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ORIGINAL PAPER

Identification and mapping of a new powdery mildew resistance gene on chromosome 6D of common wheat

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Abstract Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is one of the most serious wheat diseases. The rapid evolution of the pathogen's virulence, due to the heavy use of resistance genes, necessitates the expansion of resistance gene diversity. The common wheat line D57 is highly resistant to powdery mildew. A genetic analysis using an F_2 population derived from the cross of D57 with the susceptible cultivar Yangmai 158 and the derived $F_{2:3}$ lines indicated that D57 carries two dominant powdery mildew resistance genes. Based on mapping information of polymorphic markers identified by bulk segregant analysis, these two genes were assigned to chromosomes 5DS and 6DS. Using the $F_{2:3}$ lines that segregated in a single-gene mode, closely linked PCR-based markers were identified for both genes, and their chromosome assignments were confirmed through linkage mapping. The gene on chromosome 5DS was flanked by *Xgwm205* and *Xmag6176*, with a genetic distance of 8.3 cM and 2.8 cM, respectively. This gene was 3.3 cM from a locus mapped by the STS marker MAG6137, converted from the RFLP marker BCD1871, which was 3.5 cM from *Pm2*. An evaluation with 15 pathogen isolates indicated that this gene and *Pm2* were similar in their resistance spectra. The gene on chromosome 6DS was flanked by co-segregating *Xcfd80* and *Xmag6139* on one side and *Xmag6140* on the other, with a genetic distance of 0.7 cM and 2.7 cM, respectively. This is the first powdery mildew resistance gene identified on chromosome 6DS, and plants that carried this gene were highly resistant to all of the 15 tested pathogen isolates. This gene was designated *Pm45*. The new resistance gene in D57 could easily be transferred to elite cultivars due to its common wheat origin and the availability of closely linked molecular markers.

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Introduction

Common wheat (*Triticum aestivum* L.), one of the major staple food crops for humans, is under constant challenge from many pathogens. Powdery mildew, caused by *Blumeria graminis* f. sp *tritici* (Bgt), is a wheat foliar disease that occurs in regions with maritime and semi-continental climates and causes serious yield losses. With the employment of semi-dwarf and high-yielding varieties, together with the increased utilization of nitrogen fertilizer and the improvement of irrigation conditions, this disease has become one of the most severe wheat diseases in many wheat-growing regions (Bennett 1984). Among the measures for the control of wheat powdery mildew, breeding and utilization of disease-resistant varieties is the safest, most cost effective and environmentally friendly means.

In current wheat breeding programs, qualitative resistance, which is controlled by a single gene, is most widely utilized. Since the discovery of the dominant resistance gene *Pm1* in the common wheat cultivars Thew and Norka (Pugsley and Carter 1953), more than 70 resistance alleles, mapping to 43 loci, have been identified in the wheat genome, including the designated genes, *Pm1–Pm43*, and a few temporarily designated genes (McIntosh et al. 2009). Some of these genes have been successfully used in wheat

breeding programs. However, because qualitative resistance to powdery mildew is usually race-specific (Bennett 1984), a disadvantage of the extensive deployment of qualitative resistance genes is the rapid loss of resistance due to the co-evolution of the pathogen's virulence (McDonald and Linde 2002). Typical examples are the loss of resistance associated with *Pm2* and *Pm8* (Bennett 1984; Clarkson 2000; Huang et al. 1997b). In fact, virulent strains corresponding to many of the recognized powdery mildew resistance genes have been identified (Niewoehner and Leath 1998), which makes it a continuous challenge to discover new powdery mildew resistance genes.

Over the past decade, the availability of molecular markers has greatly accelerated the discovery of new powdery mildew resistance genes in various kinds of germplasm. With the help of molecular markers, more than 20 powdery mildew resistance genes, such as *Pm30* (Liu et al. 2002), *Pm31* (Xie et al. 2003), *Pm33* (Zhu et al. 2005), *Pm34* (Miranda et al. 2006), *Pm35* (Miranda et al. 2007), *PmY39* (Zhu et al. 2006), *PmY201* and *PmY212* (Sun et al. 2006), *PmU* (Qiu et al. 2005), *MlZec1* (Mohler et al. 2005), *Mlm2033*, *Mlm80* and *pm2026* (Yao et al. 2007; Xu et al. 2008), *PmLK906* (Niu et al. 2008) and *Pm43* (He et al. 2009), have been discovered and mapped. Moreover, molecular markers that are closely linked to these genes have greatly facilitated their utilization in breeding programs.

Common wheat and its close relatives are important sources of new resistance genes. Relative to genes in distant relatives, these genes can be directly and more easily introduced into elite cultivars through homologous recombination; their utilization is not or less limited by hybridization barriers and linkage drag. Here, we report the identification and characterization of a new powdery mildew resistance gene in a common wheat germplasm.

Materials and methods

Plant materials

The common wheat germplasm used in this study included the powdery mildew-resistant accessions, D57 and CI14118 (Ulka/8*Cc), and the powdery mildew-susceptible cultivars, Yangmai 158 and Sumai No. 3. CI14118 is a *Pm2* near-isogenic line developed using Ulka as the donor, and the susceptible cultivar chancellor as the recurrent parent (Briggle 1969). D57 is an indigenous germplasm introduced from Sichuan Academy of Agricultural Sciences with unknown pedigree. A total of 317 F_2 plants or the derived $F_{2:3}$ lines derived from the cross of Yangmai 158 × D57 were used for genetic analysis and six derived $F_{2:3}$ lines were used for mapping.

Resistance evaluation

The resistance spectrum evaluation was carried out using the detached leaf assay of Limpert et al. (1988), with some modification. Leaf segments of 2–3 cm, removed from the central part of the fully expanded primary leaves, were placed in plates containing 0.6% water agar (w/v) supplemented with 20 mg/L 6-benzylaminopurine. A set of 15 powdery mildew strains, isolated through a few rounds of single-spore separations from a Bgt mixture collected in different fields of the Nanjing area and maintained in the author's lab, was used in the inoculations. Disease symptoms were recorded 10 days after the inoculation using a scale from 0 to 5, as described by Yao et al. (2007), which represented the following: no visible symptoms, visible necrosis but without sporulation, sparse sporulation, moderate sporulation, abundant sporulation, and abundant sporulation, with more than 80% of the leaf area covered with mycelia.

Pathogen inoculation for genetic analysis was carried out by dusting Bgt conidia on one-leaf-stage plants that were grown in rectangular trays, as described by Xu et al. (2008). Two Bgt isolates, Bgt18 and Bgt19, avirulent to most of the powdery mildew resistance genes investigated on our lab, were used separately for this experiment. Sumai No. 3 and the susceptible parent were used as susceptible controls in each tray. After inoculation, the trays were placed in a growth chamber at over 80% relative humidity, and provided with 14 h of illumination and temperatures of 22°C/18°C for the day/night cycle. The disease symptoms were rated using the scale described above. The data were collected when the susceptible controls had a score of 4–5 (approximately 7 days after the inoculation).

Marker analysis

DNA was extracted from the tissues of young seedlings, following the procedures described by Ma et al. (1994). Equal amounts of DNA from 10 resistant and 10 susceptible F_2 plants derived from Yangmai 158 × D57 were combined, respectively, to produce the bulk DNA for bulk segregant analysis. DNA bulks of F_3 plants in $F_{2:3}$ families were prepared similarly for the polymorphic marker survey.

For the initial polymorphic marker survey, one simple sequence repeat (SSR) marker was chosen at approximately every 10 cM along the chromosome, according to the reported genetic maps for wheat, such as the NW map, ITMI map and consensus map (Somers et al. 2004; Song et al. 2005; Xue et al. 2008). PCR was performed in a PE9600 thermal cycler (Perkin Elmer, Norwalk, CT, USA) in a volume of 10 μl containing 10–20 ng template, 2 pmol each of the primers, 2 nmol each of the dNTPs, 15 nmol

MgCl2, 0.1 U Taq DNA polymerase and 1×PCR buffer. The PCR profile was as follows: one cycle of 94°C for 3 min; 35 cycles of 94°C for 30 s, 50–60°C (depending on the specific primers) for 30 s and 72°C for 50 s; and a final extension at 72°C for 5 min. The PCR products were separated in 8% non-denaturing polyacrylamide gels with a 19:1 or 39:1 acrylamide/bisacrylamide ratio and then silver-stained as described by Santos et al. (1993).

The RFLP marker BCD1871 that is linked to *Pm2*, seven expressed sequence tags (ESTs) mapping to the *Pm2*-containing chromosomal bin (including BE591275, BE498794, BE404603, BE5917, BE444854, BF201102 and BF484701), and the ESTs BG262421 and BE44520 mapping to the 6DS2 bin (Ma et al. 1994; Qi et al. 2004), were converted to sequence-tagged site (STS) markers. The primer sequences for these STS markers are listed in Table 1. The polymorphism survey was performed in a procedure similar to the SSR marker survey described above. When the STS markers of interest detected no polymorphism between the parents, restriction enzymes *Afa*I, *Alu*I, *Mbo*I, *Msp*I, *Hae*III, *Hind*III, *Sal*I and *Taq*I (TaKaRa Bio. Co. Ltd., Dalian, China) were selectively employed in the digestion of the PCR products. Each digestion was performed using a standard protocol in a 5 μl reaction mix with 0.05 μg DNA. The digested products were separated in 8% non-denaturing polyacrylamide gels.

Linkage Mapping

The software MAPMAKER Macintosh V2.0 (Lander et al. 1987) was used to construct linkage maps with the genetic distance calculated using the Kosambi function. A LOD score of 3.0 was used as the threshold for a declaration of linkage.

Results

Inheritance of the powdery mildew resistance in D57

One-hundred and forty-two F_2 plants, derived from the cross of Yangmai 158 × D57, and the parents were challenged with Bgt19. Seven days after the inoculation, Yangmai 158 and 12 of the F_2 plants had a disease score of 4; while the remaining plants were scored from 0 to 2, and most of these, including D57, had a score of 0. Of the 142 F_2 plants, 139 were grown to maturity and subjected to progeny testing. If plants with a score of 0–2 were viewed as resistant, and those with a score of 3–5 as susceptible, of the 11 $F_{2:3}$ lines derived from the susceptible F_2 plants, nine were homozygous susceptible, and two segregated. Of the 128 $F_{2:3}$ lines derived from the resistant F_2 plants, 60 were homozygous resistant, 67 were segregating and one was homozygous susceptible. Disagreement of the F_2 progeny test data with the F_2 data was noted for only three $F_{2:3}$ lines. The χ^2 test using the progeny test data showed that the powdery mildew resistance in the Yangmai 158 × D57 F_2 population segregated in a two dominant gene mode ($\chi^2_{7:8:1} = 0.212$). To confirm this result, another 175 $F_{2:3}$ lines were challenged with Bgt18. Seventy-two of them were homozygous resistant, 11 were homozygous susceptible and 92 were segregating. This again fitted the segregation mode of two independent, dominant resistance genes ($\chi^2_{7:8:1} = 0.504$). Thus, it was concluded that the common wheat accession D57 contains two independent, dominant resistance genes.

Chromosome assignment of the resistance genes through polymorphic marker survey

To determine the chromosomal locations of the two powdery mildew resistance genes in D57, the resistant and susceptible DNA bulks of the F_2 population as well as the parents, were initially surveyed using 412 SSR markers distributed throughout the entire genome. It was assumed that the resistant bulk DNA contained the two resistance genes, while the susceptible bulk DNA contained neither of them. The SSR markers BARC143 and BARC123 detected polymorphism between the parents and bulks (Fig. 1). Because BARC143 was described to detect loci on wheat chromosomes 3B and 5DS (Liu et al. 2005; Somers et al. 2004), and BARC123 detected loci on chromosomes 6D and 7B (Somers et al. 2004; Song et al. 2005), additional markers mapping close to *Xbarc143-3B*, *Xbarc143-5D*, *Xbarc123-6D* and *Xbarc123-7B* were surveyed. Markers CFD40, CFD67, CFD80, CFD81, CFD190, GDM108 and GWM205 detected polymorphism between the parents and the bulks. *Xcfd40*, *Xcfd67*, *Xcfd81* and *Xgwm205* have been

Table 1 STS markers developed from BCD1871 and three ESTs

Primer	Source	Forward (5′–3′)	Reverse (5′–3′)	Restriction enzymes detecting polymorphism
MAG6137	BCD1871	TTGGACTTCTGGAACAGTTGG	CTGCTATCCTTTGAGGCACC	/
MAG6139	BG262421	CACATTTCGCTATCTGGAGAGAAG	TAACCCCGCCTTTGTAGACTCG	*Rsa*I
MAG6140	BE445201	TCTTCCACCACCTGTCTTTCC	AGGCATCACCATCTTGCTTG	*Taq*I
MAG6176	BE498794	TCCATCCAAACATCCAATGC	CGTCACGCAAATCAGTCACTAAG	*Msp*I

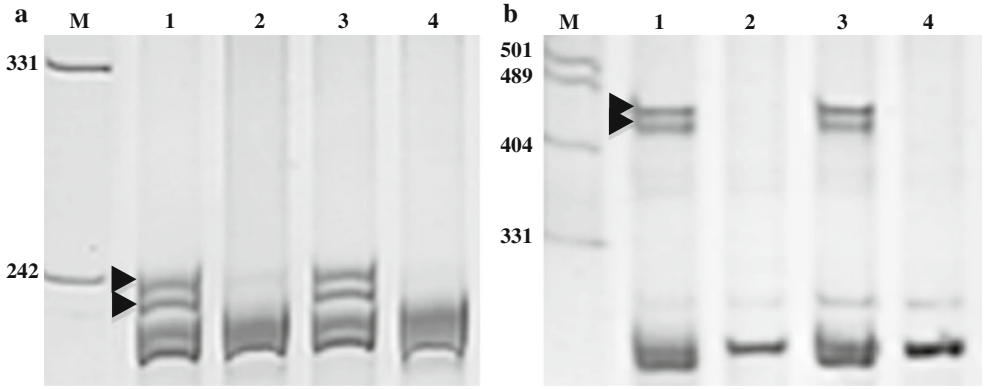

Fig. 1 Polymorphism between the parents and between the F_2 DNA bulks detected with SSR markers BARC143 (**a**) and BARC123 (**b**). Lanes *1*, *2*, *3* and *4* represent D57, Yangmai 158, resistant bulk DNA and susceptible bulk DNA, respectively. *M* size standard. The *numbers* to the *left* indicate the molecular size in bp. The *arrows* indicate the polymorphic bands

previously mapped to chromosome 5DS (Somers et al. 2004), and *Xcfd80*, *Xcfd190* and *Xgdm108* have been mapped to 6DS (Pestsova et al. 2000; Somers et al. 2004; Sourdille et al. 2004). These results implied that the two powdery mildew resistance genes in D57 likely reside on chromosomes 5DS and 6DS; thus, the genes were tentatively designated *PmD57-5D* and *PmD57-6D,* respectively.

Linkage maps of PmD57-5D and PmD57-6D

To construct the linkage maps of *PmD57-5D* and *PmD57-6D* with molecular markers, six $F_{2:3}$ lines showing the single-resistance gene segregation mode in the initial progeny tests were re-examined in a larger population size. As shown in Table 2, they all segregated for resistance in the one dominant gene mode, and the progeny test confirmed the results; therefore, they could be used for the linkage mapping.

Resistant and susceptible DNA bulks for each of the six lines were prepared and surveyed with the previously identified polymorphic markers. SSR markers BARC123, CFD80, CFD190 and GDM108 detected polymorphism between the DNA bulks derived from lines D57-9 and D57-10 in a pattern that was similar to that between the parents, but not between the DNA bulks derived from any of the other four lines. Thus, D57-9 and D57-10 were presumed to possess *PmD57-6D*. These four markers were used for mapping of *PmD57-6D*, using as the population a merger of the D57-9 and D57-10 lines (Table 2). We found that *PmD57-6D* was linked to all of these markers, with the closest, *Xcfd80*, at a distance of 0.7 cM (Fig. 2). Because these markers have been mapped to chromosome bin 6DS2 (Sourdille et al. 2004), STS markers MAG6139 and MAG6140, converted from EST sequences BG262421 and BE44520 mapping to this bin, were surveyed for polymorphism. After digestion of the PCR products using *Rsa*I and *Taq*I, a polymorphism was detected between the parents, as well as between the DNA bulks derived from line D57-9. Linkage mapping showed that *Xmag6139* and *Xmag6140* flanked *PmD57-6D* and, together with *Xcfd80,* were the loci most closely linked to the resistance gene (Fig. 2). This result confirmed that the gene resides on chromosome 6D.

Markers BARC143, CFD40, CFD67, CFD81 and GWM205 did not detect polymorphism between the DNA bulks derived from lines D57-9 and D57-10. However, CFD81 and GWM205 detected polymorphism between the

Table 2 The resistance segregation in six $F_{2:3}$ lines and their progenies

Line	Segregation ratio		Progeny test	
	R:S	$\chi^2_{(3:1)}$	RR:Rr:rr	$\chi^2_{(1:2:1)}$
D57-9	56:24	1.07	17:32:16	0.05
D57-10	63:25	0.55	16:42:21	0.95
D57-3*	55:13	1.25	–	–
D57-4	55:25	1.67	14:35:20	1.06
D57-28*	48:22	1.54	–	–
D57-148	71:21	0.23	30:31:15	8.5

* The progeny test was not conducted

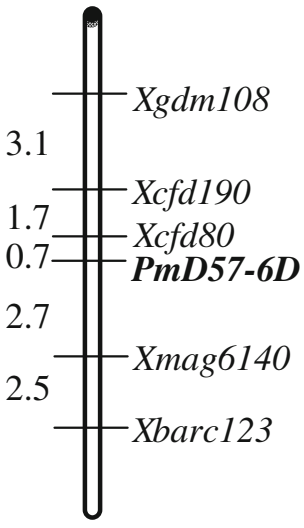

Fig. 2 The linkage map of *PmD57-6D*. The *genetic distance* is shown to the *left* of the map in cM. The *black oval* points to the telomere

DNA bulks derived from each of the remaining four $F_{2:3}$ lines, implying these four lines segregated for *PmD57-5D*. BARC143, CFD40 and CFD67 detected polymorphism between the DNA bulks derived from lines D57-3 and D57-28, but not between the DNA bulks derived from lines D57-4 and D57-148, indicating that recombination had occurred between them and *PmD57-5D*.

The linkage relationship of *Xcfd81* and *Xgwm205* with *PmD57-5D* was established using the population as a merger of lines D57-4 and D57-148 (Table 2). *Xcfd81* showed the closest linkage to the resistance gene with a distance of 4.1 cM (Fig. 3a). *Xcfd81* maps to chromosome bin 5DS5 and is linked to powdery mildew resistance gene *Pm2* by a distance of 2.0 cM (Qiu et al. 2006). Thus, to identify markers that are more closely linked, STS markers MAG6137, converted from RFLP marker BCD1871, which is closely linked to *Pm2* (Ma et al. 1994), and MAG6176, converted from the EST BE498794 that maps to the 5DS5 bin, were surveyed for polymorphism. Both markers detected polymorphic loci between the parents and the DNA bulks derived from line D57-4, either directly or after *Msp*I digestion (of the MAG6176 amplification products). *Xmag6176* was 2.8 cM away from *PmD57-5D*; *Xmag6137* was 3.3 cM from *PmD57-5D*, similar to that of *Xbcd1871* from *Pm2* (Fig. 3).

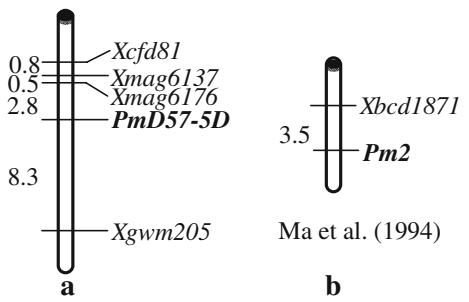

Fig. 3 Linkage maps of *PmD57-5D* (**a**) and *Pm2* (**b**). The *genetic distance* was shown to the *left* of the map in cM. The *black ovals* point to the telomeres

The resistance spectra of PmD57-5D and PmD57-6D

To examine the resistance spectra of *PmD57-5D* and *PmD57-6D,* D57, CI14118, and lines homozygous for *PmD57-5D* or *PmD57-6D* were challenged with 15 Bgt isolates (Table 3). Disease reaction of the line with *PmD57-6D* was basically similar to D57, showing necrosis 10 days after the inoculation with 14 of the 15 isolates. It differed from CI14118 by six of the 15 isolates. The resistance of CI14118 was completely overcome by four of the isolates, while the line with *PmD57-6D* (D57-6D) was resistant to them, with only necrosis observed (Table 3, Fig. 4). The line with *PmD57-5D* (D57-5D) was similar to CI14118 in its resistance spectrum (Table 3). Interestingly, when challenged with Bgt 17, both the D57-5D line and D57-6D line showed necrosis on the leaves, while D57 was immune to this isolate (Fig. 4), suggesting that *PmD57-5D* and *PmD57-6D* were cumulative in conferring the resistance.

Discussion

D57 is a common wheat germplasm, and showed resistance to all of the tested Bgt isolates. In the fields of Nanjing Agricultural University Experimental Station, it showed powdery mildew resistance during the entire growing stage when susceptible cultivars such as Sumai No. 3 and Yangmai 158 had disease ratings of 4–5, suggesting that it is a valuable source for powdery mildew resistance breeding. Genetic analyses on the F_2 population derived from the cross of D57 with the susceptible cultivar Yangmai 158, coupled with the progeny test, showed that it carries two dominant resistance genes. Using $F_{2:3}$ lines that showed single resistance gene segregation as mapping populations, one of the resistance genes was mapped to chromosome 5DS, and the other was mapped to 6DS.

PmD57-5D was mapped to the same position on 5DS as *Pm2*, based on linkage with the distal marker *Xbcd1871* or

Table 3 Reactions of *D57*, lines with *PmD57-5D* (D57-5D) and *PmD57-6D* (D57-6D), and CI14118 to infection of 15 Bgt isolates

Line	Bgt isolates														
	1	2	3	4	6	7	7-1	8	8-1	17	18	19	20	21	22
D57	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
D57-6D	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D57-5D	1	1	5	5	1	1	1	1	2	1	1	2	1	5	5
CI14118 (*Pm2*)	1	1	5	5	1	1	1	1	2	1	1	2	1	5	5

0 represents no visible symptoms, *1* represents visible necrosis but without sporulation, *2* represents sparse sporulation and *5* represents abundant sporulation

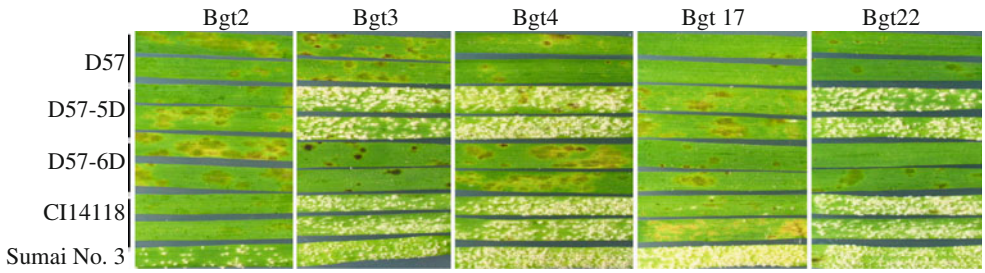

Fig. 4 The reactions of D57, lines containing *PmD57-5D* or *PmD57-6D*, CI14118 (*Pm2*) and Sumai No. 3 to infections of five different Bgt isolates

Xmag6137 (Fig. 3). Moreover, the D57-5D line and CI14118, the *Pm2* near isogenic line, had a similar resistance spectrum with the 15 Bgt isolates tested. We did note subtle variations in the reactions of these two lines to some of the isolates (Fig. 4), which might indicate that *PmD57-5D* and *Pm2* are two different alleles, but it is more likely that the differences in the genetic background caused the variations. Therefore, *PmD57-5D* was considered to be *Pm2*.

Pm2 is a widely utilized powdery mildew resistance gene and is present in many wheat varieties (Bennett 1984; Huang et al. 1997b; Lutz et al. 1995; Lutz et al. 1992; Paderina et al. 1995). However, the resistance conferred by this gene is no longer effective due to the presence of virulence in many geographic areas (Niewoehner and Leath 1998; Parks et al. 2008; Persaud and Lipps 1995; Duan et al. 2002). Although *Pm2* can no longer be used as the major resistance contributor, it may still be useful in combination with other resistance genes. Such a pyramid-like effect was illustrated after inoculation with Bgt17, D57 displayed an immune phenotype, while the lines with *PmD57-6D* displayed symptoms of necrosis (Fig. 4).

PmD57-6D is the first powdery mildew resistance gene reported on chromosome arm 6DS. *Pm24* was initially mapped to chromosome 6D (Huang et al. 1997a) but was reassigned to chromosome 1D (Huang et al. 2000). Thus, *PmD57-6D* was designated *Pm45*. We found that the lines carrying *Pm45* gave hypersensitive responses to all of the 15 tested Bgt isolates and had almost the same phenotypes as D57, with only a single exception. This result indicates that *Pm45* conferred effective seedling resistance to powdery mildew isolates collected in the Nanjing area. The common wheat origin of *Pm45* and the availability of PCR-based, closely linked flanking markers, such as *Xcfd80*, *Xmag6139* and *Xmag6140*, make it an ideal resistance gene for wheat breeding programs.

Seven powdery mildew resistance genes, including *Pm11*, *Pm12*, *Pm14*, *Pm20*, *Pm21*, *Pm27* and *Pm31,* have been identified in wheat homoeologous chromosome group 6. Unlike *Pm45*, *Pm20* maps to the long arm of chromosome 6R through the T6BS.6RL translocation line (Friebe et al. 1994), and *Pm31,* originating from wild emmer wheat, maps to the long arm of chromosome 6A (Xie et al. 2003). Based on their positions, *Pm20* and *Pm31* are obviously not orthologues of *Pm45*. The relationship of the remaining five genes to *Pm45* could not be determined with the current knowledge available. Both *Pm11* and *Pm27* are located on the short arm of chromosome 6B (Tosa et al. 1988; Järve et al. 2000). *Pm14* is located on chromosome 6B (Tosa et al. 1987). *Pm12* was transferred from chromosome 6S of *Aegilops speltoides* (Jia et al. 1996; Miller et al. 1988), and *Pm21* was transferred from chromosome 6 V of *Haynaldia villosa* (Chen et al. 1995). The discovery of *Pm45* has expanded the diversity of the powdery mildew resistance genes, which will be useful for dissecting resistance mechanisms and for wheat breeding, especially for gene pyramiding-based resistance breeding.

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