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

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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*

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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

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. kotschy* (Heyns et al. 2011), *Yr38* from *Ae. sharonensis* (Marais et al. 2010), *Yr40* from *Ae. geniculata* (Kuraparthi 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*

racess 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 1B-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 ‘AvSYr18NIL’, ‘92R137’(Yr26), ‘AvSYr29NIL’, ‘RSL65(Yr36)’ and ‘PI 192252(Yr62)’ were included in comparative response tests 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-HCl, pH 8.3), 2.0 mmol MgCl₂, 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: <i>Yr1</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr44</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr6</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr17</i> , <i>Yr24</i> , <i>Yr27</i> , <i>Yr32</i> , <i>Yr43</i> , <i>YrSP</i> , <i>YrTr1</i> , <i>Yr76</i>
CYR29	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr17</i> , <i>Yr24</i> , <i>Yr27</i> , <i>Yr32</i> , <i>YrSP</i> , <i>YrTr1</i> , <i>Yr76</i>
CYR31	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr17</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr9</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr27</i> , <i>Yr32</i> , <i>YrSP</i> , <i>YrTr1</i> , <i>Yr76</i>
CYR32	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrSP</i> , <i>YrExp2</i> , <i>Yr76</i> A: <i>Yr5</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr27Yr32</i> , <i>YrTr1</i>
CYR33	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr10</i> , <i>Yr24</i> , <i>Yr32</i> , <i>Yr44</i> , <i>YrSP</i> , <i>YrExp2</i> , <i>Yr76</i> A: <i>Yr5</i> , <i>Yr6</i> , <i>Yr17</i> , <i>Yr27</i> , <i>Yr43</i> , <i>YrTr1</i>
V26	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr9</i> , <i>Yr10</i> , <i>Yr17</i> , <i>Yr24</i> , <i>Yr27</i> , <i>Yr32</i> , <i>Yr44</i> , <i>YrSP</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr8</i> , <i>Yr15</i> , <i>Yr43</i> , <i>YrTr1</i> , <i>Yr76</i>
EK3-12	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr27</i> , <i>Yr43</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr8</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr32</i> , <i>Yr44</i> , <i>YrSP</i> , <i>Yr1Tr</i> , <i>Yr76</i>

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 breeding 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
<i>Yr5</i>	STS-7/8	STS/CAPS	0.3	TACAATTACCTAGAGT GCAAGTTTCTCCCTATT	46	439	472	Murphy et al. (2009)
<i>Yr5</i>	STS-9/10	STS/CAPS	0.7	AAAGAATACTTTAATGAA AAAGAATACTTTAATGAA	42	439		Zhang et al. (2009)
<i>Yr5</i>	S19M93	STS	0.54	TAATTGGGACCGAGAGCG TAATTGGGACCGAGAGCG	55	100	62/ 275	Smith et al. (2007)
<i>Yr5</i>	Barc349	SSR	0.4	CGA ATA GCC GCT GCA CAA CGA ATA GCC GCT GCA CAA	46	105		Murphy et al. (2009)
<i>Yr8</i>	SC-OPD11	SCAR		AGCGCATTGGGAGCTCTATGGTG AGCGCATTGGGAGCTCTATGGTG	57	1265		Niu et al. (2004)
<i>Yr9</i>	H2O-F H2O-R	Rye genome-specific		GTACTAGTATCCAGAGGTCACAAG CAGACAAACAGAGTACGGGC	56	1598		Liu et al. (2008)
<i>Yr9</i>	P6M12-P-F P6M12-P-R	STS	0.35	GTACTAGTATCCAGAGGTCACAAG CAGACAAACAGAGTACGGGC	56	250/ 350		Mago et al. (2005)
<i>Yr10</i>	E51100	SCAR		TCAAGGAGGTCAGTGACAG TCAGGGAGGTGTAGCCTAAT	56	1085		Liu et al. (2014)
<i>Yr10</i>	Yr10F	Gene specific		TCAAAGACATCAAGAGCCG	51	543		Liu et al. (2014)
<i>Yr15</i>	barc8	SSR	4.2	GCGGGAATCATGCATAGGA				
<i>Yr15</i>	gwm413	SSR		GCGGGGCGAAACATACACATAAAAACA	55	96	98	Murphy et al. (2009)
<i>Yr17</i>	URIC/LN2-F URIC/LN2-R	<i>Ae. ventricosa</i> Chromosome-specific	3.5	TGCTTGCTAGATTGCTTGGG GGTCGCCCTGGCTTGACCT	64	285	275	Helguera et al. (2003)
<i>Yr17</i>	SC-385-F SC-385-R	SCAR	3.4	TGCAGCTACAGCAGTATGTACACAAA CTGAATACAAAACAGCAAAACCAG	50	385		Jia et al. (2011)
<i>Yr18</i>	csLV34-F csLV34-R	STS	0.4	ACAGAAAAGTGATCATTTCCATC TTGATGAAACCAGTTTTTTTCTA	51	150	229	Krattinger et al. (2009)
<i>Yr18</i>	L34DINT9F- F L34PLUSR- R	Gene specific		GCCATTTAACATAATCATGATGGA TTGATGAAACCAGTTTTTTTCTA	51	517		Krattinger et al. (2009)
<i>Yr26</i>	WRS303-F WRS303-R	KASP (<i>Haynaldia villosa</i> on chromosome 1B)		GCCATTTAACATAATCATGATGGA GCTGTTAATCCTACGCCACT GCTGTTAATCCTACGCCACC	57.03			Wu et al. (2018)

Table 2 continued

Gene	Marker	Type	Distance	Sequence	Annealing temp. (°C)	(+ bp)	(– bp)	References
<i>Yr26</i>	WRS467-F	KASP (<i>Haynaldia villosa</i> on chromosome 1B)		TTTGTAACAACATCATCAGCTATTACA	57.69			Wu et al. (2018)
	WRS467-R			TTTGTAACAACATCATCAGCTATTACC				
<i>Yr29</i>	bac17R-F	STS	2.1/4.2	CCCATGCTGACATGGCCACAT	55	1700	500	Rosewarne et al. (2006)
	bac17R-R			CTCTGCTCTTTAGTAGTTGCC				
<i>Yr29</i>	wmc44-F	SSR	3.6/109	GGTCTTCTGGGCTTTTGATCCTG	57	260	~260	Rosewarne et al. (2006)
	wmc44-R			TGTTGCTAGGGACCCCGTAGTGG				
<i>Yr36</i>	Yr36E1a-F	Gene-specific		AAGGCAAAAGGCAAAAGTGG	57	911		Fu et al. (2009)
	Yr36E1a-R			TGATCTTTACCAAGCATTCG				
<i>Yr36</i>	Yr36START-F	Gene-specific		AAGGCAAAAGGCAAAAGTGG	52	871/537		Fu et al. (2009)
	Yr36START-R			TGATCTTTACCAAGCATTCG				
<i>Yr44</i>	pWB5/	STS	9.4	GGTGCAATTGAGTTTGGAGT	49	380		Sui et al. (2009)
	PWN1r1-F							
	pWB5/			GGTGTGACTGGAGAATCCG	45	820		Sui et al. (2009)
	PWN1r1-R							
<i>Yr44</i>	wgp100-F	RGAP	3.9	GCATTGGAACAAGGTGAA				
	wgp100-R			GGTGGGGTTGGGAAGACAACG	51	222		Lu et al. (2014)
<i>Yr62</i>	gwm192-F	SSR	2	GGTTTCTTTTCAGATTGCGC				
	gwm192-R			CGTTGTCTAATCTTGCCCTTGC	51	133		Lu et al. (2014)
<i>Yr62</i>	gwm251-F	SSR	3.3	CAACTGGTTGCTACACAAGCA				
	gwm251-R			GGGATGTCTGTTCCTCTTAG	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																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
	IT	 

Table 3 continued

Pedigree	Seedling IT				Adult plant response						RT	Yr gene				
	CCYR23				CYR31	CYR32	CYR33	CYR34	EK3-12	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	3	3	2	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/NEE#10/8/OPATA	2	2	2	3	3	2	2	3	2	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	3	3	1	0	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	3	3	0	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	2	3	7	2	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	9	3	3	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	9	7	7	2	2	2	5	3	5	APR	Yr29, Yr46 ^b , Yr17 ^b
WORRAKATTA/2*PASTOR//DANPHE #1	2	3	2	3	3	3	3	3	2	2	1	5	2	5	ASR	None ^a , Yr46 ^b
KRICHAUFF/2*PASTOR//CHONTE	2	5	5	5	8	9	4	4	3	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	9	9	6	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

^aMolecular marker detection, ^bpresence 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.

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