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ORIGINAL PAPER

Genetic analysis and molecular mapping of a new powdery mildew resistant gene *Pm46* in common wheat

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Abstract Powdery mildew (PM), caused by *Blumeria graminis* f. sp. *tritici* (Bgt), has become a serious disease and caused severe yield losses in the wheat production worldwide. Resistance gene(s) in wheat cultivars can be quickly overcome by newly evolved pathogen races when these genes are employed for long time or in a large area. It is urgent to search for new sources of resistance to be used in wheat breeding. Tabasco is a German resistant cultivar and a new source of resistance gene(s) to PM. An F_2 population was developed from a cross between Tabasco and a Chinese susceptible cultivar Ningnuo 1. Infection types in 472 F_2 plants and 436 F_{2-3} families were evaluated by inoculating plants with isolate Bgt19. Results showed that a single dominant gene, designed *Pm46*, controlled powdery mildew resistance in Tabasco. This gene was located to the short arm of chromosome 5D (5DS) and flanked by simple sequence repeat markers *Xgwm205* and *Xcfd81* at 18.9 cM apart. Because another resistance gene *Pm2* was also located on 5DS, 15 Bgt isolates were used to inoculate Tabasco and Ulka/8*Cc (*Pm2* carrier). The results showed that Tabasco was highly resistant to all of the 15 isolates tested, while Ulka/8*Cc was susceptible to 4 of the isolates, suggesting that Tabasco may carry resistant gene(s) different from *Pm2* gene in Ulka/8*Cc. To test the allelism between *Pm46* and *Pm2*, an F_2 population between Tabasco and Ulka/8*Cc was developed. Isolate Bgt2, avirulent to both parents, was used to evaluate the F_2 population and two susceptible plants were identified from 536 progenies with F_2 plants. This result indicated that *Pm46* is not allelic to *Pm2*. Therefore, *Pm46* is a new gene for PM resistance identified in this study.

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Introduction

Wheat is one of the earliest and most widely cultivated crops in the world. It is the staple crop for about 35 % of the human population (Huang and Röder 2004). However, as dwarf and semi-dwarf genes are deployed in more and more newly developed cultivars, more intensive cultivation systems were adopted, and more irrigation and fertilizer were used in major wheat-growing areas, the devastating effect of powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (Bgt), has spread in drier and warmer areas as well as cool and humid cropland since the green revolution (Smith and Smith 1974; Bennett 1984; Hua et al. 2009). Use of resistant cultivars proves to be an effective and environmentally safe approach to minimize crop losses due to the disease.

To date, 45 loci (*Pm1–Pm45, Pm18 = Pm1c, Pm22 = Pm1e, Pm23 = Pm4c, Pm31 = Pm21*) for resistance to PM with 64 resistance alleles have been identified on 18 different chromosomes in wheat (McIntosh et al. 2008; Xu et al. 2009; Zhang et al. 2010; Ben-David et al. 2010; Li et al. 2010; Ma et al. 2011). Most of the 45 loci show qualitative (race-specific) resistance and are easily overcome by simple genetic changes in the pathogen

(McDonald and Linde 2002; Skinnes 2002). Among them, only a few resistant genes have been successfully used in the commercial production, such as *Pm2, Pm4a Pm8, Pm21* and *Pm2* + *Pm6*. A cultivar that fits for gene-for-gene inheritance may loss its resistance soon after it is deployed in a larger cropland area because of co-evolution of host and pathogen. Some examples include that *Pm8* lost its resistance in 1980s and *Pm4a* is becoming ineffective in some areas in China. Although *Pm21* showed high and stable resistance to more than 120 isolates in both Europe and China (Huang et al. 1997; Qi et al. 1996), extensive use of *Pm21* may render it susceptible to new pathogen races. Therefore, the continuous exploration of new PM resistant genes, especially with resistance to a broad-spectrum of pathogen races, is necessary to prevent wheat from attack by the fungus.

Recently, molecular markers such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), sequence tagged sites (STS) and microsatellites, also termed simple sequence repeats (SSRs), have been widely used to tag and identify powdery mildew resistance genes in wheat using F2 and back-cross populations, near-isogenic lines (NILs), doubled haploids (DH), recombinant inbred lines (RILs) or bulked segregant analysis (BSA, Michelmore et al. 1991). High-density wheat SSR maps (Röder et al. 1998; Somers et al. 2004; Song et al. 2005) greatly facilitate the identification, mapping, and cloning of powdery resistance genes in wheat (Landjeva et al. 2007; Xu et al. 2008). Twenty-nine recently reported *Pm* genes have been tagged with different molecular markers (Alam et al. 2011). The identification of diagnostic markers closely linked to disease resistance genes can simplify breeding activities such as cultivar development (Bonnett et al. 2005), near-isogenic line development (Zhou et al. 2005), and pyramiding several resistance genes into a single cultivar by MAS.

Expressed sequence tags (ESTs) are short cDNA sequences of expressed gene. They are a valuable source of molecular markers for fine mapping of resistance genes. The sequence information of each EST can be immediately related to reference model species and used to integrate the physical and genetic maps of wheat with the genome sequence of model species such as rice (Linkiewicz et al. 2004). Using Southern hybridization to a set of Chinese Spring deletion lines, thousands of wheat ESTs have been located on specific chromosome bins (Qi et al. 2004). These physically mapped ESTs can be used to design PCR primers to develop polymorphic sequence tagged site (STS) markers to determine the chromosomal bin position of a gene of interest (Zhang et al. 2010).

Tabasco (*T. aestivum*, $2n = 6x = 42$, AABBDD) was a newly developed cultivar from Germany in 2008. It is highly resistant to powdery mildew in both Germany and in China. But the gene underlying resistance is unknown (Beschreibende Sortenliste 2009). The objective of this study was to (1) elucidate the genetic basis of powdery mildew resistance in Tabasco, (2) determine the chromosome location of the resistant gene and its relationship with previously reported genes resistant to PM, and (3) develop high-throughput PCR-based markers suitable for marker-assisted selection (MAS) in wheat breeding programs.

Materials and methods

Plant material and powdery mildew isolates

A mapping population of 472 F_2 plants and 436 F_3 families were derived from the cross between Tabasco and Ningnuo 1. Tabasco is a German cultivar (Beschreibende Sortenliste 2009) with a high resistance against all Bgt isolates currently identified in Nanjing, China. Ningnuo 1 is a new waxy cultivar susceptible to all local Bgt isolates at seedling stage. In addition, Sumai 3 is a highly susceptible cultivar to all local Bgt isolates and was used as uniform control. Ulka/8*Cc, one of the *Pm2* gene carriers, was used as another parent to develop a F_2 population, and was used for testing allelism between *Pm2* and a newly identified gene in Tabasco.

The single spore selected Bgt isolates were collected from Nanjing and kindly provided by Professor Zhengqiang Ma in The Applied Plant Genomics Laboratory of Nanjing Agricultural University, China. A differential set of 15 Bgt isolates was used for virulence tests.

Disease evaluation

All F_2 plants derived from crosses of Tabasco/Ningnuo 1 and Tabasco/Ulka/8*Cc were grown in 72-well rectangular trays with 1 plant per well. Plants in the trays were inoculated at one-leaf stage in a growth chamber with pathogen isolate Bgt19 according to Yao et al. (2007). The isolate Bgt19 is a prevalent isolate in Nanjing area. Parents Tabasco and Ningnuo 1 were randomly planted in the trays. Sumai 3 was planted as a susceptible control with two plants per parents/control in each tray. A total of 436 F_2-derived F_3 families, with 25 seedlings per family, were inoculated with Bgt19 to confirm the F_2 plant phenotypes.

Pathogenicity tests were carried out with the parents and controls in the laboratory using the detached leaf technique (Limpert et al. 1988). A set of 15 *Blumeria graminis tritici* (Bgt) isolates was used for inoculation. Primary leaf segments (3.0 cm) were floated on 0.6 % water agar (w/v) amended with 20 mg/L 6-benzylaminopurine in a petri

dish. Infection types (IT) were scored on a 0–4 scale at 9–10 days after inoculation.

An F_2 population from the cross between Tabasco and Ulka/8*Cc was inoculated with Bgt2 to test allelism of the newly identified resistant gene and a previously reported gene on the same chromosome.

Infection types (IT) were scored 7–8 days after inoculation when the susceptible controls Sumai 3 and Ningnuo 1 showed a high level of IT. IT were scored on a 0–4 scale (Liu et al. 1999), with 0 as no visible symptoms; 0, as necrotic flecks, 1 as highly resistant (necrosis with low sporulation), 2 as resistant (necrosis with medium sporulation), 3 as susceptible (no necrosis with medium to high sporulation), and 4 as highly susceptible (no necrosis with full sporulation). Reactions were finally classified into two groups, resistant (R, IT 0–2) and susceptible (S, IT 3–4).

Molecular marker analysis

DNA was extracted from young seedling tissues following Ma et al. (1994). For bulked segregant analysis (BSA), DNA bulks were prepared by combining equal amounts of DNA from six resistant (IT 0) and six susceptible (IT 4) F_2 plants based on F_2 disease data. The DNA samples of parents and bulks were for polymorphism. A total of 244 wheat SSR (barc, gwm, wmc, gpw and cfd series) covering all three wheat genomes were chosen from a consensus map (Somers et al. 2004) for parent and bulk screening. The genetic distances between selected markers were about 10–20 cM in the consensus map. Polymorphic markers between both bulks and parents were used to analyze F_2 individuals and map the PM resistant gene(s).

PCR was performed in a SensoQuest Labcycler (Germany) using a volume of 10 µl containing 20 ng of template DNA, 2 pmol of each of the primers, 2 nmol of each of the dNTPs, 15 nmol of $MgCl_2$, 0.1 U of *Taq* DNA polymerase, and 1× PCR buffer. The PCR profile included one cycle of 94 °C for 5 min followed by 35 cycles of 94 °C for 30 s, 50–61 °C (depending on the specific primers) for 30 s and 72 °C for 1 min, with a final extension at 72 °C for 10 min. PCR products were separated in 8 % non-denaturing polyacrylamide gels with a 19:1 of acrylamide and bisacrylamide, and then silver stained to visualize PCR products (Santos et al. 1993).

After initial mapping to locate the gene on 5D, 46 SSR markers located on chromosome 5D near the *Pm2* gene were further screened between parents (Sourdille et al. 2004; Xue et al. 2008) and polymorphic markers were analyzed in the F_2 population. In addition, EST-STS markers were designed using ESTs sequences of 5DS deletion maps of *Triticum aestivum* cv. Chinese Spring (http://wheat.pw.usda.gov/wEST/binmaps/wheat5_rice.html) and MACVECTOR V8.0 (Accelrys, UK). For STS, restriction enzymes, *Alu*I, *Mbo*I, *Msp*I, *Hae*III and *Taq*I (Fermentas Life Sci. China) were selectively employed to digest PCR products when the STS markers of interest were not polymorphic between the parents. PCR digestion was performed according to the manufacturer's instruction. The digested products were separated in 8 % non-denaturing polyacrylamide gels.

Identification and confirmation of chromosomal arm location of the identified gene

Chi-squared tests were used to determine the goodness-of-fit of observed data with expected segregation ratios. Linkage between molecular markers and the resistant gene was analyzed using Mapmaker 3.0, setting the LOD threshold score at 3.0.

Chinese Spring, its nulli-tetrasomic lines, and deletion lines of chromosome group 5 were used to determine chromosome location of the gene conferring powdery mildew resistance.

Results

Inheritance of the powdery mildew resistance in Tabasco

Tabasco was highly resistant to Bgt19 with IT of 0, while Ningnuo 1 and Sumai 3 were highly susceptible with an IT of 4. All 30 F_1 seedlings of Tabasco/Ningnuo 1 were highly resistant with an IT of 0. The F_2 population segregated with a ratio of 359 resistant to 113 susceptible (Table 1), fitting

Table 1 Reaction of F_2 population and F_{2-3} progenies of Tabasco × Ningnuo 1 to isolate Bgt19

Cross	Isolates	F_2 population		F_3 progeny test	
		R_:rr	$\chi^2_{3:1}$	RR:Rr:rr	$\chi^2_{1:2:1}$
Tabasco × Ningnuo 1	Bgt19	359:113	0.11	101:238:97	3.58

RR homozygous resistant, *Rr* heterozygous resistant, *rr* homozygous susceptible

$\chi^2_{0.05,1} = 3.84$, $\chi^2_{0.05,2} = 5.99$

a single dominant gene segregation ratio of 3:1 ($\chi^2_{3:1} = 0.23$, $P = 0.63$). Out of 472 F_2 individuals raised in the greenhouse, 436 plants produced F_3 seeds. Further evaluation of F_3 families for PM resistance identified 101 homozygous resistant (RR): 238 segregating (Rr): 97 homozygous susceptible (rr) F_3 families, which fits to an expected 1:2:1 ratio ($\chi^2_{1:2:1} = 3.58$, $P = 0.17$), confirming that the PM resistance in Tabasco was controlled by a single dominant gene designated as *Pm46*.

Molecular markers linked to the *Pm46*

Initially, 244 wheat SSR markers were analyzed for polymorphism between the parents and the resistant and susceptible bulks. Of these, 134 markers (55 %) were polymorphic between the parents. However, only the marker *Xgwm205* on the short arm of chromosome 5D (5DS) showed polymorphism both between parents and bulks (Fig. 1a). Linkage analysis using 472 F_2 plants showed that the marker *Xgwm205* was closely linked to the gene *Pm46*. To saturate the genomic region near *Pm46* gene, 46 additional SSR markers on 5D chromosome were selected to screen the population according to previously reported maps (Sourdille et al. 2004; Xue et al. 2008). SSRs *Xcfd81*, *Xgpw302*, *Xcfd67*, and *Xwmc608* were polymorphic and mapped close to *Pm46* (Fig. 2).

Chromosome assignment of the *Pm46* gene in Tabasco

SSR *Xgwm205*, *Xcfd81*, *Xgpw302* and *Xcfd67* were previously mapped on the short arm of chromosome 5D (Somers et al. 2004; Sourdille et al. 2004; Xue et al. 2008). Thus, *Pm46* in Tabasco was putatively assigned to the same chromosome arm. Chinese Spring and its corresponding nulli-tetrasomic lines were used to confirm the result. All four SSR amplified the expected bands in Chinese Spring (CS) and the CS N5A-T5D line, but not in the N5D-T5B line. Because the marker *Xcfd81* was also assigned to 4D and 7B and 5D (http://wheat.pw.usda.gov/GG2/index.shtml), marker *Xcfd81* was amplified in both N4D-T4B and N7B-T7D lines, respectively. Thus, all markers amplified banding pattern as expected in Chinese Spring genetic stocks and confirmed that *Pm46* was on chromosome 5DS (Fig. 3a).

Deletion lines of chromosome 5DS were used to further locate the bin position of *Pm46*. Expected PCR product of

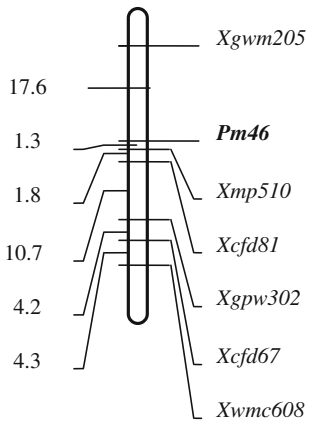

Fig. 2 Genetic linkage map of short arm of chromosome 5D to show the location of powdery mildew resistance gene *Pm46*

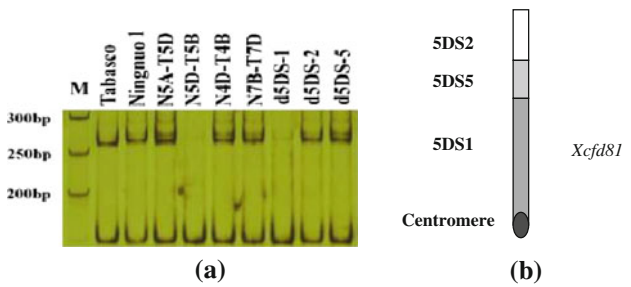

Fig. 3 Amplification patterns of SSR marker *Xcfd81* in Chinese Spring, its nulli-tetrasomic lines, and deletion bin of chromosome 5DS (**a**). The position of SSR marker *Xcfd81* on deletion maps of 5DS (**b**)

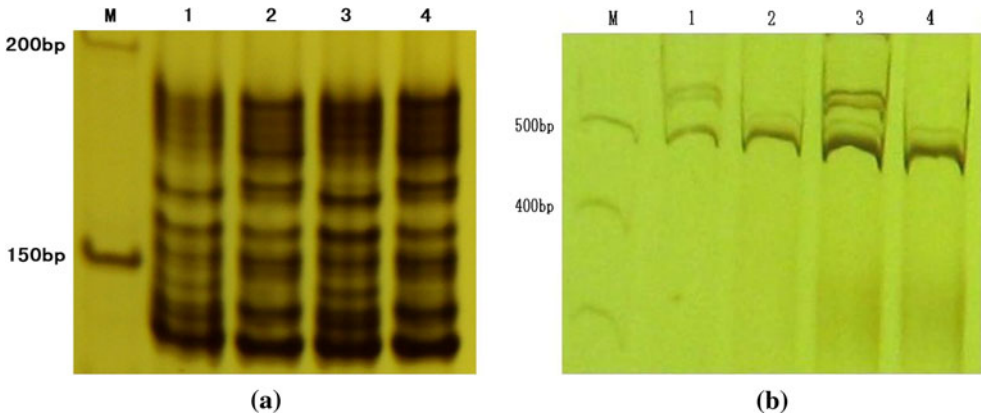

Fig. 1 Examples of amplification patterns of *Pm46*-linked polymorphic primers *Xgwm205* (**a**) and *Xmp510* (**b**). *Lanes 1, 2, 3* and *4* are corresponding to Tabasco, Ningnuo 1, resistant bulk and susceptible bulk, respectively

Xcfd81 was absent in d5DS1, while present in d5DS2 and d5DS5 (Fig. 3b), suggesting that *Pm46* was on 5DS1 in Tabasco.

STS markers linked to the *Pm46*

Fifty-three STS markers were developed from wheat ESTs that were located on several bins of 5DS. Only one STS, *Xmp510*, from the EST BE498794 with forward primer 5′-CATCCATCCAAACATCCAATGC-3′ and reverse primer 5′-ACAACACTACCACCATCACCGC-3′, was polymorphic between the parents and between bulks (Fig. 1b). After screening the F_2 population, *Xmp510* was mapped at 1.3 cM from *Pm46* in Tabasco (Fig. 2). The EST BE498794 was previously assigned to deletion bin 5DS1, the same bin *Xcfd81* was located on (Fig. 3b) according to the Graingenes' (http://wheat.pw.usda.gov/cgi-bin/gbrowse/WheatPhysicalESTMaps/#search). This further proved that the resistance gene *Pm46* is on 5DS.

Allelism test of *Pm46* and *Pm2*

In order to check if *Pm46* in Tabasco is the same gene as *Pm2*, a pathogenicity test was conducted with 15 different Bgt isolates collected from Nanjing using the detached leaf technique. Tabasco, Ulka/8*Cc (a line that carries *Pm2*), Ningnuo 1, and Sumai 3 were inoculated with all the 15 Bgt isolates (Table 2). The results showed that Tabasco was highly resistant (IT 0–1) to all isolates, while Ulka/8*Cc was resistant (IT = 0–2) to only 11 isolates (IT 0–2) and highly susceptible to 4 isolates (IT = 4) (Bgt3, Bgt4, Bgt21 and Bgt22, Fig. 4). As expected, Ningnuo 1 and Sumai 3 were highly susceptible to all isolates (IT 4). This result suggested that *Pm46* in Tabasco was most likely different from *Pm2*.

In order to further clarify the genetic relationship of *Pm46* and *Pm2*, a total of 536 F_2 plants from Tabasco// Ulka/8*Cc were inoculated with Bgt2, a isolate avirulent to both parents. Two susceptible plants were found. This result confirms that *Pm46* and *Pm2* were not in the same locus, but closely linked two genes.

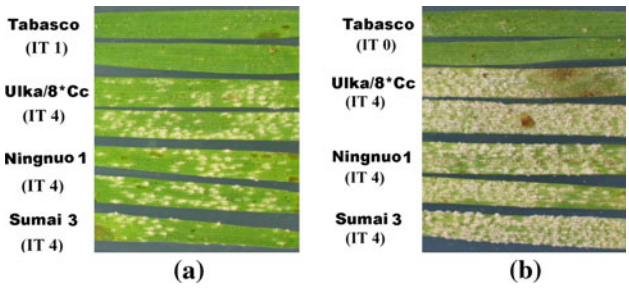

Fig. 4 The reaction of Tabasco, Ulka/8*Cc, Ningnuo 1 and Sumai 3 to Bgt3 (**a**) and Bgt22 (**b**)

Discussion

A new single dominant PM resistant gene *Pm46* was identified in a new German wheat cultivar Tabasco in this study. Genetic analysis and molecular mapping indicated that the *Pm46* was located on the chromosome 5DS and flanked by markers *Xgwm205* and *Xcfd81* based on previously reported marker data (Sourdille et al. 2004; Qiu et al. 2006). Physical mapping of the markers using Chinese Spring 5D nulli-tetrasomic genetic stocks further confirmed the result. Deletion bin mapping tentatively located the gene in bin 1 of 5DS. Using EST mapping, one EST derived STS, *Xmp510,* was 1.3 cM from Pm46 and was identified as the closest marker to *Pm46.* This marker is 1.3 cM from *Pm46*. Thus, *Xmp510* is a good marker for marker-assisted selection of *Pm46* in breeding programs.

Three PM resistant genes *Pm34, Pm35* and *Pm-M53* have been reported on chromosome 5D (Miranda et al. 2006, 2007; Li et al. 2010). *Pm34* was mapped on 5DL with three co-dominant microsatellite markers. Among the three markers, *Xbarc177* showed polymorphism between Tabasco and Ningnuo 1, but is 190 cM away from *Pm46* in this study. *Pm35* was also on 5DL (Miranda et al. 2007). A common marker *Xcfd7* that was 10.3 cM from *Pm35* was

Table 2 Differential reactions of four wheat cultivars/lines carrying different powdery mildew resistance genes after inoculation with 15 isolates of *Blumeria graminis f. sp. tritici*

Cultivar/lines	*Blumeria graminis tritici* isolates, Bgt															*Pm gene*
	1	2	3	4	6	7	7-1	8	8-1	17	18	19	20	21	22	
Tabasco	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	*Pm46*
Ulka/8*Cc	R	R	S	S	R	R	R	R	R	R	R	R	R	S	S	*Pm2*
Ningnuo 1	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	–
Sumai 3	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	–

R resistant, *S* susceptible

identified but it was mapped at 84.6 cM away from *Pm46* in this study. *Pm-M53* (Li et al. 2010) was flanked by two SSR markers *Xwmc289* and *Xgwm292*. *Xwmc289* segregated in the F_2 population used in this study, but it was 72 cM from *Pm46*. These results indicated that *Pm46* is different from *Pm34, Pm35*, and *Pm-M53*. *Pm2* was a gene previously reported on 5DS (McIntosh and Baker 1970). A SSR marker *Xcfd81* was reported to be 2.0 cM away from *Pm2* (Qiu et al. 2006). Another PM resistant gene *PmD57-5D* was also reported on 5DS in common wheat (Ma et al. 2011) and was about 4.1 cM away from *Xcfd81*. Further evaluation of resistance for these two genes found that *PmD57-5D* and *Pm2* were more likely the same gene (Ma et al. 2011). To clarify the relationship between *Pm46* and *Pm2,* 15 Bgt isolates were tested for spectrum of pathogenicity of Tabasco (with *Pm46*) and Ulka/8*Cc (with *Pm2*). The results showed that the Tabasco was highly resistant to all 15 Bgt isolates, whereas Ulka/8*Cc was highly susceptible to 4 of them. This result suggested that *Pm46* is different from *Pm2*. And *Pm46* has a wide resistance spectrum than *Pm2*. Further allelism test using 536 F_2 plants derived from the cross of Tabasco × Ulka/8*Cc identified two susceptible plants after inoculating with Bgt2 isolate. These results confirm that *Pm46* was not allelic to *Pm2,* thus a novel gene for PM resistance.

Pm2 was a widely used and very effective resistance gene against PM in China and Europe (Bennett 1984; Liu et al. 2000). Due to long time deployment of the gene, the frequency of virulent isolates to *Pm2* is arising. Recently, its resistance has been overcome in some regions (Niewoehner and Leath 1998; Persaud and Lipps 1995; Parks et al. 2008). In this study, we also found virulent isolates to *Pm2* from Nanjing. Because *Pm46* was closely linked gene to *Pm2* and has a relatively broad resistance spectrum to different PM isolates, it has a great potential to be used in commercial breeding programs. Quick development of *Pm46* has several advantages. First, a high frequency of Pm2 in commercial cultivars suggests that *Pm2* is easily transferred into different wheat cultivars, thus we expect the same for *Pm46* because *Pm2* and *Pm46* are in similar chromosome location; second, Tabasco was a predominant cultivar grown in Germany, thus carries many desirable agronomic characteristics, such as semi-dwarf plant, good adaptation, and high yield potential. Thus, undesired linkage drag may not be expected when *Pm46* is transferred to local cultivars; third, the newly developed STS marker *Xmp510* is very close to the gene and is a useful marker for marker-assisted gene pyramiding to stack *Pm46* with other resistance genes to improve PM resistance in wheat; finally, Tabasco has a wide resistant spectrum and resistance to all Bgt isolates from Nanjing region. Thence, *Pm46* shows great promise to be used as an important PM resistance gene in wheat improvement.

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