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Genetics of Durable Resistance to Leaf Rust in Bread Wheat Cultivars Capelle Desprez and Pari 73

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Summary

Bread wheat cultivars Capelle Desprez and Pari 73 have been showing adult plant leaf rust resistance in India since 20 years. To examine nature, number and mode of inheritance to leaf rust multipathotype tests were conducted on these cultivars along with reference line RL6058 and HD2009 and the susceptible cultivars WL711 and Agra Local at adult plant stages against the eight leaf rust races. F2 and F3 generations from crosses of Capelle Desprez and Pari 73 with susceptible cultivar WL711 were tested for percent disease severity against leaf rust race 77-5 which suggested the presence of three genes in Capelle Desprez and two genes in Pari 73 to leaf rust. Allelic tests using Capelle Desprez with RL6058 indicated the presence of linked genes Lr34/Yr18 however, presence of transgressive segregants in this cross indicated that the other two genes in Capelle Desprez are also involved in leaf rust resistance. The segregation for susceptible plants observed among all the crosses used for allelic tests of Pari 73 for leaf rust indicated that non-hypersensitive resistance genes in Pari 73 are different from those in RL6058, HD2009 and Capelle Desprez. Studies using 536 primers indicated that one of the three rust resistance gene(s) in cultivar Capelle Desprez is located on chromosome 1B, at a distance of 26.3cM from the primer *Xgwm* 268. Chromosome location of leaf rust resistance gene from cultivar Pari 73 could not be achieved.

Key Words: Durable resistance, Leaf rust, *Puccinia triticina*, Pari 73, Capelle Desprez

Introduction

Rusts (leaf rust, stripe rust and stem rust) are the most important and damaging pathogens of wheat [15, 20]. Among wheat rusts, viz. leaf rust *Puccinia triticina* (*Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici*), stripe rust (*P. striiformis* Pers. f. sp. *tritici*) and stem rust (P. *graminis* Pers. f. sp. *tritici* Eriks & Henn) received worldwide concern because of yield losses and quality deterioration world over [16, 20, 25] and leaf rust is the most important disease of wheat in North Western Plain Zone inflicting serious yield losses [1, 7, 27, 31, 41]

Nearly 60 leaf rust resistance genes and 48 stripe rust resistance genes have so far been identified from different germplasm collections in wheat and related species and molecular markers are available for many of them [13, 43]. Of these, only the leaf rust resistance genes *Lr34* and *Lr46* and the linked stripe rust resistance genes *Yr18* and *Yr29* respectively, have been known to confer durable resistance in wheat [32, 37, 42]. The gene *Lr34* is partially effective, and it is highly interactive and often additive in expression [5, 8, 11, 28, 34] and is also effective against stem rust [4, 12], powdery mildew [38], and barley yellow dwarf virus [2, 34]. The gene *Lr46* was identified in cultivar Pavon76 but this gene is not effective in India [37].

Availability of only one effective leaf rust resistance gene in India conferring durable resistance is a major limitation in wheat breeding, therefore; more genes conferring such resistance need to be searched from various germplasm collections. Characterization of novel sources of durable resistance and accelerated breeding in conjunction with elucidating the basis of resistance would provide at least, a sustainable resistance management strategy if, not a permanent solution.

European cultivar Capelle Desprez (Joncquoes/ Vilmorin27) and Pakistani cultivar Pari 73 (Ciano67 sib//Sonora64/Klein Rendidor/3/Penjamo 'S'/Gabo 55), have shown adult plant resistance to leaf rust in India for the past 20 years. Kaur et al suggested that leaf rust resistance of many cultivars including Pari 73 is conferred by gene(s) which may be different than *Lr34* [11]. Capelle Desprez which is resistant to yellow rust was widely cultivated without fungicide treatment in several western European countries during the 1960s and 1970s. This cultivar is therefore considered to have durable, moderate form of resistance that is effective at the adult plant stage [17, 18]. Because, only the genes *Lr34* and *Lr46* for leaf rust resistance are known to confer such resistance [32, 42], cultivars Capelle Desprez and Pari73 are additional sources of as yet undescribed genes that can confer durable leaf rust resistance in bread wheat.

The objective of our study was therefore, to determine the nature, number and chromosome location of as yet

undescribed genes that confer leaf rust resistance in wheat cultivars Capelle Desprez and Pari 73.

Material and Methods

Host material

The adult plants were raised in 10" X 12" sized earthern pots filled with a farmyard manure and sandy loam soil. Four seeds, of each cultivar were sown clockwise in 4 quarters of the pots. In the center of each pot, four seeds of susceptible check, Agra Local, were sown. When the seedlings acquired two-leaf stage, only two seedlings of each cultivar/line were allowed to grow, all others were removed in order to maintain good plant health. The pots were kept in glass house maintained at 20±1°C and relative humidity above 80% was maintained.

Cultivars Capelle Desprez and Pari 73 were crossed to susceptible cultivar WL711 and the adult plants in F_1, F_2 and F_3 generations were assessed for percent disease severity to examine the nature, number and mode of inheritance of the genes controlling leaf rust in these cultivar. Cultivar HD2009 and the reference line for the adult plant resistance gene *Lr34* RL6058 were used to compare allelic relationships of the genes for durable resistance among these cultivars.

To obtain the F1, F2 and F3 generations, the cultivars Capelle Desprez and Pari 73 were crossed with cultivar WL711, HD2009 and the thatcher line RL6058 carrying the gene Lr34 during Rabi 2002-03. A part of F1 seed was sent to the Wheat Research Station, Directorate of Wheat Research, Dalang Maidan, Lahaul and Spiti (H.P.), India to obtain F_2 seeds in off season (May-September2003). The F_3 generation was obtained by harvesting each plant from F_2 generation. During the normal season 2003-04, approximately 25-30 seeds of each F_1, F_2 and F_3 family were sown in 2m long rows placed 50cm apart. Two rows of each parent were planted on both sides of the F1 plants. The susceptible cultivar WL711 and Agra Local were sown after every 20 experimental rows as well as on all the sides of the experimental plot as disease spreader rows. The parents F_1, F_2 and F_3 generation were tested for rust reaction simultaneously in the crop season 2003-04.

Pathogen races

For characterization of adult plant leaf rust resistance, race 77 and three of its genetically defined variants i,e. 77-1, 77-2 and 77-5 and races 12-2, 162, 108 were used. Leaf rust race 77-5 is the most virulent race from the Indian sub-continent [20] and it is capable of knocking down all known leaf rust resistance genes originating from T. aestivum was used for field studies.

Inoculations

Glass House Studies

Four flag leaves of each cultivar/line grown in glasshouse were inoculated with urediniospore-talc mixture of appropriate rust culture. The plants were then incubated for 16 hours at 20+1°C and 100 percent humidity. After incubation, the pots were shifted to glasshouses.

Field Studies

Artificial rust epidemic was created by repeated inoculation of spreader rows and the experimental material with leaf rust race 77-5 suspended in mineral oil (Isopar-L from Exxon Mobil, 12 Riverside Quay, Melbourne VIC 3001 Australia). The field inoculations were done in the evening every alternate day which, were started from mid January and continued till rust appeared on susceptible cultivars.

Disease Assessment

Fourteen days after inoculation, the infection types on adult plants were scored using a modification of the scale given by Stakman et al [40]. Field assessments for leaf rust severity were based on modified Cobb scale [22], which is expressed as percent leaf area covered with rust. In the field studies, every plant was scored and based on these observations each of the F3 family was classified as resistant, segregating and susceptible. Plants showing disease severity equal to or more than the susceptible parent WL711 were classified as susceptible. All other plants were considered resistant.

Statistical analysis

Chi-square analysis was applied to test the goodness of fit of observed ratios to theoretical expectations.

DNA isolation PCR conditions, and gel electrophoresis

Total genomic DNA of 20 day old seedlings of parental lines Capelle Desprez, Pari 73, WL711 and homozygous susceptible (HS) and homozygous resistant (HR) F3 families was isolated using Cetyl trimethyl ammonium bromide (CTAB) method [24]. Quantity of the genomic DNA was assessed by agarose gel electrophoresis [28]. Approximately 20ng of DNA was used as template in a 20μl reaction volume that contained 250nM of each primer (forward and reverse), 1mM of each dNTP, 1.5mM MgCl2, 1 unit of Taq polymerase and 1X PCR buffer. A total of 279 Xgwm primers (gatersleban wheat microsatellites) [23], 156 wmc (wheat microsatellite consortium), 97 cfa, cfd (INRA clermont-Ferrand France) and 17 barc (www.scabusa.org) microsatellites uniformly distributed on all the seven homoeologous groups of chromosomes of wheat were tested for polymorphism. Amplifications were performed in an eppendorf thermal cycler for 35 cycles. These 35 cycles were useful for intensifying the bands. After an initial denaturation of 5min at 94°C, each cycle consisted of 1min at 94°C, 1min at 55-67°C, and 2min at 72°C. The 35 cycles were followed by a 7-min final extension at 72°C. Half of each sample was analysed by electrophoresis in a 2.5% agarose gel in 1X TBE buffer (2.0% CTAB, 10mM Tris-HCl, 1.4M NaCl, 20mM EDTA, 20%β-mercaptoethanol). Amplifications products were visualized by ethidium bromide (100mg/ml, Sigma ultra pure) staining and visualised under UV light and photographed using the gel documentation system (UVP Transilluminator Model GDS 7600) with GRAB IT software programme (Annotating Grabber 32 bits)

Results

The infection types displayed by the cultivars tested with eight pathotypes are presented in Table1. The test cultivar Capelle Desprez and Pari 73 showed resistant infection types at adult plant stages against races 77-5 and 162 respectively. However, HD2009 showed resistant infection types against race 77 at adult plant stage. Susceptible cultivar WL711 showed resistant Infection type at adult plant stage (1^+2) against race 162. Line RL6058 and land race Agra Local gave susceptible infection types against all the races used for the present study.

Table1. Adult plant Infection types of Capelle Desprez, Pari 73 and other cultivars/line against eight leaf rust races

Cultivar/ line	77	77-1	77-2	77-5	12-2	104-2	108	162	Postulated genes
Capelle Desprez	-	3	33+	;	3	33+	3	33+	None
Pari 73	3	33+	3	3	3	33+	x	;	Lr13
HD2009	;1	33+	33+	33+	33+	3	x	3	Lr13
RL6058	33+	33+	33+	33+	3	33+	33+	33+	None
Agra Local	33+	33+	33+	33+	33+	3	33+	33+	None
WL711 (Lr13)	3	33+	33+	33+	33+	3	1	;1	(Lr13) + ?

Table 2: Segregation for leaf rust resistance in crosses of cultivars Capelle Desprez and Pari 73 with WL711 and their intercrosses as well as crosses with RL6058 (*Lr*34) and HD2009

Crosses	Generation										
	F2					F3					
	Number of Plants*					Number of Families					
	Resistant	Susceptible	Total	Expected ratio	Chi-square (χ2)	Homozygous Resistant	Segregating	Homozygous Susceptible	Total	Expected ratio	Chi-square (χ2)
Capelle Desprez x WL711	286	6	292	63:1	0.2	59	133	5	197	26:37:1	7.7*
Pari 73 x WL711	226	22	246	15:1	2.31	160	172	15	347	15:1	2.6
Capelle Desprez x Pari 73	Segregated for susceptibility					F3 not tested					
Capelle Desprez x RL6058	No Segregation					F3 not tested					
Capelle Desprez x HD2009	Segregated for susceptibility					F3 not tested					
Pari 73 x RL6058	Segregated for susceptibility					F3 not tested					
Pari 73 x HD2009	F2 not tested**					Segregated for susceptibility					

* Significant at P = 0.05

** F2 of Pari 73 x HD2009 was not scored for leaf rust because of stripe rust infection

Inheritance studies

Capelle Desprez

The cultivars Capelle Desprez and WL711 showed leaf rust severity of 10MR-20MR percent and 70S-80S percent respectively. The F_1 plants from the cross of Capelle Desprez with WL711 displayed 20S percent leaf severity. In the F_2 generations from the cross out of 292 plants studied 286 were resistant and while plants 6 plants were susceptible. This distribution gives a perfect fit of 63:1 ratio as expected for three dominant independently inherited genes (χ^2 = 0.2). The segregation pattern of percent disease severity in F_2 and F_3 generations is given in **Table 2.** F_3 families were classified as 59 Homozygous resistant, 133 segregating and 5 Homozygous Susceptible. This pattern didn't give a perfect fit of 26:37:1, the expected pattern for three gene segregation and thus giving significant test (χ^2 = 7.7). This significant chi-square value is probably due to misclassification of resistant and segregating families those could not be differentiated because only 2m row was sown with each F_3 family accommodating not more than 20 plants.

Out of total 757 plants studied in the F_2 population from the cross Capelle Desprez with HD2009, 756 were resistant and 1 was susceptible. Whereas, the F_2 population from the cross Capelle Desprez with RL6058 did not show any susceptibility among total 263 plants studied.

Pari 73

The cultivars Pari 73 and susceptible cultivar WL711 showed leaf rust severity of 30S-40S percent and 70S-80S percent respectively. The F_1 plants obtained from the cross displayed percent disease severity of 40S similar to that of Pari 73 (40S), thus indicating partial dominant nature of gene(s) conferring low percent disease severity of Pari 73. In terms of percent disease severity out of the total 246 F_2 plants studied, 226 were resistant while 22 were susceptible. The population gave a perfect fit of 15R: 1S ratio (χ^2 = 0.34). These observations indicated presence of two dominant genes independently inherited genes. F_3 families were classified as

160 Homozygous resistant, 172 segregating and 15 Homozygous Susceptible, which fitted a digenic ratio of 7: 8: 1 (χ^2 = 0.77), thus confirming the presence of two dominant genes in cultivar Pari 73 effective against leaf rust race 77-5. The segregation pattern for percent disease severity of F_2 and F_3 is given in **Table 2.**

The F_2 generation from the crosses of Pari 73 with RL6058 and Capelle Desprez showed segregation for susceptible plants. Segregation for susceptible plants in this population also suggests that the adult plant resistance gene(s) in cultivar Pari 73 population is non allelic to *Lr34* RL6058. The F_2 generation from the cross of Pari 73 with HD2009 could not be studied for leaf rust due to heavy stripe rust infection on many plants. Therefore, the cross was studied during next season. Many F_3 families were segregating for susceptible plants and homozygous susceptible F_3 families were also observed in this population. Thus indicating that the gene(s) in cultivar Pari 73 are non-allelic to those present HD2009.

As reported by Singh and Rajaram that level of resistance *Lr34/Yr18* it confers is usually not adequate when present alone [35]. However, combinations of this gene and 3-4 additional slow rusting genes result in adequate resistance levels in most of the environments.

Molecular studies

Parental polymorphism survey between resistant cultivars Capelle Desprez, Pari 73 with respect to susceptible cultivar WL711 was done using a total of 234 *Xgwm* primers, 109 WMC, 67 cfa, 89 cfd and 19 barc primers. The 536 primers tested among resistant and susceptible parents, 120 (22.3%) primers were polymorphic between Capelle Desprez and WL711 and 134 (25%) primers were polymorphic between Pari 73 and WL711. Most of the polymorphic markers were present on chromosome 2A in both Capelle Desprez and Pari 73, while none of the primer was found to be polymorphic from 6D in both the cultivars. The results show that most of the markers which were polymorphic are present on chromosome 2A in both Capelle Desprez and Pari 73, while none of the primer was found to be polymorphic from 6D in both the cultivars.

Out of the nine primers identified as linked with bulks of Capelle Desprez X WL711, only two primers *cfa2153* (1A) and *Xgwm268* (1B) was observed to show segregation in segregating F_2 plant progenies. Whereas, six primers namely *Xgwm140* (1B), *Xgwm249* (2A), *Xgwm499* (5B), *Xgwm558* (2A), *Xgwm544* (5B), *Xgwm626* (6B) showed segregation in F_2 plant progenies of Pari 73 X WL711.

The phenotypic data for resistance to leaf rust in F_2 plant progenies against race 77-5 was used to prepare linkage map by using software MAPMAKER/EXP (version 3.0b). This analysis indicated that one of the three leaf rust resistance gene(s) in cultivar Capelle Desprez is located on chromosome 1B, at a distance of 26.3 cM from the primer *Xgwm* 268. While, in case of Pari 73 linkage between the primers used and any of the resistance genes could not be established but it is likely that non-hypersensitive resistance genes are located on chromosomes 2A and 5B.

Discussion

The Adult Plant Resistance against race 108 has been ascribed to the adult plant resistant gene *Lr13* [11]. Therefore, the resistant adult plant reaction of Pari 73 and HD2009 against race 108 indicates the presence of *Lr13* in these cultivars. Resistant reaction of cultivar WL711 to race 108 can be ascribed the gene *Lr13*. Gupta et al also reported that cultivar WL711 carries the gene *Lr13* [10]. Despite high infection types against race 77-5 in glass house tests, cultivars Pari 73, HD2009 and the line RL6058 showed low percent disease severity against this race in the filed which suggests the presence of non-hypersensitive leaf rust resistance in all these wheats. Cultivar Capelle Desprez displayed adult plant resistance against race 77-5 and susceptible infection types against rest of the races used for present study. High leaf rust reistance in cultivar Capelle Desprez may be attributed to hypersensitive resistance that expressed against race 77-5. Kaur et al have earlier reported non-hypersensitive resistance to leaf rust in cultivar Pari 73 [11]. Saini et al described low disease severity on wheats not showing hypersensitivity against a specific race as an indication of slow rusting ability of such wheats [26].

Although the wheats, having hypersensitive adult plant resistance appear to show high degree of resistance to leaf rust, such resistance being race-specific may breakdown after single step mutations in the pathogen races. However, wheats having non-hypersensitive resistance may allow a slower progress of the disease thus reducing selection pressure on the pathogen population. Such resistance will slow down the evolution of new rust races and thus it may prove to be durable.

The effective resistance against in many wheats against leaf rust is either due to *Lr34* or due to many yet undescribed genes [30, 35]. Cultivars Capelle Desprez showed leaf tip necrosis, a trait reported to be highly linked to the adult plant resistance gene. Therefore, gene *Lr34* also appears to be present in Capelle Desprez. On the other hand cultivars Pari 73 and HD2009 do not show leaf tip necrosis and thus may carry gene(s) different than *Lr34*. Absence of leaf tip necrosis both these cultivars has also been reported by Kaur et al [11]. Khanna et al reported the absence of non-hypertensive resistance genes different than *Lr34* in HD2009 [14].

The inheritance studies on leaf rust show the presence of three leaf rust resistance genes in cultivar Capelle Desprez and two leaf rust resistance genes in cultivar Pari 73. Because cultivar Capelle Desprez has shown leaf tip necrosis, therefore one of these genes is *Lr34.* McIntosh has also reprted the *Lr34* in cultivar 'Capelle Desprez". RL6058 is the reference line for non-hypersensitive adult plant resistance gene *Lr34* [19]. All the 263 F_2 plant from the cross Capelle Desprez X RL6058 were resistant indicating the presence of *Lr34* in cultivar Capelle Desprez. However, some of plants in F_2 showed percent disease severity lower than both the parents thus indicating transgression for resistance which can occur only if Capelle Desprez has gene(s) other than *Lr34*. The segregation for susceptible plants in cross Capelle Desprez X HD2009 suggested that the adult plant resistance gene(s) in cultivar Capelle Desprez and HD2009 are not allelic. Cultivar Pari 73 gave segregation in each cross thus proving that it has new sources of durable resistance against both the diseases and is devoid of durable leaf rust resistance gene *Lr34*.

Of the known *Lr* genes, *Lr11*, *Lr17*, *Lr37*, *Lr38* and *Lr45* are reported to be present on chromosome 2A [5, 3, 9, 38].

Out of these *Lr11*, *Lr17*, *Lr37* and *Lr38* show hypersensitive resistance genes whereas, gene Lr45 is alien in origin and also shows hypersensitivity. Only the *Lr18* has been reported to be present on 5B but is alien in origin. It is therefore, concluded that the genes in cultivar Pari 73 are unique.

The leaf rust resistance genes *Lr26*, *Lr46-Yr29*, *Lr51* and *Lr55* have been located on chromosome 1B. *Lr26* is the gene, which is derived from *Secale cereale*. Leaf rust resistance gene *Lr51*, located within a segment of *Triticum speltoides* Taush chromosome 1S translocated to the long arm of chromosome 1B of bread wheat and *Lr55* has been Derived from *Elymus trachycaulis*. Except *Lr46* all the other three genes are alien in origin. Therefore, the presence of these genes in cultivar Capelle Desprez is unlikely.

However, presence of gene *Lr46* although not alien in origin do not provide the host plant with complete immunity against a set of leaf rust (*Puccinia triticina*) races, instead they can delay the infection process or reduce the development of symptoms caused by a wider range of leaf rust races on adult plants was mapped distal to *Xwmc44*, approximately 5-15 cM, and proximal to *Xgwm259*, approximately 20 cM Microsatellite locus *Xbarc80* maps 10-11 cM distal to *Xgwm259* and can be used as an alternative distal marker (http://maswheat.ucdavis.edu). The contribution of gene *Lr46* to the phenotype is very low in India and thus *Lr46* is considered ineffective. Therefore, presence of *Lr46* in this cultivar is also ruled out and it is concluded from these observations that Capelle Desprez has a new and as yet undescribed APR gene.

Conclusion

In view of the use of large number of microsatellite markers it was presumed that we should be able to molecularly tag all non-hypersensitive leaf rust resistance genes conditioning resistance in cultivars Capelle Desprez and Pari 73, but only one leaf rust resistance gene in cultivar Capelle Desprez was mapped at a distance of 26.3 cM from the primer *Xgwm268*. Since no other marker was found in between the identified marker and the gene *LrCD1* further study to associate more closely linked markers with this genes will help in chromosome location and assigning a permanent symbol to the genes identified in present study in terms of international nomenclature.

More new genes need to be continuously identified from uncharacterized germplasm collections essentially for maintaining broad genetic base in breeding programme. The gene *Lr34* originally identified from Brazilian cultivar Frontana [35] is reported to confer durable resistance to leaf rust [18]. Cultivar Pari 73 released in 1978 has maintained high degree of field resistance to leaf rust for over 20 years in tests carried out in the Indian subcontinent [11]. Therefore, this cultivar is a source of durable resistance not based on the gene *Lr34*. The genetic analysis and characterization studies indicated that cultivars Capelle Desprez and Pari 73 are useful sources of leaf rust resistance that can be utilized in breeding programmes.

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