Theor Appl Genet (2012) 125:847–857
DOI 10.1007/s00122-012-1877-8

ORIGINAL PAPER

Characterization and molecular mapping of *Yr52* for high-temperature adult-plant resistance to stripe rust in spring wheat germplasm PI 183527

R. S. Ren · M. N. Wang · X. M. Chen · Z. J. Zhang

Received: 9 January 2012 / Accepted: 19 April 2012 / Published online: 5 May 2012

Abstract Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most destructive diseases of wheat worldwide. Resistance is the best approach to control the disease. High-temperature adult-plant (HTAP) stripe rust resistance has proven to be race non-specific and durable. However, genes conferring high-levels of HTAP resistance are limited in number and new genes are urgently needed for breeding programs to develop cultivars with durable high-level resistance to stripe rust. Spring wheat germplasm PI 183527 showed a high-level of HTAP resistance against stripe rust in our germplasm evaluations over several years. To elucidate the genetic basis of resistance, we crossed PI 183527 and susceptible wheat line Avocet S. Adult plants of parents, F_1, F_2 and $F_{2:3}$ progeny were tested with selected races under the controlled greenhouse conditions and in fields under natural infection. PI 183527 has a single dominant gene conferring HTAP resistance. Resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) markers in combination with bulked segregant analysis (BSA) were used to identify markers linked to the resistance gene. A linkage map consisting of 4 RGAP and 7 SSR markers was constructed for the resistance gene using data from 175 F_2 plants and their derived $F_{2:3}$ lines. Amplification of nulli-tetrasomic, ditelosomic and deletion lines of Chinese Spring with three RGAP markers mapped the gene to the distal region (0.86–1.0) of chromosome 7BL. The molecular map spanned a genetic distance of 27.3 cM, and the resistance gene was narrowed to a 2.3-cM interval flanked by markers *Xbarc182* and *Xwgp5258*. The polymorphism rates of the flanking markers in 74 wheat lines were 74 and 30 %, respectively; and the two markers in combination could distinguish the alleles at the resistance locus in 82 % of tested genotypes. To determine the genetic relationship between this resistance gene and *Yr39*, a gene also on 7BL conferring HTAP resistance in Alpowa, a cross was made between PI 183527 and Alpowa. F_2 segregation indicated that the genes were 36.5 ± 6.75 cM apart. The gene in PI 183527 was therefore designed as *Yr52*. This new gene and flanking markers should be useful in developing wheat cultivars with high-level and possible durable resistance to stripe rust.

Communicated by T. Miedaner.

Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. USDA is an equal opportunity provider and employer.

R. S. Ren and M. N. Wang made equal contributions.

Electronic supplementary material The online version of this article (doi:10.1007/s00122-012-1877-8) contains supplementary material, which is available to authorized users.

R. S. Ren · Z. J. Zhang
Department of Plant Pathology, China Agricultural University, Beijing 100193, People's Republic of China

R. S. Ren · M. N. Wang · X. M. Chen (✉)
Department of Plant Pathology, Washington State University, Pullman, WA 99164-6430, USA
e-mail: xianming@wsu.edu

X. M. Chen
US Department of Agriculture-Agricultural Research Service (USDA-ARS), Wheat Genetics, Quality, Physiology and Disease Research Unit, Pullman, WA 99164-6430, USA

Introduction

Stripe (yellow) rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss. (*Pst*), is one of the most destructive

diseases of wheat worldwide (Stubbs 1985; Chen 2005; Wan et al. 2007; Wellings 2011). Growing resistant cultivars has proven to be the most effective, economical and environmentally friendly method for control of stripe rust (Line and Chen 1995; Line 2002; Chen 2005). Two major types of resistance to stripe rust have been identified and used in breeding programs: all-stage resistance (also called seedling resistance) and adult-plant resistance (APR) (Chen 2005). All-stage resistance can be detected at the seedling stage and is effective throughout the entire growth cycle. This type of resistance is usually race-specific and readily overcome by virulent races (Line 2002; Chen 2005; Chen et al. 2010). In contrast, APR expresses at adult-plant stage. APR is mostly high-temperature adult-plant (HTAP) resistance that gradually expresses as the plants grow older and the weather becomes warmer (Qayoum and Line 1985; Chen 2005). Generally, HTAP resistance is non-race specific, often quantitatively inherited and durable (Milus and Line 1986; Chen and Line 1995a, b; Line 2002; Chen 2005). However, the level of HTAP resistance is often incomplete and is affected by plant growth stage, temperature, humidity, and the inoculum load. The combination of the two resistance types can provide high level and durable resistance to stripe rust (Chen 2005).

So far, 49 officially named and dozens of temporally named genes have been reported for resistance to wheat stripe rust (Chen 2005; Cheng 2008; McIntosh et al. 2008, 2009; Li et al. 2010). Most of these genes are all-stage resistance genes, and none is effective against all current US and world populations of *Pst*. More than 20 HTAP resistance genes (e.g. *Yr36*, *Yr39*) or QTLs (e.g. *QYrex.wgp-6AS*, *QYrex.wgp-1BL*, *QYrex.wgp-5BL*, *QYrlo.wgp-2BS*, *QYrst.wgp-6BS*) were identified and incorporated into wheat cultivars in the US Pacific Northwest (PNW) (Line 2002; Lin and Chen 2007, 2009; Santra et al. 2008; Carter et al. 2009). Most wheat cultivars grown in the PNW have HTAP resistance, and this type of resistance has been effective for over 50 years (Qayoum and Line 1985; Line 2002; Chen 2005, 2007). However, HTAP resistance in the currently grown wheat cultivars has been derived from only a few sources (Line 2002; Chen 2005). Being affected by temperature and plant development stage, the resistance level varies greatly among cultivars, and the low level of HTAP resistance in some cultivars does not provide adequate control when temperatures are low and inoculum levels are high. For example, in 2010 and 2011, cool and wet weather conditions in the PNW were extremely favorable for stripe rust development, and highly susceptible varieties had more than 60 and 90 % yield losses, respectively, whereas cultivars with low to moderate levels of HTAP resistance had 10–40 % yield losses (Chen XM, unpublished data). Therefore, it is urgent to identify new genes conferring high levels of HTAP resistance.

PI 183527 is a spring wheat line originating from India. It was deposited in the USDA-ARS National Small Grains Collection (NSGC) in 1949 (http://www.ars-grin.gov/cgi-bin/npgs/acc/search.pl?accid=PI+183527). In our germplasm evaluation program, PI 183527 was susceptible in the seedling stage to all tested predominant *Pst* races in the US at low temperatures, but consistently had high levels of resistance at adult-plant stage at high temperatures and in field tests over several years (Wang et al. 2012). These greenhouse and field data indicate that PI 183527 has HTAP resistance. The objectives of this study were to confirm HTAP resistance in PI 183527 and to identify the gene or genes conferring resistance through genetic analysis and molecular mapping.

Materials and methods

Plant material

PI 183527, obtained from the USDA National Small Grains Collection in Aberdeen, ID, is an awnless hexaploid spring wheat (*Triticum aestivum* L.) genotype. It was susceptible in seedling tests under controlled greenhouse conditions to US races PST-17, PST-37, PST-43, PST-45, and PST-100 representing predominating races from the 1970s to 2007 and collectively covering all possible virulences identified thus far in the US *Pst* population, but resistant to natural populations of the pathogen in field tests at Pullman (eastern Washington) and Mount Vernon (western Washington) since 2004 (Wang et al. 2012). PI 183527 was crossed as male parent to Avocet S (AvS), an awned Australian spring wheat genotype susceptible to most races of the stripe rust pathogen in the US (Lin and Chen 2007). Spikes on F_1 plants were bagged prior to anthesis to prevent outcrossing. An F_2 population consisting of 175 plants, obtained from seeds from a single F_1 plant grown in the greenhouse, was grown in the greenhouse to produce the same number of $F_{2:3}$ lines, which were used for genetic analysis and molecular mapping.

Chinese Spring (CS), a complete set of CS nulli-tetrasomic lines, 7BL and 7BS ditelosomic lines, and 7BL deletion lines (Del7BL-1, Del7BL-3, Del7BL-5, Del7BL-6, Del7BL-7, Del7BL-9, Del7BL-10 and Del7BL-14) were used to determine the chromosomal and specific bin position of the resistance gene in PI 183527. Seventy-four wheat cultivars and breeding lines were used to evaluate the polymorphisms of the molecular markers flanking the resistance gene in PI 183527.

As the resistance gene in PI 183527 was found on chromosome 7B and *Yr39* conferring HTAP resistance in Alpowa, a spring wheat widely grown in the western US since its release in 1994, was previously reported also on

7B (Lin and Chen 2007), a cross was made between PI 183527 and Alpowa. The F_2 population of the cross was used to determine the genetic relationship between the HTAP resistance genes in the two cultivars.

Greenhouse tests

To determine the resistance type of PI 183527, 15 plants each of PI 183527 and AvS were tested with three *Pst* races, PST-100, PST-114 and PST-127 which have been predominant in the US since 2003 (Chen 2007; Chen et al. 2010; Wan and Chen 2012), in a four-way test: seedling and adult plants tested under high- and low-temperature profiles (Chen and Line 1995a). Inoculations were done at two-leaf seedling stage and at booting. The plants were dust-inoculated with a mixture of fresh urediniospores and talc at a 1:50 ratio and kept in a dew chamber at 10 °C for 24 h without light. The inoculated plants were moved to a growth chamber for growing with programed temperature profile for rust development. The low temperature profile was set as a diurnal temperature cycle gradually changing between 4 °C at 2:00 a.m. and 20 °C at 2:00 p.m. The high-temperature profile was set as a diurnal temperature cycle gradually changed between 10 °C at 2:00 a.m. and 30 °C at 2:00 p.m. (Chen and Line 1995a). Infection type (IT) data were recorded 18–22 days after inoculation using a 0–9 scale described by Line and Qayoum (1992).

To determine the inheritance of HTAP resistance in PI 183527, 175 F_2 plants, together with three F_1 plants and three plants of each parent were tested with race PST-127 under the high temperature profile in the greenhouse.

Field test

During the 2010 crop season, the $F_{2:3}$ lines derived from the 175 F_2 plants of AvS × PI 183527 and the parents were tested for stripe rust resistance at field locations near Pullman and Mount Vernon. The two locations are about 500 km apart and are subject to different *Pst* race compositions and climatic conditions. All 175 $F_{2:3}$ lines were planted at Pullman and 138 were planted at Mount Vernon due to limited seed availability. Thirty seeds were evenly planted in a 0.5-m row in a randomized complete block design, with each line repeated three times at each location. Spreader rows of susceptible cultivar Lemhi (CI 011415) were planted every 10 rows to increase the uniformity of inoculum throughout the field. Planting dates were April 15 for Mount Vernon and April 25 for Pullman. Standard fertilizer and herbicide applications for our field research and local wheat cropping practice were used. No irrigation was used at either location because of high precipitation. Stripe rust infection types (IT) and disease severities (DS, percentage of diseased foliage) were recorded twice; on July 6 at heading and July 19 at flowering for Pullman, and on June 14 at booting and June 28 at flowering for Mount Vernon. To distinguish homozygous and heterozygous lines, a single IT and a single severity (visually estimated average percentage of leaf areas diseased) were recorded if plants in a row had uniform IT and DS; whereas variable ITs and DS values indicated heterozygosity.

During the 2011 crop season, the parents and F_1 and F_2 progeny of cross Alpowa/PI 183527 were tested in a field near Pullman. Prior to transplanting in the field, 179 F_2, 6 F_1, and 6 plants each of the parents at the first-leaf stage were vernalized at 4 °C for 1 month to synchronize plant growth because Alpowa is a facultative winter wheat. The vernalized plants were transplanted into the field with five plants per row of 1.0 m in length spaced 30 cm apart. The field was surrounded by susceptible cv. Lemhi as a rust spreader. The IT and severity on every plant were scored at heading and the milk stage.

DNA extraction, PCR amplification, electrophoresis and gel visualization

Genomic DNA was extracted from leaves of each F_2 plant and parents using the CTAB method as modified by Yan et al. (2003). After removing RNA with RNase and centrifugation, DNA was dissolved in 1 × Tris–EDTA (10 mM Tris–HCl and 1 mM EDTA, pH 8.0) buffer. DNA quality and concentrations were determined by electrophoresis (Maniatis et al. 1982) and spectrophotometry (NanoDrop ND-1000, Thermo scientific, Wilmington, DE, USA). Stock DNA solutions were diluted with sterilized dd H_2O to 30 ng/μL for use in PCR as templates.

The resistance gene analog polymorphism (RGAP) method (Chen et al. 1998; Shi et al. 2001) and simple sequence repeat (SSR) technique (Röder et al. 1998; Somers et al. 2004; Sourdille et al. 2005) were used to identify markers linked to the resistance gene. PCR was performed in a 15-μL solution comprising 1.2 μL (36 ng) template DNA, 3.0 μL Mg-free 5× PCR buffer, 0.12 μL Taq DNA polymerase solution (5 unit/μL), 3.0 μL 25 mM $MgCl_2$, 1.2 μL 2.5 mM of each dNTP, 1.0 μL (7.5 μM) of each primer solution (30 ng/μL) and 4.48 μL sterilized dd H_2O. The PCR reagents (buffer, $MgCl_2$, dNTP and Taq) were purchased from Promega Inc. (Madison, WI, USA) and the primers synthesized by Sigma-Aldrich Inc. (St. Louis, MO, USA). Amplification was performed in a GeneAmp PCR System 9700 programmed as 5 min at 94 °C for initial denaturation; 45 cycles each consisting of 1 min at 94 °C for denaturation, 1 min at either 45, 50, 55 or 60 °C [45 °C for resistance gene analog (RGA) primers, 50, 55 or 60 °C for SSR primers depending on the individual primers] for annealing, 2 min at 72 °C for extension; and finally a 7 min extension step at 72 °C. After

PCR amplification, 6 μL of formamide loading buffer [98 % formamide, 10 mM EDTA (pH 8.0), 0.5 % (W/V) xylene cyanol and 0.5 % (W/V) bromophenol blue] was added to each PCR product. After 4 min denaturation at 94 °C, 4 μL of the PCR product and loading buffer mixture for each sample was loaded for electrophoresis in a 5 % polyacrylamide gel. Gel staining and visualization were done as previously described (Chen et al. 1998).

Bulk segregant analysis

Based on the stripe rust reactions of $F_{2:3}$ lines, the corresponding F_2 individual plants were classified into three categories: homozygous resistant [RR, all plants resistant (IT 2-3)], heterozygous [Rr, most plants resistant (IT 2-3) and some susceptible (IT 7-8)] and homozygous susceptible [rr, all plants susceptible (IT 8-9)]. Resistant and susceptible bulks were constructed with equal amount of DNA from 15 RR and 15 rr F_2 plants, respectively. The DNA samples from PI 183527, AvS and bulks were used for screening primers. Twenty-seven RGA primers based on cereal resistance gene sequences were designed and synthesized by Sigma-Aldrich Inc. (St. Louis, MO, USA). Resistance gene analog (RGA) primers were randomly paired and screened on the parents and two bulks. Polymorphic bands specific to the resistant parent and resistant bulk were used to genotype the F_2 population consisting of 175 plants.

Chromosome localization of the resistance gene

To locate the resistance locus on a specific wheat chromosome, three linked RGAP markers were tested with a complete set of 21 CS nulli-tetrasomic lines and selected ditelosomic lines and deletion lines. To confirm the chromosomal location of the HTAP resistance gene indicated by RGA markers, an additional 15 SSR markers on chromosome 7BL were screened for polymorphism with genomic DNA from the parents and two bulks. Wheat SSR primers were synthesized according to sequences published in the GrainGenes database (http://www.wheat.pw.usda.gov). Polymorphic SSR markers were used to genotype the F_2 population. Sequences of relevant RGA primers and SSR primers are shown in Table 1. RGAP and SSR markers linked to the resistance locus were used to construct a linkage map.

Data analysis and linkage map construction

Phenotypic correlation coefficients between DS and IT at each site and between sites were determined using the $F_{2:3}$ data. Segregations of markers and resistance were tested for goodness-of-fit to the expected ratio using the Chi-squared test. Both analyses were done using the Excel data analysis tool and formulation of Microsoft Office 2007 (Microsoft, Redmond, WA, USA). A genetic linkage map of RGAP markers, SSR markers and the resistance locus

Table 1 Resistance gene analog (RGA) and simple sequence (SSR) primers used to identify markers for the stripe rust resistance gene in PI 183527

Primer[a]	Sequence (5′–3′)	Tm (°C)[b]	References
rga51	GGAGGCTTAGGGAAG	45	This study
rga52	GGCAAGACCACATTA	45	This study
rga56	GGAAAGACAACTTTT	45	This study
rga58	CCATATGTCATCAATGAG	45	This study
rga71	AGGTAGGTCATAGTAACT	45	This study
rga75	TGGTAGGTCCTTGTA	45	This study
cfa2040F	TCAAATGATTTCAGGTAACCACTA	60	Somers et al. (2004)
cfa2040R	TTCCTGATCCCACCAAACAT	60	Somers et al. (2004)
gwm577F	ATGGCATAATTTGGTGAAATTG	55	Röder et al. (1998)
gwm577R	TGTTTCAAGCCCAACTTCTATT	55	Röder et al. (1998)
gpw1144F	CTCGAGCGACTAACCCTGTC	60	Sourdille et al. (2005)
gpw1144R	GTGCCGAACTGACCTTGATT	60	Sourdille et al. (2005)
barc182F	CCATGGCCAACAGCTCAAGGTCTC	58	Somers et al. (2004)
barc182R	CGCAAAACCGCATCAGGGAAGCACCAAT	58	Somers et al. (2004)
barc32F	GCGTGAATCCGGAAACCCAATCTGTG	52	Somers et al. (2004)
barc32R	TGGAGAACCTTCGCATTGTGTCATTA	52	Somers et al. (2004)
wmc273F	AGTTATGTATTCTCTCGAGCCTG	51	Somers et al. (2004)
wmc273R	GGTAACCACTAGAGTATGTCCTT	51	Somers et al. (2004)
wmc276F	GACATGTGCACCAGAATAGC	51	Somers et al. (2004)
wmc273R	AGAAGAACTATTCGACTCCT	51	Somers et al. (2004)

[a] rga51, rga52, rga56, rga58, rga71 and rga75 are RGA primers designed by Meinan Wang and the remaining are SSR primers

[b] Annealing temperature

was constructed using MAPMAKER 3.0b version (Lincoln et al. 1992) and the Kosambi mapping function was employed to convert recombinant frequencies to map distances. The markers and resistance gene locus were organized into a linkage group with the GROUP command at a minimum LOD = 3 and maximum distance between two loci of 37.5 cM. Preliminary order of markers in the linkage group with seven markers was established using the COMPARE, ORDER and MAP commands. Additional markers were incorporated using the TRY command. Three-point linkage analysis was performed to determine the most likely order of markers and gene locus with the shortest distance. The linkage map was drawn using software Mapdraw 2.1 (Liu and Meng 2003).

Determination of polymorphism of flanking markers in wheat genotypes

The usefulness of a molecular marker in resistance breeding largely depends upon its polymorphism between the resistance gene donor and genotypes without the gene. To determine the usefulness of flanking markers *Xbarc182* and *Xwgp5258* in marker-assisted selection, 74 wheat genotypes (Supplement Table 1), including currently grown spring and winter cultivars, advanced breeding lines and stripe rust differentials, were evaluated. Genomic DNA of these wheat genotypes was prepared as previously described (Lin and Chen 2009; Li et al. 2010).

Results

Characterization of stripe rust resistance in PI 183527

In the four-way test under controlled greenhouse conditions, PI 183527 seedlings were susceptible (IT 8) when tested with races PST-100, PST-114 and PST-127 under both temperature profiles. Adult plants of PI 183527 were also susceptible (IT 8) at the low-temperature profile. Under the high-temperature profile, adult plants of PI 183527 were resistant (IT 2) with short necrotic stripes without uredinia on flag leaves with all three races. Lower leaves showed reduced resistance (IT 3-5) with limited uredinia. The AvS control was consistently susceptible (IT 8) with abundant uredinia in all tests. In the field tests, PI 183527 was susceptible (IT 7-9) at the seedling stage and became highly resistant (IT 2) with few short necrotic stripes on flag leaves from boot stage in both Pullman and Mount Vernon nurseries. In contrast, AvS was susceptible (IT 8-9) at both locations at each note taking. The data were consistent with the previous evaluations from 2004 to 2009 (Wang et al. 2012). Stripe rust samples collected from the Pullman and Mount Vernon locations comprised more than 10 races, whereas race PST-127 and similar races predominated at the Pullman location (data not shown). These results confirmed that PI 183527 has the typical HTAP resistance that is effective against a wide range races.

In the field tests, the IT data were almost identical at the two note-takings at both the Pullman and Mount Vernon locations, and the DS values increased from the first note-taking to the second note-taking for the susceptible lines and plants. The IT data between the two locations were completely correlated ($r = 1.0$, $P < 0.0001$), and the DS data was also highly correlated ($r = 0.97$, $P < 0.0001$). The correlation coefficient between the IT and DS data ranged from 0.95 to 0.99 with an average of 0.96 ($P < 0.0001$). These results indicated that the same gene or closely linked genes controlled IT and DS in PI 183527. The IT data of the second note-taking at Pullman were used for molecular mapping.

When adult plants of the parents, F_1 and F_2 were tested with race PST-127 under controlled greenhouse conditions at the high temperature profile, AvS was susceptible (IT 9) with long and abundant uredinial stripes and no necrosis, whereas PI 183527 was resistant (IT 2) with short necrotic stripes as in the four-way test described above. All three F_1 plants had IT 4 (necrotic stripes with limited sporulation). The 175 F_2 plants segregated in 135 resistant (IT 0-6) and 40 susceptible (IT 7-9) (Table 2), suggesting that PI 183527 has a partially dominant gene conferring HTAP resistance.

Molecular mapping of the HTAP resistance gene in PI 183527

Of 140 RGA primer pairs screened, 4 produced bands appearing to be associated with stripe rust response in the bulked segregant analysis. The associations were confirmed by genotyping all 175 F_2 plants. *Xwgp5271* was co-dominant and the remaining three (*Xwgp5175*, *Xwgp5258* and *Xwgp5668*) were dominant. The marker bands of *Xwgp5175*, *Xwgp5258* and *Xwgp5271* were in coupling with the resistance allele whereas the *Xwgp5668* band was not.

To determine the chromosomal location of the resistance gene, three RGAP markers, *Xwgp5271*, *Xwgp5258* and *Xwgp5668* which were also present in CS, were used to test the 21 CS nulli-tetrasomic lines; they amplified the fragments of 310, 430 and 650 bp in CS, respectively. As shown in Fig. 1, CS and all nulli-tetrasomic lines, except N7BT7A and CS ditelo 7BL, produced fragments of these markers, indicating that the resistance gene was located on chromosome 7BL. The three RGAP markers were further used to test a set of eight CS deletion lines of 7BL, each line carrying a different deletion bin of chromosome 7B. The target bands were not present on any of the deletion

Table 2 Observed numbers of resistant, segregating, and susceptible plants or lines for F_2 and $F_{2:3}$ progeny from Avocet S/PI 183527 tested with race PST-127 in the greenhouse and under natural infection in field plots, Chi-squared (χ^2) and probability (P) values for goodness of fit

Location	Generation	Score	No. of F_2 plants or $F_{2:3}$ lines[a]			$\chi^2_{(3:1or1:2:1)}$	P
		Taking	Res. IT 0-3	Seg. IT 2-9	Sus. IT 8-9		
Greenhouse	F_2	1st	135	–	40	0.21	0.51
	F_1	–	3	–	0	–	–
Pullman	$F_{2:3}$	1st	47	88	40	0.57	0.80
	$F_{2:3}$	2nd	47	86	42	0.34	0.84
Mount Vernon	$F_{2:3}$	1st	42	62	34	2.34	0.31
	$F_{2:3}$	2nd	42	61	35	2.57	0.29

Res. resistant F_2 plants or homozygous resistant $F_{2:3}$ lines, *Seg.* segregating $F_{2:3}$ lines; and *Sus.* susceptible F_2 plants or homozygous susceptible $F_{2:3}$ lines

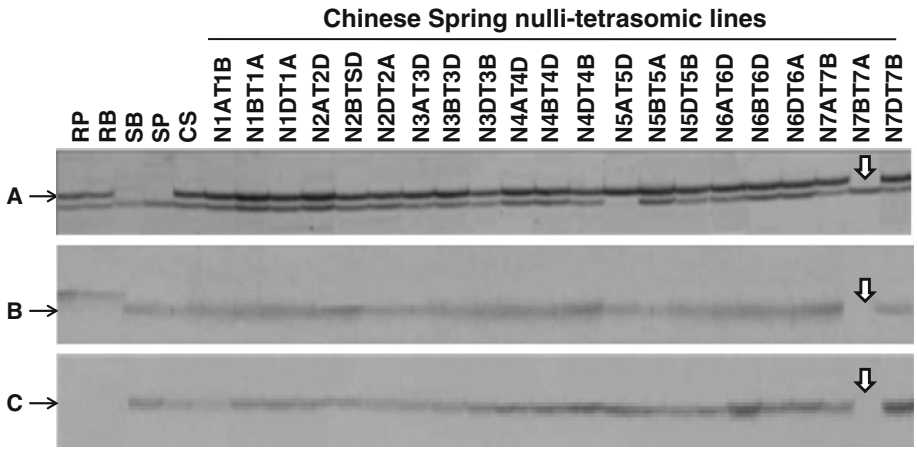

Fig. 1 Polyacrylamide gels showing resistance gene analog polymorphism (RGAP) markers *Xwgp5258* (**a**), *Xwgp5271* (**b**) and *Xwgp5668* (**c**) amplified in the resistant parent (RP, PI 183527), resistant bulk (*RB*), susceptible bulk (*SB*), susceptible parent [*SP*, Avocet Susceptible (AvS)] AvS/PI 183527; Chinese Spring (*CS*); and 21 CS nulli-tetrasomic lines

lines, including 7BL-3 which contains the whole short arm and the largest fragment (0.86) of the long arm. The results thus indicated that the markers and resistance gene were located on the distal region (0.86-1.0) of 7BL.

Fifteen SSR markers specific to chromosome 7BL were also screened in bulk segregant analysis to enrich marker density; 7 were polymorphic and associated with the resistance locus. When genotyped on the entire F_2 population, all markers, including 4 RGAP and 7 SSR markers, fitted a 3:1(dominant) or 1:2:1 (co-dominant) ratios (Table 3). Using these markers, a linkage group spanning 27.3 cM was constructed around the resistance gene locus (Fig. 2). RGAP marker *Xwgp5258* and SSR marker *Xbarc182* were the nearest flanking markers (Figs. 2, 3).

Relationship of stripe rust resistance genes on 7BL

The F_2 population of PI 183527/Alpowa was tested in the field under natural infection conditions in 2011. At seedling stage, PI 183527 and Alpowa were susceptible with IT 8-9. At heading, both PI 183527 and Alpowa displayed resistance on the flag leaves. PI 183527 had a higher level of resistance (IT 1-2 on flag leaves and IT 2-3 on lower leaves; DS 5–10 %) than Alpowa (IT 2-3 on flag leaves and IT 3-4 on lower leaves; severity 20–30 %). All six F_1 adult plants were resistant with IT 3 and severity 10–20 %. Of 179 F_2 plants, 176 were resistant with IT 0-5 and DS less than 20 % (16, 2, 144, 10 and 3 plants with IT 0, 2, 3, 4 and 5, respectively) and 3 plants were susceptible with IT 8 and DS 30–40 % at heading to milk dough stage. The segregation data indicated that the HTAP resistance gene in PI 183527 was different from *Yr39* in Alpowa, and the significant deviation from a 15R:1S ratio for independent segregation of dominant alleles at two loci ($P = 0.01$) indicated genetic linkage. Because the HTAP resistance gene in PI 183527 is different from *Yr39*, we designated the PI 183527 resistance gene as *Yr52*. Linkage of *Yr52* and *Yr39* was estimated at 36.5 ± 6.75 cM.

Polymorphism of markers flanking the *Yr52* locus in various wheat genotypes

A total of 74 wheat genotypes (56 spring and 18 winter) were tested for polymorphism at loci *Xbarc182* and *M5258*

Table 3 Resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) markers linked to the gene for HTAP resistance in wheat genotype PI 183527; their primer pairs, size and presence or absence in PI 183527, Avocet S (AvS) and Chinese Spring (CS), numbers of F_2 plants with or without the bands, and χ^2 test for goodness of fit to single locus inheritance

Marker	Primer pair	Size (bp)[a]	Band presence (+) or absence (−)			No. of F_2 plants[b]			$\chi^2_{(3:1)}$ or 1:2:1	*P*
			PI 183527	AvS	CS	RP	Both	SP		
RGAP										
Xwgp5271	rga52/rga71	300/310	300	310	310	49	86	45	0.06	0.97
Xwgp5175	rga51/rga75	450	+	−	+	132		43	0.00	0.89
Xwgp5258	rga52/rga58	650	+	−	+	134		41	0.15	0.63
Xwgp5668	rga56/rga68	430	−	+	+	130		45	0.02	0.83
SSR										
Xcfa2040	CFA2040	250/258	250	258	NT	45	87	43	0.05	0.97
Xgwm577	GWM577	150	+	−	NT	50	82	43	1.25	0.53
Xgpw1144	GWM1144	140/147	140	147	NT	51	85	39	1.79	0.41
Xbarc32	BARC32	165/175	165	175	NT	49	84	42	0.85	0.66
Xwmc273	WMC273	179	+	−	NT	132		43	0.00	0.90
Xbarc182	BARC182	75	+	−	NT	132		43	0.00	0.99
Xwmc276	WMC276	292	−	+	NT	132		43	0.00	0.90

NT not tested

[a] Fragment sizes were visually estimated based on a 50-bp DNA ladder

[b] Numbers of plants with the band of PI 183527(RP); AvS (SP); and both RP and SP (Both)

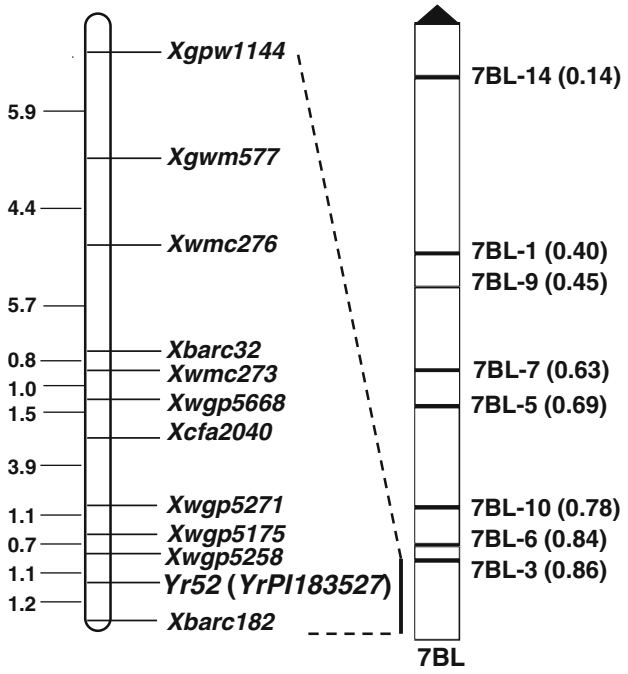

Fig. 2 Genetic map and deletion bin showing the location of the *Yr52* locus on wheat chromosome 7BL based on the AvS/PI 183527 mapping population of 175 $F_{2:3}$ lines. All resistant gene analog polymorphism (RGAP) markers (*Xwgp5271*, *Xwgp5258* and *Xwgp5175*) and simple sequence repeat (SSR) markers (*Xgpw1144*, *Xgwm577*, *Xbarc32*, *Xwmc273*, *Xcfa2040* and *Xbarc182*) were associated with the resistance allele and RGAP marker *Xwgp5668* and SSR marker *Xwmc276* were associated with the susceptibility allele

which flanked the *Yr52* locus (Supplement Table 1). The target band of *Xbarc182* was present in 19 genotypes and absent in 55, indicating a 74 % polymorphism rate. The target band of *Xwgp5258* was present in 52 genotypes and absent in 22, indicating 30 % polymorphism. Thirteen (18 %) genotypes had both flanking marker bands and therefore, the combination of the two markers can be used to distinguish the allele(s) different from the *Yr52* allele at the locus in 82 % of tested wheat genotypes, indicating that the markers could be useful in marker-assisted selection.

Discussion

PI 183527 has been highly resistant in field nurseries planted in different locations, although it was susceptible in the seedling stage to several tested races predominant in the US *Pst* population (Wang et al. 2012). In the present study, we determined that PI 183527 has a typical HTAP resistance to stripe rust because it was resistant only at the adult-plant stage at the high-temperature profile using a four-way (seedling-low temperature, seedling-high temperature, adult-low temperature and adult-high temperature) growth stage-temperature test (Chen 2005). We identified a single dominant gene conferring HTAP resistance in PI 183527 and located the gene on chromosome 7BL. We also demonstrated that the resistance gene is

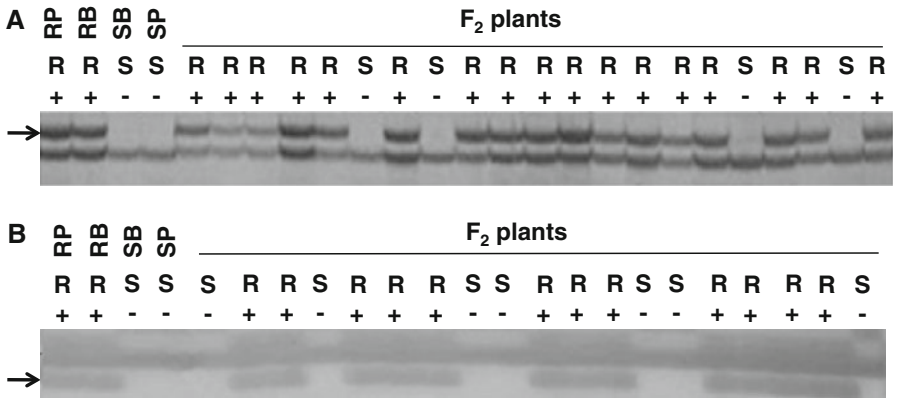

Fig. 3 Silver stained polyacrylamide gels showing resistance gene analog polymorphism (RGAP) marker *Xwgp5258* (**a**) and simple sequence repeat (SSR) marker *Xbarc182* (**b**) flanking the *Yr52* locus. RP, PI 183527; SP, AvS; RB, resistant bulk; and SB, susceptible bulk. Selected homozygous resistant (*R*) and homozygous susceptible (*S*) F_2 plants from AvS/PI 183527 were determined by the phenotypic data of $F_{2:3}$ lines

different from *Yr39* which is also located on 7BL (Lin and Chen 2007), and named the gene as *Yr52*.

Compared to other previously reported HTAP resistance genes which usually confer a low to moderate level (IT 3-7) of resistance, *Yr52* confers a higher level HTAP resistance with short necrotic stripes and very little sporulation. For comparison, under long and unusually severe epidemic conditions in 2011, lines with *Yr18* (Singh 1992) had IT 8 and DS 100 %, *Yr29* (Rosewarne et al. 2006) had IT 8 and DS 100 %, *Yr36* (Uauy et al. 2005; Fu et al. 2009) had IT 4 and DS 40 %, *Yr39* (Lin and Chen 2007) had IT 3 and DS 30 % and *QYrLo.wgp-2BS* (Carter et al. 2009) had IT 2-3 DS 30 %, whereas *Yr52* had IT 1-2 and DS 5 % in the same experimental field near Pullman, WA (Chen and associates, unpublished data). Therefore, *Yr52* may be more useful for developing wheat cultivars with high-level HTAP resistance on the basis of its greater effectiveness.

In both controlled high-temperature greenhouse conditions and naturally infected field nurseries, PI 183527 consistently expressed a necrotic reaction and low DS to stripe rust at the adult-plant stage. The IT and DS had a high correlation coefficient ($r = 0.95$, $P < 0.0001$). This is an important characteristic of the PI 183527 resistance. The correlation coefficients of IT and DS in other HTAP resistance cultivars are lower than those for PI 183527. For example, the *r* value in Louise was 0.48 (Carter et al. 2009) and in Express ranged 0.51–0.60 (Lin and Chen 2009). Disease severity is determined by both number and length of stripes and IT is determined by types of stripes (uredinia, necrosis or both). Both DS and IT can be influenced by temperature, but DS is more influenced by disease pressure. The high correlation between DS and IT indicates that both traits in PI 183527 are likely controlled by the same resistance gene (*Yr52*) and the same set of *Yr52*-regulated defense genes. For the purpose of incorporating *Yr52* into other wheat cultivars, the short necrotic stripes as a phenotypic marker of the *Yr52* resistance makes it easy and reliable to visually select plants with the gene.

There are three permanently designated stripe rust resistance genes previously reported on chromosome 7B (*Yr2*, *Yr6* and *Yr39*) (Chen 2005; Lin and Chen 2007). *Yr6* is on the short arm and the location of *Yr2* is unknown. *Yr2* confers race-specific all-stage resistance that is no longer effective against *Pst* races in the US (Chen 2005; Chen et al. 2010; Wan and Chen 2012). Therefore, it was not possible to establish the relative positions of *Yr2* and *Yr52* in the present study. *Yr52* and *Yr39* could not be distinguished by resistance types; both genes confer non-race specific HTAP resistance and both are on 7BL (Lin and Chen 2007). An F_2 population derived from PI 183527/Alpowa segregated for susceptibility and the genes were estimated to be 36.5 ± 6.8 cM apart. *Yr52* provides a higher level of HTAP resistance than *Yr39* and the two genes do not share close common markers. All results and the present discussion indicate that *Yr52* identified in PI 183527 is a new gene conferring HTAP resistance.

YrC591 in PI 189747 confers race-specific all-stage resistance; it was resistant to races PST-17 and PST-100, intermediate to PST-45, but susceptible to PST-37 and PST-43 in our seedling tests together with PI 183527 in 2004 (http://www.ars-grin.gov/cgi-bin/npgs/acc/obs.pl?1161743). Although we have not tested Zhou8425B (*YrZh84* + *Yr9*) with US races, the stripe rust resistance in this winter wheat genotype was reported to be race-specific and expressed in seedling stage (Li et al. 2009). In contrast, *Yr52* confers typical HTAP resistance that is highly effective against all tested races and field populations in the past 7 years. Furthermore, the markers linked to *YrZh84* and *Yr52* indicate that they are located at different loci. Based on the map for *YrZh84* (Li et al. 2006), the gene is located between SSR markers *Xcfa2040* and *Xbarc32* and also in the telomeric region of 7BL. However, *YrZh84* is 1.4 cM from *Xcfa2040*, while *Yr52* is 6.8 cM away from the marker locus. Therefore, *Yr52* is different from *Yr2*, *Yr6*, *YrC591* and *YrZh84* based on different resistance types, chromosomal arms, and/or marker distance.

In addition to *YrZh84* which is located on the bin 0.78–1.0 of chromosome 7BL, two QTL, *QLr.ous-7BL* and *QLr.ubo-7BL.2*, for slow rusting and durable resistance to wheat leaf rust were also mapped in this region (Xu et al. 2005; Maccaferri et al. 2008). This chromosomal region harbors the highest density of EST loci in chromosome 7B (Hossain et al. 2004), and is also known to be rich in resistance genes, resistance gene analogs and defense–response genes (Dilbirligi et al. 2004). Thus, the telomeric region of 7BL is likely a hot spot for disease resistance genes.

A number of stripe rust resistance genes (such as *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr16*, *Yr18*, *Yr29*, *Yr34*, *Yr36*, *Yr39* and *Yr48*) or QTL (such as *QYrst.wgp-6BS.1*, *QYrst.wgp-6BS.2*, *QYrex.wgp-6AS*, *QYrex.wgp-1BL*, *QYrex.wgp-3BL*, *QYrlo.wpg-2BS*, *YrR61*, *QYr.uga-6AS*, *QPst.jic-1B*, *QPst.jic-2D* and *QPst.jic-4B*) have been characterized as either adult-plant or HTAP resistance (McIntosh et al. 1995, 2008; Chen 2005; Bariana et al. 2006; Lagudah et al. 2006; Lin and Chen 2007, 2009; Cheng 2008; Melichar et al. 2008, Santra et al. 2008; Carter et al. 2009; Hao et al. 2011; Lowe et al. 2011). These genes provide different levels of resistance. Most of the QTL explained the phenotype variation less than 50 % in their tester cultivars. Although some QTL and genes behaved as major genes in their respective genetic backgrounds and were inherited as single genes, they did not explain all of the phenotypic variation. For example, *Yr39* explained 59.1 % of the variation for IT and 64.2 % of that for rAUDPC (Lin and Chen 2007), *QYrlo.wgp-2BS* explained 19–68 % of the variation for IT and 11–57 % variation for DS (Carter et al. 2009) and *YrR61* in Pioneer 26R61 explained 56 % of the phenotypic variation for disease severity (Hao et al. 2011). The phenotypes of IT and DS in the mapping population for *Yr52* were consistent across replications and locations. The limited variation among lines with the same genotype revealed that *Yr52* controls qualitative resistance, making it very easily used in breeding.

Although HTAP resistance is an important source of durable resistance to stripe rust, most of the genes or QTL identified for HTAP resistance are of the partial resistance type (Chen 2005; Uauy et al. 2005; Lin and Chen 2007, 2009; Carter et al. 2009; Lowe et al. 2011). Some of the genes do not provide an adequate protection to avoid use of fungicides, especially when temperatures are low and moisture levels are high. It is therefore important to find more genes conferring high-level HTAP resistance and to identify closely linked markers to increase the durability of resistance and to ensure sustainable wheat production (Chen 2005, Chen 2007). *Yr52* acts as a single major gene and its HTAP resistance level is similar to those of effective all-stage resistance genes. Although the gene confers a high level HTAP resistance that is likely durable, it will be better to be used in combination with other effective resistance genes to make resistance last longer. The simple inheritance simplifies the process of combining *Yr52* with other effective resistance genes. The molecular markers identified for the gene should be useful for marker-assisted selection as the flanking markers together can differentiate wheat lines with the resistance allele in most genetic backgrounds, especially for pyramiding the gene with other resistance genes. As PI 183527 is a landrace with an undesirable phenotype for modern cultivars, we selected and registered a resistant F_4 line, F4-41, from AvS/PI 183527 as PI 660057 (Wang et al. 2012). The new germplasm line is a more suitable source for *Yr52*.

Acknowledgments This research was supported by the US Department of Agriculture, Agricultural Research Service (Project No. 5348-22000-014-00D), Washington Wheat Commission (Project No. 13C-3061-3925), and Vogel Foundation (Project No. 13Z-3061-3824). PPNS No. 0592, Department of Plant Pathology, College of Agricultural, Human, and Natural Resource Sciences, Agricultural Research Center, Project Number WNP00663, Washington State University, Pullman, WA 99164-6430, USA. A scholarship from the China Scholarship Council to Runsheng Ren is gratefully acknowledged. We thank Drs. Robert McIntosh and Michael Pumphrey for critical review of the manuscript.

References

Bariana HS, Parry N, Barclay IR, Loughman R, McLean RJ, Shankar M, Wilson RE, Willey NJ, Francki M (2006) Identification and characterization of stripe rust resistance gene *Yr34* in common wheat. Theor Appl Genet 112:1143–1148

Carter AH, Chen XM, Garland-Campbell K, Kidwell KK (2009) Identifying QTL for high-temperature adult-plant resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*) in the spring wheat (*Triticum aestivum* L.) cultivar 'Louise'. Theor Appl Genet 119: 1119–1128

Chen XM (2005) Epidemiology and control of stripe rust [*Puccinia striiformis* f. sp. *tritici*] on wheat. Can J Plant Pathol 27:314–337

Chen XM (2007) Challenges and solutions for stripe rust control in the United States. Aust J Agric Res 58:648–655

Chen XM, Line RF (1995a) Gene action in wheat cultivars for durable high-temperature adult-plant resistance and interactions with race-specific, seedling resistance to stripe rust caused by *Puccinia striiformis*. Phytopathology 85:567–572

Chen XM, Line RF (1995b) Gene number and inheritability of wheat cultivars with durable, high-temperature, adult-plant resistance and race-specific resistance to *Puccinia striiformis*. Phytopathology 85:573–578

Chen XM, Line RF, Leung H (1998) Genome scanning for resistance gene analogs in rice, barley, and wheat by high-resolution electrophoresis. Theor Appl Genet 97:345–355

Chen XM, Penman L, Wan AM, Cheng P (2010) Virulence races of *Puccinia striiformis* f. sp. *tritici* in 2006 and 2007 and development of wheat stripe rust and distributions, dynamics, and evolutionary relationships of races from 2000 to 2007 in the United States. Can J Plant Pathol 32:315–333

Cheng P (2008) Molecular mapping of a gene for resistance to stripe rust in spring wheat cultivar IDO377 s and identification of a

new race of *Puccinia stiiformis* f. sp. *tritici* virulent on IDO377s. M.S. Thesis, Washington State University

Dilbirligi M, Erayman M, Sandhu D, Sidhu D, Gill KS (2004) Identification of wheat chromosomal regions containing expressed resistance genes. Genetics 166:461–481

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

Hao Y, Chen Z, Wang Y, Bland D, Buck J, Brown-Guedira G, Johnson J (2011) Characterization of a major QTL for adult plant resistance to stripe rust in US soft red winter wheat. Theor Appl Genet 123:1401–1411

Hossain KG, Kalavacharla V, Lazo GR, Hegstad J, Kianian PM, Simons K, Gehlhar S, Rust JL, Syamala RR, Obeori K, Bhamidimarri S, Karunadharma P, Chao S, Anderson OD, Qi LL, Echalier B, Gill BS, Linkiewicz AM, Ratnasiri A, Dubcovsky J, Akhunov ED, Dvora′k J, Miftahudin, Ross K, Gustafson JP, Radhawa HS, Dilbirligi M, Gill KS, Peng JH, Lapitan NL, Greene RA, Bermudez-Kandianis CE, Sorrells ME, Feril O, Pathan, Nguyen HT, Gonzalez-Hernandez JL, Conley EJ, Anderson JA, Choi DW, Fenton D, Close TJ, McGuire PE, Qualset CO, Kianian SF (2004) A chromosome bin map of 2, 148 expressed sequence tag loci of wheat homoeologous group 7. Genetics 168:687–699

Lagudah ES, McFadden H, Singh RP, Huerta-Espino J, Bariana HS, Spielmeyer W (2006) Molecular genetic characterization of the *Lr34/Yr18* slow rusting resistance gene region in wheat. Theor Appl Genet 114:21–30

Li Q, Chen XM, Wang MN, Jing JX (2010) *Yr45*, a new wheat gene for stripe rust resistance mapped on the long arm of chromosome 3D. Theor Appl Genet 122:189–197

Li Y, Niu YC, Chen XM (2009) Mapping a stripe rust resistance gene *YrC591* in wheat variety C591 with SSR and AFLP markers. Theor Appl Genet 118:339–346

Li ZF, Zheng TC, He ZH, Li GQ, Xu SC, Li XP, Yang GY, Singh RP, Xia XC (2006) Molecular tagging of stripe rust resistance gene *YrZH84* in Chinese wheat line Zhou 8425B. Theor Appl Genet 112:1098–1103

Lin F, Chen XM (2007) Genetics and molecular mapping of genes for race-specific all-stage resistance and non-race-specific high-temperature adult-plant resistance to stripe rust in spring wheat cultivar Alpowa. Theor Appl Genet 114:1277–1287

Lin F, Chen XM (2009) Quantitative trait loci for non-race-specific, high-temperature adult-plant resistance to stripe rust in wheat cultivar Express. Theor Appl Genet 118:631–642

Lincoln S, Daly M, Lander E (1992) Constructing genetic maps with Mapmarker/EXP3.0. Whitehead Institute Techn Rep, 3rd edn. Whitehead Institute, Cambridge

Line RF (2002) Stripe rust of wheat and barley in North America: a retrospective historical review. Annu Rev Phytopathol 40:75–118

Line RF, Chen XM (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, 1968–87. US Dep Agric Tech Bull 1788

Liu RH, Meng JL (2003) MapDraw: a Microsoft Excel macro for drawing genetic linkage maps based on given genetic linkage data. Heraditas 25:317–321 [in Chinese]

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

Maccaferri M, Mantovani P, Tuberosa R, Deambrogio E, Giuliani S, Demontis A, Massi A, Sanguineti MC (2008) A major QTL for durable leaf rust resistance widely exploited in durum wheat breeding programs maps on the distal region of chromosome arm 7BL. Theor Appl Genet 117:1225–1240

Maniatis TA, Frisch EF, Sambrook J (1982) Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory, Cold Spring Harbor 5.14–5.17

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC (2009) Catalogue of gene symbols for wheat: 2009 supplement. http://www.shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2009.pdf. Accessed 26 November 2011

McIntosh RA, Wellings CR, Park RF (1995) Wheat rusts: an atlas of resistance genes. Kluwer Academic Publishers, Dordrecht

McIntosh RA, Yamazaki Y, Dubcovsky J, Rogers J, Morris C, Somers DJ, Appels R, Devos KM (2008) Catalogue of gene symbols for wheat. In: Proceedings of 11th Int Wheat Genet Symp, 24–29 August 2008. http://wheat.pw.usda.gov/GG2/Triticum/wgc/2008/GeneSymbol.pdf. Accessed 26 November 2011

Melichar JPE, Berry S, Newell C, MacCormack R, Boyd LA (2008) QTL identification and microphenotype characterization of the developmentally regulated yellow rust resistance in the UK wheat cultivar Guardian. Theor Appl Genet 117:391–399

Milus EA, Line RF (1986) Number of genes controlling high-temperature adult-plant resistance to stripe rust in wheat. Phytopathology 76:93–96

Qayoum A, Line RF (1985) High-temperature, adult-plant resistance to stripe rust of wheat. Phytopathology 75:1121–1125

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:207–333

Rosewarne GM, Singh RP, Huerta-Espino J, William HM, Bouchet S, Cloutier S, McFadden H, Lagudah ES (2006) Leaf tip necrosis, molecular markers and β1-proteasome subunits associated with the slow rusting resistance genes *Lr46*/*Yr29*. Theor Appl Genet 112:500–508

Santra DK, Chen XM, Santra M, Campbell KG, Kidwell KK (2008) Identification and mapping QTL for high-temperature adult plant resistance to stripe rust in winter wheat (*Triticum aestivum* L.) cultivar Stephens. Theor Appl Genet 117:793–802

Shi ZX, Chen XM, Line RF, Leung H, Wellings CR (2001) Development of resistance gene analog polymorphism markers for the *Yr9* gene resistance to wheat stripe rust. Genome 44: 509–516

Singh RP (1992) Genetic association of leaf rust resistance gene *Lr34* with adult-plant resistance to stripe rust in bread wheat. Phytopathology 82:835–838

Somers DJ, Isaac P, Edwards K (2004) A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor Appl Genet 109:1105–1114

Sourdille P, Gandon B, Chiquet V, Nicot N, Somers D, Murigneux A, Bernard M (2005) Wheat genoplante SSR mapping data release: a new set of markers and comprehensive genetic and physical mapping data. http://wheat.pw.usda.gov/GG2/index.shtml. Accessed 26 November 2011

Stubbs RW (1985) Stripe rust. In: Roelfs AP, Bushnell WR (eds) The cereal rusts, vol II. Academic Press, New York, pp 61–101

Uauy C, Brevis JC, Chen XM, Khan IA, Jackson LF, Chicaiza O, Distelfeld A, Fahima T, Dubcovsky J (2005) High-temperature adult-plant (HTAP) stripe rust resistance gene *Yr36* from *Triticum turgidum* ssp. *dicoccoides* is closely linked to the grain protein content locus Gpc-B1. Theor Appl Genet 112:97–105

Wan AM, Chen XM (2012) Virulence, frequency, and distribution of races of *Puccinia striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* identified in the United States in 2008 and 2009. Plant Dis 96:67–74

Wan AM, Chen XM, He ZH (2007) Wheat stripe rust in China. Aust J Agric Res 58:605–619

Wang MN, Chen XM, Xu LS, Cheng P, Bockelman H (2012) Registration of 70 common spring wheat germplasm lines resistant to stripe rust. J Plant Regist 6:104–110

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

Xu X, Bai G, Carver BF, Shaner GE, Hunger RM (2005) Molecular characterization of slow leaf-rusting resistance in wheat. Crop Sci 45:758–765

Yan GP, Chen XM, Line RF, Wellings CR (2003) Resistance gene analog polymorphism markers co-segregating with the *Yr5* gene for resistance to wheat stripe rust. Theor Appl Genet 106: 636–643