Euphytica (2020)216:17
https://doi.org/10.1007/s10681-019-2541-z

Stripe rust resistance genes in a set of Ethiopian bread wheat cultivars and breeding lines

Zeray Siyoum Gebreslasie · Shuo Huang · Gangming Zhan · Ayele Badebo · Qingdong Zeng · Jianhui Wu · Qilin Wang · Shengjie Liu · Lili Huang · Xiaojing Wang · Zhensheng Kang · Dejun Han

Received: 8 May 2019 / Accepted: 30 November 2019

Abstract Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*) is one the most important diseases of wheat in Ethiopia and worldwide. To identify resistance genes, 90 bread wheat lines and 10 cultivars were tested at the seedling stage against one *Pst* race from Ethiopia and six races from China as well as evaluated for the stripe rust response in an inoculated field nursery at Yangling, Shaanxi province and in a naturally infected field in Jiangyou, Sichuan, China. Resistance genes were postulated using molecular assays for *Yr9*, *Yr17, Yr18, Yr26, Yr29, Yr36, Yr44* and *Yr62*. Of the 100 entries tested, 16 had all stage resistance to all races. Molecular markers were positive for *Yr9* in five genotypes, *Yr17* in 21 genotypes, *Yr18* in 27 genotypes, *Yr26* in ten genotypes, *Yr29* in 22 genotypes, *Yr36* in 12 genotypes, *Yr44* in 30 genotypes, and *Yr62* in 51 genotypes. No line had *Yr5*, *Yr8*, *Yr10* or *Yr15*. Complete or all stage resistance was observed in genotypes carrying gene combinations *Yr9* + *Yr18* + *Yr44* + *Yr62*, *Yr29* + *Yr62* + *Yr26* and *Yr9* + *Yr17* + *Yr26* + *Yr44* + *Yr62*. The results are helpful for developing wheat cultivars with effective and more durable resistance to stripe rust both in China and Ethiopia.

Keywords Adult plant resistance · All stage resistance · Gene combinations · Molecular markers · Stripe rust · *Triticum aestivum*

Introduction

Stripe (yellow) rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*) is a significant threat in the majority of wheat growing regions of the world (Wellings 2011) including Ethiopia (Abeyo et al. 2014). Yield losses caused by stripe rust in Ethiopia have ranged from 40 to 100% depending on the degree of susceptibility of cultivars, the time of the initial infection and environmental conditions during epidemic development (Badebo et al. 2001). In 2010, Ethiopia experienced one of the most serious stripe rust epidemics in recent times, with more than 600,000 ha of wheat affected

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10681-019-2541-z) contains supplementary material, which is available to authorized users.

Z. S. Gebreslasie · S. Huang · G. Zhan · Q. Zeng · J. Wu · Q. Wang · S. Liu · L. Huang · X. Wang · Z. Kang (✉) · D. Han (✉)
State Key Laboratory of Crop Stress Biology for Arid Areas, Northwest A&F University, Yangling 712100, Shaanxi, People's Republic of China
e-mail: kangzs@nwsuaf.edu.cn

D. Han
e-mail: handj@nwsuaf.edu.cn

A. Badebo
CIMMYT-Ethiopia, ILRI-Gurd Sholla Campus, CMC Road, P.O. Box 5689, Addis Ababa, Ethiopia

Published online: 06 January 2020

and an estimated $US3.2 million spent on fungicides (Abeyo et al. 2014).

Cultivation of resistant cultivars is the most cost effective and environmentally sensible approach to control stripe rust (Line and Chen 1995). However, durable resistance depends on the use of genetically diverse sources of resistance (Wellings 2011). Periodic outbreaks of stripe rust occur in Ethiopia due to lack of knowledge regarding the genetic resistance present in commercial cultivars and breeding populations, and inadequate monitoring of the pathogen race population (Badebo 2002). In Ethiopia, breeding for resistance is solely based on field observations at naturally infected trial sites. There is only limited information on the genetic composition of current cultivars and even less on materials undergoing selection (Dawit et al. 2012).

So far, 82 *Yr* genes have been formally designated; about 25 of these confer adult plant resistance (APR) or high temperature adult plant resistance (HTAP) while the remainder provide all stage (or seedling) resistance (ASR) (McIntosh et al. 2016, 2017; Wang and Chen 2017). Genes Yr8, *Yr9, Yr15, Yr17, Yr24/26, Yr35, Yr36, Yr53, Yr64* and *Yr65* were obtained from diploid and tetraploid wild and cultivated relatives, e.g., *Yr15* derived from *Triticum dicoccoides* (Gerechter-Amitai et al. 1989), *Yr8* from *Aegilops comosa* (Riley et al. 1968), *Yr9* from *Secale cereale* (Macer 1975), *Yr17* from *Ae. ventricosa* (Tanguy et al. 2005), *Yr28* and *Yr48* from *Ae. ventricosa* (Lowe et al. 2011; Singh et al. 2000), *Yr37* from *Ae. kotschyi* (Heyns et al. 2011), *Yr38* from *Ae. sharonensis* (Marais et al. 2010), *Yr40* from *Ae. geniculata* (Kuraparthy et al. 2009), *Yr42* from *Ae. geniculata* (Marais et al. 2009). *Yr50* from *Thinopyrum intermedium* (Liu et al. 2013), *Yr70* from *Ae. umbellulata* (Bansal et al. 2016). Other genes came from hexaploid wheat landraces (McIntosh et al. 2016). Among the permanently designated ASR genes, *Yr5, Yr15, Yr53, Yr61, Yr65 and Yr69* are still widely effective and can be used in breeding for stripe rust resistance (Xu et al. 2013; Zhou et al. 2014) provided they are not associated with detrimental linkage drag.

Following the discovery of the gene-for-gene interaction between plant hosts and their pathogens (Flor 1971), host resistance genes and their corresponding pathogen avirulence genes could be postulated. Dawit et al. (2012) tested 22 Ethiopian bread wheat cultivars and 24 differential lines with 20 *Pst* races collected from Ethiopia, France and Germany. They postulated different combinations of *Yr2, Yr3a, Yr4a, Yr6, Yr7, Yr8, Yr9, Yr27, Yr32* and *YrSU* in tested materials. Hovmøller (2007) reported *Yr1, Yr2*, *Yr3, Yr4, Yr6, Yr9, Yr15, Yr17, Yr25* and *Yr32* in 98 Danish wheat cultivars; Xia et al. (2007) detected *Yr2, Yr3a, Yr4a, Yr6, Yr7, Yr9, Yr26, Yr27*, *YrSel* and *YrSd* in 72 Chinese wheat cultivars and advanced lines; and Sharma et al. (1995) reported *Yr2, Yr6, Yr8, Yr9, Yr10, Yr15, YrA and YrSu* in tests of 52 wild emmer derivatives and advanced bread wheat lines from Nepal. The drawback of this method of gene postulation is that while it is the most effective for identifying race-specific single resistance genes or simple gene combinations at the seedling stage, it cannot be easily used to identify adult-plant, often non-specific resistance genes that tend to be more common in the case of stripe rust (Wang and Chen 2017). Knowledge of pedigrees is also very valuable and can be used to support gene postulation. For example, given that Ethiopian wheat cultivars are largely based on the CIMMYT germplasm, the presence of 'Milan' in a pedigree gives a clue as to the possible presence of *Yr17* in its derivative; the presence of a synthetic (or *Ae. squarrosa*) in a pedigree is a clue to the possible presence of *Yr24* (*Yr26*) (R.A. McIntosh personal communication). *Yr26* is located on a *Triticum aestivum/Haynaldia villosa* translocation chromosome lB-1V (Ma et al. 2001).

For the latter, more emphasis has to be placed on pedigree and molecular markers. Zeng et al. (2014) identified several *Yr* resistance genes in 330 leading cultivars and 164 advanced breeding lines from China using pedigree information and molecular markers together with gene postulation. In the present study, we opted to use seedling tests with an array of *Pst* races and adult plant responses in the field combined with pedigree and marker tests to postulate *Yr* resistance genes in the Ethiopian bread wheat cultivars and breeding lines.

Materials and methods

Plant materials

One hundred bread wheat genotypes (10 cultivars and 90 breeding lines) from the Ethiopian National Wheat Research program were tested for resistance to stripe

rust in multi-race seedling tests in a greenhouse in the State Key Laboratory of Crop Stress Biology for Arid Areas and College of Plant Protection, Northwest A&F University, Yangling, Shaanxi, China. The materials were also planted at Yangling, China during 2016–2017 and 2017–2018 growing seasons for adult plant field tests, following inoculation with a mixture of races. Lastly, the material was grown at Jiangyou in Sichuan province, China, in the same crop seasons, and exposed to a natural infection. Sichuan is one of the most stripe rust prone areas in China and resistance is an obligatory trait for cultivar release in that province. The wheat cultivars (lines) 'Mingxian 169' for seedling and 'Xiaoyan 22' for adult plant tests were used as susceptible controls, respectively. Wheat lines or cultivars such as'AvS*Yr18*NIL','92R137'(*Yr26*), 'AvS*Yr29*NIL', 'RSL65(*Yr36*)' and 'PI 192252(*Yr62*)' were included in comparative response tests in the in the stripe rust assessment Supplementary Table 2. A set of 18 wheat genotypes that carry different single known genes for resistance (Wan and Chen 2014) was included in the study as references (Supplementary Table 1).

Seedling tests

Seedling tests were conducted in a greenhouse at Yangling, China. For each wheat entry, 5–7 seedlings were grown in a 10 cm diameter pot in a disease free area. Seedlings were inoculated with fresh urediniospores mixed with talc powder in a 1:20 (v/v) ratio when the first leaves were fully expanded, and incubated in a dew chamber for 24 h at 10 °C in darkness. The seedlings were then transferred to a growth chamber with 16 h day at 16 °C and 8 h night at 13 °C. Six Chinese and one Ethiopian stripe rust races (culture EK3-12, Wan et al. 2017) were used in the study. The virulence: avirulence profiles of the actual isolates of those races are given in Table 1.

Mingxian 169 is susceptible to all known Chinese *Pst* races, and was used as the susceptible check. Infection types were recorded using the 0–9 scale, i.e. starting 15 days post-inoculation. Infection types 0–3 were considered resistant, 4–5 moderately resistant, 6–7 moderately susceptible and 8–9 susceptible, as described by Line and Qayoum (1992).

Field tests

Field tests were conducted during the 2016–2017 and 2017–2018 cropping seasons at the experimental site of Northwest A&F University, Yangling. Seeds of the 100 wheat entries were planted in two row plots, with the susceptible check, Mingxian 169, included every 20 entries. Mingxian 169 was also planted on both sides of the nursery as an inoculated stripe rust spreader. Inoculations were done during late February and early March. The inoculum used in both seasons was a mixture of urediniospores comprised of CYR33 (30%), CYR32 (30%), CYR31 (10%), CYR29 (10%), CYR23 (10%) and V26 (10%). The nurseries were managed according to agronomic practices common in the region, except that the field was irrigated twice during the epidemic development. A similar experimental design was used in the Sichuan province where the material was subjected to natural infection. In the latter trial, Xiayan22 was used as the susceptible control. Infection types and disease severities on the uppermost three leaves were recorded twice according to Line and Qayoum (1992) during mid and late May when the plants had reached the booting and milk stages respectively, and disease severities (DS) on the susceptible check exceeded 80%.

DNA extraction

The entries were grown in a greenhouse up to the two leaf stage for isolation of genomic DNA. A total of 100 mg of leaf tissue was collected from each genotype and immediately frozen in liquid nitrogen. DNA of each entry was extracted following the protocol described by Song and Henry (1994).

DNA concentration was measured using a ND-1000 spectrophotometer (Thermal Scientific, Wilmington, DE), and quality was checked by the agarose gel electrophoresis.

PCR amplification and electrophoresis

Polymerase chain reactions (PCR) were done using a S1000 Thermal Cycler (BIO-RAD, CITY). The PCR reaction (total volume = 15 µl) contained 1.0 unit of *Taq* DNA polymerase, 1.5 µl of 10× buffer (50 mmol KCl, 10 mmol Tris-HCI, pH 8.3), 2.0 mmol $MgCl_2$, 200 µmol of dNTP, 0.6 µmol of each primer and 50–100 ng of template DNA. Primers of markers for

Table 1 Virulence (V) and avirulence (A) spectra of pure isolates of seven *Pst* races from China and Ethiopia on NILs in an Avocet genetic background

Race name	V, virulent; or A, avirulent
CYR23	V: *Yr1, Yr7, Yr8, Yr9, Yr44, YrExp2*
	A: *Yr5, Yr6, Yr10, Yr15, Yr17, Yr24, Yr27, Yr32, Yr43, YrSP, YrTr1, Yr76*
CYR29	V: *Yr1, Yr6, Yr7, Yr8, Yr9, Yr43, Yr44, YrExp2*
	A: *Yr5, Yr10, Yr15, Yr17, Yr24, Yr27, Yr32, YrSP, YrTr1, Yr76*
CYR31	V: *Yr1, Yr6, Yr7, Yr8, Yr17, Yr43, Yr44, YrExp2*
	A: *Yr5, Yr9, Yr10, Yr15, Yr24, Yr27, Yr32, YrSP, YrTr1, Yr76*
CYR32	V: *Yr1, Yr6, Yr7, Yr8, Yr9, Yr17, Yr43, Yr44, YrSP, YrExp2, Yr76*
	A: *Yr5, Yr10, Yr15, Yr24, Yr27Yr32, YrTr1*
CYR33	V: *Yr1, Yr6, Yr8, Yr9, Yr10, Yr24, Yr32, Yr44, YrSP, YrExp2, Yr76*
	A: *Yr5, Yr6, Yr17, Yr27, Yr43, YrTr1*
V26	V: *Yr1, Yr6, Yr7, Yr9, Yr10, Yr17, Yr24, Yr27, Yr32, Yr44, YrSP, YrExp2*
	A: *Yr5, Yr8, Yr15, Yr43, YrTr1, Yr76*
EK3-12	V: *Yr1, Yr6, Yr7, Yr9, Yr17, Yr27, Yr43, YrExp2*
	A: *Yr5, Yr8, Yr10, Yr15, Yr24, Yr32, Yr44, YrSP, Yr1Tr, Yr76*

identifying specific *Yr* genes were synthesized by Sangon Biotech Co, Ltd (Shanghai, China)

The PCR conditions were: denaturation at 94 °C for 4 min, followed by 35 cycles (each consisting of 1 min at 94 °C, 30 s at 40–60 °C (depending upon the primers), 1 min at 72 °C), final extension for 10 min at 72 °C and a 4 °C holding step. In the case of the STS-7/8, STS-9/10 and URIC/LN2 primer pairs, after implication, the PCR products were digested with DpnII (New England Biolabs, USA) as explained by Chen et al. (2003), with some modifications. The reaction solution for enzymatic digestion contained 10 µl of PCR product, 1 µl of restriction enzyme DpnII (New England Biolabs, Beverly, MA) and 2 µl of 10× buffer for DpnII (New England Biolabs). Samples were kept at 37 °C for 4 h and the digested products were separated on agarose gels.

Yr26 was detected using SNP markers WRS303 and WRS467. SNP genotype calling and clustering were done using Illumina Genome Studio Polyploid Clustering v1.0 and Affymetrix Genotyping Console™ (GTC) software, respectively. Details of the publicly available molecular markers used to detect other resistance genes are listed in Table 2.

Results

Disease data

Seedling infection type data for the 100 tested entries inoculated with seven *Pst* races are listed in Supplementary Table 2. Fifty-six lines were highly resistant (IT 0–3) and nine lines were moderately resistant (IT 4–5) to the Ethiopian race; 40 lines were highly resistant and 8 lines moderately resistant to all Chinese races; 42 lines were highly resistant and 10 lines moderately resistant to both the Ethiopian and Chinese races. Fourteen lines and two cultivars (DANDA'A, and HULLUKA) were highly resistant (IT 0–3) to all races. Only three lines were considered susceptible in field tests in China, with infection severity ranging from 50 to 70%, including cv. MILLENIUM. This was not unexpected given the comprehensive international screening program conducted by CIMMYT and the strong emphasis on the adult plant resistance which is often provided by combinations of resistance genes individually conferring low to intermediate levels of resistance.

The presence of the 'Pastor' *Yr46* gene carrier cultivar in the pedigree of nine breeding lines such as ETBW8823, ETBW8827, ETBW8571, ETBW8663, ETBW8491, ETBW8492, ETBW8311, ETBW9470 and ETBW8848, and the presence of a synthetic (that is, of *Ae. squarrosa*) in the pedigrees of 8 lines possessing *Yr24* (*Yr26*) (Table 2) may have contributed to improved field resistance. Pedigrees, seedling and adult plant responses, and molecular marker detection for 10 bread wheat cultivars and 23 breading lines are presented in Table 3.

Each individual accession had similar adult plant stripe rust disease responses except for three entries

Table 2 Primers used to detect *Yr* resistance genes in Ethiopian bread wheat cultivars and breeding lines

Gene	Marker	Type	Distance	Sequence	Annealing temp. (°C)	(+ bp)	(− bp)	References
Yr5	STS-7/8	STS/CAPS	0.3	TACAATTCACCTAGAGT	46	439	472	Murphy et al. (2009)
				GCAAGTTTTCTCCCTATT				
Yr5	STS-9/10	STS/CAPS	0.7	AAAGAATACTTTAATGAA	42	439		Zhang et al.(2009)
				AAAGAATACTTTAATGAA				
Yr5	S19M93	STS	0.54	TAATTGGGACCGAGAGACG	55	100	62/275	Smith et al. (2007)
				TAATTGGGACCGAGAGACG				
Yr5	Barc349	SSR	0.4	CGA ATA GCC GCT GCA CAA	46	105		Murphy et al. (2009)
				CGA ATA GCC GCT GCA CAA				
Yr8	SC-OPD11	SCAR		AGCGCCATTGGGAGCTCTATGGTG	57	1265		Niu et al. (2004)
				AGCGCCATTGGGAGCTCTATGGTG				
Yr9	H2O-F	Rye genome-specific		GTACTAGTATCCAGAGGTCACAAG	56	1598		Liu et al. (2008)
	H2O-R			CAGACAAACAGAGTACGGGC				
Yr9	P6M12-P-F	STS	0.35	GTACTAGTATCCAGAGGTCACAAG	56	250/350		Mago et al. (2005)
	P6M12-P-R			CAGACAAACAGAGTACGGGC				
Yr10	E51100	SCAR		TCAAGGAGGTCAGTGACAG	56	1085		Liu et al. (2014)
				TCAGGGAGGTGTAGCCTAAT	51	543		Liu et al. (2014)
Yr10	Yr10F	Gene specific		TCAAAGACATCAAGAGCCG				
Yr15	barc8	SSR	4.2	GCGGGAATCATGCATAGGA				
				GCGGGGGCGAAACATACACATAAAAACA	55	96	98	Murphy et al. (2009)
Yr15	gwm413	SSR	3.5	TGCTTGTCTAGATTGCTTGGG				
Yr17	URIC/LN2-F	*Ae. ventricosa* Chromosome-specific		GGTCGCCCTGGCTTGCACCT	64	285	275	Helguera et al. (2003)
	URIC/LN2-R			TGCAGCTACAGCAGTATGTACACAAAA				
Yr17	SC-385-F	SCAR	3.4	CTGAATACAAACAGCAAACCAG	50	385		Jia et al. (2011)
	SC-385-R			ACAGAAAGTGATCATTTCCATC				
Yr18	csLV34-F	STS	0.4	TTGATGAAACCAGTTTTTTTTCTA	51	150	229	Krattinger et al. (2009)
	csLV34-R			GCCATTTAACATAATCATGATGGA				
Yr18	L34DINT9F-F	Gene specific		TTGATGAAACCAGTTTTTTTTCTA	51	517		Krattinger et al. (2009
	L34PLUSR-R			GCCATTTAACATAATCATGATGGA				
Yr26	WRS303-F	KASP (*Haynaldia villosa* on chromosome lB)		GCTGTTAATCCTACGCCACT	57.03			Wu et al. (2018)
	WRS303-R			GCTGTTAATCCTACGCCACC				

Table 2 continued

Gene	Marker	Type	Distance	Sequence	Annealing temp. (°C)	(+ bp)	(− bp)	References
Yr26	WRS467-F	KASP (*Haynaldia villosa* on chromosome 1B)		TTTGTACAACACATCAGCTATTACA	57.69			Wu et al. (2018)
	WRS467-R			TTTGTACAACACATCAGCTATTACC				
Yr29	bac17R-F	STS	2.1/4.2	CCCATGCTGACATGGCCACAT	55	1700	500	Rosewarne et al. (2006)
	bac17R-R			CTCTGCTCTTTAGTAGTTGCC				
Yr29	wmc44-F	SSR	3.6/109	GGTCTTCTGGGCTTTGATCCTG	57	260	~260	Rosewarne et al. (2006)
	wmc44-R			TGTTGCTAGGGACCCGTAGTGG				
Yr36	Yr36E1a-F	Gene-specific		AAGGCAAAGGCAAAGTGG	57	911		Fu et al. (2009)
	Yr36E1a-R			TGATCTTTACCAAGCATTCG				
Yr36	Yr36START-F	Gene-specific		AAGGCAAAGGCAAAGTGG	52	871/537		Fu et al. (2009)
	Yr36START-R			TGATCTTTACCAAGCATTCG				
Yr44	pWB5/PWN1r1-F	STS	9.4	GGTGCAATTTGAGTTTGGAGT	49	380		Sui et al. (2009)
	pWB5/PWN1r1-R			GGTGTTGACTGGAGAATCCG	45	820		Sui et al. (2009)
Yr44	wgp100-F	RGAP	3.9	GCATTGGAACAAGGTGAA				
	wgp100-R			GGTGGGGTTGGGAAGACAACG	51	222		Lu et al. (2014)
Yr62	gwm192-F	SSR	2	GGTTTTCTTTCAGATTGCGC				
	gwm192-R			CGTTGTCTAATCTTGCCTTGC	51	133		Lu et al. (2014)
Yr62	gwm251-F	SSR	3.3	CAACTGGTTGCTACACAAGCA				
	gwm251-R			GGGATGTCTGTTCCATCTTAG	51	133		Lu et al. (2014)

RGAP resistance gene analogs polymorphism, *SCAR* sequence characterized amplified regions, *SSR* simple sequence repeats

cM centimorgan (estimated marker gene distance), bp base pair, KASP Kompetitive Allele Specific PCR," +" the PCR product indicating the presence of the corresponded gene, "−" the PCR product indicating the absence of corresponded gene

Table 3 Pedigree, seedling and adult plant stripe rust responses and detection of resistance genes using molecular markers in an Ethiopian bread wheat cultivars and breeding lines

Pedigree	Seedling IT							Adult plant response				RT	Yr gene
	CCYR23	CCYR29	CYR31	CYR32	CYR33	CYR34	EK3-12	Yangling		Sichuan			
	IT	IT	IT	IT	IT	IT	IT	IT	DS	IT	Ds		
WAXWING*2/HEILO	6	6	7	3	6	6	3	2	10	1	10	APR	None[a]
TL/3/FN/TH/NAR59*2/4/BOL'S'	3	2	2	4	3	5	2	2	10	1	5	APR	*Yr18*[a], *Yr29*[a], *Yr62*[a]
PYN/BAU//MILAN	6	8	3	4	6	4	9	0	0	1	1	APR	*Yr17*[ab], *Yr18*[a], *Yr44a*, *Yr62a*
ALONDRA/CEP 75630//CEP75234/PAT 7219/3/BUCKBUCK/BIY/4/	2	0	1	6	6	2	6	9	50	8	50	S	Yr9[a], Yr29[a], Yr62[a]
M/4/HAR1709/3/M//24/E	2	2	6	6	3	5	3	0	0	1	1	APR	*Yr17*[a]
SOKOLL/EXCALIBUR	3	4	2	3	3	2	3	1	10	2	5	APR	*Yr29*[a]
HK-14-R251	0	6	3	2	3	4	2	0	0	1	1	APR	None
UTQUE96/3/PYN/BAU//MILAN	2	4	5	2	9	3	2	2	10	1	1	APR	None, *Yr17*[b]
KIRITATI//2*PBW65/2*SERI.1B	3	3	3	3	3	3	2	2	10	2	5	ASR	None[a]
UTQUE96/3/PYN/BAU//MILAN	2	2	2	3	3	2	2	2	10	0	0	ASR	None, *Yr17*[b]
HAR47/(BABAX/LR42//BABAX)	0	2	3	3	3	3	3	0	0	1	1	ASR	*Yr29*[a]
CHAM-4/SHUHA'S'/6/2*SAKER/5/RBS/ANZA/3/KVZ/HYS//YMH/TOB/4/BOW'S''	1	0	0	2	3	2	3	3	10	1	1	ASR	*Yr9*[ab], *Yr18*[a], *Yr44*[a], *Yr62*[a]
QT6581/4/PASTOR//SITE/MO/3/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/5/PAVON 76/JADIDA-2	33	22	33	33	33	22	22	44	220	22	55	ASR	None[a], *Yr26*[b], *Yr29*[b], *Yr46*[b]
MILAN/SHA7/3/THB/CEP7780//SHA4/LIRA/4/SHA4/CHIL/5/FARIS-6	11	00	11	22	33	33	22	11	55	11	11	ASR	*Yr9*[a], *Yr17*[ab], *Yr26*[a], *Yr44*[a], *Yr62*[a]
EALME4SA-167/FLAG-1/3/PASTOR/SERI//PFAU	33	22	33	33	33	22	33	22	110	33	110	ASR	*Yr62*[a], *Yr46*[b]
SNLG/3/EMB16/CBRD//CBRD/4/KA/NAC//TRCH	33	33	33	33	33	33	22	33	110	22	55	ASR	*Yr62*[a]
WORRAKATTA/2*PASTOR//DANPHE #1	2	3	2	3	3	3	2	1	5	2	5	ASR	None[a], Yr46[b]
SUP152//ND643/2*WBLL1/3/ND643/2*WBLL1	0	0	2	3	3	2	0	2	10	1	1	ASR	*Yr26*[a], *Yr29*[a], *Yr62*[a], *Yr36*[b]

Table 3 continued

Pedigree	Seedling IT							Adult plant response				RT	Yr gene
	CCYR23	CCYR29	CYR31	CYR32	CYR33	CYR34	EK3-12	Yangling		Sichuan			
	IT	IT	IT	IT	IT	IT	IT	IT	DS	IT	Ds		
BAVIS #1/5/W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1	2	1	3	3	3	3	2	3	10	2	5	ASR	None[a], Yr46[b]
CROC_1/AE.SQUARROSA (213)//PGO/10/ATTILA*2/9/KT/BAGE//FN/U/3/BZA/4/TRM/5/ALDAN/6/SERI/7/VEE#10/8/OPATA	2	2	2	3	2	3	2	1	10	1	1	ASR	*Yr26*[ab], *Yr44*[a], *Yr62*[a]
P1.861/RDWG//PBW343/3/MUNIA/ALTAR 84//AMSEL	2	0	0	3	3	1	0	0	0	1	1	ASR	*Yr9*[b], *Yr18*[a]
SERI.1B//KAUZ/HEVO/3/AMAD/4/PFAU/MILAN	0	2	0	3	3	3	0	0	0	1	1	ASR	None[a], *Yr17*[b]
WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBLL1/5/PRL/2*PASTOR/4/CHOIX/STAR/3/HE1/3*CNO79//2*SERI	9	2	3	2	3	7	2	1	5	1	1	APR	Yr18[a], Yr44[a], Yr62[a], Yr46[b]
WBLL1*2/BRAMBLING*2/3/ND643//2*PRL/2*PASTOR	9	6	4	3	9	3	3	3	5	2	10	APR	Yr17[a], Yr29[a], Yr36[a], Yr44[a], Yr62[a], Yr46[b]
W15.92/4/PASTOR//HXL7573/2*BAU/3/WBLL1/5/MILAN/KAUZ//DHARWAR DRY/3/BAV92	6	3	5	7	9	7	2	2	5	3	5	APR	Yr29, Yr46[b], Yr17[b]
WORRAKATTA/2*PASTOR//DANPHE #1	2	3	2	3	3	3	2	1	5	2	5	ASR	None[a], Yr46[b]
KRICHAUFF/2*PASTOR//CHONTE	2	5	5	5	8	4	3	2	10	2	10	APR	Yr62[a], Yr46[b]
ND643/2*WBLL1/3/KIRITATI//PRL/2*PASTOR/4/KIRITATI//PBW65/2*SERI.1B	9	9	9	8	9	9	6	2	5	3	15	APR	Yr29[a], Yr46[b]

IT Infection type; *DS* disease severity; *RT* resistance type; *APR* Adult plant resistance; ASR All stage resistance, CYR Chinese yellow rust

[a]Molecular marker detection, [b]presence of pedigree to those tested *Yr* genes, [ab]molecular marker detection and pedigree, [bc]gene postulation and molecular marker detection

across testing sites and years (Supplementary Table 2).

Detection of *Yr* resistance genes using molecular markers

The outcomes of molecular marker tests to predict the presence of *Yr9, Yr17, Yr18, Yr26, Yr29, Yr36, Yr44* and *Yr62* in the tested entries are provided in Supplementary Table 2. At least two molecular markers were used to identify each gene in the tested genotypes and the *Yr* gene (s) was considered to be present if both markers predicted its presence.

Yr9

Primer pairs H20 (Liu et al. 2008) and P6M12P (Mago et al. 2005) were selected to identify *Yr9*. Primer H20 F/R produced a 1598 bp diagnostic fragment (Fig. 1); primer P6M12-P F/R produced diagnostic fragments of 250 and 350 bp. Five bread wheat breeding lines and none cultivar had the *Yr9* marker.

Yr17

Resistance genes *Yr17/Lr37/Sr38* (a block of yellow, leaf and stem rust resistance genes) are located within a segment of *Ae, ventricosa* chromosome 6N that translocated to wheat chromosome 2AS (Tanguy et al. 2005). Primers URIC and LN2 amplify fragments of (+) 285 bp (from the N genome) indicating the presence of the resistance genes while (−) 275 bp (A genome) indicate their absence. Digestion of the PCR products with restriction enzyme Dpn11 facilitates differentiation between these two bands. Primer SC-385 amplifies a 385 bp fragment. Twenty-one entries tested positive for *Yr17,* including cvs HOGGANA and MERARO in Supplementary Table 2.

Yr18

A block of genes *Yr18/Lr34/Pm38* confers APR to yellow rust, leaf rust and powdery mildew. Krattinger et al. (2009) developed two primer pairs for detecting the presence (+ *Yr18*) and absence (− *Yr18*) of this block. The first multiplex reaction was developed based on primer combinations L34DINT9F/L34LUSR and csLV34 F/R, which results in amplification of either two bands (517 bp and 150 bp) which indicate the presence of *Yr18,* or one band (229 bp) which suggests the absence of *Yr18*. Of the 100 tested entries, 27 carried *Yr18*.

Yr26

Two SNP primers, WRS303 and WRS467 developed by Wu et al. (2018), were applied to detect *Yr26*. Ten breeding lines (ETBW8870, ETBW8815, ETBW8917, ETBW8777, ETBW8995, ETBW9019, ETBW9026, ETBW9015, ETBW8303 and ETBW8260) were found to carry *Yr26* (Fig. 2). Among the entries carrying *Yr26*, three (ETBW8917, ETBW9015 and ETBW8260) had all stage resistance, either the presence of noble genes or undetected gene in this study probably improved resistance of the selected entries.

Yr29

The STS marker Bac17R and the SSR marker Wmc44 (both suggested by Rosewarne et al. 2006) were used to detect this resistance gene. Primer set Bac17R amplifies a 1700 bp diagnostic fragment and primer set Wmc44 amplifies ~ a 260 bp diagnostic fragment.

Twenty-two entries had the *Yr29* associated marker polymorphisms. The seedling and adult plant resistance responses of the latter lines are shown in Table 2.

Yr36

Two gene-specific primer sets to detect the locus were developed by Fu et al. (2009). Primer set Yr36Ela amplified a 911 bp fragment and primer set Yr36 START amplified 871 or 537 bp fragments. Twelve entries were found to have *Yr36.*

Yr44

Two markers for *Yr44* were developed by Sui et al. (2009). Primer Pwb5/pWNR amplifies a 380 bp diagnostic product whereas wgp100 amplifies a 820 bp fragment. Thirty entries tested positive for *Yr44*. Among the lines with the gene, ETBW8816, ETBW8800, ETBW8917 and ETBW8260 were resistant to all races, whereas 26 showed resistance to one

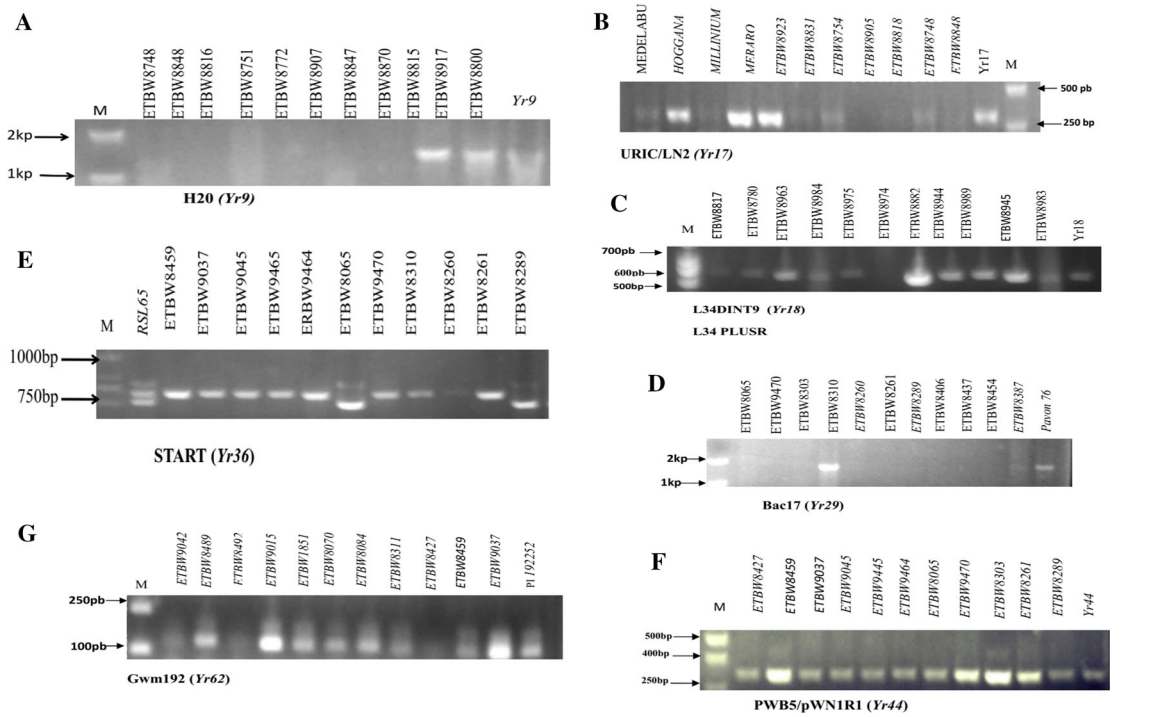

Fig. 1 Electrophoregrams produced with the use of different primers: The marker diagnostic product was confirmed using, well-established different stocks and *Yr* gene carrier cultivars **a** identification of *Yr9*, AVS/6**Yr9* is the NIL known to carry *Yr9*. **b** identification of *Yr17*, AVS/6**Yr17* is the NIL known to carry the *Yr17* gene. **c** identification of *Yr18* AvSYr18NIL is the known carry *Yr18*. **d** identification of *Yr29*, Pavon 76 known to carry *Yr29*, E, identification of *Yr36,* RSL65 know to carry *Yr36*, **f** identification *Yr44,* AvS/Zak (1-1-35-line1) is known to carry *Yr44,* and **g** identification of *Yr62,* PI 192252 know to carry *Yr62* gene. Note, M: bands in the above Fig. 1, 1598, 285, 517, 1700, 871, 380 and 223 bp DNA ladder-II (Generay Biotech (Shanghai)

or more races, indicating that these entries might also carry other effective resistance genes.

Yr62

Two SSR markers were mapped close to *Yr62* by Lu et al. (2014). These markers (Gwm192 and Gwm2511) amplified 222 bp and 133 bp diagnostic bands in the present material, respectively. Fifty-one entries were identified as likely carrying *Yr62*.

Discussion

The wide deployment and cultivation of bread wheat cultivars with *Yr9* led to serious stripe rust epidemics in many countries, including Ethiopia, when the gene became ineffective (Chen et al. 2014; Wellings 2011). Hence, it is of paramount importance to identify and develop breeding lines with effective resistance to the predominant and emerging races that threaten wheat production. To detect effective stripe resistance genes in wheat germplasm, combinations of *Pst* races with different virulence spectra should be employed in breeding material (Walker 1965). In this study, 100 entries were evaluated using a predominant *Pst* race from Ethiopia and six races representing different race categories from China. The disease phenotype data were combined with DNA marker data to postulate likely *Yr* genes for which dependable markers are available. The entries were more susceptible to Chinese races than to the Ethiopian race. We identified 14 breeding lines and two cultivars that were resistant to all races. Wan et al. (2017) also identified several genotypes resistant at the seedling stage among the tested material, using two additional *Pst* races from Ethiopia and three from the United States.

Molecular markers are helpful to identify resistance genes and speed up selection, if such markers are available (Chen 2013). In the present study, we used

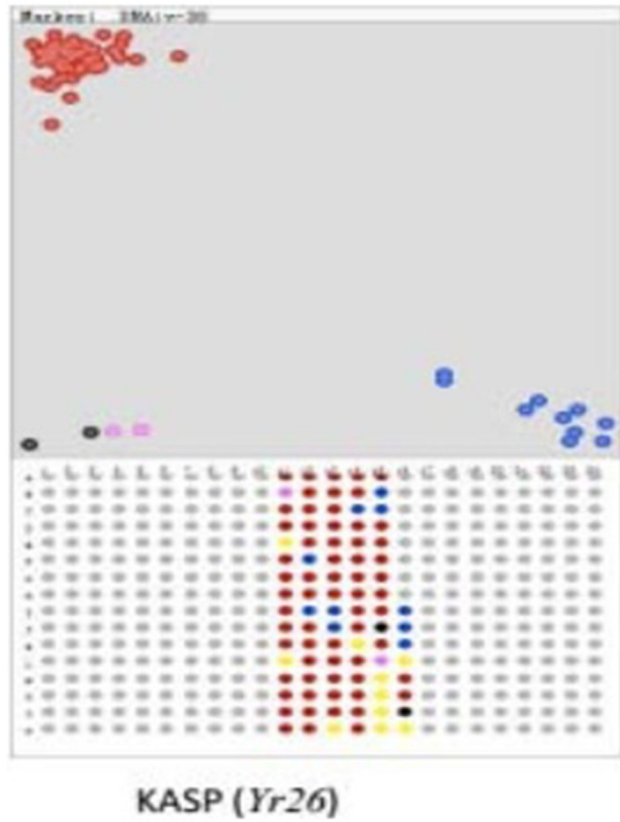

Fig. 2 **a** identification of *Yr26* resistance gene using SNP markers, genotyping data plotted using *Kluster* caller software. Genotyped samples marked red indicated absence of *Yr26* in the tested entries for the allele reported with *HEX*, those marked blue indicated that the presence of *Yr26* in the tested entries for the *FAM* allele

DNA markers to predict the presence of *Yr9, Yr17, Yr18, Yr26, Yr29, Yr36, Yr44* and *Yr62*, all of which were detected with various frequencies among the tested entries. When molecular markers were applied to identify the *Yr5, Yr15, Yr10* and *Yr8* resistance genes, indicative DNA fragments were observed only among positive controls, indicating that none of the entries carries these genes. Sixteen entries were resistant both at the seedling and adult-plant stages (ETBW8905, ETBW8800, ETBW8917, ETBW8823, ETBW8827, ETBW8583, ETBW8705, ETBW8486, ETBW8491, ETBW9015, ETBW9470, ETBW8260, ETBW8437 and ETBW8387, DANDA'A and HULLUKA) suggesting that these entries might carry either a novel resistance gene(s) or an effective combination of resistance genes. Similar to our study, Zheng et al. (2017) obtained multiple gene combinations among *Yr* resistance genes in Chinese wheat materials that were effective in the field. Chen (2013) suggested that combinations of all stage resistance genes such as *Yr5* or *Yr15* and HTAP resistance genes such as *Yr18, Yr29, Yr36, Yr39, Yr52, Yr59* and *Yr62* should be incorporated in breeding material to develop wheat cultivars with strong and durable resistance.

Yr9 was identified in five entries using both rye chromosome specific and STS markers with lines ETBW8815 and ETBW8917 being resistant to all of the tested *Pst* races, indicating that these entries probably possess another resistance gene(s) or effective gene combinations. These results are consistent with other recent studies (Wu et al. 2016; Zeng et al. 2014).

Molecular marker detection indicated that 21% of the tested entries carry *Yr17*. Zeng et al. (2014) reported that 45 of 494 Chinese wheat cultivars had *Yr17*, while Wu et al. (2016) identified *Yr17* in 10.3% of the Chinese wheat cultivars that they studied. Using gene specific markers, L34DINT9F and L34PLUSR, we determined that 27% of Ethiopian bread wheat genotypes carry *Yr18*. Yang et al. (2008) identified *Yr18* in 89.6% of 231 Chinese wheat cultivars and 6.1% of 422 landraces. *Yr26* was present in 10% of the tested entries of our study (markers WRS303 and WRS467), where as Zeng et al. (2014) reported that 15

(27.27%) of the 494 cultivars in their study had *Yr26* (detected with SSR marker WE173).

Using STS markers we identified 22 entries with *Yr29*. Twelve entries had *Yr36* (marker *Yr36* START). *Yr36* contain a kinase and a putative START lipid-binding domain and confers broad resistance to stripe rust at relatively high temperature (Fu et al. 2009). Zheng et al. (2017) also reported that few of the 672 wheat accessions tested by them had *Yr36*. In our study, *Yr44* was found in 30% of the entries using the STS marker pWB5/pWN1R. *Yr44* was first discovered in the spring wheat cv. Zak; it is located on chromosome 2B and confers race-specific or all stage resistance (Sui et al. 2009). Using SSR markers gwm192 and gwm25, we identified 51 entries with *Yr62* among 100 tested cultivars. *Yr62* was first identified in the spring wheat germplasm PI192252 and provides adult plant stripe rust resistance (Lu et al. 2014).

Pedigree analysis on 79 wheat lines showed that 51 lines had *Yr9* in their pedigree but only three lines were confirmed with molecular marker to carry of *Yr9*. Badebo et al. (1990) also identified 67% of tested 42 commercial wheat contained *Yr9*. Pedigree analysis of eight lines suggested the presence of *Yr17*; molecular markers confirmed only three. Another eight lines gives clue carried *Yr26* confirmed by molecular detection was one. Nine breeding lines possibly had *Lr67/Yr46*. These are slow-rusting resistance genes for both leaf and stripe rusts, originally identified in cv. 'Pastor' by Sybil et al. (2011).

The information obtained on the resistance profiles if various stocks tested here will contribute towards diversification and knowledge-based use of effective resistance genes in the Chinese and Ethiopian wheat breeding programs, and will be useful in attempts to develop cultivars with durable or long lasting resistance.

Acknowledgements We thank the Ethiopian national wheat breeding program based at Kulumsa, Ethiopian Institute of Agricultural Research for providing the commercial and elite breeding lines. The authors are grateful to Prof. R. A. McIntosh Plant Breeding Institute, University of Sydney for valuable advice on our research. This study was supported by the National Key Research and Development Program of China (2018YFD0200405), the National Key R&D Program of China (2018YFD02004), the Nature Science Foundation of China (31871918), and the 111 project from the Ministry of Education of China (B07049).

References

Abeyo B, Hodson D, Hundie B, Woldeab G, Girma B, Badebo A, Alemayehu Y, Jobe, T, Atilaw A, Bishaw Z, Eticha F, Gelacha S, Tadesse Z, Aliye S, Abdalla O, Fikre A, Ahmed S, Silim S (2014) Controlling wheat rusts and ensuring food security through development of resistant varieties In: Proceedings of the second international wheat stripe rust symposium. Izmir, Turkey

Badebo A (2002) Breeding bread wheat with multiple disease resistance and high yield for the Ethiopia highlands: broadening the genetic basis of yellow rust and tan spot resistance. PhD thesis. Cuvillier Verlage Goettingen, Germany

Badebo A, Stubbs RW, van Ginkel M, Gebeyehu G (1990) Identification of resistance genes to *Puccinia striiformis* in seedling of Ethiopia and CIMMY bread varieties. Neth J Plant Pathol 96:199–210

Badebo A, Andarge A, Girma B, Payne T (2001) Double sources of resistance to *Puccina striiformis* and *P. graminis* f. sp. *tritici* in CIMMYT bread wheat lines. In: Proceedings of the 9th Biannual conference, 22–23 June 1999, Addis Ababa Ethiopia. Crop Science Society of Ethiopia, Addis Ababa, Ethiopia

Bansal M, Kaur S, Dhaliwal HS, Bains NS, Barina HS, Chhuneja P, Bansal UK (2016) Mapping of *Aegilops umbellulata* derived leaf rust and stripe rust resistance loci in wheat. Plant Pathol. https://doi.org/10.1111/ppa.12549

Chen XM (2013) High-temperature adult- plant resistance, key for sustainable control of stripe rust. Amer J Plant Sci 04:608–627

Chen XM, Soria MA, Yan GP, Sun J, Dubovsky J (2003) Development of sequence tagged site and cleaved amplified polymorphic sequence markers for wheat stripe rust resistance gene *Yr5*. Crop Sci 43:2058–2064

Chen WQ, Wellings C, Chen XM, Kang ZS, Liu TG (2014) Wheat stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici*. Mol Plant Pathol 15:433–446

Dawit W, Flath K, Weber WE, Schumann E, Röder MS, Chen XM (2012) Postulation and mapping of seedling stripe rust resistance genes in Ethiopia bread wheat cultivars. J Plant Pathol 94:43–409

Flor HH (1971) Current status of the gene-for-gene concept. Annu Rev Phytopathol 9:275–296

Fu D, Uauy C, Distelfeld A, Belchl A, Epstein L, Chen X, Sela H, Fahima T, Dubcovsky J (2009) A kinase START gene confers temperature-dependent resistance to wheat stripe rust. Science 323:1357–1360

Gerechter-Amitai ZK, van SifhouCH GramaA, Kleitman F (1989) *Yr15*: a new gene for resistance to *Puccinia striiformis* in *Triticcum dicoccoides* sel. G-25. Euphytica 43:187–190

Helguera L, Khan IA, Kolmer J, Lijavetzky D, Zhong-qi L, Dubcosky J (2003) PCR assays for *Yr37-Yr17-Sr-38* cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines. Crop Sci 43:1839–1847

Heyns I, Pretorius Z, Marais F (2011) Derivation and characterization of recombinants of the *Lr54/Yr37* translocation in common wheat. Open Plant Sci J 5:1–8

Hovmøller MS (2007) Sources of seedling and adult plant resistance to *Puccinia striiformis* f. sp. *tritici* in European wheat. Plant Breed 123:225–233

Jia JQ, Li GR, Liu C, Lei MP, Yang ZJ (2011) Characterization of wheat yellow rust resistance gene *Yr17* using EST-SSR and rice syntenic region. Cereal Res. Commun 39:88–99

Krattinger SG, Lagudah ES, Spielmeyer W, Singh RP, Huerta Espino J, McFadden H, Bossolini E, Selter LL, Keller B (2009) A putative ABC transporter confer durable resistance to multiple fungal pathogens in wheat. Science 323:1360

Kuraparthy V, Sood S, See DR, Gill BS (2009) Development of a PCR assay and marker-assisted transfer of leaf rust and stripe rust resistance genes *Lr57* and *Yr40* into hard red winter wheat. Crop Sci 49:120–126

Line RF, Chen X (1995) Successes in breeding for and managing durable resistance to wheat rusts. Plant Dis 79:1254–1255

Line RF, Qayoum A (1992) Virulence, aggressiveness, evolution and distribution of races of *Puccinia striiformis* (the cause of stripe rust of wheat) in North America, 1968–1987. U.S. Department of Agriculture Technical Bulletin No. 1788

Liu C, Yang ZJ, Li GR, Zeng ZX, Zhang Y, Zhou JP, Liu ZH, Ren ZL (2008) Isolation of a new repetitive DNA sequence from *Secale africanum* enables targeting of *Secale* chromatin in wheat back ground. Euphytica 159:249–258

Liu J, Chang Z, Zhang X, Yang Z, Li X, Jia JQ, Zhan H, Guo H, Wang J (2013) Putative *Thinopyrum intermedium*-derived stripe rust resistance gene *Yr50* maps on wheat chromosome arm 4BL. Theor Appl Gene 126:265–274

Liu W, Frick M, Huel R, Nykiforuk CL, Wang X, Gaudet DA, Eudes F, Conner RL, Kuzyk A, Chen Q, Kang Z, Laroche A (2014) Stripe rust resistance gene *Yr10* encodes an evolutionary-conserved and unique CC–NBS–LRR sequence in wheat. Mol Plant 7:1740–1755

Lowe I, Jankuloski L, Chao S, Chen X, See D, Dubcovsky J (2011) Mapping and validation of QTL which confer partial resistance to broadly virulence post 2000 North American race of stripe rust in hexaploid wheat. Theor Appl Genet 123:143–157

Lu Y, Wang M, Chen X, See D, Chao S, Jing J (2014) Mapping of *Yr62* and small effect for high temperature adult plant resistance to stripe rust in spring wheat PI 192252. Theor Appl Genet 127:1449–1459

Ma JX, Zhou RZ, Dong YS, Wang LF (2001) Molecular mapping and detection of the yellow rust resistance gene *Yr26* in wheat transferred from *Triticum turgidum* L. using microsatellite markers. Euphytica 120:2019–2226

Macer RCF (1975) Plant pathology in a changing world. Trans Br Mycol Soc 65:351–374

Mago R, Miah H, Lawrence GJ, Wellings CR, Spielmeyer W, Bariana HS, McIntosh RA, Pryor AJ, Ellis JG (2005) High resolution mapping and mutation analysis separate the rust resistance genes *Sr31*, *Lr26* and *Yr9* on the short arm of rye chromosome 1. Theor Appl Genet 112:41–50

Marais GF, Marais AS, McCallum B, Pretorius ZA (2009) Transfer of leaf rust and stripe rust resistance genes *Lr62* and *Yr42* from *Aegilops neglecta* to common wheat. Crop Sci 49:871–879

Marais GF, Badenhorst PE, Eksteen A, Pretorius ZA (2010) Reduction of *Aegilops sharonensis* chromatin associated with resistance genes *Lr56* and *Yr38* in wheat. Euphytica 171:15–22

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC (2016) Catalogue of gene symbols for wheat. http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbolClassList.jsp. Accessed Dec 2018

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC (2017) Catalogue of gene symbols for wheat. http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbolClassList.jsp. Accessed Dec 2018

Murphy LR, Santra D, Kidwell K, Yan G, Chen X, Campbell KG (2009) Linkage maps of wheat stripe rust resistance genes *Yr5* and *Yr15* for use in marker-assisted selection. Crop Sci 49:1786–1790

Niu YC, Li SM, Li WF, Wu LR, Xu SC (2004) Molecular markers assisted selection for the stripe rust (*Puccinia striiformis tritici*) resistance genes*Yr8* and *Yr10* in wheat breeding lines. In: Plant protection towards the 21st century-proceeding of the XVth international plant protection congress, Beijing, China

Riley R, Chapman V, Johnson R (1968) The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synapsis. Genet Res 12:713–715

Rosewarne GM, Singh RP, Huerta-Espino J, William HM, Bouchet S, Cloutier S, McFadden H, Lagudah ES (2006) Leaf necrosis, molecular markers and beta1-proteasome subunits associated with the slow rusting resistance genes *Lr46/Yr29*. Theor Appl Genet 112:500–508

Sharma S, Louwers JM, Karki CB, Snijders CHA (1995) Postulation of resistance genes to yellow rust in wild emmer wheat derivatives and advanced wheat lines from Nepal. Euphytica 81:271–277

Singh RP, Nelson JC, Sorrells ME (2000) Mapping *Yr28* and other genes for resistance to stripe rust in wheat. Crop Sci 40:1148–1155

Smith PH, Hadfiled J, Hart NJ, Koebner RMD, Boyd LA (2007) STS markers for the wheat yellow rust resistance gene *Yr5* suggest a NBS-LRR-type resistance gene cluster. Genome 50:259–265

Song WN, Henry RJ (1994) Polymorphisms in *a*-amy1 gene of wild and cultivated barley revealed by the polymerase chain reaction. Theor Appl Genet 89:509–513

Sui XX, Wang MN, Chen XM (2009) Molecular mapping of a stripe rust resistance gene in spring wheat cultivar Zak. Phytopathology 99:1209–1215

Sybil A, Herrea F, Evans S, Lagudah, Julio HE, Mattew J, Hayden HS, Davinder S, Singh RP (2011) New slow-rusting leaf rust and stripe rust resistance genes *Lr67* and *Yr46* in wheat are pleiotropic or closely linked. Theor Appl Genet 122:239–249

Tanguy AM, Coriton O, Abélard P, Dedryver F, Jahier J (2005) Structure of the *Aegilops ventricosa* chromosome 6Nv, the donor of wheat genes *Yr17, Lr37, Sr38*, and Cre5. Genome 48:541–546

Walker JC (1965) Use of environmental factors in screening for disease resistance. Annu Rev Phytopathol 3:197–208

Wan AM, Chen XM (2014) Virulence characterization of *Puccinia striiformis* f. sp. *tritici* using a new of *Yr* single gene line differentials in the United States in 2010. Plant Dis 98:1534–1542

Wan A, Kebede T, Habtermariam Z, Bekele H, Pumphrey MO, Chen XM (2017) Virulence characterization of wheat stripe rust fungus *Puccinia striiformis* f. sp. *tritici* in Ethiopia and evaluation of wheat germplasm for resistance to race of the pathogen from Ethiopia and the United States. Plant Dis 101:73–80

Wang MN, Chen XM (2017) Stripe rust resistance. In: Chen XM, Kang ZS (eds) Stripe rust. Springer, Dordrecht, pp 353–558

Wellings CR (2011) Global status of stripe rust: a review of historical and current threats. Euphytica 179:129–141

Wu JH, Wang QL, Chen XM, Wang MJ, Mu JM, Lv XN, Huang LL, Han DJ, Kang ZS (2016) Stripe rust resistance in wheat breeding lines developed for central Shaanxi, an over-wintering region for *Puccinia striiformis* f. sp. *tritici* in China. Can J Plant Pathol 38:317–324

Wu JH, Zeng QD, Wang QL, Liu SJ, Yu SZ, Mu JM, Huang S, Sela HN, Distefeld AF, Huang LL, Han DJ, Kang ZS (2018) SNP-based pool genotyping and haplotype analysis accelerate fine-mapping of the wheat genomic region containing stripe rust resistance gene *Yr26*. Theor Appl Genet 131:1481–1496

Xia XC, Li ZF, Li GQ, Singh RP (2007) Stripe rust resistance in Chinese bread wheat cultivars and lines. In: Buck HT, Nisi JF, Salomon N (eds) Wheat production in stress environment. Springer, Amsterdam, pp 77–82

Xu LS, Wang MN, Cheng P, Kang ZS, Hulbert SH, Chen XM (2013) Molecular mapping of *Yr53*, a new gene for stripe rust resistance in durum wheat accession PI480148 and its transfer to common wheat. Theor Appl Genet 126:523–533

Yang WX, Yang FP, Liang D, He Z, Shang XW, Xia XC (2008) Molecular characterization of slow-rusting genes *Lr34/Yr18* in Chinese wheat cultivars. Acta Agron Sin 34:1109–1113

Zeng QD, Han DJ, Wang QL, Yuan FP, Wu JH, Zhang L, Wang XJ, Huang LL, Chen XM, Kang ZS (2014) Stripe rust resistance and genes in Chinese wheat cultivars and breeding lines. Euphytica 196:271–284

Zhang P, McIntosh RA, Hoxha S, Dong C (2009) Wheat stripe rust resistance genes *Yr5* and *Yr7* are allelic. Theor Appl Genet 120:25–29

Zheng SG, Li YF, Lu L, Liu Z, Zhang C, Ao DH, Li LR, Zhang CY, Liu R, Luo CP, WuY Zhang L (2017) Evaluating the contribution of *Yr* genes to stripe rust resistance breeding through marker-assisted detection in wheat. Euphytica 213:50

Zhou XL, Han DJ, Chen XM, Gou HL, Guo SJ, Rong L, Wang QL, Huang LL, Kang ZS (2014) Characterization and molecular mapping of stripe rust resistance gene *Yr61* in winter wheat cultivar Pindong 34. Theor Appl Genet 127:2349–2358