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NATURE AND INHERITANCE OF LEAF RUST RESISTANCE FROM THREE WHEAT CULTIVARS

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ABSTRACT

The nature and inheritance of leaf rust resistance of cultivars Manitou, Pavon 76 and Romany against Indian races 12, 77, 77-1, 77-3, 108 and 162 was studied. Manitou carried a dominant gene effective against race 162 that is different from *Lr13* already reported from this cultivar. Pavon 76 and Romany carried the genes *Lr1* and *Lr10* as well as a new dominant gene for low seedling reaction against race 108. In addition, Romany also carried a gene for low seedling reaction against race 77-1 and a new adult plant resistance gene against race 77-3. The field resistance of cultivars Manitou and Pavon 76 against race 77-1, without evident hypersensitive response was conditioned by duplicate genes and it is proposed to be durable. The resistance of Romany in field tests against race 77-1 was also due to duplicate genes but at least one of these genes is hypersensitive in nature.

Key words : Non-hypersensitive resistance, *Puccinia recondita*, durable resistance

Use of genetic resistance is the only effective method to combat leaf rust of wheat caused by *Puccinia recondita* f. sp. *tritici Rob.* ex Desm. So far, nearly 38 genes conferring resistance to leaf rust have been identified and designated as *Lr1* through *Lr46* [1, 2]. Other than the alien genes, only *Lr3ka, Lr12, Lr14b, Lr30* and *Lr34* from *Triticum aestivum* have remained effective in field tests in the Indian sub-continent against prevalent leaf rust races [3, 4]. Tests on many wheats showing durable resistance to leaf rust in the Indian sub-continent suggest the presence of as yet undescribed resistance genes native to *Triticum aestivum,* many of which are expressed only at the adult plant stage [5 - 7]. Additional and as yet undescribed adult plant resistance (APR) genes have been indicated from wheats tested elsewhere also [8]. Characterization of resistant wheats in terms of nature, number and usefulness of new leaf rust resistance genes is therefore, important for the use of these new genes in breeding cultivars with durable resistance. Present report deals with the characterization and inheritance of as yet undescribed leaf rust resistance genes in three resistant cultivars against six economically important and highly virulent leaf rust races from the Indian sub-continent.

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MATERIALS AND METHODS

The experimental material comprised the cultivars Manitou from Canada, Romany from Kenya and Pavon 76 developed at the International Centre for Maize and wheat Improvement (CIMMYT), Mexico. Five single gene leaf rust resistant lines (*Lr* lines) in Thatcher (Tc) background namely, Tc + *Lr1*, Tc + *Lr3* (Democrat allele), Tc + *Lr10*, Tc + *Lr12* and Tc + *Lr23* and a susceptible *Lr13* carrier wheat WL711 were used as reference stocks. Cultivar Agra Local was used as a susceptible parent in crosses. The seed source, pedigree and *Lr* gene(s) reported so far from each of the wheats used [9, 10] are given in Table 1.

Table 1. List of wheats, their seed source, pedigree and known *Lr* genes.

Cultivar/line	Seed source	Pedigree	*Lr* gene(s)
Manitou	Dr. P.L. Dyck, Agriculture Canada	Thatcher*7/Frontana/Canthatch/3/PI170125/6* Thatcher	*Lr13*[9]
Romany	Directorate of wheat research, Karnal, India	Colotana 261-51/Yakatana 54A	*Lr13*[10]
Pavon 76	Dr. R.A. McIntosh, Plant Breeding Institute, Cobittey, Australia	Vicam 71/Ciano Sib/Siete Cerros/Kalyansona/ Blue Bird	*Lr1* + *Lr10* + *Lr13*[10]
Tc + *Lr1*	Dr. P.L. Dyck, Agriculture Canada	Thatcher*6/Centenario	Lr1
Tc + *Lr3*	-do-	Thatcher*6/Democrat	*Lr3*
Tc + *Lr10*	-do-	Thatcher*6/Exchange	*Lr10*
Tc + *Lr12*	-do-	Exchange/Thatcher*6	*Lr12*
WL711 (*Lr13*)	Directorate of wheat research, Karnal, India	Sonalika/Chris// Kalyansona	*Lr13*[10]
Tc + *Lr23*	Dr. P.L. Dyck, Agriculture Canada	Lee 310/Thatcher*6	*Lr23*
Agra Local	Directorate of wheat research, Karnal, India	A leaf rust susceptible land race of India	No resistance reported so far

9 = Dyck *et al.*, 1966; 10 = Saini *et al.*, 1993

Leaf rust races 12, 77, 77-1, 77-3, 108 and 162 were used. The avirulence/virulence formulae of these six races are given in table 2. Races 12 and 162 show avirulence on Tc + *Lr1* but these races show virulence on Tc + *Lr3*. Whereas, race 108 is virulent on Tc + *Lr1* and shows avirulence on Tc + *Lr3*. The seedling reaction against races 12, 108 and 162 was, therefore, used to differentiate the resistance based on the genes *Lr1* and *Lr3*. In addition, the gene *Lr1* was also identified by its characteristic 0; reaction against races 12 and 162 [1]. Races 12 and 77 are avirulent on *Lr10* but derivative races 77-1 and 77-3 of race 77 are virulent on *Lr10*. Therefore, reaction to races 12, 77, 77-1 and 77-3 was used to detect resistance based on *Lr10*. Both the races 77-1 and 77-3 possess avirulence against *Lr23*, a gene originally transferred to hexaploid wheat from *T. turgidum* var. *durum* cv. *Gaza* [1] and frequently detected from leaf rust resistant wheats in India. Race 77-3 is differentiated from race 77-1 by its additional avirulence on *Lr20*. Reaction to races 77-1 and 77-3 was used to detect resistance due to genes other than *Lr23*. Race 77-1 was used for field tests because it is the most virulent amongst the races used and it shows virulence on all the known *Lr* genes postulated from wheats used for present study.

Table 2. List of leaf rust races used and their avirulence/virulence formulae

Sr. No.	Race	Avirulence/virulence formula
1.	12	P*Lr1, Lr2a, Lr9, Lr15, Lr18, Lr19, Lr20, Lr21, Lr23, Lr24, Lr25, Lr26, Lr27+Lr31, Lr28, Lr29, Lr32/pLr2b, Lr2c, Lr2d, Lr3, Lr10, Lr11, Lr12, Lr13, Lr14, Lr16, Lr17, Lr22, Lr30, Lr33, Lr34*
2.	77	P*Lr9, Lr10, Lr18, Lr19, Lr21, Lr24, Lr25, Lr26, Lr27+Lr31, Lr28, Lr29, Lr32/pLr1, Lr2, Lr3, Lr11, Lr12, Lr13, Lr14, Lr15, Lr16, Lr17, Lr20, Lr22, Lr23, Lr30, Lr33, Lr34*
3.	77-1	P*Lr9, Lr18, Lr19, Lr21, Lr23, Lr24, Lr25, Lr28, Lr29, Lr32/pLr1, Lr2, Lr3, Lr10, Lr11, Lr12, Lr13, Lr14, Lr15, Lr16, Lr17, Lr20, Lr22, Lr26, Lr27+, Lr31, Lr30, Lr33, Lr34*
4.	77-3	P*Lr9, Lr18, Lr19, Lr20, Lr21, Lr23, Lr24, Lr25, Lr28, Lr29, Lr32/pLr1, Lr2, Lr3, Lr10, Lr11, Lr12, Lr13, Lr14, Lr15, Lr16, Lr17, Lr22, Lr26, Lr27+Lr31, Lr30, Lr33, Lr34*
5.	108	P*Lr3, Lr9, Lr15, Lr18, Lr19, Lr21, Lr24, Lr25, Lr26, Lr27+Lr31, Lr28, Lr29, Lr30, Lr32/pLr1, Lr2, Lr10, Lr11, Lr12, Lr13, Lr14, Lr16, Lr17, Lr20, Lr22, Lr23, Lr33, Lr34*
6.	162	P*Lr1, Lr9, Lr18, Lr19, Lr20, Lr21, Lr24, Lr25, Lr26, Lr27+Lr31, Lr28, Lr29, Lr32/pLr2, Lr3, Lr10, Lr11, Lr12, Lr13, Lr14, Lr15, Lr16, Lr17, Lr22, Lr23, Lr30, Lr33, Lr34*

The leaf rust resistance of three cultivars and of the single gene *Lr* lines was assessed using each race in tests at seedling stage and adult plant stages. The first leaf of 15-20, seven day old seedlings and three flag leaves of two adult plants of each cultivar/*Lr* line were inoculated separately with uredospores of races 12, 77, 77-1, 77-3, 108 and 162 mixed in talcum powder. These were then incubated at 20 ± 1°C and 100% relative humidity for 24 hrs and shifted to glass house benches at 20 ± 8°C. The reaction types, which measure resistance in terms of hypersensitive host response, were recorded according to standard methods [11]. The reaction types 0 (zero); (fleck), 1, 2 and X were considered resistant and those of types 3 and 3 + (without hypersensitive response) were considered susceptible.

For inheritance studies the resistant cultivars were crossed to Agra Local. The F_1, F_2 and F_3 generations from crosses of Manitou, Pavon 76 and Romany with Agra Local were tested for seedling reaction types in a glass house under controlled conditions. Approximately ten seeds of each parent and F_1, up to 200 F_2 seeds from each cross and up to 25 seeds for each F_3 line were also sown in 2 m long paired rows in open experimental area. One row of the susceptible parent Agra Local was planted after every 20 experimental rows as well as around the experimental plot. Beginning from the second week of January, the experimental material was regularly sprayed with a uredospore suspension of race 77-1 in water. Inoculation of the experimental material was continued on alternate days up to the end of February. The rust scores on field grown plants were recorded twice as percentage of leaf area covered with rust according to a modification of Cobb's scale [12]. The first observation was recorded in second week of April and the second observation was recorded two weeks later to ensure maximum rust development on some late maturing segregants. The second set of observations was expressed as terminal disease severity. For studying the segregation ratios, the plants on which the rust scores were less than the minimum of that observed on susceptible parent (50MS/S) were considered resistant (R) and all others were classified as susceptible (S). Simple chi-square test was applied to fit appropriate segregation ratios in F_2 and F_3 generations. The contribution of a low seedling reaction type gene towards terminal disease severity on field grown adult plants was examined by subjecting the reaction types and adult plant terminal disease severity data of each F_3 line to joint segregation tests [13].

RESULTS AND DISCUSSION

The observations on reaction types and terminal disease severity of cultivars as well as the single gene *Lr* lines are given in Table 3. Cultivar Manitou was resistant to race 162 both at seedling stage and adult plant stage but it expressed only APR against race 108. Cultivars Pavon 76 and Romany were resistant to races

Table 3. Terminal disease severity in field tests and reaction types of cultivars and single gene *Lr* lines in glasshouse against six Indian races

Cultivar/Single gene *Lr* line	Terminal disease severity	Race, growth stage* and reaction type											
		162		12		108		77		77-1		77-3	
		SS	AP	SS	AP	SS	AP	SS	AP	SS	AP	SS	AP
Cultivars													
Manitou (*Lr13*)	5S-10S	;1	;	33+	33+	33+	X	3+	33+	33+	33+	33+	33+
Pavon 76 (*Lr1* + *Lr10* + *Lr13*)	5S-10S	0;	0;	0;	0;	X	;1–	;	;	33+	33+	33+	33+
Romany (*Lr13*)	TR-5MR	0;	0;	0;	0;	X	;	;	;	;1	;	33+	;
Single gene *Lr* lines													
Tc + *Lr1*	70S-80S	0;	0;	0;	0;	33+	33+	33+	33+	33+	33+	33+	33+
Tc + *Lr3*	70S-80S	3+	33+	33+	33+	;1	;	33+	33+	33+	33+	33+	33+
Tc + *Lr10*	70S-80S	3+	33+	;1	;	33+	33+	;1	;	33+	33+	33+	33+
Tc + *Lr12*	40S-50S	3+	33+	33+	33+	33+	33+	33+	33+	33+	33+	33+	33+
WL711 (*Lr13*)	80S-90S	33+	33+	33+	33+	33+	X+	33+	33+	33+	33+	33+	33+
Tc + *Lr23*	60S-70S	3+	33+	33+	33+	33+	33+	33+	33+	;1	;1	;1	;1
Susceptible check													
Agra Local	50S-70S	33+	33+	33+	33+	33+	33+	33+	33+	33+	33+	33+	33+

*SS = Seedling stage, AP = Adult plant stage

12, 77, 108 and 162 both at seedling stage and adult plant stage and developed a 0; reaction against races 12 and 162 which is characteristic of the gene *Lr1*. Pavon 76 was susceptible to races 77-1 and 77-3 but Romany exhibited low reaction on seedlings and adult plants against race 77-1 and only APR against race 77-3. The single gene line for *Lr1* developed a 0; reaction against races 12 and 62. The line Tc + *Lr3* was resistant to race 108, whereas Tc + *Lr10* was resistant to races 12 and 77. The single gene line Tc + *Lr12* was susceptible to all the six leaf rust races but WL711 (*Lr12*) exhibited APR against race 108. The seedlings and adult plants of the single gene line Tc + *Lr23* exhibited low reaction to races 77-1 and 77-3. The remaining race cultivar/single gene *Lr* line interactions resulted in susceptible reaction types. The terminal disease severity on Manitou and Pavon 76 varied from 5S to 10S and on Romany, it varied from TR to 5MR. The terminal disease severity on single gene *Lr* lines Tc + *Lr1*, Tc + *Lr3* and Tc + *Lr10* varied from 70S to 80S. The terminal disease severity on Tc + *Lr12* and Tc + *Lr23* was 40S to 50S and 60S to 70S, respectively. The terminal disease severity on WL711 (*Lr13*) and Agra Local varied from 80S to 90S and 50S to 70S, respectively.

The segregation for seedling reaction types against races 162 and 108 and field resistance (terminal disease severity) on adult plants against race 77-1 in F_2 and F_3 generations from different crosses is given in Table 4.

Table 4. Segregation@ for seedling and adult plant reaction in F_2 and F_3 generations from crosses of three resistant wheats with Agra Local.

Culture/Cross	Number of F_2 plants					Number of F_3 lines					
	Res.	Susc.	Total	Ratio	X^2	Res.	Segr.	Susc.	Total	Ratio	X^2
A. Seedling reaction (Reaction type)											
Race 162											
Manitou × Agra Local	227	56	283	3:1	4.10*	55	97	62	214	1:2:1	2.33
Race 108											
Pavon 76 × Agra Local	197	58	255	3:1	0.69	35	62	38	135	1:2:1	1.03
Romany × Agra Local	316	89	405	3:1	1.98	47	99	41	187	1:2:1	1.03
B. Adult plant reaction (Terminal disease severity)											
Race 77-1											
Manitou × Agra Local	156	18	174	15:1	4.98*	66	81	8	155	7:8:1	0.50
Pavon 76 × Agra Local	142	9	151	15:1	0.02	64	64	8	136	7:8:1	0.60
Romany × Agra Local	162	12	174	15:1	0.12	73	81	10	164	7:8:1	0.04

@ Res. = Resistant, Susc. = Susceptible, Segr. = Segregating. * = Significant at P = 0.05

The F_1 seedlings from crosses of cultivars Manitou, Pavon 76 and Romany with Agra Local were resistant to respective race against which these were tested. The F_2 and F_3 generations from these crosses segregated in a 3R : 1S and 1 homozygous resistant (HR) : 2 segregating (Segr.): 1 homozygous susceptible (HS) ratio, respectively. In field tests against race 77-1, the F_1 adult plants from crosses of cultivars Manitou, Pavon 76 and Romany with Agra Local showed higher disease severity levels (30S, 20S and 10S, respectively) than the respective resistant parents. The adult plants in F_2 and F_3 generations from these crosses segregated in a 15R : 1S and 7HR : 8 Segr. : 1HS ratio, respectively.

Table 5. Joint segregation* for adult plant field reaction (terminal disease severity) against race 77-1 and seedling reaction against races 108 and 162 on F_3 lines from three crosses

Race/cross		Race 77-1				
		Nature and number of lines				
		Hr	Segr.	HS	Total	χ^2(1:2:1)
Race 162						
Manitou × Agra Local	HR	15	23	2	40	
	Segr.	33	35	2	70	0.61
	HS	16	16	2	34	
	Total	64	74	6	144	
	X^2 (7:8:1)		1.07			
	X^2	4:2:1 (29.70*)	0:6:2**	0:0:1**		
Race 108						
Pavon 76 × Agra Local	HR	17	11	2	30	
	Segr.	28	26	3	57	1.60
	HS	12	22	3	37	
	Total	57	59	8	124	
	X^2 (7:8:1)		0.29			
	X^2	4:2:1 (17.68*)	0:6:2**	0:0:1**		
Romany × Agra Local	HR	25	12	2	39	
	Segr.	30	43	1	74	0.18
	HS	17	20	3	40	
	Total	72	75	6	153	
	X^2 (7:8:1)		1.74			
	X^2	4:2:1 (15.03*)	0:6:2**	0:0:1**		

@ Homozygous resistant, Segr. = Segregating, HS = Homozygous susceptible, * = Significant at P = 0.05, ** = Not calculated because one of the expected values is zero.

The observations on joint segregation for seedling reaction types against races 162 and 108, and adult plant terminal disease severity against race 77-1 in F_3 lines from crosses of cultivars Manitou, Pavon 76 and Romany with Agra Local are given in Table 5.

(i) Manitou × Agra Local: Seedling and adult plant reaction to races 162 and 77-1, respectively

Out of the 64 F_3 lines homozygous resistant (HR) to race 77-1 in field tests, 15 were HR, 33 segregated and 16 were homozygous susceptible for seedling reaction types against race 162. Only 35 of the 74 F_3 lines segregating for resistance against race 77-1 (low terminal disease severity at adult plant stage) were segregating, 23 were HR and 16 F_3 lines were HS for seedling reaction against race 162. Two of the 6 F_3 lines homozygous susceptible to race 77-1 at adult plant stage were HR, two were HS and 2 F_3 lines segregated for seedling reaction types against race 162.

(ii) Pavon 76 × Agra Local: Seedling and adult plant reaction to races 108 and 77-1, respectively

Out of the 57 F_3 lines homozygous resistant to race 77-1 in field tests, 17 were HR, 28 segregated and 12 were homozygous susceptible for seedling reaction to race 108. Only 26 of the 59 F_3 lines segregating for resistance (low terminal disease severity against race 77-1) at adult plant stage were segregating, 11 lines were HR and 22 F_3 lines were homozygous susceptible for seedling reaction to race 108. Three of the eight F_3 lines homozygous susceptible to race 77-1 at adult plant stage were HS, 3 segregated and 2 were HR for seedling reaction to race 108.

(iii) Romany × Agra Local: Seedling and adult plant reaction to races 108 and 77-1, respectively

Out of the 72 F_3 lines homozygous resistant to race 77-1 in field tests, 25 were HR, 30 segregated and 17 were homozygous susceptible for seedling reaction to race 108. Only 43 of the 75 F_3 lines segregating for resistance (low terminal disease severity against race 77-1) at adult plant stage were segregating, 12 lines were HR and 20 F_3 lines were homozygous susceptible for seedling reaction to race 108. Three of the 6 F_3 lines homozygous susceptible for adult plant reaction to race 77-1 were HS, 1 line segregated and 2 lines were homozygous resistant for seedling reaction to race 108.

Cultivar Manitou is reported to carry the adult plant resistance gene *Lr13* [9]. The APR of Manitou against race 108 is due to *Lr13* but this gene is of no value in India, because susceptibility of wheats with *Lr13* to races like 77 and 162 is already known [4, 14]. The resistance of cultivar Manitou to race 162 reported here is therefore, due to a gene different from *Lr13*.

The characteristic 0; reaction of Pavon 76 to race 77 is due to *Lr10*. The seedling reaction of cultivar Romany to races 12, 77, 77-3 and 162 suggests that the genes *Lr1* and *Lr10* are also present in this cultivar. The low seedling as well as field reaction of cultivar Romany to race 77-1 is due to a new gene and it cannot be attributed to *Lr23* because of its seedling susceptibility to race 77-3, also having avirulence on this gene. Moreover, the gene *Lr23* has not been found useful in field tests on adult plants because the line Tc + *Lr23* has shown field susceptibility against race 77-1 despite its avirulence on seedlings with the gene *Lr23*. The gene *Lr23* is known to show highly variable reaction due to changes in temperature [15]. Because the temperature in seedling tests (20 ±1°C) was different than that which prevailed during field tests, the susceptibility of Tc + *Lr23* against race 77-1 is not surprising. The seedling tests on Pavon 76 and Romany against many Australian races did not indicate *Lr3* in these two wheats [16]. Therefore, the resistance of Pavon 76 and Romany to race 108 is also due to hitherto unknown gene(s).

The genes, *Lr12*, *Lr13* and *Lr34* were identified as the only APR genes owing their origin to *T. aestivum* [1, 17]. Avirulence on *Lr34* is not known to exist in India. Therefore, detection of this gene in the present study was not possible. Because the other APR genes *Lr12* and *Lr13*, are susceptible to race 77-3, the low adult plant reaction of Romany to race 77-3 in glasshouse tests is due to new and as yet undescribed hypersensitive APR gene(s). The field performance of this new APR against race 77-1 needs to be demonstrated as yet. The terminal disease severity values of single gene *Lr* lines in field tests against race 77-1 suggest that none of the known *Lr* genes identified from cultivars Manitou, Pavon 76 and Romany is useful under field conditions and the resistance of these three cultivars to race 77-1 is due to as yet unknown gene (s). Although there is no evidence of hypersensitive resistance in cultivars Manitou and Pavon 76 against race 77-1, the resistance of cultivar Romany may be due to the new hypersensitive seedling resistance gene(s) which have remained effective against this race, in adult plants also

The low seedling reaction of Manitou to race 162 and that of the cultivars Pavon 76 and Romany to race 108 is conditioned by a dominant gene each (Table 4). The usefulness of seedling resistance of each of these cultivars against race 77-1 in field tests was tested by evaluating each F_3 line from their crosses with Agra Local for seedling reaction and terminal disease severity on adult plants (Table 5). Because some of the F_3 lines homozygous resistant for seedling reaction from each of the three crosses were homozygous susceptible for adult plant field reaction against race 77-1, the seedling resistance of Manitou to race 162 and that of cultivars Pavon 76 and Romany to race 108 did not contribute towards their field resistance against race 77-1. In field tests, duplicate genes conferred resistance to race 77-1 in each of these three cultivars. Cultivar Romany showed low hypersensitive seedling reaction against race 77-1. Since the seedling resistance genes are expected to remain effective against same race in adult plants also, the field resistance of cultivar Romany to race 77-1 may be attributed to low seedling reaction gene (s) which might have remained effective against race 77-1 in adult plants also.

High seedling as well as adult plant reaction of cultivars Manitou and Pavon 76 to race 77-1 in terms of reaction types on Stakman's scale indicates non-hypersensitive nature of duplicate genes from these wheats. A similar non-hypersensitive resistance gene from cultivar Pavon 76 has recently been designated as *Lr46* [2]. This type of resistance against leaf rust has been reported earlier also from wheat [5, 18] and barley [19]. In contrast to hypersensitive resistance, which prevents the growth of rust pathogen beyond necrotic areas, the non-hypersensitive type of resistance observed in Manitou and Pavon 76 only retards the growth of the pathogen which is ultimately expressed as low terminal disease severity in field tests. Because no selection pressure is forced on pathogen, the non-hypersensitive resistance of Manitou and Pavon 76 may be durable. The hypersensitive resistance genes often provide near complete protection in field tests, but the effective life of such resistance always depends upon ability of the pathogen to mutate and produce more virulent pathotypes. The use of such resistance for long-term control of leaf rust in India, particularly in the presence of hypervariable races like 12, 77, 104 and 108 may not be worthwhile. Therefore, it is time to understand the nature of resistance shown by different cultivars and plan plant breeding programmes on the basis of information on these important aspects.

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