

Genetic Analysis of Resistance to Blast Disease in Rice (*Oryza Sativa* L.)

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ABSTRACT

The inheritance of leaf and kernel resistance to rice blast disease was studied in five crosses involving six rice cultivars. Parents, F_1 , F_2 , and F_3 families of these crosses were grown in the field under natural and artificial infection at the Faculty of Agriculture Experimental Farm, Alexandria University, Egypt, during the 1971-1974 seasons. These crosses were classified into three groups, namely; resistant $\times$ resistant ($R \times R$), resistant $\times$ susceptible ($R \times S$), and susceptible $\times$ susceptible ($S \times S$) according to their reaction to blast. Such groups included one, two, and two crosses, respectively.

Dealing with the leaf reaction, two different duplicate dominant genes for resistance were detected in the $R \times R$ cross, G.170 $\times$ Y.M.T. Each parent probably carried one of both genes. Obviously, two dominant gene pairs governed the segregation in the two $R \times S$ crosses, G.170 $\times$ I.R.8 and G.170 $\times$ Ir.376. One of these dominant genes was the gene for resistance, present in the resistant parent (G.170), while the other might be present in each of the susceptible parents, I.R.8 and Ir.376, and conditioned the susceptibility to leaf reaction. Phenotypically, all genotypes carrying the dominant gene for resistance were resistant probably because this gene masked the expression of the dominant gene for susceptibility. Hence, the phenotypic F_2 ratio was found to be 12R:4S in these two $R \times S$ crosses. In the two $S \times S$ crosses, T.(N.)1 $\times$ Na. and T.(N.)1 $\times$ I.R.8, susceptibility was completely dominant and was conditioned by two dominant duplicate genes, each of which could be carried by each parent.

Regarding the kernel type of reaction, two different duplicate dominant genes for resistance were found in the $R \times R$ cross, G.170 $\times$ Y.M.T. A single gene pair might be carried by each resistant parent. Two pairs of dominant genes controlled the segregation in the $R \times S$ cross, G.170 $\times$ Ir.376; the gene for kernel resistance in the resistant parent (G.170) and another gene for susceptibility in the susceptible parent (Ir.376), the expression of which was masked by the former gene. The phenotypic ratio was 12R:4S. In the second $R \times S$ cross, G.170 $\times$ I.R.8, the segregation was also conditioned by two dominant genes. However, the gene for susceptibility, which could be present in the susceptible parent (I.R.8), dominated and masked the expression of the gene for resistance in the resistant parent (G.170). So, the phenotypic ratio was 4R:12S. In the two $S \times S$ crosses, two dominant duplicate genes, with complete dominance of suscept-

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ibility to kernel reaction, were detected. Each susceptible parent could carry a single gene pair.

With respect to the genetic association between leaf and kernel reactions, highly significant values were obtained in the cases of the $R \times S$ cross, G.170 $\times$ Y.M.T., and $S \times S$ cross, T.(N.)1 $\times$ I.R.8, using the F_2 data. In the $R \times S$ cross, G.170 $\times$ I.R.8, a highly significant value was detected on the basis of F_3 data. Moreover, a highly significant genetic association was obtained in the case of the $S \times S$ cross, T.(N.)1 $\times$ Na., according to the F_3 data.

INTRODUCTION

In Egypt, rice (*Oryza sativa* L.) is the second major cash-export crop after cotton. During the last five years, Egypt grew more than one million faddans (one faddan = 4,200 m²) of rice annually with an average yield of 2.4 tons per faddan.

Rice blast disease, incited by *Piricularia oryzae* Cavara, is one of the most destructive diseases which reduces the rice production in Egypt (1) as well as in several rice growing countries. The two commonly grown rice cultivars now in Egypt are Nahda and Giza 170 which are susceptible and resistant to rice blast disease, respectively.

Breeding resistant rice cultivars is an efficient way to increase the harvested yield of this important field crop. Knowledge of the genetical behaviour of the resistance to blast disease is highly beneficial to the rice breeder, since the breeding method depends mainly on the mode of inheritance for the desired trait.

The objective of the present investigation was to study the mode of inheritance of leaf and kernel resistance to the blast disease in some crosses of rice between two local and four introduced cultivars. The genetic association and correlation coefficients between leaf and kernel reactions were also determined.

MATERIALS AND METHODS

A field study was conducted at the Faculty of Agriculture Experimental Farm, Alexandria University, Egypt, during the 1971–1974 growing seasons. Six rice cultivars, showing a wide range of reaction to the blast disease, were chosen for the present work. These cultivars included two local [Nahda (Na.) and Giza 170 (G.170)] and four introduced cultivars [Yo Mon Triao (Y.M.T.), Taichung 'Native' 1 (T.(N.)1), I.R.8, and Irradiation 376 (Ir.376)]. The cultivars, Y.M.T. and Ir.376, were obtained from the Sakha Experiment Station, Ministry of Agriculture, Egypt, while the other two from the International Rice Research Institute (I.R.R.I.) in the Philippines. The cultivars, G.170 and Y.M.T., were resistant to both leaf and kernel infection, whereas the rest were susceptible.

Five crosses were made and classified into three groups as follows:

Group I: included one resistant $\times$ resistant ($R \times R$) cross, namely; G.170 $\times$ Y.M.T.

Group II: included two resistant $\times$ susceptible ($R \times S$) crosses, namely; G.170 $\times$ Ir.376 and G.170 $\times$ I.R.8.

Group III: included two susceptible $\times$ susceptible ($S \times S$) crosses, namely; T.(N.)1 $\times$ I.R.8 and T.(N.)1 $\times$ Na.

In 1971, the six parental cultivars were sown in the greenhouse on three successive dates to facilitate the artificial crossing. Crossings were made and the F_1 hybrid grains were planted in 4 m long rows and spaced at 20 cm in 1972 and 1973 seasons, respectively. Both F_1 and F_2 rows were surrounded by the corresponding parental rows. The very

susceptible local cultivar, Sabeeni, was grown as a border spreader for the disease spores around these populations.

In 1974, the F_3 families of each cross were sown in single 4 m long rows and randomly arranged in two or three pseudo-replicates, each consisted of eight to eleven sets. Each set included 25 F_3 families in addition to the two corresponding parental cultivars and bordered with the Sabeeni cultivar. Each row was planted with twenty grains spaced at 20 cm.

For the artificial infection with blast, the plants of different generations of the studied crosses, i.e.; P_1 , P_2 , F_1 , F_2 , and F_3 , were heavily sprayed twice with a spore suspension; once at the 3–4 leaf stage, while the second at flowering time.

Ou (7) classified the leaves of rice plants into eight classes according to the degree of leaf infection with blast as follows: 1–3, resistant (R); 4–5, intermediate (I); and 6–8, susceptible (S). In the present study, however, this system was modified so that the first four classes included the resistant plants, while the susceptible plants were represented by the other four classes. For kernel infection, another scale was used to classify the plants into resistant and susceptible two weeks before harvest as follows: 1) Resistant (R) class, denotes the absence or presence of rare minute dark brown spots, and 2) susceptible (S) class, represents the infection of most kernels of rice panicles.

The following genetical parameters were estimated in the present work:

1. Nature of dominance.
2. Number of gene pairs controlling the resistance to blast disease.
3. Chi-square test for independence to determine the genetic association between leaf kernel reactions.
4. Correlation coefficients between leaf and kernel reactions for the significant Chi-square values according to the following formula adopted by Spiegel (9):

$$r = \sqrt{\frac{X^2}{N(K-1)}}$$

Where, r = correlation coefficient, X^2 = Chi-square value, N = total number of plants or families, and K = number of classes.

RESULTS AND DISCUSSION

I. Leaf blast reaction

The reaction to leaf blast infection of the parental cultivars and F_1 plants of the five rice crosses to leaf blast infection in 1972 is presented in Table 1. It is clear that the F_1 plants of the $R \times R$ and $R \times S$ crosses were as resistant as the resistant parents, indicating the complete dominance of resistance to leaf blast. In the two $S \times S$ crosses, however, all F_1 plants were susceptible as their parents.

Data in Table 2 represent the segregation of F_2 plants into resistant (R) and susceptible (S) classes of leaf blast reaction. It is obvious that the F_2 plants of the $R \times R$ cross, G.170 $\times$ Y.M.T., segregated according to the ratio of 15 R:1 S, suggesting the presence of two duplicate dominant pairs of genes for resistance to leaf reaction in this cross. It was suggested that one of these two dominant duplicate gene pairs could be carried by the cultivar, Giza 170, and the other gene pair by the cultivar, Y.M.T. This was further indicated by the segregation ratio of 7 homozygous resistant (RR):8 segregating (RS):1 homozygous susceptible (SS) in the F_3 , as shown in Table 3. The presence of

Table 1 Reaction to leaf and kernel blast disease of the parental cultivars and F_1 's of the five rice crosses studied in 1972.

Rice crosses	Types of reaction	No. of plants					
		P ₁		F ₁		P ₂	
		R	S	R	S	R	S
<i>R</i> × <i>R</i> :							
G.170 × Y.M.T	Leaf & kernel	27	0	14	0	21	0
<i>R</i> × <i>S</i> :							
1. G.170 × I.R.8	Leaf	40	0	12	0	0	23
	Kernel	40	0	0	12	0	23
2. G. 170 × Ir.376	Leaf & kernel	24	0	5	0	0	26
<i>S</i> × <i>S</i> :							
1. T.(N.)1 × Na	Leaf & kernel	0	23	0	16	0	24
2. T.(N.)1 × I.R.8	Leaf & kernel	0	32	0	18	0	23

two duplicate dominant pairs of genes governing resistance to leaf blast was detected by Nelson and Atkins (6), Atkins and Johnston (2), and Hsieh (3).

The present data (Table 2) further showed that the two $R \times S$ crosses proved a good fitness to the 12R:4S ratio, as indicated by the nonsignificant values of Chi-square test. This digenic F_2 phenotypic ratio indicated that two dominant gene pairs governed the segregation in these two $R \times S$ crosses. One of these dominant genes was the gene for resistance, that might be present in the resistant parent (G.170), while the other might be carried by each susceptible parent (I.R.8 and Ir.376) and conditioned the susceptibility to leaf blast. Therefore, all genotypes carrying the dominant gene for resistance were phenotypically resistant. This reaction was probably attributed to the masking effect

Table 2 F_2 segregation of the five crosses for leaf and kernel reactions to blast disease in 1973.

Rice crosses	Types of reaction	No. of F ₂ plants			Expected Phenotypic ratios (R:S)	X ² -values ¹
		R	S	Total		
<i>R</i> × <i>R</i> :						
G. 170 × Y.M.T.	Leaf	192	9	201	15:1	1.076
	Kernel	186	15	201	15:1	0.505
<i>R</i> × <i>S</i> :						
1. G.170 × I.R.8	Leaf	168	66	234	12:4	1.282
	Kernel	48	186	234	4:12	2.513
2. G.170 × Ir.376	Leaf	222	78	300	12:4	0.160
	Kernel	238	62	300	12:4	3.004
<i>S</i> × <i>S</i> :						
1. T(N.)1 × Na	Leaf	22	278	300	1:15	0.601
	Kernel	20	280	300	1:15	0.089
2. T.(N.)1 × I.R.8	Leaf	24	276	300	1:15	1.568
	Kernel	25	275	300	1:15	2.222

^a $\chi^2_{0.05, 1 d.f.} = 3.841$.

Table 3 F_3 -family segregation in the five rice crosses with respect to leaf and kernel reactions to blast disease in 1974.

Rice crosses	Types of reaction	No. of F ₃ segregants ^a				Expected phenotypic ratio (RR:RS:SS)	X ² -values ^b
		RR	RS	SS	Total		
<i>R</i> × <i>R</i> :							
G.170 × Y.M.T.	Leaf	33	40	4	77	7:8:1	0.205
	Kernel	36	33	6	75	7:8:1	1.211
<i>R</i> × <i>S</i> :							
1. G.170 × I.R.8	Leaf	41	86	51	178	4:8:4	1.326
	Kernel	36	98	44	178	4:8:4	2.540
2. G.170 × Ir.376	Leaf	18	35	18	71	4:8:4	0.014
	Kernel	23	36	12	71	4:8:4	3.422
<i>S</i> × <i>S</i> :							
1. T.(N.)1 × Na	Leaf	6	47	23	76	1:8:7	5.620
	Kernel	5	37	34	76	1:8:7	0.056
2. T.(N.)1 × I.R.8.	Leaf	13	80	70	163	1:8:7	0.828
	Kernel	16	90	57	163	1:8:7	7.074 ^{*c}

^aRR = Homozygous resistant, RS = Segregating, and SS = Homozygous susceptible.^b $\chi^2_{0.05,2 \text{ d.f.}} = 5.991$; $\chi^2_{0.01,2 \text{ d.f.}} = 9.210$.^c = Significant at the 5% level.

displayed by the gene for resistance on the expression of the gene for susceptibility. The F_3 segregation ratio fitted the expected ratio of 4 RR:8 RS:4 SS, proving the digenic control of resistance in these crosses. This confirmed the assumption that the resistant parent, G.170, carried one dominant gene for leaf blast resistance. These results were in general agreement with those obtained by Venkataswamy (11), Tepora and Jennings (10), Hsieh *et al.* (4) Lin *et al.* (5), and Rosero (8) who found that a single dominant gene was responsible for resistance to leaf blast infection.

Furthermore, Table 2 shows that the F_2 plants of the two $S \times S$ crosses, T.(N.)1 × Na. and T.(N.)1 × I.R.8, segregated into resistant and susceptible classes which fitted a digenic ratio of 1R:15S since the Chi-square values were statistically not significant. This ratio suggested that the susceptible parents of each cross differed in two pairs of dominant duplicate genes for leaf susceptibility to leaf blast. Each susceptible parent might possess a different dominant gene controlling leaf susceptibility. The F_3 families of these crosses segregated into a ratio which was in a good fitness to the expected ratio of 1 RR:8 RS:7 SS, as presented in Table 3.

The F_3 data in Table 3 coincided with and confirmed the expected F_2 phenotypic ratios of segregation in all crosses. In this case, the segregating F_3 families (RS) represented the heterozygous resistant F_2 plants in the $R \times R$ and $R \times S$ crosses and the heterozygous susceptible F_2 plants in the $S \times S$ crosses.

II. Kernel blast reaction

Data in Table 1 showed that all F_1 plants of the $R \times R$ cross were resistant to the kernel type of reaction to blast. Data of the F_2 suggested that this resistance was conditioned by two different duplicate dominant gene pairs (Table 2) in this cross. Moreover, the gene combinations in the F_3 families of the same cross resulted in an observed

phenotypic ratio of 7 RR:8 RS:1 SS, as given in Table 3. These results confirmed those of the F_2 data. Accordingly, it was suggested that one of these two dominant genes for resistance to kernel blast could be carried by the cultivar, G.170, and the other gene by the cultivar, Y.M.T.

In the $R \times S$ cross, G.170 $\times$ Ir. 376, all F_1 plants were resistant, suggesting complete dominance of resistance to kernel blast (Table 1). The F_2 segregation showed a good fitness to the 12R:4S ratio, as presented in Table 2. This digenic F_2 phenotypic ratio confirmed the complete dominance of resistance and indicated the presence of two pairs of dominant alleles controlling segregation in this cross. That is, the gene for kernel resistance in the resistant parent (G.170) and another gene for susceptibility in the susceptible parent (Ir.376). It was suggested that the dominant gene for resistance masked the expression of the dominant gene for susceptibility. Hence, the F_2 phenotypic ratio was 12 R:4S in this cross. Furthermore, the F_3 family segregations, illustrated in Table 3, confirmed the expected ratio of 4 RR:8 RS:4 SS and agreed with the F_2 data. In the second $R \times S$ cross, G.170 $\times$ I.R.8, all F_1 plants were susceptible, indicating complete dominance of susceptibility to kernel blast. The segregation ratio for F_2 was 4R:12 S, whereas it was 4 RR:8 RS:4 SS for the F_3 families. This means that the segregation in this cross was also conditioned by two dominant genes. However, the gene for susceptibility, which might be carried by the susceptible parent (I.R.8) dominated and masked the expression of the gene for resistance in the resistant parent (G.170).

In the two $S \times S$ crosses, two dominant duplicate genes were found to be responsible for the inheritance of susceptibility to kernel blast in each cross. All F_1 plants were susceptible, the F_2 data gave a ratio of 1R:15 S, and the F_3 families resulted in the ratio of 1 RR:8 RS:7 SS. Each parent could carry one single dominant gene pair controlling susceptibility to kernel blast.

III. Genetic association

The genetic association between the genes governing the leaf and kernel reactions to blast disease was checked by the Chi-square test for independence, as summarized in Table 4. The F_2 and F_3 data of the crosses, G.170 $\times$ Y.M.T. and T.(N.)1 $\times$ I.R.8,

Table 4 Chi-square test of genetic association and correlation coefficient (r) values between leaf and kernel reactions of the five rice crosses to blast disease in F_2 and F_3 .

Rice crosses	F_2 data		F_3 data	
	X^2 -values ^a	r -values	X^2 -values ^a	r -values
$R \times R$:				
G.170 $\times$ Y.M.T.	117.128*** ^b	0.763	53.680**	0.590
$R \times S$:				
1. G.170 $\times$ I.R.8	0.028	—	13.970**	0.198
2. G.170 $\times$ Ir.376	1.646	—	4.879	—
$S \times S$:				
1. T.(N.)1 $\times$ Na	116.986	0.624	5.240	—
2. T.(N.)1 $\times$ I.R.8	116.793**	0.624	35.215**	0.329

^a $X^2_{0.01,1 \text{ d.f.}} = 6.63$; and $X^2_{0.01,4 \text{ d.f.}} = 13.28$.

^b** = Significant at the 1% level.

showed a highly significant degree of association between the genes for leaf and kernel reactions. Two possible explanations may be suggested; (a) the two types of reactions resulted from pleiotropic effects, and (b) a close linkage existed between the genes conditioning resistance in both leaves and kernels of the two crosses of rice.

Concerning the $R \times S$ cross, $G.170 \times Ir.376$, the test of association between leaf and kernel reactions revealed no correlation between the two traits in both F_2 and F_3 generations (Table 4). This means that both reactions were independently inherited. In the $S \times S$ cross, $T.(N.)1 \times Na.$, a considerable association of approximately 0.6 was obtained in the F_2 , however, there was no association between leaf and kernel reactions in the F_3 . The results of F_3 might be due to the sampling error. In the cross, $G.170 \times I.R.8$, no correlation was obtained in the F_2 . However, a slight correlation coefficient of 0.2 was recorded in the F_3 which might be considered as an unreliable measure of genetic association.

Generally speaking, the present investigation indicated that the resistance to rice blast disease was simply inherited. One or two dominant gene pairs were found to be responsible for the inheritance of blast resistance. A reliable degree of association was detected between leaf and kernel reactions of blast disease. The present results suggested the possibility of using the backcross method of breeding to incorporate the resistance to rice blast disease from the available resistant rice cultivars, such as Y.M.T., to the high yielding commercial rice cultivars which are commonly grown in Egypt, such as Nahda.

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