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ORIGINAL PAPER

Molecular mapping of leaf rust resistance gene *LrZH84* in Chinese wheat line Zhou 8425B

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Abstract Leaf rust, caused by *Puccinia triticina*, is one of the most widespread diseases in common wheat (*Triticum aestivum* L.) worldwide. With the objective of identifying and mapping new genes for resistance to leaf rust, F_1, F_2 plants and F_3 lines from a cross between resistant line Zhou 8425B and susceptible line Chinese Spring were inoculated with Chinese *P. triticina* races THTT and MBHP in the greenhouse. A total of 793 pairs of SSR primers were used to test the parents and resistant and susceptible bulks. Seven polymorphic chromosome 1B markers were used for genotyping the F_2 and F_3 populations. Zhou 8425B carried a single dominant resistance gene, temporarily designated *LrZH84*, linked to SSR markers gwm582 and barc8 with genetic distances of 3.9 and 5.2 cM, respectively. The *Xbarc8* allele co-segregated with *Lr26* in the F_3 population. The *Xgwm582* allele associated with *LrZH84* was identified as a leaf rust resistance gene and shown to be present in the Predgornaia 2 parent of Zhou 8425B. The seedling reaction pattern of *LrZH84* was different from those of lines with *Lr26, Lr33, Lr44* and *Lr46*, all of which are located in chromosome 1B. It was concluded that *LrZH84* is likely to be a new leaf rust resistance gene.

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Introduction

Leaf rust, caused by *Puccinia triticina*, is one of the most important and widespread diseases in wheat (*Triticum aestivum* L.). It is adapted to a wide range of climates, occurs wherever wheat is grown, and causes significant yield and economic losses. Given favorable conditions, leaf rust can cause yield losses of up to 40% (Knott 1989). In China, destructive epidemics of leaf rust occurred in 1969, 1973, 1975 and 1979 (Dong 2001). Over the past 10 years, it has occasionally caused destructive yield losses in the major wheat production regions, particularly in North China and the Yellow and Huai Valley wheat regions. Resistant cultivars are the most efficient, economic and environment-friendly way for reducing losses caused by leaf rust.

About 60 leaf rust resistance genes have been formally designated in wheat (McIntosh et al. 2007). Most of them confer hypersensitive reactions and interact with the pathogen in a gene-for-gene fashion (Flor 1942). The effectiveness of such genes is often short-lived in the field due to the emergence and/or increase of new virulences or

races 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 change in virulence would not be as likely to lead to loss of resistance (Watson and Singh 1952; Eriksen et al. 2004). As well as gene pyramiding, strategic gene deployment and multi-line cultivars are considered to be other useful ways to prolong race-specific resistance (McIntosh and Lagudah 2000; Wan et al. 2004). Currently, only a few designated leaf rust resistance genes, such as *Lr9*, *Lr19*, *Lr24* and *Lr38*, are effective against prevalent Chinese *P. triticina* races (Yuan et al. 2007). Hence, it is very important to search for new resistance genes to cope with the dynamic and rapidly evolving pathogen population (Chen et al. 1998).

Molecular markers are useful tools for gene pyramiding. Simple sequence repeat (SSR) markers are used more frequently than other markers due to advantages associated with co-dominance, accuracy, high repeatability, high levels of polymorphism, chromosome specificity, and ease of manipulation (Röder et al. 1995, 1998; Senior and Heun 1993). In addition to wheat (Liu et al. 2001; Raupp et al. 2001; Gupta et al. 2002) SSR markers have been widely used in maize (Senior and Heun 1993), rice (Wu and Tanksley 1993), barley (Liu et al. 1996), and other crops.

The Chinese wheat line Zhou 8425B, developed in 1984, continues to be resistant to leaf rust, stripe rust and powdery mildew under field conditions in China. At least 30 cultivars developed from Zhou 8425B have occupied an accumulated area of over six million hectares. The objective of this study was to identify the genetic basis of leaf rust resistance in Zhou 8425B and to identify associated SSR markers.

Materials and methods

Wheat germplasm and *Puccinia triticina* isolates

The resistant line Zhou 8425B, susceptible parent Chinese Spring, their F_1 offspring, F_2 plants and F_3 lines were included in the genetic analysis. Zhou 8425B originated from the cross Zhou 78A/Annong 7959. Three near-isogenic lines (TcLr26, TcLr33, and TcLr44) in the background of Thatcher with resistance genes *Lr26*, *Lr33* and *Lr44*, respectively, and Pavon 76 were kindly provided by the USDA-ARS Cereal Disease Laboratory, University of Minnesota, St Paul, USA. Cultures of 20 *P. triticina* races were used in multi-race comparisons (Table 1) and a culture of race MBHP, avirulent on both TcLr26 and Zhou 8425B, used for testing F_3 lines were available from the Biological Control Center for Plant Diseases and Plant Pests of Hebei.

Table 1 Seedling infection types produced by Zhou 8425B, Thatcher, and three Thatcher near-isogenic lines TcLr26, TcLr33, TcLr44 when inoculated with 20 *P. triticina* races

Isolate	Line				
	TcLr26	TcLr33	TcLr44	Zhou 8425B	Thatcher
PHDQ	4	4	4	2+	4
PHSS	4	4	3+	2+	4
FHNS	4	4	4	2	4
FHJS	4	3+	3+	2+	4
THSS	4	4	4	2	4
PKSS	4	4	2	4	4
FKSQ	4	4	3	2+	4
PHQS	4	4	4	2+	4
FHLQ	4	4	3-	1	4
PHSL	4	4	;, 1	4	4
FHNQ	4	4	3+	1+	4
FHBQ	4	4	3−	2+	4
PKQQ	4	4	1	2+	4
FKJS	4	4	4	1	4
PKJS	4	4	1	4	4
PHSN	4	4	;, 0	4	4
PHJG	4	4	3−	4	4
THTT	4	4	4	2	4
THDS	4	4	2+	2+	4
PTJT	4	4	4	1	4

+ uredinia somewhat larger than normal for the IT, − uredinia somewhat smaller than normal for the IT

Evaluation of leaf rust responses

Evaluation of seedling responses in the greenhouse

Zhou 8425B, Chinese Spring, 16 F_1 plants and 487 F_2 plants were inoculated with the virulent and predominant Chinese *P. triticina* race THTT. Zhou 8425B, Thatcher, and three near-isogenic lines were inoculated with 20 *P. triticina* isolates (Table 1) for comparing reaction patterns to leaf rust.

Zhou 8425B carries the 1BL.1RS translocation with *Lr26* (Li et al. 2006b). To clarify the relationship between *Lr26* and the leaf rust resistance gene in Zhou 8425B, seedlings of 136 F_3 lines were separately inoculated with race THTT (virulent on TcLr26 and avirulent on Zhou 8425B) and race MBHP (avirulent on both). Forty seedlings of each line were inoculated with each race.

Seedlings were grown in a growth chamber. When the first leaves were fully expanded, inoculations were performed by brushing condia of isolates from a fully infected susceptible genotype onto the seedlings to be tested.

Inoculated seedlings were placed in plastic-covered cages and incubated at 15°C and 100% relative humidity for 24 h. They were then transferred to a growth chamber maintained with 12 h light/12 h darkness at 18–25°C with 70% RH. Infection types were scored 10–14 days after inoculation according to the Stakman scale as modified by Roelfs et al. (1992).

Evaluation for leaf rust reactions in the field

Zhou 8425B, Chinese Spring, 136 F_2 plants and highly susceptible check cultivar Zhengzhou 5389 were planted in Baoding in the 2006–2007 cropping season. Spreader rows of cultivar Zhengzhou 5389 were planted perpendicular and adjacent to the rows of tested plants. Leaf rust epidemics were initiated by spraying an aqueous suspension of urediniospores of *P. triticina* pathotype THTT, to which a few drops of Tween 20 (0.03%) had been added, onto the spreader rows at the tillering stage. Leaf rust infection types were scored when leaves of the susceptible cultivar Zhengzhou 5389 were fully rusted. These F_2 plants were harvested and their seeds were sown for the F_3 seedling tests.

DNA extraction and bulk preparation

Genomic DNA was extracted from seedlings of individual F_2 plants and bulked F_3 lines using the CTAB protocol (Sharp et al. 1988). DNA was quantified with a UV spectrophotometer, and diluted to a final concentration of 30 ng/μl prior to further analysis.

Bulked-segregant analysis (Michelmore et al. 1991) was performed to identify molecular markers putatively linked to the leaf rust resistance gene(s) in Zhou 8425B. Genomic DNA from 20 resistant and 20 susceptible F_2 plants were mixed in equal amounts to form resistant and susceptible bulks. DNA samples of the two parents and bulks were screened for polymorphism with SSR markers.

Identification of the 1BL.1RS status of F_3 lines

Zhou 8425B was known to carry the 1BL.1RS translocation. To determine the status of this chromosome (and therefore the *Lr26/lr26* genotype), we assayed each F_3 line with a gene-specific marker for *ω-secalin* generating a 1,076-bp fragment in genotypes with the 1BL.1RS translocation (Chai et al. 2006), and a marker for *Glu-B3* generating a 636-bp fragment amplified in genotypes with the normal 1BL.1BS (de Froidmont 1998) (Table 3) following the procedure developed by Zhang et al. (2008) with minor modifications.

SSR analyses

The 793 wheat SSR loci surveyed included 240 gwm (Gatersleben wheat microsatellite) primer sequences described by Röder et al. (1998), 543 wmc primer sequences developed by the Wheat Microsatellite Consortium (wmc) (http://wheat.pw.usda.gov/ggpages/SSR/WMC), eight barc markers developed by Cregan associates (USDA-ARS Beltsville Agriculture Research Station), and two cfa markers developed by Sourdille et al. (2001). All are listed at http://www.graingenes.org.

Simple sequence repeat markers showing polymorphism between resistant and susceptible bulks were used to test the F_2 individuals and F_3 lines to determine the genetic linkage between the leaf rust resistance gene(s) and markers. Microsatellite analysis followed the procedure developed by Bryan et al. (1997) with minor modifications. PCR reactions were performed in a volume of 20 μl containing 1.0 U *Taq* DNA polymerase (Zexing Biotechnology Co. Ltd, Beijing, China), 1× buffer (50 mM KCl, 10 mM Tris–HCl, 1.5 mM $MgCl_2$, pH 8.3), 200 μM of each dNTP, 6 pmol of each primer and 60 ng of template DNA. The PCR conditions were as follows: denaturation at 94°C for 4 min, followed by 35 cycles of 94°C for 1 min, 50–61°C (depending on primer pair) for 1 min, 72°C for 1 min and a final extension for 10 min at 72°C. PCR products were mixed with 8 μl of formamide loading buffer (98% formamide, 10 mM EDTA, 0.25% bromo-phenol blue, 0.25% xylene cynol, pH 8.0) and heated at 94°C for 10 min. Each sample (5 μl) was loaded on 6% denaturing polyacrylamide gels, and run at 100 W for approximately 1.5 h and visualized by silver staining (Bassam et al. 1991).

Linkage analysis and genetic mapping

Phenotypic frequencies were tested for goodness-of-fit to postulated ratios by chi-squared tests. Linkage analysis was performed using the software MapManager QTXb20 (Manly et al. 2001) and recombination values were converted to centiMorgens using the Kosambi mapping function (Kosambi 1944).

Results

Inheritance of leaf rust resistance in Zhou 8425B

In the seeding test with race THTT, Zhou 8425B was resistant (infection type, IT 2), whereas Chinese Spring was susceptible (IT 4). F_1 plants were resistant (IT 2) and the F_2 population segregated 359 plants with IT ;–2 (resistant) and 128 plants with IT 3–4 (susceptible), indicative of a single dominant gene for resistance ($\chi^2_{3:1} = 0.43$, 1 *df*, $P > 0.5$).

Table 2 F_2 phenotypes and genotypes inferred from reactions of F_3 families inoculated with Chinese *P. triticina* race THTT and the corresponding alleles at SSR loci *Xgwm582* and *Xbarc8*

Locus name	F_2 phenotype	F_2 genotype	Allele		
			A	H	B
Xgwm582	Resistant (96)	RR (29)	24	4	1
		Rr (67)	5	61	1
	Susceptible (40)	rr (40)	0	1	39
Xbarc8 (Lr26)	Resistant (96)	RR (29)	21	7	1
		Rr (67)	10	56	1
	Susceptible (40)	rr (40)	0	0	40

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

In the field test, Zhou 8425B was resistant (IT 0–;) and Chinese Spring was susceptible (IT 4). The F_2 population segregated 96 plants IT 0–2 and 40 plants with IT 3–4, again indicating single locus segregation ($\chi^2_{3:1} = 1.41$, 1 *df*, $P > 0.1$). When 136 F_3 lines from these F_2 plants were tested as seedlings 29 lines were homozygous resistant, 67 segregated and 40 were homozygous susceptible, fitting a 1:2:1 ratio ($\chi^2_{1:2:1} = 1.81$, 2 *df*, $P > 0.25$) (Table 2). The 40 homozygous susceptible lines were the progenies of plants scored as susceptible in the field. Results from the F_2 and F_3 populations indicated that a single dominant gene, tentatively designated *LrZH84,* conferred resistance to leaf rust race THTT in Zhou 8425B.

Linkage analysis and genetic map

Of the 793 SSR markers, seven (wmc419, wmc694, wmc269, barc240, barc8, barc181, gwm582) on chromosome 1B showed polymorphisms between the resistant and susceptible bulks as well as the parents. This indicated that *LrZH84* was located on chromosome 1B. The seven polymorphic markers were then assayed in the 487 F_2 plants previously tested with leaf rust. Resistance gene *LrZH84* was closely linked to the seven SSR loci with genetic distances ranging from 3.9 to 12 cM (Fig. 2). The two closest flanking SSR loci were *Xgwm582-1B* and *Xbarc8-1B* with genetic distances of 3.9 and 5.2 cM, respectively. Gwm582 and barc8 were screened on DNA bulks from each of the 136 F_3 lines, providing comparative linkage estimates of 4.9 and 7.7 cM, respectively (Table 2). Neither value was significantly different from the estimates based on F_2 plants.

Reactions of Zhou 8425B, TcLr26, TcLr33, TcLr44 and Pavon 76 to Chinese *Puccinia triticina* isolates

In seedling tests with 20 *P. triticina* isolates (Table 1), Thatcher, TcLr26 and TcLr33 were susceptible to all isolates, TcLr44 was resistant to six races and Zhou 8425B was resistant to 15 races. Of the five races virulent on Zhou 8425B, four (PKSS, PHSL, PKJS and PHSN) produced low IT on TcLr44, indicating that the resistance gene in Zhou 8425B was different from *Lr44*. In another seedling test, Zhou 8425B and Pavon 76 (carries at least *Lr1, Lr13* and *Lr46*) (Singh and Rajaram 1991; Singh et al. 1998) were inoculated with four Chinese *P. triticina* isolates (FKJS, PKQQ, PHQS, THTT). *LrZH84* was moderately resistant to all four isolates, whereas Pavon 76 was resistant (IT 1) to PHQS and susceptible to the other three races (data not shown). These results indicated that *LrZH84* was different from *Lr26*, *Lr33*, *Lr44* and *Lr46*.

Relationship between *Lr26* and *LrZH84*

Zhou 8425B, Chinese Spring, TcLr26, and 136 F_3 lines were inoculated with races THTT and MBHP to clarify the relationship between *Lr26* and *LrZH84*. Zhou 8425B was moderately resistant (IT 2) with THTT and highly resistant (IT;) with MBHP. TcLr26 was susceptible (IT 4) to THTT and resistant (IT;) with MBHP. Chinese Spring was susceptible to both. The 31 F_3 lines genotyped *Lr26Lr26* (Table 3) based on chromosome 1B status were scored 21 homozygous resistant (HR) and 10 segregating (Seg) with

Table 3 *Lr26/lr26* genotypes for 136 F_3 lines inferred from *ω-secalin* and *Glu-B3* marker assays, leaf rust responses to two *Puccinia triticina* races and *Xbarc8* genotypes

Chromosome grouping/*Lr26/lr26* genotype	Reaction to THTT[a]			Reaction to MBHP[b]						*Xbarc8* locus[c]
	HR	Seg	HS	HR	HR:MR	MR	HR:S	MR:S	HS	
Lr26Lr26	21	10		31						A
Lr26lr26	7	56			7		56			H
lr26lr26	1	1	40			1		1	40	B

[a] HR = homozygous resistant, Seg = segregating, HS = homozygous susceptible

[b] HR = infection type;, HR:MR = infection types; and 2, MR = infection type 2, HR:S = infection types; and 4, MR:S = infection types 2 and 4, HS = infection type 4

[a] A = homozygous for the Zhou 8425B allele, H = heterozygous, B = homozygous for the CS allele

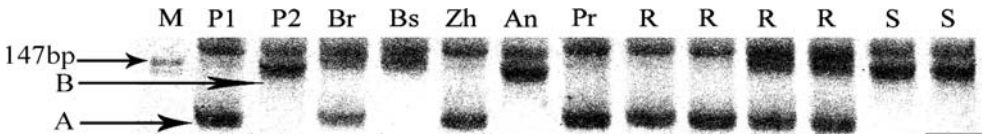

Fig. 1 Electrophoresis of PCR products amplified with SSR marker gwm582 on polyacrylamide gels. *A* allele in resistant parent Zhou 8425B (P1), *B* allele in Chinese Spring (P2), *Br* resistant bulk, *Bs* susceptible bulk, *An* Annong 7959, *Zh* Zhou 78A, *Pr* Predgornaia 2, *R* resistant F_2 plants, *S* susceptible F_2 plants

race THTT, the 63 *Lr26lr26* were scored 7HR and 56 Seg, and the 42 *lr26lr26* lines were distributed 1HR : 1 Seg : 40 homozygous susceptible (HS). This distribution was clearly not independent of the *Lr26/lr26* genotype indicating coupling linkage between the 1B centromere and *LrZH84* in chromosome 1BL. In addition all lines scored HR with race THTT were also HR with race MBHP again indicating that *LrZH84* was effective against both races. Linkage with the chromosome 1B centromere was estimated to be 7.7 cM. *Xbarc8* genotypes coincided with the chromosome 1B status (Table 3).

Origin of *LrZH84*

Zhou 8425B was derived from the cross Zhou 78A/Annong 7959. Zhou 78A was developed from the cross Predgornaia 2/Lianfeng 1//Guangmai 74 (triticale). Based on pedigree information and molecular marker analysis, Zhou 8425B is a 1B.1R translocation line with the leaf rust resistance gene *Lr26* derived from Predgornaia 2. Seedling tests with 20 Chinese *P. triticina* races, all virulent for *Lr26* (Table 1), showed that Zhou 8425B must carry a different, or a second, gene for moderate resistance to leaf rust. Seedling tests with leaf rust races THTT and FKJS indicated Zhou 78A and Predgornaia 2 were resistant (IT 1–2), whereas Annong 7959 and Lianfeng 1 were susceptible (IT 4). Seeds of Guangmai 74 were not available. It seems likely, therefore, that *LrZH84* originated from Predgornaia 2. SSR analyses with gwm582 and barc8 closely linked to *LrZH84* confirmed that Zhou 78A and Predgornaia 2 possessed the same alleles as Zhou 8425B, whereas Annong 7959 carried the same alleles as Chinese Spring (Fig. 1).

Discussion

Linkage map of leaf rust resistance gene *LrZH84*

According to Somers et al. (2004) barc8 is located in chromosome arm 1BS. In this study, it co-segregated with 1BL.1RS, indicating that it could be located in 1RS, or if it was present in 1BL, it failed to recombine with the centromere. *LrZH84* was therefore located on 1BL and showed linkage of 5.2 and 7.7 cM with the centromere in two different populations (Fig. 2). Six additional markers were

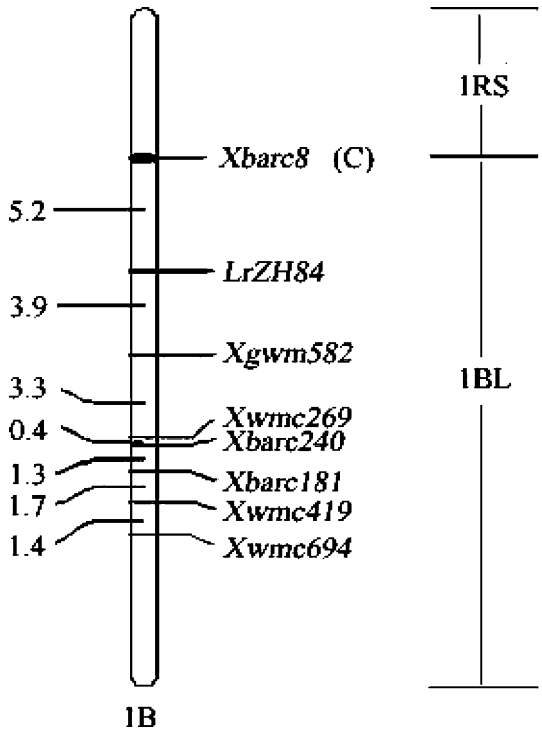

Fig. 2 Chromosome 1B linkage map of leaf rust resistance gene *LrZH84* and seven SSR loci based on 487 F_2 plants. Locus names and corresponding locations are indicated on the *right*. Map distances in centiMorgans are shown on the *left*. *C* indicates the centromere

distal to *LrZH84*. The order of these markers was consistent with the consensus map of Somers et al. (2004).

Characteristics of *LrZH84*

LrZH84 conferred moderate resistance to race THTT at the seedling stage, but Zhou 8425B was highly resistant (IT 0 to;) in the field. In seedling tests under three temperature regimes there was no obvious temperature effect on the expression of *LrZH84* (data not shown). The high level of resistance in the field was assumed to be determined by the seeding effective gene *LrZH84*.

Comparison of *LrZH84* with leaf rust resistance genes located on chromosome 1B

Six formally named leaf rust resistance genes *Lr26*, *Lr33*, *Lr44*, *Lr46*, *Lr51* and *Lr55* are located on chromosome 1B.

Lr26 was originally derived from *Secale cereale*. *Lr46* is an adult-plant resistance gene located in the terminal region of the long arm of wheat chromosome 1B (Singh et al. 1998; Rosewarne et al. 2006). *Lr33,* derived from a common wheat line, was mapped on 1BL 2.6 cM from *Lr26* (Dyck et al. 1987), and presumably the 1B centromere; this places the *Lr33* locus in the same vicinity as *LrZH84*. *Lr33* was not effective against Chinese races, and therefore it must be at least a different allele. Gene *Lr44* derived from spelt wheat was located on chromosome 1BL 5.4 cM from *Lr33* (Dyck and Sykes 1994). In the present seedling tests, races PKSS, PHSL, PKJS and PHSN virulent on Zhou 8425B produced low reactions to *Lr44* (Table 1), indicating that *LrZH84* is different from *Lr44*. *Lr51* and *Lr55* are present in alien chromosome segments derived from *Aegilops speltoides* (Helguera et al. 2005) and *Elymus trachycaulis* (McIntosh et al. 2005), respectively. Although seeds of lines with these genes were not available, it can be assumed that *LrZH84* is a different gene.

Wheat breeding for leaf rust in China

There are many sources of resistance to leaf rust in China, but very little information is available about leaf rust resistance genes and their distribution in Chinese cultivars and germplasm. Since the early 1970s, wheat cultivars with the 1B.1R translocation carrying *Lr26*, derived from Lovrin 13, Predgornaia 2, Kavkaz, Neuzucht, and various derivatives, were widely used in wheat breeding programs (He et al. 2001). Although about one-half of Chinese wheat cultivars carry 1B.1R (Wu et al. 1993; Li et al. 2006a), *Lr26* is no longer effective against prevalent Chinese races. It is therefore important that sources of resistance be documented for newer races such as PHTT and THTT. *LrZH84* appears to be a new leaf rust resistance gene and is effective against most Chinese races. If required, it could be deployed as part of a multiple resistance gene combination.

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