chhatari	1	S	0	410	—
	2	R	410	0	—
	3	S	0	410	—
	4	S	0	410	—

[a] R = resistant; MR = moderately resistant; MS = moderately susceptible; S = susceptible. The data for the F_2 progenies are numbers of plants with resistant or moderately resistant reactions (R) and with susceptible or moderately susceptible reactions (S).
[b] Chi-square test for goodness of fit to a 3:1 ratio. * = Significantly different from a 3:1 ratio at $P = 0.05$; ** = significantly different from a 3:1 ratio at $P = 0.01$.

Table 4. Reactions to four races of *Xanthomonas campestris* pv. *oryzae* of F_1 and F_2 progenies from crosses of IR22 with four resistant rice cultivars

		Disease reaction[a]			
			F_2		
	Race	F_1	R	S	X^2 (3:1)[b]
IR22 × ADT 22	1	R	430	0	—
	2	R	324	106	0.001
	3	S	0	430	—
	4	MR	430	0	—
IR22 × Mondba	1	R	480	0	—
	2	R	344	127	0.68
	3	S	0	480	—
	4	MR	478	0	—
IR22 × Hegarmanah-2					
	1	R	326	0	—
	2	R	230	96	3.20
	3	S	0	326	—
	4	MR	326	0	—
IR22 × BR116-3B-53	1	R	471	0	—
	2	R	345	126	0.68
	3	S	0	471	—
	4	MR	471	0	—

[a] R = resistant; MR = moderately resistant; S = susceptible. The data for the F_2 progenies are numbers of plants with resistant or moderately resistant reactions (R) and with susceptible or moderately susceptible reactions (S).
[b] Chi-square test for goodness of fit to a 3:1 ratio.

for reaction to race 4 did not agree with any particular ratio.

Crosses with IR22. Since ADT22, Mondba, Hegarmanah-2, and BR116-3B-53 are resistant to race 1 and moderately resistant to race 4, only these four cultivars were crossed with IR22 (Table 4). The F_1 progenies of the four crosses were resistant to races 1 and 2, susceptible to race 3, and moderately resistant to race 4. No segregation for susceptibility to race 1 was observed in any populations. Similarly, all the F_2 plants of these populations were moderately resistant to race 4. Therefore resistance to race 1 and moderate resistance to race 4 in these cultivars are conveyed by single dominant genes allelic to *Xa-4*. Resistance to race 2 in the F_1 progenies and segregation for resistance to race 2 in the F_2 progenies is due to the presence of *Xa-10* in them.

DISCUSSION

Genetic analysis showed that all seven cultivars have gene *Xa-10* for resistance to race 2. Only one cultivar with this gene was known before. Thus, the cultivars possessing *Xa-10* constitute an additional group of donors for resistance to bacterial blight. This is designated group IV, or the CAS209 group. Several other cultivars probably belonging to this group have been identified recently and are being genetically analyzed.

Four of the seven cultivars are also resistant to race 1 and moderately resistant to race 4. The genetic analysis showed that these cultivars have *Xa-4* in addition to *Xa-10*. *Xa-4* conveys a high level of resistance to race 1 and a moderate level of resistance to race 4. However, as pointed out by Saha and Khush (10), segregation for resistance to race 4 in crosses of cultivars with *Xa-4* is never very clear-cut. Similar results were observed in this study, as the crosses of CAS209 with ADT22, Mondba, Hegarmanah-2, and BR116-3B-53, which segregated for *Xa-4*, did not segregate in any specific ratio for reaction to race 4. Mondba and Hegarmanah-2 were reported earlier to have *Xa-4* by Singh et al (12) and Sidhu et al (11), respectively. However, those studies used only race 1 for inoculating the segregating populations and thus failed to detect the presence of *Xa-10* in these cultivars. The four cultivars with *Xa-4* and *Xa-10* constitute a subgroup within group IV.

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