Inheritance of Resistance to Blast in Some Traditional and Improved Rice Cultivars

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ABSTRACT

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Rice blast, caused by *Pyricularia oryzae*, is one of the most destructive rice diseases. Information on the inheritance of blast resistance is useful in breeding resistant cultivars. Five improved and four traditional cultivars were evaluated for the genetics of resistance to three Philippine isolates of *P. oryzae*. Complete isolate-specific resistance was generally controlled by one or two dominant genes. A recessive gene controlled resistance in IR54 against one isolate. Linkage analyses showed that resistance to different isolates was conditioned by genes at different loci. At least seven genes conditioned resistance to the three isolates. Linkage between genes for resistance to different isolates was detected.

Additional key words: disease resistance, *Oryza sativa* L., plant genetics, *Pyricularia oryzae* Cav.

Rice blast, caused by *Pyricularia oryzae* Cav., is one of the most important fungal diseases of rice (*Oryza sativa* L.) because it occurs in all rice culture types and can cause severe damage under favorable conditions (13). In the past, blast was perhaps the most destructive disease of tropical lowland rice. With the introduction of modern rice cultivars and the expansion of irrigation, the disease is now important only when drought occurs or when susceptible cultivars are grown, such as recently in the Indian state of Tamil Nadu (11). However, the disease continues to be an important constraint to higher productivity in rainfed lowland and upland rice. The use of resistant cultivars should be the most economical method of blast control for these rice-growing environments. Basic information on the genetics of blast resistance is required for effective blast resistance breeding and for better understanding of the interaction between *P. oryzae* and the rice plant.

Systematic genetic studies on resistance to rice blast have been conducted mostly in temperate countries, usually with japonica rices. Thirteen genes for blast resistance have been identified in Japan (10). No systematic genetic studies of the blast resistance of indica rices in the tropics have been done. Investigation is now under way at the International Rice Research Institute (IRRI) to identify the major resistance genes for tropical *P. oryzae* races (4,12). Genetic studies at IRRI (3,12) indicated that the traditional rice cultivars studied generally had one or two dominant resistance genes effective against each fungus isolate. Of 51 cultivar/isolate combinations examined, 30 had two dominant genes and 15 had a single dominant gene for resistance. Very few recessive resistance genes were identified. In most cases, resistance to different isolates was conditioned by different genes, although linkage among these genes was common (H. S. Suh and R. Srilingam, *unpublished*).

Improved rice cultivars developed at IRRI, such as IR36, are grown extensively in many countries. The inheritance of resistance to blast in such cultivars has not been studied. The objectives of this study were 1) to determine the inheritance of blast resistance to specific isolates of *P. oryzae* in improved IR cultivars and cultivars commonly used as resistant parents and 2) to identify the linkage relationships of these resistance genes.

MATERIALS AND METHODS

Five improved cultivars (IR36, IR46, IR54, IR56, and IR60) and four traditional resistant cultivars (Carreon, Pai-kan-tao, Pankhari 203, and Tetep) were used in this study. Only IR46 has one of the traditional resistant cultivars in its background. It was from a four-way cross in which one parent was derived from a cross with Tetep. IR56 and IR60 were derived from the same cross, in which IR36 was a parent. Three Philippine isolates of *P. oryzae*, PO6-6, IK81-3, and 43, belonging to the international races IB-47, IA-125, and IA-127, respectively, were used. All the cultivars are resistant to these three isolates, except IR36, IR46, and IR60, which are susceptible to isolate PO6-6. The line CR155-5029-216 served as the susceptible parent except in crosses with IR60 (for isolate IK81-3) and with Tetep (for all isolates), where the cultivar CO39 was the susceptible parent. Inheritance was determined using disease reactions of F_1, F_2, F_3 and BC_1 ($F_1 \times$ susceptible parent) generations with certain omissions, as noted under Results. Inheritance of resistance to isolate 43 in IR54, IR56, and Pankhari 203 was not studied.

Seeds were sown in three sets in separate plastic trays 37 × 26 × 11 cm. One set contained the parent cultivars, F_1, and BC_1 seeds, and

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the other sets contained F_2 and F_3 generations. About 20 F_2 seeds were uniformly planted in each of eight rows in each tray. Two sets of the F_3 lines were sown for inoculation with different isolates. About 214 F_3 lines were grown per cross, with 15–20 seedlings for each line planted in a row. The parents, F_1, BC_1, and F_2 generations of each cross were tested together, four cross combinations at a time. The F_3 generation was tested separately after the other generations were completed.

Inoculum was prepared as described previously (1). Seedlings were allowed to grow in a greenhouse and were inoculated 2–3 wk after seeding, at about the four-leaf stage, by spraying each tray with 50 ml of an aqueous spore suspension of about 5×10^4 conidia per milliliter. The inoculated seedlings were kept in a dew chamber for 24 hr at 26 C, then transferred to an air-conditioned room (24–28 C) in the greenhouse with natural lighting from a glass ceiling. Disease reactions were scored about 7 days after inoculation, when typical lesions appeared on the leaves of susceptible plants.

A five-category system (2) was used to rate each seedling: 0 = no lesions; 1 = small brown specks of pinhead size; 2 = larger brown specks; 3 = small, roundish to slightly elongated, necrotic gray spots, about 1–2 mm in diameter with a brown margin; 4 = a typical blast lesion, elliptical, longer than 2 mm. Seedlings rated 0–2 were considered resistant, and those rated 3–4 were considered susceptible. For the F_2, individual seedlings were classified as resistant or susceptible. F_3 lines were classified as resistant (R), segregating (H), and susceptible (S) on the basis of the reaction of a whole line. The grouped data from each cross combination and fungus isolate were analyzed by the chi-square method.

RESULTS

All F_1 plants from all S × R crosses were resistant to the isolates IK81-3 and 43, which indicated that resistance in the nine cultivars is dominant. The F_1 plants, except those from the cross with IR54, were resistant to isolate PO6-6. This implies that resistance to the isolate is recessive in IR54 and dominant in the other cultivars. Except for crosses with IR54 (isolate PO6-6) and IR60 (isolate 43), where many intermediate reactions were observed, distributions of disease scores were distinctly bimodal in the F_2 and BC_1 (Table 1). The F_3 data generally confirmed the ratios observed in the F_2 (Table 2).

The data for isolate PO6-6 indicate that resistance in IR56, Pai-kan-tao, Tetep, and Pankhari 203 is controlled by a single

TABLE 1. Reactions of F_2 and BC_1 populations of crosses between resistant and susceptible parents to three isolates of *Pyricularia oryzae*

Resistant parent	Generation	No. of plants observed for each class[a]					No. of plants[b]		Expected ratio	Probability
		0	1	2	3	4	R	S		
Isolate PO6-6										
IR54	F_2	40	49	25	52	253	114	305	1:3	0.25–0.50
	BC_1	0	1	2	2	46	3	48	0:1	...
IR56	F_2	278	1	0	3	93	279	96	3:1	0.75–0.90
	BC_1	17	0	0	0	22	17	22	1:1	0.50–0.75
Carreon	F_2	456	3	0	10	30	459	40	15:1	0.10–0.25
	BC_1	19	3	0	4	4	22	8	3:1	>0.99
Pai-kan-tao	F_2	229	0	0	7	36	229	43	3:1	<0.01
	BC_1	15	9	0	4	17	24	21	1:1	0.75–0.90
Pankhari 203[c]	F_2	172	0	1	11	43	173	54	3:1	0.50–0.75
Tetep	F_2	193	14	3	8	57	210	65	3:1	0.50–0.75
	BC_1	39	0	0	2	39	39	41	1:1	0.90–0.95
Isolate IK81-3										
IR36	F_2	364	1	0	9	15	365	24	15:1	0.95–0.99
	BC_1	49	1	2	8	13	52	21	3:1	0.50–0.75
IR46	F_2	331	0	1	5	34	332	39	15:1	<0.01
	BC_1	38	0	0	2	11	38	13	3:1	0.90–0.95
IR54	F_2	366	0	0	3	14	366	17	15:1	0.10–0.25
	BC_1	40	2	0	6	9	42	15	3:1	0.90–0.95
IR56	F_2	340	1	1	1	17	342	18	15:1	0.25–0.50
	BC_1	64	7	2	5	17	73	22	3:1	0.75–0.90
IR60[c]	F_2	200	1	0	6	1	201	7	15:1	0.10–0.25
Carreon	F_2	294	0	0	9	16	294	25	15:1	0.25–0.50
	BC_1	24	7	0	4	7	31	11	3:1	>0.99
Pai-kan-tao	F_2	230	0	0	2	12	230	14	15:1	0.75–0.90
	BC_1	23	4	0	6	7	27	13	3:1	0.25–0.50
Pankhari 203	F_2	233	0	0	8	6	233	14	15:1	0.75–0.90
	BC_1	28	0	0	4	6	28	10	3:1	>0.99
Tetep	F_2	238	1	0	0	13	239	13	15:1	0.50–0.75
	BC_1	57	1	1	4	16	59	20	3:1	0.90–0.95
Isolate 43										
IR36	F_2	270	4	0	10	62	274	72	3:1	0.05–0.10
	BC_1	23	0	0	0	19	23	19	1:1	0.50–0.75
IR46	F_2	269	9	0	1	22	278	23	15:1	0.25–0.50
	BC_1	82	6	0	3	25	88	28	3:1	0.90–0.95
IR60	F_2	213	32	85	44	104	330	148	3:1	<0.01
	BC_1	17	9	5	8	23	31	31	1:1	0.75–0.90
Carreon[c]	F_2	331	31	2	20	88	364	108	3:1	0.25–0.50
Pai-kan-tao[c]	F_2	368	5	1	7	12	374	19	15:1	0.25–0.50
Tetep	F_2	392	2	1	8	17	395	25	15:1	0.75–0.90
	BC_1	26	2	1	1	10	29	11	3:1	0.75–0.90

[a] Resistance was rated 0–4 as follows: 0 = no lesions; 1 = small brown specks of pinhead size; 2 = larger brown specks; 3 = small, roundish to slightly elongated, necrotic gray spots 1–2 mm diameter with a brown margin; and 4 = a typical blast lesion, elliptical, more than 2 mm long.

[b] R = resistant (scores 0–2) and S = susceptible (scores 3–4).

[c] BC_1 seed were not available for Pankhari 203 (isolate PO6-6), IR60 (isolate IK81-3), and Carreon and Pai-kan-tao (isolate 43).

dominant gene in each cultivar, whereas resistance in IR54 is controlled by a single recessive gene. The F_2 from the cross with Pai-kan-tao did not show a good fit to the expected ratio (3R:1S), but this ratio was confirmed in the BC_1 and F_3 populations. Resistance in Carreon was controlled by dominant genes at two loci. Three plants in the BC_1 population of IR54 showed resistant reactions (scores 1 and 2), presumably caused by disease escape, because even when a susceptible cultivar is inoculated using the spray method, individual seedlings sometimes escape the susceptible reaction and show scores of only 1 or 2 (15).

To isolate IK81-3, all crosses showed the segregation ratios of 15R:1S in F_2, 3R:1S in BC_1, and 7R:8H:1S in the F_3, indicating digenic dominant resistance in all the cultivars. The F_2 population of IR46 did not show a good fit to the ratio of 15R:1S, but this ratio was confirmed by testing its BC_1 and F_3 populations.

The segregation ratios from the F_2, BC_1, and F_3 populations screened against isolate 43 indicate that IR36, IR60, and Carreon possess single dominant genes for resistance and IR46, Pai-kan-tao, and Tetep possess two dominant genes for resistance to this isolate. The F_2 ratio from the cross with IR60 was confirmed through its BC_1 and F_3 populations.

Linkage analyses of F_3 lines showed that resistance to different isolates in a particular cultivar was controlled by different genes, because recombinant types always occurred (Table 3). The recessive gene for resistance to isolate PO6-6 in IR54 was inherited independently of the two dominant genes for resistance to isolate IK81-3. Likewise, the two resistance genes in Carreon to isolate PO6-6 were inherited independently of those to isolate IK81-3. The case of Tetep was not conclusive for these two isolates, and the genes may or may not be linked. The genes conferring resistance to the isolates IK81-3 and 43 in IR60 were inherited independently. Likewise, the genes for resistance to isolates PO6-6 and 43 in Pai-kan-tao were inherited independently. Fewer recombinant and more parental reaction types than expected for independent segregation were observed in the crosses involving IR56 and Pai-kan-tao to isolates PO6-6 and IK81-3 and in the crosses involving IR36, IR46, and Pai-kan-tao to isolates IK81-3 and 43. This suggests that linkage is present among the resistance genes.

DISCUSSION

Qualitative or complete resistance occurs when a fungal pathogen cannot sporulate on its host (14). In the present study, isolate-specific, complete resistance was controlled by one or two dominant genes. The number of resistance genes in Carreon and Tetep against these isolates was identical to that reported previously (12). Previous studies, however, indicated that for Pai-kan-tao a single dominant gene conferred resistance to isolates IK81-3 and 43, and for Pankhari 203 a single gene conferred resistance to isolate IK81-3. It is not clear whether these discrepancies are due to a change in the isolate, a difference in the host strains used, or the effect of environmental factors. Some workers have emphasized the instability of the blast fungus in culture (13). Conversely, work in Japan has indicated that some resistance genes are variable in expression, depending upon such factors as seedling age and inoculation method (5,8).

In three cases, the F_2 populations did not show a good fit to the expected genetic ratio. In the case of Pai-kan-tao for isolate PO6-6, the number of resistant plants was higher than expected. In IR46 with isolate IK81-3 and IR60 with isolate 43, the number of susceptible plants was higher than expected. In all these cases, the backcross and F_3 generations were used to confirm the expected genetic ratios. In the case of Pai-kan-tao, it may be possible to explain the excess of resistant plants by disease escape in the F_2 population. In the case of IR60, many intermediate reactions were observed in the F_2 (Table 1), making it more difficult to classify the plants into distinct classes. Because of plant-to-plant variability often observed in segregating populations, F_3 populations should be used whenever possible to confirm genetic ratios (9). In some cases, the number of genes and the level of dominance have been found to vary because of environmental effects (6,7). Kiyosawa (9) has advocated the use of the "cumulative distribution method" in F_3 populations for the study of blast genetics. In this method, the frequency of resistant types within each F_3 line is compared with that expected for various genetic models.

Kiyosawa (10) identified 13 genes for complete resistance, none of which were recessive. Some studies, however, have identified recessive genes for blast resistance (12,17). The present study suggests IR54 has one recessive gene for resistance to isolate PO6-6.

The presence of several resistance genes in a single cultivar makes it difficult to determine allelism of the different genes. In this study, we found at least three genes for resistance to isolate PO6-6, two for IK81-3, and two for 43. It is possible, however, that resistance to the same isolate in different cultivars is controlled by different genes. Tests for allelism will be easier when individual resistance genes have been transferred into a susceptible background (12). Such near-isogenic lines will also be useful for systematic selection of blast races for use in genetic studies.

The linkage of genes for resistance to different isolates would be an advantage in breeding for blast resistance, because all genes could be more easily transferred together into susceptible genotypes. However, the substantial number of lines showing recombinant reactions implies that resistance to one isolate does

TABLE 2. Reaction of F_3 generation of crosses between resistant and susceptible parents to three isolates of *Pyricularia oryzae*

Resistant parent	No. of lines observed[a]			Expected ratio	Probability
	R	H	S		
Isolate PO6-6					
IR54	51	104	59	1:2:1	0.50–0.75
IR56	55	111	48	1:2:1	0.50–0.75
Carreon	95	104	15	7:8:1	0.75–0.90
Pai-kan-tao	51	116	47	1:2:1	0.25–0.50
Tetep	52	113	49	1:2:1	0.50–0.75
Isolate IK81-3					
IR36	91	106	17	7:8:1	0.50–0.75
IR46	97	101	16	7:8:1	0.50–0.75
IR54	94	111	9	7:8:1	0.25–0.50
IR56	85	113	16	7:8:1	0.25–0.50
IR60	88	106	20	7:8:1	0.10–0.25
Carreon	98	100	16	7:8:1	0.50–0.75
Pai-kan-tao	103	98	13	7:8:1	0.25–0.50
Tetep	90	109	15	7:8:1	0.75–0.90
Isolate 43					
IR36	59	109	46	1:2:1	0.25–0.50
IR46	95	102	17	7:8:1	0.50–0.75
IR60	52	113	49	1:2:1	0.50–0.75
Pai-kan-tao	90	108	16	7:8:1	0.50–0.75

[a] R = all plants resistant, H = segregating, S = all plants susceptible.

TABLE 3. Reaction of F_3 lines from crosses between resistant and susceptible parents to combinations of *Pyricularia oryzae* isolates

Resistant parent	No. of lines observed[a]				Expected ratio	Probability
	R/R	R/S	S/R	S/S		
Isolates PO6-6/IK81-3						
IR54	148	7	57	2	45:3:15:1	0.25–0.50
IR56	159	7	39	9	45:3:15:1	<0.01
Carreon	185	14	13	2	225:15:15:1	0.50–0.75
Pai-kan-tao	163	4	38	9	45:3:15:1	<0.01
Tetep	158	7	41	8	45:3:15:1	0.01–0.05
Isolates IK81-3/43						
IR36	162	35	6	11	45:15:3:1	<0.01
IR46	193	5	4	12	225:15:15:1	<0.01
IR60	149	45	16	4	45:15:3:1	0.10–0.25
Pai-kan-tao	194	7	4	9	225:15:15:1	<0.01
Isolates PO6-6/43						
Pai-kan-tao	155	12	43	4	45:3:15:1	0.50–0.75

[a] R/R = resistant to both isolates, R/S = resistant to first isolate and susceptible to second, S/R = S to second isolate and R to first, and S/S = S to both isolates.

not automatically confer resistance to another. As with allelism analysis, linkage analysis is difficult when more than one resistance gene per isolate is present in a single cultivar. An increase in the number of resistance genes would decrease the proportion of plants susceptible to both isolates, thus making reliable detection of segregation ratios difficult. When a very small proportion of plants is expected in a particular class, it is difficult to confirm the segregation ratios expected. Linkage and allelism tests should focus on cultivars with only one resistance gene for each isolate so that the ratio can be more reliably detected. By backcrossing (12), isogenic lines can be developed. This approach also makes it easier to conduct a genetic analysis of cultivars with unidentified resistance genes (16).

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