Combining Single Nucleotide Polymorphism Genotyping Array with Bulk Segregant Analysis to Map a Gene Controlling Adult Plant Resistance to Stripe Rust in Wheat Line 03031-1-5 H62

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ABSTRACT

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most devastating diseases of wheat worldwide. Growing resistant cultivars is considered the best approach to manage this disease. In order to identify the resistance gene(s) in wheat line 03031-1-5 H62, which displayed high resistance to stripe rust at adult plant stage, a cross was made between 03031-1-5 H62 and susceptible cultivar Avocet S. The mapping population was tested with Chinese *P. striiformis* f. sp. *tritici* race CYR32 through artificial inoculation in a field in Yangling, Shaanxi Province and under natural infection in Tianshui, Gansu Province. The segregation ratios indicated that the resistance was conferred by a single dominant gene, temporarily designated as *YrH62*. A combination of bulked segregant analysis (BSA) with wheat 90K single nucleotide polymorphism (SNP) array was used to identify molecular markers linked to *YrH62*. A total of 376 polymorphic SNP loci identified from the BSA analysis were located on chromosome 1B, from which 35 kompetitive allele-specific PCR (KASP) markers selected together with 84 simple sequence repeat (SSR) markers on 1B were used to screen

polymorphism and a chromosome region associated with rust resistance was identified. To saturate the chromosomal region covering the *YrH62* locus, a 660K SNP array was used to identify more SNP markers. To develop tightly linked markers for marker-assisted selection of *YrH62* in wheat breeding, 18 SNPs were converted into KASP markers. A final linkage map consisting of 15 KASP and 3 SSR markers was constructed with KASP markers AX-109352427 and AX-109862469 flanking the *YrH62* locus in a 1.0 cM interval. *YrH62* explained 63.8 and 69.3% of the phenotypic variation for disease severity and infection type, respectively. *YrH62* was located near the centromeric region of chromosome 1BS based on the positions of the SSR markers in 1B deletion bins. Based on the origin, responses to *P. striiformis* f. sp. *tritici* races, and marker distances, *YrH62* is likely different from the other reported stripe rust resistance genes/quantitative trait loci on 1B. The gene and tightly linked KASP markers will be useful for breeding wheat cultivars with resistance to stripe rust.

With a total annual production of about 100 million metric tons, China remains one of the largest producers as well as the largest consumption country of wheat in the world. Wheat production is constantly threatened by various diseases, among which stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss., is one of the most devastating diseases (Chen 2005; Hovmøller et al. 2010; Stubbs 1985; Wellings 2011). Severe epidemics of stripe rust have occurred in China, causing the grain losses of millions of tons (Chen et al. 2009, 2014; Kang et al. 2010; Wan et al. 2007). The most effective strategy for control of stripe rust is breeding and growing resistant cultivars, as this approach has no additional cost to farmers and is environmentally desirable (Chen 2013; Li and Zeng 2002; Wellings 2011).

So far, there are 78 officially designated *Yr* genes for resistance to stripe rust identified in wheat, and most of them have been widely

used in different areas worldwide (Chen 2013; McIntosh et al. 2017). Moreover, most of *Yr* genes have been mapped to wheat chromosomes and many genes and their linked markers have been successfully used in breeding programs (McIntosh et al. 2014, 2017). However, some of the *Yr* genes are not effective against all races, and some markers are not tightly linked to the genes and not suitable for high-throughput screening. Nowadays, single nucleotide polymorphism (SNP) is one of the most preferred marker types because of its low cost, high genomic abundance, locus specificity, potential for high-throughput analysis, and relatively low genotyping error rates (Allen et al. 2013; Mammadov et al. 2012; Varshney et al. 2014). Several wheat SNP arrays have been developed and widely used in identifying markers closely linked to agronomic traits. These SNP arrays have accelerated molecular mapping of genes for important traits as they facilitate high-density mapping (Cavanagh et al. 2013; Cui et al. 2017; Jia and Zhao 2016; Maccaferri et al. 2015a, b; Wang et al. 2014; Winfield et al. 2016). The kompetitive allele-specific PCR (KASP), which is based on allele-specific oligo extension and utilizes fluorescence resonance energy transfer for signal generation, has become a widely used method for SNP genotyping, systematic mining of large germplasm collections for specific polymorphisms, and marker-assisted selection (Allen et al. 2013; Dreisigacker et al. 2015; Neelam et al. 2013; Ramirez-Gonzalez et al. 2014; Rasheed et al. 2016; Semagn et al. 2014).

The stripe rust pathogen is able to produce new races that may overcome race-specific resistance, leading to large-scale epidemics

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(Chen 2005; Li and Zeng 2002). As *Berberis* and *Mahonia* have been recently found to be alternate hosts for *P. striiformis* f. sp. *tritici*, sexual recombination may generate new races, in addition to mutation and somatic recombination (Jin et al. 2010; Lei et al. 2017; Wang and Chen 2013; Zhao et al. 2013, 2016). As new races are continually produced in the pathogen population, most *Yr* genes have become ineffective (Han et al. 2015; Sharma-Poudyal et al. 2013). Only a few officially named all-stage resistance genes (such as *Yr5*, *Yr15*, *Yr53*, *Yr61*, *Yr64*, *Yr65*, and *Yr69*) and several adult plant resistance (APR) or high-temperature adult plant (HTAP) resistance genes (such as *Yr18*, *Yr30*, *Yr32*, *Yr36*, *Yr39*, *Yr52*, *Yr54*, *Yr59*, and *Yr62*) are still effective against *P. striiformis* f. sp. *tritici* (Basnet et al. 2014; Cheng et al. 2014; Hou et al. 2016; Lu et al. 2014; Ren et al. 2012; Xu et al. 2013; Zeng et al. 2015; Zhou et al. 2014, 2015). Therefore, there is an urgent need to identify new genes for resistance to stripe rust and develop molecular markers for efficient incorporation of these genes into wheat cultivars.

Wheat line 03031-1-5 H62 has been highly resistant in our field nurseries in Shaanxi and Gansu provinces of China since it was started to be tested in 2008 (J. M. Mu, Q. L. Wang, J. H. Wu, D. J. Han, and Z. S. Kang, unpublished data). The objectives of the present study were to identify and map the stripe rust resistance gene(s) in 03031-1-5 H62 using the 90K and 660K SNP array and to develop molecular markers for marker-assisted selection.

MATERIALS AND METHODS

Wheat materials. Wheat line 03031-1-5 H62, provided by Z. Zhang, College of Food Science and Engineering, Northwest A&F University, was selected from cross 03031-1-5 × Jinmai 47. 03031-1-5 is a stripe rust resistant hexaploid spring wheat advanced line introduced from CIMMYT, and Jinmai 47 is a winter wheat cultivar developed and grown in Shanxi Province, but susceptible to the recently predominant *P. striiformis* f. sp. *tritici* races in China. The mapping population was developed from the cross Avocet S × 03031-1-5 H62. A total of 167 F_{2:3} lines were used for genetic mapping. Avocet S, an Australian spring wheat selection, is highly susceptible to most *P. striiformis* f. sp. *tritici* races in China and many other countries (Chen et al. 2010; Sharma-Poudyal et al. 2013; Wellings et al. 2012). The wheat cultivars (or lines) Avocet S, Mingxian 169, Jinmai 47, and Xiaoyan 22 were used as the susceptible control, 92R137 (*Yr26*), PI 660064 (*Yr64*), PI 679621 (*Yr65*), L693 (*YrL693*), H52 (*YrH52*), Alpowa (*YrAlp-1B*, *Yr39-7B*), Express (*YrExp1-1B*, *YrExp2-5B*), and Shaanmai 139 (*YrSM139-1B*) were included in tests

for response to stripe rust. A set of *Yr* single-gene lines was also included in the study as references for individual stripe rust resistance genes. A total of 158 wheat entries including winter wheat cultivars and landraces of Chinese origin and other countries were used to evaluate polymorphisms of molecular markers flanking a resistance gene identified in 03031-1-5 H62.

***P. striiformis* f. sp. *tritici* isolates.** Five *P. striiformis* f. sp. *tritici* races, HY8, CYR32, CYR33, V26/92R137, and V26/Gui22, were used in tests wheat cultivars and lines for response to stripe rust under controlled greenhouse conditions, and only race CYR32 was used to inoculate the field nursery at Yangling, Shaanxi in 2013 to 2015. A single-spore isolate was obtained for each of the five races, and their virulence/avirulence patterns of the isolates were confirmed by testing on the *Yr* single-gene lines (Table 1).

Stripe rust tests in the greenhouse. Evaluation of seedling reactions and adult plant responses to different *P. striiformis* f. sp. *tritici* races was conducted under controlled greenhouse conditions. For seedling tests, 10 seeds of each wheat cultivar or line, including both parents, Jinmai 47, 92R137, PI 660064, PI 679621, L693, H52, Shaanmai 139, Alpowa, Express, AvSYr9NIL, AvSYr10NIL, AvSYr15NIL, and AvSYr29NIL were sown in pots (9 × 9 × 9 cm³), and for adult plant tests, three plants were grown in larger pots (20 cm diameter × 15 cm height). Seedlings at the two-leaf stage (14 days after planting) and adult plant at the booting stage were separately inoculated with urediniospores of each *P. striiformis* f. sp. *tritici* isolate mixed with talc at a ratio of approximately 1:20. Inoculated plants were incubated at 10°C in a dew chamber in dark for 24 h, and then transferred to a greenhouse at 17 ± 2°C with a daily 14 h light (22,000 lx) period. Infection type (IT) data were recorded at least two times about 18 to 21 days after inoculation when rust fully developed on the susceptible check Mingxian 169, using a 0 to 9 scale as described by Line and Qayoum (1992). Plants with ITs 0 to 6 were considered resistant, and plants with ITs 7 to 9 susceptible. In order to confirm or clarify ITs of the entries, all seedling tests were conducted three times in November 2013 to March 2014, and the highest IT score of each line in each race test was used for analysis and comparison.

Stripe rust response in the fields. The parents, 10 F₁ and 174 F₂ plants of Avocet S × 03031-1-5 H62 were grown on the Northwest A&F University Research Farm in Yangling during the 2013 to 2014 wheat-growing season. Yangling is located in central Shaanxi, an overwintering region for *P. striiformis* f. sp. *tritici* (Li and Zeng 2002). F_{2:3} seeds were harvested from 169 F₂ plants, and the F_{2:3} lines were planted together with the parental lines at Yangling and Tianshui in October 2014 in a randomized complete block design with three replications. Approximately 25 plants for each line were grown in a single row of 120 cm in length with 30 cm between rows. Two rows of Xiaoyan 22 were planted after every 20 rows as a susceptible check and highly susceptible variety Mingxian 169 was planted at both ends of the nursery as spreader. In Yangling, the field was inoculated by spraying a mineral oil suspension of urediniospores of predominant race CYR32 at a ratio of approximately 1:300 in volume when flag leaves expanded. The field in Tianshui was under natural infection. During each growing season, IT and maximum disease severity (MDS) were scored for each line when the disease severities on Mingxian 169 and Avocet S reached maximum levels around 20 May in Yangling and 10 June in Tianshui. Disease severities were assessed visually using the percentage of infected leaf area based on the modified Cobb scale (Peterson et al. 1948). For the genetic analysis, the F_{2:3} lines were classified as homozygous resistant, heterozygous, and homozygous susceptible based on the IT data. A single IT and severity were recorded if plants in a row had uniform IT and DS; whereas variable IT and DS indicating heterozygosity were recorded twice or more, but later analyzed as a mean value for each line.

Statistical analyses. The infection type data of F₁, F₂, and F₃ generations were analyzed to estimate the number of genes for APR

TABLE 1. Virulence and avirulence of *Puccinia striiformis* f. sp. *tritici* races used in this study

Race	Virulence (V) and avirulence (A) to <i>Yr</i> genes
CYR32	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr18</i> , <i>Yr27</i> , <i>Yr28</i> , <i>Yr29</i> , <i>Yr31</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> , <i>YrSP</i> A: <i>Yr5</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr26</i> , <i>Yr32</i> , <i>YrTr1</i>
CYR33	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr18</i> , <i>Yr28</i> , <i>Yr29</i> , <i>Yr31</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> , <i>YrSP</i> A: <i>Yr5</i> , <i>Yr8</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr26</i> , <i>Yr27</i> , <i>Yr32</i> , <i>YrTr1</i>
V26/Gui22	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr10</i> , <i>Yr17</i> , <i>Yr18</i> , <i>Yr24</i> , <i>Yr26</i> , <i>Yr27</i> , <i>Yr28</i> , <i>Yr29</i> , <i>Yr31</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> , <i>YrSP</i> A: <i>Yr5</i> , <i>Yr15</i> , <i>Yr32</i> , <i>YrTr1</i>
V26/92R137	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr18</i> , <i>Yr24</i> , <i>Yr26</i> , <i>Yr28</i> , <i>Yr29</i> , <i>Yr31</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> , <i>YrTr1</i> A: <i>Yr5</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr27</i> , <i>Yr32</i> , <i>YrSP</i>
HY8	V: <i>Yr1</i> , <i>Yr6</i> , <i>Yr7</i> , <i>Yr8</i> , <i>Yr9</i> , <i>Yr17</i> , <i>Yr18</i> , <i>Yr28</i> , <i>Yr29</i> , <i>Yr31</i> , <i>Yr43</i> , <i>Yr44</i> , <i>YrExp2</i> A: <i>Yr5</i> , <i>Yr10</i> , <i>Yr15</i> , <i>Yr24</i> , <i>Yr26</i> , <i>Yr27</i> , <i>Yr32</i> , <i>YrTr1</i> , <i>YrSP</i>

resistance in 03031-1-5 H62. χ^2 test (χ^2) was used to determine the goodness of fit of observed numbers of the classes to a theoretical segregation ratio for the classes using the Excel data analysis available in Microsoft Office 2013. Mean IT and MDS of each $F_{2:3}$ line were used for analysis of variance (ANOVA), using the PROC GLM in the statistical analysis system (SAS) software package (SAS Institute, V9.0, Cary, NC). The broad-sense heritability (h_b^2) of stripe rust resistance were calculated using the formula $h_b^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2/e + \sigma_e^2/re)$ (Allard 1960), where genetic variance σ_g^2 is calculated as $(MS_f - MS_{fe})/re$, genotype $\times$ environment interaction variance σ_{ge}^2 is calculated as $(MS_{fe} - MS_e)/r$, and σ_e^2 is the value of MS_e ; in which, σ_e^2 is the error variance, MS_f is the mean square of genotype, MS_{fe} is the mean square of genotype $\times$ environment interaction, MS_e is the mean square of error, r the number of replications, and e the number of environments. Pearson's correlation coefficients were calculated between traits with the PROC CORR procedure based on mean values across the two environments.

DNA extraction and bulk segregant analysis. Genomic DNA was extracted from leaf samples of each F_2 plant and the parents using the sodium dodecyl sulfonate (SDS) method (Song et al. 1994). The quality and quantity of DNA were determined using 1% agarose gel electrophoresis and a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA). A resistant bulk (RB) and susceptible bulk (SB) were made by comprising equal amount DNA from 10 homozygous resistant and 10 homozygous susceptible F_2 plants, respectively based on their IT (=1 for RB; 8 or 9 for SB) and severity (<5% for RB; > 90% for SB) values in 2014 and the uniformity of their derived $F_{2:3}$ lines in both Yangling and Tianshui fields in 2015. The bulk segregant analysis (BSA), as described by Michelmore et al. (1991), was used to screen primers with the bulk and parental DNA samples for identifying markers associate to resistance.

SNP analysis. The two bulks and parents were genotyped with the 90K and 660K SNP arrays by CapitalBio Corporation (Beijing, China; <http://www.capitalbio.com>). SNP genotype calling and clustering was performed with software Genome Studio Polyploid Clustering v1.0 (Illumina, <https://www.illumina.com>). The monomorphic and poor-quality SNP markers, which had more than 20% missing values, ambiguous SNP calling, or minor allele frequencies below 5%, were excluded from further analyses. The polymorphic SNP loci associated with resistance in BSA included homozygous and heterozygous differences, but only homozygous polymorphic loci were localized to chromosomes based on the high-density 90K genetic map (Wang et al. 2014) and the 660K genetic map provided by J. Jia, the Institute of Crop Science, Chinese Academy of Agricultural Sciences. The sequences of all SNP markers were used to search the IWGSC RefSeq v 0.4 (<http://www.wheatgenome.org/>) to determine their physical positions using BLAST.

Validation of chromosomal location with simple sequence repeat (SSR) markers. When a chromosome was identified according to the polymorphic SNP loci, SSR markers in the chromosome were screened with the parents and bulks based on the previous reports (Maccaferri et al. 2015a; Somers et al. 2004). Polymerase chain reaction (PCR) amplification was performed in a S1000 Thermal Cycler (BIO-RAD, Hercules, CA) in a 15 μ l reaction mixture containing 50 to 100 ng of template DNA, 1.0 U of *Taq* DNA polymerase, 1.5 μ l of 10 $\times$ buffer (50 mM KCl, 10 mM Tris-HCl, pH 8.3), 2.0 mM of $MgCl_2$, 200 mM of dNTPs, and 1.0 mM of the forward and reverse primers. The PCR program was: denaturation at 94°C for 4 min, followed by 15 cycles of 94°C for 30 s, touchdown starting at 65°C for 45 s (decreasing 1.0 per cycle), 72°C for 1 min, 20 cycles of 94°C for 30 s, 50°C for 45 s, 72°C for 1 min, and a final extension at 72°C for 10 min. PCR products were separated in 6% denaturing polyacrylamide gels, visualized using silver staining for polyacrylamide gels, and photographed.

Development of KASP markers. Based on the consensus 90K SNP map (Maccaferri et al. 2015a, b) and the IWGSC RefSeq v 0.4, the polymorphic SNP loci for a specific chromosomal region were selected for conversion into KASP markers using the method described in Ramirez-Gonzalez et al. (2015). KASP assays were conducted in the Laboratory of National Wheat Improvement Center, Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing, China. The end-point fluorescence data were visualized with a microplate reader (Synergy HT, BioTek, USA) and analyzed using Klustering Caller software (<http://www.lgcgroup.com/>). A reaction mixture was comprised of a final volume of 5 μ l containing, 2.5 μ l of 2 $\times$ KASP V4.0 Mastermix (LGC Genomics, Middlesex, UK), 0.056 μ l of assay primer mix (12 mM of each allele-specific primer and 30 mM of the common primer) and 50 to 100 ng of genomic DNA. The reaction was performed in a S1000 Thermal Cycler (Bio-Rad) in the cycling conditions: 94°C for 15 min, 9 cycles of 94°C for 20 s, touchdown starting at 65°C for 60 s (decreasing 0.8 per cycle), 32 cycles of 94°C for 20 s, and 57°C for 60 s.

Construction of a genetic linkage map and quantitative trait loci (QTL) analysis. Linkages between markers and the stripe rust resistance gene locus in 03031-1-5 H62 were calculated using software JOINMAP V4.0 (Van Ooijen 2006). Genetic distances were determined using the Kosambi mapping function (Kosambi 1943) and a logarithm of odds (LOD) score of 3.0 as a threshold. The genetic linkage map was drawn with software Mapchart V2.3 (Voorrips 2002). The resistance locus was assigned to a chromosomal bin based on the flanking markers using the deletion maps (Sourdille et al. 2004). QTL mapping was conducted using mean MDS (maximum disease severity) and IT data of the $F_{2:3}$ lines of both field locations. A stripe rust resistance QTL was mapped in the population using the inclusive composite interval mapping (ICIM) analysis in software QTL IciMapping V4.1 (Meng et al. 2015; Wang 2009) (<http://www.isbreeding.net/>). A value of phenotypic variance explained by an individual QTL was determined also using ICIM. A LOD default threshold of 2.5 was set to declare a significant QTL.

Bioinformatics analysis of candidate genes. In order to identify candidate genes controlling the stripe rust APR in 03031-1-5 H62, the sequences of SNP markers located in the target region were blasted the Ensembl Plants website (<http://plants.ensembl.org/index.html>) using BLASTn to find corresponding wheat genes. Their amino acid sequences were used to blast against the NCBI database (<https://www.ncbi.nlm.nih.gov/>) using BLASTp. BLAST hits were filtered with an e value threshold of 10^{-5} and sequence similarity higher than 95%.

RESULTS

Stripe rust resistance in 03031-1-5 H62. As shown in Figure 1 and Table 2, Avocet S displayed high susceptibility (IT = 9, DS $\geq$ 90%), whereas 03031-1-5 H62 was highly resistant (IT = 1, DS $\leq$ 5%). All 10 F_1 plants had IT 2 and DS 10%, indicating that the APR in 03031-1-5 H62 was dominant. The F_2 segregation of 134 resistant (IT = 0 to 3): 40 susceptible (IT = 7 to 9) fitted the 3:1 ratio ($\chi^2 = 0.38$, $P = 0.54$). Because seven F_2 plants failed to produce seeds, 167 $F_{2:3}$ lines were tested in both Yangling and Tianshui locations. The segregation of the $F_{2:3}$ lines at both locations fit a 1 resistant: 2 segregating: 1 susceptible ratio (Table 2). All susceptible $F_{2:3}$ lines that were derived from the 34 susceptible F_2 plants were homozygous susceptible, indicating that the same gene conferred resistance in both locations. The above results showed that 03031-1-5 H62 had a single dominant gene conferring the stripe rust resistance. The gene was temporarily named *YrH62*.

When the mean IT and mean MDS values were used to show the frequencies of different resistance levels, both data sets indicated a continuous variation with one peak (Fig. 2A and B). The IT data between the two locations were highly correlated

($r = 0.92$, $P < 0.01$), and the mean MDS data were also highly correlated ($r = 0.82$, $P < 0.01$). ANOVA revealed significant differences ($P < 0.01$) in MDS and IT among lines, environments, and line–environment interactions (Table 3), indicating that the APR resistance in 03031-1-5 H62 was influenced by different environments. Broad-sense heritability (h_2) was estimated at 0.88 for the IT data and 0.86 for the mean MDS data across both locations (Table 3), indicating that the APR resistance is highly inheritable and it should be relatively easy to be incorporated into other wheat cultivars.

Polymorphic SNP loci from the 90K SNP array and construction of a genetic map. A total of 883 SNP loci from the 90K SNP array showed homozygous polymorphisms between the two parents and two bulks, of which 376 were in 1B and the others distributed on other chromosomes from 1 to 61 SNPs (Fig. 2C), indicating that 1B was likely the chromosome carrying the stripe rust resistant QTL. Based on the density of SNPs in 1B, SNPs located within the interval 280–350 Mb (Fig. 2D) were most likely linked to the resistance locus, and therefore, 35 SNPs in this region were selected for conversion to KASP markers. Nine KASP markers successfully showed polymorphism between the parents and bulks. In addition, 3 of 84 wheat SSR markers on chromosome 1B were also polymorphic between the parents and bulks, indicating linkage with the stripe rust resistance locus. All polymorphic markers obtained through BSA were used to genotype the F_2 population. Combining the IT data and the genotyping data of the $F_{2:3}$ lines, the stripe rust resistance locus was initially mapped in a 3.35 cM interval flanked by KASP markers *IWB11553* and *IWB9149*.

Saturation of the linkage map using the 660K SNP array. A total of 5,256 SNP loci from the 660K SNP array were polymorphic between the parents and bulks and were located in the 21 chromosomes, of which 2,287 were located on chromosome 1B and the others were distributed in other chromosomes (Fig. 2E). These results were consistent with the 90K genotyping result. Of the 2,287

SNP loci located on 1B, more than 500 were positioned in the interval between *IWB11553* and *IWB9149* (280 to 330 Mb) according to the wheat genome assembly (Fig. 2F). To saturate the *YrH62* region and develop improved markers for routine breeding applications, 18 SNPs located within the interval 295 to 315 Mb (Fig. 2F) were converted into KASP markers and six polymorphic KASP markers were used to genotype the mapping population. The sequences of all KASP markers are listed in Supplementary Table S1. A final linkage map spanning 15.3 cM in chromosome 1B was constructed (Fig. 3A) and the stripe rust resistance locus was located within a 1.04 cM interval. The order of the markers and QTL is as follows: *IWB1153*—1.1 cM—*AX-108995142/AX-110071821*—0.4 cM—*AX-109871410/AX-109472792/AX-109352427*—0.3 cM—*YrH62*—0.7 cM—*AX-109862469*—0.8 cM—*IWB9149*. According to the positions of the SSR markers in the 1B deletion bin map, the gene was located in the 1BS region close to the centromere.

QTL mapping for stripe rust resistance. Based on the ICIM analysis using the mean MDS and IT data in each environment, a major QTL, corresponding to *YrH62*, was also mapped within a 1.04 interval flanked by KASP markers *AX-109871410/AX-109472792/AX-109352427* and *AX-109862469* on chromosome 1B. This QTL explained 67.8% of the phenotypic variation in MDS at Yangling and 59.8% at Tianshui. The corresponding variances explained on the basis of IT were 73.6 and 64.9% for the two locations, respectively (Table 4). It is worth mentioning that there were still more than 100 SNP loci positioning in the interval *AX-109352427* and *AX-109862469*, and they are the putative markers for fine mapping *YrH62*.

Comparison of *YrH62* with other *Yr* genes in chromosome 1B. Wheat line 03031-1-5 H62 (*YrH62*) was compared with *AvSYr9NIL* (*Yr9*), *AvSYr10NIL* (*Yr10*), *AvSYr15NIL* (*Yr15*), *AvSYr29NIL* (*Yr29*), *92R137* (*Yr26*), *Shaanmai139* (*YrSM139-1B*), *PI 660064* (*Yr64*), *PI 679621* (*Yr65*), *L693* (*YrL693*), *H52* (*YrH52*), *Alpowa* (*YrAlp-1B*, *Yr39-7B*), and *Express* (*YrExp1-1BL*,

Fig. 1. Phenotypic reactions of the wheat lines to *Puccinia striiformis* f. sp. *tritici*. **A**, Seedling reaction of 03031-1-5 H62 in Tianshui. **B**, Phenotypes of Avocet S (left) and 03031-1-5 H62 (right) in the Yangling field. **C**, Adult plant responses on leaves of (from left to right) 03031-1-5 H62, F_1 , Avocet S, and Jinmai 47.

TABLE 2. Genetic analysis of stripe rust resistance in different generations of Avocet S $\times$ 03031-1-5 H62 in the fields of Yangling and Tianshui

Location	Parents and generation	Observed number of F_2 plants or F_3 lines ^a			Expected ratio	χ^2	P
		R (ITs 0–3)	Seg. (ITs 0–9)	S (ITs 7–9)			
Yangling	03031-1-5 H62	30		0	–	–	–
	Avocet S	0		28	–	–	–
	F_1	10			–	–	–
	F_2	134		40	3:1	0.38	0.54
	$F_{2:3}$	43	90	34	1:2:1	1.98	0.37
Tianshui	03031-1-5 H62	25		0	–	–	–
	Avocet S	0		20	–	–	–
	$F_{2:3}$	40	93	34	1:2:1	2.03	0.36

^a R: homozygous resistant line, Seg.: segregating line, and S: homozygous susceptible line.

YrExp2-5BL, *QYrex.wgp-1BL*, *QYrex.wgp-3BL*, and *QYrex.wgp-6AS*) using five *P. striiformis* f. sp. *tritici* isolates at seedling and adult plant stage. As shown in Table 5, 03031-1-5 H62 was susceptible to most isolates except CYR32 and HY8 in the seedling tests, in which it conferred resistance to all races in the adult plant tests. The response of 03031-1-5 H62 (*YrH62*) was different from the lines with *Yr9*, *Yr10*, *Yr15*, *Yr26*, *Yr29*, *Yr64*, *Yr65*, *YrL693*, *YrH52*, *YrSM139-1B*, *YrAlp-1BL*, and *YrExp1-1BL*.

Polymorphisms of KASP markers flanking *YrH62*. One hundred and fifty-eight wheat genotypes were tested for polymorphism at loci *AX-109871410*, *AX-109472792*, *AX-109352427*, and *AX-109862469* near the *YrH62* locus (Supplementary Table S2). The 03031-1-5 H62 allele of *AX-109352427* was present in 17 genotypes and absent in 137 genotypes, indicating an 89% polymorphism rate. The 03031-1-5 H62 allele of *AX-109862469* was present in 5 genotypes and absent in 151 genotypes,

Fig. 2. Stripe rust phenotype distribution and the numbers and percentages of polymorphic single nucleotide polymorphisms (SNPs). Frequency distributions of **A**, infection type and **B**, maximum disease severity of 167 $F_{2,3}$ lines of AvS $\times$ 03031-1-5 H62. The number and percentage of **C**, polymorphic SNP loci in each of the 21 wheat chromosomes and the number of **D**, SNPs in each 1 Mb region of chromosome 1B identified using the 90K SNP array and those identified with the 660K SNP array (**E** and **F**, respectively). SNPs in the black dotted boxes were analyzed in the mapping population using the KASP assay.

indicating a 97% polymorphism rate. None of the tested wheat genotypes had the resistant parent allele of both flanking marker SNPs, indicating that the combination of the two markers can be used for marker-assisted selection of *YrH62*. Furthermore, the combination of KASP markers *AX-109352427* and *AX-109862469* can completely differentiate *YrH62* from other genes on chromosome 1B (Supplementary Fig. S1).

Candidate genes for stripe rust resistance in the target region. A search by the BLAST procedure revealed that nine genes were identified in the target region and many SNPs were mapped in a single gene (Supplementary Table S3). In the *YrH62* region, *Traes_1BL_D48C0BE54* was especially interesting as it is a nuclear transporter found in bread wheat and its progenitor wheat *T. urartu* and was involved in stress responses and plant immune activation. The product encoded by *Traes_1BL_869ED1456* was probably related to sugar kinase in *T. urartu*.

DISCUSSION

Wheat chromosome 1B is known for its rich of disease resistance genes. To date, 12 *Yr* genes have been reported on chromosome 1B: *Yr9*, *Yr10*, *Yr15*, *Yr24/26/CH42*, *Yr29/Lr46*, *Yr64*, *Yr65*, *YrH52*, *YrL693*, *YrSM139*, *YrAlp*, and *YrExp1* (Cheng et al. 2014; Huang et al. 2014; Lin and Chen 2007, 2008; Nagy et al. 2003; Peng et al. 1999; Sun et al. 1997; Wang et al. 2002; William et al. 2003; Zhang et al. 2013, 2016). All of these genes except *Yr29/Lr46* confer all-stage resistance (ASR) or race-specific resistance in the previous reports. *Yr9*, present in the 1RS segment of rye, was ineffective to current Chinese *P. striiformis* f. sp. *tritici* races (Wan et al. 2007). *Yr10* in Turkish hexaploid wheat accession PI 178383 is overcome by race V26. *Yr15*, *YrH52*, and *YrSM139-1B* are derived from wild emmer wheat (*T. dicoccoides*), which were reported to confer resistance against all Chinese races (Zeng et al. 2015; Zhang et al. 2016; J. Peng, *personal communication*). Durum wheat lines are the donors of *Yr24/26/CH42*, *Yr64* and *Yr65*. Cheng et al. (2014) reported that resistance in PI 331260 (*Yr64*) and PI 480016 (*Yr65*) was characterized as ASR to all tested races, including those virulent to *Yr10* and *Yr24/26/CH42*. *Thinopyrum intermedium*-derived *YrL693* exhibits ASR to all tested Chinese *P. striiformis* f. sp. *tritici* races including CYR32, CYR33, and V26 (Huang et al. 2014). Express and Alpowa had nonrace specific, high-temperature adult plant (HTAP) resistance as well as race-specific, seedling resistance (*YrExp1-1BL* and *YrExp1-5BL* in Express and *YrApl-1B* in Alpowa (Lin and Chen 2007, 2008). In our comparison test, *Yr9*, *YrExp1-1B*, and *YrApl-1B* were susceptible to all tested races; V26/Gui22 was virulent to both *Yr10* and *Yr26*; *Yr15*, *Yr65*, *YrL693*, and *YrH52* conferred resistance against all tested races. These phenotypic responses are consistent with the published results. However, ASR genes *Yr64* and *YrSM139-1B* were susceptible when tested with race V26/Gui22 in this study. All of the above genes showed race-specific resistance. *Yr29/Lr46* as an APR gene was susceptible to all tested races at both seedling and adult plant stage. *YrH62*

originally from the CIMMYT-derived common wheat advanced line confers resistance in adult plants despite possessing small effects in seedlings. These comparisons indicated the uniqueness of *YrH62* in this study. Moreover, the 90K SNP and SSR markers can be used to compare relative distances of *YrH62* and other genes. *YrH62* was located within a 3.6 cM interval flanked by markers *Xgwm273*—*IWB9735*—*IWB11553* and *IWB9149/IWB35383*—*Xbarc137*. According to the consensus maps (Cheng et al. 2014; Maccaferri et al. 2015a), the order of genes on 1B is: *Yr10*—(3.5 cM)—*Yr9*—(27.4 cM)—*YrAl*—9.1 cM—*Yr15*—3.7 cM—*YrH52*—1.8 cM—*Yr64*—*YrSM139-1B*—3.2 cM—*YrL693*—0.5 cM—*YrH62*—4.4 cM—*Yr65*—2.8 cM—*Yr24/26/CH42*—54.4 cM—*YrExp1*—33.7 cM—*Yr29/Lr46*. Based on the molecular markers, the resistance origins, seedling and adult plant responses to the tested *P. striiformis* f. sp. *tritici* races, and the comparison of relative distances, it can be concluded that *YrH62* is different from the reported resistance genes in 1B.

In addition, several stripe rust APR QTL in chromosome 1B have been reported, most of which were connected to the *Lr46/Yr29* locus (Rosewarne et al. 2013; Singh et al. 1998). Rosewarne et al. (2012) reported a small effect QTL flanked by DArT markers *wPT-8168* and *wPT-6240* on chromosome 1BS in cultivar Pastor. According to the consensus 90K SNP map (Maccaferri et al. 2015a), *wPT-8168* is near *IWB47638* that is linked to *YrH62*, whereas *IWB47638* is about 5 cM from *YrH62*. Another QTL named *QYr.cau-1BS*, explaining about 10% of the phenotypic variation, was located in the region *gwm374* — *gwm264* — *barc194* near the distal region far away from *YrH62* (Quan et al. 2013). In the near centromere region, Naz et al. (2012) also reported a major effective QTL for stripe rust seedling resistance, *QYrs.Z86-1B*, originated from *T. turgidum* subsp. *dicoccoides* and it was finally considered as *Yr15*. These results indicated that *YrH62* is very likely a novel gene in chromosome 1B.

The wheat SNP arrays facilitate constructing high density genetic maps at a relatively low cost in wheat. High-resolution maps and SNP-based consensus maps have been constructed with the 90K SNP in tetraploid wheat and hexaploid wheat (Maccaferri et al. 2015a, b; Marone et al. 2012; Wang et al. 2014). Based on the SNP location information in these maps, we can rapidly position a single gene candidate region by a combination of SNP array and BSA. Chromosome-specific SNP loci were selected and converted to KASP markers to be screened in BSA according to the density of SNPs. Using this method, 35 SNP loci from 90K SNP and 18 SNP loci from 660K SNP were converted to KASP markers, and together with SSR markers, a genetic map was generated with 15 SNP and 3 SSR. In general, SNP array is an efficient marker system for SNP discovery and it is useful for QTL identification and mapping when it is validated with KASP-SNP assays. Using KASP-SNP assays in this study, *YrH62* was mapped in a 1.0 cM interval which is a good candidate region for map-based cloning. Moreover, more than 100 polymorphic SNP loci were identified in this region by 660K SNP array that established an important foundation for such work.

TABLE 3. Analysis of variance of maximum disease severity (MDS) and infection type (IT) scores for F_{2:3} lines derived from AvS × 03031-1-5 H62^a

Source of variation	MDS			IT		
	df	Mean square	F value	df	Mean square	F value
Line	166	1,943.04	19.10**	166	12.11	14.16**
Environment	1	37,099.97	364.70**	1	87.46	102.27**
Line × environment	166	275.26	2.71**	166	1.76	2.05**
Error	661	101.73		661	0.86	
σ_g^2	307.81			2.82		
h_b^2	0.86			0.88		

^a *, Significant at *P* < 0.01. **, Significant at *P* < 0.001.

Studies on molecular genetics of APR to rusts has indicated that there is not just only one single model for the genetics or mechanisms of durable resistance (Brown 2015). *Lr34* encodes a member of the ABC transporter G family (Krattinger et al. 2009); *Lr67* encodes an H⁺/monosaccharide transporter similar to STP13 of *Arabidopsis thaliana* (Moore et al. 2015); the YR36 protein contains both kinase and START domains (Fu et al. 2009). Based on the functions of these identified proteins, vesicle

trafficking and protein/metabolite transportation are probably common physiological processes involved in APR (Niks et al. 2015). In the present study, bioinformatics analysis of the mapped SNPs in the target region for stripe rust resistance showed that wheat gene *Traes_1BL_D48C0BE54* corresponds to nuclear transporting (Ling et al. 2013; Lopato et al. 2006). Nuclear transporting macromolecular proteins, immune receptors, signal transducers, and transcription factors is a crucial regulatory

B	Individuals	28	1	3	2	1	1	1	2	1	2	1	1	1	2	1	72	1	3	3	1	1	1	1	2	2	2	1	5	1	25	
	IWA1949	A	A	A	A	A	A	A	H	H	H	H	H	H	H	H	H	.	H	H	H	H	H	H	H	B	B	B	B	B	B	
	Xgwm273	A	A	A	A	A	A	A	A	A	H	H	H	H	H	H	H	H	H	H	H	H	H	H	B	H	B	B	B	B	B	
	IWB9735	A	A	A	A	A	A	C	A	A	A	C	C	C	.	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	
	IWB1569	A	A	A	A	A	A	H	A	A	A	A	H	H	H	H	H	H	H	H	H	H	H	H	B	H	H	B	B	B	B	
	IWB11553	A	A	A	A	A	A	H	A	A	A	A	H	H	H	H	H	H	H	H	H	H	H	H	B	B	H	H	B	B	B	
	AX-108995142	A	A	A	A	A	A	H	A	.	A	A	A	H	H	H	H	H	H	H	H	H	H	B	B	B	H	H	H	B	B	B
	AX-110071821	A	A	A	A	A	A	H	A	A	A	A	A	H	H	.	H	.	H	H	H	H	B	B	B	H	H	H	B	B	B	
	AX-109871410	A	.	A	A	A	H	H	A	A	A	A	A	H	H	H	H	H	H	H	H	H	B	B	B	H	H	H	B	B	B	
	AX-109472792	A	.	A	A	A	H	H	A	A	A	A	A	H	H	H	H	.	H	H	H	H	B	B	B	H	H	H	B	B	B	
	AX-109352427	A	.	A	A	A	H	H	A	A	A	A	A	H	H	H	H	H	H	H	H	H	B	B	B	H	H	H	B	B	B	
	YrH62	R	.	R	R	H	H	H	R	R	R	R	R	H	H	H	H	.	H	H	H	H	S	S	S	H	H	H	S	S	S	
	AX-109862469	A	A	A	A	H	H	H	A	A	A	A	A	A	H	H	H	H	H	H	H	B	B	B	B	H	H	H	B	B	B	
	IWB9149	A	A	A	A	H	H	H	A	A	A	A	A	A	A	H	H	H	H	H	H	B	B	B	B	H	H	H	B	.	B	
	IWB35383	D	D	D	D	D	D	D	D	.	D	D	D	D	D	D	D	D	D	D	D	B	B	B	B	D	D	D	B	B	B	
	Xbarc137	A	A	A	A	H	H	H	A	A	A	A	A	A	A	H	H	H	H	H	B	B	B	B	B	H	H	H	B	B	B	
	IWB820	A	A	A	H	H	H	H	A	A	A	A	A	A	A	A	H	H	H	H	B	B	B	B	B	H	H	H	B	B	B	
	IWB820	D	D	D	D	D	D	D	D	D	D	D	D	D	.	D	D	D	D	B	B	B	B	B	B	D	D	D	D	B	B	
	Xbarc181	A	A	A	H	H	H	H	A	A	A	A	A	A	A	A	H	H	B	B	B	B	B	B	B	H	H	H	H	B	B	
	IWB51640	A	A	H	H	H	H	H	A	A	A	.	A	A	A	A	H	H	B	B	B	B	B	B	.	B	H	H	H	H	B	

Fig. 3. A, Linkage map of *YrH62* on chromosome 1BS in comparison with the consensus (Maccaferri et al. 2015a, b) and deletion maps (<https://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/>) and **B**, the numbers of $F_{2:3}$ lines for each allelic genotype of the 18 markers linked to the *YrH62* locus. The alleles are abbreviated according to their origin: A, 03031-1-5 H62; B, AvS; H, Heterozygous; C, AvS + heterozygous; and D, 03031-1-5 H62 + heterozygous. The phenotypes are abbreviated as R, homozygous resistant line; H, segregating line; and S, homozygous susceptible line. Missing calls are indicated by a dot.

mechanism for plant immune activation and responses to abiotic stress (Gu et al. 2016; Reddy and Ali 2011). The protein encoded by *Traes_1BL_869ED1456* was corresponding to sugar kinase. As a super gene family, sugar kinases can be divided into many distinct nonhomologous families and they were involved in regulating many activities in plant cells such as energy metabolism and transport (Bork et al. 1993; Conway and Josef 2016; Usuda et al. 1997). The function of energy metabolism and transport is similar to *Lr34/Yr18* or *Lr67/Yr46*. Prediction of candidate genes is a basis for the next step in the process of map-based cloning. Nevertheless, further genetic studies and more detailed analyses are needed to confirm the roles of these genes in stripe rust response.

Marker-assisted selection provides a desirable approach to quickly detect APR to stripe rust in breeding programs (Chen 2013). In this study, *AX-109352427* and *AX-109862469* are the two closest flanking markers for *YrH62* and showed similar effects which remain valuable markers for MAS. They can increase

selection accuracy when used together. Pyramiding stripe rust resistance genes has showed promises in prolonging durability of major gene resistance (Chen 2013; Li and Zeng 2002). Growing cultivars with stacking effective race-specific resistance and durable adult plant resistance should be a strategy for control of stripe rust in the area where the disease occurs frequently (He et al. 2011). In the present study, wheat line 03031-1-5 H62 is not only an ideal germplasm for resistance to stripe rust, but it also has many desirable agronomic traits which make it a good intermediate material for breeding. Closely linked molecular markers can be used to pyramid *YrH62* with additional resistance genes into wheat cultivars.

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TABLE 4. Marker interval, logarithm of odds score (LOD), additive effect (Add), and percentage of the phenotypic variance explained (PVE) by stripe rust resistance QTL detected in the AvS × 03031-1-5 H62 F_{2:3} population

Location	Marker interval	LOD	Add	PVE
Infection type				
Yangling	<i>AX-109352427</i> — <i>AX-109862469</i>	47.8	−2.5	73.6
Tianshui	<i>AX-109352427</i> — <i>AX-109862469</i>	37.6	−2.3	64.9
Average				69.3
Maximum disease severity				
Yangling	<i>AX-109352427</i> — <i>AX-109862469</i>	40.6	−27.9	67.8
Tianshui	<i>AX-109352427</i> — <i>AX-109862469</i>	32.8	−21.0	59.8
Average				63.8

TABLE 5. Seedling infection types and adult plant responses of wheat lines produced by inoculation with five races of *Puccinia striiformis* f. sp. *tritici* and in fields by artificial inoculation (Yangling) or natural infection (Tianshui)

Wheat lines	Stage	Greenhouse					Field	
		CYR32	CYR33	V26/Gui22	HY8	V26/92R137	Tianshui	Yangling
Mingxian 169	Seedling	9	9	9	9	9	9	— ^a
	Adult plant	100S ^b	90S	100S	95S	100S	100S	100S
Avocet S	Seedling	9	9	9	9	9	9	—
	Adult plant	100S	90S	100S	80S	100S	100S	100S
Jinmai 47	Seedling	8	9	9	9	9	9	—
	Adult plant	100S	90MS	100S	90S	80S	100S	100S
03031-1-5 H62	Seedling	6	8	8	6	7	8	—
	Adult plant	5R	2R	5R	1R	1R	5R	5R
AvSYr9NIL	Seedling	9	9	9	8	9	9	—
	Adult plant	90S	80S	90S	80S	90S	100S	100S
AvSYr10NIL	Seedling	1	2	9	2	4	8	—
	Adult plant	1R	5R	70S	10R	10MR	70MS	5R
AvSYr15NIL	Seedling	0	1	2	1	1	1	—
	Adult plant	5R	2R	10R	1R	5R	5R	5R
AvSYr29NIL	Seedling	8	9	8	9	9	8	—
	Adult plant	70MS	40S	60S	70S	60S	80S	90S
92R137 (<i>Yr26</i>)	Seedling	1	2	9	2	8	8	—
	Adult plant	10R	10R	80MS	10R	60MS	70MS	5R
Alpowa (<i>YrAlp</i>)	Seedling	8	7	9	9	9	8	—
	Adult plant	40M	30M	60MS	60MS	50MS	40R	60S
Express (<i>YrExp1</i>)	Seedling	8	7	9	9	9	7	—
	Adult plant	20R	10R	20R	20R	20R	10R	10R
Shaanmai139 (<i>YrSM139</i>)	Seedling	1	2	7	2	6	8	—
	Adult plant	5R	10R	20MS	5R	20MS	40MS	5R
PI 660064 (<i>Yr64</i>)	Seedling	2	2	8	9	3	8	—
	Adult plant	5R	10R	60S	50S	40MR	80MS	10R
PI 679621 (<i>Yr65</i>)	Seedling	2	1	4	2	1	—	—
	Adult plant	10R	5R	10R	5R	1R	—	—
L693 (<i>YrL693</i>)	Seedling	1	2	2	1	2	—	—
	Adult plant	5R	5R	10R	1R	5R	—	—
H52 (<i>YrH52</i>)	Seedling	1	1	2	2	1	—	—
	Adult plant	1R	5R	5R	10R	5R	—	—

^a —, not tested.

^b R = resistant (IT 0 to 3), MR = moderately resistant (IT 4 to 6), MS = moderately susceptible (IT 7 to 8), and S = susceptible (IT 9).

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LITERATURE CITED

- Allard, R. W. 1960. Principles of Plant Breeding. John Wiley and Sons, Inc., New York.
- Allen, A. M., Barker, G. L. A., Wilkinson, P., Burrige, A., Winfield, M., Coghill, J., Uauy, C., Griffiths, S., Jack, P., Berry, S., Werner, P., Melichar, J. P. E., McDougall, J., Gwilliam, R., Robinson, P., and Edwards, K. J. 2013. Discovery and development of exome-based, co-dominant single nucleotide polymorphism markers in hexaploid wheat (*Triticum aestivum* L.). *Plant Biotechnol. J.* 11:279-295.
- Basnet, B. R., Singh, R. P., Ibrahim, A. M. H., Herrera-Foessel, S. A., Huerta-Espino, J., Lan, C., and Rudd, J. C. 2014. Characterization of *Yr54* and other genes associated with adult plant resistance to yellow rust and leaf rust in common wheat Quaiu 3. *Mol. Breed.* 33:385-399.
- Bork, P., Sander, C., and Valencia, A. 1993. Convergent evolution of similar enzymatic function on different protein folds: The hexokinase, ribokinase, and galactokinase families of sugar kinases. *Protein Sci.* 2:31-40.
- Brown, J. K. M. 2015. Durable resistance of crops to disease: A Darwinian perspective. *Annu. Rev. Phytopathol.* 53:513-539.
- Cavanagh, C. R., Chao, S. M., Wang, S. C., Huang, B. E., Stephen, S., Kiani, S., Forrest, K., Saintenac, C., Brown-Guedira, G. L., Akhunova, A., See, D., Bai, G., Pumphrey, M., Tomar, L., Wong, D., Kong, S., Reynolds, M., Da Silva, M. L., Bockelman, H., Talbert, L., Anderson, J. A., Dreisigacker, S., Baenziger, S., Carter, A., Korzun, V., Morrell, P. L., Dubcovsky, J., Morell, M. K., Sorrells, M. E., Hayden, M. J., and Akhunov, E. 2013. Genome-wide comparative diversity uncovers multiple targets of selection for improvement in hexaploid wheat landraces and cultivars. *Proc. Nat. Acad. Sci.* 110:8057-8062.
- Chen, W. Q., Wellings, C., Chen, X. M., Kang, Z. S., and Liu, T. G. 2014. Wheat stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici*. *Mol. Plant Pathol.* 15:433-46.
- Chen, W. Q., Wu, L. R., Liu, T. G., Xu, S. C., Jin, S. L., Peng, Y. L., and Wang, B. T. 2009. Race dynamics, diversity, and virulence evolution in *Puccinia striiformis* f. sp. *tritici*, the causal agent of wheat stripe rust in China from 2003 to 2007. *Plant Dis.* 93:1093-1101.
- Chen, X. M. 2005. Epidemiology and control of stripe rust [*Puccinia striiformis* f. sp. *tritici*] on wheat. *Can. J. Plant Pathol.* 27:314-337.
- Chen, X. M. 2013. Review Article: High-temperature adult-plant resistance, key for sustainable control of stripe rust. *Am. J. Plant Sci.* 4:608-627.
- Chen, X. M., Penman, L., Wan, A. M., and 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., Xu, L. S., Wang, M. N., See, D. R., and Chen, X. M. 2014. Molecular mapping of genes *Yr64* and *Yr65* for stripe rust resistance in hexaploid derivatives of durum wheat accessions PI 331260 and PI 480016. *Theor. Appl. Genet.* 127:2267-2277.
- Conway, L. P., and Josef, V. 2016. Functional analysis of anomeric sugar kinases. *Carbohydr. Res.* 432:23-30.
- Cui, F., Zhang, N., Fan, X. L., Zhang, W., Zhao, C. H., Yang, L. J., Pan, R. Q., Chen, M., Han, J., Zhao, X. Q., Ji, J., Tong, Y. P., Zhang, H. X., Jia, J. Z., Zhao, G. Y., and Li, J. M. 2017. Utilization of a Wheat660K SNP array-derived high-density genetic map for high-resolution mapping of a major QTL for kernel number. *Sci. Rep.* 7:3788.
- Dreisigacker, S., Wang, X., Martinez Cisneros, B. A., Jing, R. L., and Singh, P. K. 2015. Adult-plant resistance to Septoria tritici blotch in hexaploid spring wheat. *Theor. Appl. Genet.* 128:2317-2329.
- Fu, D. L., Uauy, C., Distelfeld, A., Blechl, A., Epstein, L., Chen, X. M., Sela, H., Fahima, T., and Dubcovsky, J. 2009. A kinase-START gene confers temperature-dependent resistance to wheat stripe rust. *Science* 323: 1357-1360.
- Gu, Y. N., Zebell, S. G., Liang, Z. Z., Wang, S., Kang, B. H., and Dong, X. N. 2016. Nuclear pore permeabilization is a convergent signaling event in effector-triggered immunity. *Cell* 166:1526-1538.
- Han, D. J., Wang, Q. L., Chen, X. M., Zeng, Q. D., Wu, J. H., Xue, W. B., Zhan, G. M., Huang, L. L., and Kang, Z. S. 2015. Emerging *Yr26*-virulent races of *Puccinia striiformis* f. sp. *tritici* are threatening wheat production in the Sichuan Basin, China. *Plant Dis.* 99:754-760.
- He, Z. H., Lan, C. X., Chen, X. M., Zou, Y. C., Zhuang, Q. S., and Xia, X. C. 2011. Progress and perspective in research of adult-plant resistance to stripe rust and powdery mildew in wheat. *Sci. Agric. Sin.* 44: 2193-2215.
- Hou, L. Y., Jia, J. Q., Zhang, X. J., Li, X., Yang, Z. J., Ma, J., Guo, H. J., Zhan, H. X., Qiao, L. Y., and Chang, Z. J. 2016. Molecular mapping of the stripe rust resistance gene *Yr69* on wheat chromosome 2AS. *Plant Dis.* 100: 1717-1724.
- Hovmøller, M. S., Walter, S., and Justesen, A. F. 2010. Escalating threat of wheat rusts. *Science* 329:369.
- Huang, Q., Li, X., Chen, W. Q., Xiang, Z. P., Zhong, S. F., Chang, Z. J., Zhang, M., Zhang, H. Y., Tan, F. Q., Ren, Z. L., and Luo, P. G. 2014. Genetic mapping of a putative *Thinopyrum intermedium*-derived stripe rust resistance gene on wheat chromosome 1B. *Theor. Appl. Genet.* 127:843-853.
- Wang, J. K. 2009. Inclusive composite interval mapping of quantitative trait genes. *Acta Phytopathol. Sin.* 35:239-245.
- Jia, J. Z., and Zhao, G. Y. 2016. Wheat660 SNP array developed by CAAS. https://wheat.pw.usda.gov/ggpages/topics/Wheat660_SNP_array_developed_by_CAAS.pdf
- Jin, Y., Szabo, L. J., and Carson, M. 2010. Century-old mystery of *Puccinia striiformis* life history solved with the identification of *Berberis* as an alternate host. *Phytopathology* 100:432-435.
- Kang, Z. S., Zhao, J., Han, D. J., Zhang, H. C., Wang, X. J., Wang, C. F., Han, Q. M., Guo, J., and Huang, L. L. 2010. Status of wheat rust research and control in China. Pages 50-69 in: BGRI 2010 Technical Workshop Oral Presentations. Borlaug Global Rust Initiative.
- Kosambi, D. D. 1943. The estimation of map distances from recombination values. *Ann. Eugen.* 12:172-175.
- Krattinger, S. G., Lagudah, E. S., Spielmeier, W., Singh, R. P., Huerta-Espino, J., McFadden, H., Bossolini, E., Selter, L. L., and Keller, B. 2009. A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. *Science* 323:1360-1363.
- Lei, Y., Wang, M. N., Wan, A. M., Xia, C. J., See, D. R., Zhang, M., and Chen, X. M. 2017. Virulence and molecular characterization of experimental isolates of the stripe rust pathogen (*Puccinia striiformis*) indicate somatic recombination. *Phytopathology* 107:329-344.
- Li, Z. Q., and Zeng, S. M. 2002. Wheat Rust in China. China Agriculture Press, Beijing.
- Lin, F., and Chen, X. M. 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., and Chen, X. M. 2008. Molecular mapping of genes for race-specific overall resistance to stripe rust in wheat cultivar Express. *Theor. Appl. Genet.* 116:797-806.
- Line, R. F., and 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. Dep. Agric. Tech. Bull. No.1788: 74.
- Ling, H. Q., Zhao, S., Liu, D., Wang, J., Sun, H., Zhang, C., Fan, H., Li, D., Dong, L., Tao, Y., Gao, C., Wu, H., Li, Y., Cui, Y., Guo, X., Zheng, S., Wang, B., Yu, K., Liang, Q., Yang, W., Lou, X., Chen, J., Feng, M., Jian, J., Zhang, X., Luo, G., Jiang, Y., Liu, J., Wang, Z., Sha, Y., Zhang, B., Wu, H., Tang, D., Shen, Q., Xue, P., Zou, S., Wang, X., Liu, X., Wang, F., Yang, Y., An, X., Dong, Z., Zhang, K., Zhang, X., Luo, M. C., Dvorak, J., Tong, Y., Wang, J., Yang, H., Li, Z., Wang, D., Zhang, A., and Wang, J. 2013. Draft genome of the wheat A-genome progenitor *Triticum urartu*. *Nature* 496: 87-90.
- Lopato, S., Borisjuk, L., Milligan, A. S., Shirley, N., Bazanova, N., and Langridge, P. 2006. Systematic identification of factors involved in post-transcriptional processes in wheat grain. *Plant Mol. Biol.* 62: 637-653.
- Lu, Y., Wang, M. N., Chen, X. M., See, D., Chao, S. M., and Jing, J. X. 2014. Mapping of *Yr62* and a small effect QTL for high-temperature adult-plant resistance to stripe rust in spring wheat PI 192252. *Theor. Appl. Genet.* 127: 1449-1459.
- Maccaferri, M., Zhang, J. L., Bulli, P., Abate, Z., Chao, S. M., Cantu, D., Bossolini, E., Chen, X. M., Pumphrey, M., and Dubcovsky, J. 2015a. A genome-wide association study of resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*) in a worldwide collection of hexaploid spring wheat (*Triticum aestivum* L.). *G3 (Bethesda)* 5:449-465.
- Maccaferri, M., Ricci, A., Salvi, S., Milner, S. G., Noli, E., Martelli, P. L., Casadio, R., Akhunov, E., Scalabrin, S., Vendramin, V., Ammar, K., Blanco, A., Desiderio, F., Distelfeld, A., Dubcovsky, J., Fahima, T., Faris, J., Korol, A., Massi, A., Mastrangelo, A. M., Morgante, M., Pozniak, C., N'Diaye, A., Xu, S., and Tuberosa, R. 2015b. A high-density, SNP-based consensus map of tetraploid wheat as a bridge to integrate durum and bread wheat genomics and breeding. *Plant Biotechnol. J.* 13:648-663.

- Mammadov, J., Aggarwal, R., Buyyarapu, R., and Kumpatla, S. 2012. SNP markers and their impact on plant breeding. *Int. J. Plant Genomics* 2012: 728398.
- Marone, D., Laido, G., Gadaleta, A., Colasuonno, P., Ficco, D. B., Giancaspro, A., Giove, S., Panio, G., Russo, M. A., De Vita, P., Cattivelli, L., Papa, R., Blanco, A., and Mastrangelo, A. M. 2012. A high-density consensus map of A and B wheat genomes. *Theor. Appl. Genet.* 125:1619-1638.
- McIntosh, R. A., Dubcovsky, J., Rogers, W. J., Morris, C., Appels, R., and Xia, X. C. 2014. Catalogue of gene symbols for wheat: 2013-2014 Supplement. <http://shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2013.pdf>
- McIntosh, R. A., Dubcovsky, J., Rogers, W. J., Morris, C., and Xia, X. C. 2017. Catalogue of gene symbols for wheat: 2017 Supplement. <http://shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2017.pdf>
- Meng, L., Li, H. H., Zhang, L. Y., and Wang, J. K. 2015. QTL IciMapping: Integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. *Crop J.* 3:269-283.
- Michelmore, R. W., Paran, I., and Kesseli, R. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. *Proc. Nat. Acad. Sci.* 88:9828-9832.
- Moore, J. W., Herrera-Foessel, S., Lan, C. X., Schnippenkoetter, W., Ayliffe, M., Huerta-Espino, J., Lillemo, M., Viccars, L., Milne, R., Periyannan, S., Kong, X. Y., Spielmeier, W., Talbot, M., Bariana, H., Patrick, J. W., Dodds, P., Singh, R., and Lagudah, E. 2015. A recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. *Nat. Genet.* 47: 1494-1498.
- Nagy, E. D., Eder, C., Molnár-Láng, M., and Lelley, T. 2003. Genetic mapping of sequence-specific PCR-based markers on the short arm of the 1BL.1RS wheat-rye translocation. *Euphytica* 132:243-249.
- Naz, A. A., Kunert, A., Flath, K., Pillen, K., and Léon, J. 2012. Advanced backcross quantitative trait locus analysis in winter wheat: Dissection of stripe rust seedling resistance and identification of favorable exotic alleles originated from a primary hexaploid wheat (*Triticum turgidum* ssp. *dicoccoides* × *Aegilops tauschii*). *Mol. Breed.* 30:1219-1229.
- Neelam, K., Brown-Guedira, G., and Huang, L. 2013. Development and validation of a breeder-friendly KASPar marker for wheat leaf rust resistance locus *Lr21*. *Mol. Breed.* 31:233-237.
- Niks, R. E., Qi, X. Q., and Marcel, T. C. 2015. Quantitative resistance to biotrophic filamentous plant pathogens: Concepts, misconceptions, and mechanisms. *Annu. Rev. Phytopathol.* 53:445-470.
- Peng, J. H., Fahima, T., Röder, M. S., Li, Y. C., Dahan, A., Grama, A., Ronin, Y. I., Korol, A. B., and Nevo, E. 1999. Microsatellite tagging of the stripe-rust resistance gene *YrH52* derived from wild emmer wheat, *Triticum dicoccoides*, and suggestive negative crossover interference on chromosome 1B. *Theor. Appl. Genet.* 98:862-872.
- Peterson, R. F., Campell, A. B., and Hannah, A. 1948. A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. *Can. J. Res.* 26: 496-500.
- Quan, W., Hou, G. L., Chen, J., Du, Z. Y., Lin, F., Guo, Y., Liu, S., and Zhang, Z. J. 2013. Mapping of QTL lengthening the latent period of *Puccinia striiformis* in winter wheat at the tillering growth stage. *Eur. J. Plant Pathol.* 136:715-727.
- Ramirez-Gonzalez, R. H., Segovia, V., Bird, N., Fenwick, P., Holdgate, S., Berry, S., Jack, P., Caccamo, M., and Uauy, C. 2014. RNA-Seq bulked segregant analysis enables the identification of high-resolution genetic markers for breeding in hexaploid wheat. *Plant Biotechnol. J.* 13:613-624.
- Ramirez-Gonzalez, R. H., Uauy, C., and Caccamo, M. 2015. PolyMarker: A fast polyploid primer design pipeline. *Bioinformatics* 31:2038-2039.
- Rasheed, A., Wen, W. E., Gao, F. M., Zhai, S. N., Jin, H., Liu, J. D., Guo, Q., Zhang, Y. J., Dreisigacker, S., Xia, X. C., and He, Z. H. 2016. Development and validation of KASP assays for genes underpinning key economic traits in bread wheat. *Theor. Appl. Genet.* 129:1843-1860.
- Stubbs, R. W. 1985. Stripe rust. Pages 61-101 in: *The Cereal Rusts*. Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, New York.
- Reddy, A. S. N., and Ali, G. S. 2011. Plant serine/arginine-rich proteins: Roles in precursor messenger RNA splicing, plant development, and stress responses. *Wiley Interdiscip. Rev. RNA* 2:875-889.
- Ren, R. S., Wang, M. N., Chen, X. M., and Zhang, Z. J. 2012. Characterization and molecular mapping of *Yr52* for high-temperature adult-plant resistance to stripe rust in spring wheat germplasm PI 183527. *Theor. Appl. Genet.* 125:847-857.
- Rosewarne, G. M., Herrera-Foessel, S. A., Singh, R. P., Huerta-Espino, J., Lan, C. X., and He, Z. H. 2013. Quantitative trait loci of stripe rust resistance in wheat. *Theor. Appl. Genet.* 126:2427-2449.
- Rosewarne, G. M., Singh, R. P., Huerta-Espino, J. S., Herrera-Foessel, A., Forrest, K. L., Hayden, M. J., and Rebetzke, G. J. 2012. Analysis of leaf and stripe rust severities reveals pathotype changes and multiple minor QTLs associated with resistance in an Avocet × Pastor wheat population. *Theor. Appl. Genet.* 124:1283-1294.
- Semagn, K., Babu, R., Hearne, S., and Olsen, M. 2014. Single nucleotide polymorphism genotyping using kompetitive allele specific PCR (KASP): overview of the technology and its application in crop improvement. *Mol. Breed.* 33:1-14.
- Sharma-Poudyal, D., Chen, X. M., Wan, A. M., Zhan, G. M., Kang, Z. S., Cao, S. Q., Jin, S. L., Morgounov, A., Akin, B., Mert, Z., Shah, S. J. A., Bux, H., Ashraf, M., Sharma, R. C., Madariaga, R., Puri, K. D., Wellings, C., Xi, K. Q., Wanyera, R., Manninger, K., Ganzalez, M. I., Koyda, M., Sanin, S., and Patzek, L. J. 2013. Virulence characterization of international collections of the wheat stripe rust pathogen, *Puccinia striiformis* f. sp. *tritici*. *Plant Dis.* 97:379-386.
- Singh, R. P., Mujeeb-Kazi, A., and Huerta-Espino, J. 1998. *Lr46*: A gene conferring slow-rusting resistance to leaf rust in wheat. *Phytopathology* 88: 890-894.
- Somers, D. J., Isaac, P., and Edwards, K. 2004. A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.* 109:1105-1114.
- Song, W. N., Ko, L., and Henry, R. J. 1994. Polymorphisms in the α -amyl gene of wild and cultivated barley revealed by the polymerase chain reaction. *Theor. Appl. Genet.* 89:509-513.
- Sourdille, P., Singh, S., Cadalen, T., Brown-Guedira, G. L., Gay, G., Qi, L., Gill, B. S., Dufour, P., Murigneux, A., and Bernard, M. 2004. Microsatellite-based deletion bin system for the establishment of genetic-physical map relationships in wheat (*Triticum aestivum* L.). *Funct. Integr. Genomics* 4:12-25.
- Sun, G. L., Fahima, T., Korol, A. B., Turpeinen, T., Grama, A., Ronin, Y. I., and Nevo, E. 1997. Identification of molecular markers linked to the *Yr15* stripe rust resistance gene of wheat originated in wild emmer wheat, *Triticum dicoccoides*. *Theor. Appl. Genet.* 95:622-628.
- Usuda, Y., Kawasaki, H., Shimaoka, M., and Utagawa, T. 1997. Molecular cloning and transcriptional analysis of a guanosine kinase gene of *Brevibacterium acetylum* ATCC 953. *J. Bacteriol.* 179:6959-6964.
- Van Ooijen, J. W. 2006. JoinMap4, Software for the Calculation of Genetic Linkage Maps in Experimental Populations. Kyazma BV, Wageningen, The Netherlands.
- Varshney, R. K., Terauchi, R., and McCouch, S. R. 2014. Harvesting the promising fruits of genomics: Applying genome sequencing technologies to crop breeding. *PLoS Biol.* 12:e1001883.
- Voorrips, R. E. 2002. MapChart: Software for the graphical presentation of linkage maps and QTLs. *J. Hered.* 93:77-78.
- Wan, A. M., Chen, X. M., and He, Z. H. 2007. Wheat stripe rust in China. *Crop Pasture Sci.* 58:605-619.
- Wang, J. 2009. Inclusive composite interval mapping of quantitative trait genes. *Acta Agron. Sin.* 35:239-245.
- Wang, L. F., Ma, J. X., Zhou, R. H., Wang, X. M., and Jia, J. Z. 2002. Molecular tagging of the yellow rust resistance gene *Yr10* in common wheat, PI178383 (*Triticum aestivum* L.). *Euphytica* 124:71-73.
- Wang, M. N., and Chen, X. M. 2013. First report of Oregon grape (*Mahonia aquifolium*) as an alternate host for the wheat stripe rust pathogen (*Puccinia striiformis* f. sp. *tritici*) under artificial inoculation. *Plant Dis.* 97: 839.
- Wang, S. C., Wong, D., Forrest, K., Allen, A., Chao, S. M., Huang, B. E., Maccaferri, M., Salvi, S., Milner, S. G., Cattivelli, L., Mastrangelo, A. M., Whan, A., Stephen, S., Barker, G., Wieseke, R., Plieske, J., Lillemo, M., Mather, D., Appels, R., Dolferus, R., Brown-Guedira, G., Korol, A., Akhunova, A. R., Feuillet, C., Salse, J., Morgante, M., Pozniak, C., Luo, M. C., Dvorak, J., Morell, M., Dubcovsky, J., Ganai, M., Tuberosa, R., Lawley, C., Mikoulitch, I., Cavanagh, C., Edwards, K. J., Hayden, M., and Akhunova, E. 2014. Characterization of polyploid wheat genomic diversity using a high-density 90 000 single nucleotide polymorphism array. *Plant Biotechnol. J.* 12:787-796.
- Wellings, C. R. 2011. Global status of stripe rust: A review of historical and current threats. *Euphytica* 179:129-141.
- Wellings, C. R., Boyd, L. A., and Chen, X. M. 2012. Resistance to stripe rust in wheat: Pathogen biology driving resistance breeding. Pages 63-83 in: *Disease Resistance in Wheat*. I. Sharma, ed. CAB International, Wallingford, U.K.
- William, M., Singh, R. P., Huerta-Espino, J., Islas, S. O., and Hoisington, D. 2003. Molecular marker mapping of leaf rust resistance gene *Lr46* and its association with stripe rust resistance gene *Yr29* in wheat. *Phytopathology* 93:153-159.
- Winfield, M. O., Allen, A. M., Burrige, A. J., Barker, G. L., Benbow, H. R., Wilkinson, P. A., Coghill, J., Waterfall, C., Davassi, A., Scopes, G., Pirani, A., Webster, T., Brew, F., Bloor, C., King, J., West, C., Griffiths, S., King, I., Bentley, A. R., and Edwards, K. J. 2016. High-density SNP genotyping array for hexaploid wheat and its secondary and tertiary gene pool. *Plant Biotechnol. J.* 14:1195-1206.
- Xu, L. S., Wang, M. N., Cheng, P., Kang, Z. S., Hulbert, S. H., and Chen, X. M. 2013. Molecular mapping of *Yr53*, a new gene for stripe rust

- resistance in durum wheat accession PI 480148 and its transfer to common wheat. *Theor. Appl. Genet.* 126:523-533.
- Zeng, Q. D., Shen, C., Yuan, F. P., Wang, Q. L., Wu, J. H., Xue, W. B., Zhan, G. M., Yao, S., Chen, W., Huang, L. L., Han, D. J., and Kang, Z. S. 2015. The resistance evaluation of the *Yr* genes to the main prevalent pathotypes of *Puccinia striiformis* f. sp. *tritici* in China. *Acta Phytopathol. Sin.* 45: 641-650.
- Zhang, H., Zhang, L., Wang, C. Y., Wang, Y. J., Zhou, X. L., Lv, S. K., Liu, X. L., Kang, Z. S., and Ji, W. Q. 2016. Molecular mapping and marker development for the *Triticum dicoccoides*-derived stripe rust resistance gene *YrSM139-IB* in bread wheat cv. Shaanmai 139. *Theor. Appl. Genet.* 129: 369-376.
- Zhang, X. J., Han, D. J., Zeng, Q. D., Duan, Y. H., Yuan, F. P., Shi, J. D., Wang, Q. L., Wu, J. H., Huang, L. L., and Kang, Z. S. 2013. Fine mapping of wheat stripe rust resistance gene *Yr26* based on collinearity of wheat with *Brachypodium distachyon* and rice. *PLoS One* 8:e57885.
- Zhao, J., Wang, L., Wang, Z. Y., Chen, X. M., Zhang, H. C., Yao, J. N., Zhan, G. M., Chen, W. Q., Huang, L. L., and Kang, Z. S. 2013. Identification of eighteen *Berberis* species as alternate hosts of *Puccinia striiformis* f. sp. *tritici* and virulence variation in the pathogen isolates from natural infection of barberry plants in China. *Phytopathology* 103: 927-34.
- Zhao, J., Wang, M. N., Chen, X. M., and Kang, Z. S. 2016. Role of alternate hosts in epidemiology and pathogen variation of cereal rusts. *Annu. Rev. Phytopathol.* 54:207-228.
- Zhou, X. L., Han, D. J., Chen, X. M., Gou, H. L., Guo, S. J., Rong, L., Wang, Q. L., Huang, L. L., and Kang, Z. S. 2014. Characterization and molecular mapping of stripe rust resistance gene *Yr61* in winter wheat cultivar Pindong 34. *Theor. Appl. Genet.* 127:2349-2358.
- Zhou, X. L., Zhan, G. M., Huang, L. L., Han, D. J., and Kang, Z. S. 2015. Evaluation of resistance to stripe rust in eighty abroad spring wheat germplasms. *Sci Agric Sin.* 48:1518-1526.