

Molecular mapping of a powdery mildew resistance gene in common wheat landrace Baihulu and its allelism with *Pm24*

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Abstract Powdery mildew is one of the most devastating diseases of wheat in areas with cool and maritime climates. Chinese wheat landrace Baihulu confers a high level of resistance against a wide range of *Blumeria graminis* DC f. sp. *tritici* (*Bgt*) races, especially those currently prevailing in Shaanxi. The objectives of this study were to determine the chromosome bin location of the *mlbhl* gene from Baihulu and its allelism with *Pm24*. To investigate the inheritance of powdery mildew resistance and detect adjacent molecular markers, we constructed a segregating population of 301 F₂ plants and corresponding F_{2:3} families derived from Baihulu/Shaanyou 225. Genetic analysis revealed that a single dominant gene was responsible for seedling stage powdery mildew resistance in Baihulu. A genetic map comprising *Xgwm106*, *Xgwm337*, *Xgwm1675*, *Xgwm603*, *Xgwm789*, *Xbarc229*, *Xgpw4503*, *Xcfd72*, *Xcfd83*, *Xcfd59*, *Xcfd19*, and *mlbhl* spanned 28.2 cM on chromosome 1D. *Xgwm603/Xgwm789* and *Xbarc229* were flanking markers tightly linked to *mlbhl* at genetic distances of 1.5 and 1.0 cM, respectively. The *mlbhl* locus was located in chromosome bin 1DS 0.59–1.00 delimited by the SSR markers *Xgwm337* and *Xbarc229*. When tested

with a differential array of 23 *Bgt* isolates Baihulu displayed a response pattern that was clearly distinguishable from that of Chiyacao and varieties or lines possessing documented *Pm* genes. Allelism analysis indicated that *mlbhl* is a new gene, either allelic or closely linked with *Pm24*. The new gene was designated *Pm24b*.

Introduction

Powdery mildew of common wheat (*Triticum aestivum* L. em Thell.), caused by *Blumeria graminis* (DC.) E. O. Speer f. sp. *tritici*, is a serious fungal disease in the wheat growing areas of the world. Deployment of resistant cultivars provides an effective approach for disease control, eliminates the use of fungicides and minimizes crop losses. To date, more than 60 genes conferring resistance to powdery mildew have been identified at 41 gene loci (*Pm1-Pm45*) (<http://www.shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2011.pdf>) in wheat and its wild relatives. Five of these loci (*Pm1a-Pm1e*, *Pm3a-Pm3k*, *Pm4a-Pm4d*, *Pm5a-Pm5e* and *Pm8/Pm17*) have multiple alleles (Hsam and Zeller 1997; Huang et al. 2003; Singrün et al. 2003; Yahiaoui et al. 2009; Schmolke et al. 2012). A significant problem is that powdery mildew resistance genes are frequently overcome by virulent races within a short time period after introduction to agriculture. Consequently, it is necessary to search for new powdery mildew resistance genes/alleles and to pyramid several resistance genes in a single cultivar using linked markers, to achieve effective resistance.

The most widely used resistance sources in wheat are the wild relatives. Introgressions from relatives may involve large alien segments that are barriers to recombination. Wheat landraces, on the other hand, are valuable sources of resistance genes, especially in regard to ease of

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transfer in breeding programs. Three formally designated powdery mildew resistance genes/alleles (*Pm5d*, *Pm5e* and *Pm24*) (Huang et al. 2003; Nematollahi et al. 2008; Huang and Röder 2011) have been identified from Chinese wheat landraces. Indeed, there are numerous unidentified genes for resistance to a wide range of diseases in wheat landraces (Zeven 1998; Newton et al. 2010).

As part of a program to identify powdery mildew resistance in Chinese wheat landraces, we assembled a collection of more than 1,000 accessions, which were screened with mixed *Bgt* isolates or by exposure to natural infection in the field. A more detailed analysis of selected landraces revealed that some might possess novel genes or alleles that have not been identified. Baihulu is one of them. A previous study located powdery mildew resistance gene *mlbhl* on chromosome 1D in Baihulu and showed that it was linked to marker *Xgwm337* (Zhao et al. 2010). The major objectives of this study were to (1) map gene *mlbhl* by means of molecular markers and (2) investigate allelism between *mlbhl* and *Pm24*.

Materials and methods

Plant materials

The mapping population derived from a cross between Baihulu and Shaanyou 225 comprised 301 F₂ plants and the derived F₃ families. Fifteen plants of each F₃ family were tested to identify the genotypes of corresponding F₂ plants. Shaanyou 225 and Chancellor which carry no known powdery mildew resistance genes were used as susceptible controls in the disease reaction tests. Baihulu served as a resistant parent and resistant control.

Chinese Spring (CS) and chromosome 1D deletion lines (Table 1) kindly provided by Drs Takashi Endo and Shuheji Nasuda, Kyoto University, Japan, were used for chromosomal arm assignment and bin mapping of the molecular markers. A set of 40 differential wheat genotypes (Table 2) possessing known powdery mildew resistance genes were evaluated for response to 23 *Bgt* isolates. Chinese wheat landrace Chiyacao carrying resistance gene *Pm24*, together with Baihulu and a total of 560 F₂ plants from the cross Baihulu/Chiyacao were employed to test the allelism of *mlbhl* and *Pm24*.

B. graminis f. sp. *tritici* pathotypes

Twenty-three *Bgt* differential isolates were used to postulate and differentiate resistance genes *mlbhl* and *Pm24*. The *Bgt* isolates were collected from different areas of China and purified at least twice from single colonies. They were continuously maintained in isolation on seedlings of

Table 1 Chinese Spring chromosome 1D deletion lines used for chromosomal bin mapping

Number	Deletion line	Fraction length (FL)
LPGKU1047	1DL-02	0.41
LPGKU1049	1DL-04	0.18
LPGKU1053	1DS-01	0.59
LPGKU1055	1DS-03	0.48
LPGKU1057	1DS-05	0.70

Chancellor at the institute of Plant Protection, CAAS, Beijing. Isolate E09 was used in host genetic studies as it is avirulent on both Chiyacao and Baihulu. The parents, F₂ population, and F_{2:3} progenies from Baihulu/Shaanyou 225 were inoculated with isolate E09, which was also used to evaluate the F₂ population from Baihulu/Chiyacao.

Scoring for powdery mildew response

Seedlings were grown in the greenhouse at 16–20 °C and inoculated when they were at the 2- to 3-leaf stage. Seedlings were inoculated by dusting conidia from infected seedlings of Chancellor. Approximately 12 days later, infection types were scored when the control varieties Shaanyou 225 and Chancellor were fully infected. Infection types (IT) were scored on a scale of zero to four (Sheng 1988). For analysis two main classes of host reactions were distinguished as resistant (IT = 0, 0₁, 1 and 2) and susceptible (IT = 3 and 4).

Molecular marker analysis

Genomic DNA of parents and progenies were extracted from seedling leaves according to the CTAB protocol (Saghai-Maroo et al. 1984). Molecular markers were evaluated by bulked segregant analysis (BSA) (Michelmore et al. 1991) to identify markers linked to the powdery mildew resistance gene in Baihulu. Resistant and susceptible bulks were made by pooling equal amounts of DNA from ten resistant and ten susceptible F₂ plants, respectively. Wheat SSR markers located on chromosome 1D were selected from primer sets of the GWM (Röder et al. 1998), WMC (Somers et al. 2004), BARC (Song et al. 2005), CFD (Guyomarc'h et al. 2002), and GPW series (<http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/>). Previously published wheat genetic maps of EST-SSR markers (CWEM set) (Peng and Lapitan 2005) and EST-STS markers (MAG set) (Xue et al. 2008) assigned to chromosome 1DS were also screened for polymorphisms between the parents and bulks. Polymorphic markers were further checked for linkage to *mlbhl*, using the entire F_{2:3} mapping population. Primer sequences were

Table 2 Differential reactions of 40 wheat cultivars/lines possessing known powdery mildew resistance genes after inoculation with 23 isolates of *Blumeria graminis* f. sp. *tritici*

Cultivar/Line	Pm gene (s)	Isolate																						
		E01	E02	E05	E06	E07	E09	E11	E13	E15	E16	E17	E18	E20	E21	E231	E232	E26	E301	E302	E31	E32	E49	E50
Axminster/8*Cc	<i>Ia</i>	S	I	S	I	S	S	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Ulka/8*Cc	<i>2</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Asosan/8*Cc	<i>3a</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Chul/8*Cc	<i>3b</i>	S	I	S	I	I	S	I	S	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Sonora/8*Cc	<i>3c</i>	S	S	S	S	S	S	S	S	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Kolibri	<i>3d</i>	I	I	S	I	S	I	I	I	S	S	I	S	S	I	I	I	I	I	I	I	I	I	I
W150	<i>3e</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Mich. Amber/8*Cc	<i>3f</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Khapli/8*Cc	<i>4a</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Armada	<i>4b</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Hope/8*Cc	<i>5a</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Xiaobaidong	<i>xbd</i>	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I	S	I
Timgalen	<i>6</i>	S	S	/	S	S	/	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Coker 747	<i>6</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
CI 14189	<i>7</i>	S	S	/	S	S	/	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Kavkaz	<i>8</i>	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Wembley Der.	<i>I2</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
R4A	<i>I3</i>	I	I	S	I	I	I	I	S	I	I	/	I	I	S	I	I	I	I	I	I	I	I	I
Brigand Der.	<i>I6</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Amigo	<i>I7</i>	S	S	S	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
M1 N	<i>I8 (Ic)</i>	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
XX 186	<i>I9</i>	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
PI 583795	<i>20</i>	I	I	I	S	I	/	I	I	I	S	I	S	I	I	I	I	/	I	I	I	/	I	I
Yangmai 5/Sub.6 V	<i>21</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
81-7241	<i>23 (4c)</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
NC96BGTAS	<i>25 + 3a</i>	S	S	S	I	S	S	I	S	I	S	S	S	S	S	S	S	S	S	S	S	S	S	S
5P27	<i>30</i>	I	I	I	/	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
NC97BGTD7	<i>34</i>	S	I	I	S	S	S	I	S	I	S	I	S	S	S	S	S	I	I	I	S	S	S	I
NC96BGTD3	<i>35</i>	I	I	I	I	S	S	S	S	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Maris Huntsman	<i>2 + 6</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Maris Dove	<i>2 + mld</i>	I	I	I	/	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Bairman 3	<i>4 + 8</i>	I	I	I	I	I	I	I	I	S	I	S	I	S	S	I	I	I	I	I	I	S	I	I
Mission	<i>4b + Mli</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Aquila	<i>Mli</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I

Table 2 continued

Cultivar/Line	Pm gene (s)	Isolate																							
		E01	E02	E05	E06	E07	E09	E11	E13	E15	E16	E17	E18	E20	E21	E231	E232	E26	E301	E302	E31	E32	E49	E50	
Coker 983	5 + 6	s	s	r	s	s	s	s	s	r	s	s	s	s	s	s	s	r	r	r	r	s	s	s	s
Era	?	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Funo	-	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
Chancellor	-	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
Chiyacao	Pm24	r	r	s	s	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Baihulu	mlbhl	r	r	s	r	s	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r

r resistant, s susceptible, - no resistance gene, ? unknown, / not tested, 8*Cc seven times backcrossed to Chancellor, Der. derivative

obtained from the GrainGenes database (<http://wheat.pw.usda.gov/GG2/index.shtml>). Unpublished primer sequences *Xgwm603* and *Xgwm789* were kindly provided by Dr. M. Röder, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany. *Xgwm1675* and *Xgwm1291* were kindly provided by Dr. M. Ganai, TraitGenetics GmbH, Gatersleben, Germany.

The PCR were done in total volumes of 10 μ L, including 1 \times PCR reaction buffer, 1.5 mM MgCl₂, 0.2 mM dNTPs, 0.25 U *Taq* DNA polymerase, 0.5 μ M of each primer, and 40–100 ng total DNA. PCR was performed in an S1000 thermocycler (Bio-Rad, California, USA) using the following program: initial denaturation at 94 $^{\circ}$ C for 3 min, followed by 35 cycles of 30 s at 94 $^{\circ}$ C, 45 s at 50–60 $^{\circ}$ C (based on the primer information from the GrainGenes database), 50 s at 72 $^{\circ}$ C, and a final extension step of 10 min at 72 $^{\circ}$ C before cooling to 4 $^{\circ}$ C. PCR products were resolved in 8 % non-denaturing polyacrylamide gel (37.5 acrylamide: 1 bisacrylamide) electrophoresis and visualized by silver staining.

Physical bin mapping

The chromosome bin assignments of markers linked to the resistance gene on chromosome arm 1DS were obtained using CS and CS chromosome 1D deletion lines produced by Endo and Gill (1996).

Data analysis

Chi-squared tests for goodness of fit were used to test for deviation of observed segregation ratios from theoretic Mendelian ratios by SAS 8.0 software. Linkages between markers and the resistance gene were established using JoinMap 4.0 (<http://www.kyazma.nl/index.php/mc.JoinMap/sc.General/>), with a LOD threshold of 3.0. The genetic map was drawn with the software Mapdraw V2.1 (Liu and Meng 2003).

Results

Inheritance of powdery mildew resistance in Baihulu

Seedlings of 301 F₂ plants and the derived F_{2:3} families produced from the cross Baihulu/Shaanyou 225, and parents were inoculated with *Bgt* isolate E09. Shaanyou 225 was susceptible with IT 4, whereas Baihulu was highly resistant with IT 0, 0; and 1 (necrotic or small pustules). F₂ segregation of 223:78 was consistent with a 3:1 ratio ($\chi^2 = 0.134, P = 0.714, \chi^2_{0.05,1} = 3.841$). Similarly, the observed ratio of the F_{2:3} families (73 homozygous resistant:150 segregating:78 homozygous susceptible) fitted the

expected 1:2:1 ratio ($\chi^2 = 0.169, P = 0.919, \chi^2_{0.05,2} = 5.991$). The combined F₂ and F₃ family data indicated that resistance in Baihulu was conferred by a single dominant gene.

Molecular marker analysis and chromosome bin location

To determine the chromosomal bin location of *mlbhl*, resistant and susceptible DNA bulks as well as the parents were initially employed in BSA using 61 SSR markers located on chromosome 1D. Markers *Xgwm106*, *Xgwm337*, *Xgwm1675*, *Xgwm603*, *Xgwm789*, *Xbarc229*, *Xgpw4503*, *Xcfd72*, *Xcfd83*, *Xcfd59* and *Xcfd19* were polymorphic between the parents and bulks and showed expected patterns for linked markers after being tested on individual F₂ plants. All were inherited co-dominantly (Fig. 1). A linkage map of gene *mlbhl* and closely linked markers with a total map length of 28.2 cM are shown in Fig. 2. Gene *mlbhl* was flanked by loci *Xgwm603/Xgwm789* and *Xbarc229* at genetic distances of 1.5 and 1.0 cM, respectively. *Xgwm1291*, that co-segregated with *Pm24* in earlier work (Huang and Röder 2011), was not polymorphic between Baihulu and Shaanyou 225. None of the eight

EST-based markers previously mapped on 1DS showed linkage with *mlbhl*.

CS and CS deletion lines of chromosome 1D were used to locate flanking markers *Xgwm337* and *Xbarc229*, and therefore *mlbhl*, to a specific segment of the chromosome arm. Fragments of both *Xgwm337* and *Xbarc229* were missing in 1DS-01 and 1DS-03, and *Xgwm337* was also missing in 1DS-05, indicating that *Xgwm337* was located in the distal deletion bin 1DS-05 (0.70–1.00), whereas *Xbarc229* was in bin 1DS-01 (0.59–0.70) (Fig. 3); thus *mlbhl* was placed in bin 0.59–1.00. A comparison with published genetic maps (Huang and Röder 2011) suggested that *mlbhl* was located in the same or a similar chromosomal region to *Pm24* (Fig. 2).

The relationship of *Pm24* and *mlbhl*

A comparison of the responses of Baihulu and Chiyacao and lines possessing other identified resistance genes when inoculated with the 23 differential isolates is shown in Table 2. Baihulu was resistant to 14 isolates and susceptible to nine. The responses of Baihulu and Chiyacao differed for six isolates: five avirulent to the former and one avirulent to the latter. Thus the resistance gene in Baihulu

Fig. 1 Polyacrylamide gel electrophoresis of PCR products amplified with *mlbhl* linked polymorphic markers *Xgwm337*, *Xgwm603*, *Xgwm789*, *Xbarc229*, *Xcfd83* and *Xcfd72* in the F₂ population of Baihulu/Shaanyou 225. 1 Baihulu, 2 Shaanyou 225, 3 resistant bulk, 4 susceptible bulk, 5–10 homozygous susceptible individuals, 11–16 heterozygous resistant individuals, 17–22 homozygous resistant individuals. Arrows indicate the polymorphic amplification products. M D2000 ladder

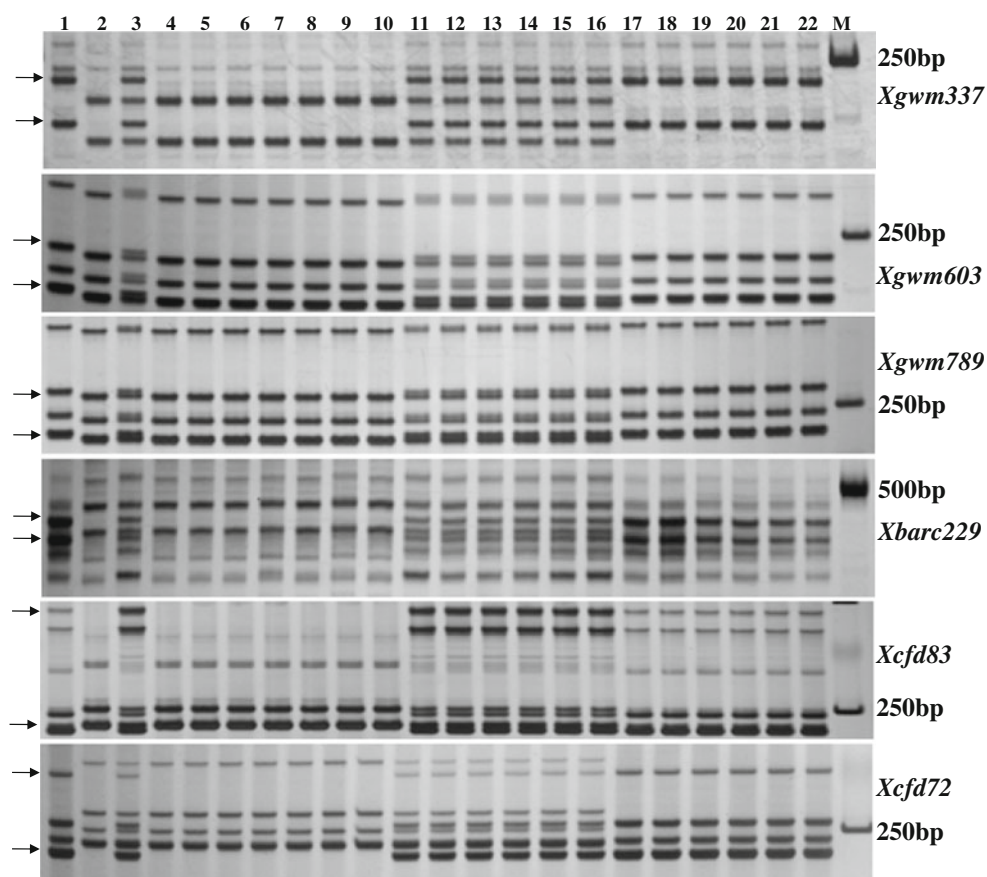


Fig. 2 Comparative view of the *Pm24* (a) and *mlbhl* (b) linkage maps with respect to the 1D physical bin map (c). Locus names and Kosambi map distances (cM) are shown on the right and left side of the a and b maps, respectively. Fraction lengths are indicated on the right side of map c

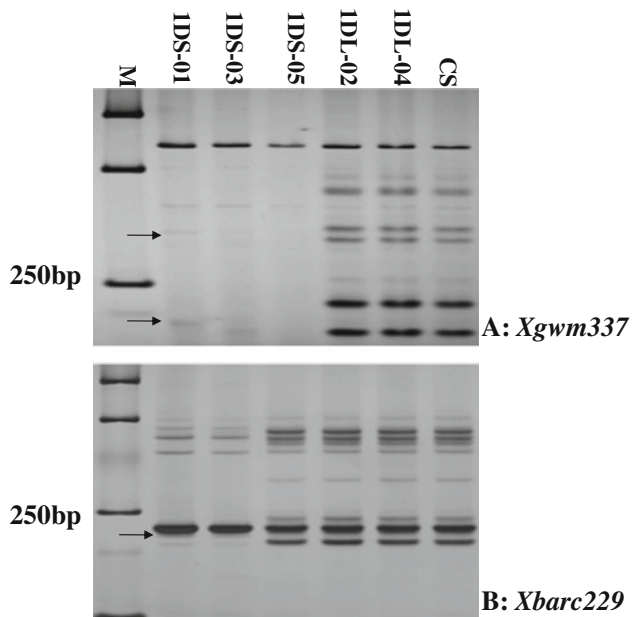
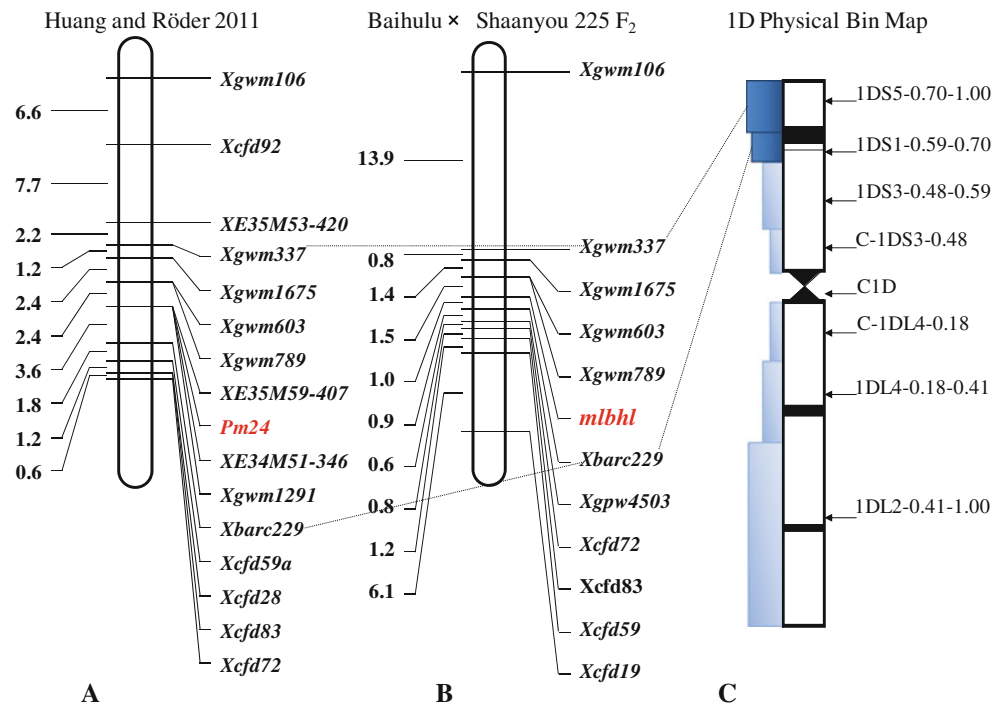


Fig. 3 PCR amplifications of SSR loci *Xgwm337* (a) and *Xbarc229* (b) in Chinese Spring and its five deletion lines of chromosome 1D. Arrows indicate the locations of missing bands. *M* D2000 ladder

was different from *Pm24*, as well as being different from all other genes represented in Table 2.

All 560 F_2 plants from Baihulu/Chiyacao, inoculated with isolate E09 were resistant. On the basis of these results, and the fact that the molecular maps for the present work and for *Pm24* (Huang and Röder 2011) are very similar, we propose that the resistance gene in Baihulu be

designated *Pm24b* and that the former *Pm24* be designated *Pm24a*.

Discussion

Many landraces have tolerances to biotic and abiotic stresses (Zeven 1998). Wheat landraces are abundant in China. Useful traits can be easily transferred from landraces to elite common wheat cultivars. To date, three powdery mildew resistance genes have been identified in Chinese wheat landraces, viz. *Pm24* (Chiyacao), *Pm5d* (CI 10904), and *Pm5e* (Fuzhuang 30) (Huang et al. 2000b, 2003; Nematollahi et al. 2008). In addition to formally named powdery mildew resistance genes, other Chinese wheat landraces were reported to have powdery mildew resistance genes, temporarily designated as *mlxbd* (Xiaobaidong) and *PmH* (Hongquanmang) (Huang et al. 2000a; Zhou et al. 2005). Further resistant genotypes were identified among 3,000 landraces, some of which are immune or highly resistant, such as Youbailan, Bensanyuehuang, Mangmai, Baiyouyantiao, Shangeda, Hongtutou, Hongkema, and Mazhamai (Duan unpublished; Sheng et al. 1992; Xue et al. 2009). Gene *Pm24b* named in this study was present in a largely unexploited reservoir of Chinese wheat landraces. This new gene is highly effective in the field in Shaanxi. Despite its inferior agronomic traits (e.g. low grain yield, lodging), Baihulu can serve as a valuable resistance resource for common wheat improvement.

So far, *Pm24* is the only known wheat powdery mildew resistance locus that was located on chromosome arm 1DS. It was initially mapped in the vicinity of the centromere (Huang et al. 2000b), but was later assigned to bin 1DS5-0.70–1.00 (Huang and Röder 2011). The markers flanking *Pm24a* were *Xgwm789/Xgwm603* and *Xbarc229* at 2.4 and 3.6 cM, respectively. It was also near *Xgwm337* and co-segregated with *Xgwm1291* (Huang and Röder 2011). In our research a genetic map containing 11 markers linked to *Pm24b* was constructed and markers *Xgwm337* and *Xbarc229* flanked it at genetic distances of 3.7 and 1.0 cM, respectively. According to Sourdille et al. (2004) these markers are close to the 1D centromere, but in the present study the *Pm24b* region was shown to be in deletion bin 1DS-0.59–1.00 (Fig. 3). Therefore, *Pm24* must be physically located in the distal region of chromosome 1DS.

We investigated the response spectra of 40 wheat genotypes including a set of differentials carrying known resistance genes. The response arrays of Baihulu and Chiyacao were different from all other reference sources and from each other. The lack of segregation in the intercross, and the very similar map locations of both genes, indicated they are allelic or very closely linked. The present study provides a springboard for fine mapping of *Pm24b* and for its use in wheat breeding programs using the closely linked markers to combine it with other resistance genes as a means of achieving durable resistance.

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