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Molecular tagging of stripe rust resistance gene *YrZH84* in Chinese wheat line Zhou 8425B

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Abstract Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (PST), is one of the most damaging diseases in common wheat (*Triticum aestivum* L.). With the objective of identifying and tagging new genes for resistance to stripe rust, F_1, F_2 and F_3 populations from the cross Zhou 8425B/Chinese Spring were inoculated with Chinese PST isolate CYR32 in the greenhouse. A total of 790 SSR primers were used to test the parents and resistant and susceptible bulks. The resulting seven polymorphic markers on chromosome 7BL were used for genotyping F_2 and F_3 populations. Results indicated that Zhou 8425B carries a single dominant resistance gene, temporarily designated *YrZH84*, closely linked to SSR markers *Xcfa2040-7B* and *Xbarc32-7B* with genetic distances of 1.4 and 4.8 cM, respectively. In a seedling test with 25 PST isolates, the reaction patterns of *YrZH84* were different from those of lines carrying *Yr2* and *Yr6*. It was concluded that *YrZH84* is probably a new stripe rust resistance gene.

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Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (PST), is a major disease of common wheat (*Triticum aestivum* L.) in cool and moist production regions (Singh et al. 2000). In terms of area affected by stripe rust, China is the largest epidemic region in the world (Stubbs 1988). Stripe rust is most destructive to autumn-sown wheat in northwest and southwest China when susceptible cultivars are grown and the weather is favorable for the disease (Wan et al. 2004). Destructive epidemics of stripe rust in China occurred in 1950, 1964, 1990, and 2002, which caused yield losses of 6.0, 3.2, 1.8, and 1.3 million tonnes, respectively (Z.F. Li and S.M. Zeng; Wan et al. 2004). The most recent country-wide epidemic in 2002 was caused by a new Chinese PST isolate designated CYR32 (Wan et al. 2004).

The use of resistant cultivars is the most economical and environmentally sound method to reduce damage caused by stripe rust. Currently, 40 resistance genes at 37 loci (*Yr1*-*Yr37*) and 23 temporarily designated genes are identified (McIntosh et al. 2003, 2004, 2005). Most of these described genes are race-specific and confer a low infection type at the seedling stage. Such genes often prove to be short-lived in the field due to selection of previously rare races or to the emergence of new virulences in the pathogen population (Kilpatrick 1975). As a consequence, breeders have emphasized the need to deploy resistances based on gene combinations assuming that any single changes in virulence would be less damaging on production (Eriksen et al. 2004). Gene pyramiding, gene deployment, and multi-line cultivars are considered useful for prolonging race-specific resistance (Watson and Singh 1952; McIntosh and Lagudah 2000). Currently, a number of designated seedling

resistance genes, except *Yr5*, *Yr10*, *Yr15*, *Yr24*, and *Yr26*, are ineffective to CYR32 in China based on seedling tests (Ma et al. 2001; Yang et al. 2003). It is, therefore, very important to identify new resistance genes for wheat breeding programs.

Molecular markers, including RAPD, RFLP, SSR, and RGAP, are useful tools for gene mapping in wheat. Many stripe rust resistance genes have been mapped to wheat chromosomes during the past years (Sun et al. 1997; Chague et al. 1999; Peng et al. 1999; Robert et al. 1999; Ma et al. 2001; Shi et al. 2001; Sun et al. 2002; Wang et al. 2002; Chen et al. 2003; Yan et al. 2003; Lin et al. 2005; Chicaiza et al. 2006). In particular, SSR loci are employed much more frequently than other markers due to their advantages with a higher level of polymorphism, known map location, accuracy, repeatability, and PCR-based amplification. Closely linked SSR markers can provide a powerful tool for pyramiding stripe rust resistance genes and marker-assisted selection in breeding programs (Röder et al.1998; Narvel et al. 2001; Karakousis et al. 2003; Somers et al. 2004).

Zhou 8425B, developed in 1984, continues to be resistant to stripe rust. It was widely used as a parent in wheat breeding programs and at least seven hybrid derivatives have been released as cultivars. Among them, Zhoumai 11 and Zhoumai 12 have covered over half million hectares annually from 1997 to 2005. It is likely that newly developed derivatives such as Zhoumai 16 and Aikang 58 will also play a leading role in future production. The objective of this study was to map the stripe rust resistance gene in the Chinese wheat line Zhou 8425B using molecular markers.

Materials and methods

Wheat germplasm and PST isolates

The resistant line Zhou 8425B, susceptible parent Chinese Spring, their F_1 offspring, 611 F_2 plants and 97 F_3 lines were included in the genetic analysis. Zhou 8425B originated from cross Zhou 78A/Annong 7959. Three cultivars, Maris Huntsman, Heines VII, and Clement, with different resistance genes were kindly provided by Dr. Y.C. Niu, Institute of Plant Protection, Chinese Academy of Agricultural Sciences (CAAS). The near-isogenic line *Yr6*/6*Avocet S was kindly provided by Dr. C. R. Wellings, Plant Breeding Institute, University of Sydney, Australia. The 25 PST isolates used for comparative studies were collected from China and other countries (Table 1).

Seedling tests

The parents and genetic populations were inoculated with PST isolate CYR32. Zhou 8425B. Four selected lines with different known resistance genes were inocu-

Table 1 Seedling reactions of Zhou 8425B and four other cultivars and lines with known resistance genes to 25 PST isolates tested

Isolate	Origin[a]	Cultivar or line and their resistance genes to stripe rust				
		Yr6/6*Avocet S *Yr6*	Maris Huntsman *Yr2, Yr3a, Yr4a, Yr13*	Heines VII *Yr2, Yr25*	Clement *Yr9, YrCle*	Zhou 8425B *Yr9, YrZH84*
CYR29	China	4	4	4	4	1^+, 2
CYR32	China	4	4	3^+, 4	4	1^+, 2
86094	Kenya	4	0;	0	3	2
86107	Ethiopia	3	0, 0;	3	4	2
72107	–	3	0;	0;, 1	0	0
76088	Afghanistan	3	0	0;	0	0
86036	Bolivia	0;$^+$	0;$^+$	0;$^+$	0;	0
82061	Chile	3	4	4	4	3
85019	Chile	4	4	2	0;	0
CYR26	China	3^+	3^+	3	0	0
CYR27	China	3	3	4	0	0;
Su-1	China	3	0;	2^+	0	0
74187	Ecuador	0	0;$^+$	0, 0;	0,0;	0
75078	Egypt	2^+	3	3, 3^+	0	0
86106	Ethiopia	4	0;	4	0	0
82517	France	1^+, 2	4	4	0	0
60105	Germany	0;$^+$	0;$^+$, 1^+	0;$^+$, 2^+	0	0
78028	Israel	4	0;	1, 2^+	0	0
PE92	Italy	3^+, 4	1^+, 2^+	2	0	0
78080	Mexico	4	4	3	0	0
59791	Netherlands	0;	3	3	0	0
61009	Netherlands	0;, 2	0;	0	0	0
68009	Netherlands	4	4	4	0	0
80551	Netherlands	2^+	3	3	4	3^+, 4
76093	Pakistan	3^+, 4	0;	1^+	0	0

[a]Information on the origins of 25 isolates based on Niu et al. (2000), – = unknown

lated with 25 PST isolates for comparison of the stripe rust responses of Zhou 8425B and genotypes possessing *Yr2*, *Yr6* and *Yr9* in the spring of 2004, and this test was repeated for confirmation of the results in the spring of 2005 (Table 1).

Inoculations were conducted as described by Stubbs (1988) and Sun et al. (2002). Seedlings were grown in a growth chamber. Inoculations were performed by brushing conidia of isolates from a fully infected susceptible genotype onto the seedlings to be tested, when the first leaf was fully expanded. Inoculated seedlings were placed in plastic-covered cages and incubated at 9°C and 100% relative humidity (RH) for 24 h. Seedlings were then transferred into a growth chamber with identical conditions, i.e., the day/night regime of 14 h light (22,000 lx) at 17°C and 10 h of darkness at 12°C, with 70% RH. Infection types (IT) were scored 15–16 days after inoculation based on a 0–4 scale (Bariana and McIntosh 1993), when the susceptibility of the check, Mingxian 169, was fully expressed. Plants with ITs 0; to 2 were considered to be resistant and those with ITs 3 to 4, susceptible.

SSR analysis

Genomic DNA was extracted from seedlings (Sharp et al. 1988) of individual F_2 plants and bulked F_3 families. Resistant and susceptible bulks were established from equal amounts of DNA from 20 resistant and 20 susceptible F_2 plants, respectively. SSR markers linked to the resistance locus were identified by bulked segregant analysis (BSA) (Michelmore et al. 1991).

Of the 790 pairs of wheat SSR primers surveyed, 240 gwm (Gatersleben wheat microsatellite) primer sequences were described by Röder et al. (1998), 543 WMC primer sequences were developed by the Wheat Microsatellite Consortium (wmc), a private effort coordinated by Somers and Isaac (http://www.wheat.pw.usda.gov/ggpages/SSR/WMC/), five barc markers on chromosome 7B were developed by Cregan, Song and associates (the USDA-ARS Beltsville Agriculture Research Station), and two cfa markers on chromosome 7B were developed by Sourdille et al. (2001).

Microsatellite analysis followed the procedure of Bryan et al. (1997) with minor modifications. PCR reactions were performed in a PTC200 Peltier Thermal Cycler in a volume of 20 µl containing 1.0 U of *Taq* DNA polymerase, 2 µl of 10× buffer (50 mmol of KCl, 10 mmol of Tris–HCl, 1.5 mmol of $MgCl_2$, pH 8.3), 200 µmol of each of dNTPs, 6 pmol of each of primers, and 50 ng of template DNA. Cycling conditions were an initial denaturation step of 5 min at 94°C, followed by 35 cycles of 1-min denaturation at 94°C, 1-min annealing at 50–61°C (depending on primers), 1-min extension at 72°C, and a final extension at 72°C for 10 min. After amplification, PCR products were denatured by adding 4 µl of formamide buffer (98% formamide, 10 mM EDTA, pH8.0, 0.25% bromo-phenol blue, and 0.25% xylene cyanol) and heated at 94°C for 5 min. Each sample (5–7 µl) was loaded on 6% denaturing polyacylamide gels [(19 acrylamide:1 Bis), 8 M urea and 1× TBE (0.09 M Tris–borate, 2 mM EDTA, and pH 8.3)], which were run at 80 W for approximately 1.5 h, and visualized by silver staining (Bassam et al. 1991).

Statistical analyses

Chi-squared (χ^2) tests were used to evaluate the goodness of fit for the observed and expected ratios of segregation in F_2 and F_3 populations. Linkage analysis was conducted with the software MapManager QTXb20. The Kosambi (1944) function was used to calculate the map distance, and a highly significant P value ($P < 10^{-6}$) was used as a threshold for declaration of linkage.

Results

Inheritance of stripe rust resistance in Zhou 8425B

In the seedling test, Zhou 8425B was resistant (infection type (IT) 0;−2) to CYR32, whereas Chinese Spring was susceptible (IT 4). Eight F_1 plants were resistant (IT 2) and the F_2 population segregated in 121 plants with IT 0; 88 plants with IT 1, 231 plants with IT 2, 25 plants with IT 3, and 146 plants with IT 4, which conformed to 3R:1S segregation ratio ($\chi^2 = 2.91$, 1 *df*, $P > 0.05$), suggesting that the stripe rust resistance in Zhou 8425B was conferred by a single dominant gene, tentatively designated *YrZH84*. The 97 F_3 families segregated in a 1:2:1 ratio ($\chi^2 = 1.268$, 2 *df*, $P > 0.5$), confirming the single gene segregation hypothesis (Table 2).

Linkage analysis and genetic map

Of the 790 SSR markers employed in this study, 258 markers showed clear polymorphisms between two

Table 2 F_2 genotypes inferred from seedling reactions of F_3 families and the corresponding alleles at SSR loci *Xcfa2040-7B* and *Xbarc32-7B*

Marker	Genotype	Allele			Total
		A	H	B	
Xcfa2040-7B	RR	29			29
	Rr	1	43	2	46
	rr		3	19	22
	Total	30	46	21	97
Xbarc32-7B	RR	27	2		29
	Rr	2	41	3	46
	rr		2	20	22
	Total	29	45	23	97

RR homozygous resistant, *Rr* segregating, *rr* homozygous susceptible, *A* homozygous for the Zhou 8425B, *B* homozygous for the Chinese Spring, *H* heterozygous

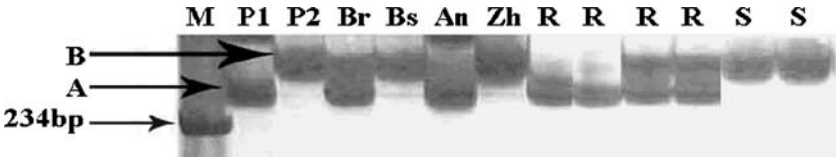

Fig. 1 Electrophoresis of PCR product amplified with SSR marker *Xcfa2040-7B* in polyacrylamide gel. *A* allele for resistant parent Zhou 8425B (*P1*); *B* allele for Chinese Spring (*P2*); *Br* resistant bulk; *Bs* susceptible bulk; *An* Annong 7959; *Zh* Zhou 78A; *R* resistant F_2 plants; *S* susceptible F_2 plants

parents, in which seven SSR loci on chromosome 7BL were polymorphic between the resistant (Br) and susceptible (Bs). This indicated that *YrZH84* was located on chromosome 7BL. Subsequent linkage analysis, based on the phenotyped and genotyped data of the F_2 population with the seven polymorphic markers, indicated that the resistance gene *YrZH84* was closely linked to the seven SSR loci with genetic distances ranging from 1.4 to 12.0 cM (Figs. 1, 2). The two closest flanking SSR loci were *Xcfa2040-7B* and *Xbarc32-7B* with genetic distances of 1.4 and 4.8 cM, respectively.

The linkage analysis based on the data from F_3 families genotyped with the most closely linked markers

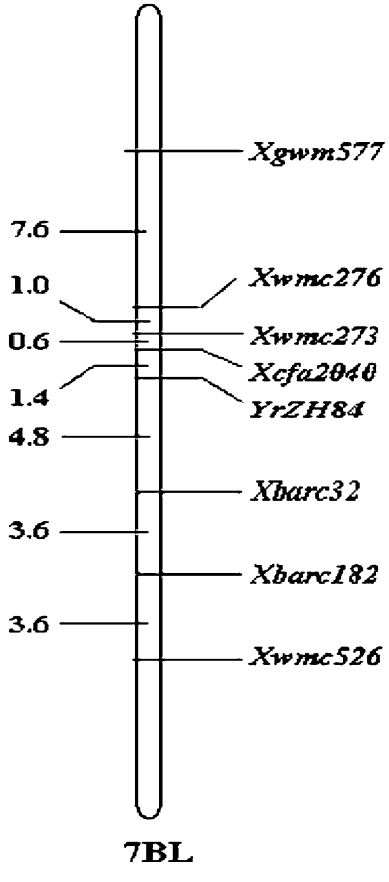

Fig. 2 Linkage map of stripe rust resistance gene *YrZH84* and seven SSR markers on chromosome 7BL. Locus names and corresponding locations on the genetic map are indicated on the *right side*. Map distances (Kosambi) in centi-Morgans are shown on the *left side*

Xcfa2040-7B and *Xbarc32-7B* confirmed F_2-based observation (Table 2). Of the 97 F_3 families, 29 homozygous resistant genotypes (RR) carried the same allele as that of resistant parent Zhou 8425B at the SSR locus *Xcfa2040-7B*, while for the 46 segregating F_3 families (Rr), 43 were detected to have heterozygous genotypes, one had the same allele as Zhou 8425B and two were the same as that of susceptible parent Chinese Spring, and 19 of the homozygous genotypes carried the Chinese Spring allele, whereas three genotypes were heterozygous at the *Xcfa2040-7B* locus in the 22 uniformly susceptible F_3 families (rr). Based on the method of maximum likelihood linkage analysis with the phenotyped and genotyped data of the F_3 families, *YrZH84* was flanked by *Xcfa2040-7B* and *Xbarc32-7B* with 5.7 and 5.6 cM, respectively.

Reactions of lines with *YrZH84, Yr2*, *Yr6*, and *Yr9* to 25 PST isolates

Based on the gene-for-gene relationship, in many of the instances where Zhou 8425B produced IT 0, resistance could be due to one or more of genes. In all instances where Clement produced IT 0 or 0;, Zhou 8425B also produced IT 0 indicating the likely presence of *Yr9*. Of the six cultures virulent on Clement, four cultures (CYR29, CYR32, 86094 and 86107) produced intermediate responses on Zhou 8425B, two cultures (80551 and 82061) were virulent. The intermediate responses with CYR29, CYR32, 86094, and 86107 was attributed to *YrZH84*. *Yr2* and *Yr6* were highly susceptible to CYR29 and CYR32, indicating that *YrZH84* is a different resistance gene from *Yr2* and *Yr6* (Table 1).

Origin of the stripe rust resistance gene *YrZH84*

The wheat line Zhou 8425B was derived from cross Zhou 78A/Annong 7959. Based on pedigree information and molecular marker analysis, Zhou 8425B is a 1B/1R translocation line with the stripe rust resistance gene *Yr9* derived from Predgornaia 2. Seedling tests with 25 PST isolates indicated that Zhou 8425B contained *Yr9* and a new gene that was designated *YrZH84* (Table 1). The Chinese wheat cultivar Annong 7959 was resistant to the isolate CYR32 (IT 0;−2) in a seedling test, whereas Zhou 78A was highly susceptible (data not shown). SSR analyses with *Xcfa2040-7B* and *Xbarc32-7B* showed that

Annong 7959 possessed the same allele as that of Zhou 8425B, whereas Zhou 78A carried the same allele as Chinese Spring (Fig. 1). These results indicated that *YrZH84* originated from Annong 7959. Annong 7959 was developed from the cross St2422-464/Nainari 60 (Zhuang 2003). The line St2422-464 was inoculated with the isolate CYR32 and displayed a high seedling infection type (data not shown). Therefore, *YrZH84* might be derived from Nainari 60. Wellings et al. (1988) reported that Nainari 60 possessed gene *YrA*. However, the reaction of Funo that carries *YrA*, to the 25 PST isolates used in Table 1 was different from that of *YrZH84* (data not shown).

Discussion

Comparison of *YrZH84* with *Yr2* and *Yr6* located on chromosome 7B

Stripe rust resistance genes *Yr2* and *Yr6* have been located to chromosome 7B (Labrum 1980; Chen et al. 1995). Lin et al. (2005) found that *Yr2* was 5.6 cM from SSR marker *Xwmc364-7B*. According to available maps (http://www.graingenes.org/cgi-bin/ace/pic/graingenes?name=Ta-SSR-2004-7B&class=Map) *Xwmc364* is 83 cM from *Xcfa2040-7B* that is closely linked to *YrZH84*. Therefore, the locations of *YrZH84* and *Yr2* are very different. El-Bedewy and Robbelen (1982) located *Yr6* to chromosome 7BS, whereas *YrZH84* mapped to 7BL in this study. In addition, lines with *Yr2* and *Yr6* were highly susceptible to Chinese isolates CYR29 and CYR32, whereas Zhou 8425B produced an intermediate response (Table 1; Wan et al. 2004). Based on the reaction patterns and chromosomal locations, it can be concluded that *YrZH84* is different from both *Yr2* and *Yr6*, and is probably a new stripe rust resistance gene.

Wheat breeding for stripe rust resistance in China

Since the early 1970s, wheat cultivars with the 1B/1R translocation carrying *Yr9*, derived from Lovrin 13, Predgornaia 2, Kavkaz, or Neuzucht, and their derivatives, have been widely used in wheat breeding programs in China (He et al. 2001). Around one-half of Chinese wheat cultivars have *Yr9* and succumbed to destructive stripe rust epidemics in 1990 and 2002 (Wu et al. 1993; Wan et al. 2004). In southwest China, wheat cultivars derived from Fan 6 were widely grown on 1.5–2 million ha each year. They were highly resistant for 20 years (Niu and Wu 1997), but became susceptible to the new Chinese PST isolates CYR31 and CYR32, leading to serious yield losses in 2002 (Wan et al. 2004). Recently, 92R137, 92R178, and other lines with *Yr26* have been used widely in wheat breeding programs in Gansu, Sichuan, and Yunnan provinces (Ma et al. 2001), where climatic conditions are favorable for stripe rust every year. In the seedling tests with 26 PST isolates on 98 Chinese cultivars and advanced lines, 42 were postulated to carry *Yr9* and 19 possess *Yr26* (data not shown). The danger of using limited sources of resistance has become a great concern to wheat breeders and pathologists. It is imperative that new stripe rust resistance genes be identified and utilized in breeding programs.

Cultivars Zhoumai 11 and Zhoumai 12 derived from Zhou 8425B have been grown on large areas in Henan province. They show intermediate seedling responses to PST isolate CYR32 and are highly resistant in the field (data not shown). Data in Table 1 indicate that *YrZH84* is already ineffective against two cultures among an international group and more effort is required to assemble such genes in more durable combinations using molecular markers.

In conclusion, the stripe rust resistance gene *YrZH84*, mapped on chromosome 7BL, is different from other known resistance genes and shows resistance to prevailing Chinese PST isolates both at seedling stage and in the field. Seven SSR markers were identified to be closely linked to this gene, which can certainly benefit its use through marker-assisted selection in wheat breeding programs. It must, however, be crossed to a wheat known to carry gene *Yr2* to confirm its genetic independence before assigning a formal gene symbol.

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