

## Dominance Reversal of a Bacterial Blight Resistance Gene in Some Rice Cultivars

G. S. Sidhu and Gurdev S. Khush

Postdoctoral Fellow and Plant Breeder, International Rice Research Institute, Los Baños, Philippines.  
Accepted for publication 21 September 1977.

### ABSTRACT

SIDHU, G. S., and G. S. KHUSH. 1978. Dominance reversal of a bacterial blight resistance gene in some rice cultivars. *Phytopathology* 68: 461-463.

The inheritance of resistance to *Xanthomonas oryzae* isolate PXO61 (from the Philippines) in five rice cultivars was studied. The same gene confers resistance in the five cultivars. The pattern of segregation indicates a monogenic recessive factor when the plants are inoculated at the booting stage, but it is monogenic dominant when the plants are inoculated

during flowering. The dosage effect of the resistance gene causes this reversal of dominance because the heterozygous plants are susceptible at booting and resistant during flowering. This gene, designated *Xa6*, is linked to *Xa4*, another dominant gene for resistance, with a crossover value of 26%.

*Additional key words:* *Oryza sativa* L., *Xanthomonas oryzae*, allelic relationships, dominant, recessive, monogenic.

Previous work (6) showed that a single gene governs resistance to bacterial blight, which is caused by *Xanthomonas oryzae* (Uyeda and Ishiyama) Dowson, in two breeding lines of rice (*Oryza sativa* L.), IR944-102 and IR1698-241. Allele tests revealed that these lines have allelic genes for resistance, and like their parents Malagkit Sungsong (M. Sungsong) and Zenith, respectively, are susceptible at the seedling and maximum-tillering (40-45 days after sowing) stages. However, these lines are resistant at booting (70-75 days after sowing) and at flowering (90-95 days after sowing).

When segregating populations were inoculated at booting, the gene for resistance in IR944-102 and IR1698-241 appeared to be recessive. However, the pattern of segregation was monogenic-dominant when the plants were inoculated after flowering. This reversal of dominance suggested that the dominance relationship depends upon the stage of growth of the plant when exposed to the inoculum (6). Heterozygous plants may be susceptible at booting but resistant at flowering.

The present study was designed to investigate the possibility of reversal of dominance and to analyze the allelic relationships of genes for resistance in five rices which appeared to have a similar type of gene action.

### MATERIALS AND METHODS

The rice cultivars used in the study are listed in Table 1. A dwarf cultivar from Taiwan, Taichung Native 1 (TN1), which is susceptible to bacterial blight, was used as a susceptible parent in the crosses. Cultivar IR22, homozygous for *Xa4*, a dominant gene for resistance to bacterial blight, and breeding line IR1545-339, homozygous for *xa5*, a recessive gene for resistance to bacterial blight (7), were used in crosses for allele tests.

Four of the remaining five cultivars are tall traditional

cultivars from the Philippines. All five cultivars are susceptible to bacterial blight at the seedling stage but are resistant at booting and flowering. Malagkit Sungsong and Nagkayat are glutinous rices and have identical morphology. Dayaggot Qan Binuggon (D. Binuggon) and Pinidwa Qan Qipugo Qekek (P. Qekek) originated from the mountain provinces of the Philippines. Zenith is a semi-improved cultivar from the USA.

Five tall cultivars were crossed with TN1 and the F<sub>1</sub>, F<sub>2</sub>, and F<sub>3</sub> progenies were evaluated for bacterial blight reaction. The F<sub>1</sub> progenies were evaluated at booting and at flowering. The F<sub>2</sub> and F<sub>3</sub> progenies of all crosses, except TN1 × M. Sungsong, were evaluated at booting only. However, the F<sub>2</sub> and F<sub>3</sub> progenies of TN1 × M. Sungsong were evaluated at both booting and flowering. The reaction of each F<sub>3</sub> family of this cross was compared with the reaction of ancestral F<sub>2</sub> plants at booting and flowering.

Four tall cultivars, D. Binuggon, Nagkayat, P. Qekek,

TABLE 1. Reaction of rice cultivars to bacterial blight

Cultivar	IRRI <sup>a</sup> Acc. No.	Origin	Reaction
Taichung Native 1 (TN1)	105	Taiwan	Susceptible
IR22	11356	IRRI	Resistant
IR1545-339	32624	IRRI	Resistant
Dayaggot Qan Binuggon (D. Binuggon)	9134	Philippines	Resistant <sup>b</sup>
Malagkit Sungsong (M. Sungsong)	755	Philippines	Resistant <sup>b</sup>
Nagkayat	584	Philippines	Resistant <sup>b</sup>
Pinidwa Qan Qipugo Qekek (P. Qekek)	23360	Philippines	Resistant <sup>b</sup>
Zenith	4038	U.S.A.	Resistant <sup>b</sup>

<sup>a</sup>Acc. No. = Accession number in IRRI germplasm bank.

<sup>b</sup>Susceptible at the seedling stage but resistant at booting and at flowering.

and Zenith, were crossed with M. Sungsong for allele tests within this group. Both F<sub>1</sub> and F<sub>2</sub> progenies of these crosses were tested for bacterial blight resistance. The tall varieties also were crossed with IR22 and the F<sub>1</sub> and F<sub>2</sub> progenies were evaluated for bacterial blight resistance. Only the F<sub>1</sub> progenies from the crosses of IR1545-339 with tall cultivars were tested for resistance.

Isolate PXO61 of *Xanthomonas oryzae* from the Philippines was used to inoculate the parents and hybrid populations. This isolate is similar to isolate PXO25 used by Olufowote et al. (6) in the reactions it elicits on a set of varieties. The plants were inoculated by the clipping technique (3) and inoculum was prepared from cultures grown on modified Wakimoto's medium (2) for 5 days at 28 C and suspended in distilled water at a concentration of about 10<sup>9</sup> cells/ml.

Disease scores were recorded 2 wk after inoculation, based on the scoring system of Kauffman et al. (3). In the F<sub>1</sub> and F<sub>2</sub> populations, the individual plants were classified as resistant or susceptible. Individual plants in the F<sub>3</sub> families were scored and each family was then classified as resistant, segregating, or susceptible.

### RESULTS

**Inheritance studies.**—The F<sub>1</sub> progenies of the crosses of TN1 with resistant varieties were susceptible at booting (Table 2) but resistant at flowering. The F<sub>2</sub> populations and F<sub>3</sub> families were inoculated at booting. All the F<sub>2</sub> populations segregated in the ratio of one resistant to three susceptible plants. This indicated that resistance at booting in all of the cultivars is governed by a single recessive gene. The F<sub>3</sub> data of four crosses also fitted the 1:2:1 ratio expected for monogenic control of resistance. The F<sub>3</sub> families from the cross TN1 × Nagkayat were not studied because Nagkayat and M. Sungsong are similar in plant morphology.

The F<sub>1</sub> and F<sub>2</sub> progenies from the crosses of M. Sungsong with the other four were all resistant (Table 2), suggesting that the same gene confers resistance in all five varieties.

**Reversal of dominance.**—In testing the hypothesis of reversal of dominance, the F<sub>2</sub> plants from the cross TN1 × M. Sungsong were inoculated at booting and at flowering and the reactions of the F<sub>3</sub> lines were compared with the reactions of ancestral F<sub>2</sub> plants at both stages. The one resistant (129 plants) to three susceptible (313 plants) ratio ( $\chi^2 = 4.17$ ) expected for monogenic recessive control of resistance was noted after the plants were inoculated at booting (Table 2). When the same population was inoculated at flowering, the ratio of three resistant (314 plants) to one (128 plants) susceptible, expected for monogenic dominant control of resistance, was obtained.

Of 201 F<sub>3</sub> families derived from randomly harvested F<sub>2</sub> plants of this cross, 59 were susceptible, 55 were resistant, and 87 were segregating. All 59 susceptible families originated from F<sub>2</sub> plants which were classified as susceptible at both stages of growth. All of the 55 resistant families originated from F<sub>2</sub> plants which were classified as resistant at both stages. All of the 87 segregating families originated from plants which were classified as susceptible at booting and resistant at flowering. As expected, in the segregating families there were more susceptible than resistant plants when inoculated at booting, whereas more resistant than susceptible plants were recorded when the plants were inoculated at flowering.

**Allele tests with other resistance genes.**—The F<sub>1</sub> hybrids of IR1545-339 crossed with five cultivars were susceptible when inoculated at booting. This indicates that the gene which governs resistance in these five cultivars is non-allelic to *xa5*. As expected, the F<sub>1</sub> progenies of the cross of five cultivars with IR22 were resistant. In the F<sub>2</sub> populations of these crosses (inoculated at flowering), a few susceptible plants were observed (Table 3). The proportion of susceptible plants in these populations, however, was lower than expected on the basis of independent segregation of two dominant genes. The  $\chi^2$  values for a 15:1 ratio were significant. The data suggest that these two genes are linked with a crossover value of 26%. Similar observations were made by Murty et al. (5) and Olufowote et al. (6).

TABLE 2. Classification of F<sub>1</sub> and F<sub>2</sub> plants and F<sub>3</sub> families for bacterial blight resistance from crosses of TN1 and Malagkit Sungsong with resistant cultivars

Cross	F <sub>1</sub>			F <sub>2</sub>			F <sub>3</sub>			
	Booting	Flowering		R <sup>a</sup>	S	$\chi^2$ 1:3	R	Segr.	S	$\chi^2$ 1:2:1
TN1 ×										
M. Sungsong	S	R	Booting	129	313	4.17	55	87	59	3.79
			Flowering	314	128	3.69 <sup>b</sup>	25	72	23	4.89
D. Binuggon	S	R	Booting	148	370	3.42	...	...	...	...
Nagkayat	S	R	Booting	125	313	4.17	...	...	...	...
P. Qelek	S	R	Booting	99	256	1.57	22	60	38	4.26
Zenith	S	R	Booting	145	355	4.26	30	59	41	2.96
M. Sungsong ×										
D. Binuggon	R		Booting	441	0					
Nagkayat	R		Booting	442	0					
P. Qelek	R		Booting	424	0					
Zenith	R		Booting	576	0					

<sup>a</sup> Number of plants that were: R=resistant; S=susceptible; or Segr.=segregating.

<sup>b</sup>  $\chi^2$  for 3:1.

TABLE 3. Classification of F<sub>2</sub> plants for bacterial blight resistance from the crosses of IR22 with resistant cultivars inoculated at flowering

Cross	F <sub>2</sub>		$\chi^2$ 15:1	r value <sup>a</sup>
	Resistant (no.)	Susceptible (no.)		
IR22 × D. Binuggon	503	5	24.03	0.20
IR22 × M. Sungsong	487	7	19.64	0.24
IR22 × Nagkayat	532	8	20.94	0.25
IR22 × P. Qelek	432	10	11.98	0.30
IR22 × Zenith	528	12	14.94	0.31
Pooled	2,482	42	18.38	0.26

<sup>a</sup>r: recombination value.

### DISCUSSION

The reactions of all the F<sub>3</sub> families from the cross TN1 × M. Sungsong agreed with that expected on the basis of dosage effect of the resistance gene. Apparently, the gene can express itself at booting, only when in two dosages. Heterozygous plants with one dose of the resistance allele are susceptible at booting. However, at flowering, one dose is enough for expression of resistance. Therefore, the reversal of dominance can be explained on the basis of the dosage effect of the resistance gene at a specific stage of growth of the plant when exposed to bacterial inoculum.

Five rice cultivars, Zenith, M. Sungson, Nagkayat, D. Binuggon, and P. Qelek, appear to have the same gene for resistance to the Philippine isolate PXO61 of the bacterial blight organism. According to the international rules of nomenclature (1) we have assigned gene symbol *Xa6* to this locus.

Of the five cultivars known to possess *Xa6*, four are

from the Philippines and one (Zenith) is from USA. Many of the USA. rice cultivars were bred from crosses involving cultivars introduced from the Philippines in the earlier part of this century. Thus, Zenith may have inherited *Xa6* from introduced Philippine germplasm. The distribution of *Xa6* seems to be limited to the Philippine cultivars. Similarly, all the cultivars with *xa5* originated from the Indian subcontinent. In contrast, however, *Xa4* is more widely distributed (4).

### LITERATURE CITED

1. INTERNATIONAL RICE COMMISSION. 1959. Genetic symbols for rice recommended by the International Rice Commission. IRC Newslett. 8:1-6.
2. KARGANILLA, A., M. P. NATURAL, and S. H. OU. 1973. Comparative study on the different media for *Xanthomonas oryzae*. Philipp. Agric. 57:141-152.
3. KAUFFMAN, H. E., A. P. K. REDDY, S. P. Y. HSIEH, and S. D. MERCA. 1973. An improved technique for evaluating resistance of rice varieties to *Xanthomonas oryzae*. Plant Dis. Rep. 56(6):537-541.
4. LIBROJO, V., H. E. KAUFFMAN, and G. S. KHUSH. 1976. Genetic analysis of bacterial blight resistance in four varieties of rice. Sabrao J. 8:105-110.
5. MURTY, V. V. S., G. S. KHUSH, and N. F. JENSEN. 1973. Inheritance of resistance to bacterial leaf blight, *Xanthomonas oryzae* (Uyeda and Ishiyama) Dowson in rice. I. Allelic relationships of resistance genes in donor varieties. Japn. J. Breed. 23:325-328.
6. OLUFOWOTE, J. O., G. S. KHUSH, and H. E. KAUFFMAN. 1977. Inheritance of bacterial blight resistance in rice. Phytopathology 66:772-775.
7. PETPISIT, V., G. S. KHUSH, and H. E. KAUFFMAN. 1977. Inheritance of resistance to bacterial blight in rice. Crop Sci. 17:551-554.