

STUDIES ON THE INHERITANCE OF LEAF BLAST RESISTANCE IN RICE¹

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ABSTRACT

Studies on the inheritance of leaf blast resistance in seven differential varieties of rice tested against two Indian isolates of the international races IA-11 and ID-1 of *Pyricularia oryzae* Cav. under standardized experimental conditions revealed the presence of three dominant genes, one each in Zenith, Tetep and Ginga conferring resistance to IA-11 and two, one each in Zenith and Tetep, to the race ID-1. The genes of Zenith were independent of those of Tetep. C.I. 5309 possessed inhibitory genes inhibiting the resistance of Zenith but not of Tetep. Mode of segregation of resistance of Norin 20 to the race IA-11 was found to be anomalous. Studies on the crosses among susceptible varieties showed the existence of dominant genes conferring susceptibility, two each in P.I. 180061 and Yakeiko. This is a new feature of the present studies and its utility in evolving homozygous recessive resistant varieties have been pointed out.

INTRODUCTION

Sasaki (1922) reported that the leaf blast resistance in rice varieties were controlled by genetic factors. Since then several workers have studied the mode of inheritance of leaf blast resistance in rice in Japan, U.S.A., Taiwan, Philippines, Thailand and India.

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Ramiah and Ramaswamy (1936), initiating the studies on genetics of blast resistance in India, reported that the blast resistance of the variety GEB. 24 as simple recessive and that of Co. 4 as complicated under field conditions. They believed that such variations were due to the occurrence of physiologic races of the pathogen and also due to the environmental influences on the disease reaction. Bhapkar and D'Cruz (1960) reported that resistance to blast was dominant over susceptibility and was dependent upon one, two or more factors. Further, variations in susceptibility among the F_2 survivors were under polygenic control. Padmanabhan (1965) observed that leaf blast resistance of Co. 25 was dominant and was controlled by two or three genes, along with modifiers. Resistance to neck blast was also conditioned by two or three genes and was influenced by modifiers. The two phenomena were independent of each other. In further studies with forty crosses tested to the Indian race 11B (US 8), Padmanabhan *et al.*, (1967) recorded that F_1 hybrids of $R \times M$, $R \times S$ and $M \times M$ combinations were resistant except for the cross C.I. 5309 \times Zenith where it was susceptible. All F_1 plants of $S \times S$ combinations were susceptible while those of $M \times S$ combinations were variable (R, MR or S). Segregations in F_2 generation showed that the varieties Zenith, BJ.1, S.67 and Co.4 possessed one gene each conferring resistance against the race 11B.

A careful study of the available data on leaf blast resistance revealed that there was a wide range of variation in the number of genes controlling resistance, their dominant-susceptibility relationship and also in their mode of inheritance. Therefore, a study was undertaken with the object of determining the number of genes governing resistance, their expression in hybrids and their mode of inheritance so that the light thrown on these phenomena might help the breeders in introducing such known genes into any desirable high yielding rice variety. In the present studies differential varieties of the host were inoculated with specific physiologic races of the pathogen under standardized experimental conditions so as to minimize the variations in the expression of the disease reaction.

MATERIALS AND METHODS

Seven differential varieties of rice were selected from the list of differentials used in U.S.A. (Latterell *et al.*, 1960) and Japan (Goto and Yamanaka, 1961). Origin and pathological reactions of the parents were as follows (Padmanabhan *et al.*, 1967):

Variety	Pathological reaction		Remarks
	IA-11	ID-1	
<i>Indica</i>			
1. Zenith ..	R	R	Resistance is inhibited by the Inhibitory genes of C.I. 5309
2. Tetep ..	R	R	More resistant than Zenith
3. P.I.1 80061 ..	S	S	..
4. C.I. 5309 ..	S	S	Possessed inhibitory genes inhibiting the resistance of Zenith
<i>Japonica</i>			
5. Norin 20 ..	R	S	..
6. Ginga ..	R	S	..
7. Yakeiko ..	S	S	Used to study the genetics of both <i>indicas</i> and <i>japonicas</i>

Two isolates, *viz.*, OR-13 and MR-3, belonging to the races IA-11 and ID-1, respectively, of *P. oryzae* were selected from a stock of the races maintained at the Central Rice Research Institute, Cuttack. Both the races were isolated in 1964 and were virulent and sporulating on culture media. They were also widely distributed in different parts of India. OR-13 was isolated from the infected material of MTU-15 collected from Deras, Orissa, while MR-3 was obtained from the infected material of Ambemohar-157, collected at Manjari in Maharashtra State.

Parents were raised at intervals of 15 days in pots for synchronization of flowering at the time of crossing. Crossing between parents of desired combinations (*vide* Tables II and III) was undertaken during July-August, 1968 by the emasculation technique. Seeds of crossed origin were harvested after 25-30 days. The seeds were dried and stored.

Cross seeds were dehusked, treated with 0.1% mercuric chloride for 1-2 minutes and then allowed to germinate in petridishes with moist blotters. The seedlings were planted in trays (3' x 2') with proper N, P and K levels along with the parents and the standard susceptible variety, Co. 13. After 25 to 30 days, the trays containing the test material were transferred to glass chambers with wooden frames of 5' x 3.5' x 3.5'. The chambers were provided with devices for maintaining high humidity (over 90%).

Fifteen-day-old cultures of the fungus isolates, grown on oat meal agar medium supplemented with thiamine (3 mg/l) and biotin (0.5 mg/l) were used for inoculation. The colonies were removed from agar slants and inoculum was prepared by homogenizing them in a Warring blender. The spore concentration was adjusted at 5–10 spores per microscopic field ($\times 100$). The inoculum was sprayed on test plants during night hours when the air temperature was below 26° C. Separate atomizers and separate chambers were used for different races.

Inoculated plants were incubated in the same chambers without any disturbance for 7–10 days until Co. 13 showed typical symptoms. The infection was scored on the maximum infected leaf by a scale of 0–3 E (Padmanabhan and Ganguly, 1959). F_1 plants, after scoring the disease reaction, were transplanted and maintained in pots with proper care. At the time of flowering, each F_1 plant was tested for its hybridity with the help of specific morphological characters available with a cross combination and the plants suspected to be of selfed origin (only two) were rejected. F_1 plants were harvested twice, once during January–February, 1969 and again in May–June, 1969. The seeds were dried and stored. F_2 seeds along with the parents and the standard susceptible were raised in trays and tested for their leaf blast reaction as in testing F_1 plants.

Sixteen frequency classes (0–3 E) of the disease reaction were grouped as resistant (0–3 B) or susceptible (1C–3E). The data were subjected to chi-square test for goodness of fit for estimating the number of factors involved.

EXPERIMENTAL RESULTS

The data on the reaction of the parents tested to the races IA-11 and ID-1 of *P. oryzae* are presented in Table I.

It may be seen from Table I that the parents Zenith and Tetep are resistant to both the races while P.I. 180061, Yakeiko and C.I. 5309 are susceptible. The varieties Norin 20 and Ginga are resistant to the race IA-11 and susceptible to ID-1. The parental reactions are distinct and homozygous.

The data on the reaction of F_1 hybrids of different crosses tested to the races IA-11 and ID-1 of *P. oryzae* are presented in Table II.

TABLE I

Leaf blast reaction of the parents tested against the races IA-11 and ID-1 of P. oryzae

Parent	Race IA-11			Race ID-1		
	<i>a</i> *	<i>b</i> *	<i>c</i> *	<i>a</i>	<i>b</i>	<i>c</i>
Zenith ..	115	..	R	115	..	R
Tetep ..	136	..	R	134	..	R
Norin 20 ..	70	..	R	..	66	S
Ginga ..	68	..	R	..	68	S
P.I. 180061	135	S	..	102	S
Yakeiko	183	S	..	198	S
C.I. 5309	81	S	..	20	S

* *a* = number of resistant plants, *b* = number of susceptible plants *c* = reaction of the parent.

It may be seen from Table II that F_1 plants of the crosses 1, 2, 4, 5, 6, 7, 11, 12 and 13 are resistant to the race IA-11 while those of the crosses 3, 8, 9 and 10 are susceptible. Similarly, the F_1 plants of the crosses 1, 2, 4, 5, 6 and 7 are resistant to the race ID-1 and those of the crosses 3, 8, 9, 10, 11, 12 and 13 are susceptible.

The data on the reaction of F_2 progenies of different crosses and their reciprocals tested to the races IA-11 and ID-1 of *P. oryzae* are presented in Table III.

It may be seen from Table III that F_2 progenies of the crosses 1, 2, 5, 6, 7 and 12 tested to the race IA-11 and of the crosses 1, 2, 5, 6 and 7 tested against the race ID-1 segregate in a ratio of 3R : 1S. F_2 progenies of the crosses 3 and 11 tested against IA-11 and those of cross 3 tested against ID-1 segregate in the proportion of 3R : 13S. F_2 plants of the cross 4 tested to both the races segregate as 15R : 1S while those of the crosses 8 and 9 tested to the race IA-11 and those of 8 tested to ID-1 segregate as 1R : 15S. All F_2 progenies of the cross 13 were resistant to the race IA-11 while those of the crosses 9, 10, 11, 12 and 13 are susceptible to ID-1.

TABLE II

Reaction of F₁ hybrids of different crosses tested against the races IA-11 and ID-1 of P. oryzae

Cross*	Race IA-11						Race ID-1					
	Cross			Reciprocal			Cross			Reciprocal		
	a**	b**	c**	a	b	c	a	b	c	a	b	c
1. Z×P ..	5	..	R	2	..	R	6	.	R	3	..	R
2. Z×Y ..	2	..	R	4	..	R	2	..	R	3	..	R
3. Z×C	6	S	..	3	S	..	4	S	..	3	S
4. Z×T ..	3	..	R	2	..	R	3	..	R	2	..	R
5. T×P ..	3	..	R	3	..	R	2	..	R	3	..	R
6. T×Y ..	2	..	R	6	..	R	4	..	R	6	..	R
7. T×C	3	..	R	4	..	R
8. Y×P	5	S	..	4	S	..	4	S	..	3	S
9. Y×C	2	S	..	3	S	..	2	S	..	4	S
10. P×C	1	S	..	1	S	..	1	S	..	1	S
11. Y×N ..	5	..	R	4	..	R	..	10	S	..	4	S
12. Y×G ..	5	..	R	5	..	R	..	6	S	..	2	S
13. G×N ..	7	..	R	6	..	R	..	8	S	..	3	S

* Z = Zenith, T = Tetep, P = P.I. 180061, C = C.I. 5309, Y = Yakeiko, N = Norin 20 and G = Ginga.

** a = resistant, b = susceptible, c = disease reaction of F₁.

DISCUSSION

The data presented for the crosses 1 and 2 showed that Zenith possessed one dominant gene conferring resistance to each of the races of the pathogen. Monogenic dominant resistance to the leaf blast fungus in the variety Zenith was also recorded by Atkins *et al.* (1965), Atkins and Johnston (1966), Kiyosawa (1967 *a*), Rosero (1967) and Padmanabhan *et al.* (1967). Thus the results obtained confirm the earlier records.

TABLE III

Inheritance of leaf blast reaction in F₂ progenies of different crosses tested against the races IA-11 and ID-1 of P. oryzae

Cross*	Race IA-11				Race ID-1			
	Observed frequency		Expected frequency	P	Observed frequency		Expected frequency	P
	R	S	(R : S)		R	S	(R : S)	
1. Z × P ..	212	66	3 : 1	.80-.70	206	91	3 : 1	.20-.10
P × Z ..	208	65	3 : 1	.50-.30	203	83	3 : 1	.50-.30
2. Z × Y ..	179	49	3 : 1	.50-.30	228	61	3 : 1	.50-.30
Y × Z ..	199	58	3 : 1	.50-.30	165	45	3 : 1	.50-.30
3. Z × C ..	67	196	3 : 13	.10-.05	48	163	3 : 13	.50-.30
C × Z ..	53	177	3 : 13	.30-.20	51	165	3 : 13	.50-.30
4. Z × T ..	268	14	15 : 1	.70-.50	223	12	15 : 1	.70-.50
T × Z ..	200	10	15 : 1	.70-.50	161	15	15 : 1	.50-.30
5. T × P ..	145	52	3 : 1	.80-.76	204	55	3 : 1	.50-.30
P × T ..	209	78	3 : 1	.70-.50	155	63	3 : 1	.50-.30
6. T × Y ..	158	49	3 : 1	.90-.80	174	49	3 : 1	.50-.30
Y × T ..	179	48	3 : 1	.50-.30	155	55	3 : 1	.80-.70
7. T × C
C × T ..	110	55	3 : 1	.10-.05	99	42	3 : 1	.30-.20
8. Y × P ..	23	202	1 : 15	.20-.10	24	235	1 : 15	.30-.20
P × Y ..	27	240	1 : 15	.20-.10	25	270	1 : 15	.30-.20
9. Y × C ..	14	120	1 : 15	.10-.05	0	194	0 : 1	1.00
C × Y ..	11	161	1 : 15	.99-.98	0	138	0 : 1	1.00
10. P × C ..	0	156	0 : 1	1.00	0	162	0 : 1	1.00
C × P ..	0	144	0 : 1	1.00	0	123	0 : 1	1.00
11. Y × N ..	69	219	3 : 13	.10-.05	0	272	0 : 1	1.00
N × Y ..	72	219	3 : 13	.20-.10	0	263	0 : 1	1.00
12. Y × G ..	209	76	3 : 1	.80-.70	0	270	0 : 1	1.00
G × Y ..	205	76	3 : 1	.50-.30	0	277	0 : 1	1.00
13. G × N ..	294	0	1 : 0	1.00	0	291	0 : 1	1.00
N × G ..	271	0	1 : 0	1.00	0	275	0 : 1	1.00

* Z = Zenith, T = Tetep, Y = Yakeiko, P = P.I. 180061, C = C.I. 5309, N = Norin 20 and G = Ginga.

The data presented for the crosses 5, 6 and 7 suggested the presence of one dominant gene in Tetep conferring resistance to each of the races of

P. oryzae under consideration. Kiyosawa (1967 *b*) has indicated the presence of at least three genes conditioning resistance in this variety one of which was located at *Pi-k* locus. The difference between the observations made by Kiyosawa and those of the present studies suggest that "variety-race combination" might be involved in such discrepancies. Since these are the two analyses available on the genetic control of this highly resistant variety, it is desirable that further studies be undertaken with this variety along with the Phillippino variety, Tadukan, and its derivatives as the latter has been used to distinguish the T-races of *P. oryzae* in Japan.

The results obtained for cross 4 showed that the genes governing resistance in Zenith were independent of those of Tetep. Occurrence of independent genes conferring leaf blast reaction in different rice varieties have been demonstrated earlier (Kiyosawa, 1967 *b*, 1969). He pointed out that one of the genes of Zenith, *Pi-z*, was on a locus independent of the genes *Pi-a*, *Pi-k*, *Pi-k^s*, *Pi-k^p*, *Pi-ta*, *Pi-ta 2* and *Pi-m*. It was, however, loosely linked with the gene *Pi-i* of Ishikari Shiroke. It was evident from the data presented by Padmanabhan *et al.* (1967) that the gene conferring resistance in Zenith was independent of the one present in BJ.1.

The results presented for cross 3 demonstrated the presence of inhibitory genes in the variety, C.I. 5309, inhibiting the resistance of Zenith to each of the races under study, thus confirming the earlier findings of Padmanabhan *et al.* (1967). These inhibitory genes, however, did not inhibit the resistance conferred by the genes of Tetep.

The mode of inheritance of resistance of Norin 20 (cross 11) to the race IA-11 showed an anomalous situation, in that, F_1 plants were resistant while F_2 progenies segregated in a ratio of 3R : 13S. This anomaly of reversal in the expression of resistance could neither be explained in terms of the operation of an inhibitory gene, since the F_1 plants were resistant, nor by mutation in pathogenicity of the fungus strain because of the normal behaviour in crosses 12 and 13 which were inoculated with cultures from the same stock on the same day. The results, therefore, need further verification. It was of interest to note that Hsieh (1965) obtained similar results and attributed them to the environmental influences.

The resistance of Ginga to IA-11 was found to be monogenic-dominant (cross 12) and was homologous with the resistant factor of Norin 20 (cross 13). Kiyosawa (1970) reported that Ginga possessed three genes of higher activity against the Japanese races of the pathogen and segregation patterns were complicated.

The genes for susceptibility of Yakeiko were inherited independently of those of P.I. 180061 for both the races and of C.I. 5309 tested to the race IA-11. The genes for susceptibility of Yakeiko to the race ID-1 was homologous to that of C.I. 5309. Similarly, genes conferring susceptibility in the varieties P.I. 180061 and C.I. 5309 were identical or closely linked. Thus, there are two sets of dominant genes conferring susceptibility to each of the races, IA-11 and ID-1, one set in P.I. 180061 and the other in Yakeiko. There are no earlier records of dominant independent genes conferring susceptibility to different races of *P. oryzae* in rice varieties. Detection of genes for susceptibility was, therefore, a new finding of the present investigation. It would appear that the earlier observations of recessive resistance for blast by Ramiah and Ramaswamy (1936), Oka and Lin (1957), Goto (1959, 1960) and Jennings (1966) could be explained on the basis of elimination of dominant genes controlling susceptibility.

Some workers were of the opinion that leaf blast resistance of *indica* varieties were higher than the *japonicas* (Hashioka, 1950; Okeda and Maeda, 1956; Abumiya, 1959; Somoto and Ouchi, 1968). On the other hand, the workers at Central Rice Research Institute, Cuttack and at the International Rice Research Institute (Ann. Rep., 1965) did not observe the existence of any such phenomenon. The data presented for the inter-racial crosses (crosses 2, 6, 8 and 9) clearly demonstrated that inheritance of resistance as well as of susceptibility genes was a characteristic of variety-race combination and was independent of racial differences. This confirmed the views of the latter group of workers.

Since several methods are available for the symbolisation of *Pyricularia*-resistance genes (*Pi*), this problem is dealt separately.

It may be inferred from the present investigations that leaf blast reaction in rice varieties to different races of the pathogen is controlled mainly by dominant genes. A few reports on the recessiveness of blast resistance could be accounted by the absence of genes governing susceptibility in a given variety. Certain varieties might contain inhibitory genes inhibiting blast resistance of certain sources. The mode of inheritance is not complicated by inter-racial or inter-varietal differences.

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