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Mapping a stripe rust resistance gene *YrC591* in wheat variety C591 with SSR and AFLP markers

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Abstract Stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* (PST), is one of the most destructive diseases of common wheat (*Triticum aestivum* L.). To determine inheritance of stripe rust resistance and map the resistance gene(s) in wheat variety C591, F_1, F_2, and F_3 progenies derived from the Taichung 29 × C591 cross were inoculated with Chinese PST race CY32 in the greenhouse. Genetic analysis identified a single dominant gene, temporarily designated *YrC591*. A total of 178 SSR and 130 AFLP markers were used to test the parents and resistant and susceptible bulks. From the bulk segregant analysis, seven polymorphic SSR and two AFLP markers were selected for genotyping the F_2 population. SSR marker *Xcfa2040-7B*, and SCAR marker *SC-P35M48* derived from AFLP marker $P35M48_{373}$ were identified to be closely linked to the resistance gene with genetic distances of 8.0 and 11.7 cM, respectively. The SSR markers mapped the resistance gene on chromosome arm 7BL. In the seedling test with five PST races, the reaction patterns of C591 were different from wheat cultivars or lines carrying *Yr2* or *Yr6* that also are found on chromosome 7B. The results indicate that *YrC591* is probably a novel stripe rust resistance gene.

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Introduction

Wheat stripe rust or yellow rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* (PST), is one of the most damaging diseases of common wheat (*Triticum aestivum* L.), and is especially destructive in China. Epidemics of stripe rust, that occurred in 1950, 1964, and 1990, caused wheat yield losses of 6.0, 3.2, and 2.65 million metric tonnes, respectively (Li and Shang 1989; Niu and Wu 1997; Wang et al. 1995). In 2002, the epidemic caused by a new virulent Chinese PST race CY32 resulted in a yield loss of 1.31 million metric tons (Wan et al. 2004).

It has been demonstrated that growing resistant cultivars is the most effective, economic and environment-friendly strategy to reduce damage caused by stripe rust. So far, more than 40 officially named *Yr* genes at 40 loci (*Yr1-Yr40*) and many temporarily designated genes have been reported (McIntosh et al. 1995, 1998, 2003, 2007). However, as the frequently emerging virulent races, cultivars carrying a single race-specific resistance gene are often overcome by new virulent races and then become susceptible a few years after being grown for commercial production (Wellings and McIntosh 1990; Chen et al. 2002;

Wan et al. 2004). Gene pyramiding, gene deployment and multi-lines strategies were considered useful for protecting and prolonging the resistance of developed resistant cultivars (Line and Chen 1995; Kumar 1999; Wu and Niu 2000). At present, most of the reported seedling resistance genes, except for *Yr5*, *Yr10*, *Yr15*, *Yr24*, and *Yr26*, etc., are ineffective against race CY32 in China (Yang et al. 2003). Therefore, there is a pressing need to identify new *Yr* genes with resistance to CY32 and newly emerged virulent races for wheat breeding programs.

Wheat variety C591, originally from India, is highly resistant in both seedling and adult-plant stages to prevailing PST races (including CY32) in China. The variety has not been widely used in breeding programs, but winter wheat variety 'Zhongzhi 1', which was developed with C591 and other varieties by the Institute of Plant Protection, Chinese Academy of Agricultural Sciences (IPP, CAAS), showed resistance in fields in Gansu China in recent years. The objective of this study was to identify the stripe rust resistance gene(s) in C591 and map the gene(s) using molecular markers.

Materials and methods

Wheat materials

C591 was crossed with susceptible variety Taichung 29 with the latter as the female parent. The parents and 10 F_1 and 633 F_2 plants were used for genetic analysis. Randomly selected 127 F_2 plants and their corresponding F_3 families were used for molecular mapping. Wheat varieties or lines Heines Peko, Heines Kolben, Heines VII, *Yr6*/6*Avocet S, Soissonais Desprez, and Kalyansona that have *Yr2* or *Yr6* were used in the seedling test. Wheat variety Chinese Spring (CS) and its 21 nulli-tetrasomic (NT) lines were used to confirm the location of *YrC591*.

Seedling test and PST isolates

The parents, F_1, F_2, and F_3 plants were inoculated with Chinese PST race CY32. C591 and varieties carrying *Yr2* or *Yr6* were inoculated with Chinese PST races CY19, CY26, CY29, CY31, and CY32, respectively, to compare their responses in the greenhouse. Seedlings were grown in the greenhouse under controlled temperature, humidity and illumination conditions. When the first leaves were fully expanded, all seedlings were inoculated with fresh urediniospores of a race that were increased on susceptible wheat variety Mingxian 169 using the brushing method (Roelfs et al. 1992). Inoculated seedlings were placed in dew chambers at 10°C for 24 h and then transferred into a controlled greenhouse with a daily cycle of 14 h of light at 17°C and 10 h of dark at 12°C. Infection types (ITs) were scored 16 days after inoculation based on a 0–4 scale (McIntosh et al. 1995).

DNA preparation

Genomic DNA of the second leaves of 127 randomly selected F_2 plants, which were not emerged at the time of inoculation, were extracted using the sodium dodecyl sulfate (SDS) method (Dellaporta et al. 1983). The concentration of DNA was determined using the mini-gel method (Sambrook and Russell 2001). Based on the results of seedling test inoculated with race CY32, 20 resistant (IT 0;) and 20 susceptible (IT 4) F_2 plants were randomly selected to make the bulk of resistance (BR) and the bulk of susceptible (BS) according to the bulked segregant analysis (BSA) method (Michelmore et al. 1991).

SSR analysis

A total of 178 SSR markers covering all wheat chromosomes, including *Xgwm* series from Röder et al. (1998, personal communication) and the *Xwmc*, *Xcfa*, *Xcfd*, and *Xbarc* series from the internet website (http://wheat.pw.usda.gov), were used for identifying markers associated to the stripe rust resistance in C591. SSR analysis was performed according to Röder et al. (1998) with minor modification. PCR reactions were performed in a 25 µl reaction volume, containing 80 ng of template DNA, 120 nM of each of primers, 20 µM of each of dNTPs, 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 15 mM $MgCl_2$, and 1 unit of *Taq* DNA polymerase. Amplification was performed in a PTC-200D Thermal Cycler (MJ Research Corp Ltd) with cycling program consisted of initial denaturation of 1 min at 95°C, followed by 35 cycles of 1 min denaturation at 96°C, 1 min annealing at 50–61°C (depending on primers), 2 min extension at 72°C, and a final extension at 72°C for 10 min. After amplification, PCR products were mixed with 2 µl of formamide buffer (98% formamide, 10 mM EDTA, 0.5% bromophenol blue, and 0.5% xylene cyanol, pH 8.3) and denatured at 95°C for 5 min, and then 4 µl of the mixture for each sample was loaded on a 1% agarose gel to check for the success of amplification.

PCR products were then separated on 6% denaturing polyacrylamide gels containing 8 M urea. The polymerized gels were pre-run in 1× TBE buffer (90 mM of Tris–borate, 2 mM of EDTA, pH 8.3) for 40–60 min at 2,300 V. After urea and gel debris were removed from the well, 7 µl of samples were loaded and the gels were run at 2,200 V for approximately 1.5–2 h (depending on bands of interest), and visualized by silver staining (Tixier et al. 1997).

AFLP analysis

A total of 130 combinations from 10 *Pst*I-primers and 13 *Mse*I-primers were used for AFLP analysis according to Vos et al. (1995). Genomic DNA (250 ng) was double-digested with restriction endonucleases *Pst*I and *Mse*I at 37°C for 2 h, and then ligated with the standard *Pst*I-(5 pM) and *Mse*I-(50 pM) adaptors. Pre-amplification was performed in 40 μl of reaction volume containing 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 15 mM $MgCl_2$, 75 ng of each of pre-amplification primers P_X (X = A, G, C or T) and M_X (X = A, G, C or T), 250 μM of each of dNTPs, 1 unit of *Taq* DNA polymerase, and 5 μl of the ligation products as template DNA. PCR cycling program consisted of initial denaturation at 94°C for 1 min, followed by 22 cycles of 30-s denaturation at 94°C, 1-min annealing at 60°C, 2-min extension at 72°C, and a final extension at 72°C for 10 min.

Selective amplifications were performed in 20 μl of reaction volume containing 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 15 mM $MgCl_2$, 1.6 ng of each primer, 300 μM of each of dNTPs, 1 unit of *Taq* DNA polymerase, and 5 μl 20-time diluted pre-amplification product. PCR cycling program consisted of initial denaturation at 94°C for 2 min, followed by 30 cycles of 30-s denaturation at 94°C, 30-s annealing at 56°C, 1-min extension at 72°C, and a final extension at 72°C for 5 min. PCR products were separated on 5% denaturing polyacrylamide gels containing 8 M urea. Electrophoresis and silver-staining was the same as those described for SSR analysis.

Conversion of AFLP markers into SCAR markers

The polymorphic AFLP fragments were recovered according to the protocol of DNA recovery kit (Promega). Recovered DNA were then linked with pGEM T-easy vector and transformed into *Escherichia coli*, and incubated at 37°C on solid SOB medium with Amp^+ antibiotic for 12 h. White colonies (recombinants) were picked, cultured, from which plasmid DNA were extracted and digested with *Eco*RI at 37°C for 1 h. The target DNA fragments were sequenced on a 737 sequencer by Invitrogen Corporation using the dideoxy chain termination method. Based on the sequences, SCAR (sequence characterized amplified region) primers were designed with the Primer Premier 5.0 software. The SCAR primers were used in PCR to amplify the parents and the F_2 mapping population to confirm the linkage of the SCAR markers with the resistance gene.

Statistical analysis

Chi-square (χ^2) test was used to evaluate the goodness of fit for the observed and expected ratios of segregation in the F_2 population. Probability (*P*) values of chi-square test were calculated using the chi test formula in the Excel program of Microsoft Office (version 2003). Linkage analyses were conducted with the software MAPMAKER 3.0b/EXP (Lander et al. 1987). The logarithmic odds ratio (LOD) score 3.0 was used as the threshold for declaration of linkage and the Kosambi function was used to calculate the map distance. The genetic linkage map was drawn with the software GENEMAP version 1.0.

Results

Genetic analysis of stripe rust resistance in C591

In the seedling test with race CY32, C591 was resistant (IT 0;), whereas Taichung 29 was susceptible (IT 4). Ten F_1 plants were resistant (IT 0;−1), and the 633 F_2 plants segregated in 475 resistant (21 with IT 0, 218 with IT 0;, 155 with IT 1 and 81 with IT 2) and 158 susceptible (81 with IT 3 and 77 with IT 4), which fitted a 3R:1S ratio ($\chi^2_{3:1} = 0.0005$, $P > 0.95$). The results indicated that the resistance to CY32 in C591 was conferred by a single dominant gene, tentatively designated as *YrC591*. When the 127 F_3 families were tested with the same race, 34 of the 99 families derived from resistant F_2 plants (R-) were homozygous resistant (RR), 61 were heterozygous resistant (Rr) and 4 were homozygous susceptible (rr); 26 of the 28 families derived from susceptible F_2 plants were homozygous susceptible (rr) and 2 were heterozygous resistant (Rr). The segregation of the F_3 families in a 1RR:2Rr:1rr ratio ($\chi^2_{1:2:1} = 0.2598$, $P > 0.80$) confirmed the single gene for resistance (Table 1).

Table 1 F_2 genotypes inferred from seedling reactions of F_3 families and the corresponding alleles at SSR loci *Xbarc32-7B* and *Xcfa2040-7B*

Markers	Genotypes	Allele			Total
		A	H	B	
Xbarc32-7B	RR	30	4	0	34
	Rr	3	51	9	63
	rr	1	2	27	30
	Total	34	57	36	127
Xcfa2040-7B	RR	33	1	0	34
	Rr	2	52	9	63
	rr	1	2	27	30
	Total	36	55	36	127

RR homozygous resistant, *Rr* segregating, *rr* homozygous susceptible, *A* homozygous for C591, *B* homozygous for Taichung 29, *H* heterozygous

SSR markers and genetic linkage analysis

Of the 178 SSR markers employed in this study, 43 showed clear polymorphisms between two parents, of which seven SSR loci on wheat chromosome 7BL were polymorphic between the resistant bulk (BR) and susceptible bulk (BS) (Fig. 1). The results of subsequent linkage analysis based on the phenotype and genotype data of the 127 F_2 plants indicated that *YrC591* was linked to the seven SSR loci, and the closest SSR locus to *YrC591* were *Xcfa2040-7B* with a genetic distance of 8.0 cM. As an example, the association of SSR marker *Xbarc32-7B* with the resistance in C591 is shown in Fig. 2. Furthermore, the seven polymorphic SSR loci were analyzed with 21 CS NT lines. All seven SSR markers were absent only in N7BT7A (Fig. 3), confirming that they were on the long arm of chromosome 7B. These results indicated that *YrC591* was located on wheat chromosome arm 7BL.

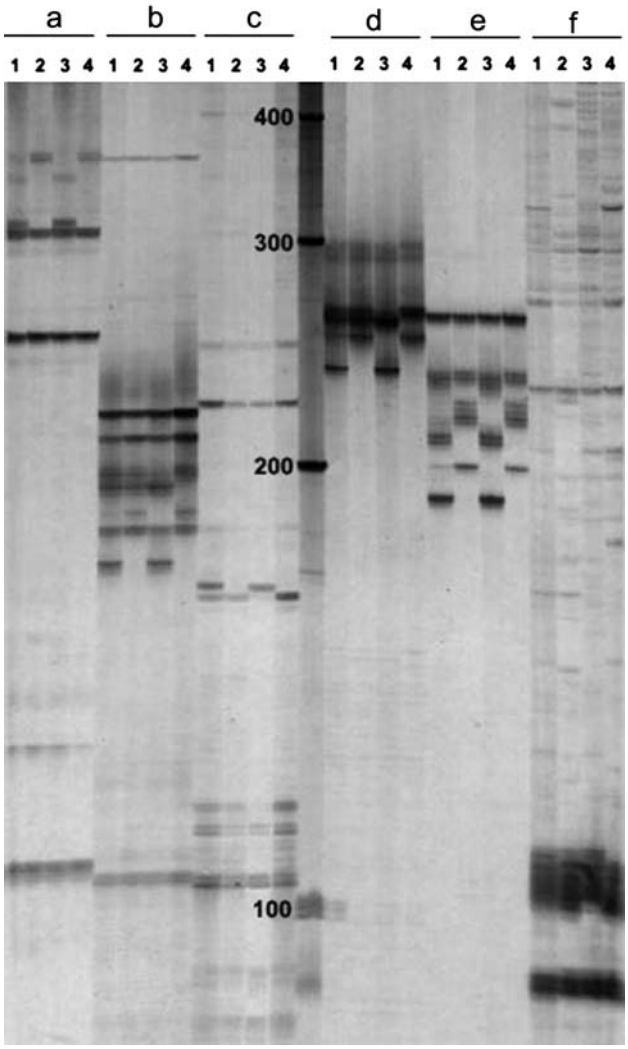

Fig. 1 Electrophoresis of PCR products amplified with SSR markers *Xwmc166* (**a**), *Xwmc273* (**b**), *Xbarc32* (**c**), *Xcfa2040* (**d**), *Xgwm984* (**e**) and *Xwmc311* (**f**) in polyacrylamide gel. *1* BR; *2* BS; *3* C591 and *4* Taichung 29

The linkage analysis based on the data from F_3 families genotyped with the most closely linked SSR markers *Xcfa2040-7B* and *Xbarc32-7B* confirmed the F_2 results (Table 1). Of the 127 F_3 families, for the 34 homozygous resistant genotypes (RR), 33 carried the same allele as that of C591 at the SSR locus *Xcfa2040-7B* and one was detected heterozygous; for the 63 segregating F_3 families (Rr), 52 had a heterozygous genotype, two had the same allele as C591 and nine had the same allele as Taichung 29; for the 30 homozygous susceptible genotypes (rr), 27 carried the same allele as Taichung 29, whereas one had the same allele as C591 and two were heterozygous.

AFLP markers linked with *YrC591*

Of the 130 AFLP markers employed in this study, $P34M50_{190}$, $P35M48_{373}$, $P38M48_{218}$, and $P41M48_{258}$ showed clear polymorphisms between the two parents and two bulks, which were then confirmed linked to *YrC591* through PCR amplification with resistant and susceptible F_2 plants (Fig. 4). Two of the four polymorphic AFLP markers were converted successfully into SCAR markers (Fig. 5); they were *SC-P35M48*$_{373}$ (left: 5′-GTTCAGAC ACAGCACAACTCGG-3′, right: 5′-CCTGAGTAACAC AGTACGGATG-3′), and *SC-P41M48*$_{258}$ (left: 5′-GAC-AAGCTGGCGCACTATAACAT-3′, right: 5′-GGACTCA TTGTGCCTTTTCGTTA-3′). The SCAR markers had the same segregating pattern and the same association with the resistant and susceptible phenotype in the F_2 plants as the AFLP markers.

Mapping of the resistance gene *YrC591*

Based on the method of maximum likelihood linkage analysis with the phenotype and genotype data of the F_2 plants and F_3 families, *YrC591* was flanked by *Xcfa2040-7B* and *SC-P35M48* with genetic distances of 8.0 and 11.7 cM, respectively (Fig. 6).

Reactions of wheat lines with *YrC591*, *Yr2*, and *Yr6* to Chinese PST races

To determine the relationships of *YrC591* with *Yr2*, and *Yr6* that have been reported on chromosome 7B, wheat varieties Kalyansona, Soissonais Desprez, *Yr6*/6*Avocet S, Heines Peko, Heines Kolben, and Heines VII, which have either *Yr2* or *Yr6* were tested together with C591 with five Chinese PST races. The results indicated that except for CY19, Kalyansona, Soissonais Desprez, *Yr6*/6*Avocet S, Heines Peko, Heines Kolben, and Heines VII were susceptible to races CY26, CY29, CY31, and CY32 with ITs

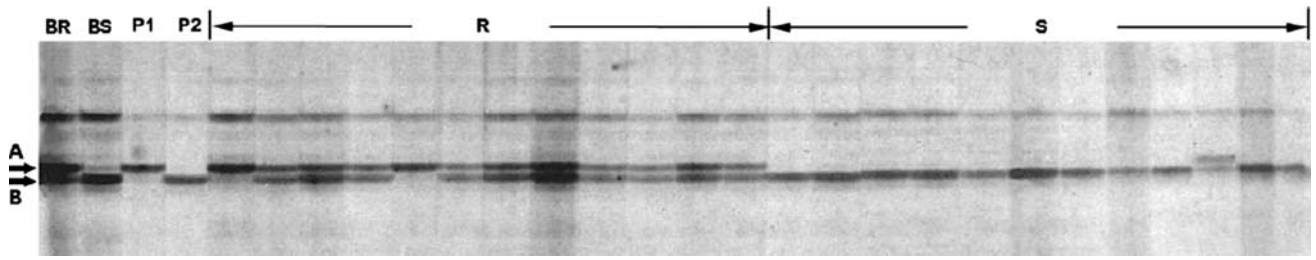

Fig. 2 Electrophoresis of PCR products amplified with SSR marker *Xbarc32-7B* in polyacrylamide gel. *A* allele for resistant parent C591 (*P1*), *B* allele for susceptible parent Taichung 29 (*P2*), *R* resistant F_2 plants, *S* susceptible F_2 plants

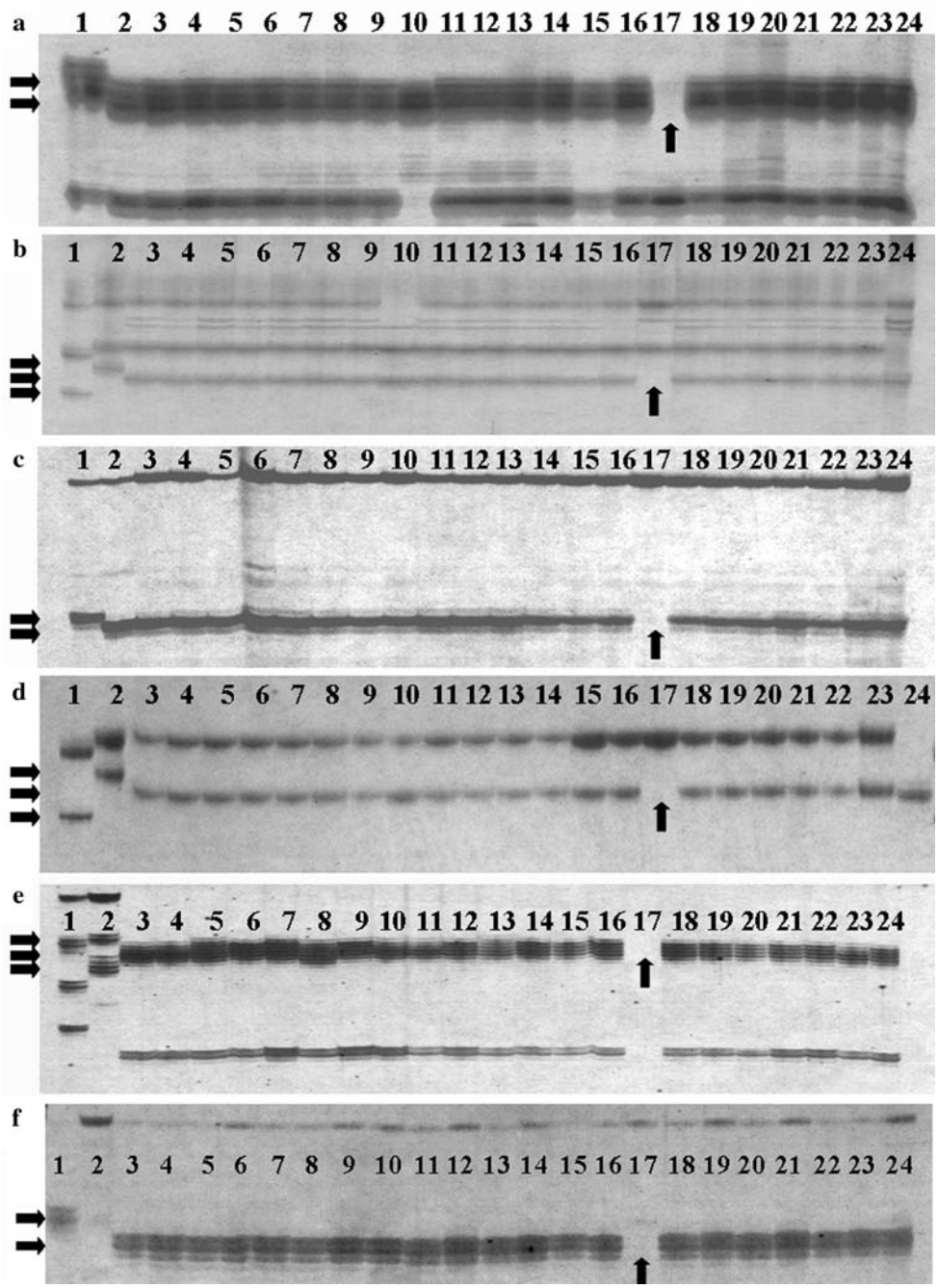

Fig. 3 Nulli-tetrasomic (*NT*) analysis of SSR markers *Xwmc311* (**a**), *Xwmc273* (**b**), *Xbarc32* (**c**), *Xcfa2040* (**d**), *Xgwm984* (**e**) and *Xgwm577* (**f**) linked to *YrC591*. *1* C591, *2* Taichung 29, *3* CS, and *4–24* the 21 Chinese Spring (*CS*) NT lines (*4* N1AT1B, *5* N2AT2D, *6* N3AT3B, *7* N4AT4D, *8* N5AT5B, *9* N6AT6B, *10* N7AT7B, *11* N1BT1A, *12* N2BT2A, *13* N3BT3A, *14* N4BT4A, *15* N5BT5A, *16* N6BT6A, *17* N7BT7A, *18* N1DT1A, *19* N2DT2A, *20* N3DT3A, *21* N4DT4A, *22* N5DT5A, *23* N6DT6A and *24* N7DT7A). *Arrows* indicate the SSR bands and the NT line without 7B

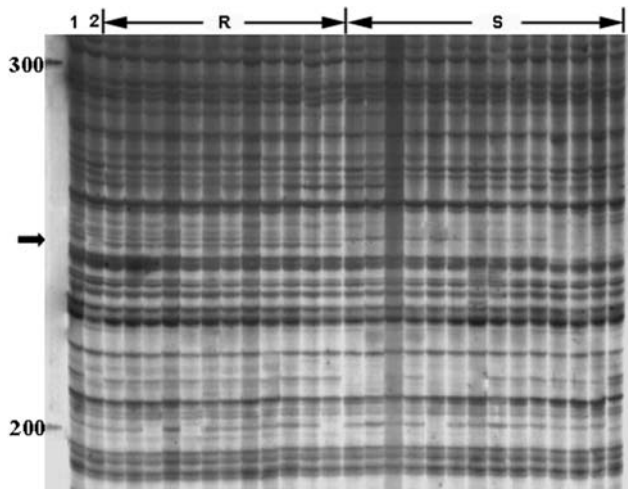

Fig. 4 Electrophoresis of products amplified by AFLP primers P41/M48. *1* C591, *2* Taichung 29, *R* resistant F_2 plants and *S* susceptible F_2 plants. *Arrow* indicates the polymorphic band

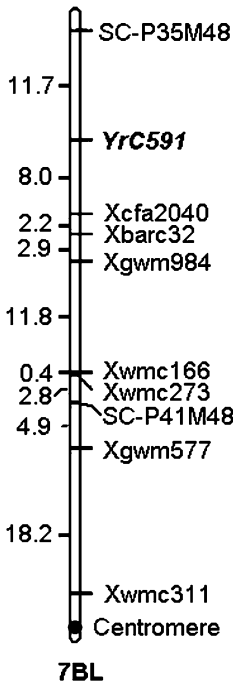

Fig. 6 Linkage map of stripe rust resistance gene *YrC591*, flanking with seven SSR markers and two SCAR markers on wheat chromosome 7BL. Locus name and corresponding locations were indicated on the *right* side, and genetic distances between them were indicated on the *left* side

ranging from 3 to 4, while C591 for *YrC591* was resistant to these five races with ITs from 0; to 1 (Table 2). The results indicated that *YrC591* is different from *Yr2* and *Yr6*.

Discussion

In this study, we identified a single dominant gene *YrC591* in wheat variety C591 and mapped it on wheat chromosome arm 7BL. We also showed that the gene is different from previously reported genes, *Yr2* and *Yr6*, on chromosome 7B, and therefore, is first described in this study. Because of its effectiveness against prevailing Chinese PST races, *YrC591* is valuable for developing wheat cultivars with stripe rust resistance. The molecular markers closely linked to the gene should be useful in marker-assisted selection for incorporating the gene into new wheat varieties or pyramiding it with other effective *Yr* genes to develop varieties with durable resistance to stripe rust.

In addition to *YrC591*, *Yr2* and *Yr6* have been previously located on wheat chromosome 7B. *Yr2* was first reported in Heines VII by Lupton and Macer (1962) and located on chromosome 7B using monosomic analysis (Labrum 1980; Chen et al. 1995b). We have tested wheat varieties including Heines VII, Heines Peko, Kalyansona, and Sonissonais Desprez, which have been previously reported to have *Yr2* (McIntosh et al. 1998) and found that these cultivars were susceptible to Chinese PST race CY32, and Wan et al. (2004) also reported that Heines VII and Heines Peko were susceptible to the race. Thus, *YrC591* is different from *Yr2*. *Yr6* was first reported in Heines Kolben and located on chromosome 7B by Macer (1966). The location of *Yr6* on chromosome 7B was later confirmed by Labrum (1980) and Chen et al. (1995a). In this study, the cultivars Heines Kolben and Heines Peko, that have been previously reported to carry *Yr6*, and the *Yr6* near-isogenic line *Yr6*/6*Avocet S were found susceptible to race CY32 with ITs 3 and 4, and the same results were also reported by Wan et al. (2004). Furthermore, *Yr6* was located on 7BS by El-Bedewy and Röbbelen (1982), but *YrC591* was mapped on 7BL. From the different reactions to PST races and chromosome locations, we conclude that *YrC591* is at a different locus from *Yr6*.

As C591 is a hexaploid wheat, it should be relatively easy to incorporate its resistance gene into different wheat

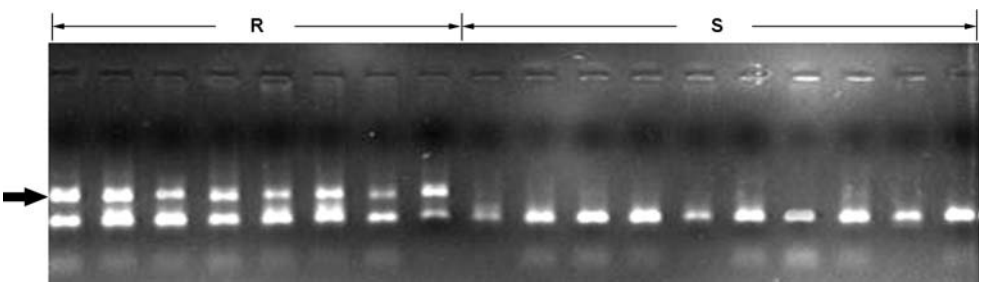

Fig. 5 Electrophoresis of PCR products amplified by SCAR marker *SC-P41M48* primers derived from AFLP marker $P41M48_{258}$ in an agarose gel. *Arrow* shows the polymorphic band. *R* resistant and *S* susceptible F_2 plants

Table 2 Infection types of C591 and wheat varieties with known *Yr* genes to five races of *Puccinia striiformis* f. sp. *tritici* (PST)

Cultivar or line	Yr genes	Infection types[a] produced by PST races				
		CY19	CY26	CY29	CY31	CY32
C591	*YrC591*	0;	0;	0;	1	0;
T29	–	3	4	4	4	4
Kalyansona	*Yr2*	0;	3	4	3	3^-
Soissonais Desprez	*Yr2*	0;	3	3	4	4
Yr6/6*Avocet S	*Yr6*	0;	3^+	4	4	4
Heines Peko	*Yr2*, *Yr6*	0;	3	4	4	4
Heines Kolben	*Yr6*	0;	3^+	4	3	4
Heines VII	*Yr2*, *Yr25*, *YrHVII*	0;	3	4	3	4
Mingxian 169	–	4	4	4	4	4

[a] Infection types were based on the 0–4 scale, in which 0 = no visible infection, 0; = necrotic or chlorotic flecks without sporulation, 1 = small uredia with necrosis, 2 = small to medium uredia with necrosis and chlorosis, 3 = medium-sized uredia with chlorosis, and 4 = large uredia without chlorosis

cultivars, compared to other exotic sources. The high resistance controlled by a single dominant gene, common wheat background, and many other good agronomic traits make C591 a desirable resistant donor to wheat breeding programs. In fact, C591 has been used in breeding programs a few years ago in China; winter wheat variety 'Zhongzhi 1' and some resistance lines have been developed with C591 by IPP, CAAS and showed resistance to prevailing PST races in fields of Gansu province. Unfortunately, with the lack of genetic information and molecular markers of *YrC591*, the use of the gene in breeding programs is still limited. The demonstration of *YrC591* as a new gene and the availability of the flanking SCAR and SSR markers identified in this study should accelerate its application in breeding programs.

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