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ORIGINAL PAPER

Identification of the gene *Pm47* on chromosome 7BS conferring resistance to powdery mildew in the Chinese wheat landrace Hongyanglazi

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Abstract Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is an important disease that causes substantial yield losses in wheat (*Triticum aestivum*) in China and other parts of the world. This foliar disease can be effectively managed by host resistance. The Chinese landrace Hongyanglazi from Shaanxi province is highly resistant to many *Bgt* isolates at the seedling stage. Genetic analysis using an $F_{2:3}$ population derived from a cross between Hongyanglazi and susceptible cultivar Zhongzuo 9504 indicated that Hongyanglazi carried a single recessive gene (tentatively designated *PmHYLZ*) conferring its resistance to *Bgt* isolate E09. *PmHYLZ* was flanked by EST marker *BE606897* and microsatellite marker *Xgwm46* on chromosome 7BS at genetic distances of 1.7 and 3.6 cM, respectively. This gene differed from *Pm40*, also located on 7BS, by origin, linked markers, and reactions to 13 *Bgt* isolates. Based on these findings, *PmHYLZ* was permanently designated as *Pm47*.

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Introduction

Common wheat (*Triticum aestivum*), a staple food crop for approximately one-third of the world population, is constantly challenged by pathogens. *Blumeria graminis* f. sp. *tritici* (*Bgt*) causes powdery mildew, one of the most important diseases in many wheat-producing regions worldwide. Powdery mildew often occurs in the regions with cool and humid climates, resulting in severe yield reductions (Everts and Leath 1992). In China, the disease is exacerbated by irrigated conditions, heavy applications of nitrogenous fertilizers, high planting density, and dwarf high-yielding susceptible cultivar growth (Zhuang and Li 1993; Zhuang 2003). In the last decade, powdery mildew has affected more than 6 million hectares of area annually (http://www.agri.gov.cn/). Although fungicides can be used to control the disease, resistant cultivars are a preferable means of control to circumvent environmental problems associated with fungicide use.

The development of powdery mildew resistant cultivars relies on the availability of sources of resistance. At present, about 60 resistance genes or alleles have been designated at 46 loci (*Pm1–Pm46*) (McIntosh et al. 2008, 2009, 2011; Ma et al. 2011). Six of these loci (i.e., *Pm1*, *Pm3*, *Pm4*, *Pm5*, *Pm8*, and *Pm24*) contain more than one resistance allele. Among these genes or alleles, 30 were derived from *T. aestivum*, whereas the others originated either from species closely related to common wheat, such as *T. monococcum*, *T. turgidum*, *T. timopheevii*, *Aegilops speltoides*, *Ae. tauschii*, *Ae. longissina*, *Ae. ovata*, and *Ae. umbellulata*, or more distantly related species, such as *Secale cereale*, *Haynaldia villosa*, and *Elytrigia intermedium*. Because of their qualitative mode of inheritance, most genes become ineffective within a short period of use in agriculture due to virulence changes in the pathogen

populations (Hsam and Zeller 2002). Therefore, a continuous effort is necessary to search for new resistance genes for sustainable protection of wheat from powdery mildew. Since the 1990s, the saturation of genetic maps with different classes of molecular markers has facilitated the identification of genes for resistance to powdery mildew (Huang and Röder 2004; McIntosh et al. 2008, 2011). In particular, PCR-based microsatellite or simple sequence repeat (SSR) markers have been widely used to localize powdery mildew resistance genes in the genome, e.g., *Pm30–Pm46* (Feuillet and Keller 2004; McIntosh et al. 2008; Schmolk et al. 2012).

Chinese landraces indigenous to different regions of China represent a class of valuable wheat germplasm resources. They had not only dominated wheat production throughout the country for a long time before they were replaced by improved cultivars from the 1950s but also served as primary parents in the initial stages of cross breeding (He et al. 2001). Chinese landraces have contributed several genes for resistance to powdery mildew. *Pm5e* is located on chromosome 7BL of Fuzhuang 30 selected from the landrace cross Liquan Heshangtou × Huaxian Qisifeng (Huang et al. 1997, 2003). *Pm24* and *Pm24b* were localized on chromosome 1DS of Chinese landraces Chiyacao (Huang et al. 2000b) and Baihulu (Xue et al. 2012), respectively. Numerous other efforts have been made to find other sources of resistance in large collections of Chinese landraces. These have resulted in identification of powdery mildew-resistant cultivars such as Hongquanmang, Mazhamai, and Xiaobaidongmai (Sheng et al. 1992; Xiong et al. 1995; Wang et al. 1996; Hu et al. 2007; Zhai et al. 2008; Cao et al. 2010). Genetic studies indicated that many landraces carry one or two genes for resistance (Hu et al. 2007; Zhai et al. 2008). These studies demonstrated that it is possible to identify many powdery mildew resistance genes in Chinese landraces.

In a project aimed at identifying the sources of resistance to powdery mildew in Chinese wheat germplasm, many landraces and improved cultivars were tested (Li et al. 2011). Hongyanglazi, a landrace from Shanyang county, Shaanxi province, was highly resistant to *Bgt* isolates. The present study was carried out to map the gene(s) conferring resistance to powdery mildew in Hongyanglazi.

Materials and methods

Plant materials

Hongyanglazi was crossed with the susceptible cultivar Zhongzuo 9504 and F_1, F_2, and $F_{2:3}$ populations were generated for genetic analysis. Jingshuang 16 was used as the susceptible control. Chinese Spring (CS), selected nullisomic–tetrasomic lines (viz. N7A–T7D, N7B–T7A, N7B–T7D, N7D–T7A, and N7D–T7B), ditelosomic lines (Dt7BS and Dt7BL), and deletion lines (7BS-1, 7BL-6, 7BL-7, and 7BL-10), kindly provided by WJ Raupp and BS Gill, Wheat Genetics Resource Centre, Kansas State University, USA, were used in chromosome assignment of the molecular markers associated with the powdery mildew resistance gene in Hongyanglazi.

Evaluation of powdery mildew response

To study the inheritance of resistance to powdery mildew in Hongyanglazi, the *Bgt* isolate E09, a prevailing pathotype in the Beijing area, was used to inoculate Hongyanglazi and Zhongzuo 9504, as well as the hybrid populations. Isolate E09 is virulent to resistance genes *Pm1a*, *Pm3a*, *Pm3c*, *Pm5a*, *Pm7*, *Pm8*, *Pm17*, and *Pm19* but avirulent on Hongyanglazi. Seedlings at the one-leaf-stage in rectangular plastic trays were dusted with conidiospores of isolate E09 newly increased on susceptible cultivar Zhongzuo 9504. The inoculated plants were grown under controlled greenhouse conditions set at 18–22 °C with a 12-h light/12-h dark photoperiod. Twenty seedlings from each $F_{2:3}$ family were evaluated to confirm the phenotypes and to predict the genotypes of the parental F_2 individuals. Disease symptoms were rated on a 0–4 scale about 15 days after inoculation when the susceptible control Jingshuang 16 displayed severe symptoms (Xie et al. 2003).

The response spectra of Hongyanglazi and other materials were evaluated using detached leaf segments as described by Limpert et al. (1988). Thirteen *Bgt* isolates, collected from different parts of China and increased from single-spore progenies, were used to compare the reactions of Hongyanglazi and wheat lines with known resistance genes, including Fuzhuang 30 (*Pm5e*) (Huang et al. 2003), Xiaobaidongmai (*mlxbd*) (Xue et al. 2009), Hongquanmang (*PmH*) (Zhou et al. 2005), and GRY19 (*Pm40*) (Luo et al. 2009), to determine whether the resistance gene(s) in Hongyanglazi was different from known powdery mildew resistance genes on chromosome 7B. All isolates were avirulent for genes *Pm1c*, *Pm5e*, *Pm13*, *Pm16*, *Pm20*, *Pm21*, and *Pm24*, but virulent for *Pm3a* and *Pm3c* (Song et al. 2012). Primary leaf segments 2–3 cm in length were placed on 0.6 % water agar (w/v) supplemented with 50 mg L^{-1} benzimidazole in clear plastic boxes and separately inoculated with the *Bgt* isolates by gently shaking sporulating Zhongzuo 9504 plants over the leaf segments. The plastic boxes containing the inoculated wheat leaf segments were then placed in a growth cabinet at 80 % relative humidity with 14 h of illumination and day/night temperatures of 22/18 °C. Infection types (ITs) were scored using a 0–4 scale 10 days after inoculation when the leaf segments of the susceptible control showed obvious

symptoms (Xie et al. 2003). Reactions to powdery mildew were classified into two groups; plants with IT 0–2 were resistant, and those with IT 3–4 were susceptible.

PCR amplification, electrophoresis, and band visualization

Genomic DNA was extracted from the leaf tissues of young seedlings using the CTAB protocol (Sharp et al. 1988). Equal amounts of DNA from ten homozygous resistant and ten homozygous susceptible F_2 plants were separately bulked to produce resistant and susceptible DNA pools for bulked segregant analysis (Michelmore et al. 1991). The SSR markers and EST markers, mapped in wheat (http://wheat.pw.usda.gov/; Huang et al. 2003; Zhu et al. 2008; Luo et al. 2009; Xue et al. 2009), were used to test for polymorphisms between Hongyanglazi and Zhongzuo 9504 and the DNA bulks. The resulting polymorphic markers were used to map the resistance gene in Hongyanglazi. DNA amplification was performed in a Biometra T3000 Thermocycler (ABI, New York, USA) with the reaction mixture (20 μL) containing 50 ng of template DNA, 0.2 μM of the forward and reverse primers, 1 U of *Taq* polymerase, 0.4 mM dNTPs, and 2 μL 10× buffer with 20 mM Mg^{2+}. The amplification program was initiated at 94 °C for 4 min, followed by 38 cycles of 94 °C for 1 min, 50–60 °C for 1 min, and 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR products were mixed with 2 μL loading buffer (98 % formamide, 10 mM EDTA, 0.25 % bromophenol blue, and 0.25 % xylene cyanol), separated on 1 % agarose gels or 8 % non-denaturing polyacrylamide gels (Acr:Bis = 19:1 or 39:1) at room temperature with 1× TBE buffer (90 mM Tris–borate, pH 8.3, 2 mM EDTA), and visualized following silver staining (Bassam et al. 1991).

Statistical analysis

The goodness-of-fit of observed phenotypes and expected segregation ratios was determined by Chi-square tests (χ^2). Linkage between molecular markers and the resistance gene was estimated using Mapmaker/Exp Version 3.0b with the LOD score threshold of 3.0 (Lincoln et al. 1992). Map distances were derived from recombination values using the Kosambi function (Kosambi 1944).

Results

Inheritance of the powdery mildew resistance in Hongyanglazi

When inoculated with isolate E09, Hongyanglazi exhibited a hypersensitive reaction (IT 0;), whereas Zhongzuo 9504 was highly susceptible (IT 4). F_1 plants of Hongyanglazi × Zhongzuo 9504 were susceptible with IT 3 or 4. The F_2 population segregated 64 resistant and 200 susceptible plants, respectively, fitting to a ratio of 1:3 ($\chi^2 = 0.0808$, df = 1, $P = 0.7762$). The reactions of 210 $F_{2:3}$ families were classified into 48 homozygous resistant, 108 segregating, 54 homozygous susceptible types, respectively, agreeing with a ratio of 1:2:1 ($\chi^2 = 0.5143$, df = 2, $P = 0.7733$). These results indicated that a single recessive gene, tentatively designated *PmHYLZ*, conferred the resistance in Hongyanglazi to isolate E09.

Molecular mapping of the powdery mildew resistance gene in Hongyanglazi

Among 967 SSR markers examined, 331 (34.2 %) displayed polymorphism between the two parents Hongyanglazi and Zhongzuo 9504. Four markers, *Xgwm46*, *Xgpw2119*, *Xgpw2107*, and *Xgwm350* on chromosome 7BS were polymorphic between the contrasting DNA bulks, indicating linkage with the resistance gene in Hongyanglazi. These markers were used to genotype the F_2 population of Hongyanglazi × Zhongzuo 9504 for mapping gene *PmHYLZ*. The closest marker *Xgwm46*, 3.6 cM away from *PmHYLZ*, was located on the bin 7BS-1-0.27-1.00 (Figs. 1, 2a). The polymorphisms of 50 EST markers previously mapped on this chromosome bin (http://wheat.pw.usda.gov/cgi-bin/westsql/bin_candidates.cgi?bin=7BS1-0.27-1.00) were further tested against both parents and the DNA bulks, resulting in two polymorphic markers *BE606897* and *BE638122* (Fig. 2b).

The genetic distances of *BE606897* and *BE638122* from *PmHYLZ* were 1.7 cM and 9.1 cM from *PmHYLZ*, respectively (Fig. 1).

Since *Pm40* originating from *E. intermedium* was located on chromosome 7BS (Luo et al. 2009), markers linked to this gene were tested against the F_2 mapping population of Hongyanglazi × Zhongzuo 9504. Although *Xgwm297* was polymorphic between the parents and the DNA bulks, this marker was not linked to *PmHYLZ*. Other markers *Xwmc426*, *Xwmc335*, *Xwmc364*, and *Xwmc476* flanking *Pm40* were not polymorphic between Hongyanglazi and Zhongzuo 9504 (Table 1). The genotyping results of the markers that were linked to genes *Pm5e* (*Xgwm1267* and *UBC405-628*), *mlxbd* (*Xgwm577*), *PmH* (*Xgwm611*), and *Mlmz* (*Xwmc396*) on the long arm of chromosome 7B demonstrated that they all were either monomorphic or not linked to *PmHYLZ* (Table 1). Together, these results indicated that *PmHYLZ* was different from *Pm40* on 7BS, as well as *Pm5e*, *mlxbd*, *PmH*, and *Mlmz* on 7BL. Because of its unique position on chromosome 7BS, *PmHYLZ* resides on new locus and is renamed *Pm47*.

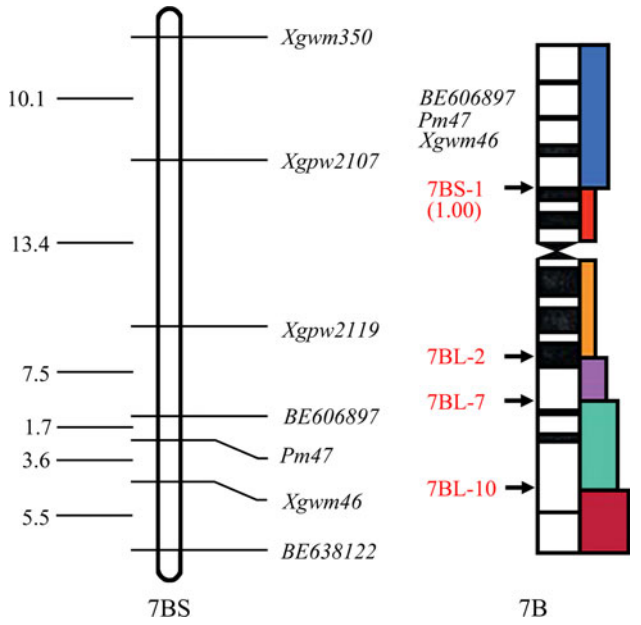

Fig. 1 Linkage map and chromosome bin physical map of *PmHYLZ* on chromosome 7BS. Genetic distances are shown to the *left* in cM

Chromosome assignment of *Pm47*

The EST marker *BE606897* and the SSR marker *Xgwm46* that flanked *Pm47* amplified identical banding patterns in nulli–tetrasomic lines CS N7A-T7D, CS N7D-T7A, CS N7D-T7B, and Chinese Spring, but did not produce any product in the lines without chromosome 7B, indicating that these marker loci were located on chromosome 7B (Fig. 3). The presence of the diagnostic bands of these markers in Dt7BS and absence in Dt7BL indicated that these loci were located on the chromosome arm 7BS. Furthermore, these markers amplified no products in the deletion line for bin 7BS-1-0.27-1.00, but amplified the same products in the 7BL-6, 7BL-7 and 7BL-10 deletion lines (Fig. 3). Therefore, *Pm47* was located on the bin 7BS-1-0.27-1.00 of chromosome arm 7BS.

Comparative reactions of Hongyanglazi and the lines with known powdery mildew resistance genes on chromosome 7B to a panel of *Bgt* isolates

The reactions of *Pm47* to 13 different *Bgt* isolates were compared with those of lines possessing genes previously mapped on chromosome 7B. The responses of GRY19 with *Pm40* differed from those of Hongyanglazi when tested with isolates E09, E11, E16, E20, E21, E22, and Bg30. The reactions of lines with *Pm5a*, *Pm5e*, and *mlxbd* on 7BL also differed from Hongyanglazi, but Hongyanglazi showed a similar pattern to Hongquanmang with *PmH* (Table 2). Zhongzuo 9504 and Jingshuang 16 were susceptible to all isolates.

Discussion

The Chinese wheat landrace Hongyanglazi is resistant to most *Bgt* isolates in China. Resistance was controlled by a single recessive gene, designated *PmHYLZ*, and was mapped on chromosome arm 7BS. Since no gene for powdery mildew resistance derived from genus *Triticum* was previously located on this chromosome arm, *PmHYLZ* represents a new locus. The gene was therefore designated *Pm47*.

Although *Pm40* is also localized on chromosome arm 7BS (Luo et al. 2009), its alien origin allows for a different designation in wheat. Line GRY19 with *Pm40* also displayed a different pattern of powdery mildew responses compared to Hongyanglazi (Table 2). The putative chromosome segment containing *Pm40* was described as a cryptic translocation from *E. intermedium* (Luo et al. 2009) and there is no

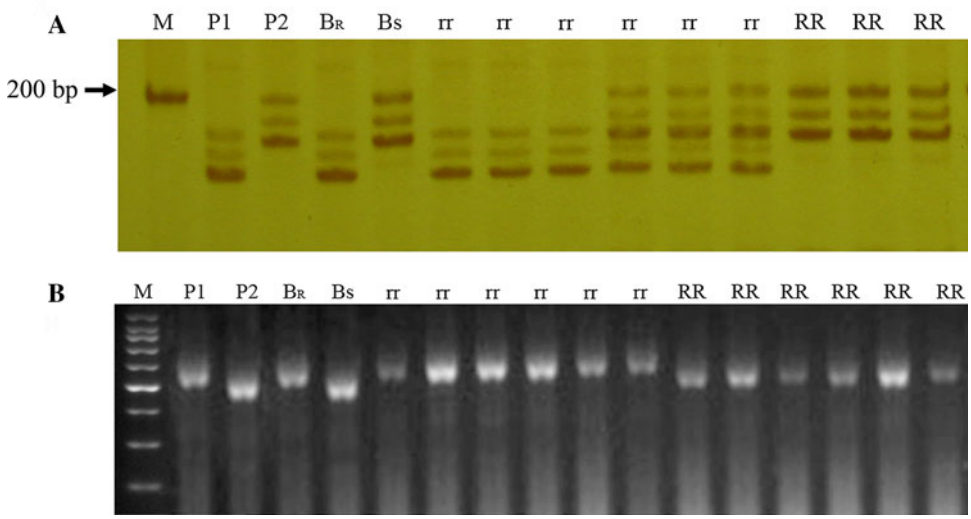

Fig. 2 Amplification patterns of SSR marker *Xgwm46* (**a**) and EST marker *BE606897* (**b**) from selected F_2 plants of Hongyanglazi × Zhongzuo 9504 *P1* Hongyanglazi, *P2* Zhongzuo 9504, B_R resistant bulk, B_S susceptible bulk, *rr* homozygous resistant plants, *Rr* heterozygous susceptible plants, *RR* homozygous susceptible plants, *M* 100 bp DNA ladder

Table 1 Detection of polymorphism in the *PmHYLZ* mapping population with the SSR markers associated with known powdery mildew resistance genes on chromosome 7B

Marker	Resistance gene[a]	Chromosome arm	Polymorphism[b]		Linkage to *PmHYLZ*
			Parents	Bulks	
Xwmc425	*Pm40*	7BS	−	−	−
Xwmc335	*Pm40*	7BS	−	−	−
Xgwm297	*Pm40*	7BS	+	+	−
Xwmc364	*Pm40*	7BS	−	−	−
Xwmc426	*Pm40*	7BS	−	−	−
Xwmc476	*Pm40*	7BS	−	−	−
Xgwm1267	*Pm5e*	7BL	+	+	−
UBC405-628	*Pm5e*	7BL	−	−	−
Xgwm577	*mlxbd*	7BL	+	+	−
Xgwm611	*PmH*	7BL	−	−	−
Xwmc396	*Mlmz*	7BL	−	−	−

[a] *Pm40*, Luo et al. (2009); *Pm5e*, Huang et al. (2003); *mlxbd*, Huang et al. (2000a); *PmH*, Zhou et al. (2005); and *Mlmz*, Zhai et al. (2008)

[b] +, polymorphic or linked; −, non-polymorphic or unlinked

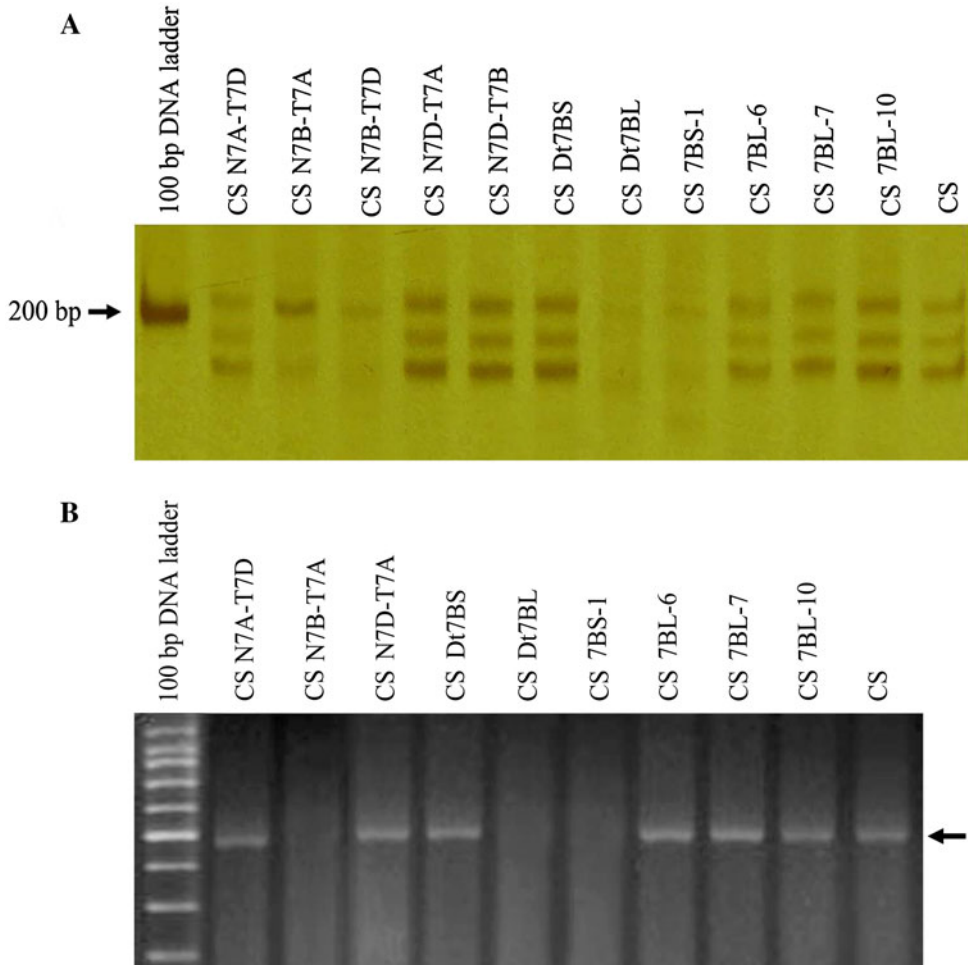

Fig. 3 Chromosomal localizations of SSR marker *Xgwm46* (**a**) and EST marker *BE606897* (**b**) using the Chinese Spring homoeologous group 7 nulli-tetrasomics, ditelosomics, and deletion lines. The *arrow* in **b** indicates the diagnostic band of marker *BE606897*

evidence, apart from pedigree, for its alien origin. However, even if it is derived from wheat, the marker evidence suggests that the two genes must be present at different loci. The positions of SSR markers *Xwmc426*, *Xwmc335*, *Xgwm297*, *Xwmc364*, and *Xwmc476*, closely linked to *Pm40* were at positions 53, 28, 34, 29, and 60 cM on the consensus map of wheat, respectively (http://wheat.pw.usda.gov/CMap/). The order of these loci in the *Pm40* mapping population was *Xwmc426–Xwmc335–Pm40–Xgwm297–Xwmc364*–Xwmc4-76 (Luo et al. 2009). In the consensus genetic map, the positions of SSR markers associated with *Pm47*, i.e., *Xgwm350*, *Xgpw2107*, *Xgpw2119*, and *Xgwm46*, were 17, 18, 37, and 41 cM, respectively. Therefore, *Pm47* and *Pm40* must be at different loci.

Table 2 Comparative responses of Hongyanglazi and wheat genotypes with known powdery mildew resistance genes on chromosome 7B to *Bgt* isolates

Cultivar/line[a]	*Pm* gene	Chromosome arm	*Bgt* isolates												
			E03	E09	E11	E16	E18	E20	E21	E22	Bgt2	Bgt12	Bgt30	Bgt32	Bgt36
Hongyanglazi	*PmHYLZ*	7BS	0	0;	0	0	0;	0;	0;	0	0	1	0	3	1
GRY19	*Pm40*	7BS	1	3	3	3	0	3	3	3	0	0;	3	3	0;
CI 14125	*Pm5a*	7BL	3	3	3	0	0;	3	3	3	3	3	3	3	3
Fuzhuang 30	*Pm5e*	7BL	0;	0;	0	0	0; + 1	0;	1	0	0;	1	0	0	0
Hongquanmang	*PmH*	7BL	0	0	0;	1	0	0;	0	0;	0	0	0;	3	0
Xiaobaidongmai	*mlxbd*	7BL	0	0;	0;	1	0;	1	0	0	0; + 1	0	0;	0	0;
Zhongzuo 9504	–	–	4	4	4	4	4	4	4	4	4	4	4	4	4
Jingshuang 16	–	–	4	4	4	4	4	4	4	4	4	4	4	4	4

[a] GRY19, Luo et al. (2009); CI 14125, Law and Wolfe (1966); Fuzhuang 30, Huang et al. (2003); Hongquanmang, Zhou et al. (2005); Xiaobaidongmai, Huang et al. (2000a)

The SSR markers linked to *Pm40* were tested against the mapping population of Hongyanglazi × Zhongzuo 9504. Unfortunately, no polymorphism was detected for any of the SSR markers between the parental lines Hongyanglazi and Zhongzuo 9504, and thus, could not be used to map *Pm47* (Table 1). The marker *Xgwm297* was not linked to *Pm47* even though it was polymorphic in the present study. The SSR mapping results indicated that *Pm40* was closely linked to SSR marker *Xgwm297* that was previously physically mapped to bin 7BS-1-c-0.27 near the centromere; however, *Pm47* was linked to *BE606897* and *Xgwm46* that was physically mapped to bin 7BS-1-0.27-1.0 (http://wheat.pw.usda.gov/wEST/binmaps/; Sourdille et al. 2004), indicating that *Pm47* was located on this region of chromosome 7BS. This provides further evidence supporting the conclusion that the *Pm47* has a different location from *Pm40*. Furthermore, the identification of EST markers tightly linked to *Pm47* allows fine mapping of the target gene using comparative genomics approach with the available genomic sequences of the model plant species, such as *Brachypodium* and rice (*Oryza sativa* L.), because of the good colinearity of wheat chromosomes and the chromosome regions of these plant species (Bossolini et al. 2007; Qin et al. 2011). The recently published wheat genome sequence will facilitate developing high-density map of the gene *PmHYLZ* (Brenchley et al. 2012).

Previously, several genes for resistance to powdery mildew originating from Chinese landraces were mapped on chromosome 7B, for example, *Pm5e* (Huang et al. 2000a), *mlxbd* (Huang et al. 2000a; Xue et al. 2009), and *PmH* (Zhou et al. 2005). However, they all were located on the long arm of this chromosome. So, these genes are most unlikely associated with *Pm47* even though *PmH* shares similar patterns in reaction to the *Bgt* isolates tested. Chinese wheat landraces have contributed several genes conferring resistance to powdery mildew. Since wheat has a long history of cultivation in China, numerous landraces were grown throughout the country before modern cross-breeding was initiated in the 1950s (He et al. 2001). Currently, about 14,000 accessions of wheat landraces are conserved in the national gene bank. It is not surprising to discover more landraces with resistance to powdery mildew.

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