

## MOLECULAR MAPPING OF STRIPE RUST RESISTANCE GENE *YrSE5756* IN SYNTHETIC HEXAPLOID WHEAT AND ITS TRANSFER TO COMMON WHEAT

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### Abstract

Synthetic hexaploid wheat is an important germplasm resource for transfer of beneficial genes from alien species to common wheat (*Triticum aestivum* L.). Synthetic hexaploid wheat SE5756 confers a high level of resistance against a wide range of races of *Puccinia striiformis* West. f. sp. *tritici* Eriks. et Henn. (*Pst*). The objectives of this study were to determine the inheritance pattern, adjacent molecular markers, and chromosomal location of the stripe rust resistance gene in SE5756 and to develop new germplasm. We constructed a segregating population of 116 F<sub>2</sub> plants and corresponding F<sub>2,3</sub> families from a cross between SE5756 and Xinong979 with *Pst* races CYR32. Genetic analysis revealed that a single dominant gene, tentatively designated as *YrSE5756*, was responsible for seedling stage stripe rust resistance in SE5756. A genetic map, encompassing *Xwmc626*, *Xwmc269*, *Xgwm11*, *Xbarx137*, *Xwmc419*, *Xwmc85*, *Xgpw5237*, *Xwmc134*, *WE173*, *Xwmc631*, and *YrSE5756*, spanned 70.1 cM on chromosome 1BS. *Xwmc419* and *Xwmc85* were flanking markers tightly linked to *YrSE5756* at genetic distances of 2.3 and 1.8 cM. Typical adult plant responses of the SE5756, varieties of the carrier *Yr10* and *Yr15*, Chuanmai 42 (*Yr24/Yr26*), Yuanfeng 175 (*Yr24/Yr26*) and Huixianhong resistant to mixture *Pst* races (CYR32, CYR33 and V26) were experimented. The results showed that *YrSE5756* was likely a new resistance stripe rust gene different from *Yr24/Yr26*, *Yr10* and *Yr15*. From cross and backcross populations of SE5756/Xinong 979, we developed four new wheat lines with large seeds, stripe rust resistance, and improved agronomic traits: N07178-1, N07178-2, N08256-1, and N08256-2. These new germplasm lines could serve as sources of resistance to stripe rust in wheat breeding. SE5756 has the very vital significance in the development of breeding and expand our resistance germplasm resource gene pool.

**Key words:** Synthetic hexaploid wheat; Stripe rust; Resistance gene; Genetic mapping; Germplasm utilization.

### Introduction

Stripe rust (yellow rust), caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most devastating diseases of wheat (*Triticum aestivum* L.) worldwide. In China, stripe rust is most destructive to autumn-sown wheat in northwestern and southwestern China when susceptible cultivars are grown and the weather is favorable for the disease (Wan *et al.*, 2004). Growing resistant cultivars is the most effective, economical, and environmentally friendly strategy for controlling the disease, but race-specific resistance genes are usually overcome by new virulent *Pst* races shortly after such genes become widely deployed in commercial cultivars (Lin & Chen, 2008). Discovery of new stripe rust resistance genes, development of associated molecular markers, and breeding of new wheat varieties is thus critical.

To date, 56 genes for stripe rust resistance have been designated and located at 54 loci (*Yr1-Yr54*) on different wheat chromosomes (Chen, 2005; Marais *et al.*, 2006; Lin *et al.*, 2007; Kuraparthi *et al.*, 2007; Marais *et al.*, 2009; Ren *et al.*, 2012; Xu *et al.*, 2013). Forty-one of these genes originated from common wheat (Lin *et al.*, 2008; Deng *et al.*, 2004; Xu *et al.*, 2013; Basnet *et al.*, 2014), with the remaining genes derived from wheat relatives (Yan *et al.*, 2003; Sun *et al.*, 1997; Dadkhodaie *et al.*, 2011; Uauy *et al.*, 2005; Liu *et al.*, 2013). Molecular markers have been widely used for tagging these stripe rust resistance genes in wheat.

Screening of 138 synthetic wheat lines with mixed *Pst* in the field to uncover more stripe rust resistance genes has resulted in the identification of various lines that may possess novel genes or alleles, such as SE5756. Our study had two objectives. The first goal was to determine the inheritance pattern, adjacent molecular markers, and chromosomal location of the stripe rust resistance gene in SE5756. The second objective was to transfer this gene into common wheat and to breed new germplasm possessing the identified gene using typical cross and backcross populations of SE5756 × Xinong979. The transfer of resistance genes can broaden the narrow genetic base of wheat varieties and expand our resistance germplasm resource gene pool.

### Materials and Methods

**Plant materials and evaluation of stripe rust reactions:** SE5756 is a synthetic hexaploid wheat, which was provided by Dr. Lihui Li from the Institute of Crop Science Chinese Academy of Agricultural Sciences, Beijing, China. Its pedigree is 68.111/RGB-U//WARDResel/3/Stil/4/*Ae. squarrosa* 783. The wheat cultivars Xinong 979, Huixianhong, susceptible control were included in comparative response tests. The mapping population derived from SE5756/Xinong 979 comprised F<sub>2</sub> plants and their derived F<sub>2,3</sub> families. Fifteen plants of each F<sub>3</sub> family were tested to identify genotypes of corresponding F<sub>2</sub> plants. The cultivar Huixianhong was used as a susceptible control in disease reaction tests.

SE5756 served as a resistant parent and a resistant control, Xinong 979 served as a susceptible parent. The parents, the F<sub>2</sub> population, and F<sub>2:3</sub> progenies from SE5756/ Xinong 979 were inoculated with *Pst* race CYR32. Seedlings were grown in the greenhouse at 12–17°C and inoculated with Chinese *Pst* races CYR32 when their first leaves were fully expanded. After inoculation, seedlings were placed in a dew chamber at 9°C and 100% relative humidity for 24 h, and then transferred to a greenhouse maintained at 12–17°C under a 14-h light and 10-h dark photoperiod. Infection types (ITs) were recorded 14–15 days after inoculation, when rust was fully developed on the susceptible control Huixianhong. ITs were based on a 0–4 scale (Yang *et al.*, 2013). Two main classes of host reactions were distinguished: resistant (IT = 0, 0, 1, or 2) and susceptible (IT = 3 or 4).

The response of wheat cultivar Chuanmai 42, which carries *Yr24/Yr26* (Li *et al.*, 2006a; Liu *et al.*, 2010), Yuanfeng 175, produced from the cross 92R149/Xian87 (30)// Xiaoyan No. 6, which carries *Yr24/Yr26* (Ali *et al.*, 2010), varieties of the carrier *Yr10* and *Yr15* were compared with that of SE5756 using mixture *Pst* races (CYR32, CYR33 and V26). Among these *Pst* races, V26 differs from others in China because of its virulence on *Yr24/Yr26* genotypes (Huang *et al.*, 2014). SE5756, Chuanmai 42, Yuanfeng 175, varieties of the carrier *Yr10* and *Yr15* were planted in a randomized design with 20–30 plants in 2.5 m rows with 25 cm spacing. Susceptible control plants (Huixianhong) used to spread disease was planted in every third row to ensure that all plants had the same opportunity for infection. Huixianhong was inoculated with the predominant mixture *Pst* races (CYR32, CYR33 and V26) at the elongation stage according to previously described methods (Liu *et al.*, 2013). The reactions of adult plants were scored at the milk stage using the previously described rating scale (Luo *et al.*, 2008). These seeds were provided by the College of Agronomy, Northwest A & F University, Yangling, Shaanxi, China. These *Pst* races CYR32 and mixture *Pst* races (CYR32, CYR33 and V26) were provided by the College of Plant Protection, Northwest A & F University.

**Molecular marker analysis:** Genomic DNA of parents and progenies were extracted from seedling leaves according to the CTAB protocol (Wang *et al.*, 2013). Molecular markers were evaluated by bulked segregant analysis (Michelmore *et al.*, 1991) to identify markers linked to the stripe rust resistance gene in SE5756. Resistant and susceptible bulks were created by pooling equal amounts of DNA from 10 resistant and 10 susceptible F<sub>2</sub> plants, respectively. We synthesized 498 wheat SSR primer pairs based on sequences published in the Grain Genes database (<http://www.wheat.pw.usda.gov>), and screened them against the parents and bulks. Polymorphic markers were further checked for linkage to resistance gene using the entire F<sub>2:3</sub> mapping population.

PCRs were performed in 10- $\mu$ L reaction volumes containing 1 $\times$  PCR reaction buffer, 1.5 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 0.25 U *Taq* DNA polymerase, 0.5  $\mu$ M of each primer, and 40–100 ng total DNA. Reactions were

performed in an S1000 thermocycler (Bio-Rad, Hercules, California, USA) using the following program: initial denaturation at 94°C for 3 min, followed by 35 cycles of 94°C for 30 s, 50–60°C (depending on primers) for 45 s, and 72°C for 50 s, with a final extension step of 72°C for 10 min followed by chilling at 4°C. PCR products were resolved by electrophoresis on an 8% nondenaturing polyacrylamide gel (37.5:1 acrylamide-bis) and visualized by silver staining.

**Data analysis:** Chi-squared tests were used to evaluate the goodness of fit of observed and expected segregation ratios of stripe rust reaction and molecular markers. Linkages between markers and the resistance gene were established using JoinMap 4.0 (Van Ooijen, 2006). A genetic map was created using Mapdraw V2.1 (Liu & Meng, 2003).

**Utilization of *YrSE5756*:** We selected plants exhibiting excellent agronomic characters and resistance to *Pst* races from cross (N07178: SE5756/Xinong979) and backcross (N08256:SE5756/Xinong979//Xinong979) populations in the field.

## Results

**Inheritance of stripe rust resistance in SE5756:** In seedling tests with CYR32, SE5756 and 10 F<sub>1</sub> plants from the cross SE5756/Xinong 979 were highly resistant (IT = 0–0 ;), whereas Xinong979 and Huixianhong were highly susceptible (IT = 4) (Fig. 1). A genetic mapping population derived from a cross between SE5756 and Xinong979, comprising 116 F<sub>2</sub> plants and their derived F<sub>2:3</sub> families, was inoculated along with their parents with CYR32. The resulting 90 resistant: 26 susceptible F<sub>2</sub> segregation ratios were consistent with the expected 3:1 ratio ( $\chi^2=0.4137$ ). Similarly, the observed ratio of the F<sub>2:3</sub> families (25 homozygous resistant: 65 segregating: 26 homozygous susceptible) fit well with the expected 1:2:1 ratio ( $\chi^2=1.7069$ ). The combined F<sub>2</sub> and F<sub>2:3</sub> family data indicated that resistance in SE5756 was conferred by a single dominant gene, temporarily designated as *YrSE5756*.

**Bulked segregant and linkage analyses:** To determine the chromosomal location of SE5756, 498 wheat SSR primer pairs were screened against the parents and resistant and susceptible DNA bulks. Markers *Xpsp3000*, *Xwmc626*, *Xwmc269*, *Xgwm11*, *Xbarc137*, *Xwmc419*, *Xwmc85*, *Xgpw5237*, *Xwmc134*, *WE173* (EST-STS of *Yr26*), *Xwmc631*, *Xgwm273*, *Xgwm18*, and *Xgwm498* on chromosome 1BS were polymorphic between the parents and bulks, and showed expected patterns for linked markers after being tested on individual F<sub>2</sub> plants (Fig. 2). All markers were inherited as co-dominant markers, except for *Xgwm273*, *Xgwm18*, and *Xgwm498*. A linkage map of the gene *YrSE5756* and closely linked markers, with a total map length of 70.1 cM, is shown in Fig. 3. The *YrSE5756* gene was flanked by loci *Xwmc419* and *Xwmc85* at genetic distances of 2.3 and 1.8 cM, respectively.

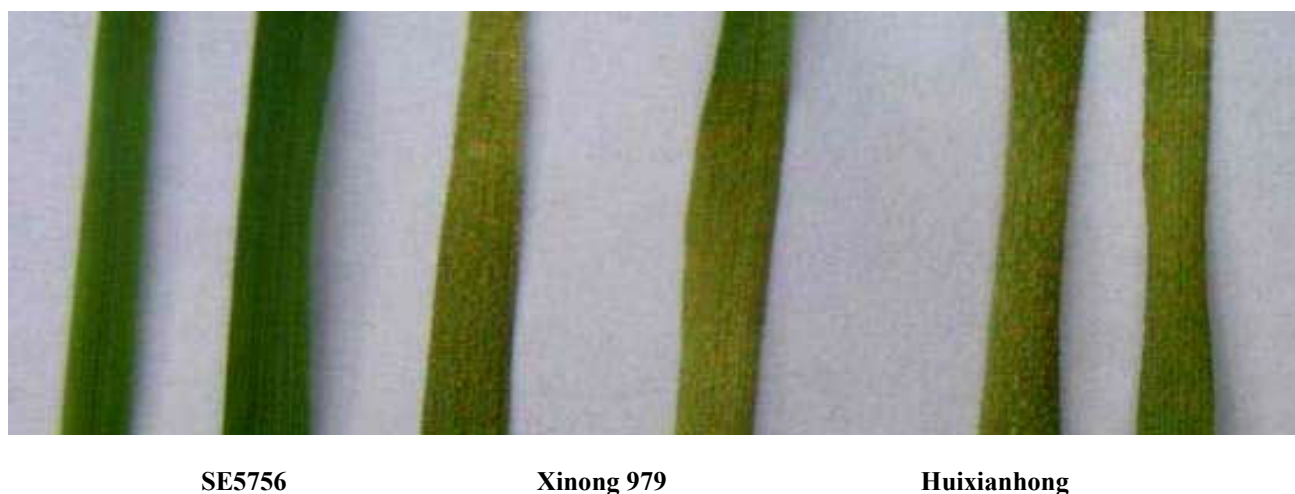


Fig. 1. Resistance reaction of Synthetic hexaploid wheat SE5756, Xinong979, and Huixianhong inoculated with stripe rust races CYR32 in the seedling stage.

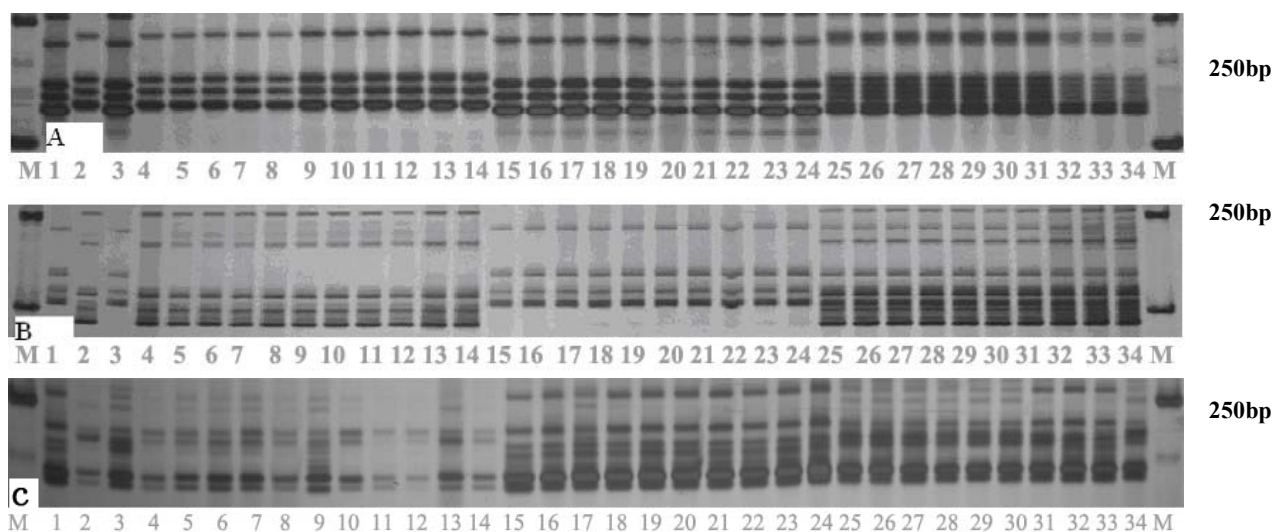


Fig. 2. Polyacrylamide gel electrophoresis of PCR products obtained using markers **a** *Xbarc137*, **b** *Xwmc419*, and **c** *Xwmc85* in the  $F_2$  population of SE5756/Xinong 979 M: D2000 ladder; 1: SE5756; 2: Xinong979; 3: susceptible bulk; 4: resistant bulk; 5-14: homozygous susceptible individuals; 15-24: homozygous resistant individuals; 25-34: heterozygous resistant individuals

**Stripe rust response:** Typical adult plant responses of the SE5756, varieties of the carrier *Yr10* and *Yr15*, Chuanmai 42, Yuanfeng175 and Huixianhong resistant segregants to mixture *Pst* races (CYR32, CYR33 and V26) are showed in Fig. 4. Responses of the SE5756 is highly resistant (IT 0-0), varieties of the carrier *Yr10* and *Yr15*, Chuanmai 42, Yuanfeng175 were susceptible varying degrees (IT 3-4), that is to say, *YrSE5756* was likely a new resistance stripe rust gene different from *Yr24/Yr26*, *Yr10* and *Yr15*.

**Utilization of *YrSE5756*:** To transfer strip rust resistance genes to common wheat, we selected plants (N07178 and N08256) displaying disease resistance to two combinations of races CYR32 and CYR33. After 6-7 years, we obtained four morphologically identical germplasm lines showing resistance in the field to races CYR32 and CYR33, which we named N07178-1, N07178-2, N08256-1, and N08256-2. Compared with their parents, the new plants were shorter than the maternal parent; they resembled common wheat, and

tillered profusely with vigorous growth (Fig. 5). The average main spike length was also significantly higher than that of either parent. The spikelet number of the main spike was significantly higher than that of the maternal parent, and the spike had a wheat-like morphology. In addition, the four new germplasm lines produced plump white seeds (Fig. 6) that resembled those of SE5756 and that had a comparatively high thousand kerner weight (TKW) (> 50 g). Plant height, spike length, kernels per spike, and TKW of parents and new lines are listed in Table 1. Agronomic traits of backcross plants (N08256-1 and N08256-2) were superior to those of selfed plants (N07178-1 and N07178-2) (Table 1).

SE5756, Xinong979, and the four new germplasm lines were field-tested to determine their responses to stripe rust races during the adult plant stage in the field. We found that SE5756 and the four new lines were highly resistant (IT 0-0 ; ) to mixture *Pst* races (CYR32, CYR33 and V26). In contrast, Xinong979 was susceptible (IT 3-4) (Table 1).

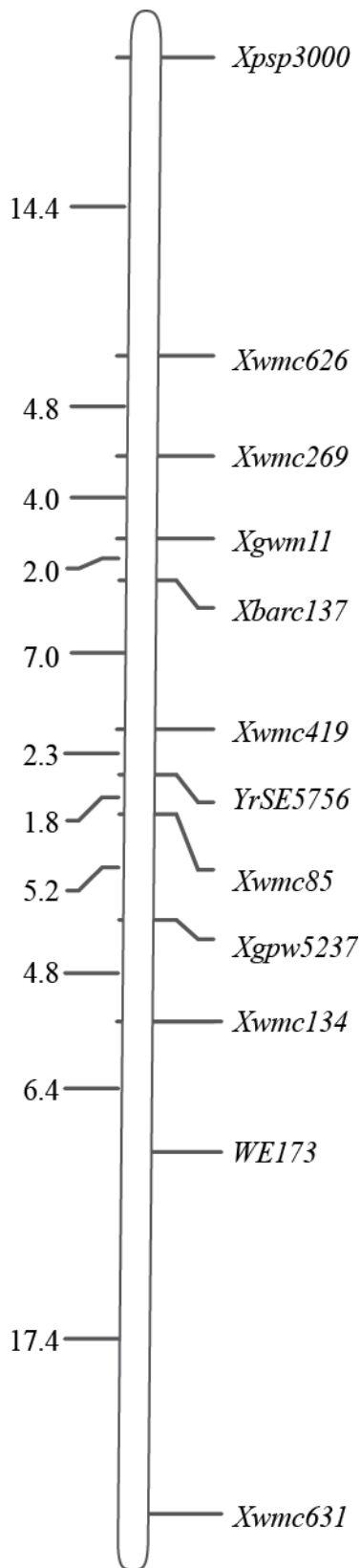


Fig. 3. Linkage map for *YrSE5756* and 11 markers on chromosome 1BS. Locus names and Kosambi map distances (cM) are indicated on right and left sides of the map, respectively. Note: Locus names are indicated on the right side of the map. Kosambi map distances (cM) are shown on the left side.

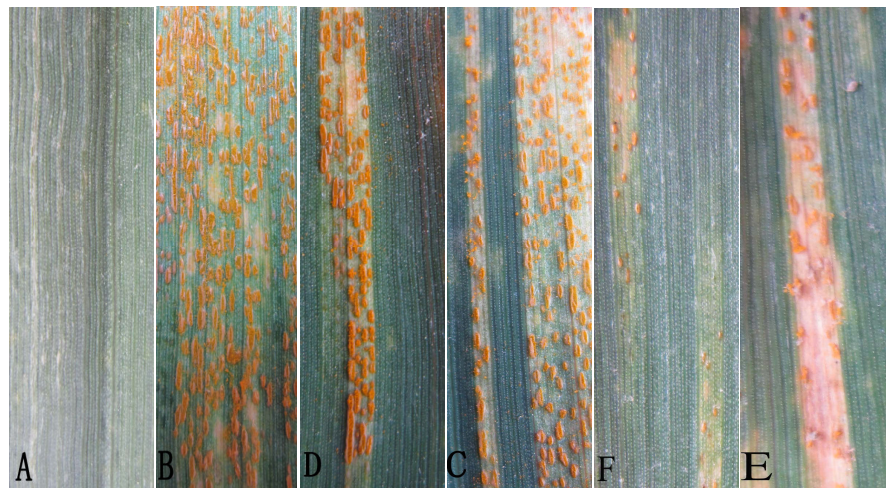


Fig. 4. Resistance reaction of Synthetic hexaploid wheat SE5756 (A), Huixianhong (B), Chuanmai 42 (C), Yuanfeng 175 (D), varieties of the carrier *Yr10* (E) and *Yr15* (F) inoculated with mixture *Pst* races (CYR32, CYR33 and V26) in the field.

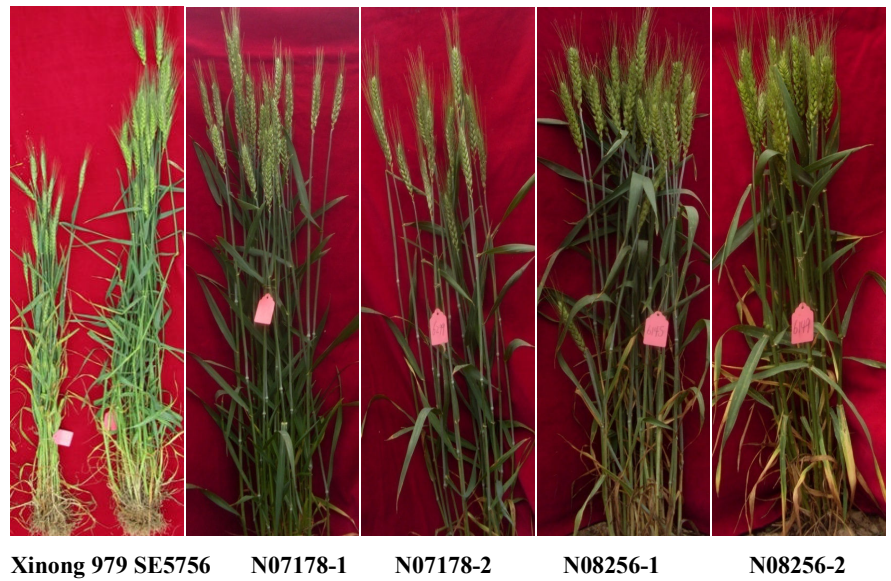


Fig. 5. Plants of SE5756, Xinong979, N07178-1, N07178-2, N08256-1, and N08256-2.

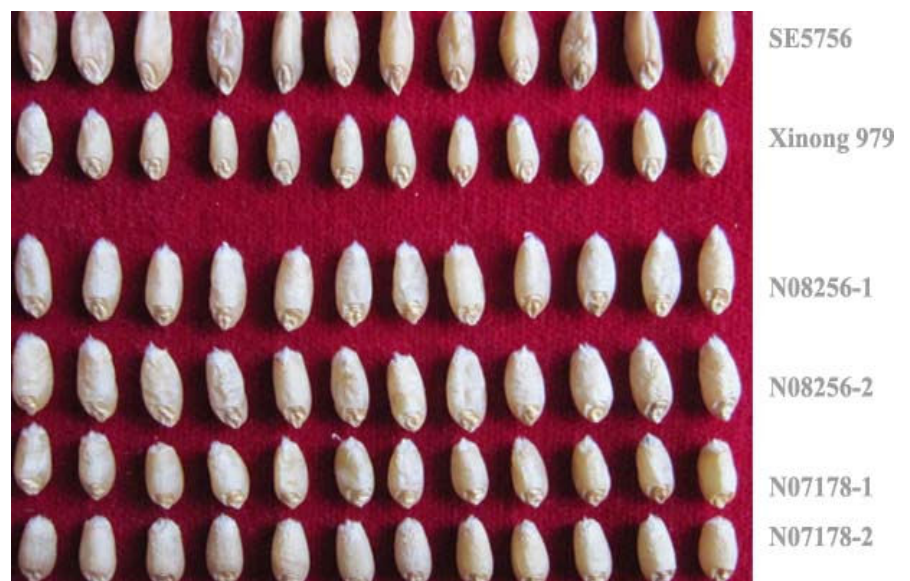


Fig. 6. Seeds of SE5756, Xinong979, N07178-1, N07178-2, N08256-1, and N08256-2.

**Table 1. Biological traits of four new germplasm lines and their parents.**

Materials	TKW (g)	Plant height (cm)	Spike length (cm)	Kernels per spike	Infection type of mixture Pstraces (CYR32, CYR33 and V26)
SE5756	56.2	114.2	8.5	42	0-0;
Xinong979	44.5	76.6	9.1	45	3-4
N07178-1	51.1	95.1	8.9	41	0-0;
N07178-2	52.3	87.2	8.6	42	0-0;
N08256-1	54.5	81.8	8.8	45	0-0;
N08256-2	56.1	80.1	9.2	43	0-0;

## Discussion

### Comparison of *YrSE5756* with *Yr10*, *Yr15*, *Yr24*, *Yr26*, *YrH52*, *YrCH42*, and *YrCI42* located on chromosome 1BS:

In recent years, molecular markers have played a significant role in tagging stripe rust resistance (*Yr*) genes in wheat. In this study, the chromosomal location of a resistance gene in the synthetic hexaploid wheat line SE5756 was confirmed using SSR markers, with the markers *Xwmc419* and *Xwmc85* closely linked to *YrSE5756* at distances of 2.3 and 1.8 cM, respectively. Based on the linkage map and chromosomal location, *YrSE5756* is located near the centromere of chromosome 1BS. Of the resistance genes identified on 1BS, *Yr10*, *Yr15*, *Yr24*, *Yr26*, *YrH52*, *YrCH42*, and *YrCI42* have been located on chromosome 1BS near the centromere (Ma *et al.*, 2001; Smith *et al.*, 2002; Li *et al.*, 2006; Lin & Chen 2007; Wang *et al.*, 2009; Fahima *et al.*, 1999). *Yr10* is derived from *T. spelta*, and is closely linked to the marker *Xpsp3000*, being separated by a distance of  $1.2 \pm 1.1$  cM (Wang *et al.*, 2002). *Yr15* originated from *T. dicoccoides*, and is closely linked to the RAPD marker *Norl* (Fahima *et al.*, 1999). *Yr24* originated from *T. turgidum* var. *durum* K733. *Yr24*, *Yr26*, and *YrCH42* are reported to represent the same locus, and *YrCH42* is flanked by markers *Xbarc187* and *Xgwm498*, at genetic distances of 2.2 and 1.5 cM, respectively (Li *et al.*, 2006). *YrH52* is flanked by markers *Xgwm273* and *Xgwm413* mapping to chromosome 1BS. *YrCH42* and *YrH52* are located on 1BS near the centromere (Peng *et al.*, 2000). *YrCI42* is derived from *Aegilops. tauschii*, and is closely linked to the SSR marker *Xgwm273* located 0.8 cM distant (Wang *et al.*, 2009). Based on the *YrSE5756* linkage map, the SSR marker *Xpsp3000* is 38.5 cM linked to *YrSE5756*, while the EST-STS marker *WE173*, closely linked to *Yr26* at a distance of 1.4 cM, and is linked to *YrSE5756* at a distance of 17.2 cM. Based on the pedigree of SE5756—68.111/RGB-U//WARDResel/3/Stil/4/*Ae. squarrosa* 783—the resistance gene may be derived from tetraploid wheat. In regard to origin and gene location on chromosome 1BS, *YrSE5756* and other genes on chromosome 1BS are very different, suggesting that they are derived from different genetic backgrounds. Based on the results of previous studies, *Yr10*, *Yr15*, *Yr24*, and *Yr26* confer resistance to CYR32 (Yang *et al.*, 2003; Wan & Wu, 2003; Wan *et al.*, 2004); In addition, a new race referred to as V26 is virulent to *Yr24/Yr26*, and varieties in the region possessing *Yr24/Yr26* are now vulnerable to stripe rust epidemics (Huang *et al.*, 2014). So, stripe rust response test in typical adult plant responses of the SE5756, varieties of the carrier *Yr10* and *Yr15*, Chuanmai

42, Yuanfeng175 and Huixianhong resistant segregants to mixture *Pst* races (CYR32, CYR33 and V26) are shown in Fig. 4, *YrSE5756* was likely a new resistance stripe rust gene different from *Yr24/Yr26*, *Yr10* and *Yr15*.

### Wheat breeding for stripe rust resistance using synthetic hexaploid wheat:

Synthetic hexaploid wheat derived from crossing tetraploid durum wheat with diploid *Ae. tauschii* provides germplasm for wheat improvement, and features resistance to leaf and stem rust, powdery mildew, and loose smut, and superior grain and bread-making qualities. The use of synthetic hexaploid wheat allows desirable properties of both *Ae. tauschii* and tetraploid wheat to be transferred to common wheat hybrids. The International Maize and Wheat Improvement Center (CIMMYT) wheat breeding program has produced 1,014 new synthetic hexaploids that have harnessed almost all the diversity of global *Ae. tauschii* accessions. Screening of this huge genetic diversity array has allowed assembly of sub-groups for particular traits; this demonstrates that synthetic wheat lines can be useful for identification of new, agriculturally important loci that can be used to modify flowering and grain maturation in hexaploid wheat (Nguyen *et al.*, 2013). Synthetic wheat lines are useful resources for the identification of agronomically important loci that function in hexaploid wheat. Previous studies (Kerber, 1987; Ma *et al.*, 1995; Mujeeb-Kazi *et al.*, 1996) have shown that numerous alleles applicable to wheat breeding can be identified in natural populations of wild progenitors of common wheat. In China, Chuanmai42 is the first breeding wheat variety derived from synthetic wheat, and was authorized as a national variety in 2004 (No. 2004002). Its pedigree is SynCD768/SW3243//Chuan6415. The parent SynCD768 is a synthetic hexaploid wheat with stripe rust resistance. Through stripe rust response test, *YrSE5756* was likely a new resistance stripe rust gene different from Chuanmai 42. By crossing and backcrossing SE5756 and national authorized variety Xinong979 and selecting for agronomic traits and disease resistance over several years, four germplasm lines with improved agronomic traits, resistance to stripe rust, and similar morphology to common wheat were selected: N07178-1, N07178-2, N08256-1, and N08256-2. In addition, we found that backcross plants had superior agronomic traits compared with plants obtained by selfing. Stripe rust response test in typical adult plant responses of the N07178-1, N07178-2, N08256-1, and N08256-2 resistant segregants to mixture *Pstraces* (CYR32, CYR33 and V26) are shown disease resistant, the resistance gene *YrSE5756* was transferred to common wheat with the expectation that disease resistant,

high-quality germplasm resources and varieties can be obtained. The transfer of resistance genes can broaden the narrow genetic base of wheat varieties and expand our resistance germplasm resource gene pool.

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### References

- Ali, M., W.Q. Ji, Y.G. Hu, G.M. Baloch, H. Zhang and C.Y. Wang. 2010. Molecular implications from SSR markers for stripe rust (*Puccinia striiformis* f. sp. *tritici*) resistance gene in bread wheat line N95175. *Pak. J. Bot.*, 42: 383-390.
- Basnet, B.R., R.P. Singh, A.M.H. Ibrahim, S.A.H. Foessel, J.H. Espino, C. Lan and J.C. Rudd. 2014. Characterization of *Yr54* and other genes associated with adult plant resistance to yellow rust and leaf rust in common wheat Quaiu 3. *Mol. Breeding*, 33: 385-399.
- Chen, X.M. 2005. Epidemiology and control of stripe rust (*Puccinia striiformis* f. sp. *tritici*) on wheat. *Can. J. Plant Pathol.*, 27: 314-337.
- Dadkhodaie, N.A., H. Karaoglou and R.F.W. Park. 2011. Mapping genes *Lr53* and *Yr35* on the short arm of chromosome 6B of common wheat with microsatellite markers and studies of their association with *Lr36*. *Theor. Appl. Genet.*, 122: 479-487.
- Deng, Z.Y., X.Q. Zhang, X.P. Wang, J.K. Jing and D.W. Wang. 2004. Identification and molecular Mapping of a stripe rust resistance gene from a common wheat line Qz180. *Acta. Bot. Sin.*, 46: 236-241.
- Fahima, T., G.L. Sun, A. Beharav, T. Krugman, A. Beiles and E. Nevo. 1999. RAPD polymorphism of wild emmer wheat populations, *Triticum dicoccoides*, in Israel. *Theor. Appl. Genet.*, 98: 434-447.
- Huang, Q., X. Li, W.Q. Chen, Z.P. Xiang, S.F. Zhong, Z.J. Chang, M. Zhang, H.Y. Zhang, F.Q. Tan, Z.L. Ren and P.G. Luo. 2014. Genetic mapping of a putative *Thinopyrum intermedium*-derived stripe rust resistance gene on wheat chromosome 1B. *Theor. Appl. Genet.*, 127: 843-853.
- Kerber, E.R. 1987. Resistance to leaf rust in hexaploid wheat: *Lr32*, a third gene derived from *Triticum tauschii*. *Crop Sci.*, 27: 204-206.
- Kuraparthi, V., P. Chhuneja, H.S. Dhaliwal, S. Kaur, R.L. Bowden and B.S. Gill. 2007. Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes *Lr57* and *Yr40* in wheat. *Theor. Appl. Genet.*, 114: 1379-1389.
- Li, G.Q., Z.F. Li, W.Y. Wang, Y. Zhang, Z.H. He, S.C. Xu, R.P. Singh, Y.Y. Qu and X.C. Xia. 2006. Molecular mapping of stripe rust resistance gene *YrCH42* in Chinese wheat cultivar Chuanmai 42 and its allelism with *Yr24* and *Yr26*. *Theor. Appl. Genet.*, 112: 1434-1440.
- Lin, F. and X.M. Chen. 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 X.M. Chen. 2008. Molecular mapping of genes for race-specific overall resistance to stripe rust in wheat cultivar Express. *Theor. Appl. Genet.*, 116: 797-806.
- Liu, J., Z.J. Chang, X.J. Zhang, Z.J. Yang, X. Li, J.Q. Jia, H.X. Zhan, H.J. Guo and J.M. Wang. 2013. Putative *Thinopyrum intermedium*-derived stripe rust resistance gene *Yr50* maps on wheat chromosome arm 4BL. *Theor. Appl. Genet.*, 126: 265-274.
- Liu, R.H. and J.L. Meng. 2003. MapDraw: a Microsoft Excel macro for drawing genetic linkage maps based on given genetic linkage data. *Hereditas*, Beijing, 25: 317-321.
- Liu, T.G., Y.L. Peng, W.Q. Chen and Z.Y. Zhang. 2010. First detection of virulence in *Puccinia striiformis* f. sp. *tritici* in China to resistance genes *Yr24* (= *Yr26*) present in wheat cultivars Chuanmai 42. *Plant Dis.*, 94: 1163.
- Luo, P.G., X.Y. Hu, Z.L. Ren, H.Y. Zhang, K. Shu and Z.J. Yang. 2008. Allelic analysis of stripe rust resistance genes on wheat chromosome 2BS. *Genome*, 51: 922-927.
- Ma, H., P. Singh and A. Mujeeb-Kazi. 1995. Resistance to stripe rust in *Triticum turgidum*, *T. tauschii* and their synthetic hexaploids. *Euphytica*, 82: 117-124.
- Ma, J.X., R.H. Zhou, Y.C. Dong, F. Lan, X.M. Wang and J.Z. Jia. 2001. Molecular mapping and detection of the yellow rust resistance gene *Yr26* in wheat transferred from *Triticum turgidum* L. using microsatellite markers. *Euphytica*, 120: 219-226.
- Marais, F., A. Marais, B. McCallum and Z. Pretorius. 2009. Transfer of leaf rust and stripe rust resistance genes *Lr62* and *Yr42* from *Aegilops neglecta* Req. ex Bertol. to Common Wheat. *Crop Sci.*, 49: 871-879.
- Marais, G.F., B. McCallum and A.S. Marais. 2006. Leaf rust and stripe rust resistance genes derived from *Aegilops sharonensis*. *Euphytica*, 149: 373-380.
- Michelmore, R.W., I. Paran and R.V. Kesseli. 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 segregation populations. *Proc. Natl. Acad. Sci., USA*, 88: 9828-9832.
- Mujeeb-Kazi, A., V. Rosas and S. Roldan. 1996. Conservation of the genetic variation of *Triticum tauschii* (Coss.) Schmalh. (*Aegilops squarrosa* auct. non L.) in synthetic hexaploid wheats (*T. turgidum* L. s.lat. × *T. tauschii*; 2n = 6× = 42, AABBDD) and its potential utilization for wheat improvement. *Genet. Resour. Crop Evol.*, 43: 129-134.
- Nguyen, A.T., J.C.M. Iehisa, T. Kajimura, K. Murai and S. Takumi. 2013. Identification of quantitative trait loci for flowering-related traits in the D genome of synthetic hexaploid wheat lines. *Euphytica*, 192: 401-411.
- Peng, J.H., T. Fahima, M.S. Röder, Q.Y. Huang, A. Dahan, Y.C. Li, A. Grama and E. Nevo. 2000. High-density molecular map of chromosome region harbouring stripe-rust resistance genes *YrH52* and *Yr15* derived from wild emmer wheat. *Genetica*, 109: 199-210.
- Ren, R.S., M.N. Wang, X.M. Chen and Z.J. Zhang. 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.
- Smith, P.H., R.M.D. Koebner and L.A. Boyd. 2002. The development of a STS marker linked to a yellow rust resistance derived from the wheat cultivar Moro. *Theor. Appl. Genet.*, 104: 1278-1282.
- Sun, G.L., T. Fahima, A.B. Korol, T. Turpeinen, A. Grama, Y.I. Romin and E. Nevo. 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.
- Uauy, C., J.C. Brevis, X.M. Chen, I. Khan, L. Jackson, O. Chicaiza, A. Distelfeld, T. Fahima and J. Dubcovsky. 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.

- Van Ooijen, J.W. 2006. JionMap 4.0, Software for the calculation of genetic linkage maps in experimental populations. Kyazma B. V., Wageningen, Netherlands.
- Wan, A.M. and L.R. Wu. 2003. Pathogenic changes of stripe rust fungus of wheat in China during 1997-1999. *Acta. Phytopathol Sin.*, 33: 261-266.
- Wan, A.M., Z.H. Zhao, X.M. Chen, Z.H. He, S.L. Jin, Q.Z. Jia, G. Yao, J.X. Yang, B.T. Wang, G.B. Li, Y.Q. Bi and Z.Y. Yuan. 2004. Wheat stripe rust epidemic and virulence of *Puccinia striiformis* f. sp. *tritici* in China in 2002. *Plant Dis.*, 88: 896-904.
- Wang, L.F., J.X. Ma, R.H. Zhou, X.M. Wang and J.Z. Jia. 2002. Molecular tagging of the yellow rust resistance gene *Yr10* in common wheat, P.I. 178383 (*Triticum aestivum* L.). *Euphytica*, 124: 71-73.
- Wang, L.M., Z.Y. Zhang, H.J. Liu, S.C. Xu, M.Z. He, H.X. Liu and O.Z.Y. Veisz. 2009. Identification, gene postulation and molecular tagging of a stripe rust resistance gene in synthetic wheat CI142. *Cereal Res. Communications*, 37: 209-215.
- Wang, Y.J., C.Y. Wang, H. Zhang, Z.N. Yue, X.L. Liu and W.Q. Ji. 2013. Genetic analysis of wheat (*Triticum aestivum* L.) and related species with SSR markers. *Genet. Resour. Crop Evol.*, 60: 1105-1117.
- Xu, L.S., M.N. Wang, P. Cheng, Z.S. Kang, S.H. Hulbert and X.M. Chen. 2013. Molecular mapping of *Yr53*, a new gene for stripe rust resistance in durum wheat accession PI480148 and its transfer to common wheat. *Theor. Appl. Genet.*, 126: 523-533.
- Yan, G., X. Chan, R. Line and C. Wellings. 2003. Resistance gene-analog polymorphism markers co-segregating with the *Yr5* gene for resistance to wheat stripe rust. *Theor. Appl. Genet.*, 106: 636-643.
- Yang, B.J., W.Q. Ji, C.Y. Wang, F. Xue, M. Ali, Y.J. Wang, H. Zhang and X.L. Liu. 2013. Chromosome location and SSR markers of a stripe rust resistance gene from wheat (*Triticum aestivum*) line N9738. *Pak. J. Bot.*, 45: 719-724.
- Yang, Z.M., C.J. Xie and Q.X. Sun. 2003. Situation of the sources of stripe rust resistance of wheat in the Post-CY32 era in China. *Acta. Agron. Sin.*, 29: 161-168.

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