ORIGINAL ARTICLE

Identification of a recessive gene YrZ15-1370 conferring adult plant resistance to stripe rust in wheat-Triticum boeoticum introgression line

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Abstract

Key message A novel recessive gene YrZ15-1370 derived from Triticum boeoticum confers adult–plant resistance to wheat stripe rust.

Abstract Stripe rust, caused by Puccinia striiformis f. sp. tritici (Pst), is one of the most damaging diseases of wheat globally and resistance is the effectively control strategy. Triticum boeoticum Boiss (T. monococcum L. ssp. aegilopoides, 2n = 2x = 14, ABAbb) accession G52 confers a high level of adult–plant resistance against a mixture of the Chinese prevalent Pst races. To transfer the resistance to common wheat, a cross was made between G52 and susceptible common wheat genotype Crocus. A highly resistant wheat-T. boeoticum introgression line Z15-1370 (F5 generation) with 42 chromosomes was selected cytologically and by testing with Pst races. F1, F2, and F2:3 generations of the cross between Z15-1370 and stripe rust susceptible common wheat Mingxian169 were developed. Genetic analysis revealed that the resistance in Z15-1370 was controlled by a single recessive gene, tentatively designated YrZ15-1370. Using the bulked segregant RNA-Seq (BSR-Seq) analysis, YrZ15-1370 was mapped to chromosome 6AL and flanked by markers KASP1370-3 and KASP-1370-5 within a 4.3 cM genetic interval corresponding to 1.8 Mb physical region in the Chinese Spring genome, in which a number of disease resistance-related genes were annotated. YrZ15-1370 differed from previously Yr genes identified on chromosome 6A based on its position and/or origin. The YrZ15-1370 would be a valuable resource for wheat resistance improvement and the flanking markers developed here could be useful tools for marker-assisted selection (MAS) in breeding and further cloning the gene.

Introduction

Common wheat (Triticum aestivum L.) is one of the most important staple cereal crops for mankind, providing approximately 19% of the food calories and over 20% of the protein consumed by the world population (Braun et al. 2010). Stripe rust (Puccinia striiformis f. sp. tritici, Pst) is one of the most serious fungal diseases affecting wheat production worldwide (Wellsing 2011). Breeding resistant cultivars is the most economical and sustainable method for stripe rust control.

Host resistance of wheat against Pst could be classified as either all-stage resistance (ASR) or adult–plant resistance (APR). Whereas ASR can be observed in seedling stage and is effective through all stages of plant growth, APR is susceptible in seedling stage and mainly effective at the late stages of plant growth (Chen and Kang 2017). The ASR confers high levels of resistance that is mostly race-specific and is vulnerably overcome by the emergence of new virulent races (Ellis et al. 2014). In contrast, APR generally provides a partial level of resistance that is non-race specific and, in some cases, has proven to be more durable than ASR (Ellis et al. 2014).

To date, more than 80 stripe rust resistance genes (Yr1–Yr83) have been permanently named (McIntosh et al. 2017; Li et al. 2020a). Most of them belonging to ASR genes have been overcome due to the rapidly evolving of new Pst races (Wellsing 2011). APR genes, such as Yr18 (Lagudah...
et al. 2009), Yr29 (William et al. 2003), and Yr46 (Herrera-Foessel et al. 2011), provide durable partial resistance to several fungal pathogen species. Among the officially designated genes, only a few genes are recessive, such as Yr3a (Chen and Line 1995), Yr6 (El-Bedewy and Robbelon 1982), and Yr51 (Randhawa et al. 2014), whereas the remaining genes are dominant.

*Triticum boeoticum* (*2n = 2x = 14, A^b^A^b^), the wild progenitor of *T. monococcum* L. ssp. *monococcum* (*2n = 2x = 14, A^m^A^m^), exhibits high variability in a number of biotic and abiotic stress responses (Lebedeva and Peusha 2006; Singh et al. 1998; Vasu et al. 2000). Several resistance genes have been transferred from *T. boeoticum* to wheat, such as *PmTb7A.1*, *PmTb7A.2*, and *Pm25* for powdery mildew resistance (Elkot et al. 2015; Chhuneja et al. 2015; Shi et al. 1998); *Sy22* for stem rust resistance (Gerechter-Amitai et al. 1971; The 1973, 1975; Paull et al. 1994). The *T. boeoticum* accessions are also valuable resistance source for wheat stripe rust (Chhuneja et al. 2008). For example, *QYrtm.pau-5A* confers APR to stripe rust has been mapped on the chromosome 5A^b^ of *T. boeoticum* accession pau5088 and was successfully transferred to hexaploid wheat using *T. durum* as a bridge (Chhuneja et al. 2008).

Although the potential of *T. boeoticum* for wheat improvement has been recognized for a long time, the available genetic diversity remains largely underexploited (Rey et al. 2015). In the current study, a resistant wheat-*T. boeoticum* introgression line Z15-1370 was obtained from common wheat cultivar *Crocus* as female crossed with *T. boeoticum* accession G52 as male. The objectives of this study were: (1) to evaluate the response of Z15-1370 to *Pst*; (2) to characterize the Z15-1370 by multicolor fluorescence in situ hybridization (mc-FISH), singlecolor genomic in situ hybridization (sc-GISH), multicolor genomic in situ hybridization (mc-GISH), and 55 K SNP array; (3) to map the stripe rust resistance gene in Z15-1370 using Bulked Segregant RNA-Seq (BSR-Seq) analysis.

### Materials and methods

#### Plant materials

Common wheat *Crocus*, *T. boeoticum* accession G52 and their derivative line Z15-1370 (selected from F_3_ progenies of *Crocus x G52*, Fig. S1) were used in this study. *Crocus* and G52 were kindly provided by George Fedak at the Ottawa Research and Development Centre in Canada. The wheat-*T. boeoticum* introgression line Z15-1370 was crossed with common wheat Mingxian169 to develop F_1_, F_2_, and F_2.3_ populations, which were used in stripe rust resistance assessments and gene mapping. Mingxian169, widely used as a spreader for stripe rust evaluation, is highly susceptible to currently prevailing Chinese *Pst* races (Wang et al. 2017).

### Cytological observations

Multicolor FISH was conducted based on the methods provided by Tang et al. (2014) and Zhao et al. (2018). Oligo-pTa535 and Oligo-pSc19.2 were used as probes to differentiate individual chromosomes of Z15-1370. All probes were labeled with either 6-carboxyfluorescein (6-FAM) or 6-carboxytetramethylrhodamine (Tamra) by the TsingKe Biological Technology Company (Chengdu, China).

After stripping off the FISH oligo probes, the same slides were analyzed by sc-GISH and mc-GISH. Sc-GISH was conducted according to Wang et al. (2019a). Total genomic DNA from G52 was labeled with fluorescein-12-dUTP (Roche Diagnostics Australia, Castle Hill, NSW) using nick translation. Total genomic DNA of wheat Chinese Spring was used for blocking. The probe to blocker ratio was ~1:2.2. Chromosomes were counter-stained with DAPI and pseudo-colored red. Mc-GISH was conducted based on the methods provided by Han et al. (2004). Total genomic DNA of *T. urartu* was labeled with digoxigenin-11-dUTP and that of *Aegilops tauschii* with biotin-16-dUTP using the nick translation method. Total genomic DNA of *Ae. speltoides* was used for blocking. Hybridization signals were visualized and captured using an Olympus BX-63 epifluorescence microscope equipped with a Photometric SenSys DP70 CCD camera (Olympus, Tokyo, Japan). Raw images were processed using Photoshop v.7.1 (Adobe Systems Inc., San Jose, CA, USA).

Chromosome pairing observation in pollen mother cells (PMCs) was performed as described by Zhang et al. (2007). For meiotic analysis, at least 50 PMCs were observed for Z15-1370. Ring bivalents (ring II) and rod bivalents (rod II) were counted, and their average numbers were calculated.

#### SNP genotyping

Genomic DNA was extracted from fresh leaves using a plant genomic DNA kit (Tiangen Biotech, Beijing, China). Chip-based genotyping was carried out using the Wheat 55 K SNP array containing 53,063 markers by CapitalBio Technology (Beijing, China) (www.capitalbio.com). Markers showed homozygous genotype among Z15-1370, G52, and *Crocus* were used to analyze the G52 donor segments in Z15-1370. The ratios of same SNP to the total SNPs scored between Z15-1370 and its two parents were calculated using a sliding window of 10 Mb and step length of 1 Mb as described by Hao et al. (2019). Only results from windows with > 30 markers were treated as effective data. The genome regions of Z15-1370 covered by windows with higher ratio of same SNP to G52 compared to that of *Crocus* and values larger
than 0.6 were defined as the G52 introgression fragments. Graphical representations were constructed using the R package ggplot2 (v.2.2.1) (Wickham 2016).

**Stripe rust resistance response**

Crocus, G52, Z15-1370, and F1 individuals derived from Mingxian169 × Z15-1370 were tested for seedling stripe rust resistance at growth chamber. The highly virulent *Pst* race CYR34 (virulent on *Yr1*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr17*, *Yr18*, *Yr24*, *Yr26*, *Yr27*, *Yr29*, *Yr31*, *Yr43*, *Yr44*, *YrExp2*, and *YrSP*) (Wang et al. 2019b) was used to inoculate the plants at the second leaf stage. Urediniospores used for inoculation of leaf tissue were first suspended in isodecane and then sprayed as described previously (He et al. 2020). Disease severity was evaluated and characterized 14–21 days after inoculation using a 0–9 scale of infection type (IT) (Line and Qayoum 1992). Plants with ITs 1–3, 4–6, and 7–9 were considered resistant, intermediate resistant, and susceptible, respectively.

A field evaluation for adult–plant stripe rust resistance of parents, F1, and F2 individuals as well as their corresponding F2:3 families was performed at the experimental field of the Triticeae Research Institute, Sichuan Agricultural University, Wenjiang. The highly susceptible spreader variety SY95-71 and Mingxian169 were planted around the experimental field as spreader rows. A mixture of the Chinese prevalent races (CYR32, CYR33, CYR34, Zhong4, and HY46) (Bai et al. 2018; Hu et al. 2012), kindly provided by the Research Institute of Plant Protection, Gansu Academy of Agricultural Sciences, was used to inoculate the adult plants. Stripe rust response was scored on a 1–9 scale (Wellings and Bariana 2004), with 1 being highly resistant and 9 highly susceptible. ITs were recorded for three times at 7-day intervals when susceptibility of flag leaves of SY95-71 was fully expressed. The final rating of each wheat line was used for analysis.

**Bulked segregant RNA-Seq (BSR-Seq)**

The phenotypically contrasting F2:3 families against stripe rust races in the field were used to construct the resistant and susceptible RNA pools for RNA-Seq. Equal amounts of RNA from 30 homozygous resistant and 30 homozygous susceptible families each were pooled for conducting bulked segregant analysis (Li et al. 2020b). The RNA samples were sequenced on the Illumina HiSeq platform at the Beijing Novogene Technology (Beijing, China) (https://www.novogene.com/). Sequence quality was controlled using software Trimmomatic v0.36 (Bolger et al. 2014). RNA reads of the resistant and susceptible bulks were aligned to the Chinese Spring reference genome sequence v1.0 (IWGSC 2018) using software STARv2.5.1b (Dobin et al. 2013). The unique and confident alignments were applied to call SNP variants using software GATK v3.6 (McKenna et al. 2010). The SNP variants with *P*-values of Fisher’s exact test (FET) < 1e−8 and allele frequency difference (AFD) > 0.6 were considered to be associated with the disease resistance and further used as templates to develop SNP markers (Li et al. 2020b).

**Kompetitive allele-specific PCR (KASP) assays**

The resistance-associated SNPs and the 500 bp flanking sequences served to design the KASP primers and tested polymorphisms on the parental lines, the resistant and susceptible DNA bulks. Polymorphic markers that could be reliably scored were genotyped on the F2 segregation population of Mingxian169 × Z15-1370. For each KASP assay, 10 µl reaction volum containing 5 µl of 2 KASP mastermix (Biosearch Technologies), 1.4 µl primer mix (mixture of 0.168 µM each forward A1 and A2 primers and 0.42 µM of reverse primer), 100 ng of genomic DNA and 2.6 µl of ddH2O was prepared. The CFX96Touch™ real-time PCR detection system (BioRad, USA) was used for amplification under the following conditions: 15 min at 94 °C, 10 touchdown cycles of 20 s at 94 °C, 60 s at 65–57 °C (decreasing by 0.8 °C per cycle), and 32 cycles of 20 s at 94 °C, 60 s at 57 °C.

**Data analysis**

The Chi-square (χ²) tests were used to determine goodness of fit for the observed segregation and expected ratios of the F2 and F3 populations. Linkage analysis was performed using MAPMAKER/EXP v3.0b (Lander et al. 1987). The Kosambi function was used to convert recombination values to genetic distances (Kosambi 1943). A logarithmic odds (LOD) ratio of 3.0 and maximum distance of 50.0 cM was set as a threshold for the declaration of linkage. The genetic linkage map was drawn using Mapdraw V2.1 software (Liu and Meng 2003).

**Candidate gene analysis**

The corresponding sequences of markers *KASP-1370-3* and *KASP-1370-5* linked to *YrZ15-1370* were used to BLAST against the genomes of common wheat cv. Chinese Spring (IWGSC 2018) and *T. urartu* accession G1812 (Ling et al. 2018). Gene annotations between the flanking markers of the two genomes were retrieved from the online databases (http://202.194.139.32/). Five sets of primers specific to chromosome 6A were designed based on the kinase protein genes sequences of Chinese Spring or *T. urartu* to amplify candidate genes in G52, Crocus, and Z15-1370 (Table S1).
Purified PCR fragments were sent to commercial company for gene cloning and sequencing.

**Results**

**Cytological characterization of the introgression line Z15-1370**

Mc-FISH and mc-GISH analysis indicated that the Z15-1370 has 42 chromosomes with 14 A-genome, 14 B-genome, and 14 D-genome chromosomes, respectively (Fig. 1a, b). Sc-GISH using *T. boeoticum* genomic DNA as a probe confirmed the existence of 14 chromosomes from A-genome in Z15-1370 (Fig. 1c). All 42 chromosomes of Z15-1370 paired as bivalents in PMCs (observed PMCs > 50) at metaphase I (Fig. 1d), with the pairing configuration 17.45 ring II (±1.00) + 3.55 rod II (±1.00), suggesting a normal meiosis.

**Genetic analysis of the stripe rust resistance in Z15-1370**

The introgression line Z15-1370 and its male parent G52 were susceptible (IT = 7–9; in a 0–9 scale, Line and Qayoum 1992) to *Pst* race CYR34 at the seedling stage (Fig. 2a), whereas both of them showed high resistance (IT = 1–2; in a 1–9 scale, Wellings and Bariana 2004) to the mixture *Pst* races (CYR32, CYR33, CYR34, Zhong4, and HY46) (Fig. 2b) at the adult plant stage. The common wheat Mingxian169 and Crocus were completely susceptible (IT = 9). The resistant Z15-1370 was then crossed with Mingxian169 to develop F1, F2, and F2:3 populations for genetic analysis of the adult plant stripe rust resistance in Z15-1370. The infection type of all F1 plants was similar to that of the susceptible parent Mingxian169 (Fig. 2b). The F2 population segregated in 136 resistant (IT = 1–3) and 406 susceptible (IT = 7–9), fitting a 1R: 3S ratio ($\chi^2 = 0.001, p = 0.98$) (Fig. 2b; Table 1), indicating that the stripe rust resistance was conferred by a single recessive gene tentatively designated as *YrZ15-1370*. The F2:3 population consisting of 273 families showed a segregation...
of 134 (homozygous resistant): 276 (heterozygous): 123 (homozygous susceptible) ($\chi^2 = 1.128$, $p = 0.569$), in agreement with the results from the F2 population (Table 1).

### Molecular mapping of $YrZ15-1370$

Sixty-three out of the 116 clustered SNPs on 6AL were chosen to develop KASP markers. Five of them were successfully converted into KASP markers ($KASP-1370-2$, $KASP-1370-3$, $KASP-1370-5$, $KASP-1370-6$, and $KASP-1370-7$) and scored reliably on the parents as well as the resistant and susceptible bulks (Table 2). Subsequently, these KASP markers were used to genotype 273 F2 plants derived from the cross between resistant Z15-1370 and susceptible Mingxian169. Linkage analysis indicated that $KASP-1370-5$ was potentially mapped 2.5 cM proximal and $KASP1370-3$ was placed 1.8 cM distal to $YrZ15-1370$ (Fig. 4a).

### Evaluation of the G52 introgression segments on 6A chromosome of Z15-1370

The five KASP markers used for developing the genetic map described above were also used to genotype common wheat Crocus, G52 and their derivative line Z15-1370, as well as Mingxian 169. All tested markers exhibited identical
haplotypes between Z15-1370 and G52 while distinct from those of Crocus and Mingxian 169 (Table 3). SNP genotyping analysis revealed five potential G52 donor segments on chromosome 6A of Z15-1370 (0–3.0 Mb, 6.0–24.0 Mb, 43.1–82.1 Mb, 405.1–434.0 Mb, 519.0–607.8 Mb, based on the physical positions of Chinese Spring). One of them (519.0–607.8 Mb) overlapped the genome region of YrZ15-1370 defined by its linked KASP markers (600.4–604.4 Mb) (Fig. 4).

Table 2 Primer sequences of KASP markers used for genetic mapping of YrZ15-1370

| Maker    | Physical position (Mb) | Allele 1 primer\(^a\) | Allele 2 primer\(^b\) | Common/reverse primer |
|----------|------------------------|------------------------|------------------------|-----------------------|
| KASP-1370-2 | 600.4 | GCA TAT AAG AGA CGG GGT GAC | GCATATAAGAGACGCGGTGAC | AGCAGAACACATATACACAC |
| KASP-1370-3 | 601.5 | AGGAGAAAGATGAGCCAAAAA | AGGAGAAAGATGAGCCAAAAA | CCAAGATCGCTCCTCTACTC |
| KASP-1370-5 | 603.3 | TTCAGTTTGAGCTGAGGAC | TTCTAGTTTGAGCTGAGGAT | CAGATGGCCATGAAGGCAGT |
| KASP-1370-6 | 604.4 | CGACTAGCTAGCTAGCTACAA | CGACTAGCTAGCTAGCTACAG | GGCTAGCGGAGCGGATCATGG |
| KASP-1370-7 | 604.4 | ATCAATGTAAACAAAATTTGGG | ATCAATGTAAACAAAATTTGGG | GAGCTAGTTCATGGATCG |

\(^a\)A1 primer labelled with FAM: GAAGGTGACCAAGTTTCAGCT
\(^b\)A2 primer labelled with HEX: GAAGGTGACCAAGTTTCAGCT

Gene analysis of the YrZ15-1370 genomic region

The sequences of closely linked markers KASP-1370-3 and KASP-1370-5 were blasted against the Chinese Spring genome and the T. urartu genome to obtain their physical positions, respectively. The YrZ15-1370 was physically mapped to the region between the 601.5 Mb to 603.3 Mb positions of 1.8 Mb in the Chinese Spring 6AL chromosome and between 557.4 Mb to 560.2 Mb (2.8 Mb) in the T. urartu 6AL chromosome. There were 71 and 59 predicted genes in the target physical regions in Chinese Spring and T.
In Chinese Spring genome, six genes may be associated with plant defense responses to pathogens (Chen et al. 2020; Klymiuk et al. 2018; Noman et al. 2019), including five kinase protein genes (\textit{TraesCS6A01G584000LC}, \textit{TraesCS6A01G384700}, \textit{TraesCS6A01G384900}, \textit{TraesCS6A01G385000}, \textit{TraesCS6A01G385100}) and one Myb-like transcription factor gene (\textit{TraesCS6A01G385500}). Four kinase protein genes (\textit{TuG1812G0600004115.01}, \textit{TuG1812G0600004116.01}, \textit{TuG1812G0600004117.01}, and \textit{TuG1812G0600004133.01}) were found in \textit{T. urartu} genome which had good collinearity relationship with those of Chinese Spring (Fig. S2). The homologous gene of \textit{TuG1812G0600004133.01} in Chinese Spring is \textit{TraesCS6A01G386800} which located outside the \textit{YrZ15-1370} region in Chinese Spring genome.

**Discussion**

\textit{Triticum boeoticum} represents a valuable source of disease resistance for wheat improvement (Gill et al. 1988; Ma et al. 1997; Ahmed et al. 2014), whereas the transferring of the disease resistance genes from this species has been relatively lagging behind. In the present study, a new stripe rust resistance gene, tentatively named \textit{YrZ15-1370}, was mapped on 6AL in a wheat-\textit{T. boeoticum} introgression line Z15-1370.

A previous study had reported the transferring of the stripe rust resistance gene \textit{QYrtb.pau-5A} from \textit{T. boeoticum} to hexaploid wheat, using \textit{T. durum} as a bridging species (Chhuneja et al. 2008). In the current study, the resistant line Z15-1370 was obtained by direct hybridization between common wheat and \textit{T. boeoticum}. SNP genotyping analysis revealed that part chromatin of \textit{T. boeoticum} G52 was successfully introgressed into Z15-1370. The genomic interval of one G52 donor fragment on 6AL of Z1370 was 88.8 Mb (519.0–607.8 Mb), which overlapped the physical interval...
of YrZ15-1370 locus (601.5 to 603.3 Mb) in the Chinese Spring reference genome (Fig. 4b). The SNP genotyping together with the KASP assay (Table 3) demonstrated that the YrZ15-1370 segment on 6AL was derived from the 6A\textsuperscript{b} chromosome of T. boeoticum.

To date, three stripe rust resistance genes (Yr38, Yr42, and Yr81) have been assigned on chromosome 6A. Yr81 located in the short arm of chromosome 6A, was detected in an Australian common wheat landrace Aus27430 (Gessese et al. 2019). Yr38 (Marais et al. 2006) and Yr42 (Marais et al. 2009) are present in translocated segments from wild relatives Ae. sharonensis (2n = 14, S\textsubscript{a}S\textsubscript{b}) and Ae. neglecta (2n = 28, UUMM), respectively. All these genes confer ASR to stripe rust, whereas YrZ15-1370 is an APR gene. To our best knowledge, there was only one APR gene QYrtb.pau-5A from T. boeoticum had been mapped, while this gene was located on chromosome 5A (Chhuneja et al. 2008). Taken together, YrZ15-1370 reported here is a new stripe rust resistance gene found in T. boeoticum.

Five and four kinase protein genes in the YrZ15-1370 genomic region were annotated in Chinese Spring and T. urartu, respectively. Since relatively good collinearity were observed between these genes, we isolated part genomic sequences of four Chinese Spring kinase protein genes (except TraesCS6A01G5840000LC) and one T. urartu gene TuG1812G0600004133.01 in G52, Crocus, and Z15-1370. Sequence alignment results showed that TraesCS6A01G384700, TraesCS6A01G384900, and TraesCS6A01G385100 were identical among the three genotypes (data not shown). TraesCS6A01G385000 and TuG1812G0600004133.01 were identical in G52 and Z15-1370, while SNPs were detected in exons of TraesCS6A01G385000 and TuG1812G0600004133.01 in Crocus (Figs. S3, S4). These SNPs could be used to develop molecular markers for fine mapping and cloning of YrZ15-1370.

Among stripe rust resistance genes listed in the wheat gene catalogue, the majority show dominant inheritance, whereas a small number of them, such as Yr51 (Randhawa et al. 2014), yrCH45 (Yang et al. 2016), yrGn22 (Li et al. 2016), and yrMY37 (Ren et al. 2015) were recessive and usually confer all-stage resistance. YrZ15-1370 in wheat-T. boeoticum line Z15-1370 is another case of recessive gene, while confer adult plant resistance. Most of the reported APR genes do not confer adequate levels of resistance when present alone. For example, APR genes Yr18 (Lagudah et al. 2009), Yr29 (William et al. 2003), Yr36, and Yr46 (Herrera-Foessel et al. 2011) provide partial resistance to a wide spectrum of Pst races. The YrZ15-1370 gene identified during this study provides a high level of APR to a mixture of the Chinese prevalent races (CYR32, CYR33, CYR34, Zhong4, and HY46), indicating its suitability for wheat stripe rust resistance improvement.

The Z15-1370 has crossed with several wheat cultivars in Sichuan province to facilitate the transfer of YrZ15-1370 in wheat breeding. Flanking markers KASP-1370-3 and KASP-1370-5 would be used as efficient tools in marker assisted selection (MAS). In addition, the recessive nature of YrZ15-1370 made the homozygous resistant plants can be easily selected through phenotypic selection. Although YrZ15-1370 is effective against the Chinese prevalent Pst races, there is a possibility of its resistance to be overcome by the emergence of new virulent races. Therefore, YrZ15-1370 should be stacked with other Yr genes to achieve durable resistance.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00122-021-03866-3.

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**Author contribution** D.C. L., L.Z., L.H., M.H., Z.Y., and S.N. designed the experiments. M.Z., X.L., T.P., D.W., D.Y.L., X.J.C., B.J., H.L., and X.C. performed the experiments. D.C.L., L.Z., L.H., M.H., and M.Z. discussed results and wrote the paper.

**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no competing interests.

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