Journal of Integrative Agriculture 2015, 14(4): 603–609

Available online at www.sciencedirect.com

ScienceDirect

RESEARCH ARTICLE

Comparative genetic mapping revealed powdery mildew resistance gene *MlWE4* derived from wild emmer is located in same genomic region of *Pm36* and *Ml3D232* on chromosome 5BL

ZHANG Dong, OUYANG Shu-hong, WANG Li-li, CUI Yu, WU Qiu-hong, LIANG Yong, WANG Zhen-zhong, XIE Jing-zhong, ZHANG De-yun, WANG Yong, CHEN Yong-xing, LIU Zhi-yong

State Key Laboratory for Agrobiotechnology/Beijing Key Laboratory of Crop Genetic Improvement/Key Laboratory of Crop Heterosis Research & Utilization, Department of Plant Genetics & Breeding, China Agricultural University, Beijing 100193, P.R.China

Abstract

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is one of the most devastating wheat diseases. Wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*) is a promising source of disease resistance for wheat. A powdery mildew resistance gene conferring resistance to *B. graminis* f. sp. *tritici* isolate E09, originating from wild emmer wheat, has been transferred into the hexaploid wheat line WE4 through crossing and backcrossing. Genetic analyses indicated that the powdery mildew resistance was controlled by a single dominant gene, temporarily designated *MlWE4*. By mean of comparative genomics and bulked segregant analysis, a genetic linkage map of *MlWE4* was constructed, and *MlWE4* was mapped on the distal region of chromosome arm 5BL. Comparative genetic linkage maps showed that genes *MlWE4*, *Pm36* and *Ml3D232* were co-segregated with markers *XBD37670* and *XBD37680*, indicating they are likely the same gene or alleles in the same locus. The co-segregated markers provide a starting point for chromosome landing and map-based cloning of *MlWE4*, *Pm36* and *Ml3D232*.

Keywords: wild emmer, powdery mildew resistance gene, *Pm36*, comparative genomics

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important food crops in many parts of the world, providing about one-fifth of the calories consumed globally (FAO 2011). Wheat powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is a serious disease worldwide, especially in humid areas, which results in partial or total loss of grain yield on susceptible cultivars when climatic conditions are favorable. The most effective strategy for controlling powdery mildew is to make full use of resistance cultivars. Identification of powdery mildew resistance genes and reliable molecular markers are essential for developing powdery mildew resistance cultivars using marker assisted selection (MAS) approach in wheat breeding program.

Wild emmer (*T. turgidum* var. *dicoccoides*, 2n=4x=28, AABB), which shares the same genomes as durum wheat (*T. durum* Desf.) and contributes two genomes to bread wheat, is the progenitor of cultivated wheat. It possesses many important beneficial traits, including powdery mildew resistance. To date, more than 60 genes/alleles for resis-

Received 26 February, 2014 Accepted 23 April, 2014
Correspondence LIU Zhi-yong, Tel: +86-10-62731211, E-mail: zhiyongliu@cau.edu.cn

doi: 10.1016/S2095-3119(14)60774-7

tance to powdery mildew have been identified at 46 loci (*Pm1 to Pm50*, *Pm18=Pm1c*, *Pm22=Pm1e*, *Pm23=Pm4c*, *Pm31=Pm21*) on 20 different chromosomes (McIntosh *et al.* 2013). Twelve of these genes/alleles originated from wild emmer, including *Pm16* (Reader and Miller 1991), *Pm26* (Rong *et al.* 2000), *Pm30* (Liu *et al.* 2002), *MlZec1* (Mohler *et al.* 2005), *MlIW72* (Ji *et al.* 2008), *Pm36* (Blanco *et al.* 2008), *Pm41* (Li *et al.* 2009), *Pm42* (Hua *et al.* 2009), *PmG16* (Ben-David *et al.* 2010), *Ml3D232* (Zhang H T *et al.* 2010), *MlIW170* (Liu *et al.* 2012), *PmAS846* (Xue *et al.* 2012), and *PmG3M* (Xie *et al.* 2012).

Molecular markers are powerful tools to identify parts of DNA that are located near a gene of interest. Restriction fragment length polymorphisms (RFLP), simple sequence repeats (SSR), random amplified polymorphisms DNA (RAPD), sequence tagged site (STS), and amplified fragment length polymorphisms (AFLP) have been used to map more than 30 powdery mildew resistance genes. However, a saturated genetic map with co-segregated or tightly linked markers is necessary for map-based cloning and MAS of the targeted gene.

Mapping and cloning genes from plant genomes largely depend on the availability of a reference genome. Up to date, genome sequences of major grass species, including rice (*Oryza sativa*), maize (*Zea mays*), sorghum (*Sorghum bicolor*), and *Brachypodium distachyon* are available (International Rice Genome Sequencing Project 2005; Paterson *et al.* 2009; Schnable *et al.* 2009; International *Brachypodium* Initiative 2010). High levels of collinearity have been detected among the grass family (Devos and Gale 1997). The genome sequences of rice, sorghum, maize and *Brachypodium* are very useful in developing molecular markers linked to wheat genes by performing comparative genomic analysis. Recently, the shotgun draft sequences of hexaploid wheat Chinese Spring (Brenchley *et al.* 2012), *Triticum urartu* (Ling *et al.* 2013), *Aegilops tauschii* (Jia *et al.* 2013), and individual flow-sorted bread wheat Chinese Spring chromosome arms sequences (http://www.wheatgenome.org) have been released, providing more information to develop tightly linked or even co-segregated markers for a particular gene.

In this paper, we have described the identification and genetic mapping of a powdery mildew resistance gene *MlWE4* derived from wild emmer and comparative genetic mapping of *MlWE4*, *Pm36* and *Ml3D232* located on chromosome arm 5BL.

2. Results

2.1. Genetic analysis of the powdery mildew resistance

Lines WE4, 5BIL-29 (*Pm36*) and 3D232 were highly resistant to *Bgt* isolate E09 (IT 0) whereas Xuezao, 81086A, 87-1, and Yumai 18 were highly susceptible (IT 4). The F_1 seedlings of 81086A/5BIL-29, Xuezao/WE4, and Xuezao/3D232 were resistant (IT 0), indicating dominant nature of the resistance genes in WE4, 5BIL-29 and 3D232. The F_2 populations segregated as 106 resistant:31 susceptible for 81086A/5BIL-29, 116 resistant:46 susceptible for Xuezao/WE4 and 477 resistant:153 susceptible for Xuezao/3D232, fitting the 3:1 single Mendelian loci ratio (Table 1). The F_3 progenies were classified as 40 homozygous resistant:76 segregating, and 46 homozygous susceptible for Xuezao/WE4, 33 homozygous resistant:73 segregating, and 31 homozygous susceptible for 81086A/5BIL-29, and 157 homozygous resistant:320 segregating, and 153 homozygous susceptible for Xuezao/3D232, fitting the expected 1:2:1 ratio of single gene segregation ratio (Table 1). The powdery mildew resistance gene in WE4 was temporarily designated *MlWE4*.

2.2. Identification of molecular markers linked to *MlWE4*

Wheat SSR and expressed sequence tag (EST) markers were tested for polymorphisms between Xuezao and WE4 as well as the resistant and susceptible F_2 DNA bulks. Five markers, *Xgwm499*, *Xgwm639*, *XFCP1*, *XCD862323*, and *XCJ832481* were polymorphic between Xuezao and WE4, as well as the resistant and susceptible DNA bulks and could be linked to *MlWE4* after genotyping the 162 individual F_2 plants. *MlWE4* was co-segregated with EST marker *XCJ832481* (*XBD37680*) and flanked by markers *XCD862323* (*XBD37380*) and *XFCP1* (Fig. 1). Both *XCD862323* (Zhang H T *et al.* 2010) and *XFCP1* (Lu and Faris 2006) have been mapped to the deletion bin 5BL 0.75–0.76, indicating that *MlWE4* is also located in the same chromosome bin interval.

2.3. Comparative genomics analysis of the *MlWE4* genomic region

The EST marker *XBJ261635* was tightly linked to *Pm36* (Blanco *et al.* 2008) and *XCJ832481* was tightly linked to *Ml3D232* (Zhang H T *et al.* 2010) and *MlWE4*. Both *BJ261635* and *CJ832481* are orthologous to *Brachypodium* gene *Bradi4g37680*. The SSR marker *XFCP1* (Faris *et al.* 2010) was derived from BAC 1154L7 that is tightly linked to the homologous of *Brachypodium* gene *Bradi4g37980*. The EST *CD862323* is orthologous to *Brachypodium* gene *Bradi4g37380*. In order to develop a high-density genetic linkage map of *MlWE4*, the 450-kb genomic region from *Bradi4g37380* to *Bradi4g37980* in *Brachypodium* was selected for comparative genomic analyses with rice and

Table 1 Genetic analysis of powdery mildew resistance genes *MlWE4*, *Pm36* and *Ml3D232*[1)]

Mapping population	Resistance	Susceptible	Total	χ^2	$\chi^2_{0.05}$
WE4	20				
Xuezao		20			
Xuezao/WE4	20				
Xuezao/WE4 F_2	116	46	162	0.32	3.84
Xuezao/WE4 F_3	40(A)+76(H)	46(B)	162	0.59	5.99
5BIL-29 (*Pm36*)	20				
81086A		20			
81086A/*Pm36* F_1	20				
81086A/*Pm36* F_2	106	31	137	0.41	3.84
81086A/*Pm36* F_3	33(A)+73(H)	31(B)	137	0.65	5.99
3D232	20				
Xuezao		20			
Xuezao/3D232	20				
Xuezao/3D232 F_2	477	153	630	0.17	3.84
Xuezao/3D232 F_3	157(A)+320(H)	153(B)	630	0.21	5.99

[1)] A, H and B represent homozygous resistance, heterozygous and homozygous susceptible, respectively.

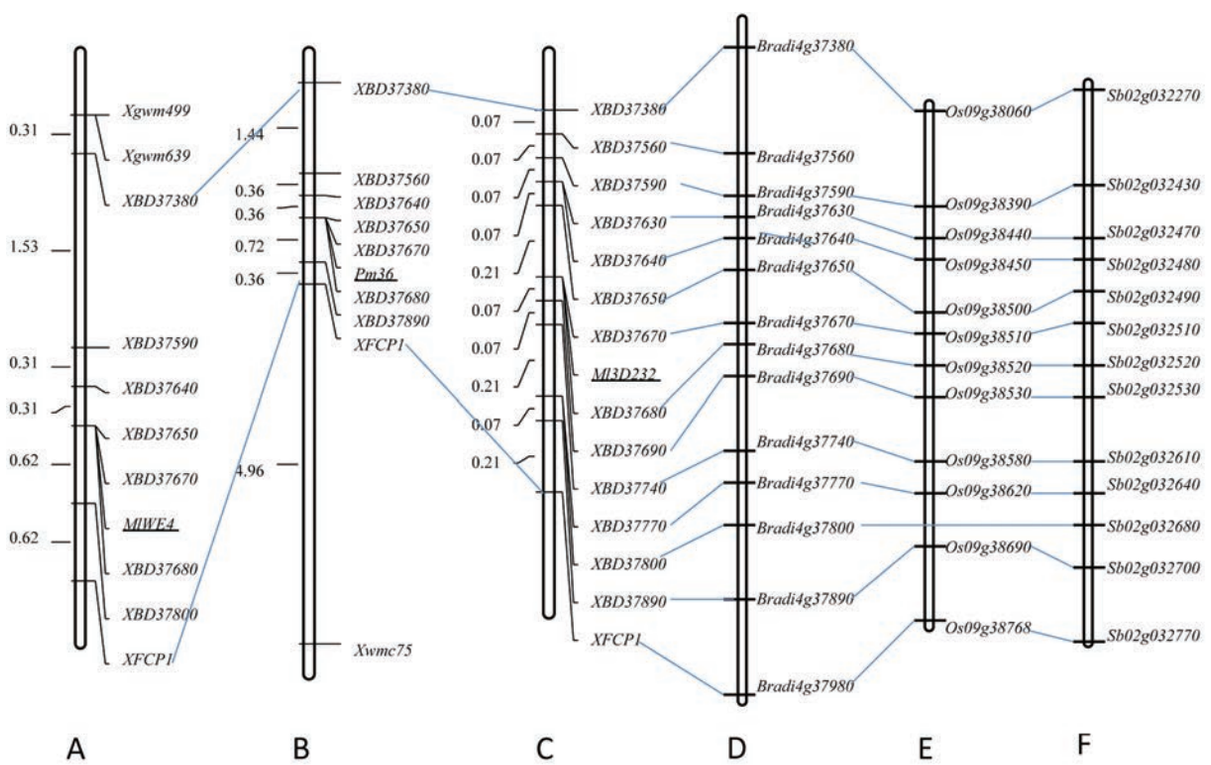

Fig. 1 Comparative genetic and genomics linkage map of powdery mildew resistance genes *MlWE4*, *Pm36*, and *Ml3D232* on wheat chromosome 5BL. The *MlWE4* (A), *Pm36* (B) and *Ml3D232* (C) loci are in underline with genetic distances in cM shown on the left, and markers shown on the right. The markers served as anchors, establishing colinearity between the genetic map and the genes of *Brachypodium*, rice and sorghum, are connected with solid lines. The orthologous genomic region of *Brachypodium* chromosome 4 (450 kb) with putative genes on the left (D). The orthologous genomic region of rice chromosome 9 (347 kb) with putative genes on the right (E). The orthologous genomic region of sorghum chromosome 2 (370 kb) with putative genes on the right (F). Bd4, Os9 and Sb2 represent *Brachypodium* chromosome 4, rice chromosome 9 and sorghum chromosome 2, respectively.

sorghum using the OrthoMCL platform (http://orthomcl.org). Conserved collinearity was observed between genomic regions of *Brachypodium Bradi4g37380*–*Bradi4g37980*, rice *Os09g38060*–*Os09g38770* (347 kb), and sorghum *Sb02g032270*–*Sb02g032770* (370 kb). In the corresponding genomics regions, 38 of 61 predicted *Brachypodium* genes are orthologs to 35 of 72 predicted rice genes and 35 of 51 predicted sorghum genes. There are 32 ortholo-

gous gene pairs among rice, *Brachypodium* and sorghum (Table 2), indicating highly micro-colinearity of gene orders in those genomic regions among the three species.

2.4. Comparative genetic mapping of *MlWE4*, *Pm36* and *Ml3D232*

Since powdery mildew resistance genes *Pm36* and *Ml3D232* were also derived from wild emmer and mapped on chromosome 5BL, molecular markers linked to *MlWE4* were tested in the segregating populations of 81086A/5BIL-29 (*Pm36*) and Xuezao/3D232 (*Ml3D232*). The putative orthologous genes with the same order and high level of synteny among *Brachypodium*, rice and sorghum are likely to have the same order and synteny as those of the wheat genes on chromosome 5BL, and these were preferentially used to develop molecular markers linked to *MlWE4*, *Pm36* and *Ml3D232*. After screening 75 intron-flanking primer pairs and 10 SSR primer pairs, polymorphic markers were developed and integrated into the genetic linkage maps of *MlWE4*, *Pm36* and *Ml3D232* (Fig. 1). The *MlWE4*, *Pm36* and *Ml3D232* were mapped in the same genetic interval and co-segregated with markers *XBD37670* and *XBD37680* (Fig. 1).

3. Discussion

3.1. Comparison of *MlWE4* with other powdery mildew resistance genes derived from wild emmer

Wild emmer is an important germplasm for diversified powdery mildew resistance genes. More than 13 alleles in 8 loci conferring powdery mildew resistance have been identified from wild emmer and mapped in 7A, 2B, 3B, 5B, and 6B chromosomes (Reader and Miller 1991; Rong *et al.* 2000; Liu *et al.* 2002, 2012; Mohler *et al.* 2005; Blanco *et al.* 2008; Ji *et al.* 2008; Hua *et al.* 2009; Li *et al.* 2009; Ben-Davis *et al.* 2010; Zhang H T *et al.* 2010; Xie *et al.* 2012; Xue *et al.* 2012). Among them, *Pm36*, *Ml3D232* and *PmAs846* were mapped within the same genetic interval of the chromosome arm 5BL (Blanco *et al.* 2008; Zhang H T *et al.* 2010; Xue *et al.* 2012).

Comparative genetic linkage maps of *MlWE4*, *Pm36* and

Table 2 Colinearity between wheat, *Brachypodium*, rice, and sorghum in the syntenic genomic region

Wheat markers	*Brachypodium*	Rice	Sorghum	Wheat markers	*Brachypodium*	Rice	Sorghum
XBD37380	Bradi4g37380	Os09g38060	Sb02g032270	XBD37690	Bradi4g37690	Os09g38530	Sb02g032530
	Bradi4g37390	Os09g38070	Sb02g032280		Bradi4g37700	Os09g38540	Sb02g032540
	Bradi4g37400		Sb02g032290		Bradi4g37710	Os09g38550	
	Bradi4g37410	Os09g38090	Sb02g032300		Bradi4g37720	Os09g38560	Sb02g03 2580
	Bradi4g37420	Os09g38100	Sb02g032310		Bradi4g37730	Os09g38570	Sb02g032600
	Bradi4g37430	Os09g38110	Sb02g032320	XBD37740	Bradi4g37740	Os09g38580	Sb02g032610
	Bradi4g37440				Bradi4g37750		Sb02g032620
	Bradi4g37450	Os09g38130	Sb02g032330		Bradi4g37760	Os09g38610	Sb02g032630
	Bradi4g37460			XBD37770	Bradi4g37770	Os09g38620	Sb02g032640
	Bradi4g37470				Bradi4g37780	Os09g38630	
	Bradi4g37480				Bradi4g37790	Os09g38650	Sb02g032660
	Bradi4g37490	Os09g38300	Sb02g032340	XBD37800	Bradi4g37800		Sb02g032680
	Bradi4g37500	Os09g38310	Sb02g032350		Bradi4g37810		
	Bradi4g37510				Bradi4g37820		
	Bradi4g37520	Os09g38320	Sb02g032370		Bradi4g37830		
	Bradi4g37530	Os09g38330	Sb02g032380		Bradi4g37840		
	Bradi4g37540	Os09g38340	Sb02g032400		Bradi4g37850		
	Bradi4g37550				Bradi4g37860		
XBD37560	Bradi4g37560				Bradi4g37870		
	Bradi4g37570	Os09g38350			Bradi4g37880		
	Bradi4g37580	Os09g38370	Sb02g032420	XBD37890	Bradi4g37890	Os09g38690	Sb02g032700
XBD37590	Bradi4g37590	Os09g38390	Sb02g032430		Bradi4g37900		
	Bradi4g37600				Bradi4g37910	Os09g38710	Sb02g032725
	Bradi4g37610	Os09g38410	Sb02g032440		Bradi4g37920	Os09g38720	Sb02g032730
	Bradi4g37620	Os09g38420	Sb02g032450		Bradi4g37930	Os09g38740	Sb02g032740
XBD37630	Bradi4g37630	Os09g38440	Sb02g032470		Bradi4g37940		
XBD37640	Bradi4g37640	Os09g38450	Sb02g032480		Bradi4g37950	Os09g38750	Sb02g032750
XBD37650	Bradi4g37650	Os09g38500	Sb02g032490		Bradi4g37960	Os09g38755	Sb02g032760
	Bradi4g37660				Bradi4g37970		
XBD37670	Bradi4g37670	Os09g38510	Sb02g032510		Bradi4g37980	Os09g38768	Sb02g032770
XBD37680	Bradi4g37680	Os09g38520	Sb02g032520				

Ml3D232 revealed that these genes are located in the same genetic interval co-segregated with markers *XBD37670* and *XBD37680*. The EST marker *XBJ261635*, homologous to *Brachypodium* gene *Bradi4g37680*, was also tightly linked to *PmAS846* (Xue *et al.* 2012). Both *Ml3D232* (Zhang H T *et al.* 2010) and *PmAS846* (Xue *et al.* 2012) provide a broad-spectrum of resistance to 21 *Bgt* isolates collected from different regions of China. These *Bgt* isolates were also used to test the reactions of *Pm36* and *MlWE4*. Both *Pm36* and *MlWE4* showed same resistance reaction patterns as that of *Ml3D232* and *PmAS846*, indicating that *Ml3D232*, *PmAS846*, *Pm36*, and *MlWE4* are most likely the same gene or different alleles in the same locus.

3.2. Micro-collinearity of the *Pm36* genomic region in *Brachypodium*, rice and sorghum

Recently, the colinearity among the wheat, sorghum, rice and *Brachypodium* genomes has been exploited for saturation and fine mapping genes in wheat, such as *Lr34/Yr18* (Spielmeyer *et al.* 2008), *H26* (Yu *et al.* 2009), *Eps1* (Faricelli *et al.* 2010), *Sr35* (Zhang W J *et al.* 2010), *Ml3D232* (Zhang H T *et al.* 2010), *Cdu1* (Wiebe *et al.* 2010), *Snn3-D1* (Zhang *et al.* 2011), *MlIW170* (Liu *et al.* 2012), and *PmAS846* (Xue *et al.* 2012). Comparative analysis of the *Tsn1* genomic region of wheat chromosome 5B with the homologous region of rice and *Brachypodium* indicated a conserved level of colinearity with rice chromosome 9 and *Brachypodium* chromosome 4, fascinating the map-based cloning of *Tsn1* (Faris *et al.* 2010).

In this study, 12 polymorphic markers linked to *Ml3D232* were developed and integrated into the genetic linkage map of *Ml3D232*. High level of synteny in gene order was observed between wheat and *Brachypodium* (*Bradi4g37380*–*Bradi4g37980*) in the *Pm36* and *Ml3D232* genomic region. The *Ml3D232* was narrowed to a 0.14-cM genetic interval flanked by markers *XBD37650* and *XBD37690* and co-segregated with *XBD37670* and *XBD37680*. Sequence annotations revealed no resistance gene analog (RGA) appeared in *Brachypodium* between *Bradi4g37650* to *Bradi4g37690*. Since there is still no assembled reference genome sequences available for wheat (Brenchley *et al.* 2012; Ling *et al.* 2013; Jia *et al.* 2013), the *MlWE4/Ml3D232/Pm36* co-segregated markers *XBD37670* and *XBD37680* could serve as a starting point for chromosome landing and toward map-based cloning of the powdery mildew resistance gene locus.

4. Materials and methods

4.1. Plant materials

Wild emmer accession G-84-1M, kindly provided by Dr. Gerechter-Amitai Z K of the Agricultural Research Organization, the Volcani Center, Israel and highly resistant to a local prevailing *Bgt* isolate E09 at Beijing, China, was used as resistance gene donor. Line WE4 is a powdery mildew resistance derivative of G-84-1M crossed with a common wheat line 87-1 followed by 6 times of backcrossing with Yumai 18, a widely cultivated elite cultivar in Henan Province, China. Both 87-1 and Yumai 18 were highly susceptible to the *Bgt* E09. Line WE4 was crossed with a highly susceptible common wheat line Xuezao to develop a population for mapping the powdery mildew resistance gene in WE4. A reconstructed mapping population of *Ml3D232* (Zhang H T *et al.* 2010) was also used for comparative linkage map construction.

Durum wheat line 5BIL-29 (*Pm36*), kindly provided by Dr. Antonio Blanco of the University of Bari, Italy, was crossed with durum wheat line 81086A to develop a mapping population for comparative analysis of *Pm36* and the powdery mildew resistance gene in WE4.

4.2. Evaluation of powdery mildew resistance

B. graminis f. sp. *tritici* isolate E09, kindly provided by Dr. Duan Xiayu of the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, was used for evaluation of powdery mildew reactions of the parental lines and mapping populations. Isolate E09 was virulent on powdery mildew resistance genes *Pm1*, *Pm3a*, *Pm3c*, *Pm5*, *Pm7*, *Pm8*, *Pm17*, and *Pm19* (Zhou *et al.* 2005) and Xuezao, but avirulent on lines WE4, 3D232 and 5BIL-29. Xuezao was also used for the live production and preservation of the *Bgt* pathogen. Seedlings of Xuezao, WE4, 87-1, Yumai 18, 5BIL-29, 81086A, and 3D232 were inoculated with E09 by brushing conidia from neighbor sporulating susceptible seedlings of Xuezao onto the tested seedlings when the first leaf was fully expanded in the controlled greenhouse conditions. Infection types (IT) were scored 15–18 days after inoculation when the control (Xuezao) was heavily infected using a scales of 0, 0;, 1, 2, 3, and 4 (Liu *et al.* 2002). Thirty plants per line and F_3 lines of the mapping populations were tested. Phenotypes were classified into two groups, resistant (R, IT 0–2) and susceptible (S, IT 3–4).

4.3. DNA extraction and molecular marker analysis

Genomic DNA was extracted from the uninfected seedling leaves of each F_2 plant by the CTAB method (Allen *et al.* 2006). For bulked segregant analysis (Michelmore *et al.* 1991), equal amounts of DNA samples from 10 homozygous resistant and 10 homozygous susceptible F_3 families were pooled respectively for polymorphic marker screening with wheat SSRs (*Xgwm*, *Xwmc*, *Xbarc*, and *Xcfd* series;

GrainGenes website http://wheat.pw.usda.gov) and expressed sequence tags (EST) (http://wheat.pw.usda.gov/SNP/primers/contig_primer_list.xls).

Polymerase chain reaction (PCR) amplifications were carried out in a 10-μL reaction volume under the following conditions: 94°C for 5 min, followed by 35 cycles at 94°C for 45 s, 50–60°C (depending on annealing temperature of the primer pair) for 45 s, and 72°C for 60 s, with a final extension at 72°C for 10 min. PCR products mixed with 2 μL of loading buffer were separated on 8% non-denaturing polyacrylamide gels with a 39:1 of acrylamide:bisacrylamide and 1× TBE buffer. PCR products were visualized with silver staining and photographed.

4.4. Comparative genomic analysis and marker design

The corresponding sequences of polymorphic EST markers were used to perform a BLAST search against the genome sequences of *Brachypodium*, rice and sorghum to identify orthologous gene pairs. The orthologous genomic regions were identified through comparative genomics analysis of the putative highly conserved gene pairs in *Brachypodium*, rice and sorghum. The putative gene pairs with high level of collinearity among *Brachypodium*, rice and sorghum were preferentially used to search homologous wheat sequences to develop new polymorphic markers. Amplicons targeted the intronic sequences between two exons were preferred to be tested to find more polymorphisms. Intron-flanking primers were designed based on the intron/exon information of wheat sequences using BatchPrimer3 (You *et al.* 2008).

4.5. Data analysis

Chi-squared (χ^2) tests for goodness-of-fit were used to test for deviation of observed data from theoretically expected segregation ratios. Linkage analysis of markers and the resistance genes were conducted using Mapmaker 3.0 software with a LOD score threshold of 3.0 (Lander *et al.* 1987).

Acknowledgements

This work was financially supported by the National High-Tech R&D Program of China (2011AA100104), the National Basic Research Program of China (2013CB127705), the National Natural Science Foundation of China (31030056, 31210103902), and the Introducing Talents of Disciplines to Universities, Ministry of Education (MOE) of China (111-02-3).

References

Allen G C, Flores-Vergara M A, Krasynanski S, Kumar S. 2006. A modified protocol for rapid DNA isolation from plant tissues using cetyltrimethylammonium bromide. *Nature Protocols*, **1**, 2320–2325.

Ben-David R, Xie W, Peleg Z, Saranga Y, Dinoor A, Fahima T. 2010. Identification and mapping of *PmG16*, a powdery mildew resistance gene derived from wild emmer wheat. *Theoretical and Applied Genetics*, **121**, 499–510.

Blanco A, Gadaleta A, Cenci A, Carluccio A V, Abdelbacki A M, Simeone R. 2008. Molecular mapping of the novel powdery mildew resistance gene *Pm36* introgressed from *Triticum turgidum* var. *dicoccoides* in durum wheat. *Theoretical and Applied Genetics*, **117**, 135–142.

Brenchley R, Spannagl M, Pfeifer M, Barker G L, D'Amore R, Allen A M, McKenzie N, Kramer M, Kerhornou A, Bolser D, Kay S, Waite D, Trick M, Bancroft I, Gu Y, Huo N, Luo M C, Sehgal S, Gill B, Kianian S, *et al.* 2012. Analysis of the bread wheat genome using whole-genome shotgun sequencing. *Nature*, **491**, 705–710.

Devos K M, Gale M D. 1997. Comparative genetics in the grasses. *Plant Molecular Biology Reporter*, **35**, 3–15.

Faricelli M E, Valarik M, Dubcovsky J. 2010. Control of flowering time and spike development in cereals: the earliness per se *Eps-1* region in wheat, rice, and *Brachypodium*. *Functional & Integrative Genomics*, **10**, 293–306.

Faris J D, Zhang Z C, Lu H J, Lu S, Reddy L, Cloutier S, Fellers J P, Meinhardt S W, Rasmussen J B, Xu S S, Oliver R P, Simons K J, Friesen T L. 2010. A unique wheat disease resistance-like gene governs effector-triggered susceptibility to necrotrophic pathogens. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 13544–13549.

Hua W, Liu Z J, Zhu J, Xie C J, Yang T M, Zhou Y L, Duan X Y, Sun Q X, Liu Z Y. 2009. Identification and genetic mapping of *pm42*, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). *Theoretical and Applied Genetics*, **119**, 223–230.

International *Brachypodium* Initiative. 2010. Genome sequencing and analysis of the model grass *Brachypodium distachyon*. *Nature*, **463**, 763–768.

International Rice Genome Sequencing Project. 2005. The map-based sequence of the rice genome. *Nature*, **436**, 793–800.

Ji X L, Xie C J, Ni Z F, Yang T M, Nevo E, Fahima T, Liu Z Y, Sun Q X. 2008. Identification and genetic mapping of a powdery mildew resistance gene in wild emmer (*Triticum dicoccoides*) accession IW72 from Israel. *Euphytica*, **159**, 385–390.

Jia J, Zhao S, Kong X, Li Y, Zhao G, He W, Appels R, Pfeifer M, Tao Y, Zhang X, Jing R, Zhang C, Ma Y, Gao L, Gao C, Spannagl M, Mayer K F, Li D, Pan S, Zheng F, *et al.* 2013. *Aegilops tauschii* draft genome sequence reveals a gene repertoire for wheat adaptation. *Nature*, **496**, 91–95.

Lander E S, Green P, Abrahamson J, Barlow A, Daly M J, Lincoln S E, Newberg L A. 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics*,

1, 174–181.

Li G Q, Fang T L, Zhang H T, Xie C J, Li H, Yang T M, Nevo E, Fahima T, Sun Q X, Liu Z Y. 2009. Molecular identification of a new powdery mildew resistance gene *Pm41* on chromosome 3BL derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). *Theoretical and Applied Genetics*, **119**, 531–539.

Ling H Q, Zhao S, Liu D, Wang J, Sun H, Zhang C, Fan H, Li D, Dong L, Tao Y, Gao C, Wu H, Li Y, Cui Y, Guo X, Zheng S, Wang B, Yu K, Liang Q, Yang W, *et al.* 2013. Draft genome of the wheat A-genome progenitor *Triticum urartu*. *Nature*, **496**, 87–90.

Liu Z J, Zhu J, Cui Y, Liang Y, Wu H, Song W, Liu Q, Yang T M, Sun Q X, Liu Z Y. 2012. Identification and comparative mapping of a powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*) on chromosome 2BS. *Theoretical and Applied Genetics*, **124**, 1041–1049.

Liu Z Y, Sun Q X, Ni Z F, Nevo E, Yang T M. 2002. Molecular characterization of a novel powdery mildew resistance gene *Pm30* in wheat originating from wild emmer. *Euphytica*, **123**, 21–29.

Lu H J, Faris J D. 2006. Macro- and microcolinearity between the genomic region of wheat chromosome 5B containing the *Tsn1* gene and the rice genome. *Functional & Integrative Genomics*, **6**, 90–103.

McIntosh R A, Yamazaki Y, Dubcovsky J, Rogers J, Morris C, Appels R, Xia X C. 2013. Catalogue of gene symbols for wheat. In: *Proceedings of the 12th International Wheat Genetics Symposium.* Yokohama, Japan.

Michelmore R W, Paran I, Kesseli R V. 1991. Identification of markers linked to disease-resistance genes by Bulked Segregant Analysis **—** A rapid method to detect markers in specific genomic regions by using segregating populations. *Proceedings of the National Academy of Sciences of the United States of America*, **88**, 9828–9832.

Mohler V, Zeller F J, Wenzel G, Hsam L K. 2005. Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 9. Gene *MlZec1* from the *Triticum dicoccoides*-derived wheat line Zecoi-1. *Euphytica*, **142**, 161–167.

Paterson A H, Bowers J E, Bruggmann R, Dubchak I, Grimwood J, Gundlach H, Haberer G, Hellsten U, Mitros T, Poliakov A, Schmutz J, Spannagl M, Tang H, Wang X, Wicker T, Bharti A K, Chapman J, Feltus F A, Gowik U, Grigoriev I V, *et al.* 2009. The *Sorghum bicolor* genome and the diversification of grasses. *Nature*, **457**, 551–556.

Reader S M, Miller T E. 1991. The introduction into bread wheat of a major gene for resistance to powdery mildew from wild emmer wheat. *Euphytica*, **53**, 57–60.

Rong J K, Millet E, Manisterski J, Feldman M. 2000. A new powdery mildew resistance gene: Introgression from wild emmer into common wheat and RFLP-based mapping. *Euphytica*, **115**, 121–126.

Schnable P S, Ware D, Fulton R S, Stein J C, Wei F, Pasternak S, Liang C, Zhang J, Fulton L, Graves T A, Minx P, Reily A D, Courtney L, Kruchowski S S, Tomlinson C, Strong C, Delehaunty K, Fronick C, Courtney B, Rock S M, *et al.* 2009. The B73 maize genome: complexity, diversity, and dynamics. *Science*, **326**, 1112–1115.

Spielmeyer W, Singh R P, McFadden H, Wellings C R, Huerta-Espino J. 2008. Fine scale genetic and physical mapping using interstitial deletion mutants of *Lr34/Yr18*: a disease resistance locus effective against multiple pathogens in wheat. *Theoretical and Applied Genetics*, **116**, 481–490.

Wiebe K, Harris N S, Faris J D, Clarke J M, Knox R E, Taylor G J, Pozniak C J. 2010. Targeted mapping of *Cdu1*, a major locus regulating grain cadmium concentration in durum wheat (*Triticum turgidum* L. var. *durum*). *Theoretical and Applied Genetics*, **121**, 1047–1058.

Xie W, Ben-David R, Zeng B, Distelfeld A, Roder M S, Dinoor A, Fahima T. 2012. Identification and characterization of a novel powdery mildew resistance gene *PmG3M* derived from wild emmer wheat, *Triticum dicoccoides*. *Theoretical and Applied Genetics*, **124**, 911–922.

Xue F, Ji W, Wang C, Zhang H, Yang B. 2012. High-density mapping and marker development for the powdery mildew resistance gene *PmAS846* derived from wild emmer wheat (*Triticum turgidum* var. *dicoccoides*). *Theoretical and Applied Genetics*, **124**, 1549–1560.

You F M, Huo N, Gu Y Q, Luo M C, Ma Y, Hane D, Lazo G R, Dvorak J, Anderson O D. 2008. BatchPrimer3: a high throughput web application for PCR and sequencing primer design. *BMC Bioinformatics*, **9**, 253.

Yu G T, Cai X W, Harris M O, Gu Y Q, Luo M C, Xu S S. 2009. Saturation and comparative mapping of the genomic region harboring Hessian fly resistance gene *H26* in wheat. *Theoretical and Applied Genetics*, **118**, 1589–1599.

Zhang H T, Guan H Y, Li J T, Zhu J, Xie C J, Zhou Y L, Duan X Y, Yang T, Sun Q X, Liu Z Y. 2010. Genetic and comparative genomics mapping reveals that a powdery mildew resistance gene *MI3D232* originating from wild emmer co-segregates with an NBS-LRR analog in common wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics*, **121**, 1613–1621.

Zhang W J, Olson E, Saintenac C, Rouse M, Abate Z, Jin Y, Akhunov E, Pumphrey M, Dubcovsky J. 2010. Genetic maps of stem rust resistance gene *Sr35* in diploid and hexaploid wheat. *Crop Science*, **50**, 2464–2474.

Zhang Z C, Friesen T L, Xu S S, Shi G J, Liu Z H, Rasmussen J B, Faris J D. 2011. Two putatively homoeologous wheat genes mediate recognition of *SnTox3* to confer effector-triggered susceptibility to *Stagonospora nodorum*. *The Plant Journal*, **65**, 27–38.

Zhou R, Zhu Z, Kong X, Huo N, Tian Q, Li C, Jin P, Dong Y, Jia J. 2005. Development of wheat near-isogenic lines for powdery mildew resistance. *Theoretical and Applied Genetics*, **110**, 640–648.

(Managing editor WANG Ning)