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Evaluating stripe rust resistance in Indian wheat genotypes and breeding lines using molecular markers

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ABSTRACT

Stripe rust (yellow rust), caused by *Puccinia striiformis f. sp. tritici* (*Pst*), is a serious disease of wheat worldwide, including India. Growing resistant cultivars is the most cost-effective and eco-friendly approach to manage the disease. In this study, 70 publically available molecular markers were used to identify the distribution of 35 *Yr* genes in 68 wheat genotypes. Out of 35 *Yr* genes, 25 genes amplified the loci associated with *Yr* genes. Of the 35, 18 were all-stage resistance ASR (All-stage resistance) genes and 7 (*Yr16*, *Yr18*, *Yr29*, *Yr30*, *Yr36*, *Yr46* & *Yr59*) were APR (Adult-plant resistance) genes. In the field tests, evaluation for stripe rust was carried out under artificial inoculation of *Pst*. Fifty-three wheat genotypes were found resistant to yellow rust (ITs 0), accounting for 77.94% of total entries. Coefficients of infection ranged from 0 to 60 among all wheat genotypes. Two genotypes (VL 1099 & VL 3002) were identified with maximum 15 *Yr* genes followed by 14 genes in VL 3010 and HI8759, respectively. Maximum number of all-stage resistance genes were identified in RKD 292 (11) followed by ten genes in DBW 216, WH 1184 and VL 3002. Maximum number of adult-plant resistance gene was identified in VL 3009 (6), HI 8759 (5) and Lassik (4) respectively. Genes *Yr26* (69.2%), *Yr2* (69.1%), *Yr64* (61.7%), *Yr24* (58.9%), *Yr7* (52.9%), *Yr10* (50%) and *Yr 48* (48.5%) showed high frequency among selected wheat genotypes, while *Yr9* (2.94%), *Yr36* (2.94%), *Yr60* (1.47%) and *Yr32* (8.8%) were least frequent in wheat genotypes. In future breeding programs, race specific genes and non-race specific genes should be utilised to pyramid with other effective genes to develop improved wheat cultivars with high-level and durable resistance to stripe rust. Proper deployment of *Yr* genes and utilizing the positive interactions will be helpful for resistance breeding in wheat.

1. Introduction

Stripe (yellow) rust caused by *Puccinia striiformis f. sp. tritici (Pst)* is the most destructive fungal disease for wheat, especially in cool temperate and humid environment of wheat producing regions like India, China, US, Australia and the middle east [1,2]. Wheat is a widely cultivated cereal crop and acts as staple food to 35% of the world's population, providing 8 to 15% proteins, up to 20% of calories intake and nearly 55% of the carbohydrate [3]. In India, yellow rust (YR) severely affects wheat production in North-Western plain zone as well as Northern hills zone due to the favourable environment for rust pathogens [4,5]. The rust fungus can travel by wind through

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urediniospores over thousands of kilometres from the initial infection sites [6] and exerts greatest damage by preventing transport of water and nutrients through the host. It causes decrease in seed vigour leading to shrivelled grains, loss in number of grains per spike and of grain weight. Disease loss can range up to 10–70% to complete crop failure [7]. The predominant pathotypes *i.e.* 46S119 and 78S84 are adversely affecting wheat production in the northern wheat growing region of India [8,9]. A Yellow rust pathotypes profiling in Punjab showed the dominance of race 46S119 in 84% of collected yellow rust samples [10]. Since 2011, the frequency of 46S119 has increased up to 74% whereas that of 78S84 has reduced to 18.5%, due to the favourable cold and humid climate over the years [11]. This shift in virulence and rapid emergence of new races has resulted in breakdown of major resistance genes *Yr2*, *Yr9* and *Yr27*, rendering widely-planted wheat varieties (PBW 343 and HD 2967) susceptible [11]. YR genes such as *Yr5, Yr10, Yr11, Yr12, Yr13, Yr14, Yr15, Yr24, Yr26, YrSp*, and *Yrsk* are still effective and could be used in breeding programs, while *Yr2, Yr3, Yr4, Yr6, Yr7, Yr8, Yr9, Yr17, Yr18, Yr19, Yr21, Yr22, Yr23, Yr25, Yr27* and *YrA* have become ineffective to the currently prevalent or new races [12]. Presently, 76 *Yr* genes have been catalogued in wheat [13] in which mostly confer race-specific all-stage resistance, and some confer adult-plant or high temperature adult-plant (HTAP) resistance [7,14]. Breeding for resistant cultivars is considered the most effective, economic and environmentally friendly approach to control stripe rust [15,16]. Race-specific resistance with single resistance gene is often short lived. Gene pyramiding strategies deploying race-specific and non-race specific resistance genes is required to achieve durable resistance [17]. However, detailed knowledge of resistance genes present in wheat cultivars is a prerequisite in resistance breeding. Therefore, evaluation and distribution of *Yr* genes needs to be done in breeding wheat genotypes to identify and select resistant cultivar. Molecular marker assisted detection is the most convenient and reliable method to identify the presence of *Yr* genes [18,19]. A wide range of markers are reported to be associated with *Yr* genes in wheat including STS (*Yr5*- [20]), SSR (*Yr10*- [21]; *Yr15, Yr26, YrH52*- [22]), EST (*Yr26*- [23]), STS/CAPS ([24]; *YrMoro*- [25]), STS (*Yr61*- [26]), DArt (*Yr51*- [27]), RGAP/SSR (*Yr59*- [28]) and SSR (*Yr 50*- [29]; *Yr64* and *Yr65*- [30]). Canadian YR resistant wheat varieties were identified with *Yr 10, Yr17*, *Yr18* and *Yr 36* linked markers [31]. Ullah et al. [32] screened 99 wheat genotypes using markers linked with *Yr5, Yr10, Yr17* and *Yr9*. Iqbal et al. [33] studied the allelic variation for markers *Xgwm 11*, *CYS5*, *Xpsp3000*, *S19M93-140, cSLv34, VENTRIUP/LN2* and *Barc181* linked with *Yr5*, *Yr9, Yr10, Yr17, Yr26* in 67 Pakistani wheat varieties. Kumar et al. [34] evaluated 19,460 Indian wheat accessions to identify new sources of resistance to rust using molecular markers. Similar studies were performed using 330 cultivars and 164 breeding genotypes from China [35]. Zheng et al. [36] studied the distribution of 36 *Yr* genes in 672 wheat accessions in USA and observed significant additive effects in some gene combinations, such as *Yr9 + Yr18* and *Yr30 + Yr46*.

The present study was conducted to explore the rust resistance potential of advanced wheat genotypes and varieties using molecular markers linked with YR resistance genes. The information generated on gene sources of rust resistance will prove vital for developing pre-breeding potential genotypes and high yielding rust resistant varieties. The gene specific rust resistant wheat varieties so developed and deployed would not only reduce cost of cultivation spent on fungicides but would also save environment from pollution.

2. Materials and methods

2.1. Plant materials

A total of 68 wheat genotypes (Table 1) were used for molecular and field evaluation at the Chaudhary Charan Singh Haryana Agricultural University (CCS HAU), Hisar, India.

2.2. Molecular markers

Two or three closely linked markers of each YR gene were chosen to identify its presence or absence in the wheat genotypes, except a few genes for which only one closely linked marker was reported. A total of 70 markers (SSR, CAPS, RGAP, STS, EST-SSR) were used for profiling the wheat genotypes. Sequences of available markers (Table 2) along with their previously determined chromosomal locations were obtained from Graingenes database (http://wheat.pw.usda.gov/). Primers were synthesized from Eurofins Genomics India Pvt. Ltd, Bangalore and Imperial life sciences Pvt. Ltd. India.

2.3. DNA extraction, PCR amplification and electrophoresis

Genomic DNA was isolated from 100 mg fresh leaf tissue collected from each line using the CTAB extraction method of Murray and Thompson [37] as modified by Saghai-Maroof et al. [38] and Xu et al. [39]. The DNA stock solution was adjusted to a concentration of 100–150 ng/μl with nuclease free sterile water as the working concentration for the polymerase chain reaction (PCR) and stored at -20° C. PCR reactions were performed using a Benchtop thermocycler in 25 μl of a PCR mixture containing 100–150 ng of genomic DNA, 2 units of Taq DNA polymerase (Promega), 1X PCR buffer (10 mM Tris HCL), 2.5 mM of $MgCl_2$, 100 μM of each dNTP, and 10 μM of each primer. The Touchdown PCR protocol was used to increase the specificity and sensitivity in PCR amplifications. The annealing temperature for Touchdown PCR was optimized using the melting temperature recommended by the primer synthesis user's guide. The initial program provided for a decrease of 0.5 °C for 40 s per 5 cycles from 65 to 60 °C; the second one started at 60 °C with a decrease of 0.5 °C for 40 seconds per 30 cycles. PCR products were separated on 1.5–2.5% agarose gels (depending on gene product size) or 6% denaturing polyacrylamide gel and visualized under UV light using the digital gel imaging system (MultiDoc-It). For the primer pair *URIC/LN2*, the PCR products were

Table 1
List of the genotypes used for molecular and field evaluation.

Sr. No.	Genotype	Sr. No.	Genotype	Sr. No.	Genotype
1	HI 8759 (d)	**25**	WB 2	**49**	WH 1184
2	PBW 723	**26**	AKAW 4842	**50**	HS 580
3	HI 8774 (d)	**27**	DBW 179	**51**	VL 1009
4	HPPAU 05	**28**	DBW 216	**52**	UP 2954
5	HPW 423	**29**	DBW 217	**53**	UP 2955
6	HPW 433	**30**	DBW 219	**54**	VL 3002
7	HS 622	**31**	DDK 1050 (dic.)	**55**	VL 3010
8	HS 623	**32**	DDK 1051 (dic.)	**56**	VL 3011
9	HS 626	**33**	GW 477	**57**	VL 3012
10	HS 628	**34**	MACS 5044 (dic.)	**58**	WH 1181
11	PBW 725	**35**	MACS 5046 (dic.)	**59**	WH 1216
12	PBW 756	**36**	NW 6094	**60**	WH 1310
13	PBW 757	**37**	PBW 621	**61**	HD 3171
14	PBW 760	**38**	RKD 292 (d)	**62**	Lassik
15	RKD 283 (d)	**39**	VL 4001	**63**	WH 711
16	TL 3006 (T)	**40**	WH 1215	**64**	PBW 343
17	TL 3007 (T)	**41**	DBW 220	**65**	WH 542
18	TL 3008 (T)	**42**	HPBW 02	**66**	WH 1105
19	TL 3009 (T)	**43**	HPPAU 08	**67**	HD 2967
20	UAS 459 (d)	**44**	HPPAU 10	**68**	Kharchia
23	HI 1605	**47**	NW 6046		
24	K 1317	**48**	PDW 344 (d)		

digested with *Dpn II* (New England Biolabs, USA) according to Chen et al. [20] before electrophoresis. The restriction digestion mixture contained 10 μl of PCR product, 1U of restriction enzyme *Dpn II* (New England Biolabs) and 2 μl of 10 X buffer for *Dpn II* (New England Biolabs). Samples were incubated at 37 °C for 4 h and the digested products were separated in a 6% polyacrylamide gel.

2.4. Field evaluation under artificial inoculation of Puccinia striiformis f. sp. tritici for stripe rust

All 68 wheat genotypes were evaluated under epiphytotic condition by artificial inoculation of mixture of pathotypes including 46S119, 110S119, 110S84 & 78S84 (10^6/ml) at seedling/tillering stage of *Pst* through spray for stripe rust reaction in the research field of CCS HAU, Hisar (latitude 29°10 'N, longitude 75°46 'E, altitude 215.2 m) in India during the 2016–17 cropping season. Sowing was done in mid November. Approximately, 10 g seeds of each of the 68 wheat genotypes were planted in 2 m furrow length with a distance of 25 cm between each furrow in the field. The infectors (mixture of susceptible cv. i.e. Kharchia, Agra Local, WH143, Lal Bahadur & Bajara Yellow) were sown after every 20 furrows and around the plots as natural spreaders of stripe rust inoculum. Infection types (ITs) of seedlings were recorded in late January and early February when the plants were at tillering/stem elongation stage and disease severity (DS) data was also recorded. In late March, terminal disease severity was also recorded using modified Cobb's scale [40]. The immune plant with no visible symptoms was scored as IT-0, the highly resistant plant with little necrotic flecks and no sporulation was scored as IT-1, the moderately resistant plant with a few necrotic flecks and trace sporulation was scored as IT-2, the moderately susceptible plant with necrotic blotches and moderate sporulation was scored as IT-3, the highly susceptible plant with chlorotic stripes and abundant sporulation was scored as IT-4. Disease severities were assessed based on the percentage of leaf area affected (0, 1, 5, 10, 20, 30, 40, 60, 80, and 100%) [41]. Disease severity were recorded as R (Resistant) when small necrotic areas and no uredia were present, MR (moderately resistant) when small uredia with slight sporulation, chlorosis or necrosis, MS (moderately susceptible) when medium-size uredia with moderate sporulation, and some chlorosis may still be present, and S (susceptible) when large uredia with abundant sporulation, and often coalesced to form lesions without evidence of stripes on visible chlorosis or necrosis [42].

3. Results and discussion

3.1. Adult-plant stage rust evaluation in field under artificial conditions

At the adult-plant stage, disease data on infection types and severity was recorded on 68 wheat genotypes as depicted in Tables 3 and 4. Fifty-three genotypes were found resistant (ITs 0), accounting for 77.94% of total genotypes, 3 genotypes (4.4%) (RKD 292, VL 3002, and DBW 179) showed trace resistance (ITs 1), 7 genotypes (10.3%) (HD 3209, AKAW 4842, DDK 1050, GW 477, MACS 5044, MACS 5046 and NW 6094) were moderately susceptible (ITs 3) and 5 genotypes (7.35%) (HD 3171, DDK 1051, Infector, WH 711 and PBW 343) were susceptible (ITs 4). According to disease severity, 53 lines exhibited immune response, 7 genotypes (10.3%) (HD 3209, AKAW 4842, DDK 1050, GW 477, MACS 5044, MACS 5046 and NW 6094) showed 10 percentage severity of moderately susceptible type (10MS), one genotype (1.5%) HD 3171 contracted 5 percentage severity of susceptible type (5S), 4 genotypes (5.9%) (DDK 1051, WH 711, PBW 343 and Infector) obtained 60 percentage severity of

Table 2
Primers' name, sequences, distance, location, product size, annealing temperature, and references for stripe rust resistance genes.

Gene	Linkage	Chromosome position	Source genotypes	Type of resistance conferred	Marker name	Type of Marker	Primer sequence	Annealing Temperature	Distance (cm)	Product size	References
Yr2		7B		RS	*Wmc364*	SSR	ATCACAATGCTGGCCCTAAAAC CAGTGCCAAAATGTCGAAAGTC	56	5.6	200 (+), 190 (–)	Feng et al. [113]
Yr5	*Yr7* (allelic or linked)	2B	*Triticum aestivum subsp. spelta 'Album'*	RS, AS	*Wmc175*	SSR	GATAAAATCATTATTGGGTGTCCTTT TTCAAATAATCTTTCATCAGTCAAATG	55	1.1	Not amplified	Sun et al. [46]
					Xgwm501	SSR	ACTTACATGAATTATCTTTCTTGGTCC CGTATTCAAATAATCTTTCATCAGTCA	55	10.5–13.3	100, 150, 176 (+)	Sun et al. [46]
					STS7/8	STS	GTACAATTCACCTAGAGT GCAAGTTTTCTCCCTATT	45	0.3	500 (+)	Murphy et al. [48]
					S19M93	STS	TAATTGGGACCGAGAGACG TTCTTGCAGCTCCAAAACCT	58	0	100 (+)	Smith et al. [47]
					Barc349	SSR	CGAATAGCCGCTGCACAAG TATGCATGCCTTTCTTTACAAT	58	0.4	100, 105 (+), 120, 140, 220	Murphy et al. [48]
					Barc167	SSR	AAAGGCCCATCAACATGCAAGTACC CGCAGTATTCTTAGTCCCTCAT	55	2.6	Not amplified	Smith et al. [47]
Yr7	*Sr9 g*	2BL	*T. turgidum (lumillo durum)*	RS, AS	*Xgwm526*	SSR	CAATAGTTCTGTGAGAGCTGCG CCAACCCAAATACACATTCTCA	55	5.6	75, 78, 95, 140, 145 (+)	Yao et al. [51]
					CFD77	SSR	CTGCTTCAGGGATTGGAGAG GTTTCCTGGGCTAAACCACA	58		220	USDA
Yr9	*Sr31/Lr26/Sr50*	1RS/1BL	*Secalis cereal (Imperial rye)*	RS, AS	*Xgwm582*	SSR	AAGCACTACGAAAATATGAC TCTTAAGGGGTGTTATCATA	45	3.7	150 (+), null	Cabuk et al. [54]
					STS (Sr31)	STS	CTCTGTGGATAGTTACTTGATCGA CCTAGAACATGCATGGCTGTTACA	58	0	Not amplified	USDA
					IB-267	SSR	GCAAGTAAGCAGCTTGATTTAGC AATGGATGTCCCGGTGAGTGG	56	0	267 (+), null	Mago et al. [55]
					Xwgp8	RGAP	CTCTGTATACGAGTTGTC GAGGAAGGACAGGTTGCC	60		Not amplified	USDA
Yr10		1BS	*'Moro'*	RS, AS	*Xpsp3000*		GCAGACCTGTGTCATTGGTC	52		240 (–),	Bariana et al. [60]
						SSR	GATATAGTGGCAGCAGGATACG		1.5	220 (+), 260 (+), 285 (+)	
Yr15	*YrCH52 (close)*	1BS	*T. turgidum var. dicoccoides G-25*	RS, AS	*Xgwm413*	SSR	TTTTTGGCTTATTAGACTGACTT TTGCCATAAAATACAAAATCC	50	4.3	90, 95 (+), 100 (–)	Murphy et al. [48]
					Xgwm11	SSR	AAAAGGAACCTCAAGTGACA GAAAATGAGGGAGTGAGATG	52		Not amplified	Cheng et al. [30]
					Xgwm273	SSR	ATTGGACGGACAGATGCTTT AGCAGTGAGGAAGGGGAT C	58	0.4	156 (+), 165 170, 180, 190, 200	Revathi et al. (2010) [114]
					Xbarc8	SSR	GCGGGAATCATGCATAGGAAAACAGAA GCGGGGGCGAAACATACACATAAAAACA	56	4.2	260 (+), 280	Murphy et al. [48]
					Xgwm18	SSR	TGGCGCCATGATTGCATTATCTC GGTTGCTGAAGAACCTTATTTAGG	52		Not amplified	Cabuk et al. [54]
					Xgwm33	SSR	GGAGTCACACTTGTTTGTGCA CACTGCACACCTAACTACCTGC	55	4.5	Not amplified	Somers et al. [128]
Yr16		2AS, 2DS	*Capelle-Desprez*	NRS, AP	*Xgwm102 (QTL)*	SSR	TCTCCCATCCAACGCCTC TGTTGGTGGCTTGACTATTG	57		150 (–), 155 (+), 200 (+)	Agenbag et al. [63]
					Xgwm 249	SSR	CAAATGGATCGAGAAAGGGA CTGCCATTTTTCTGGATCTACC	58		120–160	Agenbag et al. [63]

Table 2 (*Continued*)

Gene	Linkage	Chromosome position	Source genotypes	Type of resistance conferred	Marker name	Type of Marker	Primer sequence	Annealing Temperature	Distance (cm)	Product size	References
Yr17	*Lr37/Sr38*	2AS	*T. ventricosa*	RS, AS	*VENTRIUP-LN2*		AGGGGCTACTGACCAAGGCT TGCAGCTACAGCAGTATGTACACAAAA	58	*T. ventricosum chromosome specific*	259 (+), null	Halguera et al. (2003) [24]
					URIC/LN2	CAPS	GGTCGCCCTGGCTTGCACCT TGCAGCTACAGCAGTATGTACACA AAA	58		285 (+), 166 (–), 109 (–)	Halguera et al. (2003) [24]
Yr18	*Lr34*	7D	*Frontana*	NRS, AP	*csLV34*		GTTGGTTAAGACTGGTGATGG TGCTTGCTATTGCTGAATAGT	58	0.4	150 (+), 229 (–)	Lagudah et al. [65]
					Cssfr1	Gene based	TTGATGAAACCAGTTTTTTTTCTA GCCATTTAACATAATCATGATGGA	56	0	Not amplified	Lagudah et al. [129]
					Cssfr2	Gene based	TTGATGAAACCAGTTTTTTTTCTA TATGCCATTTAACATAATCATGAA	55	0	517 (+), null	Lagudah et al. [129]
					Cssfr5	Gene based	TTGATGAAACCAGTTTTTTTTCTA TATGCCATTTAACATAATCATGAA	57	0	Not amplified	Lagudah et al. [129]
					Xgwm295	SSR	GTGAAGCAGACCCACAACAC GACGGCTGCGACGTAGAG	55		Variable bands	Bariana et al. [117]
					CHR5	RGAP	GCATTGGAACAAGGTGAA GGIGGIGTIGGIAAIACIAC		0	Not amplified	Wen et al. [69]
Yr24	*Yr24, YrCH42*	1BS	*T. turgidum*	RS, AS	*Barc181*	SSR	CGCTGGAGGGGGTAAGTCATCAC CGCAAATCAAGAACACGGGAGAAAGAA	58	6.7	180 (+), 220 (–)	Wang et al. [68]; Zhang et al. [23]
Yr25		1D		RS, AS	*Xgwm6*	SSR	CGTATCACCTCCTAGCTAAACTAG AGCCTTATCATGACCCTACCTT	52		150	[131]
Yr26	*Yr24, YrCH42*	1BS	*Haynaldia villosa*	RS, AS	*Barc187*	SSR	GTGGTATTTCAGGTGGAGTTGTTTTA CGGAGGAGCAGTAAGGAAGG	57	2.3	200 (+), 220 (–), 225	Wen et al. [69]
					CON-6 (EST)	ESTSSR	GCCGATGGGGAACTGAAT GTTGAACCGCTTGAACACC	52	0	Not amplified	Zhang et al. [23]
					CYS-5	RGAP	GCATTGGAACAAGGTGAA GGIGGIGTIGGIAAIACIAC	58	0	Not amplified	Wen et al. [69]
					Xgwm498	SSR	GGTGGTATGGACTATGGACACT TTTGCATGGAGGCACATACT	60	1.6	160 (+), null	Li et al. [67]
Yr27	*Lr13*	2BS	*Selkirk*	RS, AS	*Xgwm630*	SSR	GTGCCTGTGCCATCGTC CGAAAGTAACAGCGCAGTGA	55	10	124 (+)	Seyfarth et al. (2000) [119]
Yr29	*Lr46, YrChk*	1BL	*Lalbahadur*	NRS, AP	*Xgwm259*	SSR	AGGGAAAAGACATCTTTTTTTTC CGACCGACTTCGGGTTC	56	*(Yrchk*: 9.1)	Not amplified	Lilemo et al. (2008) [120]
					Wmc44	SSR	GGTCTTCTGGGCTTTGATCCTG TGTTGCTAGGGACCCGTAGTGG	58	3.6 *(Yrchk*: 8.3)	205, 210, 220, 240, 260 (+), 280, 300, 320	Rosewarne et al. [75]; Liu et al. (2007) [121]
Yr30	*Sr2, Lr27*	3BS	*Opata 85*	NRS, AP	*Xgwm533*	SSR	AAGGCGAATCAAACGGAATA GTTGCTTTAGGGGAAAAGCC	57		100, 120 (+), 130, 140, 150	Spielmeyer et al. (2003) [122]
					csSr2	*CAPS*	CAAGGGTTGCTAGGATTGGAAAACA AGATAACTCTTATGATCTTACA TTTTTCTGA	56	0	Not amplified	Mago et al. (2011) [123]
Yr32		2AL	*Carstens V*	RS, AS	*Wmc198*	SSR	CACGCTGCCATCACTTTTAC TTGAAGTGGTCATTGTTGCT	58	2	180, 200	Eriksen et al. [80]
Yr35	*Lr53*	6BS			*T. dicoccoides*	RS, AS	*CFD1* CCTCCATGTAGGCGGAAATA TGTGTCCCATTCACTAACCG	SSR 57	4.1	Not amplified	Dadkhodaie et al. [132]
Yr36	*Gpc-B1*	6BS			*T. dicoccoides*	NRS, HTAP	*Barc101* GCTCCTCTCACGATCACGCAAAG GCGAGTCGATCACACTATGAGCCAATG	SSR 58	2	116, 124 (+), 138, 160, 165	Uauy et al. [82]
					ASA (Gpc-B1)	Gene based	CTACCATCGAAAGTTGATAGGGA TTCACAAACTAAGGGGAGGGA	57	0.3	1.6Kb (+), null	Uauy et al. [82]
					WKS1	Gene based	ATCCATTGCCAAGTCAACCAC TCACTTCCATGAAGGAGGTC	55	0	128 (+), null	Fen et al. (2009) [83] Fu et al. (2009) [[130]]

Table 2 (*Continued*)

Gene	Linkage	Chromosome position	Source genotypes	Type of resistance conferred	Marker name	Type of Marker	Primer sequence	Annealing Temperature	Distance (cm)	Product size	References
Yr39		7BL	*Alpowa*	NRS, HTAP	*Xwgp36: Pto kin1/RLK For*	RGAP	GCATTGGAACAAGGTGAA GAYGTNAARCCIGARAA	55	0.8	Not amplified	Lin and Chen [115]
					Xwgp45:Pto kin1/XLRR For	RGAP	GCATTGGAACAAGGTGAA CCGTTGGACAGGAAGGAG	52	6.6	Not amplified	
Yr40	*Lr57*	5DS	*Aegilops geniculata*	RS, AS	*Xfbb276*	SSR	AACAGCTATGACCATG GTAAAACGACGGCCAGT	48		1 kb, 2 kb, null	Kuraparthy et al. [84]
Yr45		3DL		RS, AS	*Xwgp115*	RGAP	AGTGTCTTGTAGGGTATC TCAGGCCGTGAAAAATAT	46	4.8	Not amplified	Li et al. (2011) [124]
					Xwgp118	RGAP	AAGTGGAACAAGGTTACG ACACTGGTCCATGAGGTT	48	5.8	Not amplified	Li et al. (2011) [124]
Yr46	*Lr67/Sr55/Pm46*	4DL	*Thatcher*	RS, AS	*CFD71*	SSR	CAATAAGTAGGCCGGGACAA TGTGCCAGTTGAGTTTGCTC	52		148 (+), 150, 152	Hiebert et al. (2010) [125]
					CFD23	SSR	TAGCAGTAGCAGCAGCAGGA GCAAGGAAGAGTGTTCAGCC	55		211 (+), 214 (+)	Hiebert et al. (2010) [125]
Yr47	*Lr52*	5BS	*T. aestivum*	RS, AS	*Cfb309*	SSR (BAC Contig)	TAGGGCATATTTCCAACACT TAAGTCCGCGTATTAGCATT	58	8–12	600 (+), 350 (–)	Bansal et al. [86]
Yr51		4AL		RS, AS	*Sun104*	STS	TGCTATGTGCGTGATGATGA TTACATGCTCCAGCGACTTG	56	2.5	225 (+), null (–)	Randhawa et al. [27]
					owm45F3R3	SSR	GGCTCGTCTACACCAACGAC TTGGGGTCTTTAGGCATGAG	56	1.2	1 kb (non conclusive)	Randhawa et al. [27]
Yr59		7BL	*Alpowa*	NRS, HTAP	*Barc32*	SSR	GCGTGAATCCGGAAACCCAATCTGTG TGGAGAACCTTCGCATTGTGTCATTA	62	2.1	165 (+), 175, 190, 250	Zhou et al. [26]
					Wmc557	SSR	GGTGCTTGTTCATACGGGCT AGGTCCTCGATCCGCTCA	56	< 2.1	315 (+), 500	Zhou et al. [26]
Yr60		4AL	*T. aestivum*	RS, AS	*Wmc776*	SSR	CCATGACGTGACAACGCA ATTGCAGGCGCGTTGGTA	56	< 0.6	150, 160, 170 (+)	Herrera-Foessel et al. [85]
					Wmc313	SSR	GCAGTCTAATTATCTGCTGGCG GGGTCCTTGTCTACTCATGTCT	60.3	0.6	180, 200 (+)	Herrera-Foessel et al. [85]
					Wmc219	SSR	TGCTAGTTTGTCATCCGGGCGA CAATCCCGTTCTACAAGTTCCA	57	0.6	200 (+), 220	Herrera-Foessel et al. [85]
YrCH52	*Yr15*	1BS	*T. turgidum*	RS, AS	*Xgwm273*	SSR	ATTGGACGGACAGATGCTTT AGCAGTGAGGAAGGGGATC	48	2.7	170, 180, 190, 200	Cabuk et al, (2011) [54]
YrSpP		2B	*Spaldings Profilic*	RS, AS	*Wmc441*	SSR	TCCAGTAGAGCACCTTTCATT ATCACGAAGATAAACAAACGG	56	12.1	Not amplified	Guan et al. (2005) [116]
Yr48		5AL	*Aegilops tauschii*	NRS, AP	*cfa2149*	SSR	CTT GGA GCT CGG GTA GTA GC AAG GCA GCT CAA TCG GAG TA	52	0.06	225 (+), 250	Lowe et al. (2011) [126]
					SNF-A2	SSR	TCCGTCTCCATCATTCAACA GTGTTGCGCAAGTTTGTGAC	58	0.18	150 (+), 180, 200 (–)	Lowe et al. (2011) [126]
					BE495011	SSR	TGATTACTGTAGCTACCTCCTCCT GGTGCAAGATGTGCCTGTAA	56	0.09	220 (+), null	Lowe et al. (2011) [126]
YrCN19		2BS	*AIM6*	RS, AS	*Xgwm410*	SSR	GCTTGAGACCGGCACAGT CGAGACCTTGAGGGTCTAGA	57	0.3	Not amplified	Luo et al. (2008) [117]
YrZH84		7B		RS, AS	*Barc32*	SSR	GCGTGAATCCGGAAACCCAATCTGTG TGGAGAACCTTCGCATTGTGTCATTA	56	4.8	165 (+), 170, 190, 250	Zhou et al. ([26]; [125])
YrMor		4B	*Moro*	RS, AS	*S26M47*	SSR	TTTACAGGTTGGAATCTA GAATATACCTTTTCTTCAA	55	0	250 (+), null	Smith et al. [25]
YrHua				RS, AS	*PM14*	STS	GTACATGCAGACAGAAAGAGAGAA TGATGAGTCCTGAGTAACTC	58	5.4	Not amplified	Cao et al. (2008) [127]
YrExp1				RS, AS	*Wmc631*	SSR	TTGCTCGCCCACCTTCTACC GGAAACCATGCGCTTCACAC	60	3.4	Not amplified	Lin and Chen (2008) [118]

RS: Seedling resistance; AS: all stage resistance; APR; adult plant resistance; CAPS cleaved amplified polymorphism sequences, DArT diversity arrays technology, EST expressed sequence tag, RGAP resistance gene analogs polymorphisms, SCAR sequence characterized amplified regions, SSR simple sequence repeats, STS sequence tagged site, cM centimorgan, bp base pair, "+" the PCR product indicating the existence of corresponded gene, "-" the PCR product indicating the absence of corresponded gene.

Table 3
Field response, severity, and coefficient of infection of wheat genotypes.

Genotypes	Field Severity response & symbol	No. of Lines	Average Coefficient of Infection (ACI)
RKD 292, VL3002, DBW179	Ts (R)	3	0.2
HD 3209, AKAW 4842, DDK 1050, GW 477, MACS 5044, MACS 5046, NW 6094	10MS	7	8.0
HD 3171	5S	1	5.0
DDK1051, Infector, WH 711, PBW 343	60S	4	60.0
Remaining genotypes	Immune	53	0

Ts: traces, MS: moderately susceptible, S: susceptible, R: resistant.

Table 4
Data on infection types (ITs) in the selected wheat genotypes.

Wheat genotypes	Infection response (field)	Total No. of genotypes	ITs
RKD 292, VL3002, DBW179	Ts	3	1
HD3209, AKAW4842, DDK 1050, GW477, MACS 5044, MACS 5046, NW6094	MS	7	3
HD3171, DDK1051, Infector, WH711, PBW343	S	5	4
All remaining genotypes	R	53	0

susceptible type (60S). Infector rows expressed 60 percentage severity of susceptible type (60S). Coefficient of infection ranged from 0 to 60 among all wheat genotypes in which 0 CI is associated with the immune and resistant genotypes and 60 CI is associated with susceptible genotypes. Overall 60 genotypes expressed yellow rust resistance under field conditions against predominant yellow rust pathotypes *i.e.* 46S119, 110S119, 110S84 &78S84.

3.2. Detecting stripe (yellow) rust resistance genes using molecular markers

Marker assisted detection of 35 *Yr* genes in wheat genotypes was carried out using 70 *Yr* gene linked markers. The results indicated the effectiveness of these markers for specific *Yr* gene which also identified the resistant lines containing multiple *Yr* genes. Details of *Yr* resistance genes in wheat genotypes are presented in Table 5. Molecular identification of various genes is discussed below.

3.3. Molecular identification of Yr2

SSR marker *Wmc364* linked to the yellow rust resistance gene is located on chromosome 7B at the distance of 5.6 cM [43]. *Wmc364* amplified two alleles (+200 bp/−190 bp) for distinguishing gene positive and negative genotypes. A total of 31 genotypes (45%) amplified 200 bp alleles whereas 16 genotypes (23.5%) amplified both the alleles (HI 8759, HI 8774, HPPAU 05, WB 2, DBW 179, DBW 216, DBW 217, DBW 219, DDK 1050, DDK 1051, MACS 5044, RKD 292, DBW 220, HS 580, VL 3012 and WH 1310). Twenty-one genotypes (30.8%) amplified 190 bp allele (HS 626, RKS 283, TL 3006, TL 3007, TL 3008, TL 3009, UAS 459, Infector, HD 3209, HI 1605, K 1317, AKAW 4842, NW 6046, PDW 344, VL 3002, VL 3011, WH 1216, Lassik, WH 542, Kharchia and WH711). On the basis of screening at genotypic level, 47 genotypes (69.1%) were postulated to carry resistant allele for *Yr2* gene. Since the distance between marker and gene is far, it is not recommended for marker assisted breeding.

3.4. Molecular identification of Yr5

Yellow rust resistance gene *Yr5*, originally derived from *Triticum spelta* var *album* [44] is a race-specific R-gene effective at both seedling and all plant growth stages and located on the chromosome 2BL [45]. Four microsatellite markers *Xgwm501, Wmc175, Barc349, Barc167* [46] and two STS markers *S19M93-100* [47], *STS7/8* [48] linked with yellow rust resistance gene *Yr5* were used to confirm and evaluate the diagnostic potential of these markers in wheat genotypes. Microsatellite marker *Wmc175* and *Barc167* failed to yield any amplicons whereas *S19M93-140* located at 0.54 cM from *Yr5* amplified one 100 bp allele. Screening with *S19M93* marker produced the expected 100 bp band associated with *Yr5* gene in 30 genotypes (44.1%), while the other 38 wheat genotypes (55.8%) failed to amplify the gene. Another marker *STS7/8* is proximally located 0.3 cM from the *Yr5* gene and amplified 500 bp bands in 23 genotypes (33.8%) with *Yr5* gene. Dominant SSR marker *Barc349* is located 0.4 cM distally [48] and amplified 5 alleles (100 bp, 105 bp, 120 bp, 140 bp, 220 bp). Product size 105 bp that is linked with presence of *Yr5* gene was observed in 32 lines (47%). SSR marker *Xgwm501* is located 10.5–13.3 cM from *Yr5* gene [49] and amplified 3 alleles (100 bp, 150 bp, 176 bp). Thirty-one genotypes (45%) produced the expected 176 bp band which indicated that they may contain *Yr5*. However, the genetic distance between the markers *Xgwm501* and *Yr5* is too far to be used in marker-assisted selection. On the basis of proximal and distal distance of *Yr5* linked markers, 12 genotypes (17.64%) (HS 626, TL 3007, HD 3209, K 1317, DDK 1051, PDW 344, WH 1184, HS 510, VL 3010, VL 3011, VL 3012 and WH 1181) were identified with *Yr5* gene.

Table 5
Details of *Yr* resistance genes in wheat genotypes.

S. no.	Genotypes	RS, AS genes	APR genes	Total number of RS, AS genes	Total number of APR genes	Total number of genes	Resistant Types
1	HI 8759 (d)	*Yr2, Yr7, Yr10, Yr15, Yr24, YrcH52, Yr47, YrZH84*	*Yr16, Yr18, Yr29, Yr30, Yr48, Yr59*	8	6	14	R
2	PBW 723	*Yr2, Yr9, Yr24, YrZH84*	*Yr16, Yr30, Yr59*	4	3	7	R
3	HI 8774 (d)	*Yr2, Yr7, Yr10, Yr24, Yr40, Yr60*	*Yr18, Yr30, Yr48*	6	3	9	R
4	HPPAU 05	*Yr2, Yr7, Yr9, Yr10, Yr15, Yr24, Yr26, Yr64, YrMor*	*Yr18, Yr30, Yr36*	9	3	12	R
5	HPW 423	*Yr2, Yr10, Yr24, Yr26, Yr64*	*Yr18, Yr30*	5	2	7	R
6	HPW 433	*Yr2, Yr7, Yr10, Yr26, Yr47, YrMor*	*Yr18, Yr48*	6	2	8	R
7	HS 622	*Yr2, Yr7, Yr24, Yr26*	*Yr30*	4	1	5	R
8	HS 623	*Yr2, Yr7, Yr26, YrMor*	*Yr18, Yr29, Yr30*	4	3	7	R
9	HS 626	*Yr5, Yr7, Yr10, Yr24, Yr26, Yr40, Yr47, Yr64*	*Yr16, Yr29, Yr30*	8	3	11	R
10	HS 628	*Yr2, Yr7, Yr15, YrcH52, Yr64*	*Yr30*	5	1	6	R
11	PBW 725	*Yr2, Yr15, Yr24, Yr26, Yr64*	*Yr29, Yr30*	5	2	7	R
12	PBW 756	*Yr2, Yr10, Yr64*	*Yr30*	3	1	4	R
13	PBW 757	*Yr2*	*Yr59*	1	1	2	R
14	PBW 760	*Yr2, Yr7, Yr24, YrMor*	*Yr59*	4	1	5	R
15	RKD 283 (d)	*Yr7, Yr10, Yr24, Yr64*	*Yr59*	4	1	5	R
16	TL 3006 (T)	*Yr24, Yr64*	*Yr18, Yr30*	2	2	4	R
17	TL 3007 (T)	*Yr5, Yr10, Yr15, Yr26, Yr40, Yr47*	*Yr18, Yr29, Yr30, Yr59*	6	4	10	R
18	TL 3008 (T)	*Yr10, Yr26, Yr64, YrMor*	*Yr29*	4	1	5	R
19	TL 3009 (T)	*Yr10, Yr24, Yr26, Yr47, YrZH84*	*Yr29, Yr48, Yr59*	5	3	8	R
20	UAS 459 (d)	*Yr10, Yr26, Yr64*	*Yr29, Yr48*	3	2	5	R
21	INFECTOR		*Yr46*	0	1	1	30S
22	HD 3209	*Yr5, Yr15, Yr26, Yr47*	*Yr29, Yr30*	4	2	6	‘10MS
23	HI 1605	*Yr10, Yr24, Yr26, Yr40, Yr64*		5	0	5	R
24	K 1317	*Yr5, Yr10, Yr24, Yr26, Yr40, Yr64*	*Yr30, Yr46*	6	2	8	R
25	WB 2	*Yr2, Yr5, Yr7, Yr10, Yr26, YrcH52, Yr64*	*Yr29, Yr30*	7	2	9	R
26	AKAW 4842	*Yr7, Yr15, Yr24, Yr26, YrcH52, Yr32, Yr40, Yr64*	*Yr36*	8	1	9	10MS
27	DBW 179	*Yr2, Yr7, Yr15, Yr24, YrcH52, Yr40, Yr47, Yr64*	*Yr16, Yr29*	8	2	10	TS
28	DBW 216	*Yr2, Yr7, Yr10, Yr15, Yr26, YrCH52, Yr32, Yr40, Yr64, YrMor*	*Yr29*	10	1	11	R
29	DBW 217	*Yr2, Yr7, Yr15, Yr24, Yr26, YrCH52, Yr40, Yr47, Yr64*	*Yr16, Yr30*	9	2	11	R
30	DBW 219	*Yr2, Yr10, Yr15, Yr24, Yr26, Yr32*	*Yr16, Yr29, Yr46*	6	3	9	R
31	DDK 1050 (dic.)	*Yr2, Yr7, Yr15, Yr24, Yr26, Yr40, YrMor, YrZH84*	*Yr29, Yr30, Yr59*	8	3	11	10MS
32	DDK 1051 (dic.)	*Yr2, Yr5, Yr7, Yr24, Yr26, YrcH52, Yr47, YrZH84*	*Yr16, Yr29, Yr30*	8	3	11	10MS
33	GW 477	*Yr2, Yr10, Yr15, Yr24, YrcH52*	*Yr30, Yr63*	5	2	7	10MS
34	MACS 5044 (dic.)	*Yr2, Yr15, Yr24, YrCH52, Yr47, Yr64*	*Yr16, Yr18, Yr29, Yr46, Yr64*	6	4	10	10MS
35	MACS 5046 (dic.)	*Yr2, Yr10,Yr15, Yr24, YrcH52, Yr47, Yr64*	*Yr18, Yr29*	7	2	9	10MS
36	NW 6094	*Yr2, Yr10, Yr24, YrcH52, Yr47, Yr64*	*Yr18, Yr48*	6	2	8	R
37	PBW 621	*Yr2, Yr7, Yr10, Yr15, Yr24, Yr26, YrcH52,Yr64*	*Yr16, Yr30, Yr48*	8	3	11	TS
38	RKD 292 (d)	*Yr2, Yr7, Yr10,Yr15, Yr24, Yr26, YrcH52, Yr47, YrZH84, Yr64,YrMor*		11	0	11	R
39	VL 4001	*Yr2, Yr10,Yr15, Yr24, YrcH52, Yr40, Yr47, Yr63, YrMor*	*Yr30*	9	1	10	R
40	WH 1215	*Yr2, Yr15, Yr24, Yr26, YrcH52, Yr47, Yr64*	*Yr46*	7	1	8	R
41	DBW 220	*Yr2, Yr10, Yr15, Yr26, YrCH52, Yr40, Yr64*	*Yr16, Yr18, Yr30, Yr46*	7	4	11	R
42	HPBW 02	*Yr2, Yr7, Yr10, Yr15, Yr17, Yr64*	*Yr18, Yr46*	6	2	8	R
43	HPPAU 08	*Yr2, Yr10, Yr24, Yr26, YrcH52, Yr64, YrMor*	*Yr16, Yr18, Yr29, Yr30*	7	4	11	R
44	HPPAU 10	*Yr2, Yr15, Yr24, Yr26, Yr64*	*Yr16, Yr18, Yr29, Yr30*	5	4	9	R
45	HPW 424	*Yr2, Yr15, Yr24, Yr26, Yr63, YrMor*	*Yr18, Yr29, Yr30*	6	3	9	R
46	HS 627	*Yr2, Yr7, Yr10, Yr15, Yr26, Yr64*	*Yr29, Yr30*	6	2	8	R

Table 5 (*Continued*)

S. no.	Genotypes	RS, AS genes	APR genes	Total number of RS, AS genes	Total number of APR genes	Total number of genes	Resistant Types
47	NW 6046	*Yr5, Yr7, Yr10, Yr24, Yr26*	*Yr29, Yr30*	5	2	7	R
48	PDW 344 (d)	*Yr7, Yr10, Yr24, Yr26, YrcH52*	*Yr29, Yr30, Yr48*	5	3	8	R
49	WH 1184	*Yr2, Yr5, Yr7, Yr10, Yr26, YrcH52, Yr40, Yr64, YrMor*	*Yr29, Yr30, Yr48*	9	3	12	R
50	HS 580	*Yr2, Yr5, Yr7, Yr10, Yr26, YrcH52, Yr40, Yr64*	*Yr18, Yr29, Yr30, Yr46,*	8	4	12	R
51	VL 1009	*Yr2, Yr7, Yr10, Yr26, YrcH52, Yr32, Yr40, Yr64, YrZH84*	*Yr16, Yr18, Yr29, Yr30, Yr46, Yr59*	9	6	15	R
52	UP 2954	*Yr2, Yr7, Yr10, Yr24, Yr26, YrcH52, Yr64, YrZH84*	*Yr16, Yr29, Yr46, Yr59*	8	4	12	R
53	UP 2955	*Yr2, Yr7, Yr24, YrcH52, Yr47, Yr48, Yr64*	*Yr16, Yr46*	7	2	9	R
54	VL 3002	*Yr5, Yr7, Yr24, Yr26, YrcH52, Yr40, Yr47, Yr48, Yr60, Yr64*	*Yr16, Yr18, Yr29, Yr30, Yr46*	10	5	15	Ts
55	VL 3010	*Yr2, Yr5, Yr7, Yr10, Yr15, Yr26, YrCH52, Yr40, Yr47*	*Yr16, Yr18, Yr29, Yr30, Yr46*	9	5	14	R
56	VL 3011	*Yr5, Yr7, Yr10, Yr26, YrCH52, Yr40*	*Yr18, Yr29, Yr30, Yr46*	6	4	10	R
57	VL 3012	*Yr2, Yr5, Yr10*	*Yr29, Yr30, Yr46*	3	3	6	R
58	WH 1181	*Yr2, Yr5, Yr7, Yr10, Yr64*	*Yr16, Yr29, Yr30*	5	3	8	R
59	WH 1216	*Yr7, Yr10, YrCH52, Yr64, YrMor*	*Yr16, Yr30*	5	2	7	R
60	WH 1310	*Yr2, Yr7, Yr10, Yr40*	*Yr16, Yr30, Yr48*	4	3	7	R
61	HD 3171	*Yr2, Yr7, Yr10, Yr40, YrMor*	*Yr16, Yr30*	5	2	7	R
62	Lassik	*Yr17, Yr26*	*Yr18, Yr29, Yr30, Yr36, Yr48*	2	5	7	R
63	WH711		*Yr16, Yr30*	0	2	2	S
64	PBW343	*Yr2, Yr26*	*Yr16, Yr30*	2	2	4	S
65	WH542	*Yr64*	*Yr16, Yr18, Yr30, Yr59*	1	4	5	R
66	WH1105	*Yr2, Yr10*	*Yr16, Yr30*	2	2	4	R
67	HD2967	*Yr2, Yr7, Yr24, Yr64*	*Yr30*	4	1	5	S
68	Kharchia	*Yr7, Yr24*	*Yr16, Yr30*	2	2	4	S

3.5. Molecular identification of Yr7

Yr7 was first identified in wheat cultivar 'Lee' (*Triticum turgidum* (lumillo durum) [50] and mapped on chromosome 2BL [51]. *Yr7* is allelic to *Yr5* and linked with *Sr9g* [52]. Microsatellite marker *Xgwm526* linked with *Yr7* locus at 2.3 cM was used to detect the presence of *Yr7*. Thirty-nine genotypes (57.4%) showed 145 bp fragment associated with the presence of *Yr7*. The remaining 29 wheat genotypes did not show 145 bp products, indicating likely absence of *Yr7*. SSR marker CFD77 amplified a 220 bp allele in all the genotypes indicating non-diagnostic behaviour of that marker. Overall 36 genotypes (52.9%) were postulated to harbour the *Yr7* gene.

3.6. Molecular identification of Yr9

Yr9, located on the short arm of rye chromosome 1R, was transferred to wheat through chromosomal translocation of 1BL.1RS. Four markers *STSSr31* [53], *Xgwm582*, *IB267* and *Xwgp8* were chosen to amplify *Yr9* gene. STS marker *Sr31* and RGAP marker *Xwgp8* failed to give amplification reactions. *Xgwm582* is present on chromosome 1BL at 3.7 cM distance of *Yr9* and amplified 150 bp product size in 23 genotypes (33.9%) carrying *Yr9* gene [54]. *IB267* marker is completely linked at 0 cM [55] and produced *Yr9* specific 267 bp bands in 2 genotypes (PBW 723 and HPPAU 05). Based on 2 sets of primer pairs, PBW 723 and HPPAU 05 genotypes amplified both of the primers and were postulated to carry *Yr9*.

3.7. Molecular identification of Yr10

Dominant gene, *Yr10* was isolated from Moro [21] and located on chromosome 1BS, 2 cM apart from *Rg1* locus that confers brown glume colour [56] and 5 cM from locus *Gli-1B* [57]. Microsatellite marker *Xpsp3000* located 1.3 cM proximal to *Yr10* [58] was used to determine the presence or absence of the gene in wheat genotypes. On screening with marker *Xpsp3000*, a varied range of allelic variation (220 bp, 240 bp, 260 bp and 285 bp) at *Yr10* locus was observed. Thirty-four genotypes produced 260 bp fragment associated with the presence of *Yr10* allele [59], 16 genotypes showed 285 bp fragment specific for *Yrvav* allele [60], 48 genotypes amplified 240 bp fragment specific for susceptible allele. Seven genotypes showed amplification of both 285 and 260 bp allele (*Yr10 + Yrvav*) (K 1317, DBW 216, PDW 344, WH 1184, HS 580, VL 3011, HPBW 02), 15 genotypes amplified both 260 bp and 240 bp alleles (HI 8759, HI 8774, PBW 756, RKD 283, TL 3007, TL 3008, TL 3009, WH 1214, GW 477, UAS 459, MACS 5046, NW 6046, HPPAU 10, WH 542, WH 1105). Five genotypes amplified all four alleles (HPW 423, DBW 179, PBW 621, VL 4001 and HPPAU 08) and 31 genotypes amplified a 220 bp allele in combination with other alleles indicating the presence of a novel allele at *Yr10* loci. One Genotype, WB2 was identified

carrying 260 bp allele. Both 260 bp and 285 bp bands are associated with the presence of resistance gene. On this basis, 34 genotypes (50.0%) carried *Yr10* gene.

3.8. Molecular identification of Yr15

Dominant gene *Yr15*, derived from *Triticum dicoccoides*, is located on chromosome 1BS [61]. Murphy et al. [48] showed that *Xbarc8* and *Xgwm413* were closely linked with *Yr15*. The *Yr15* gene was mapped to a 6.4 cM interval flanked by marker *Barc8*, located 3.9 cM to the distal side, and by *Xgwm413* and *Xgwm273* located 2.5 cM and 2.1 cM to the proximal side. Six markers, *Xgwm11*, *Xgwm18*, *Xgwm 33*, *Xgwm273*, *Barc8* and *Xgwm413* linked with *Yr15* were used for validation purpose. SSR marker *Barc8,* produced 2 alleles (260 bp and 280 bp), respectively. Thirty genotypes (44.1%) amplified 260 bp bands associated with *Yr15* gene while 37 genotypes (54.4%) amplified 280 bp without *Yr15* gene. SSR locus *Xgwm 413* located 3.5 cM proximally produced 3 alleles (90 bp, 95 bp and 100 bp) among wheat genotypes used in this study. A huge variation in allelic profile of *Xgwm413* was observed. Forty-three genotypes amplified 90 bp specific alleles, 64 genotypes amplified 95 bp alleles, 36 genotypes amplified 100 bp alleles, 17 genotypes produced both the 95 bp and 100 bp alleles, 25 genotypes amplified 90 bp and 95 bp alleles and 17 genotypes amplified all the three alleles (90 bp, 95 bp and 100 bp). *Xgwm273* marker is present 0.4 cM from *Yr15* and amplified 7 alleles (156 bp, 165 bp, 180 bp, 200 bp, 350 bp, 400 bp and 500 bp), respectively. Sixteen genotypes (23.5%) produced 156 bp bands specific for *Yr15* [62]. *Xgwm11* and *Xgwm18* failed to give amplifications. *Xgwm33* produced inconclusive results. On the basis of proximal and distal distance of linked markers 25 genotypes (36.7%) (HI 8774, HPPAU 05, HS 628, PBW 725, TL 3007, HD 3209, AKAW 4842, DBW 179, DBW 216, DBW 217, DBW 219, DDK 1050, GW 477, MACS 5044, MACS 5046, PBW 621, RKD 292, VL 4001, WH 1215, DBW 220, HPBW 02, HPPAU 10, HPW 424, HS 627 and VL 3010) were predicted with *Yr15*.

3.9. Molecular identification of Yr16

Yr16 was originally originated from the French cultivar *Capelle-Desprez* and mapped on chromosome 2DS. SSR, *Xgwm102* corresponding to the QTLs (*QYr.ufs-2D*) is reported to be linked with gene *Yr16* and was used to screen the wheat genotypes [63]. SSR marker, *Xgwm249* linked to *Yr16* gene showed polymorphism in present investigation with product size ranging from 120 to 160 bp. Since, no specific product size information is available for this marker. Screening results could not be associated with *Yr16* gene. Marker *Xgwm102* amplified three alleles 150 bp, 155 bp and 200 bp, respectively. Twenty-two wheat genotypes (32.3%) produced the 155 bp and 200 bp allele confirming the likely presence of this gene [63].

3.10. Molecular identification of Yr17

Three rust resistance genes i.e. *Yr17, Lr37* and *Sr38* were translocated into the short arm of wheat chromosome 2A of bread wheat from 2NS chromosome of *Triticum ventricosum* [64]. The presence of *Yr17* gene in Indian wheat genotypes was investigated with the primers *VENTRIUP/LN2* [24]. All the wheat genotypes amplified a 259 bp fragment specific for *Yr17* gene, indicating either the presence of *Yr17* in all the genotypes or the non-diagnosing behaviour of this marker in the Indian wheat background. Therefore, further confirmation of *Yr17* was done with the help of primers *URIC/LN2* which amplifies the two fragments of 285 bp (N-allele) and 275 bp (A-allele). Subsequent digestion of the undigested PCR products with restriction enzyme *DpnII* yields the 275 bp and the 166, 109 bp fragments corresponding to the presence and absence of gene. None of the wheat genotypes, other than the positive control Lassik gave positive restriction digestion results for *Yr17* gene, confirming the likely absence of *Yr17* gene in this panel of Indian wheat genotypes.

3.11. Molecular identification of Yr18

The presence of yellow rust resistance gene *Yr18* was assayed using STS marker *csLV34,* gene specific marker *cssfr2* and SSR marker *Xgwm295*. The STS marker *csLV34* located 0.4 cM distal to *Yr18* [65] produced two allelic variants i.e. *csLV34b* and *csLV34ba*. The 150-bp band (*csLV34b)* and 229-bp band (*csLV34ba)* indicated the presence and absence of *Yr18* gene, respectively. Twenty-four genotypes (35.3%) amplified 150 bp fragments, suggesting the presence of *Yr18*-associated allele. Forty-four genotypes (64.7%) produced 229 bp band associated with *csLV34a* allele indicating absence of *Yr18* gene. The gene specific marker *cssfr2* produced 517 bp products with *Yr18*. Thirty-five genotypes (51.5%) amplified *cssfr2* marker. A total of 42 genotypes (61.8%) showed the association with *Yr18* gene by using any of the markers while 20 genotypes (29.4%) (HI 8759, HI 8774, HPPAU 05, HPW 423, HPW 433, HS 623, TL 3006, TL 3007, MACS 5044, MACS 5046, NW 6094, HPBW 02, HPW 424, HS 580, VL 1009, VL 3002, VL 3010, VL 3011, Lassik and WH 542) were positive with both the markers. SSR marker *Xgwm295* produced variable results and could not be linked with the presence of gene.

3.12. Molecular identification of Yr24/26

Yr24 confers ASR to yellow rust and was originally identified in *T. turgidum* var. *durum* accession K733. Yellow rust resistance gene *Yr26*, carried by *T. turgidum* durum line and was located on chromosome 1B [66]. *Yr26* and *Yr24* are considered to be identical genes due to their disease reaction against rust isolates [67]. Two markers *Barc181* and *Barc187*, were used to detect the presence/absence of *Yr24/Yr26* genes. The SSR marker *Barc187* linked with *Yr24* at the distance of 2.3 cM [68], amplified three alleles; 200 bp, 220 bp and 225 bp, respectively. Forty genotypes (58.9%) amplified 200 bp indicating the likely presence of *Yr24,* whereas 31 genotypes (45.6%) produced 220 bp and 225 bp alleles, without *Yr24*. Microsatellite marker *Xbarc181* is 6.7 cM distal to *Yr26* [68] and produced 2 alleles 180 bp and 200 bp, respectively. Thirty-eight

genotypes (69.2%) produced 180 bp allele associated with *Yr26* gene while 34 genotypes amplified the 200 bp specific allele. Four genotypes (HS623, HS626, DDK1051 and DBW220) amplified both the alleles. Combined results with both the markers exhibited the presence of *Yr24/Yr26* in 19 genotypes (27.9%) *i.e.* HPPAU 05, HPW 423, HS 622, PBW 725, TL 3009, HI 1606, K 1317, AKAW 4842, DBW 217, DBW 219, DDK 1050, PBW 621, WH 1215, HPBW 02, HPPAU 08, HPPAU 10, HS 627, NW 6046 and VL 1009.

3.13. Molecular identification of YrCH52

Xgwm498 located at 1.6 cM produced 160 bp associated with *YrCH52* in 25 genotypes (36.7%), EST based marker *CON-6* (0 cM) and STS marker *CYS-5* (0.5 cM) developed from resistance gene analogues [69] did not produce any results.

3.14. Molecular identification of Yr25

Xgwm6 linked with *Yr25* gene produced monomorphic bands of 150 bp in all the genotypes indicating non-diagnosing nature of the primer.

3.15. Molecular identification of Yr27

Yr27, originated from the cultivar McMurachy and is located on chromosome 2BS [70]. The chromosomal region of *Yr27* harbours *Lr13*, *Lr23* and *Lr31* rust resistance genes. SSR marker *Xgwm630* is located 10 cM from *Lr13* (Seyfarth *et al*., 1999). Since, *Yr27* is linked with *Lr13*; *Xgwm630* was used to check the abundance of *Yr27* gene in wheat genotypes [71]. *Xgwm630* primer amplified a 124 bp allele in all the genotypes marking either the 100% abundance of *Yr27* or its absence. Nevertheless, the genetic distance (10 cM) is too large for use of *Xgwm630* for MAS. *Yr27* is an all plant stage resistant gene that shows the durability in combination with *Lr34* and other resistance genes [72]; however, as a single gene *Yr27,* is no longer effective in most wheat growing areas (McIntosh *et al.,* 1995) [73].

3.16. Molecular identification of Yr29

Yr29 was originally identified in cultivar Pavon 76 and was assigned to chromosome 1BL [74]. *Yr29* confers moderate level slow-rusting APR to yellow rust. *Yr29* gene is closely linked to *Lr46* for leaf rust resistance. *Wmc44* flanks *Yr29* 3.6 cM proximally [75] and amplified 8 alleles (205 bp, 210 bp, 220 bp, 240 bp, 260 bp, 280 bp, 300 and 310 bp), respectively. Twenty-six genotypes (38.2%) specific as predicted for (260 bp) with *Yr29* and 49 lines (72%) without *Yr29* were identified. SSR *Xgwm 259* gave inconclusive results.

3.17. Molecular identification of Yr30

Yr30 is a minor APR gene introgressed from Yaroslav emmer wheat into bread wheat along with the stem rust resistance gene *Sr2* [76] and is located on chromosome 3BS [77]. *Yr30* is closely linked with *Sr2* for stem rust resistance and *Lr27* for leaf rust resistance [78]. SSR marker *Xgwm533* (+120 bp) has been used in MAS for incorporating the *Sr2* gene into wheat cultivars (Spielmeyer *et al*., 2003) hence *Xgwm533* can be potentially used to select *Yr30* gene containing genotypes. Screening with *Xgwm533* amplified 5 alleles 100 bp, 120 bp, 130 bp, 140 bp and 150 bp, respectively. Forty-six genotypes (67.6%) produced 120 bp bands specific for *Yr30* while 10 genotypes (14.7%) failed to yield any amplicons. CAPS marker *csSr2* failed to amplify any of the genotypes.

3.18. Molecular identification of Yr32

Yr32 was originally detected from cultivar Carstens V [79] and is located on chromosome 4D. SSR marker *WMC198* is closely linked to *Yr32* at 0.2 cM [80] and amplified two alleles 180 bp and 200 bp, respectively. Six genotypes (8.8%) (HD 3209, AKAW 3842, DBW 216, DBW 219, RKD 292 and VL 1009) produced bands associated with *Yr32* while the remaining genotypes failed to amplify the gene.

3.19. Molecular identification of Yr35

Yr35 confers effective all-stage resistance. It was derived from *T. dicoccoides* and was located on chromosome 6BS [81]. SSR marker *cfd1* located at 4.1 cM from *Yr35* and 3.0 cM to *Lr53* gene didn't amplify in any of the genotypes indicating absence of *Yr35* gene in all genotypes.

3.20. Molecular identification of Yr36

Yr36 is derived from *T. turgidum ssp. dicoccoides* accession *FA15-3* and confers high level of HTAP resistance. It is located on chromosome 6B. Three primers, *ASA* at 0.3 cM [82], SSR *Barc101* [82] at 2 cM and *WKS1* (gene based) [83] linked with *Yr36* were used to screen the wheat genotypes. *ASA* primer amplified 1.6 kb product size in 3 genotypes (4.5%) i.e. HPPAU 05, AKAW 3842 & Lassik. *Barc101* amplified 5 alleles 116 bp, 124 bp, 138 bp, 160 bp and 165 bp respectively. Twenty-seven genotypes (39.7%) produced a 165 bp band associated with *Yr36.* Remaining genotypes showed absence of this allele. *WKS1* is HTAP gene-based marker and amplified 128 bp product sizes in two genotypes (HPPAU 05 and Lassik).

3.21. Molecular identification of Yr40

Yr40 originated from ovate goat grass, *Ae. geniculata* Roth (syn. *Ae. ovata* L.) is located on chromosome 4D and confers effective ASR to yellow rust. *Yr40* and *Lr57* was either closely linked genes or they are the same gene with pleiotropic effect [84]. SSR *Xfbb276* amplified 1 kb and 2 kb alleles in 20 lines (29.4%) indicating likely presence of *Yr40*.

3.22. Molecular identification of Yr46

Yr46 confers APR to yellow rust and is located in the middle of chromosome 4DL. *Cfd71* and *Cfd23* markers are associated with *Lr47* gene [85]. *Cfd71* amplified 3 alleles 148 bp (+), 150 bp and 152 bp while *Cfd23* amplified two alleles of 214 bp and 211 bp in 20 genotypes (29.4%). On

the basis of both primers 13 genotypes (19.1%) (K 1317, DBW 219, MACS 5044, WH 1215, DBW 220, HPBW 02, HS 580, VL 1009, UP 2954, UP 2955, VL 3002, VL 3011 and VL 3012) identified with *Yr46* gene.

3.23. Molecular identification of Yr47

Yr47 (*YrW1*) originated from Iranian wheat landraces and was located on chromosome 5BS [86]. SSR marker *cfb309*, estimated to be about 8–12 cM from *Yr47*. *Yr47* is linked with leaf rust resistance gene *Lr52* with a genetic distance of 3–6 cM [86]. *Cfb309* amplified 2 alleles of 350 bp and 600 bp. Allele 600 bp is associated with the presence of *Yr47* and was found in 6 genotypes (8.8%) while 15 genotypes (22.05%) produced both alleles indicating heterozygosity of the gene. Four genotypes (5.8%) produced 350 bp allele confirming absence of this gene. Remaining genotypes didn't amplify any product. Twenty-one genotypes (30.9%) are presumed to include the *Yr47* gene.

3.24. Molecular identification of Yr48

Yr48, derived from wheat genotype PI610750 is a QTL conferring APR to yellow rust and located on chromosome 5AL [87]. Marker-assisted breeding programs uses closely linked markers *SNF-A2* (0.18 cM proximal of *Yr48*), *BE495011* (0.09 cM proximal of *Yr48*) and *cfa2149* (0.06 cM distal of *Yr48*) for selection of *Yr48* gene. SSR *cfa2149* produced 2 alleles of 225 bp and 250 bp. Twenty-two Genotypes (32.4%) showed both 225 bp and 250 bp alleles, 2 genotypes (2.9%) showed 225 bp, 2 genotypes (2.9%) showed 250 bp alleles. *SNF-A2* amplified 3 alleles of 150 bp, 180 bp and 220 bp. Two genotypes (2.9%) (TL 3009, UAS 459) produced 150 bp alleles and were associated with *Yr48*. Two genotypes (2.9%) gave 180 bp and 220 bp alleles, five genotypes produced 180 bp allele and eight genotypes produced 220 bp allele. *BE495011* amplified one allele of 220 bp in 18 genotypes (26.5%) confirming presence of this gene. Overall 32 genotypes (48.5%) confirmed positive with all these markers. Combining proximal and distal position, 12 genotypes (17.6%). HI 8759, HI 8774, HPW 433, UAS 459, NW 6094, PBW 621, PDW 344, WH 1184, UP 2955, WH 1310 and Lassik were postulated to carry *Yr48*.

3.25. Molecular identification of Yr51

Yr51 is recessive in nature and confers ASR to yellow rust. *Yr51* is delimited by markers *owm45F3R3* at 1.2 cM proximal and *sun104* at 2.5 cM distal, respectively, locating *Yr51* on the long arm of chromosome 4B. Since, *Yr51* is not present in modern wheat genotypes, positive validation was not feasible. Marker *sun104* amplifies 225 bp in resistant lines and a null in susceptible lines. Negative validation using *sun104* produced null allele in all 68 genotypes confirming absence of *Yr51* gene. Marker *owm45F3R3*, amplified in 10 genotypes (14.8%). Since, no earlier data on this marker is available this marker was considered unsuitable for diagnostic purpose. Therefore, *sun104* can be used for marker-assisted selection of *Yr51* in wheat genotypes lacking the resistance linked 225 bp allele. Marker assisted detection for *Yr51* revealed the absence of this gene in Indian wheat genotypes. Similar results were obtained by Randhawa et al. [27].

3.26. Molecular identification of Yr59/YrZH84

Yr59, identified from an Iraqi spring wheat landrace, PI 178759, codes for HTAP resistance and is located on chromosome 7BL [28]. SSR locus *Xbarc32*, located proximal to *Yr59* (< 2.1 cM) produces a 165 bp product in the resistant line and a 175 bp product in the susceptible line. On screening with this primer, 4 alleles were amplified 165 bp (+), 175, 190 bp and 250 bp, respectively. Eleven genotypes (16.2%) were found to contain this gene, while the remaining genotypes did not amplify the 165 bp allele associated with *Yr59*. On the distal side *Xwmc 557* is located (> 2.2 cM). Screening with this primer amplified 2 alleles, 315 bp and 500 bp. Thirteen genotypes showed presence of this gene indicating 19.2% polymorphism rate. Over all 17, genotypes (25%) amplified either of the primers while 4 genotypes (HI 8759, DDK 1050, VL 1009 and UP 2954) showed amplification with both of these primer pairs.

3.27. Molecular identification of Yr60

Yr60 (*YrLalb*) resistance gene is developed from the Mexican wheat line 'Almop' (Wiliam *et al.*, 2003) [88] and located on the distal end of chromosome arm 4AL. This gene confers moderate resistance at both the seedling and the adult-plant stages. *SSR locus* wmc776 located < 0.6 cM away amplified 3 alleles 150 bp, 160 bp and 170 bp respectively. Fourteen genotypes (20.6%) amplified this gene with 150 bp, 160 bp and 170 bp respectively. Wmc313 is located 0.6 cM distal to Yr60 *and amplified 180 bp and 200 bp alleles in 20 genotypes (29.3%)* whereas wmc219 which is also located 0.6 cM to *Yr60* amplified 200 bp and 220 bp alleles in 16 genotypes (23.6%). Remaining genotypes didn't amplify any product confirming absence of this gene. Combined results using all the markers predicted *Yr60* in HI 8774 (d).

3.28. Molecular identification of Yr64

Yr64 confers ASR to yellow rust and is located on chromosome 1BS. SSR *Xgwm413* is linked to *Yr64* gene distally at 3.5cM [30]. Screening of wheat genotypes with *Xgwm413* led to the amplification of 95 bp allele in 42 genotypes, predicting its likely presence in the Wheat breeding lines.

3.29. Molecular identification of YrMor

S26M47 amplified 250 bp product size associated with the presence of the gene in 10 genotypes (14.8%) i.e. HPPAU 05, HPW 433, PBW 760, TL 3000, DBW 316, VL 4001, HPPAU 08, WH 1216 & HD 3171.

PM47 marker specific for *YrHua* gene, *Xgwm410* specific for *YrCN19/Yr41*, *WMC631* specific for *YrExp*1 gene and *WMC441* associated with *YrSPp* gene did not produce any

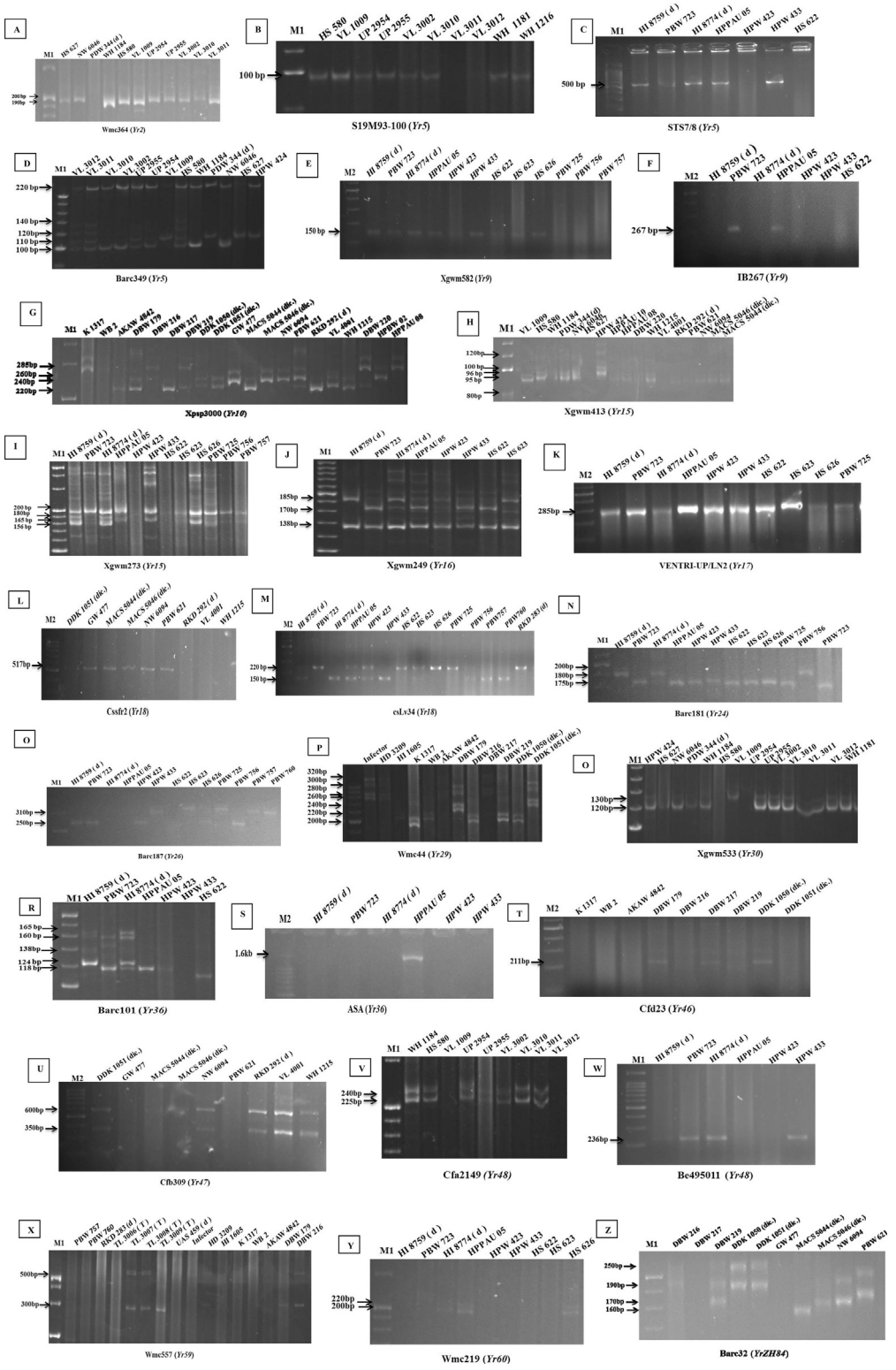

Fig. 1. Electrophoretogram of the primers for different *Yr* resistance genes. The corresponding Primers of *Yr2*, *Yr5*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr18*, *Yr24*, *Yr26*, *Yr29*, *Yr30*, *Yr36*, *Yr46*, *Yr47*, *Yr48*, *Yr59*, *Yr60*, and *YrZH84* were used to screen the elite wheat lines and varieties (A–Z). Although no control accession was used, the postulated bands were easy to be distinguished according to previously reported base pairs of the PCR product. The presence or absence of gene is marked with an arrow. Note: M1, 20 bp DNA Ladder (Fermentas life sciences); M2: 100 bp Ladder (G Biosciences).

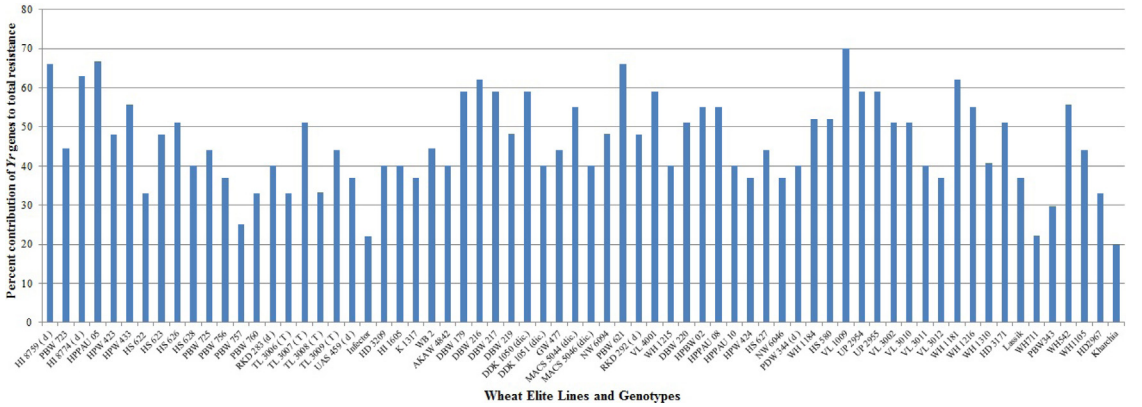

Fig. 2. Percent contribution of *Yr* genes to the total resistance in wheat genotypes.

result confirming either the absence of this gene in wheat genotypes or non-diagnostic behaviour of markers used for the screening purposes. RGAP markers linked with *Yr9*, *Yr45* also didn't yield satisfactory results may be due to non-specificity of the markers in diverse wheat background. Electrophoretograms of various *Yr* genes are given in Fig. 1.

4. Discussion

The severe yellow rust problem on the predominant wheat varieties of India is due to the excessive dependence on seedling resistance genes *Yr2*, *Yr9* and *Yr27* in isolation from other APR genes and absence of major avirulent (*Yr10*, *Yr15* & *Yr24/Yr26*) genes in the adopted varieties. Rapid evolving and virulent races of *Pst* have overcome the resistance of these major single genes deployed in widely cultivated varieties with the passage of time [89]. The breakdown of resistance has alarmed wheat breeders in the need for broadening the genetic base of future Indian wheat varieties by incorporating multiple yellow rust resistance genes. Identification of novel genes for yellow rust resistance can help breeders to efficiently and accurately incorporate those genes into breeding material by MAS to reduce the disease incidences. Deployment of specific gene combinations provides durable and improved resistance versus using single genes because single specific gene is subject to become susceptible due to genetic shifts in the pathogen [90]. Therefore, 70 closely linked markers specific for 35 *Yr* genes were used to detect the likely presence of *Yr* genes among the wheat genotypes and evaluate their contribution to the current status of *Pst* resistance. Most of the genes were amplified by using 1–5 linked markers for better accuracy of results. The combined results of all the markers were used for confirming the presence of genes. However, those markers which are gene based have better accuracy and can be considered alone for evaluation of resistance genes in wheat breeding programmes. Our molecular screening results correlated with the published reports for the size of expected PCR product and provides useful information for choosing specific resistant genes and an opportunity to pyramid the resistant genes against *Pst* pathotypes in a single wheat genotype. Out of 35 *Yr* genes, 25 genes amplified in wheat genotypes under study. The distribution of 25 *Yr* resistance genes among 68 wheat genotypes is illustrated in Fig. 2.

Two genotypes (VL 1009 & VL 3002) were identified with maximum 15 *Yr* genes followed by 14 genes in VL 3010 and HI 8759, respectively. Both of these genotypes exhibited resistance response at field level. Most 11 seedling resistance genes were identified in RKD 292 followed by 10 genes in DBW 216, WH 1184 and VL 3002 while most six APR genes were identified in HI 8759 and VL 3009 followed by five genes in, Lassik respectively. Even though RKD292 contained the major *Yr* genes (*Yr*10, *Yr*15, *Yr*24 & *Yr*26) and none of the APR gene, it still exhibited resistance response at field level concluding the major effects of these genes. Lowest numbers of two *Yr* genes were detected in genotypes PBW 757 and WH 711 susceptible genotypes. No major *Yr* genes were identified in susceptible genotypes. None of the RS/ASR genes were identified in genotype WH 711 while PBW 757 had one gene, followed by two genes in TL 3006, WH 1105, Kharchia and PBW 343 genotypes, respectively. Genotypes (HI 1605 and RKD 292) were identified with none of the APR genes but presence of *Yr10*, *Yr24* & *Yr26* imparted resistance response at field testing.

The genotypes carrying multiple *Yr* genes might be useful for pyramiding *Pst* resistance sources into commercial varieties [35]. The ratio of RS and APR genes to the total resistance among wheat genotypes is illustrated in Fig. 3. The higher frequency of RS genes over APR genes in Indian genotypes indicates an erosion of APR genes resulting from preferred use of dominant RS and ASR genes which were easier to select and breed into existing crop cultivars in Indian breeding programs. Genes *Yr26* (69.2%), *Yr2* (69.1%), *Yr64* (61.7%), *Yr24* (58.9%), *Yr7* (52.9%), *Yr10* (50%) and *Yr 48* (48.5%) showed high frequency among our panel of wheat genotypes, while *Yr9* (2.94%), *Yr36* (2.94%), *Yr60* (1.47%) and *Yr32* (8.8%) were least frequent in wheat genotypes (Fig. 4). Similar frequency of *Yr* genes among genotypes was observed in previous studies [18,91]. Zheng et al. [16] also studied the molecular

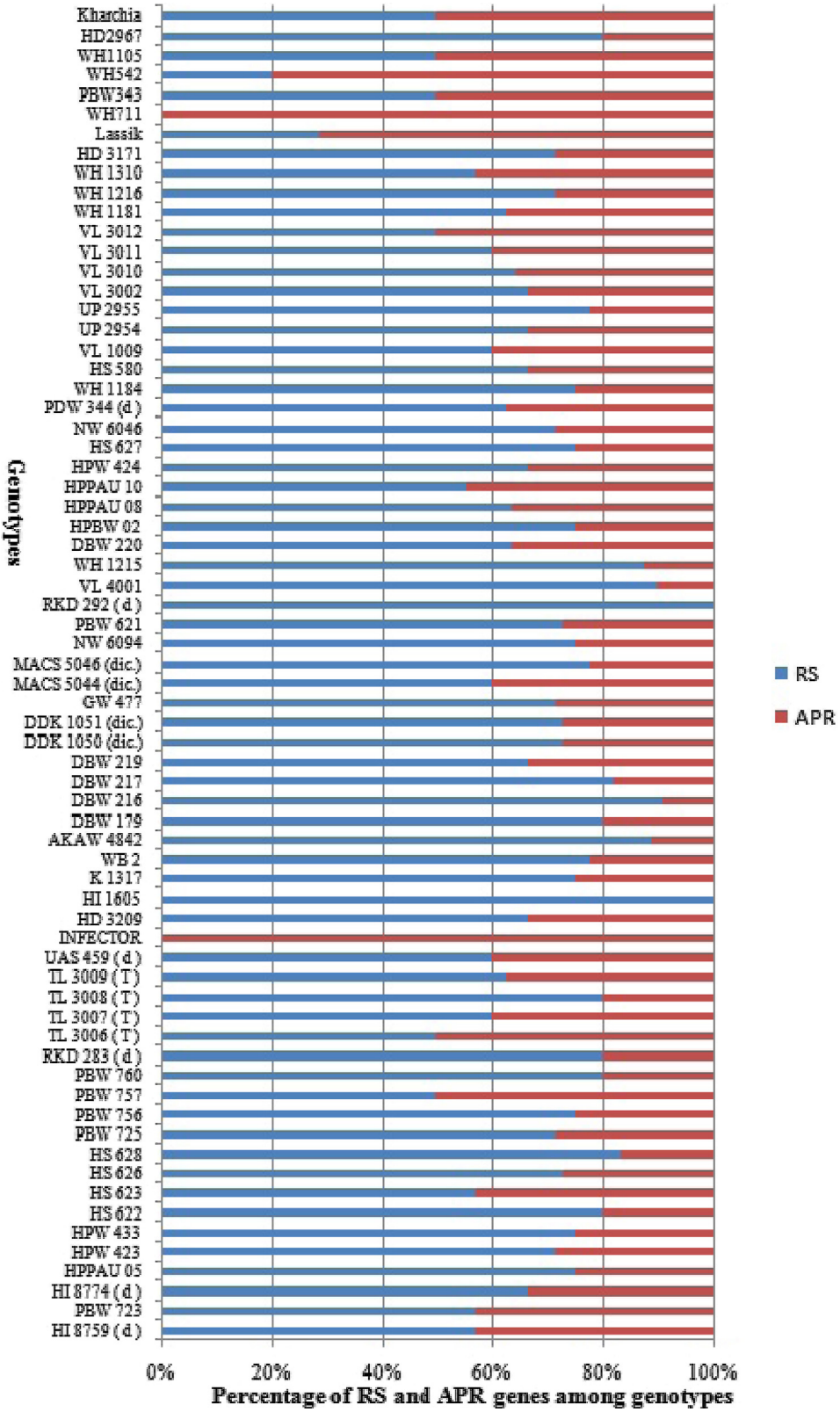

Fig. 3. Contribution of all-stage resistance genes (RS) and adult-plant resistance (APR) genes in wheat genotypes.

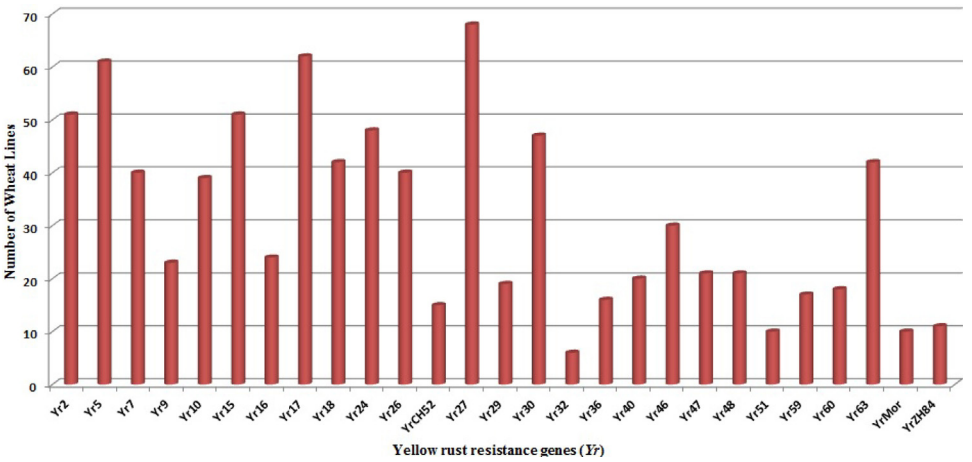

Fig. 4. Abundance of individual *Yr* genes in wheat genotypes.

characterisation of 330 leading wheat cultivars and 164 advanced breeding lines in China and identified *Yr9*, *Yr17*, *Yr18* and *Yr26* in 134 (29.4%), 45 (9.1%), 10 (2%) and 15 (3%) entries, respectively.

Yr5 is found to be effective against all rust virulent races in North America [7,20,92], Iran, China [7,93], India and Turkey [94]. *Yr5* gene is still resistant to major races in India and has potential to become an effective source of yellow rust resistance if deployed in combination with other *R*-genes. On screening with *S19M93* marker specific for *Yr5* gene, polymorphic rate of 44.1% was observed among wheat genotypes. Ullah et al. [32] obtained 89% polymorphic rate of *Yr5* gene in 99 Pakistan wheat lines on screening with *S19M93* molecular marker. Our findings for *Yr5* gene were also in accordance with the screening results of Iqbal et al. [33]. On the basis of combined results of the entire *Yr5* markers, all of the *Yr5* gene containing twelve genotypes (TL3007, K1317, WB2, NW6046, WH1184, HS580, VL3010, VL3011, VL3012, WH1181, HD3209, DDK1051 & VL3002) showed fairly good to moderate resistance response at field testing. A total of 52.9% genotypes showed the presence of *Yr7* gene. *Yr7* is known to be allelic to *Yr5* and linked with stem rust *Sr9 g* gene [52]. These genotypes can be further tested against stem rust pathotypes to be used as donor in stem rust breeding programmes. *Yr10* gene has also been reported to be effective against all races in India, Pakistan, China, Iran and USA [95]. Bariana et al. [60] reported two alleles for *Yr10 i.e. Yr10* and *Yrvav* and described that varieties with *Yr10* amplify a 258–260 bps fragment, 285 bp with *Yrvav* allele and 240 bp for lacking the *Yr10* gene. In our study, a 220 bp allele was also identified among the thirty-one wheat genotypes. Yaniv et al. [96] also reported the presence of 220 bp in Pakistani wheat varieties and linked it to the *Yr10* resistance gene. Totally, 50% genotypes exhibited the presence of *Yr10* resistant allele. Most of the *Yr10* alleles co-segregated together indicating the heterozygosity of *Yr10* locus. Similar, heterozygous pattern was reported in 28% varieties using *Xpsp3000* marker by Talha et al. [97]. However, close genetic distances have been reported to exist between reported marker gene combinations. Though the chance of recombination is very low but could not be neglected. Therefore, the allelic variability among genotypes also emphasizes the need of gene-based markers for efficient selection in marker assisted programmes. A close association between *Xpsp3000* marker and *Gli-B1* gene has also been reported [57]. *Gli-B1* encodes a wheat storage protein which improves plant resistance to abiotic stresses. This association of *Yr10vav* and *Yr10* with specific alleles of *Gli-B1* and *Xpsp3000* can be useful in marker-assisted selection and gene pyramiding. Marker validation depends on effective marker/trait linkage. To further validate the presence of *Yr5* and *Yr10*, an independent F_2 population can be developed from cross between positive parents and a highly susceptible line which can be tested for phenotypic segregation in field and genotypic segregation by proposed markers for respective genes.

The *Lr34/Yr18* gene for rust resistance has been used in agriculture for centuries. In contrast to many other resistance sources against leaf rust and stripe rust, it has remained effective and no virulence has been reported. In our study, the frequency of *Yr18* allele (29.4%) seemed to be comparatively higher in Indian breeding lines than the previously reported studies. All the genotypes exhibited resistant response at field testing. One genotype, MACS 5046 showed moderate response. Wu et al. [98] found that many Chinese wheat landraces that were predicted to possess the *Yr18* resistance allele by marker assays were highly susceptible to yellow rust in the field. This indicated that such landraces either contained susceptible allelic variations at the *Yr18* locus or a suppressor of gene function. Yang et al. [99] identified *Lr34/Yr18* genes in 231 Chinese wheat cultivars and 422 landraces using the STS marker *csLV34* with a frequency of 6.1% and 89.6% respectively. Similarly, Alma et al. [100] characterized elite wheat germplasm from Central Asia using molecular markers linked to the *Lr34/Yr18* and found a 16.7% frequency of the csLV34b-allele. As this gene complex provides durable adult-plant resistance, its deployment

should be increased in future wheat varieties of India so that their genetic base can be broadened against the continually evolving new races of *P. striiformis tritici*.

Yr24, *Yr26* and *YrCH42* are considered to be identical genes due to their similar infection types against rust isolates [67]. Combined results with markers exhibited the presence of *Yr24/Yr26/YrCH52* in 19 genotypes (27.9%). All these genotypes exhibited significant lower ACI values. *Yr24/Yr26/YrCH52* imparts race specific seedling resistance therefore, in wheat breeding programs; it should be used in combination with other major or minor resistance genes. Yang et al. [101] suggested the importance of gene pyramiding in improvement of durability of rust resistance.

Marker assisted detection for *Yr51* using negative validation by *sun104* marker revealed the absence of this gene in Indian wheat genotypes. Similar results were obtained by Randhawa et al. [27]. The genetic association of yellow rust resistance with other traits also allows indirect or direct selection for resistance in breeding. Examples include *Yr18/Lr34/Sr34*, *Yr9/Lr26/Sr31*, *Yr17/Lr37/Sr38*, *Yr18/Lr34/Pm38*, *Yr29/Lr46*, *Yr40/Lr57* and *Yr46/Lr67/Sr55. Yr60* gene was identified in one genotype HI 8774 (d). Apart from *Yr60* gene, *Wmc219* and *Wmc313* markers are also linked with leaf rust resistance gene (*Lr28)* and *Septoria tritici* blotch resistance gene (*Stb7)* at 5 cM [102] and 0.5–1.1 cM, respectively [103]. Genotype, HI 8774 can be tested at field level for the presence of leaf rust and septoria blotch resistance for durable rust breeding programmes.

Lines with these genes can be utilised alone or in combination with other ASR and APR genes containing lines. This type of resistance has been used in CIMMYT programs for improvement of leaf rust resistance) [104]. Some genotypes showed good frequency of APR genes such as *Yr18* (29.4%) loci which also coincides with leaf rust, stem rust and powdery mildew disease resistance locus, *Yr 30* (67.6%), *Yr 59* (19.2%) and *Yr46* (19.1%). Disease severity response was recorded from resistant to moderate susceptible (0–10 MS) among the genotypes containing these APR genes. *Yr30* is a minor APR gene and is closely linked with *Sr2* for stem rust resistance and *Lr27* for leaf rust resistance [78]. Forty-six genotypes (67.6%) postulated with *Yr30* showed effective resistance in the field testing. Since *Yr30* is linked with *Sr2*, it can be effective source in stem rust breeding programmes. *Yr46* is a pleiotropic gene and confers APR to yellow rust. It is also known to confer resistance to stem rust (*Sr55*), leaf rust (*Lr67*), powdery mildew (*Pm46*) and also leaf tip necrosis (*Ltn3*) [105]. The frequency of *Yr46* gene was found to be 19.1% among wheat genotypes. Genotypes MACS5044, DBW219, K1317, DBW220, HS580, HPBW02, UP2954, WH1215, VL1009, UP2955, VL3002, VL3010, VL3011 and VL3012 were found to be carrying *Yr46* and exhibited resistant to moderate field response. *Yr46* is widely distributed in older, tall wheat landraces from Punjab regions in India and Pakistan before modern wheat cultivars were grown in this region and was effective in field tests in Pakistan, India, Mexico and Australia and displayed durable resistance [106]. *Yr40* and *Lr57* is the same gene with pleiotropic effect [84]. Twenty genotypes (29.4%) HI8774, HS626, TL3007, HI1605, K1317, AKAW4842, DBW179, DBW216, DBW217, VL4001, DBW220, WH1184, HS580, VL1009, VL3002, VL3010, VL3011, DDK1050, WH1310 AND HD3171) indicating likely presence of *Yr40*.

Non-race-specific *Yr59* gene, confers a high level of HTAP resistance (IT 2) and is effective against all tested North American *Pst* races [26]. Eleven genotypes (WH 542, UP 2954, VL 1009, DDK 1050, TL 3009, RKD 283, PBW 760, PBW 757, PBW 723 and HI 8759) identified with *Yr59* can be used to strengthen durable breeding programmes. *Yr48,* is another QTL which confers APR to yellow rust. Twelve genotypes (17.6%) HI 8759, HI 8774, HPW 433, UAS 459, NW 6094, PBW 621, PDW 344, WH 1184, UP 2955, WH 1310 and Lassik were postulated to carry *Yr48*. An APR gene imparts durable resistance when pyramided together. Hussain et al. [107] showed that genotypes with combinations of slow rusting genes such as *Yr18, Yr29* and *Yr30* were high yielding with better resistance. This combination is very interesting as it provides protection against three types of rusts (Leaf rust, yellow rust and stem rust). In our study, out of 68 genotypes, ten genotypes (HI 8759 (d), HPPAU 08, HPPAU 10, HPW 424, HS 580, VL1009, VL3002, VL3010, VL3011 and Lassik) showed the combination of three designated slow rusting/durable genes (*Yr18 + Yr29 + Yr30*). All these ten genotypes also showed immune response at field testing. Asghar et al. [108] studied the stacking effect of combination of yellow and leaf rust resistance genes *Yr18/Lr34, Yr17/Lr37, Yr29/Lr46* and *Lr47* in 50 spring wheat genotypes using PCR based markers. *Yr18/Lr34* gene or loci was observed in 39 genotypes, *Yr17/Lr37* in 43 genotypes, *Yr29/Lr46* in 33 genotypes and *Lr47* was found in 34 wheat genotypes, respectively which exhibited better response towards rust diseases. Our results also showed similar trend with these findings. Madenova et al. [109] identified one genotype with *Lr34/Yr18* genes and two genotypes with complex genes *Lr37/Sr38/Yr17* using *csLv34* and *VENTRIUP/LN2* primers. Zheng et al. [36] demonstrated the significant additive effect of *Yr9 + Yr18* gene combination in Chinese wheat genotypes. One genotype, HPPAU 05 was identified with the gene combination of *Yr9 + Yr18* displaying effective resistance at field testing.

IB267, the translocation carrying resistance gene *Sr50* was transferred from Imperial rye into wheat in chromosome 1BL.1RS and 1DL.1RS [55]. It was found to be effective against stem rust race *Ug99* and is being used in various Australian wheat breeding program [110]. In our study, two genotypes (PBW 723 & HPPAU 05) were identified with IB267 translocation, which can be useful for incorporating stem rust resistance in wheat breeding programmes. *Yr36* is an HTAP gene which is closely linked to Grain protein content gene (*Gpc-B1*). Two genotypes AKAW 4842 and HI 8774, along with positive control Lassik were found to be carrying *Gpc-B1* allele. Genotype HI 8774 also showed linkage with *WKS1* gene. These genotypes can be directly utilised in bio-fortification and durable resistance breeding programme.

Among race specific genes *Yr5, Yr10, Yr15, Yr24* and *Yr26* are still protective against current predominant races in India. Breeding lines containing these genes can be utilised directly in resistance breeding. By analysing the molecular

evaluation data, one genotype (VL 3010) was identified with *Yr5*, *Yr10*, *Yr15* and *Yr26* genes. Six genotypes (VL 3011, HS 626, K 1317, WB 2, WH 184 and HS 580) were identified positively for *Yr5, Yr10* and *Yr24/Yr26* genes. Eight genotypes (PBW 725, AKW 4842, DBW 179, DBW 217, DDK 1050, VL 4001, WH 1215 and HPW 424) showed the presence of *Yr15* and *Yr24/26* genes. All these lines displayed high immune response at field testing. Moreover, the genotypes with multiple *Yr* genes identified in this study might be useful as parental lines for diversifying *Pst* resistance sources in wheat breeding. Indeed, *Yr15* gene has been combined with *Yr24* and *Yr5* in all the commercial varieties in California covering 14% of the acreage of common wheat and proved to be very useful in controlling the yellow rust epidemics in California. The stacking of genes also has not shown any negative traits associated with the introgression of either of these genes [96]. Several combinations of *Yr* gene such as (*Yr5, Yr9, Yr18, Yr26, Yr29*), (*Yr10, Yr17, Yr18, Yr26, Yr29*), (*Yr10, Yr17, Yr18, Yr26, Yr29*) and (*Yr5, Yr10, Yr18, Yr26, Yr29*) was also reported by Begum et al. [111] in Pakistani wheat lines.

Out of 53 parental lines showing field resistance, 9 lines PBW723, HS622, HS623, PBW757, PBW760, TL3006, UP2955, Lassik and WH542 showed a resistant response to yellow rust races but molecular studies indicates these genotypes do not carry *Yr5*, *Yr10* and *Yr15*. Genotype, PBW 757 showed least number of *Yr* genes but exhibited immune response in field testing. For genotypes, exhibiting positive reaction in the field for rust resistance but not showing likely presence of major rust resistance *Yr5, Yr10* and *Yr15* genes, must be having other effective combination of ASR and APR genes or other effective genes which could not be detected with the linked markers used in the study or lack the corresponding allele which could be as a result of genetic recombination [112].

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Compliance with ethical standards

Disclosure of interest

The authors declare that they have no competing interest.

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