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Genetic analysis of blast resistant gene in rice (*Oryza sativa* L.) cultivars

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ABSTRACT

The inheritance investigation uncovered that blast resistance in R 1013-2307-1-1, R 1124-91-2-73, R 1518-762-3-564-1, R 1558-2423-3-1445-1 and R 1559-2425-2-1449-1 was controlled by a single dominant gene, while two independent dominant genes governed resistance in R 1519-781-5-598-1 and R 1540-1888-1278-1. The allelic studies revealed that genes for resistance present in R 1013-2307-1-1, R 1518-762-3-564-1 and R 1558-2423-3-1445-1 was allelic to Pi-z5 (IRBL 10 and 5173). Among the blast differential genes (monogenic lines) tested, only 'Pi-z5' gene consistently imparted complete resistance against the blast population in the Northern Hilly Region of Chhattisgarh, Pi-z, Pi-9 and Pi-kh provided variable level of resistance. On the other hand four genes, Pi-z5, Pi-z, Pi-9 and Pi-kh are functional in Bastar Plateau (Jagdalpur). The severity of blast disease was considerably higher at Ambikapur station than at Jagdalpur so only one center (Ambikapur) could be reliably used to conduct screening trials. The race of the fungus at these two sites seems to be different. Eight genotypes viz., R 1518-762-3-564-1, R 1519-781-5-598-1, R 1540-1888-1278-1, R 1558-2423-3-1445-1, B 6441-FMR-6-0-0, F 7-10, IR42221-145-2-3-2 and 5173 showed consistently stable resistant reaction over the years.

Key words: *Rice, blast resistance, genetics, inheritance, allelic study*

INTRODUCTION

Rice is the staple food for more than half of the world's population. Demand for rice continues to increase due to the ever-increasing rice consumer base. However, the present rate of increase in rice production (2000-09) has slowed down (1.21%) compared with that of previous decades (2.49%) during 1970-79 and (1.70%) in 1990-2000, due to various biotic and abiotic stresses (Khush and Jena, 2009). Among the biotic stresses, blast disease is the most devastating disease in rice cultivation by causing heavy losses ranging from 35 to 50% (Padmavathi et al., 2005) and maximum up to 90% yield loss (Ramkumar et al., 2010). The fungus is adaptable to adverse environmental conditions of widely-fluctuating temperatures and relative humidity. It is considered as a major constraint in rice production in different rice ecosystems ranging from irrigated (40-100%) to rainfed (70%) and upland rice area (63%) in major rice growing countries of the world, except in Australia (Vera Cruz et al., 2007). In general, the disease causes 10-20% yield reduction in susceptible varieties, but in severe cases, the loss may be upto 80% (Koutroubas et al., 2009). This usually occurs when the pathogen (virulent) found the environmental conditions favourable, that is, relatively high humidity (up to 85% and above), low night temperatures, high or excessive nitrogen (N) fertilizer application, the presence of dew and drought stress, and cases where the host is susceptible (Idowu et al., 2013).

Due to the extreme sensitivity of rice cultivars to blast disease, farmers are forced to apply frequent fungicides (Mousanejad et al., 2010), which can lead to environmental pollution (Pasha et al., 2013). However, the use of resistant cultivars is the most economical and environmentally friendly method for the management of rice blast (Haq et al., 2002). Identification and incorporation of different blast resistance genes with overlapping resistance spectra

have long been main objectives of rice breeding program worldwide (Wang et al., 2007). However, because of either the rapid evolution of new pathogen races or the selection of a rare component of the pathogen population that is already virulent, resistance is rendered ineffective in many cultivars. Thus, breeding for more durable resistant cultivars therefore has become a priority in rice improvement.

Chhattisgarh state, considered as the 'rice bowl', has 3.76 million hectare under rice cultivation and a production of about 7.70 million tonnes (Anonymous, 2016). The prevailing environment in some areas of Chhattisgarh such as Bastar Plateau and Northern Hilly Region favors the development of blast to epidemic proportions and has been considered as "hot spots" for the blast. Severe blast (S, >50%) was recorded in plateaus of Jharkhand and Chhattisgarh (Production -oriented survey report, 1994-2006) and that was higher than the plains in the same region (Variar, 2007). Though in Chhattisgarh some rice varieties and breeding lines, as sources of blast resistance, were identified (Persuad, 2006). However, a proper understanding of this disease is of utmost importance, thus the study was carried out to identify the functional resistance conferring genes, detection of variability in the pathogen population, inheritance-allelic pattern.

MATERIALS AND METHODS

The research work was carried out in the Department of Plant Breeding and Genetics, College of Agriculture, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Raipur, Chhattisgarh. Collaboration was made with College of Agriculture and Research Station Ambikapur and Jagdalpur to facilitate screening against blast. The studies were extended over a period of five cropping seasons *viz.*, wet season (kharif) 2007, 2008, 2009, and dry season (rabi) 2008, and 2009. The experimental materials consisted of a set of thirty one blast monogenic / differential lines along with seventy nine other genotypes including breeding lines, resistant and susceptible checks, were tested at blast 'hot spots' Ambikapur for three years (2007-2009) and Jagdalpur in 2007, (b) F_1, F_2, and F_3 populations of the 63 crosses attempted for the genetic dissection (28 for inheritance and 35 for allelic studies) were screened against the blast population at Ambikapur to ascertain the genetic ratios. The experiment was conducted under field conditions and all the standard agronomic practices were followed during cultivation of the crop. Screening techniques employed as Uniform Blast Nursery (UBN) test procedure (Ou, 1965). Evaluation was done about 30-35 days after seeding, when susceptible check reached 9 score, using the Standard Evaluation System (SES) based on a 0-9 scale as given by International Network for Genetic Evaluation of Rice, INGER (1996). For the genetic studies, score 4 and 5 were clubbed with susceptible. In F_1 and F_2, plants were individually scored. The F_3 progenies were classified as breeding true for resistance (all plants in the line being resistant), segregating (both resistant and susceptible were observed) or breeding true for susceptibility (all plants in the line being susceptible). For the genetic studies, score upto 3 were kept as resistant while score 4 and 5 were clubbed with susceptible. The Chi-Square test was employed to test the significance of deviation of an observed segregation ratio from a theoretical one for the purpose of working out the genetic ratios in F_2 and F_3.

RESULTS AND DISCUSSION

Rice blast screening

Blast monogenic lines and new rice genotypes were screened along with eight susceptible checks (Mahisugandha, Dubraj, Poornima, Danteshwari, Swarna, Mahamaya, Cheptigurmatia, and HR12) against blast population over the years 2007-2009 at Ambikapur. The primary aim was to identify effective blast resistance genes conferring resistance in Chhattisgarh. The reactions of these genes over the years are given in Table 1. Highly susceptible reaction (score 9) was consistently observed for all eight checks over the years. This served as a benchmark for the reliability of reaction of the test entries.

Of the thirty-one monogenic lines tested at Ambikapur during *kharif* 2007, only IRBL 9, IRBL 10, IRBL 22, IRBL 31 and IRBL 8 possessing the genes Pi-z, Pi-z5, Pi-9, Pi-z5 and Pi-kh respectively provided resistance (score 1 & 3), while the remaining 26 lines / genes proved highly susceptible and same as the checks. During *kharif* 2008, resistant reaction was recorded for four entries *viz.*, IRBL 10, IRBL 31 (both possessing Pi-z5 gene), IRBL 22 (Pi-9) and IRBL 9 (Pi-z) (score 1 & 3), while IRBL 8 (Pi-kh) was moderately resistant and all other entries were highly

Table 1. Reaction of blast in Rice lines at Ambikapur and Jagadalpur, Chhattisgarh.

SN	Genotypes	Designation	Target gene	Blast score & reaction					
				Jagdalpur	Ambikapur			Maximum	Reaction
				kh. 2007	*kh*.2007	*kh*.2008	*kh*.2009	Score	
1.	IRBL 1	IRBLa-A	Pi-a	9	9	9	9	9	S
2.	IRBL 2	IRBLa-C	Pi-a	9	9	9	9	9	S
3.	IRBL 3	IRBLi-F5	Pi-i	9	9	9	9	9	S
4.	IRBL 4	IRBLks-F5	Pi-ks	9	9	9	9	9	S
5.	IRBL 5	IRBLks-S	Pi-ks	9	9	9	9	9	S
6.	IRBL 6	IRBLk-ka	Pi-k	9	9	9	9	9	S
7.	IRBL 7	IRBLkp-K60	Pi-kp	9	9	9	9	9	S
8.	IRBL 8	IRBLkh-K3	Pi-kh	3	3	5	5	3	R
9.	IRBL 9	IRBLz-Fu	Pi-z	1	1	3	5	1	R
10.	IRBL 10	IRBLz5-CA	Pi-z5 = Pi-2(t)	1	1	1	3	1	R
11.	IRBL 11	IRBLzt-T	Pi-zt	9	9	9	9	9	S
12.	IRBL 12	IRBLta-K1	Pi-ta = Pi-4(t)	9	9	9	9	9	S
13.	IRBL 13	IRBLta-CT2	Pi-ta	9	9	9	9	9	S
14.	IRBL 14	IRBLb-B	Pi-b	9	9	9	9	9	S
15.	IRBL 15	IRBLt-K59	Pi-t	9	9	9	9	9	S
16.	IRBL 16	IRBLsh-S	Pi-sh	9	9	9	9	9	S
17.	IRBL 17	IRBLsh-B	Pi-sh	9	9	9	9	9	S
18.	IRBL 18	IRBL1-CL	Pi-1	9	9	9	9	9	S
19.	IRBL 19	IRBL3-CP4	Pi-3	9	9	9	9	9	S
20.	IRBL 20	IRBL5-M	Pi-5(t)	9	9	9	9	9	S
21.	IRBL 21	IRBL7-M	Pi-7(t)	9	9	9	9	9	S
22.	IRBL 22	IRBL9-W	Pi-9	1	1	3	5	1	R
23.	IRBL 23	IRBL12-M	Pi-12(t)	9	9	9	9	9	S
24.	IRBL 24	IRBL19-A	Pi-19	9	9	9	9	9	S
25.	IRBL 25	IRBLkm-Ts	Pi-km	9	9	9	9	9	S
26.	IRBL 26	IRBL20-IR24	Pi-20	9	9	9	9	9	S
27.	IRBL 27	IRBLta2-Pi	Pi-ta2	9	9	9	9	9	S
28.	IRBL 28	IRBLta2-Re	Pi-ta2	9	9	9	9	9	S
29.	IRBL 29	IRBLta-CP1	Pi-ta	9	9	9	9	9	S
30.	IRBL 30	IRBL11-Zh	Pi-11(t)	9	9	9	9	9	S
31.	IRBL 31	IRBLz5-CA(R)	Pi-z5	1	1	1	3	1	R
32.	IR-64			1	1	3	3	3	R
33.	MTU 1065			5	7	7	7	7	S
34.	MTU 1075			5	7	7	9	9	S
35.	OR 1898-18			7	9	9	9	9	S
36.	R 714-5-55-2-1			5	3	5	5	5	S
37.	R 979-67-2-44-1			5	5	7	7	7	S
38.	R 979-1528-2-1			7	3	5	5	5	S
39.	R 1013-2307-1-1			3	1	3	3	3	R
40.	R 1022-1803-1-1			5	3	5	5	5	S
41.	R 1027-2238-3-1			7	3	5	5	5	S
42.	R 1060-30-2-41-1			3	3	5	5	5	S
43.	R 1124-69-1-45-1			5	3	5	5	5	S
44.	R 1124-91-2-73			3	3	3	3	3	R
45.	R 1130-80-1-52-1			5	3	7	7	7	S
46.	R 1207-257-5-1			7	3	3	5	5	S
47.	R 1219-650-2-314-1			7	5	7	7	7	S
48.	R 1238-692-820-1-1			5	3	7	7	7	S
49.	R 1238-1820-1-1			5	3	5	7	7	S
50.	R 1240-913-2-1031-1			3	3	3	7	7	S
51.	R 1240-927-3-1056-1			5	5	7	5	5	S
52.	R 1247-1936-1-1			3	1	5	5	5	S
53.	R 1248-1489-2-822-1			7	9	9	9	9	S
54.	R 1250-1557-1-895-1			3	1	3	3	3	R

Contd....

SN	Genotypes	Designation	Target gene	Blast score & reaction					
				Jagdalpur	Ambikapur			Maximum	Reaction
				kh. 2007	*kh*.2007	*kh*.2008	*kh*.2009	Score	
55.	R 1262-1667-1-1			3	1	5	5	5	S
56.	R 1262-1668-2-1			5	1	5	5	5	S
57.	R 1264-1670-1-1			5	3	3	5	5	S
58.	R 1327-483-1-1			3	7	7	7	7	S
59.	R 1448-153-65-2-1			3	9	7	7	7	S
60.	R 1448-578-2-473-1			3	3	1	3	3	R
61.	R 1454-87-50-4-1			5	7	7	7	7	S
62.	R 1454-171-96-1			7	7	7	9	9	S
63.	R 1456-199-3-180-1			3	5	3	5	5	S
64.	R 1462-243-100-7-1-1			7	5	7	7	7	S
65.	R 1470-345-338-2-1			1	3	3	3	3	R
66.	R 1473-529-249-4-1			7	1	1	3	3	S
67.	R 1475-468-564-2-1			5	3	5	5	5	S
68.	R 1493-625-3-499-1			3	3	5	3	5	S
69.	R 1502-643-784-1-1			3	3	3	5	5	S
70.	R 1518-762-3-564-1			1	1	1	3	3	R
71.	R 1518-767-4-569-1			3	1	5	5	5	S
72.	R 1519-769-2-574-1			1	1	3	3	3	S
73.	R 1519-773-5-583-1			7	3	3	3	3	R
74.	R 1519-778-2-590-1			3	1	3	3	3	R
75.	R 1519-781-5-598-1			1	1	1	3	3	R
76.	R 1519-784-1-599-1			3	1	1	3	3	R
77.	R 1520-936-1-811-1			3	9	7	9	9	S
78.	R 1528-1139-3-1003-1			7	3	5	5	5	S
79.	R 1529-1166-1-1020-1			7	3	3	3	3	S
80.	R 1529-1183-1-1041-1			5	1	1	3	3	S
81.	R 1529-1183-3-1043-1			5	1	1	3	3	S
82.	R 1530-1194-2-1061-1			5	1	3	5	5	S
83.	R 1537-1566-1-1210-1			7	3	5	5	5	S
84.	R 1538-1614-1-1221-1			9	3	5	5	5	S
85.	R 1539-1785-1-1263-1			3	1	3	3	3	R
86.	R 1540-1888-1278-1			3	1	1	1	1	R
87.	R 1543-1966-1-1290-1			3	3	3	3	3	R
88.	R 1551-2169-1-1354-1			3	3	3	3	3	R
89.	R 1558-2419-2-1442-1			3	3	3	3	3	R
90.	R 1558-2423-3-1445-1			3	1	1	1	1	R
91.	R 1559-2425-2-1449-1			3	1	1	3	3	R
92.	R 1559-2427-1-1450-1			3	1	1	3	3	R
93.	R 1559-2427-2-1451-1			3	1	3	3	3	R
94.	R 1560-2442-1-1456-1			3	1	3	3	3	R
95.	R 1723-2271-1-1404-1			3	1	3	3	3	R
96.	B 6441-FMR-6-0-0			1	1	1	1	1	R
97.	F 7-10			1	1	1	1	1	R
98.	IR 42221-145-2-3-2			1	1	1	1	1	R
99.	5173			1	1	1	1	1	R
100.	Abhaya			1	1	3	3	3	R
101.	G 95-02			1	1	3	3	3	R
102.	BR 240			1	1	3	3	3	R
103.	Mahisugandha (ch)			9	9	9	9	9	S
104.	Dubraj (ch)			9	9	9	9	9	S
105.	Swarna (ch)			9	9	9	9	9	S
106.	Poornima (ch)			9	9	9	9	9	S
107.	HR 12 (ch)			9	9	9	9	9	S
108.	Mahamaya (ch)			9	9	9	9	9	S
109.	Cheptigurmatia (ch)			9	9	9	9	9	S
110.	Danteshwari (ch)			9	9	9	9	9	S

kh = *kharif* season, ch = Susceptible check, R=Resistant, S=Susceptible

susceptible (score 9). But only two blast monogenic lines *viz.*, IRBL 10, IRBL 31 (both possessing Pi-z5 gene) were recorded resistant reaction (score 3) and other three monogenic lines IRBL 9 (Pi-z), IRBL 22 (Pi-9) and IRBL 8 (Pi-kh) were found moderately resistant (score 5) during the *kharif* 2009. Thus, the Pi-z5 gene should be utilized in developing blast resistant varieties for the Chhattisgarh state. This gene is providing durable and stable resistance in the region. Identification of functional blast resistance gene(s) for a particular region is a prerequisite for their meaningful deployment (Shridhar et al., 1999).

Overall, twenty nine genotypes *viz.*, IR 64, R 1013-2307-1-1, R 1124-91-2-73, R 1250-1557-1-895-1, R 1448-578-2-473-1, R 1470-345-338-2-1, R 1518-762-3-564-1, R 1519-769-2-574-1, R 1519-778-2-590-1, R 1519-781-5-598-1, R 1519-784-1-599-1, R 1539-1785-1-1263-1, R 1540-1888-1278-1, R 1543-1966-1-1290-1, R 1551-2169-1-1354-1, R 1558-2419-2-1442-1, R 1558-2423-3-1445-1, R 1559-2425-2-1449-1, R 1559-2427-1-1450-1, R 1559-2427-2-1451-1, R 1560-2442-1-1456-1, R 1723-2271-1-1404-1, B 6441-FMR-6-0-0, F 7-10, IR 42221-145-2-3-2, 5173, Abhaya, G 95-02 and BR 240 proved to be resistant over the years (2007-2009) at Ambikapur.

The Colombian cultivar 5173 has Pi-z5 gene, proved highly resistant with scores of 1 over three years testing at Ambikapur. Also score of 1 and 3 were observed from 2007-2009 for monogenic lines IRBL 10 and IRBL 31 that were representatives of Pi-z5 gene and both the lines were derived from C101 A51. The reason why 5173 showed better (less) score than all these NIL's is possibly due to additional effective minor genes / QTL's that may be present in cultivar 5173 which supported the resistance of gene Pi-z5. The same may be the case with IR42221-145-2-3-2 that possess Pi-z5 gene.

The gene present in Guyanese strains B 6441-F-MR-6-0-0 (Pi-48), F 7-10 (Pi-49) were reported to be new blast resistant gene (Persaud, 2006). Both showed highly resistant score of 1, so they can be used as new donors for the blast resistant gene. F 7-10 has extra-long slender grain and high production potential. The other two Guyanese strains BR 240 and G 95-02 were also imparting resistance of variable level.

Genetical study

Sixty-three crosses were made to analyze the inheritance and allelic relationships of the genes involved in the resistant parents. The F_1, F_2, and F_3 populations of the crosses were screened against the blast population prevailing at Ambikapur for classification of the plants / progenies to fit the appropriate genetic ratios. The reactions of the various populations are presented in Table 2 & 3.

(A) Inheritance of resistance

Twenty eight crosses were made to analyze the inheritance pattern of the genes involved in the resistant parents. The F_1, F_2 and F_3 populations of the crosses were screened against the blast population prevailing at Ambikapur for classification of the plants / progenies to fit the appropriate genetic ratios. The reactions of the various populations are presented in Table 2. Seven resistant parents *viz.*, R 1013-2307-1-1, R 1124-91-2-73, R 1518-762-3-564-1, R 1519-781-5-598-1, R 1540-1888-1278-1, R 1558-2423-3-1445-1 and R 1559-2425-2-1449-1 were crossed with four susceptible parents (HR12, Swarna, Mahamaya and Cheptigurmatia). The F_1 populations of all the crosses showed resistant reaction against the blast population. This indicated the dominant nature of the resistance gene(s) involved. The F_2 population of the crosses of R 1013-2307-1-1, R 1124-91-2-73, R 1518-762-3-564-1, R 1558-2423-3-1445-1 and R 1559-2425-2-1449-1 with susceptible parents segregated in a frequency of three resistant plants: one susceptible plant (3R:1S). This suggested the presence of single dominant gene in the resistant parent. Further, the F_3 progenies of these crosses for each resistant parent were analyzed. A segregation pattern of one homozygous resistant: two segregating (heterozygous): one homozygous susceptible, (1R:2Sg:1S) was observed for these crosses as expected following simple Mendelian inheritance. This confirmed the inheritance of a single dominant gene present in these resistant parents, while the segregation behavior of F_2 population of the crosses of R 1519-781-5-598-1 and R 1540-1888-1278-1 with susceptible parents fit well in fifteen resistant plants: one susceptible plant ratio (15R:1S) that signifying the possibility of two independent dominant genes controlling resistance. Further, the F_3 progenies of these crosses were evaluated and classified into seven

Table 2. Reaction of F_1, F_2 and F_3 population to Magnaporthe oryzaein twenty eight crosses of rice.

SN	Cross combination	F_1	Reaction of F_2 plants						Reaction of F_3 progenies						
		Rea-ction	No. of Plants			Expect-ed Ratio	χ^2-value	P-value	No. of progenies				Expect-ed Ratio	χ^2-value	P-value
			R	S	Total	R:S			R	Sg	S	Total	R:Sg:S		
1.	R 1013-2307-1-1 x Swarna	R	331	94	425	3:1	1.883	0.20-0.10	29	63	39	131	1:2:1	1.718	0.50-0.30
2.	R 1013-2307-1-1 x HR 12	R	287	78	365	3:1	2.565	0.20-0.10	37	62	26	125	1:2:1	1.944	0.50-0.30
3.	R 1013-2307-1-1 x Mahamaya	R	315	113	428	3:1	0.449	0.50-0.30	41	72	33	146	1:2:1	0.904	0.70-0.50
4.	R 1013-2307-1-1 x Cheptigurmatia	R	362	114	476	3:1	0.280	0.70-0.50	35	78	41	154	1:2:1	0.494	0.80-0.70
5.	R 1124-91-2-73 x Swarna	R	405	118	523	3:1	1.658	0.20-0.10	37	71	30	138	1:2:1	0.826	0.70-0.50
6.	R 1124-91-2-73 x HR 12	R	253	102	355	3:1	2.638	0.20-0.10	35	68	26	129	1:2:1	1.636	0.50-0.30
7.	R 1124-91-2-73 x Mahamaya	R	288	81	369	3:1	1.829	0.20-0.10	29	77	35	141	1:2:1	1.709	0.50-0.30
8.	R 1124-91-2-73 x Cheptigurmatia	R	262	86	348	3:1	0.015	0.95-0.90	37	80	35	152	1:2:1	0.474	0.80-0.70
9.	R 1518-762-3-564-1 x Swarna	R	322	90	412	3:1	2.188	0.20-0.10	26	59	23	108	1:2:1	1.093	0.70-0.50
10.	R 1518-762-3-564-1 x HR 12	R	299	104	403	3:1	0.140	0.80-0.70	24	59	32	115	1:2:1	1.191	0.70-0.50
11.	R 1518-762-3-564-1 x Mahamaya	R	313	95	408	3:1	0.641	0.50-0.30	31	79	32	142	1:2:1	1.817	0.50-0.30
12.	R 1518-762-3-564-1 x Cheptigurmatia	R	280	79	359	3:1	1.717	0.20-0.10	29	58	22	109	1:2:1	1.349	0.70-0.50
13.	R 1519-781-5-598-1 x Swarna	R	352	24	376	15:1	0.011	0.95-0.90	49	53	8	110	7:8:1	0.273	0.90-0.80
14.	R 1519-781-5-598-1 x HR 12	R	372	17	389	15:1	2.346	0.20-0.10	58	78	7	143	7:8:1	1.344	0.70-0.50
15.	R 1519-781-5-598-1 x Mahamaya	R	369	27	396	15:1	0.218	0.70-0.50	48	58	6	112	7:8:1	0.235	0.90-0.80
16.	R 1519-781-5-598-1 x Cheptigurmatia	R	345	21	366	15:1	0.164	0.70-0.50	47	55	7	109	7:8:1	0.020	0.99-0.98
17.	R 1540-1888-1278-1 x Swarna	R	371	32	403	15:1	1.965	0.20-0.10	53	67	6	126	7:8:1	0.782	0.70-0.50
18.	R 1540-1888-1278-1 x HR 12	R	470	41	511	15:1	2.743	0.10-0.05	60	78	7	145	7:8:1	1.073	0.70-0.50
19.	R 1540-1888-1278-1 x Mahamaya	R	443	33	476	15:1	0.379	0.70-0.50	58	75	8	141	7:8:1	0.583	0.80-0.70
20.	R 1540-1888-1278-1 x Cheptigurmatia	R	433	22	455	15:1	1.554	0.30-0.20	60	66	8	134	7:8:1	0.064	0.98-0.95
21.	R 1558-2423-3-1445-1 x Swarna	R	328	106	434	3:1	0.077	0.80-0.70	33	73	30	136	1:2:1	0.868	0.70-0.50
22.	R 1558-2423-3-1445-1 x HR 12	R	281	75	356	3:1	2.936	0.10-0.05	33	76	25	134	1:2:1	3.373	0.20-0.10
23.	R 1558-2423-3-1445-1 x Mahamaya	R	294	104	398	3:1	0.271	0.70-0.50	34	70	28	132	1:2:1	1.030	0.70-0.50
24.	R 1558-2423-3-1445-1 x Cheptigurmatia	R	263	84	347	3:1	0.116	0.80-0.70	32	81	35	148	1:2:1	1.446	0.50-0.30
25.	R 1559-2425-2-1449-1 x Swarna	R	265	75	340	3:1	1.569	0.30-0.20	28	62	22	112	1:2:1	1.929	0.50-0.30
26.	R 1559-2425-2-1449-1 x HR 12	R	290	79	369	3:1	2.537	0.20-0.10	33	78	28	139	1:2:1	2.439	0.30-0.20
27.	R 1559-2425-2-1449-1 x Mahamaya	R	298	103	401	3:1	0.101	0.80-0.70	38	69	30	137	1:2:1	0.942	0.70-0.50
28.	R 1559-2425-2-1449-1 x Cheptigurmatia	R	275	109	384	3:1	2.347	0.10-0.05	36	68	31	135	1:2:1	0.378	0.90-0.80

In F_2: R = Resistant, S = Susceptible. In F_3: R = Breeding true for resistance, Sg = Segregating, S = Breeding true for susceptibility.

Table 3. Reaction of F_1, F_2 and F_3 population to *Magnaporthe oryzae* in thirty five crosses of rice.

SN	Cross combination	F_1	Reaction of F_2 plants						Reaction of F_3 progenies						
		Rea-ction	No. of Plants			Expect-ed Ratio	χ^2-value	P-value	No. of progenies				Expect-ed Ratio	χ^2-value	P-value
			R	S	Total	R:S			R	Sg	S	Total	R:Sg:S		
1.	R 1013-2307-1-1 x B 6441-FMR-6-0-0	R	329	25	354	15:1	0.398	0.70-0.50	58	70	6	134	7:8:1	0.814	0.70-0.50
2.	R 1013-2307-1-1 x F 7-10	R	301	25	326	15:1	1.120	0.30-0.20	60	73	9	142	7:8:1	0.131	0.95-0.90
3.	R 1013-2307-1-1 x 5173	R	387	0	387	-	-	-	145	0	0	145	-	-	-
4.	R 1013-2307-1-1 x IRBL 10	R	364	0	364	-	-	-	138	0	0	138	-	-	-
5.	R 1013-2307-1-1 x IRBL 22	R	375	28	403	15:1	0.335	0.70-0.50	56	68	12	136	7:8:1	1.647	0.50-0.30
6.	R 1124-91-2-73 x B 6441-FMR-6-0-0	R	380	32	412	15:1	1.618	0.30-0.20	59	71	5	135	7:8:1	1.582	0.50-0.30
7.	R 1124-91-2-73 x F 7-10	R	385	30	415	15:1	0.679	0.50-0.30	62	70	5	137	7:8:1	1.586	0.50-0.30
8.	R 1124-91-2-73 x 5173	R	376	34	410	15:1	2.920	0.10-0.05	56	67	6	129	7:8:1	0.628	0.80-0.70
9.	R 1124-91-2-73 x IRBL 10	R	287	24	311	15:1	1.142	0.30-0.20	56	65	7	128	7:8:1	0.141	0.95-0.90
10.	R 1124-91-2-73 x IRBL 22	R	461	0	461	-	-	-	140	0	0	140	-	-	-
11.	R 1518-762-3-564-1x B 6441-FMR-6-0-0	R	397	34	431	15:1	1.975	0.20-0.10	56	74	6	136	7:8:1	1.471	0.50-0.30
12.	R 1518-762-3-564-1x F 7-10	R	484	41	525	15:1	2.179	0.20-0.10	54	67	7	128	7:8:1	0.337	0.90-0.80
13.	R 1518-762-3-564-1x 5173	R	418	0	418	-	-	-	129	0	0	129	-	-	-
14.	R 1518-762-3-564-1x IRBL 10	R	569	0	569	-	-	-	138	0	0	138	-	-	-
15.	R 1518-762-3-564-1x IRBL 22	R	333	30	369	15:1	2.226	0.20-0.10	52	64	5	121	7:8:1	1.087	0.70-0.50
16.	R 1519-781-5-598-1 x B 6441-FMR-6-0-0	R	477	12	489	63:1	2.527	0.20-0.10	-	-	-	-	-	-	-
17.	R 1519-781-5-598-1x F 7-10	R	417	9	426	63:1	0.838	0.50-0.30	-	-	-	-	-	-	-
18.	R 1519-781-5-598-1x 5173	R	411	0	411	-	-		135	0	0	135	-	-	
19.	R 1519-781-5-598-1x IRBL 10	R	385	0	385	-	-		134	0	0	134	-	-	
20.	R 1519-781-5-598-1x IRBL 22	R	356	9	365	63:1	1.936	0.20-0.10	-	-	-	-	-	-	-
21.	R 1540-1888-1278-1 x B 6441-FMR-6-0-0	R	337	8	345	63:1	1.283	0.20-0.10	-	-	-	-	-	-	-
22.	R 1540-1888-1278-1 x F 7-10	R	447	11	458	63:1	2.097	0.20-0.10	-	-	-	-	-	-	-
23.	R 1540-1888-1278-1 x 5173	R	429	0	429	-	-		136	-	-	136	-	-	
24.	R 1540-1888-1278-1 x IRBL 10	R	416	0	416	-	-		138	-	-	138	-	-	
25.	R 1540-1888-1278-1x IRBL 22	R	488	10	498	63:1	0.643	0.50-0.30	-	-	-	-	-	-	-
26.	R 1558-2423-3-1445-1 x B 6441-FMR-6-0-0	R	534	44	578	15:1	1.831	0.20-0.10	55	78	9	142	7:8:1	1.509	0.70-0.50
27.	R 1558-2423-3-1445-1 x F 7-10	R	462	39	501	15:1	2.013	0.20-0.10	56	66	10	132	7:8:1	0.424	0.90-0.80
28.	R 1558-2423-3-1445-1 x 5173	R	376	0	376	-	-		131	0	0	131	-	-	
29.	R 1558-2423-3-1445-1 x IRBL 10	R	342	0	342	-	-		121	0	0	121	-	-	
30.	R 1558-2423-3-1445-1 x IRBL 22	R	393	33	426	15:1	1.628	0.30-0.20	54	63	5	122	7:8:1	0.977	0.70-0.50
31.	R 1559-2425-2-1449-1 x B 6441-FMR-6-0-0	R	367	22	389	15:1	0.235	0.70-0.50	57	64	5	126	7:8:1	1.129	0.70-0.50
32.	R 1559-2425-2-1449-1 x F 7-10	R	386	22	408	15:1	0.512	0.50-0.30	55	66	4	125	7:8:1	2.058	0.30-0.20
33.	R 1559-2425-2-1449-1 x 5173	R	337	28	365	15:1	1.258	0.30-0.20	54	64	5	123	7:8:1	1.042	0.70-0.50
34.	R 1559-2425-2-1449-1x IRBL 10	R	347	30	377	15:1	1.876	0.20-0.10	51	61	4	116	7:8:1	1.613	0.50-0.30
35.	R 1559-2425-2-1449-1 x IRBL 22	R	381	0	381	-	-	-	125	0	0	125	-	-	

In F_2: R = Resistant, S = Susceptible. In F_3: R = Breeding true for resistance, Sg = Segregating, S = Breeding true for susceptibility.

homozygous resistant: eight segregating (heterozygous): one homozygous susceptible (7R:8Sg:1S) ratio ratifying the existence of two independent dominant genes in these resistant parents.

Resistant parents R 1013-2307-1-1, R 1124-91-2-73, R 1518-762-3-564-1, R 1558-2423-3-1445-1 and R 1559-2425-2-1449-1 possess only one gene for resistance which is dominant. In many of the earlier studies, resistance has been reported to be governed by one dominant gene (Persaud, 2002; Persaud, 2006 and Nagaty et al., 2007), although resistance to blast has also been reported to be controlled by recessive genes (Marchetti et al., 1987).

The strains R 1519-781-5-598-1 and R 1540-1888-1278-1 have two dominant genes for resistance. Resistance to blast has been noted by several workers to be governed by two dominant genes (Persaud, 2002; Persaud, 2006 and Nagaty et al., 2007). Even three dominant genes have been found to control resistance (Zhoa et al., 1998).

Control of a trait by a dominant gene is considered to be an advantage to the breeder as it makes the identification of the resistant plants easier, which is also expressed, in heterozygous condition. In-depth understanding of the inheritance of the resistance gene greatly enhances the breeder's ability to plan an appropriate breeding strategy to exploit/transfer the target gene(s). Since, the resistance genes in the parents studied are inherited independently they are expected to be transferred quite easily.

(B) Allelic test

The segregation behavior of the F_2 populations of the cross between unknown resistant parents R 1013-2307-1-1, R 1518-762-3-564-1, and R 1558-2423-3-1445-1 with known resistant donors B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)) and IRBL 22 (Pi -9) showed a 15R:1S ratio pointing out that two independently dominant gene were involved in each of these crosses. The reaction of the F_3 progenies of all these crosses tested were partitioned into 7R:8Sg:1S segregation classes. This corroborate that the gene identified in R 1013-2307-1-1, R 1518-762-3-564-1 and R 1558-2423-3-1445-1 were different from those found in B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)) and IRBL 22 (Pi-9I. The F_2 and F_3 populations of the crosses involving R 1013-2307-1-1, R 1518-762-3-564-1 and R 1558-2423-3-1445-1 with IRBL 10 (Pi-z5) and 5173 (Pi-z5) did not segregate for blast resistance. This signified that the gene(s) involved in R 1013-2307-1-1, R 1518-762-3-564-1, and R 1558-2423-3-1445-1were allelic to that of IRBL 10 (Pi-z5) and 5173 (Pi-z5). This indicates the presence of the gene Pi-z5 gene in these parents (R 1013-2307-1-1, R 1518-762-3-564-1 and R 1558-2423-3-1445-1).

Unknown resistant parents R 1124-91-2-73 and R 1559-2425-2-1449-1 were tested for their allelic relationship with B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)), IRBL 10 (Pi-z5) and 5173 (Pi-z5). The F_2 reactions of these crosses were classified into 15R:1S segregation ratio demonstrating that the single gene present in these parents were inherited independently and were non-allelic to the B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)), IRBL 10 (Pi-z5) and 5173 (Pi-z5). However, the F_2 and F_3 populations of the crosses of R 1124-91-2-73 and R 1559-2425-2-1449-1 with IRBL 22 (Pi9) did not segregate for blast resistance. This confirmed that the gene present in R 1124-91-2-73 and R 1559-2425-2-1449-1 was allelic to Pi9 gene of IRBL 22.

The resistance to rice blast involving the parents R 1519-781-5-598-1 and R 1540-1888-1278-1 found to possess two independent dominant genes did not segregate in F_2 and F_3 populations of its crosses with parents having only one resistant gene (Pi-z5) in 5173 and IRBL 10. This pointed out that one of the gene present in R 1519-781-5-598-1, R 1540-1888-1278-1 was allelic to (*i.e.*, same as) the gene Pi-z5. Furthermore, the F_2 population of the crosses of these two unknown resistant parents with other known resistant parents B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)) and IRBL 22 (Pi-9) segregate in a ratio of 63:1, indicating that the genes in those unknown parents were non allelic to the gene present in B 6441-FMR-6-0-0 (Pi-48(t)), F 7-10 (Pi-49(t)) and IRBL 22 (Pi-9). The gene for blast resistance in R 1124-91-2-73 and R 1559-2425-2-1449-1 was allelic to Pi-9 gene of IRBL 22. Likewise, one of the gene present in R 1519-781-5-598-1, R 1540-1888-1278-1 was allelic to the gene Pi-z5. The blast population in the Northern Hilly Region proved highly unpredictable and comprised of more than two highly virulent races. Breakdown of many resistant strains and genes occurred during the study, which could be attributed to changes in the frequency of pathogenic

races prevailing over the years.

From the above study one can conclude that only 'Pi-z5' gene consistently imparted complete resistance against the blast population in the Northern Hilly Region of Chhattisgarh while gene Pi-z, Pi-9 and Pi-kh provided variable level of resistance. Eight strains viz., R 1518-762-3-564-1, R 1519-781-5-598-1, R 1540-1888-1278-1, R 1558-2423-3-1445-1, B 6441-FMR-6-0-0, F 7-10, IR42221-145-2-3-2 and 5173 showed consistently stable resistant reaction over the years. New resistant parents R 1013-2307-1-1, R 1124-91-2-73, R 1518-762-3-564-1, R 1558-2423-3-1445-1 and R 1559-2425-2-1449-1 possess only one dominant gene for resistance against blast whereas, strains R 1519-781-5-598-1 and R 1540-1888-1278-1 have two dominant genes for resistance.

CONCLUSION

This study was intended in developing a comprehensive understanding of the mode of inheritance, the allelic relationships of the resistance conferring genes in donors in Chhattisgarh along with the functional resistance genes for the region are identified, and the variation in the fungus population has been detected. This study would enable the breeders and pathologist to have a greater insight into the nature of the genetic interactions between the blast fungus and its host. The stability of resistance conferring genes in given rice cultivar is determined by how the blast pathogen changes and the way the resistance is deployed (Ahn, 1994). Thus the ability of the breeders to develop varieties with effective durable blast resistance for the region is likely to be enhanced with the results obtained in this study.

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