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ORIGINAL PAPER

Genetic mapping of a putative *Thinopyrum intermedium*-derived stripe rust resistance gene on wheat chromosome 1B

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Abstract
Key message **Stripe rust resistance transferred from *Thinopyrum intermedium* into common wheat was controlled by a single dominant gene, which mapped to chromosome 1B near *Yr26* and was designated *YrL693*.**
Abstract Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*) is a highly destructive disease of wheat (*Triticum aestivum*). Stripe rust resistance was transferred from *Thinopyrum intermedium* to common wheat, and the resulting introgression line (L693) exhibited all-stage resistance to the widely virulent and predominant Chinese pathotypes CYR32 and CYR33 and to the new virulent pathotype V26. There was no cytological evidence that L693 had alien chromosomal segments from *Th. intermedium*. Genetic analysis of stripe rust resistance was performed by crossing L693 with the susceptible line L661. F_1, F_2, and $F_{2:3}$ populations from reciprocal crosses showed that resistance was controlled by a single dominant gene. A total 479 $F_{2:3}$ lines and 781 pairs of genomic simple sequence repeat (SSR) primers were employed to determine the chromosomal location of the resistance gene. The gene was linked to six publicly available and three recently developed wheat genomic SSR markers. The linked markers were localized to wheat chromosome 1B using Chinese Spring nulli-tetrasomic lines, and the resistance gene was localized to chromosome 1B based on SSR and wheat genomic information. A high-density genetic map was also produced. The pedigree, molecular marker data, and resistance response indicated that the stripe rust resistance gene in L693 is a novel gene, which was temporarily designated *YrL693*. The SSR markers that co-segregate with this gene (*Xbarc187-1B*, *Xbarc187-1B-1*, *Xgwm18-1B*, and *Xgwm11-1B*) have potential application in marker-assisted breeding of wheat, and *YrL693* will be useful for broadening the genetic basis of stripe rust resistance in wheat.

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Introduction

Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*) continues to be one of the most devastating diseases threatening wheat (*Triticum aestivum* L.) yields worldwide, especially in wheat-growing areas with cool, moist climates. Based on survey data collected over the last 10 years, China is the largest region for wheat stripe rust in the world, with an average of 4 million hectares potentially affected each year (Li et al. 2006b; Liu et al. 2013). For example, 6.6, 4.9, and 4.08 million hectares of wheat in China were affected by stripe rust in 2002, 2003, and 2009, respectively (Kang et al. 2010).

Stripe rust is most destructive to wheat production in northwest and southwest China (Luo et al. 2005; Wan et al. 2004). With the prevalence of *Pst* races CYR32 and CYR33, stripe rust has become existing major threat to wheat production because only a few of the known resistance genes (*Yr5*, *Yr10*, *Yr15*, *Yr18*, *Yr24*/*Yr26*, *Yr36*, *Yr39*, and *Yr41*) are effective against these races (Chen et al. 2009; Kang et al. 2010; Li et al. 2006a, b, c; Luo et al. 2009a; Wan et al. 2004). Additionally, a recently identified race, V26, overcomes the resistance gene *Yr24*/*Yr26*/*YrChuanmai42* present in a number of varieties grown in the region (Han et al. 2012; Liu et al. 2010).

The development of host resistance by selective breeding is the most effective, economical, environmentally sound, and consistently used method of controlling stripe rust in wheat (Chen 2005). To date, more than 60 designated resistance genes or alleles and more than 40 temporarily assigned genes have been identified on all wheat chromosomes except 1A and 7A (http://wheat.pw.usda.gov/; Xu et al. 2013; McIntosh pers. comm.). Among these genes, only *Yr9* and *Yr24*/*Yr26* have been widely used to develop stripe rust-resistant cultivars in wheat breeding programs in China. In hexaploid wheat (AABBDD), microsatellites or simple sequence repeats (SSRs) have been used to locate and map many stripe rust resistance genes within specific wheat chromosomes or chromosomal arms; these genes include *Yr5* (Sun et al. 2002), *Yr17* (Jia et al. 2011), *Yr18* and *Yr29* (Lillemo et al. 2008), *Yr24*/*Yr26* (Li et al. 2006a), *Yr36* (Uauy et al. 2005), *Yr41* (Luo et al. 2008), *Yr43* and *Yr44* (Cheng and Chen 2010), *Yr45* (Li et al. 2011), *Yr46* (Herrera-Foessel et al. 2011), *Yr47* (Bansal et al. 2011), *Yr48* (Lowe et al. 2011), *Yr50* (Liu et al. 2013), *Yr52* (Ren et al. 2012), and *Yr53* (Xu et al. 2013).

Alien gene transfer is an important means of increasing the genetic diversity of disease resistance in wheat. Of the permanently named *Yr* genes, 14 were transferred from wild relatives, including *Aegilops comosa* Sm., *Ae. geniculata* Host, *Ae. kotschyi* Boiss, *Ae. neglecta* Bertol, *Ae. sharonensis* Eig., *T. dicoccoides* Körn., *T. tauschii* Coss., *T. ventricosum* Ces., *Dasypyrum villosum* L., and cereal rye (*Secale cereale* L.) (http://wheat.pw.usda.gov/; Chen 2005; Xu et al. 2013). *Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey (2n = 6x = 42; JJJ^{s}J^{s}SS) (syn. *Elytrigia intermedia* [Host] Nevski) has been hybridized extensively with wheat and has also proven to be a useful source of disease resistance in hexaploid wheat (*T. aestivum* L.) (2n = 42; AABBDD) (Liu et al. 2013; Luo et al. 2009a).

A considerable body of evidence supports the hypothesis that *Th. intermedium* is a valuable gene pool for wheat disease resistance because of its resistance to wheat streak mosaic virus (Friebe et al. 1996), Fusarium head blight (FHB) (Fedak and Han 2005), leaf rust (Autrique et al. 1995), stem rust (Fedak 1999), and powdery mildew (Liu and Wang 2005). Two powdery mildew resistance genes, *Pm40* and *Pm43*, and one stripe rust resistance gene, *Yr50*, were transferred from *Th. intermedium* to common wheat (He et al. 2009; Liu et al. 2013; Luo et al. 2009b). The wheat line L693, which is resistant to stripe rust, powdery mildew, and FHB, was developed from $F_{6:7}$ families of a cross between Mianyang 11 (MY11) and YU25. The latter was derived from *Th. intermedium* by an interspecific cross (Zhang et al. 2011). The stripe rust resistance in L693 is conferred by the temporarily designated gene *YrYU25* (Luo et al. 2009a). The objectives of the present study were to study the inheritance of stripe rust resistance in L693, to identify the chromosomal location of the resistance gene, and to map the gene with the eventual objective of marker-assisted selection, fine mapping, and map-based cloning.

Materials and methods

Plant materials

Wheat line L693, which is resistant to stripe rust, and susceptible line L661 were selected from $F_{6:7}$ families of a cross between the susceptible line MY11 and the resistant line YU25. Stripe rust resistance in YU25 is derived from *Th. intermedium* (Luo et al. 2009a, b; Zhang et al. 2011). The sister lines were used as parents to study the inheritance of stripe rust resistance. The wheat cultivars (or lines) YU25, MY11, Chuanmai 42, L693, and L661 and susceptible control SY95-71 were included in comparative response tests. *Th. intermedium* and common wheat line Chinese Spring were used as controls for the detection of alien chromatin in YU25 and L693. Chinese Spring nulli-tetrasomic (NT) lines were used to identify the chromosomal location of the resistance gene and linked markers. F_1, F_2, and $F_{2:3}$ populations from the reciprocal crosses L661/L693 and L693/L661 were used for genetic analysis of stripe rust response. A total 479 $F_{2:3}$ lines were used in genetic mapping.

Evaluation of stripe rust reactions

Nine wheat cultivars or lines, including four resistant lines (L658, L693, L696, and L699) and one susceptible line (L661), were derived from the same $F_{6:7}$ families of MY11/YU25. The response of wheat cultivar Chuanmai 42 (CM42), which carries *Yr24*/*Yr26* (Li et al. 2006a; Liu et al. 2010), was compared with that of YU25 and its derived lines using six representative Chinese *Pst* races (CYR31, CYR32, CYR33, SY11-4, SY11-7, and V26). Among these *Pst* races, V26 differs from others in China because of its virulence on *Yr24*/*Yr26* genotypes. Wheat plants at the three-leaf stage were inoculated with urediniospores of a single race, and their reactions were evaluated according to

previously described methods (Luo et al. 2005). Inoculated seedlings were kept sufficiently moist during incubation at 10 °C with 100 % relative humidity in the dark for 24 h, after which they were subjected to a 24 h cycle of 16 h of light (at 18 °C) and 8 h of darkness (at 10 °C). When the pustules on susceptible checks were fully developed (14–21 days after inoculation), infection types (IT) were classified using a 0–4 rating scale (Luo et al. 2008).

To determine the genetics of resistance in YU25, race CYR32, which is avirulent on YU25 and virulent on SY95-71, was employed to test F_1, F_2, and $F_{2:3}$ populations of L661/L693 and L693/L661. All seeds used for genetic analysis were planted in a greenhouse; 20–30 plants of each parental line and F_1, 396 F_2 plants and 207 $F_{2:3}$ lines derived from L661/L693, and 582 F_2 plants and 272 $F_{2:3}$ lines derived from L693/L661 (Table 1) were planted in a randomized design with 20–30 plants in 2.5 m rows with 25 cm spacing. Susceptible control plants (SY95-71) used to spread disease were planted in every third row to ensure that all plants had the same opportunity for infection. SY95-71 was inoculated with the predominant race CYR32 at the seedling 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).

DNA extraction and bulked segregant analysis

Total DNA was extracted from 5-week-old seedling leaves using a previously described method (Tai and Tanksley 1990). Equal amounts of DNA at a concentration of 60 ng/μl from 10 homozygous resistant and 10 homozygous susceptible F_2 individuals (genotypes based on the reactions of $F_{2:3}$ lines) were mixed to construct resistant (B_R) and susceptible (Bs) bulks, respectively, for bulked segregant analysis (BSA) (Michelmore et al. 1991). Markers that were polymorphic between the resistant and susceptible parents and bulks were used to genotype the $F_{2:3}$ lines and in linkage analysis.

Microsatellite marker analysis

Genomic DNA of parents and individual F_2 plants derived from the L661/L693 and L693/L661 crosses was used for molecular analyses. For the initial polymorphic marker survey, selected *gwm* (Röder et al. 1998) and *wmc* (Gupta et al. 2002) SSR markers spaced at intervals of 3–4 cM along the chromosome according to the consensus map of Somers et al. (2004) were used in BSA to screen for markers linked to the resistance gene. PCRs (25 μl volume) were performed in a PTC-200 thermocycler (MJ Research, Watertown, MA, USA). SSR analysis was performed following a previously described procedure (Röder et al. 1998) with minor modifications. For each PCR, the 25 μl mixture consisted of each SSR primer at a concentration of 200 nmol/l, 0.2 mmol/l dNTPs, 1.5 mmol/l $MgCl_2$, 1 unit of Taq polymerase, and 60 ng of template DNA. PCR was performed following a previously described program (Luo et al. 2008). Each PCR product was mixed with 3 μl of loading buffer (98 % formamide, 10 mM EDTA [pH 8.0], 0.25 % bromophenol blue, and 0.25 mg/ml xylene cyanol), denatured at 95 °C for 5 min, and chilled on ice. Subsequently, a 6 μl aliquot of each sample was loaded onto a 6 % polyacrylamide gel (19:1 acrylamide:bis-acrylamide, 8 M urea and 1 × TBE [90 mM tris–borate (pH 8.3), 2 mM EDTA]) prior to separation at 80 W for approximately 1.5 h and visualization by silver staining (Bassam et al. 1991).

Development of novel SSR markers

To increase the marker density of the map, we chose various *Xcfd*, *Xbarc*, and *Xgdm* SSR markers situated close to two markers that co-segregated with the resistance locus in BSA. The contig sequences carrying the markers that mapped to chromosome 1B can be found in the draft wheat genome sequence (Brenchley et al. 2012; Jia et al. 2013; Ling et al. 2013) using BLAST. This contig was used to search for additional SSR loci. Using primer3 (Rozen and Skaletsky 2000), we developed 19 novel genomic SSR

Table 1 Resistance phenotypes in F_1, F_2, and $F_{2:3}$ populations obtained from L661/L693 and L693/L661 crosses upon exposure to *Pst* race CYR32

Cross	Generation	Observed number of F1, F2and F2:3 individuals			Expected ratio	χ^{2a}
		Homozygous resistant/F2 resistant	Segregating	Homozygous susceptible/F2 susceptible		
L661/L693	F_1		11			
	F_2	304	–	92	3:1	0.660
	$F_{2:3}$	52	103	52	1:2:1	0.005
L693/L661	F_1		16			
	F_2	368	–	114	3:1	0.467
	$F_{2:3}$	67	137	68	1:2:1	0.022

[a] Value for significance at $P = 0.05$ is 3.84

Table 2 New SSR markers based on a contig from the draft wheat genome sequence on chromosome 1B

Name	Forward primer 5′-3′	Reverse primer 5′-3′	Contig no[c]	Polymorphism	Type
Xbarc137-1B[a]	GGCCCATTTCCCACTTTCCA	CCAGCCCCTCTACACATTTT	3480801	Y	Codominant
Xbarc137-1B-1[b]	TTGGAGGAAAAATGGTTTGG	CAGACACATAACGAACATG-TATAGG		N	
Xbarc187-1B[a]	GTGGTATTTCAGGTGGAGTT-GTTTTA	CGGAGGAGCAGTAAGGAAGG	3460958	Y	Codominant
Xbarc187-1B-1[b]	GCAGTAAGGAAGGGGATCAA	TGGTATTTCAGGTGGAGTTGTTT		Y	Codominant
Xcfd2-1B[a]	GGTTGCAGTTTCCACCTTGT	CATCTATTGCCAAAATCGCA	3894989	N	
Xcfd2-1B-1[b]	ACCGATGCCTAGGTGAACTG	TTGCAGTTAGGAGCCAGGAT		N	
Xcfd2-1B-2[b]	GTCGTGACCATCCTCCAGAT	TGGATGGTTTCGCTTGTGTA		N	
Xcfd2-1B-3[b]	TATTGCCAAAATCGCAGCTT	TGTTTTGTGCTCATGAATTGC		N	
Xcfd2-1B-4[b]	ATGCTGGAGGAGAGCAGAAC	CGTGCAGGTTTGTGATTGAG		N	
Xcfd2-1B-5[b]	GGTTTGGAGGGAGAGGAGAG	TCCTCCCACCTCTGTCACTT		N	
Xcfd2-1B-6[b]	TCAACTACCCCACACGATCA	CACGCACGGTAAGGTTCTTT		N	
Xcfd65-1B[a]	AGACGATGAGAAGGAAGCCA	CCTCCCTTGTTTTTGGGATT	3920499	N	
Xcfd65-1B-1[b]	AAGCCAACTGTGGCAAGTCT	GGCGCAAAAGAACAAGTCTC		Y	Codominant
Xcfd65-1B-2[b]	CAAGAGCCACTCACAAGCAT	CACCCCTACTCCTGCATGTT		Y	Dominant
Xcfd65-1B-3[b]	GGGTTCATCATCCTCATTGG	AAAGTTCATCGGATCCCAAA		N	
Xgpw1239-1B[a]	TCGCCTTTACTACGGAGTGG	AACAATCGACCAACAAAGCC	3828766	N	
Xgpw1239-1B-1[b]	AAAAGGGGTGCAGTCAGTGT	GCCACCATGTGATCTTCCTT		N	
Xgpw1239-1B-2[b]	TTAAGACCCCTCCCTCTTCC	TGTGCATACCATGGCAATCT		N	
Xgpw1239-1B-3[b]	TGGACTTCAGCCCAGATTTT	ACTGAGATGGCTTCCACCAC		N	
Xwmc597-1B[a]	AACACACCTTGCTTCTCTGGGA	GACTAGGGTTTCGGTTGTTGGC	3480535	N	
Xwmc597-1B-1[b]	GCTACGTCCGGTGATTTCAT	AGACGATGGGAGGAGGAGTG		Y	Dominant
Xwmc597-1B-2[b]	AGAACTGCTCCAGTGCGTTT	AGAACTGCTCCAGTGCGTTT		N	
Xwmc597-1B-3[b]	TTCCGATGCAATGAAACAAA	AAGTAGCGAGAATCCGAGTTTT		N	
Xwmc611-1B[a]	GGTTCGCTTTCAAGGTCCACTC	CGGGACACTAGTGCTCGATTCT	3422054	N	
Xwmc611-1B-1[b]	TTTGTCACTGCCTCACTGGA	TTCGCTTTCAAGGTCCACTC		Y	Codominant
Xwmc626-1B[a]	AGCCCATAAACATCCAACACGG	AGGTGGGCTTGGTTACGCTCTC	3417264	Y	Dominant
Xwmc626-1B-1[b]	GTGCACAGGGGAGTAGAGGT	CACCCTTCTTTTTCGTGCAT		Y	Codominant

Y yes, *N* no

[a] Published SSR markers on chromosome 1B

[b] Newly developed SSR markers on chromosome 1B

[c] Contig from which the marker was derived

markers based on 8 contigs carrying 8 different public SSR loci (Table 2). The novel markers were named after previously identified public SSR markers by adding a second number. Because the public markers and newly developed markers are located within the same contig, they are physically close and, therefore, useful for fine genetic mapping. Thus, these markers were employed to screen additional polymorphic markers and subsequently used to construct the high-density genetic map.

Chromosomal location

To further ensure that the chromosomal locations of the linked microsatellite markers used in this study were accurate, the following lines were used: Chinese Spring nullisomic 1A tetrasomic 1B (N1AT1B), nullisomic 1A tetrasomic 1D (N1AT1D), nullisomic 1B tetrasomic 1A (N1BT1A), nullisomic 1B tetrasomic 1D (N1BT1D), nullisomic 1D tetrasomic 1A (N1DT1A), and nullisomic 1D tetrasomic 1B (N1DT1B). All lines were kindly provided by Prof. D.C. Liu, Triticeae Research Institute, Sichuan Agricultural University, Chengdu, Sichuan.

Statistical analysis and linkage mapping

Chi-squared tests were performed to determine the goodness-of-fit of the segregation data with hypothesized 1:2:1 ratios for $F_{2:3}$ lines using Sigmaplot 2001 software (SPSS Inc., Chicago, IL, USA). Recombination fractions were converted to map distances (cM) between loci using the

Kosambi mapping function (Kosambi 1944). Loci showing no significant deviations ($P > 0.05$) were used in the linkage analysis. The order of the linked SSR markers and the resistance gene was determined using JoinMap 4 (Wageningen, Netherlands). A total of 207 $F_{2:3}$ lines derived from L661/L693 and 272 $F_{2:3}$ lines derived from L693/L661 (Table 1) were used to construct two different genetic maps using JoinMap 4 with an LOD threshold of 3.0. An integrated genetic linkage map of the resistance gene was constructed by integrating the two different genetic maps from L661/L693 and L693/L661 using the map integration function of JoinMap 4.

Results

Stripe rust response

The low ITs on nine wheat lines inoculated with six *Pst* races (CYR31, CYR32, CYR33, SY11-4, SY11-7, and V26) showed that line YU25 and its derived lines L658, L693, L696, and L699 were resistant (IT 0-0) to all six races, whereas MY11 and SY95-71 were susceptible (IT 3-4). CM42, which carries *Yr24*/*Yr26*, was susceptible (IT 4) only to the V26 race. Typical adult plant responses of the parents and resistant segregants to race CYR32 are shown in Fig. 1. Thus, the resistance gene in YU25 was likely present in wheat lines L658, L693, L696, and L699.

Fig. 1 Stripe rust reaction on flag leaves of parental lines L693 (*left*) and L661

Inheritance of resistance in L693

To map the resistance gene in L693 using molecular markers, F_1 plants, 978 F_2 individuals and 479 $F_{2:3}$ lines from the reciprocal L661/L693 crosses (Table 1) were infected from the susceptible spreader line SY95-71, which was inoculated with race CYR32. F_1 plants were resistant, and their response was similar to that of L693, indicating that resistance was dominant. The F_2 and $F_{2:3}$ lines segregated for a single dominant gene (Table 1), which was provisionally designated *YrL693*.

Identification of microsatellite markers linked with *YrL693*

Only 41 (5.2 %) of 781 microsatellites (from the *gwm* and *wmc* series) were polymorphic between the susceptible line L661 and resistant line L693. Primer pairs *Xgwm273-1B*, *Xgwm18-1B*, *Xgwm11-1B*, and *Xwmc269-1B* produced identical bands in the resistant (B_R) F_2 bulks (and in L693) and polymorphic bands in the susceptible (B_S) F_2 bulks (and in L661), demonstrating that these markers were linked with *YrL693*. Of the five *Xbarc*, *Xcfd*, and *Xwmc* serial primer pairs close to *YrL693*, *Xbarc137-1B* and *Xbarc187-1B* were linked with *YrL693* (Fig. 2). In addition, three of 19 newly developed SSR primer pairs (Table 2), *Xbarc187-1B-1*, *Xcfd65-1B-1* and *Xwmc626-1B-1*, were closely linked to *YrL693*. Because six of the nine linked markers were previously shown to be located on wheat chromosome 1B and the contigs containing the other three linked markers must also be located on wheat chromosome 1B, we hypothesize that *YrL693* is located on this chromosome.

Chromosomal assignment and genetic map of *YrL693*

Based on the published chromosomal locations of the six linked microsatellite markers (Röder et al. 1998; Somers et al. 2004; Song et al. 2002) and the reported chromosomal locations of the contigs containing the other three linked microsatellite markers (http://www.wheatgenome.org/), *YrL693* was localized to the centromeric region of wheat chromosome 1B, and the order of SSR loci agreed well with the established SSR maps on chromosome 1B (http://wheat.pw.usda.gov/cgi-bin/graingenes). However, microsatellite markers are not always chromosome-specific because some wheat chromosomes share partial homology (Plaschke et al. 1996). Eight of the nine linked markers were verified on chromosome 1B using Chinese Spring nulli-tetrasomic lines, and only *Xwmc626-1B-1* was not assigned to chromosome 1B (Fig. 3).

The relationship between the stripe rust resistance gene and the marker genotypes is shown in Supplemental

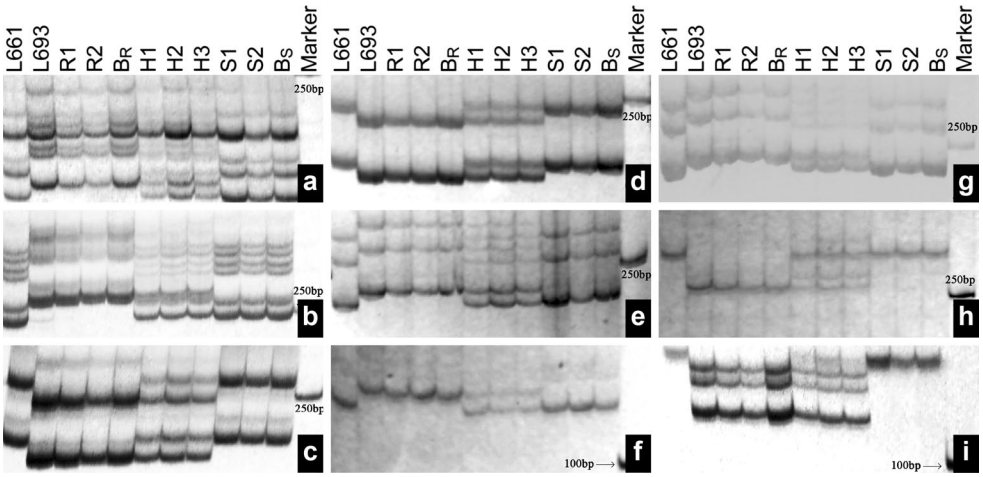

Fig. 2 Silver-stained polyacrylamide gels showing simple sequence repeat (SSR) markers: *Xgwm273-1B* (**a**), *Xbarc137-1B* (**b**), *Xgwm11-1B* (**c**), *Xgwm18-1B* (**d**), *Xbarc187-1B* (**e**), *Xwmc269-1B* (**f**), *Xbarc187-1B-1* (**g**), *Xcfd65-1B-1* (**h**), and *Xwmc626-1B-1* (**i**) linked with *YrL693*. *L661*susceptible parent; *L693* resistant parent; *R1* and *R2* resistant F_2 individuals; B_R resistant F_2 DNA pool; *H1*, *H2*, and *H3* resistant F_2 individuals; *S1* and *S2* susceptible F_2 individuals; B_S susceptible F_2 DNA pool; Marker, 50 bp DNA ladder

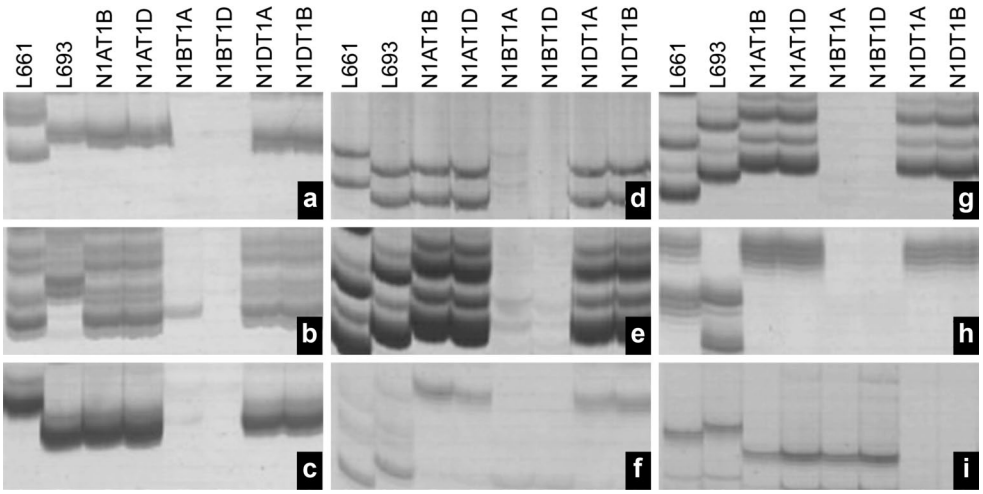

Fig. 3 Chromosomal localization of the microsatellite markers *Xgwm273-1B* (**a**), *Xbarc137-1B* (**b**), *Xgwm11-1B* (**c**), *Xgwm18-1B* (**d**), *Xbarc187-1B* (**e**), *Xwmc269-1B* (**f**), *Xbarc187-1B-1* (**g**), *Xcfd65-1B-1* (**h**), and *Xwmc626-1B-1* (**i**) linked with *YrL693* in L661 (S), L693 (R), and a nulli-tetrasomic line of homoeologous group 1. With the exception of *Xwmc626-1B-1*, no PCR products were generated in nullisomic 1B (N1BT1A and N1B1D)

Table 1. Each marker locus exhibited a 1:2:1 segregation ratio. No crossovers were found between *YrL693* and the markers *Xgwm18-1B*, *Xgwm11-1B*, *Xbarc187-1B*, and *Xbarc187-1B-1* in the forward cross (L661/L693) (Supplemental Table 1; Fig. 4a); *YrL693* was, therefore, narrowed to a 0.39 cM interval flanked by markers *Xbarc137-1B* and *Xwmc269-1B*/*Xcfd65-1B-1* (Fig. 4a). Additionally, no crossovers were found between *YrL693* and the markers *Xbarc137-1B*, *Xgwm273-1B*, *Xgwm18-1B*, *Xgwm11-1B*, *Xbarc187-1B*, *Xbarc187-1B-1*, and *Xwmc626-1B-1* in the reverse cross (L693/L661); however, the markers *Xcfd65-1B-1* and *Xwmc269-1B* were distally linked to *YrL693* with genetic distances of 1.3 and 1.5 cM, respectively (Fig. 4b). The locus order in the forward cross agreed well with that in the reverse cross (Fig. 4a, b). An integrated map was produced from the two genetic maps using the regression mapping algorithm in JoinMap 4 (Fig. 4c). In the integrated map, *YrL693* co-segregated with four microsatellite markers (*Xgwm18-1B*, *Xgwm11-1B*, *Xbarc187-1B*, and *Xbarc187-1B-1*), and it was narrowly flanked by the markers *Xgwm273-1B* and *Xwmc626-1B-1*, with distances of 0.08 and 0.07 cM, respectively.

Discussion

Origin and mode of inheritance for *YrL693*

The discovery of novel stripe rust resistance genes and development of new resistant cultivars is the most effective method of controlling stripe rust in wheat. *Th. intermedium* is an important perennial Triticeae species and is a valuable

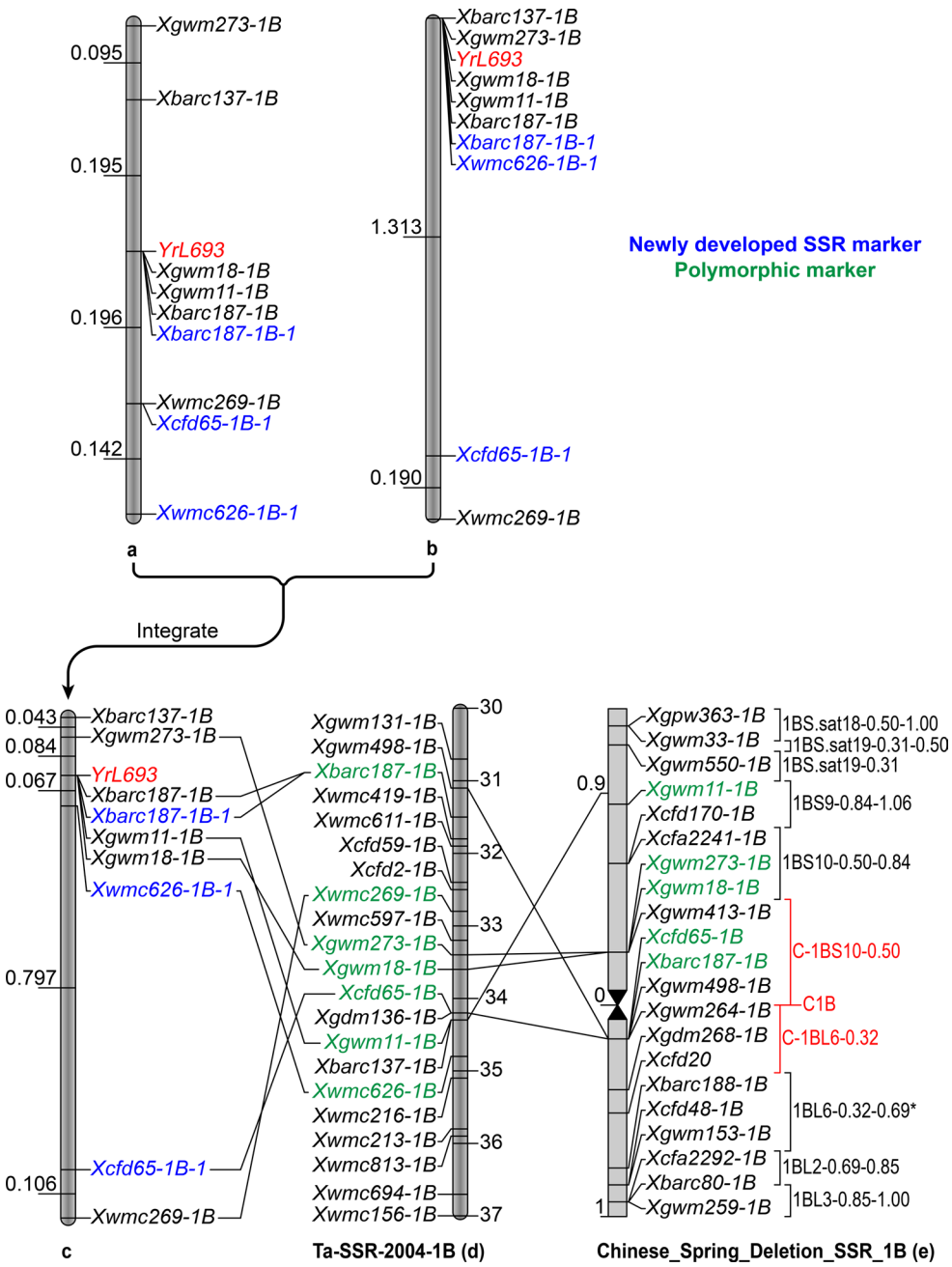

Fig. 4 Genetic mapping of *YrL693* on chromosome 1B in reciprocal crosses L661/L693 (**a**), and L693/L661 (**b**), the integrated map (**c**), the order of SSR markers in the reference map (**d**), and the wheat deletion map (**e**) (http://wheat.pw.usda.gov/cmap/)

source of resistance to stripe rust (Liu et al. 2013; Luo et al. 2009a). The wheat line L693 and its resistant parent YU25 are derivatives of *Th. intermedium*, and because all common wheat parents in the pedigree of these lines are highly susceptible, the resistance in L693 was likely derived from *Th. intermedium*. Genetic segregation data clearly indicate the presence of a single dominant resistance gene in L693 (Table 1) and its resistant parent YU25 (Luo et al. 2009a). Of the formally named wheat genes for stripe rust resistance, only *Yr53* is derived from this donor species. Because of its different chromosomal location the resistance gene in L693 is likely to be novel.

Chromosomal location of *YrL693*

The microsatellite markers *Xgwm273-1B*, *Xgwm18-1B*, *Xgwm11-1B*, *Xwmc269-1B*, *Xbarc137-1B*, and *Xbarc187-1B*, which were previously assigned to chromosome 1B (Gupta et al. 2002; Röder et al. 1998; Somers et al. 2004; Song et al. 2002), were closely linked with the stripe rust resistance gene in L693. Additionally, the contigs containing the other three linked microsatellite markers were also on chromosome 1B (http://www.wheatgenome.org/). More importantly, eight of the linked markers (except for *Xwmc626-1B-1*) were verified to be located on

chromosome 1B using the Chinese Spring nulli-tetrasomic line (Fig. 3). Furthermore, the order of these SSR loci agreed well with the established SSR maps of chromosome 1B (http://wheat.pw.usda.gov/cgi-bin/graingenes), and the genetic distances between these markers and *YrL693* were <1 cM (Fig. 4c). These data provide solid evidence that *YrL693* is also on chromosome 1B and is located in the centromeric region, where it is narrowly flanked by the markers *Xgwm273-1B* and *Xwmc626-1B-1* at distances of 0.08 and 0.07 cM, respectively. *Xgwm273-1B* mapped to the wheat chromosome deletion bin C-1BS-10-0.50, whereas *Xwmc626-1B-1* is not mapped to a chromosome. However, *Xcfd65-1B*, which is located in the same contig as *Xcfd65-1B-1* is distal to *Xwmc626-1B-1* on the opposite side of *Xgwm273-1B*, proximal to the centromere in deletion bin C-1BL-6-0.32 (http://wheat.pw.usda.gov/cmap/). The co-segregating marker *Xgwm18-1B* was also mapped to wheat chromosome deletion bin C-1BS-10-0.50, indicating that *YrL693* may be located within wheat chromosome deletion bin C-1BS-10-0.50.

Of the permanently named stripe rust resistance genes, *Yr26* is located in the centromeric region of chromosome 1B (Zhang et al. 2013). *Yr26* was mapped to chromosome 1B using microsatellite markers, and a 1.9 cM genetic distance between *Yr26* and *Xgwm11-1B*/*Xgwm18-1B* was estimated using an F_2 population of 109 individuals (Ma et al. 2001). The genetic distance between *Yr26* and *Xgwm11-1B*/*Xgwm18-1B* was reported to be 3.2 cM in a study utilizing 500 $F_{2:3}$ families (Wang et al. 2008). However, another study using 787 F_2 plants and 165 F_3 lines reported that *Xgwm11-1B*, *Xgwm18-1B*, and *Xbarc187-1B* were closely linked with *Yr26*, with genetic distances of 4.2, 3.9, and 2.5 cM, respectively (Wen et al. 2008). The differences among the reported distances between a single marker and *Yr26* may result from errors in genotyping and differences in population size and genetic backgrounds of the materials studied because similar mapping software and LOD thresholds were used in the different experiments. Thus, although variable genetic distances were reported between *Yr26* and markers *Xgwm11-1B*, *Xgwm18-1B*, and *Xbarc187-1B* in independent experiments, no crossovers were detected between *YrL693* and *Xgwm11-1B*, *Xgwm18-1B*, or *Xbarc187-1B* in the present reciprocal crosses (Fig. 4c). More importantly, recent studies have confirmed that *Yr26* maps to wheat chromosome deletion bin C-1BL-6-0.32 (Wen et al. 2008; Zhang et al. 2013), whereas the present work indicates that *YrL693* might be located within wheat chromosome deletion bin C-1BS-10-0.50. A comparison of the available mapping information regarding *Yr26* and *YrL693* tends to support the hypothesis that the *YrL693* locus is not an allele of *Yr26*. The new *Pst* race V26 is virulent to *Yr24*/*Yr26* (Liu et al. 2010; Han et al. 2012) but avirulent to *YrL693*. The pedigree of L693 indicates that *YrL693* should be derived from *Th. intermedium*, whereas *Yr26* is derived from *Triticum turgidum* (Ma et al. 2001).

Of the permanently named stripe rust resistance genes, *Yr15* is also located on wheat chromosome 1BS and genetically close to the centromere, but physically could be some distance from it (McIntosh et al. 1996; Sun et al. 1997; Peng et al. 2000). Several lines of evidence indicate that *YrL693* is different from *Yr15* and *YrH52*. First, *Yr15* and *YrH52* are from *Triticum dicoccoides* (McIntosh et al. 1996; Peng et al. 2000), whereas *YrL693* is potentially from *Th. intermedium*. Moreover, the presence of *YrL693* in L693, together with resistances to powdery mildew and FHB (Luo et al. 2009b; Zhang et al. 2011), further excludes the possibility that *YrL693* is by *Yr15* or *YrH52*. Moreover, *Yr15* is located on the short arm within 5.7 cM of *Xgwm273-1B* in the high-density molecular map (Peng et al. 2000), whereas *YrL693* is on the long arm within 0.08 cM of *Xgwm273-1B* based on genetic mapping (Fig. 4c). These data suggest that the locus of *YrL693* is different from that of *Yr15*. Among the formally named stripe rust resistance genes, only *Yr9* and *Yr17* confer resistant to *Pst* race V26, whereas *YrL693* was effectively resistant to V26 (Han et al. 2012).

Thus, based on pedigree, inheritance, results of molecular marker experiments, gene location, and response specificity, it can be concluded that *YrL693* differs from *Yr26* and *Yr15* and is apparently a new gene.

Transfer of resistance by cryptic translocation is possible

Alien chromosomal translocation is a classic and useful method for transferring genes from wild relatives to common wheat. Despite the potential to carry valuable genes, many alien translocations have questionable value in wheat breeding because the large transferred chromosome segments often carry additional genes for undesirable traits or do not adequately compensate for the wheat genes they replace, resulting in 'linkage drag' (e.g., Young and Tanksley 1989). However, traits of interest have been occasionally transferred to recipient genotypes by cryptic translocation without detectable cytological or genetic changes (Kuraparthy et al. 2007). Previous studies have indicated that the wheat genotype YU25 the resistant parent of L693, does not have a cytologically detectable alien chromosome segment and, therefore, may have a cryptic translocation (Luo et al. 2009a, b). Alien chromosomal segments resulting from such small translocations are not easily detected by standard cytogenetic methods other than high-resolution FISH.

In the present study, nearly all of the 781 SSR primer pairs amplified wheat-specific products that were evenly distributed over all the chromosomal arms with 3–4 cM spacing in L661 and L693; however, only 41 (5.2 %) of the 781 SSR primer pairs revealed polymorphisms between

L693 and L661. These polymorphisms were located on all chromosomes except 7A, 7B, 1D, 3D, and 6D. This result, which was not unexpected because L661 and L693 are sister lines (Zhang et al. 2011), but they also indicate that a large foreign chromosomal segment is not present in L693. This observation is similar to what was observed in YU25 (Luo et al. 2009a, b). Furthermore, the amplified products of all linked markers in L693 were the same size as those in YU25. Additional evidence for the absence of a large alien chromosomal segment in line L693 includes the following: First, wheat primers linked with the resistance gene produced wheat-specific PCR products in genotype L693, and the SSR loci closely flanking *YrL693* (with distances of 0.07 and 0.8 cM) did not show significant alterations in order or between-marker distances compared with the consensus genetic map (Fig. 4); second, L693 is genetically and agronomically uniform based on several years of observations; and third, the resistance gene in L693 behaved as a discrete Mendelian unit (Table 1). Moreover, we could not detect in situ hybridization signals in the resistant parent YU25 using *Th. intermedium* genomic DNA as a probe (data not shown, personal communication with Prof. F.P. Han, Institute of Genetics and Developmental Biology, Chinese Academy of Science, Beijing). Taken together, these data indicate that L693 does not possess a large alien chromosomal segment and may instead contain a cryptic translocation. The pedigree provides the only evidence that L693 carries a resistance gene from *Th. intermedium*. Hence, one of the goals for further study is to seek new information concerning the source of stripe rust resistance at the DNA level.

Potential role of *YrL693* in the improvement of wheat resistance

Although many wheat stripe rust resistance genes have been identified and incorporated into commercial cultivars, most of them have been overcome by virulent races. In recent years, several physiological races of *Pst*, including CYR30, CYR31, and CYR32, have become prevalent in southwestern China. These races are virulent to almost all the cultivars developed in this region (Luo et al. 2005). 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 (Liu et al. 2010; Han et al. 2012). The present study identified a novel stripe rust resistance gene located on chromosome 1B in L693 that displayed normal inheritance. Approximately, 66.7 % of the alien genes that confer resistance to wheat stripe rust are located on B chromosomes (http://wheat.pw.usda.gov/), indicating that wheat B chromosomes may be more tolerant to the presence of alien chromatin. Hence, loss, gain, or replacement of genetic material in this genome is likely to have minimal detrimental effects. L693 displays effective resistance to all predominant *Pst* races in the region. In addition, this line exhibits excellent resistances to powdery mildew (afforded by *Pm40* [Luo et al. 2009b]) and FHB (Zhang et al. 2011), but those resistances are not linked to *YrL693*. Markers that co-segregate with or are closely linked to *YrL693* can be used to accelerate the incorporation of this gene into commercial cultivars by marker-assisted selection. Therefore, there is a high likelihood that the material described in the present study can be utilized by breeders, especially in southwestern China.

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Conflict of interest The authors declare that they have no conflict of interest.

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