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Validation of race non-specific, adult plant leaf rust resistance genes *Lr34* and *Lr67* in some common wheat (*Triticum aestivum* L.) cultivars

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Abstract

Twelve common wheat cultivars with *Lr34* postulated based on leaf tip necrosis and other observations were studied for adult plant resistance to leaf rust (*Puccinia triticina*) pathotype 77-5 (121R63-1), and validation of *Lr34* and *Lr67* through allelic tests. Line 897 and Frontana, known *Lr34* carriers, served as checks. Resistance was governed by one dominant gene each in C 306, Kalyansona, Line 897, NI 5439 and WH 147; and by two dominant genes each in Frontana, GW 173, HD 2189, HI 1077, HP 1744, K 9107, PBW 175, PBW 373, and UP 2338. Allelic tests showed presence of *Lr34* in Frontana, GW 173, HD 2189, HP 1744 and Line 897; and of *Lr67* in C 306, NI 5439 and K 9107. Comparison is drawn with reports based on molecular markers. Our findings should be useful in multiple disease resistance breeding as *Lr34* and *Lr67* are associated with resistance to multiple wheat pathogens.

Key words: Adult plant resistance, race non-specific resistance, *Lr34*, *Lr67*, multiple disease resistance

Introduction

Seventy two leaf rust resistance genes in wheat have been designated (McIntosh et al. 2013; Herrera-Foessel et al. 2014a), of which *Lr34*, *Lr46*, *Lr67*, and *Lr68* are known to confer race non-specific adult plant resistance (APR) (Kolmer 2013). APR is receiving worldwide attention as durable resistance has been mostly of this kind. Best known and characterized of these genes is *Lr34*. Besides providing broad spectrum leaf rust resistance, *Lr34* is pleiotropic or closely linked with *Yr18*, *Sr57*, and *Pm38* (McIntosh et al. 2013), genes for resistance to stripe rust, stem rust, and powdery mildew pathogens, respectively. It also shows tolerance to barley yellow dwarf (*Bdv1*), resistance to spot blotch pathogen (*Sb1*), and leaf tip necrosis (*Ltn*) (McIntosh et al. 2013).

Lr34 was postulated in many common wheat cultivars including C 306, GW 173, HD 2189, HI 1077, HP 1744, K 9107, Kalyansona, NI 5439, PBW 175, PBW 373, UP 2338 and WH 147 based on leaf tip necrosis and few other observations (Nayar et al. 1999). However, presence of *Lr34* in C 306 was ruled out by us based on allelic tests (Mishra et al. 2005). Like C306, higher leaf rust scores were observed on HI 1077, Kalyansona, NI 5439, PBW 373 and WH 147, while GW 173, HD 2189, HP 1744, K 9107, PBW 175, and UP 2338 exhibited resistance phenotype similar to or stronger, compared to near-isogenic *Lr34* lines. Hence, it was planned to study inheritance of leaf rust resistance in these cultivars, and validate postulation of *Lr34* in them through allelic tests using near-isogenic lines RL 6058 and RL 6077. The latter was thought to carry *Lr34*, though translocated to another chromosome (Dyck et al. 1994) at the time our study was planned. Later, gene-specific markers revealed that *Lr34* was absent in RL6077 (Lagudah et al. 2009), and the gene present was designated *Lr67* (Hiebert et al. 2010; Herrera-Foessel et al. 2011). Allelic tests with RL 6077 could therefore confirm the presence of *Lr67* in the cultivars studied. Like *Lr34*, besides imparting race non-specific, adult plant leaf rust resistance, *Lr67* is pleiotropic or closely linked with *Yr46*, *Sr55* and *Pm46* for resistance to stripe rust, stem rust, and powdery mildew pathogens, respectively, and is associated with leaf tip necrosis (Herrera-Foessel et al. 2011; 2014b).

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Materials and methods

The above listed 12 common wheat cultivars and two known *Lr34* carriers: Line 897 (Thatcher (Tc) *6/ Terenzio) (Lagudah et al. 2006) and Frontana (Lagudah et al. 2009) were crossed with susceptible variety ‘Lalbahadur’, which served as female parent, and with RL 6058 (Tc*6/PI58548) and RL 6077 (Tc*6/ PI250413), which served as male parents. Seedling and adult-plant tests were conducted using the most prevalent (Bhardwaj et al. 2010) and virulent (Mishra et al. 2009) *Puccinia triticina* pathotype 77-5 (121R63-1). Parental lines and F_1s were seedling tested at 20-22^{o}C ± 2^{o}C in glasshouse using standard procedures (Roelfs et al. 1992). Adult-plant tests were conducted in nurseries isolated with paired maize rows using recommended cultivation practices. Seeds of parental lines, F_1s and F_2 s were dibbled with 10 cm spacing between seed-to-seed in 2.0 m long rows, planted 30 cm apart. Two-hundred F_2 seeds collected individually from two F_1 plants of each of the crosses involving Lalbahadur, and 400 F_2 seeds from two-to-three F_1 plants of each of the crosses involving RL 6058 or RL 6077 were sown. Rust spreader rows of highly susceptible varieties were planted after every 20 test rows, and all around experimental plot, and were inoculated using hypodermic syringes and sprays with uredospores of the pathotype 77-5 (121R63-1). Leaf rust scores were recorded on ‘flag-minus-one’ using modified Cobb scale (Peterson et al. 1948), and host response (Roelfs et al. 1992). The F_2 plants were grouped in to ‘resistant’ and ‘susceptible’ classes. Those classified “susceptible” were progeny tested to confirm F_2 observations. Fifty seeds from each of such plants were hand-drilled in 2.5 m long rows planted 30 cm apart. Chi-squared test was used to test the goodness-of-fit of observed F_2 ratios to the expected ones on the basis of Mendelian segregation.

Results and discussion

In glasshouse tests, all the test lines and their F_1s exhibited high infection types (‘33+’, ‘34’, ‘4’) showing seedling susceptibility (Table 1). In field tests, leaf rust resistance similar to the resistant parent was exhibited by F_1s of susceptible/resistant crosses, indicating dominant inheritance of resistance (Table 1). Optimum or enhanced levels of resistance were displayed by F_1s of resistant parent/RL 6058 or RL 6077 crosses (Table 1). Lines carrying *Lr34* and *Lr67* individually showed 10-20MSS and 30-40MSS reactions, respectively, while F_1s combining the two genes exhibited reactions in the range of 5-10MS (Table 1). However, NI 5439 and its F_1 with *Lr34* (RL 6058) displayed comparatively higher reactions *viz*., 30-40S and 10-20 MSS, respectively (Table 1), perhaps due to background effect.

In each F_2 population, plants as susceptible as the susceptible parental line (Lalbahadur) were grouped in susceptible class, and all the remaining plants were considered resistant. The F_2 ratios indicated that resistance was governed by one dominant gene each in C 306, Kalyan Sona, Line 897, NI 5439, WH 147, RL 6058, and RL 6077; and by two each in Frontana, GW 173, HD 2189, HI 1077, HP 1744, K 9107, PBW 175, PBW 373, and UP 2338 (Table 2).

No susceptible segregants were observed in crosses of RL 6058 with Frontana, GW 173, HD 2189, HP 1744 and Line 897 (Table 3) confirming the presence of *Lr34* in them; and in those from crosses of RL 6077 with C 306, NI 5439 and K 9107 (Table 4) showing the presence of *Lr67* in them. The remaining crosses involving RL 6058 or RL 6077 showed F_2 segregation for the expected ratio of 15 or 63 resistant:1 susceptible plants based on the inheritance of two or three independent dominant genes showing the absence of *Lr34* or *Lr67* in the cultivars involved (Tables 3 and 4). However, number of susceptible plants was higher than the expected in Kalyansona/ RL 6077 and WH 147/RL 6077 crosses (Table 4), which we are unable to explain. The absence of *Lr67* in cultivars Kalyansona and WH 147 is obvious from the segregation for susceptible plants in the above crosses. In progeny tests, ‘susceptible’ F_2 segregants were found to be true breeding for susceptibility thereby confirming the F_2 observations.

Pedigree analysis suggests that GW 173 could have inherited *Lr34* from TW 275-7-6-10 through ‘Norin 10’ (Lagudah et al. 2009), HD 2189 from Lerma Rojo 64 or Tezanos Pintos Precoz (Kolmer et al. 2008), and HP 1744 from ‘Parula’ (Kolmer et al. 2008). During recent years, molecular markers have been developed for gene identification due to difficulties in *Lr34* postulation based on leaf tip necrosis and slow rust development as their expression is influenced by environment and genetic background (Dakouri et al. 2010). The ‘*csLV34*’ marker has been used for characterizing *Lr34* in Indian wheat germplasm (Priyamvada et al. 2008; 2009; Pawar et al. 2013). Comparing our results revealed that these three studies reported the allele *csLV34b* in HD 2189, confirming the presence of *Lr34*. Also, there was total agreement between our findings and the marker based

Table 1. Seedling infection types in the glasshouse and terminal leaf rust scores on the flag-1 (flag-minus-one) leaf of the wheat parental lines and their F_1s in the field in response to *Puccinia triticina* pathotype 77-5 (121R63-1)

Parents/ F_1s	Seedling ITs	Terminal leaf rust scores on flag-1 leaf	Parents/F_1s	Seedling ITs	Terminal leaf rust scores on flag-1 leaf
C 306, Lalbahadur (Lb)/C 306	34, 34	30-40MSS, 40MSS-50S	Line 897, Lb/Line 897	33+, 33+	10-20MSS, 20MSS-30S
C 306/RL 6058, C 306/RL 6077	34, 34	5-10MS, 30-40MSS	Line 897/RL 6058, Line 897/ RL 6077	33+, 33+	10-20MSS, 5-10MS
Frontana (Fn), Lb/Fn	33+, 33+	TMR-5MRMS, 5-10MS	NI 5439, Lb/NI 5439	34, 34	30-40S, 50-60S
Fn/RL 6058, Fn/RL 6077	33+, 33+	TMR-5MRMS, TMR-5MR	NI 5439/RL 6058, NI 5439 / RL 6077	34, 34	10-20MSS, 30-40S
GW 173, Lb/GW 173	33+, 33+	5-10MRMS, 10-20MSS	PBW 175, Lb/PBW 175	33+, 33+	10-20MRMS, 20MS-30MSS
GW 173/RL 6058, GW 173/RL 6077	33+, 33+	5-10MRMS, 5-10MR	PBW 175/RL 6058, PBW 175/ RL 6077	33+, 33+	5-10MRMS, 10-20MRMS
HD 2189, Lb/HD 2189	33+, 33+	5-10MSS, 10MSS-20S	PBW 373, Lb/PBW 373	33+, 33+	10-20S, 20-30S
HD 2189/RL 6058, HD 2189/RL 6077	33+, 33+	5-10MSS, TMS-5MS	PBW 373/RL 6058, PBW 373/ RL 6077	33+, 33+	10-20MSS, 20-30MSS
HI 1077, Lb/HI 1077	34, 34	10-20S, 20-30S	UP 2338, Lb/UP 2338	33+, 33+	10-20MRMS, 20-30MS
HI 1077/RL 6058, HI 1077/RL 6077	34, 34	10-20MSS, 20-30MSS	UP 2338/RL 6058, UP 2338 / RL 6077	33+, 33+	5-10MRMS, 10-20MRMS
HP 1744, Lb/HP 1744	33+, 33+	5-10MSS, 10MSS-20S	WH 147, Lb/WH 147	4, 4	60-80S, 70-90S
HP 1744/RL 6058, HP 1744/RL 6077	33+, 33+	5-10MSS, 5-10MRMS	WH 147/RL 6058, WH 147/RL 6077	34, 34	10-20MSS, 30-40MSS
K 9107, Lb/K 9107	33+, 33+	10-20MSS, 20MSS-30S	Lalbahadur	4	90-100S
K 9107/RL 6058, K 9107/RL 6077	33+, 33+	5-10MRMS, 10-20MSS	RL 6058	33+	10-20MSS
Kalyansona (KS), Lb/KS	34, 34	40-60S, 60-80S	RL 6077	33+	30-40MSS
KS/RL 6058, KS/RL 6077	34, 34	10-20MSS, 30-40MSS			

ITs = Infection types are based on a '0-4' scale where '3' and '4' = medium and large uredinia, respectively, without chlorosis or necrosis; and '+' = uredinia somewhat larger than normal for infection type; R = resistant or miniature uredinia surrounded by necrosis and chlorosis, MR = moderately resistant or small uredinia surrounded with chlorosis or necrosis, MS = moderately susceptible or moderate-sized uredinia without chlorosis or necrosis and S = susceptible or large uredinia without chlorosis and necrosis

observations regarding absence of *Lr34* in C 306, HI 1077, Kalyansona, and PBW 175 (Priyamvada et al. 2008; 2009); and in WH 147 (Kolmer et al. 2008; Priyamvada et al. 2008; 2009; Pawar et al. 2013). There was partial agreement with regard to absence of *Lr34* in NI 5439 and PBW 373 (Priyamvada et al. 2009 agreed, but Pawar et al. 2013 did not). However, presence of *Lr34* in GW 173 was not confirmed by marker-based studies (Priyamvada et al. 2008; Pawar et al. 2013). No marker-based information regarding HP 1744, K 9107 and UP 2338 is available, and hence, no comparison could be drawn. Thus, overall there was good agreement between our findings and *csLV34* based observations. However, *csLV34* is "diagnostic", and not a "perfect" marker based on high resolution mapping (Lagudah et al. 2006). Hence, *Lr34* status of any genotype needs to be confirmed through the gene-based markers (Lagudah et al. 2009; Dakouri et al. 2010).

Allelic tests confirmed the presence of *Lr67* in C 306, NI 5439 and K 9107. To our knowledge, this is the first report on the occurrence of *Lr67* in any wheat genotypes based on allelic tests. C 306 was observed to be positive for *Lr67* when probed with linked SSR marker *Xcfd71* (Prakasha T.L. personal communication). *Lr67* was detected based on linked marker *Lr67SNP* in 'Sujata' (Lan et al. 2013), a selection from C 306 (Jain 1994). *Lr67* in Sujata and NP 876 is likely derived from common parent C 591 (Lan et al. 2013), derived fromTYPE 9/8B (Jain 1994). NP 710, a parent of NI 5439, was derived from NP 52/NP 165, NP 52 having originated from NP 6/9D (Jain 1994). TYPE 9, 8B and 9D were local selections made

Table 2. Segregation for adult plant resistance to *P. triticina* pathotype 77-5 (121R63-1) in the F_2 populations derived from crosses of resistant genotypes with susceptible parental line Lalbahadur (Lb)

Cross	R	S	Total	χ^2	P value
Lb / C 306	133	51	182	0.88 (3R:1S)	0.35
Lb / Frontana	171	8	179	0.97 (15R:1S)	0.32
Lb / GW 173	168	16	184	1.88 (15R:1S)	0.17
Lb / HD 2189	170	13	183	0.23 (15R:1S)	0.63
Lb / HI 1077	163	17	180	3.14 (15R:1S)	0.08
Lb / HP 1744	172	12	184	0.023 (15R:1S)	0.88
Lb / K 9107	170	15	185	1.09 (15R:1S)	0.30
Lb / Kalyansona	129	53	182	1.65 (3R:1S)	0.20
Lb / Line 897	143	38	181	1.55 (3R:1S)	0.21
Lb / NI 5439	125	56	181	3.40 (3R:1S)	0.06
Lb / PBW 175	164	14	178	0.79 (15R:1S)	0.37
Lb / PBW 373	171	12	183	0.029 (15R:1S)	0.86
Lb / UP 2338	167	15	182	1.23 (15R:1S)	0.27
Lb / WH 147	128	52	180	1.45 (3R:1S)	0.23
Lb / RL 6058	134	49	183	0.31 (3R:1S)	0.58
Lb / RL 6077	138	47	185	0.016 (3R:1S)	0.90

R = Resistant; S = Susceptible. True breeding for susceptibility, confirmed through progeny tests

Table 3. Segregation for adult plant resistance to *P. triticina* pathotype 77-5 (121R63-1) in the F_2 populations derived from crosses of resistant genotypes with tester line RL 6058 (Thatcher + *Lr34*)

Cross	R	S	Total	χ^2	P value
C 306/RL 6058	349	22	371	0.065 (15R:1S)	0.80
Frontana/RL 6058	383	0	383	6.07 (63R:1S)	0.014
GW 173/RL 6058	385	0	385	6.11(63R:1S)	0.013
HD 2189/RL 6058	382	0	382	6.06 (63R:1S)	0.014
HI 1077/RL 6058	371	4	375	0.60 (63R:1S)	0.44
HP 1744/RL 6058	381	0	381	6.04 (63R:1S)	0.014
K 9107/RL 6058	370	2	372	2.54 (63R:1S)	0.11
Kalyansona/RL 6058	355	20	375	0.54 (15R:1S)	0.46
Line 897/RL 6058	379	0	379	25.27 (15R:1S)	<0.01$^{\#}$
NI 5439/RL 6058	352	18	370	1.21 (15R:1S)	0.27
PBW 175/RL 6058	374	8	382	0.70 (63R:1S)	0.40
PBW 373/RL 6058	380	4	384	0.68 (63R:1S)	0.41
UP 2338/RL 6058	375	3	378	1.46 (63R:1S)	0.23
WH 147/RL 6058	352	29	381	1.20 (15R:1S)	0.27

R = Resistant; S = Susceptible. True breeding for susceptibility, confirmed through progeny tests; $^{\#}$ = 0.00001

Table 4. Segregation for adult plant resistance to *P. triticina* pathotype 77-5 (121R63-1) in the F_2 populations derived from crosses of resistant genotypes with tester line RL 6077 (Thatcher + *Lr67*)

Cross	R	S	Total	χ^2	P value
C 306/RL 6077	373	0	373	24.85 (15R:1S)	<0.01$^{\#}$
Frontana/RL 6077	371	6	377	0.002 (63R:1S)	0.96
GW 173/RL 6077	374	7	381	0.19 (63R:1S)	0.66
HD 2189/RL 6077	369	5	374	0.12 (63R:1S)	0.73
HI 1077/RL 6077	368	3	371	1.37 (63R:1S)	0.24
HP 1744/RL 6077	373	7	380	0.19 (63R:1S)	0.66
K 9107/RL 6077	377	0	377	5.98 (63R:1S)	0.014
Kalyansona/RL 6077	335	36	371	7.55 (15R:1S)	0.006
Line 897/RL 6077	353	28	381	0.79 (15R:1S)	0.37
NI 5439/RL 6077	379	0	379	25.27 (15R:1S)	<0.01$^{\#}$
PBW 175/RL 6077	368	3	371	1.37 (63R:1S)	0.24
PBW 373/RL 6077	373	9	382	1.57 (63R:1S)	0.21
UP 2338/RL 6077	369	2	371	2.54 (63R:1S)	0.11
WH 147/RL 6077	348	35	383	5.45 (15R:1S)	0.019

R = Resistant; S = Susceptible. True breeding for susceptibility, confirmed through progeny tests; $^{\#}$ = 0.00001

in undivided Indian Punjab during the early 20th century at Lyallpur (Jain 1994), now in Pakistan. In fact, RL 6077 was developed by transferring a leaf rust resistance gene (now designated *Lr67*) from accession PI 250413 collected in Pakistan (Dyck and Samborski 1979). K 68, a parent of K 9107 originated from NP 773/K 13 (Jain 1994). While K 13 is a local selection, pedigree of NP 773 is not known (Jain 1994). However, *Lr67* in K 9107 could have been derived from any one of them considering the frequency of this gene in Indian land races, and NP series wheats.

Thus, three each out of the 12 common wheat cultivars studied were found to possess *Lr34* or *Lr67*. None of the cultivars carried both the genes. However, they need to be characterized for other APR genes associated with leaf tip necrosis like *Lr46* (Sivasamy et al. 2014) and *Lr68* (Herrera-Foessel et al. 2012). For example, besides *Lr34*, the second gene in HP 1744 could be *Lr46* or *Lr68* inherited from 'Parula' which carries all the three genes (Herrera-Foessel et al. 2012). Specific combinations of slow-rusting leaf rust resistance genes can contribute to effective and stable resistance as additive gene effects have been demonstrated among particular combinations of such genes, optimally expressed under certain environmental conditions (Herrera-Foessel et al. 2012; Sivasamy et al. 2014). Additive effects, if any, of the linked genes for resistance to stem rust, stripe rust and powdery mildew pathogens also need to be studied. Such information can be very useful in breeding for multiple disease resistance in wheat.

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