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Microsatellite mapping of a *Triticum urartu* Tum. derived powdery mildew resistance gene transferred to common wheat (*Triticum aestivum* L.)

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Abstract A powdery mildew resistance gene from *Triticum urartu* Tum. accession UR206 was successfully transferred into hexaploid wheat (*Triticum aestivum* L.) through crossing and backcrossing. The F_1 plants, which had 28 chromosomes and an average of 5.32 bivalents and 17.36 univalents in meiotic pollen mother cells (PMC), were obtained through embryos rescued owing to shriveling of endosperm in hybrid seed of cross Chinese Spring (CS) × UR206. Hybrid seeds were produced through backcrossing F_1 with common wheat parents. The derivative lines had normal chromosome numbers and powdery mildew resistance similar to the donor UR206, indicating that the powdery mildew resistance gene originating from *T. urartu* accession UR206 was successfully transferred and expressed in a hexaploid wheat background. Genetic analysis indicated that a single dominant gene controlled the powdery mildew resistance at the seedling stage. To map and tag the powdery mildew resistance gene, 143 F_2 individuals derived from a cross UR206 × UR203 were used to construct a linkage map. The resistant gene was mapped on the chromosome 7AL based on the mapped microsatellite makers. The map spanned 52.1 cM and the order of these microsatellite loci agreed well with the established microsatellite map of chromosome arm 7AL. The resistance gene was flanked by the microsatellite loci *Xwmc273* and *Xpsp3003*, with the genetic distances of 2.2 cM and 3.8 cM, respectively. On the basis of the origin and chromosomal location of the gene, it was temporarily designated *PmU*.

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Introduction

Powdery mildew, caused by *Blumeria graminis* f.sp. *tritici* (syn. *Erysiphe graminis* f.sp. *tritici*), is one of the most important diseases of bread wheat (*Triticum aestivum* L.). Growing resistant cultivars is the most economical and environmentally safe approach to eliminate the use of fungicides and to reduce production losses due to this disease. Because of the co-evolution of host and pathogen, race-specific resistance genes can be overcome by new races of the pathogen possessing corresponding virulence genes, especially when a single resistance gene is deployed over a wide area. Hence, it is necessary to search for novel resistance genes for use in wheat breeding. So far, 49 genes/alleles for resistance to powdery mildew that map to 33 loci (*Pm1–Pm33*) have been identified (McIntosh et al. 1998, 2003; Hsam et al. 2003; Zhu et al. 2005), of which some have been transferred from related species to bread wheat. *Triticum* species carry ancestral or homoeologous genomes to those of cultivated wheat; a great hope for future crop genetic improvement lies in exploiting the genetic resources available in the wild relatives of crop plants. The wild gene pool of wheat contains many economically important alleles for resistance to diseases and pests, high grain-protein content, tolerance to many kinds of ecological stresses, and earliness, which might be transferred to cultivated wheat and utilized in its improvement (Feldman and Sears 1981). *Triticum urartu* Tum. ($2n = 2x = 14$; genome AA) is the A-genome donor of cultivated tetraploid ($2n = 2x = 28$; genome AABB) and hexaploid wheat ($2n = 2x = 42$; genome AABBDD) (Dvořák et al. 1988, 1993), and its chromosomes are homologous to chromosomes of the A genome of bread wheat. Thus, direct hybridization enables efficient

transfer of desirable alleles from every 'wild' chromosome into its 'cultivated' homologue. *T. urartu* carries many agronomically important traits that can be exploited for wheat improvement, including resistance to different wheat diseases (our unpublished data). But up till now, no powdery mildew resistance gene has been transferred into hexaploid wheat from *T. urartu*.

Molecular markers, such as restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs), random amplified polymorphic DNAs (RAPDs) and microsatellites, have been widely used to tag and identify powdery mildew resistance genes in wheat. So far, RFLP markers for *Pm1, Pm2, Pm3, Pm4, Pm6, Pm12, Pm13, Pm17* and *Pm26* (Hartl et al. 1993, 1995; Ma et al. 1994; Donini et al. 1995; Jia et al. 1996; Tao et al. 2000; Hsam et al. 2000; Rong et al. 2000), RAPD markers for *Pm1, Pm13, Pm21* and *Pm25* (Qi et al. 1996; Hu et al. 1997; Shi et al. 1998; Cenci et al. 1999; Liu et al. 1999), and AFLP markers for *Pm1c, Pm4a, Pm17, Pm22, Pm24* and *Pm29* (Hartl et al. 1999; Hsam et al. 2000; Huang et al. 2000; Zeller et al. 2002; Singrün et al. 2003) have been established.

Microsatellites, also termed simple sequence repeats (SSRs), can be used in different species of the genus *Triticum* to track the same chromosome, including *T. aestivum* (AABBDD), *T. durum* (AABB), *T. monococcum* (AA), *T. tauschii* (DD) (Röder et al. 1998), *T. aethiopicum* (Plaschke et al. 1995), and *T. dicoccoides* (Fahima et al. 1998), and have the advantages of being easy to handle, inexpensive and reliable. Such markers in wheat are chromosome-specific and detect high levels of polymorphism (Plaschke et al. 1995; Röder et al. 1995). Microsatellite markers were successfully used to tag *Pm3g* (Bougot et al. 2002), *Pm4a* (Ma et al. 2004), *Pm5e* (Huang et al. 2003), *Pm22* (Singrün et al. 2003), *Pm24* (Huang et al. 2000), *Pm27* (Järve et al. 2000), *Pm30* (Liu et al. 2002), *Pm31* (Xie et al. 2003) and *Pm33* (Zhu et al. 2005). But among the documented *Pm* genes, only *Pm3b* was recently isolated by positional cloning method (Yahiaoui et al. 2004).

The present paper reports transfer and mapping of a novel powdery mildew resistance gene derived from *T. urartu* by using microsatellite markers.

Materials and methods

Plant materials

Triticum urartu accession UR206 (original code No. 1010015), UR203 (original code No. 1010004) and UR204 (original code No.1010013) were generously provided by Mr. Reader from John Innes Centre, Norwich, UK. Accession UR206 (with IT value 0) was used as the donor of the powdery mildew resistance gene, and crossed to the susceptible accession UR203 (with IT value 4). The resulting F_1 hybrids were self-pollinated to produce the F_2 segregating population. The 143 F_2 individuals of cross UR206/UR203 were assessed for linkage of microsatellite markers and powdery mildew resistance gene.

Embryo rescue and transfer of resistance gene

In order to transfer the powdery mildew resistance gene into hexaploid wheat, susceptible bread wheat cultivar Chinese Spring (CS) (with IT value 4) was used as the female parent to cross to resistant *T. urartu* accession UR206. Because of shriveling of endosperm in hybrid seed, the immature embryos must be rescued. Twelve to sixteen days post-pollination, the mother spikes were cold treated at 4°C for 24 h prior to the excision of embryos. Dehusked immature seeds were sterilized with 75% ethanol for 1 min, followed in 0.1% $HgCl_2$ solution for 10 min and rinsed four times in sterile water. Immature embryos of hybrids were cultured on N6 basal medium supplemented with 0.5 mg/l indolebutyric acid (IBA) and 0.2 mg/l α-naphthalene acetic acid (NAA) in glass tubes that were sealed to avoid contamination and to maintain high humidity. The F_1 seedlings were transferred to N6 basal medium supplemented with 10 mg/l indoleacetic acid (IAA) and 80 g/l sucrose. All cultures were incubated in a growth room at 21–25°C with a 12 h light/12 h dark photoperiod, under fluorescent light of 2,000 lux. The plantlets were transferred to pots at the three-leaf stage.

The F_1 plants of the cross CS/UR206 were sterile but could be backcrossed with elite common wheat line PI29 (with IT value 4) from our institute. The plants with 42 chromosomes generated from the progenies of cross CS/UR206//2*PI29 were selected for further work.

Chromosome observation

Meiotic chromosome pairing in pollen mother-cells (PMC) was analyzed at metaphase I. Immature spikes from F_1 plants at the appropriate stage were collected; anthers of spikes were fixed with 3:1 absolute alcohol–glacial acetic acid for 24 h and stored at 4°C in 70% alcohol until used. Anthers were stained with Schiff reagent and squashed in 45% acetic acid. Every PMC was scored for the presence of univalents, bivalents and trivalents; the number of chromosomes involved and their configurations were recorded.

The somatic chromosome numbers were studied from root-tips cells taken from the sprouted seeds that were pretreated in ice-water for 24 h, fixed with 3:1 absolute alcohol–glacial acetic acid, hydrolyzed in 1 mol/l HCl at 60°C for 8–10 min, and finally stained in leuco basic fuchsin for at least 20 min. Those with 42 complete chromosomes were selected from the progenies by root-tip examination.

Evaluation of resistance reactions

The *Blumeria graminis tritici* (*Bgt*) isolates used for the differentiation of documented major resistance genes were collected from different wheat growing regions of China and selected from single spore progenies. Powdery mildew resistance reactions were surveyed on agar-detached primary leaf segments. The methods of inoculation, conditions of incubation, and disease assessment were according to Huang et al. (1997). In the postulation of resistance genes using differential *Bgt* isolates, three major classes of host reactions were distinguished: r = resistant (0–20% infection relative to susceptible control cv.), i = intermediate (30–50% infection), and s = susceptible (more than 50% infection).

To follow powdery mildew segregation, we utilized *Bgt* isolate E09, virulent to *Pm1a, Pm3a, Pm5a*, *Pm7, Pm8*, *Pm17* and *Pm19*, but avirulent to UR206 and its derivatives. Inoculations were performed in the greenhouse by brushing conidia on the first leaf when it had fully expanded. The test results were scored about 10 days after inoculation when the susceptible control Jingshuang16 was heavily infected. The infection types (IT 0 to 4) was used to classify the disease reaction (Stakman et al. 1962).

Microsatellite markers analysis

Genomic DNA was extracted from leaf tissue samples following the procedure of Sharp et al. (1988). Microsatellite markers linked to the resistance locus were identified by bulked segregation analysis (BSA), a screening method described by Michelmore et al. (1991). The resistant bulk (B_R) and the susceptible bulk (B_S) were made by separately pooling with equal amounts of DNAs from 10 resistant and 10 susceptible plants from the segregating F_2 population. The candidate markers were subsequently identified in DNA of each plant of the F_2 and CS/UR206 // 2^* PI29 F_1 segregating for powdery mildew resistance.

PCR amplification and product analysis

Wheat microsatellite primers ('WMS', 'WMC' and 'CFA') were synthesized according to the sequences published in the GrainGenes database (http://wheat.pw.usda.gov/). 'PSP' were kindly provided by Dr. P. Stephenson, John Innes Centre, UK.

Microsatellite analysis followed the procedure of Bryan et al. (1997) with some modifications. Each PCR reaction was conducted in a total volume of 25 μl containing 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.8 mM $MgCl_2$, 200 μM of each dNTP, 200 nM of each primer, 50 to 100 ng genomic DNA, and 1.25 U *Taq* DNA polymerase. The amplifications were performed in a *MJ PTC-225* Thermocycler at 94°C for 4 min, followed by 35 cycles at 94°C for 1 min, at 50 to 61°C (depending on the microsatellite primer pair) for 1 min, and at 72°C for 1 min, with a final extension at 72°C for 5 min. Each PCR product was mixed with one-tenth volume of loading buffer (50 mM Tris-HCl, pH 8.0, 50 mM EDTA, 1% SDS, 0.25% bromo-phenol blue, 0.25% xylene cyanol and 50% glycerol), denatured at 95°C for 5 min and chilled on ice. Five to seven microliter 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 1,000 V, 50 W for approximately 2 h. Gels were then silver stained and photographed.

Data analysis

Chi-square (χ^2) tests for goodness-of-fit were used to test for deviation of observed data from theoretically expected segregation. The recombination frequencies were calculated using MAPMAKER/Exp version 3.0b (Lincoln et al. 1992) and converted to centi-Morgans (cM) using the Kosambi (1944) mapping function. The commands "group" and "ripple", and LOD scores ≥3.0 were used to develop the linkage map.

Results

Identification and mapping the gene for powdery mildew resistance

The disease response patterns of 18 wheat cultivars and lines with known resistance genes were compared with those of the resistant parent UR206 and susceptible parent UR203. *T. urartu* accession UR206 showed full resistance to each of the 15 different *Bgt* isolates, and the disease responses were different from those of the known genes except *Pm12*, *Pm13*, *Pm16*, *Pm18*, *Pm20* and *Pm21* (Table 1). There were a total of 143 F_2 individuals from the cross UR206/UR203. Of these, 103 plants showed complete resistance (IT 0) and 40 plants showed complete susceptibility (IT 4) to isolate E09 of *Blumeria graminis* f.sp. *tritici*, and the χ^2 test indicated a good fit to a 3:1 segregation for resistance ($\chi^2_{3:1} = 0.525 < \chi^2_{0.05} = 3.84$), suggesting that the powdery mildew resistance in *T. urartu* accession UR206 was controlled by a single dominant gene. The gene in accession UR206 is tentatively designated *PmU*.

On the basis of the microsatellite map of wheat, 242 microsatellite markers mapped on the A genome of wheat were chosen to identify polymorphism between UR206 and UR203, and 126 (52%) of these markers showed polymorphism between the parents. The polymorphic microsatellite markers were further used to screen the resistant bulk (B_R) and the susceptible bulk (B_s) of F_2 segregating population; two microsatellite primer pairs, *Xwmc273* and *Xwmc346* showed polymorphism between the bulks. After testing among 143

Table 1 Differential reactions of 18 wheat cultivars/lines possessing different known powdery mildew resistance genes after inoculation with 15 isolates of *Blumeria graminis* f.sp. *tritici*

Cultivar/Line	*Pm* gene	*Blumeria graminis tritici* isolate														
		E02	E03	E05	E06	E07	E09	E11	E13	E15	E17	E18	E20	E21	E23	E25
Festival	*Pm1a*	s[b]	s	s	s	s	s	s	s	s	s	s	s	s	s	s
Ulka/8*Cc[a]	*Pm2*	r	r	r	r	r	r	s	s	r	r	s	s	s	r	r
Asosan/8*Cc	*Pm3a*	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
Khapli/8*Cc	*Pm4a*	s	r	r	r	r	r	r	r	s	s	s	s	s	r	r
VPM	*Pm4b*	s	r	r	r	r	r	s	r	r	r	s	s	s	r	r
CI14125	*Pm5a*	r	s	s	s	s	s	s	s	s	r	s	s	s	s	s
Coker 747	*Pm6*	s	r	r	s	r	r	s	r	i	s	s	s	s	r	s
CI14189	*Pm7*	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
PI361879	*Pm8*	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
Line 31	*Pm12*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
R1A	*Pm13*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Line Pm16	*Pm16*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Amigo	*Pm17*	r	s	s	s	s	s	s	s	r	i	s	s	s	s	s
M1N	*Pm18*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
96–286	*Pm19*	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s
96–287	*Pm20*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
R43	*Pm21*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
Line 81–7241	*Pm23*	r	r	r	r	r	r	r	r	r	r	s	s	s	r	r
UR203	–	r	r	r	r	r	s	s	s	s	s	s	s	s	r	r
UR206	*PmU*	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r

[a]Seven times backcrossed to cv. Chancellor
[b]r, resistant; i, intermediate; s, susceptible

DNA samples of the F_2 segregating population, the polymorphic fragments amplified by two microsatellite primer pairs were *Xwmc273*/240 and *Xwmc346*/205 which segregated with the resistance gene *PmU*, and *Xwmc273*/216 and *Xwmc346*/214 with its susceptible allele, respectively, indicating that *Xwmc273* and *Xwmc346* were linked to the *PmU* locus.

On the wheat microsatellite map constructed by Gupta et al. (2002), *Xwmc273* was mapped on the long arm of chromosome 7A; other primer pairs located on chromosome arm 7AL were further tested to search for polymorphic markers. Eight more markers, *Xpsp3003, Xpsp3094, Xcfa2257, Xcfa2040, Xcfa2293, Xcfa2019, Xwmc525* and *Xgwm63*, detected polymorphism between the resistant and susceptible plants, and were also found to be linked to *PmU*. A typical amplification pattern generated by *Xwmc273* is shown in Fig. 1. Among 10 microsatellite loci, 9 exhibited co-dominance, with the remaining marker, *Xpsp3003*/198, being dominant. The microsatellite loci exhibited perfect Mendelian inheritance.

Linkage analysis between each microsatellite marker and *PmU* using MAPMAKER 3.0b indicated the locus order and genetic distance between *PmU* and the 10 microsatellite markers. A microsatellite genetic map involving the *PmU* region was constructed with a total map length of 52.1 cM (Fig. 2). In the present study, the powdery mildew resistance gene *PmU* was flanked by the microsatellite loci *Xwmc273* and *Xpsp3003* with the genetic distances of 2.2 cM and 3.8 cM, respectively. *Xcfa2040*, *Xwmc525*, *Xcfa2257*, *Xwmc346* and *Xcfa2293* were relatively close to *PmU*, with genetic distances of 5.8, 6.5, 9.9, 10.1 and 22.7 cM, respectively. Other *PmU*-linked microsatellite loci were *Xcfa2019*, *Xgwm63* and *Xpsp3094*, though with larger genetic distances of 31.1, 38.8 and 42.4 cM (Fig. 2).

Microsatellite loci *Xpsp3094*, *Xcfa2257*, *Xcfa2040*, *Xcfa2293*, *Xcfa2019* and *Xgwm63* were also located on

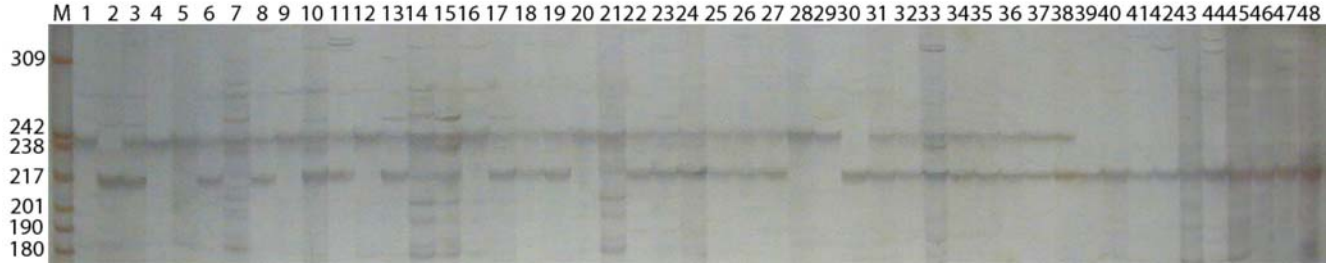

Fig. 1 Amplification products by wheat microsatellite primer *Xwmc273* in resistant parent UR206 (Lane 1), susceptible parent UR203 (Lane 2), 36 resistant F_2 individuals (Lanes 3–38) and 10 susceptible F_2 individuals (Lanes 39–48). Line 30, exchanged plant. M, pBR322 DNA/MSP I marker

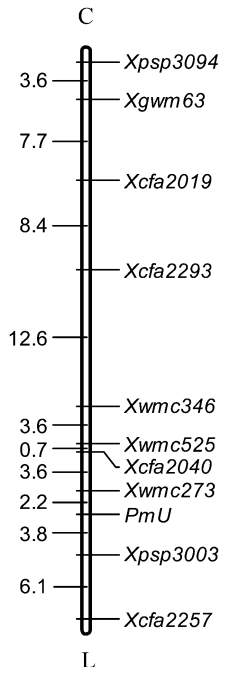

Fig. 2 Microsatellite linkage map of powdery mildew resistance gene *PmU* and linked microsatellite loci on chromosome 7AL. *C*, Centromere; *L*, long arm

chromosome arm 7AL (Röder et al. 1998; Stephenson et al. 1998; Sourdille et al. 2004); the order of these microsatellite loci agreed well with the established microsatellite maps of chromosome arm 7AL (http://wheat.pw.usda.gov/ggpages/SSRclub/GeneticPhysical/). On the basis of the above analysis, we concluded that *PmU* was located in the distal region of chromosome 7AL.

Transfer of *PmU* from *T. urartu* to common wheat

T. urartu accession UR206 was crossed as male with common wheat cultivar CS, and the ratio of hybrid embryos was 27.6%. The immature embryos must be rescued due to lack of endosperm in hybrids. The F_1 plants of cross CS/UR206 were hybridized with wheat elite line PI29, and seed set was 12.89% in the first backcross, and 52.05% (28.7–71.7%) in subsequent backcrosses to PI29.

Observation of the chromosome configurations of F_1 pollen mother cell (PMC) of cross CS/UR206 at metaphase I (MI) showed that the chromosome number was 28, with an average of 17.36 univalents and 5.32 bivalents (Table 2). The chromosome numbers in partially fertile F_1 plants of cross CS/UR206//PI29 ranged from 36 to 41, and the average chromosome pairing of F_1 PMC at MI were 16.54 bivalents, 6.6 univalents and 0.19 trivalents (Table 2), but no plants with $2n = 42$ chromosomes were observed. An additional backcross of the F_1 with the corresponding susceptible parent PI29 was made in order to obtain plants with normal chromosome number. After observation of chromosome number from root-tips cells of F_1 plants of cross CS/UR206//2*PI29, more than a half plants had $2n = 42$ chromosomes.

The F_1 plants of cross CS/UR206 were immune to powdery mildew, and segregation to powdery mildew resistance in the F_1 of cross CS/UR206//PI29 was observed. Fifty-one BCF_1 progeny from the cross CS/UR206//2*PI29 were derived from one F_1 resistant plant that segregated 23 resistant (IT 0-2) and 28 susceptible (IT 3-4) individuals, and this was a good fit to a 1:1 segregation for resistance ($\chi^2_{1:1} = 0.314 < \chi^2_{0.05} = 6.64$).

PmU was identified using *PmU*-linked microsatellite markers *Xwmc346* in 34 DNA samples of progenies of cross CS/UR206//2*PI29 (including 16 resistant plants and 18 susceptible plants) owing to no polymorphism between parents amplified by microsatellite primer pair *Xwmc273*, and 18 heterozygous resistant genotypes, 16 homozygous susceptible genotypes were observed. The ratio of genotypes accorded well with 1:1 segregation of phenotypes ($\chi^2_{1:1} = 0.029 < \chi^2_{0.05} = 6.64$). This indicated that the microsatellite markers that were closely linked to *PmU* could be used for marker-assisted selection (MAS) in wheat breeding.

From F_2 progeny of cross CS/UR206//2*PI29, 10 powdery mildew resistant lines with 42-chromosomes (with IT value 0) were obtained, indicating that the resistance to powdery mildew conferred by *PmU* was successfully transferred into bread wheat. The resistance reaction to powdery mildew in the F_1 progenies of cross CS/UR206 and the F_1, F_2 progenies of cross CS/UR206//2*PI29 demonstrated that the resistance gene from *T. urartu* accession UR206 was expressed in the bread wheat background.

Table 2 Chromosome pairing at MI in hybrid F_1 from crosses between CS/UR206 and CS/UR206//PI29

Crosses	No. of chromosome	No. of PMC	Mean number per cell				
			Bivalents			Univalents	Trivalents
			Rod	Ring	Total		
CS/UR206	28	53	2.14 (1 – 4)[a]	3.18 (1–4)	5.32 (4–6)	17.36 (16–20)	
CS/UR206 // PI29	40 (36–41)	109	3.84 (1–7)	12.66 (10–17)	16.54 (13–19)	6.6 (3–11)	0.19 (0–2)

[a]Range is given in parenthesis

Discussion

A new resistance gene found in closely related species can be successfully introduced into hexaploid wheat by crossing, using embryo rescue (if required), and in subsequent backcrosses, recombination can occur between the homologous chromosomes. Eleven genes/alleles *Pm1b*, *Pm3h*, *Pm4a*, *Pm4b*, *Pm5a*, *Pm16*, *Pm19*, *Pm25*, *Pm26*, *Pm30* and *Pm31* were introduced into hexaploid wheat by this way. Among them, *Pm1b* derived from *T. monococcum* (Hsam et al. 1998), *Pm25* from *T. boeoticum* (Shi et al. 1998), and the stem rust (*Puccinia graminis* Pers.:Pers. f.sp. *tritici* Eriks. & Henn.) resistance gene *Sr22* from *T. boeoticum* (Paull et al. 1994), demonstrate the successful transfer of disease resistance genes from diploid einkorn to hexaploid wheat.

The resistance genes in chromosome 7A and relation between *PmU* and *Pm1*

Among the 33 catalogued and allocated powdery mildew resistance genes, *Pm1* (*Pm1a, Pm1b* and *Pm1d*), *Pm1c* (formerly *Pm18*), *Pm1e* (*Pm22*) and *Pm9* are located on chromosome 7AL. *Pm1a, Pm1c, Pm1e* and *Pm9* originated from common wheat, *Pm1b* from *T. monococcum* and *Pm1d* from *T. spelta* (Sears and Briggle 1969; Hsam et al. 1998; Singrün et al. 2003). Singrün et al. (2004) found a recessive powdery mildew resistance gene *mlRD30* from common wheat line RD30 and located it in the terminal region of chromosome 7AL. In our study, *PmU* derived from the *T. urartu* accession UR206 was also mapped on chromosome 7AL by the aid of microsatellite markers. The fact that a resistance gene derived from another *T. urartu* accession UR204 was also mapped to the same complex region in chromosome 7AL (our unpublished data) indicates that chromosome 7AL in wheat may thus be an important carrier of a cluster of disease resistance genes.

The powdery mildew resistance gene *Pm1* was observed to co-segregate with RFLP marker *Xcdo347* that is located in the distal region of chromosome 7AL (Ma et al. 1994), and linked to *Pm9* with the distance of 8.5 cM (Schneider et al. 1991). Hartl et al. (1995) found RFLP marker *Xwhs178* closely linked to *Pm18* with a distance of 4.4 ± 3.6 cM, and suggested that *Pm1* and *Pm18* were closely linked at a distance of about 7 cM (2.8 ± 4.4 cM) from each other, with *Xwhs178* placed in between. In the study of Neu et al. (2002), the RFLP marker *Xmwg2062* mapped 0.4 cM proximal to *Pm1* in population Chancellor × Axminster/8*Chancellor and co-segregated in population Frisal × Sappo, while *Xsts638* showed no recombination to *Pm1* in both populations. Singrün et al. (2003) found *Pm1e* to map 0.9 cM and 17.7 cM from the microsatellite loci *Xgwm344-7A* and *Xgwm282/Xgwm332-7A*, and estimated the genetic distance between *Pm1c* and *Pm1e* at 0.9–2.4 cM through identification of AFLP markers. On the microsatellite genetic map constructed by Röder et al. (1998), microsatellite locus *Xgwm63* locates near to microsatellite loci *Xgwm282/Xgwm332* with the distance of 2.4 cM in the chromosome 7AL. In our study, *PmU* was linked to *Xgwm63* at a distance of 38.8 cM, therefore, it may represent a separate locus (Fig. 2). However, because the genetic distance often varies between mapping population, confirmation that *PmU* and *Pm1* represent different loci, will require further experiments.

The homologous relationships of the A genome of *T. urartu* and bread wheat

This study suggest that recombination can occur between bread wheat and *T. urartu* chromosomes, and that normal chromosome pairing facilitates the transfer of genes from diploid to hexaploid wheat. After only two backcrosses, or a backcross and an intercross, self-fertility and the normal chromosome number were restored. This indicates that the chromosomes of *T. urartu* and A genome of common wheat have high homology. The lack of complete pairing (presence of 5.32 bivalents in PMCs) may be caused by the chromosome 4A rearrangement with chromosome 5AL and 7BS, which was already well explored by Chapman et al. (1976).

The cytological observations indicate that *T. urartu* has five to six chromosomes homologous to A genome of *T. aestivum*, and the map, constructed by using F_2 population of cross UR206 × UR203, which spans 52.1 cM of the distal region of chromosome arm 7AL, is in accordance with the established hexaploid wheat microsatellite map of chromosome arm 7AL, indicating that 7A chromosome of *T. urartu* is sytenous to that of hexaploid wheat. Further research will be required to identify the chromosomes that differ.

The gene expression transferred from diploid *T. urartu* to hexaploid wheat

The powdery mildew resistance gene derived from *T. urartu* accession UR206 was transferred into hexaploid wheat and expressed in the new background. Powdery mildew resistance at the hexaploid level of introgressive lines introduced from *T. urartu* was as high as at the diploid level. There are some reports that the degree of resistance conferred by genes introduced from a diploid donor to a higher level of ploidy can be diluted (Dyck and Kerber 1970; Kerber and Dyck 1973) or completely suppressed (Villareal et al. 1992; Ma et al. 1995, 1997). We synthesized 20 hexaploid wheat lines (AABBDD) from tetraploid wheat (AABB) and *T. tauschii* (DD) carrying powdery mildew resistance. However, all 20 lines were susceptible to powdery mildew, suggesting that the resistance from *T. tauschii* was suppressed in hexaploid wheat. An interesting topic for further research will be to find the reason why the resistance from the A genome of *T. urartu* was expressed in a synthesized

hexaploid wheat but not in the gene from the D genome of *T. tauschii*.

Resistance against powdery mildew in many Chinese wheat cultivars has gradually decreased. The diploid *T. urartu* accessions showed a high degree of differentiation with respect to hexaploid wheat and such diversity could potentially be of interest to breeders as a source of genes for introgression. The rapid introduction of new resistance genes from related species into wheat has become a high priority for wheat breeding in China. The resistance gene *PmU* conferred full resistance to all of the *Bgt* isolates used in the present study, and no virulence for *PmU* has been found in China. Therefore, introgression of *PmU* may be beneficial to future wheat breeding programs searching for resistance to powdery mildew.

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