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ORIGINAL PAPER

Characterization and chromosomal location of *Pm40* in common wheat: a new gene for resistance to powdery mildew derived from *Elytrigia intermedium*

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Abstract Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is a very destructive wheat (*Triticum aestivum*) disease. Resistance was transferred from *Elytrigia intermedium* to common wheat by crossing and backcrossing, and line GRY19, that was subsequently selected, possessed a single dominant gene for seedling resistance. Five polymorphic microsatellite markers, *Xgwm297*, *Xwmc335*, *Xwmc364*, *Xwmc426* and *Xwmc476*, on chromosome arm 7BS, were mapped relative to the powdery mildew resistance locus in an F_2 population of Mianyang 11/GRY19. The loci order *Xwmc426–Xwmc335–Pm40–Xgwm297–Xwmc364–Xwmc476*, with 5.9, 0.2, 0.7, 1.2 and 2.9 cM genetic distances, was consistent with published maps. The resistance gene transferred from *Elytrigia intermedium* into wheat line GRY19 was novel, and was designated *Pm40*. The close flanking markers will enable marker assisted transfer of this gene into wheat breeding populations.

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Introduction

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is one of the most destructive foliar diseases of wheat (*Triticum aestivum*) in China (Zhuang and Li 1993). In southwest China, powdery mildew probably exceeds stripe rust as the most damaging disease, especially under cooler conditions with high inputs of irrigation and nitrogenous fertilizer. Race-specific resistance to powdery mildew is usually short-lived, especially when a single resistance gene is deployed over a wide area, and ongoing searches are required to identify new sources of resistance for use in breeding programs. More than 60 resistance alleles located at 37 loci for resistance to powdery mildew (*Pm1–Pm39*) have been identified and designated in wheat (McIntosh et al. 1998, 2006; Miranda et al. 2007). Among them, 25 were derived from *Triticum aestivum*, six from *T. turgidum*, two from *T. monococcum*, two from *Aegilops speltoides*, one from *A. longissina*, one from *A. ovata*, one from *A. umbellulata*, two from *T. timopheevi*, four from *Secale cereale*, one from *Haynaldia villosa* and four from *A. tauschii*. No resistance gene came from *Elytrigia intermedium* (2n = 42; $E_1E_1E_2E_2StSt$), a grass relative of wheat reported to be immune to wheat powdery mildew (Wang et al. 2000a). This species is easily hybridized with wheat and therefore is of potential value for wheat improvement. Various disomic addition lines and translocation lines resistant to powdery mildew have been produced in China (Li and Wang 2002; Lin et al. 2005). The wheat derivative YU25 is immune to powdery mildew. Genetic analysis showed that resistance in YU25 is controlled by two genes (Ma et al. 2007). The location of these genes on chromosomes and the identification of markers closely linked to them should be beneficial to their utilization in wheat breeding programs.

Molecular markers are now widely used for gene tagging, gene mapping, and other genetics research because they are not influenced by environmental conditions and growth stage. Molecular markers tightly linked to genes conferring traits of interest can be used in marker-assisted selection (MAS) to improve the efficiency of conventional plant breeding (Gupta et al. 1999). Among the various molecular marker systems currently available to wheat workers, microsatellites, or simple sequence repeats (SSR), are the most widely utilized and several microsatellite maps of wheat have been reported (Röder et al. 1998; Stephenson et al. 1998; Pestsova et al. 2000; Gupta et al. 2002; Somers et al. 2004). SSR loci are evenly distributed along the chromosome maps providing excellent coverage of the wheat genome. SSR markers were successfully used to tag a number of powdery mildew resistance genes (Huang et al. 2000; Jarve et al. 2000; Liu et al. 2002; Xie et al. 2003, 2004; Zhu et al. 2005; Miranda et al. 2006, 2007).

The purposes of the present study were to use microsatellite markers to characterize and locate a mildew resistance gene, already introgressed into wheat from *Elytrigia intermedium*.

Materials and methods

Plant materials

Wheat lines or cultivars GRY19, YU24, YU25, CM107, TAI7047, Taiyuan768 and 76(64), and *E. intermedium* were used in powdery mildew response tests. Chuanmai107 (CM107) as maternal parent was crossed with octoploid *Trititrigia* TAI7047, derived from the interspecific cross *T. aestivum* cv. Taiyuan768/*Elytrigia intermedium*// *T. aestivum* line 76(64). Two wheat lines, Yuan24 (YU24) and Yuan25 (YU25) selected from an F_5 population of the cross exhibited immune responses to powdery mildew over several years of observation. GRY19, selected from an F_4 population of Mianyang 11 (MY11)/YU25, is also immune. F_1 plants, reciprocal backcross F_1s and F_2s, and F_3 families (about 50 seedlings per family per test) and reciprocal BCF_2 populations derived from the cross MY11/GRY19, were used in genetic studies. Chancellor and Sy95-7 were used as susceptible controls.

Pathogen materials

An isolate of the prevailing local *B. graminis* f. sp. *tritici* (*Bgt*) race 15 (Xie et al. 2003) was used in the seedling stage assays. Inoculations were performed by dusting conidia from sporulating seedlings of Chancellor on to the test seedlings. Infection types (ITs) produced on individual plants or lines were recorded about 2 weeks after inoculation. Although recordings are usually based on a six IT scale only plants with IT 0 (immune) or IT 4 (Xie et al. 2003) were observed on the parental segregating materials.

Preparation of genomic DNA

Total DNA was extracted from 5-weeks-old seedling leaves according to the method of Luo et al. (2004).

PCR amplification and product analysis

Genomic DNA of parents and individual F_2 plants derived from MY11/GRY19 were used for molecular analysis. SSR markers linked to the resistance gene were identified by bulked segregant analysis (BSA). PCR were performed in volumes of 25 µl in a MJ RESEARCH (PTC-200) thermocycler, using publicly available GWM (Bryan et al. 1997; Röder et al. 1998) and WMC (Gupta et al. 2002) primer pairs. SSR analysis followed the procedure of Röder et al. (1998) with minor modifications. PCR followed the program described by Luo et al. (2008). Each PCR product was mixed with 3 µl of loading buffer (98% formamide, 10 mM EDTA, pH 8.0, 0.25% bromo-phenol blue, and 0.25 xylene cyanol), denatured at 95°C for 5 min and chilled on ice. Six microliters of each sample was loaded on 6% polyacrylamide (19:1 acrylamide : Bis, 8 M urea and 1× TBE [90 mM tris-borate (pH 8.3), 2 mM EDTA] gels, which were run at 80 W for approximately 1.5 h, and visualized by silver staining (Bassam et al. 1991).

Statistical analysis and linkage analysis

The goodness of fit of segregation data with hypothesized ratios was determined by chi-squared tests using Sigmaplot 2001 software (SPSS Inc., Chicago, IL, USA). Linkage distances between markers and the resistance gene were determined using MAPMAKER 3.0 (Lander et al. 1987). Markers were accepted at a LOD threshold of 3.0, and the linkage map was constructed by the method of Lincoln et al. (1992). Map distances were based on the Kosambi function (Kosambi 1944).

Results

Powdery mildew responses

Infection types produced by nine wheat lines, octoploid *Tritelyitrigia* TAI7047, and *E. intermedium* after

inoculation with Bgt race 15 showed that GRY19, YU24, YU25, TAI7047, *E. intermedium* were immune (IT 0), and that MY11, CM107, 76(64), Taiyuan768, Chancellor, and Sy95-7 were susceptible (IT 4). This confirmed that one or more genes for resistance had been transferred from *E. intermedium* into wheat lines GRY19, YU24 and YU25.

Response segregation and inheritance

For mapping the resistance gene in GRY19 using molecular markers, F_1 plants, 396 F_2 individuals, and 213 F_3 families from the cross MY11/GRY19, 161 BC_1F_2 families from MY11/GRY19//MY11, and 132 BC_1F_2 families from MY11/GRY19//GRY19 were inoculated with race 15. F_1 plants were as resistant as GRY19 indicating that resistance was dominant. The F_2 population segregated 294 resistant: 102 susceptible ($\chi^2_{3:1} = 0.121$, $P > 0.7$), and as shown in Table 1 the F_3 lines segregated 1 homozygous resistant, 2 segregating:1 homozygous susceptible, F_2 lines from the backcross to MY11 segregated 1 segregating:1 homozygous susceptible, and the backcross to GR19 segregated 1 homozygous resistant:1 segregating. These results clearly showed that GRY19 carried a single dominant gene for powdery mildew resistance.

Identification of microsatellite markers linked to the powdery mildew resistance gene

A total of 238 (34.3%) of 683 microsatellite primer pairs, mapped to wheat chromosomes amplified clear bands, and gave polymorphisms between MY11 and GRY19. Among them, *Xgwm297*, *Xwmc335*, *Xwmc364*, *Xwmc426* and *Xwmc476* amplified identical bands in the resistant (B_R) F_2 bulks and GRY19, and contrasting bands in the susceptible (B_S) F_2 bulks and MY11 (Fig. 1), indicating that these markers were linked with *Pm40*. Because all five primer pairs, previously located on wheat chromosome arm 7BS, amplified only single bands, *Pm40* was likely also located on that chromosome arm. The relationships between the powdery mildew resistance response genotypes and molecular genotypes are shown in Table 2. Each marker locus exhibited a 1:2:1 segregation ratio. The locus order

Table 1 Responses of F3 lines and reciprocal backcross F2 populations of MY11//GRY19 to *Bgt* race 15

Cross	Generation (families)	Responses			Expected ratio	χ^{2a}
		HR	Seg	HS		
MY11/GRY19	F_3	56	106	51	1:2:1	0.239
MY11/GRY19//MY11	BC_1F_2		78	83	1:1	0.078
MY11/GRY19//GRY19	BC_1F_2	62	70		1:1	0.242

[a] Values for significance at $P = 0.05$ are 3.84 (1 *df*), 5.99 (2 *df*)

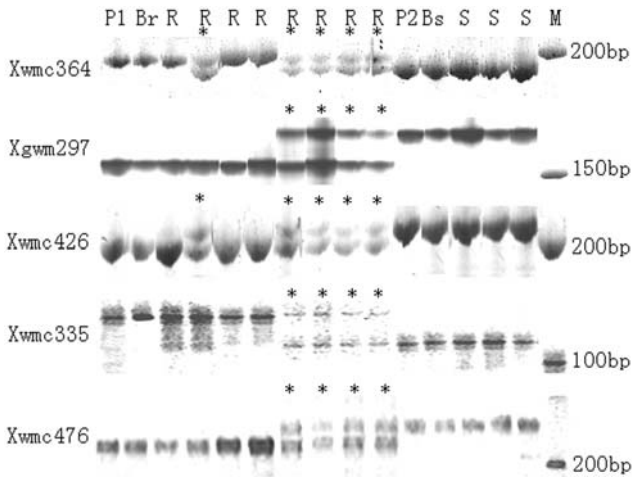

Fig. 1 Amplified PCR products with SSR primer pairs *Xgwm297*, *Xwmc335*, *Xwmc364*, *Xwmc426* and *Xwmc476* in polyacrylamide gels. *P_1* GRY19, *Br* resistant bulk, *R* resistant F_2 plants, *P_2* MY11, *Bs* susceptible bulk, *S* susceptible F_2 plants, *M* marker (with100 bp ladder); *asterisk* heterozygous loci

Table 2 Marker and powdery mildew response genotypes for the MY11/GRY19 F_2 population

Marker	Resistance genotype	Marker genotype			Total
		A	H	B	
Xgwm297	RR	55	1		56
	Rr		105	1	106
	rr		1	50	51
	Total	55	107	51	213
	$\chi^2_{1:2:1} = 0.155$; $P = 0.925$; linked with *Pm40* (0.7 cM)				
Xwmc335	RR	56			56
	Rr		105	1	106
	rr			51	51
	Total	56	105	52	213
	$\chi^2_{1:2:1} = 0.192$; $P = 0.908$; linked with *Pm40* (0.2 cM)				
Xwmc364	RR	56			56
	Rr		104	2	106
	rr		4	47	51
	Total	56	108	49	213
	$\chi^2_{1:2:1} = 0.502$; $P = 0.778$; linked with *Pm40* (1.9 cM)				
Xwmc426	RR	53	3		56
	Rr	3	95	8	106
	rr		8	43	51
	Total	56	106	51	213
	$\chi^2_{1:2:1} = 0.239$; $P = 0.887$; linked with *Pm40* (6.1 cM)				
Xwmc476	RR	56			56
	Rr	4	99	3	106
	rr		3	48	51
	Total	60	102	51	213
	$\chi^2_{1:2:1} = 0.141$; $P = 0.565$; linked with *Pm40* (4.8 cM)				

A homozygous for the GRY19 allele, *H* heterozygous, *B* homozygous for the MY11 allele

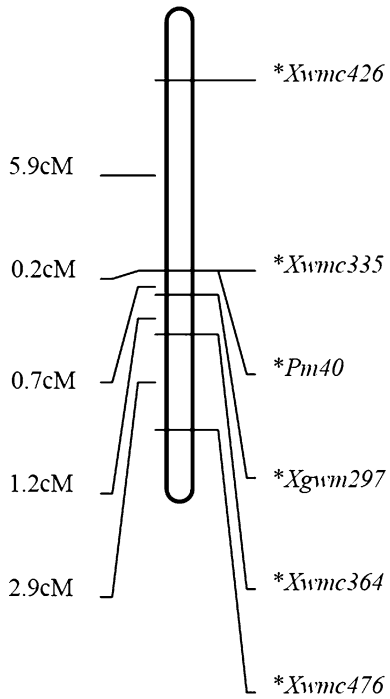

Fig. 2 Chromosome 7BS genetic map based on F_2 genotypes for *Pm40* and five microsatellite markers. Locus names and Kosambi map distances (cM) are shown on the *right and left sides* of the map, respectively

was *Xwmc426–Xwmc335–Pm40–Xgwm297–Xwmc364–Xwmc476*, with genetic distances of 5.9, 0.2, 0.7, 1.2, and 2.9 cM, respectively (Fig. 2).

Discussion

Origin of the resistance gene and its mode of inheritance

Intermediate wheatgrass can be used as a potential source of resistance to wheat powdery mildew (Wang et al. 2000a,b). GRY19 is a derivative of that species and all common wheat parents involved in its pedigree were highly susceptible indicating that the resistance should have come from *E. intermedium*. Genetic segregation data clearly showed the presence of a single dominant gene for resistance. Since no current formally named wheat gene for powdery mildew resistance is derived from this donor species the resistance gene must be novel.

Chromosomal location of the powdery mildew resistance gene

The microsatellite markers *Xgwm297*, *Xwmc335*, *Xwmc364*, *Xwmc426* and *Xwmc476*, earlier placed on chromosome 7BS (Röder et al. 1998; Gupta et al. 2002; Somers et al. 2004) were closely linked with the powdery mildew resistance gene in GRY19. The genetic distances between four of the markers (except for *Xwmc426*) and the resistance gene were less than 5 cM (Table 2 and Fig. 2), making them useful for molecular MAS, especially the flanking *Xwmc335* and *Xgwm297* alleles separated by <1 cM. Somers et al. (2004) reported the same markers in the sequence *Xwmc426–Xwmc335–Xgwm297–Xwmc476/Xwmc364* with separating intervals of 5.1, 0.4 and 2.7 cM, respectively. Both the order and distances for these loci closely agreed with those in Fig. 2. The unique chromosomal location suggested that the resistance gene for powdery mildew is new locus and it is named *Pm40*.

The transferred resistance appears to be present in a cryptic translocation

Chromosome translocation is a common and useful method for transferring alien genes from wild relatives to common wheat. Many alien translocations, despite carrying potentially useful genes, have questionable value in wheat improvement, because the often large transferred chromosome segments do not adequately compensate for the wheat genes they replace, or carry additional genes conferring undesirable traits. However, in a few instances, traits of interest were transferred to recipient genotypes without detectable cytological or genetic changes (Multani et al. 1994; Ren and Zhang 1997; Dong et al. 2004; Kuraparthy et al. 2007). Wheat primers did not span the resistance gene. Wheat SSR primers yielded PCR products on wheat genotype GRY19 and SSR marker loci closed flanked the *Pm40* without significant changes in the order and distance when compared to the consensus genetic map. Previously study showed that YU24 and its sister selection, YU25, were genetically ($2n = 42$, 21 II) and agronomically uniform (Ma et al. 2007). The resistance gene in GRY19 behaved as a normal Mendelian unit. Moreover, we could not detect in situ hybridization signals using *E. intermedium* genomic DNA as a probe (data not shown). This persuaded us to conclude that wheat genotype GRY19 does not have a large alien chromosomal segment. Thus the only evidence that GRY19 carries resistance from *E. intermedium* is pedigree. Genetic analysis showed that YU25 carries two genetically independent genes for resistance to powdery mildew (Ma et al. 2007), and that YU24 probably carries the same two genes (unpublished data). One of the genes confers immunity (IT 0), and the other, an intermediate response. GRY19 apparently inherited only the immunity factor.

Prospects of *Pm40* in wheat resistance breeding programs

In China, especially southwest China, powdery mildew is the most common wheat disease due to the temperate rainy

environment during the wheat growing season (Zhuang and Li 1993). In recent years, powdery mildew levels have increased because almost all previously deployed resistances are no longer effective (Liu et al. 2002). The single resistance gene located in chromosome 7BS in GRY19 showed normal inheritance. Group 7 chromosomes in wheat are highly tolerant to the presence of alien chromatin as evidenced by the observation that homologous group 7 nullisomics (especially nulli-7B) are the most normal of all wheat nullisomics. Hence the loss or gain (or replacement) of genetic material in this chromosome is likely to have minimal detrimental effects. The closely linked SSR markers and the defined location of *Pm40* should accelerate its incorporation into commercial cultivars by MAS. Therefore, there is a high likelihood that the present material can be utilized by breeders, especially when it is realized that the only currently effective highly resistant alternate source of resistance in southwestern China is *Pm21* which is also derived from an alien source, namely *H. villosa*.

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