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INHERITANCE OF ADDITIONAL RESISTANCE FROM NEAR-ISOGENIC LINES FOR THE GENE *LR3* AGAINST INDIAN LEAF RUST RACES

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ABSTRACT

Near-isogenic leaf rust resistant lines Thatcher + *Lr*3Ka, Prelude+*Lr*3Ka and Prelude+*Lr*3s in were found to carry a yet undescribed field resistance effective against a mixture of highly virulent variants 77-1 and 77-2 of the Indian leaf rust race 77. Against another highly virulent culture from race 108 showing avirulence on *Lr*3, these three lines as well as the near-isogenic lines Thatcher+*Lr*3do and Thatcher+*Lr*3bg were resistant both at seedling and adult plant stages. The seedling resistance of each of these five near-isogenic lines to race 108 was caused by a recessive gene. The seedling resistance of Thatcher+*Lr*3do and Thatcher+*Lr*3bg to race 108 was due to the same gene or a gene tightly linked to *Lr*3. This resistance segregated independently of the recessive seedling resistance gene identified from the near-isogenic lines Thatcher+*Lr*3ka, Prelude+*Lr*3ka and Prelude+*Lr*3sin. The field resistance of isogenic lines Thatcher+*Lr*3ka, Prelude+*Lr*3ka and Prelude+*Lr*3sin was due to a dominant and a recessive gene in each. The factors causing field resistance in each of these three near-isogenic lines were different.

Key words: *Puccinia recondita*, *Triticum aestivum*, allelic tests, adult plant resistance.

Leaf rust caused by *Puccinia recondita* Rob ex. Desm. f. sp. *tritici* is an important and most widely distributed disease of wheat (*Triticum aestivum* L.). Use of genetic resistance is an efficient and effective method to reduce losses caused by this disease. So far over 40 leaf rust resistance genes (*Lr* genes) have been identified from different sources and designated as *Lr1* through *Lr44* [1]. Identification of majority of these genes became possible using the leaf rust cultures available in India, but accurate detection of some genes is not possible because the reference lines for these genes (near-isogenic lines) also carry additional genes effective against the Indian rust cultures [2]. The identification of an important seedling resistance gene, *Lr3*, was difficult in India because of similar reasons. A dominant gene originally identified from each of the cultivars Democrat and Mediterranean [3] was later designed as *Lr*3do [4]. Gene *Lr3* was also proposed for the cultivars Bage, Klein Aniversario and

Sinvalocho, and was temporarily designated as *Lr3*bg, *Lr3*ka, and *Lr3*sin, respectively [5]. The gene *Lr3* from different sources was subsequently transferred to Thatcher (Tc) and Prelude (Pr) backgrounds, and the lines thus developed are being used as reference lines for *Lr3* by various workers throughout the world. However, tests on seedlings and adult plants of these five isogenic lines for *Lr3* against Indian leaf rust cultures indicate presence of additional resistance in some of these lines. The present investigation, therefore, aims to examine the nature of leaf rust resistance from five near-isogenic lines for the gene *Lr3*.

MATERIALS AND METHODS

Three genetically defined rust cultures, one isolated from race 108 and one each from the variants 77-1 and 77-2 of race 77, were used. Race 108 is avirulent on seedlings as well as adult plants of the wheats carrying only the genes *Lr3* and *Lr15* from *T. aestivum*. At the same time, variants 77-1 and 77-2 show virulence against any of the *Lr* genes so far identified from *T. aestivum* at seedling as well as adult plant stages. The five near-isogenic lines, i.e. Thatcher*6/Democrat (TC+*Lr3*do), Thatcher*6/Bage (TC+*Lr3*bg), Thatcher*6/Klein Aniversario (TC+*Lr3*ka), Prelude*6/Klein Aniversario (Pr+*Lr3*ka), and Prelude*6/Sinvalocho (Pr+*Lr3*sin) were intercrossed as well as crossed to the susceptible cultivar Agra Local.

The F_1, F_2 and F_3 generations obtained from the crosses of near-isogenic lines with Agra Local and the F_2 generations obtained from the intercross of the near-isogenic lines were tested for seedling reaction (infection types) against race 108. A part of the F_1, F_2 and F_3 generations from the cross Tc+*Lr3*ka x Agra Local, Pr+*Lr3*ka x Agra Local, and Pr+*Lr3*sin x Agra Local as well as intercrosses of TC+*Lr3*ka, Pr+*Lr3*ka and Pr+*Lr3*sin used for seedling tests was also grown under field conditions and tested for disease severity at adult plant stage against a mixture of the variants 77-1 and 77-2.

The seedlings and adult plants of five near-isogenic lines and the background cultivars Thatcher and Prelude were studied for infection types (ITs) against race 108 and the variants 77-1, 77-2. These lines were also evaluated for terminal disease severity at adult plant stage in field tests. Agra Local was used as a susceptible parent for all purpose.

For seedling tests, the seedlings were raised and tested at $20 \pm 1^{\circ}C$ in a growth house. About 20–30 seedlings of each near-isogenic line, the background cultivar, F_1 and F_2 plant progeny (F_3 family), and at least 200 F_2 seedlings from each cross were tested. The primary leaf of 7-day-old seedlings was inoculated using a homogeneous mixture of the respective rust culture and inert talcum powder. The inoculated seedlings were incubated in a humidity chamber for 24 h and then kept on benches for rust development.

For adult plant tests, four plants of each line were sown in a 25 x 30 cm earthen pot. Two pots of each line were sown as replication. Three flag leaves from each plant were inoculated at boot leaf stage using a uridospore talc mixture of race 108 with the variants 77-1 and 77-2 separately. The inoculated pots were incubated and shifted to a glasshouse maintained at 25 $\pm$ 8°C. The infestation types on seedlings as well as adult plants were recorded 14 days after inoculation as per the standard procedures [6].

For field tests, the F_1, F_2 and F_3 generations, near-isogenic lines, and background cultivars were planted in 2 m long rows. Up to 20 seeds of each near-isogenic line, background cultivar and F_1, 200 F_2 seeds obtained from each cross and 20–30 seeds from each F_2 plant progeny were sown. Rust epidemic was created in the field by repeated inoculations with a mixture of variants 77-1 and 77-2 of race 77. The terminal disease severity of each plant was recorded as percent leaf area covered with rust according to a standard visual scale [7]. For all purposes the plants showing terminal disease severity up to 40S/MS/MR were considered resistant. Simple χ^2 test was applied to test the fitness of different genetic ratios.

RESULTS AND DISCUSSION

The infection types and disease severity recorded on seedlings as well as adult plants of five near-isogenic lines, background cultivars, and the susceptible check Agra Local are presented in Table 1. The seedlings as well as adult plants of near-isogenic lines were resistant to race 108. The background cultivar Thatcher was susceptible to race 108 but

Table 1. The infection types and disease severity on near-isogenic lines for *Lr3*, background cultivars and cv. Agra Local of wheat

Line/cultivar	Infection at different growth stages						Disease severity
	108		77-1		77-2		
	seeding	adult	seedling	adult	seedling	adult	
Near-isogenic lines:							
Tc+*Lr3*do	;1-	0;	3+	3+	3+	3+	80S
Tc+*Lr3*bg	;1-	0;	3+	3+	3+	3+	80S
Tc+*Lr3*ka	2+	;1-	3+	33+	33+	33+	20S
Pr+*Lr3*ka	;1+	0;	33+	33+	3+	33+	30MR/MS
Pr+*Lr3*sin	X=	0;	33+	33+	3+	33+	40MR/MS
Background cultivars:							
Thatcher	3	3	3+	3+	3+	3+	70S
Prelude	3	X+	33+	33+	33+	33+	20MR/MS
Susceptible check:							
Agra Local	3+	3+	3+	3+	3+	3	90S

Prelude showed adult plant resistance. Cultivars Thatcher and Prelude and the five near-isogenic lines for *Lr3* were susceptible to the variants 77-1 and 77-2 at both developmental stages. Agra Local was susceptible to race 108 as well as variants 77-1 and 77-2 at both developmental stages. The disease severity on Tc+*Lr3*do, Tc+*Lr3*bg, Thatcher and Agra Local varied from 70S to 90S in field tests. The disease severity on Tc+*Lr3*ka, Pr+*Lr3*ka, Pr+*Lr3*sin and Prelude varied from 20S to 40MR/MS. In spite of susceptible infection types on the adult plants of Tc+*Lr3*ka, Pr+*Lr3*ka, Pr+*Lr3*sin and Prelude against the variants 77-1 and 77-2, the terminal disease severity on adult plants of these lines was low in field tests. Since the adult plants of Tc+*Lr3*ka, Pr+*Lr3*ka, Pr+*Lr3*sin and Prelude developed fully susceptible infection types and did not show hypersensitive response to the variants 77-1 and 77-2, it is concluded that field resistance of these three near-isogenic lines and cv. Prelude is due to new and yet undescribed nonhypersensitive resistance gene(s). In spite of significant reduction in development of disease under field conditions, such genes do not force selection pressure on the pathogen. Such resistance is believed to be durable [8]. The wheat varieties having such resistance can be identified by testing for hypersensitive resistance as judged by seedling and adult plant infection types and terminal disease severity on adult plants in field tests.

Against the race 108, the F_1 seedlings from the crosses of isogenic lines with cv. Agra Local were susceptible (IT = 33+). The disease severity on F_1 adult plants from the crosses of Tc+*Lr3*ka, Pr+*Lr3*ka and Pr+*Lr3*sin against the mixture of the variants 77-1 and 77-2 was 20S, 40MR and 50MR, respectively. The segregation pattern for seedling reaction against race 108 and disease severity against the mixture of variants 77-1 and 77-2 on field grown adult plants in F_2 and F_3 generations is given in Table 2. The F_2 and F_3 seedlings from the crosses of all the five near-isogenic lines with cv. Agra Local segregated in 1 resistant : 3 susceptible ratio and 1 homozygous resistant : 2 segregating : 1 homozygous susceptible ratio, respectively, against race 108. These observations suggest that each of the near-isogenic lines for *Lr3* and its alleles carries a recessive seedling resistance gene effective against race 108.

In the field tests on adult plants, the crosses of Tc+*Lr3*Ka, Pr+*Lr3*Ka and Pr+*Lr3*sin with cv. Agra Local segregated in the ratios of 13 resistant : 3 susceptible in F_2 and 7 homozygous resistant : 8 segregating : 1 homozygous susceptible in F_2. These observations suggest the presence of one dominant and one recessive gene for field resistance in each of the lines Tc+*Lr3*Ka, Pr+*Lr3*Ka and Pr+*Lr3*sin.

The segregation data for susceptible and resistant seedlings and adult plants in F_2 generations of the intercrosses among the near-isogenic lines are given in Table 3. All F_2 seedlings of the cross Tc+*Lr3*do x Tc+*Lr3*bg were resistant to race 108, which is avirulent against *Lr3* and its alleles. The F_2 generations from all other intercrosses segregated susceptible seedlings. This suggests that seedling resistance of Tc+*Lr3*do and Tc+*Lr3*bg

Table 2. Segregation for seedling infection types and adult plant disease severity in F_2 and F_3 generations of wheat

Stage of growth	No. of F_2 plants				No. of F_3 families				
	R	S	Ratio tested	χ^2	R	Segr.	S	Ratio tested	χ^2
				Tc+*Lr3*(Do) x Agra Local					
Seedling	51	133	1:3	0.73	84	166	94	1:2:1	1.00
				Tc+*Lr3*(Bg) x Agra Local					
Seedling	53	145	1:3	0.33	70	156	67	1:2:1	1.30
				Tc+*Lr3*(Ka) x Agra Local					
Seedling	42	110	1:3	0.56	39	67	39	1:2:1	0.83
Adult	128	30	13:3	0.01	31	50	6	7:8:1	2.33
				Pr+*Lr3*(Ka) x Agra Local					
Seedling	29	120	1:3	2.44	33	55	38	1:2:1	2.43
Adult	99	26	13:3	0.35	58	45	8	7:8:1	3.98*
				Pr+*Lr3*sin x Agra Local					
Seedling	43	99	1:3	2.11	36	60	3	1:2:1	0.77
Adult	74	21	13:3	0.70	80	75	11	7:8:1	1.56

*Significant at 5% level.

against race 108 is due to the same gene or a gene tightly linked to *Lr3*. The remaining three near-isogenic lines carry a seedling resistance against race 108 which is not due to *Lr3*.

The adult F_2 plants in the intercrosses of the near-isogenic lines Tc+*Lr3*Ka, Pr+*Lr3*Ka and Pr+*Lr3*sin segregated for susceptible plants in the disease severity tests against a mixture

Table 3. Segregation for susceptible seedlings and adult plants in F_2 generation from intercrosses among near-isogenic lines of wheat for *Lr3* gene for leaf rust resistance

Female parent	Stage	F_2 performance with different male parents			
		Tc+Lr3bg	Tc+Lr3ka	Pr+Lr3ka	Pr+Lr3sin
Tc+*Lr3*do	Seedling	All resistant	Segregates	Segregates	Segregates
Tc+*Lr3*bg	Seedling		Segregates	Segregates	Segregates
Tc+*Lr3*ka	Seedling			Segregates	Segregates
	Adult			Segregates	Segregates
Pr+*Lr3*ka	Seedling				Segregates
	Adult				Segregates

Note. Seedling stage tested against race 108, and adult plant stage against mixture of variants 77-1 and 77-2.

of variants 77-1 and 77-2. These observations suggest that field resistance of each of these three near-isogenic lines is due to different resistance factors.

Additional nonhypersensitive field resistance effective against the mixture of the highly virulent variants 77-1 and 77-2 of the Indian leaf rust race 77 has been detected in the isogenic lines Tc+*Lr3*Ka, Pr+*Lr3*Ka, and Pr+*Lr3*sin. This additional resistance might have been transferred to the near-isogenic lines for *Lr3*Ka and *Lr3*sin under investigation from cvs. Klein Aniversario and Sinvalocho, respectively. The field resistance of Pr+*Lr3* can also be attributed to cv. Prelude. Leaf rust resistance due to factors other than *Lr3* has already been reported in the cultivars Bage and Klein Aniversario and the near-isogenic lines for *Lr3* in Thatcher background [9, 10]. Therefore, detection of additional resistance from the near-isogenic lines for *Lr3* in the Prelude background is also not unexpected. Such new resistances can always be expected due to genetic differences in the pathogen cultures originating from different countries. It is absolutely essential to understand this variation at the global level through collaborative international effort.

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