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Molecular identification of *Pm12*-carrying introgression lines in wheat using genomic and EST-SSR markers

Wei Song · Hao Xie · Qing Liu · Chaojie Xie · Zhongfu Ni · Tsomin Yang · Qixin Sun · Zhiyong Liu

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Abstract *Pm12*, transferred from *Aegilops speltoides* ($2n = 2x = 14$, genome SS) to wheat, confers effective resistance to powdery mildew worldwide. By applying bulked segregant analysis in a BC_3F_2 segregating population consisting of 305 plants, 18 wheat genomic and EST-SSR markers linked to the resistance gene were identified. *Pm12* was located in the 6SS portion of the T6BS-6SS.6SL translocation chromosome based on the physical bin positions of the genomic and EST-SSR markers in the Chinese Spring group six deletion stocks and their linkage relationship to the resistance gene. Twenty eight recombinants among 305 F_2 plants indicated a low frequency of recombination between the alien chromosome segment and wheat chromosome 6B. Since recombination events occurred on both sides of *Pm12*, the materials generated provide opportunities for further reduction of alien chromatin by intercrossing selected individuals and using markers to select the required plants.

Keywords Powdery mildew resistance · *Pm12* · *Aegilops speltoides* · SSR · Introgression lines

Wei Song and Hao Xie are contributed equally to this work.

W. Song · H. Xie · Q. Liu · C. Xie · Z. Ni · T. Yang · Q. Sun (✉) · Z. Liu (✉)
Department of Plant Genetics & Breeding and State Key Laboratory for Agrobiotechnology/Key Laboratory of Crop Genomics and Genetic Improvement, Ministry of Agriculture/Beijing Key Laboratory of Crop Genetic Improvement/Key Laboratory of Crop Heterosis Research & Untilization, Ministry of Education, China Agricultural University, Beijing 100094, P. R. China
e-mail: qxsun62@public.bta.net.cn

H. Xie
e-mail: zhiyongliu@cau.edu.cn

Present Address:
H. Xie
Beijing University of Agriculture, Beijing 102206, P. R. China

Introduction

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is one of the most important fungal diseases of wheat (*Triticum aestivum* L.) worldwide. Breeding for resistance to powdery mildew is the most economical and effective way to control the disease. However, evolution of the pathogen population often leads to virulence that enables the pathogen to overcome the host resistance, a situation made worse when single resistance genes are deployed in monocultures over wide areas. New and diversified sources of resistance to powdery mildew are needed to broaden the availability of resistant germplasm for wheat breeders. To date, 34 powdery mildew resistance gene loci have been characterized and assigned to specific chromosomes in common wheat (McIntosh et al. 2003; Hsam et al. 2003; Zhu et al. 2005;

Miranda et al. 2006). Some of them were introduced from related species.

Diploid species with the S genome belong to the *Aegilops* section Sitopsis, and are part of the the secondary gene pool for common wheat improvement. The S genome is considered to be closely related to the B genome of *T. aestivum*. *Ae. speltoides* was proposed to be the B genome donor of both common and durum wheat (Huang et al. 2002; Kimber and Athwal 1972; Dvorak and Zhang 1990). It is the source of several disease resistance genes, including leaf rust resistance genes *Lr28* (T4AS.4AL-7S#2S, McIntosh et al. 1982), *Lr35* (Kerber and Dyck 1990), *Lr36* (Dvorak and Knott 1990), *Lr47* (Dubcovsky et al. 1998) and *Lr51* (Dvorak 1977), stem rust resistance genes *Sr32* (Friebe et al. 1996) and *Sr39* (Kerber and Dyck 1990), and powdery mildew resistance genes *Pm12* (Miller et al. 1988) and *Pm32* (Hsam et al. 2003), that were transferred to wheat and are being used for wheat improvement.

Pm12 was first introgressed into hexaploid wheat cultivar Wembley in UK and a chromosome translocation involving group-6 chromosomes was identified (Miller et al. 1988). RFLP mapping indicated that the chromosome carrying *Pm12* was a 6BS-6SS.6SL translocation (Jia et al. 1996), involving the entire long arm and most of the short arm of chromosome 6S. *Pm12* was highly effective against powdery mildew isolates in China (Duan et al. 1998), Europe (Huang and Röder 2004) and the United States (Niewoehner and Leath 1998). However, due to the large amount of alien chromatin, lines with *Pm12* appear to have yield depression and the gene has not contributed to commercial wheat cultivar production.

Molecular markers have been widely used to map powdery mildew resistance genes in wheat. So far, 18 of 34 wheat powdery mildew resistance genes have been mapped by RFLP, RAPD, AFLP and SSR approaches (Huang and Röder 2004; McIntosh et al. 2003, Hsam et al. 2003; Zhu et al. 2005, Miranda et al. 2006). Microsatellite markers, or simple sequence repeats (SSRs), have the advantages of being inexpensive, safe and easy to handle compared to RFLP markers. In the last decade, genetic (Röder et al. 1998b; Stephenson et al. 1998; Pestsova et al. 2000; Gupta et al. 2002; Song et al. 2002; Somers et al. 2004) and physical (Sourdille et al. 2004) maps of wheat microsatellites have been developed, and they greatly facilitate the molecular tagging of agronomically important genes. Several powdery mildew resistance genes, such as *Pm5e* (Huang et al. 2003), *Pm24* (Huang et al. 2000), *Pm27* (Järve et al. 2000), *Pm30* (Liu et al. 2002), *Pm33* (Zhu et al. 2005) and *MlZec1* (Mohler et al. 2005) were mapped with microsatellite markers. Recently, a new kind of microsatellite marker, EST-SSR, derived from expressed sequence tags (ESTs) and more likely physically associated with the coding regions of the genome, provided additional PCR-based markers that could be used for genome mapping, and marker assisted selection (Cho et al. 2000; Scott et al. 2000; Eujayl et al. 2002, Yu et al. 2004).

In the present paper, we report (1) the genomic SSR and EST-SSR mapping of the powdery mildew resistance gene *Pm12*, and (2) the molecular identification of *Pm12* introgression lines containing smaller segments of *Ae. speltoides* chromosome 6S.

Materials and methods

Plant materials

The Wembley line carrying *Pm12*, Line #31, was kindly provided by Dr. XY Duan, Chinese Academy of Agricultural Sciences (originally from Dr. MD Gale, JI Centre, Norwich, UK). Susceptible elite commercial common wheat lines 87-1, Jing 411, Nongda 101, Jin 190, and Jin 207 were used as parents in crosses with Line #31 and then used as recurrent parents for backcrossing to improve the agronomic traits. Five resistant plants of each cross were selected in each cycle to make further backcrosses with the recurrent parents. A BC_3F_2 population derived from Line #31/3*Jin 207 was chosen to construct a linkage map. A total of 305 BC_3F_2 plants and their progenies were used for powdery mildew evaluations and microsatellite analysis. Five resistant and 5 susceptible plants selected from the progenies of Line #31/8*Jing 411, Line #31/6*87-1, Line #31/3*Nongda 101 and Line #31/3*Jin 190 were used for marker validation.

Chinese Spring (CS) nullisomic-tetrasomics, ditelosomics and deletion lines of homoeologous group 6 (kindly provided by Drs. WJ Raupp and BS Gill, Wheat Genetics Resource Centre, Kansas State University, USA) were used for chromosomal arm

assignments and physical mapping of the microsatellite markers.

Powdery mildew evaluations

The powdery mildew seedling reactions of the BC_3F_2 mapping population and BC_3F_3 progenies were determined as described by Liu et al. (2002). A local prevailing isolate of *B. graminis* f. sp. *tritici* E09 was used for inoculation. Reactions were scored on a 0, 0;, and 1 to 4 infection type (IT) scale, with 0 representing no visible symptoms, 0; representing necrotic flecks, and 1, 2, 3, 4 for highly resistant (necrosis with low sporulation), resistant (necrosis with medium sporulation), susceptible (no necrosis with medium to high sporulation), and highly susceptible (no necrosis with full sporulation) reactions, respectively. The reaction of each BC_3F_3 line was based on 20 seedlings and the reaction of each F_2 plant was scored homozygous resistant (RR), heterozygous resistant (Rr) and homozygous susceptible (rr).

Genomic DNA isolation and microsatellite analysis

Genomic DNA was extracted from uninfected leaves by the cetyltrimethylammonium bromide method (Saghai-Maroof et al. 1984). Resistant and susceptible DNA pools were constructed by separately bulking equal amounts of DNA from 10 homozygous resistant (IT 0) and 10 homozygous susceptible (IT 4) plants.

Microsatellite markers from homoeologous group-6 chromosomes were used to screen the two DNA pools to find polymorphic markers. They were divided into two groups: genomic-SSRs, including GWM (Röder et al. 1998a, b), GDM (Pestsova et al. 2000), BARC (Song et al. 2002), CFD (Guyomarc'h et al. 2002), WMC (Gupta et al. 2002), and EST-SSRs, including PK (Gupta et al. 2003), KSUM (Yu et al. 2004) and CAU. The CAU primers were designed according to flanking sequences of microsatellite motifs in wheat ESTs from public EST databases in GenBank (Table 1). Each PCR reaction was performed in a total volume of 10 µl containing 10 mM Tris–HCl, pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$, 0.2 mM of dNTP, 25 ng of each primer, 50–100 ng genomic DNA and 0.75 U Taq DNA polymerase. Amplifications were performed at 94°C for 3 min, followed by 45 cycles at 94°C for 1 min, 50–60°C for 1 min, and 72°C for 2 min, with a final extension at 72°C for 10 min. PCR products were separated on 8% non-denaturing polyacrylamide gels for the mapping population analysis and 5% denaturing polyacrylamide gels for chromosome arm assignments. Gels were silver stained and photographed.

Linkage analysis

Linkage between *Pm12* and linked markers was determined using MAPMAKER (Lander et al. 1987), with an LOD threshold of 3.0. The Kosambi mapping function was used to calculate map distances (Kosambi 1944).

Physical mapping of the SSR and EST-SSR markers

Genomic SSR and EST-SSR markers linked to *Pm12* were located using a set of Chinese Spring nullisomic-tetrasomics, ditelosomics and deletion lines. Each marker was mapped to a chromosome bin flanked by breakpoints of the largest deletion possessing the fragment and the smallest deletion lacking it after comparing the amplification patterns. A consensus deletion map of chromosome 6 was constructed by

Table 1 CAU EST-SSR primer sequences linked to *Pm12*

Primer	Forward sequence (5′–3′)	Reverse sequence (5′–3′)	Wheat EST
CAU24	GCTCCTCTCCAAACCTCTCC	TGCTCTAGGGATAGGCCAGC	CJ670530
CAU44	CCTTACCACAACAAGGAGCC	GTCGAAGGCTATGTAGGCCC	CA681143
CAU127	TAGAGCAATCCAACTCACGG	AAGGGACTGACCCATCAGC	CA640857
CAU186	ACATGCCACCGAACAACG	TGGAACAGTAACCATGCAGC	CA608922
CAU196	AAGAATAGAATAAGGGTACACGGC	ATTTGTGATTGTAGCCACGG	CA637078

placing the breakpoints of 11 deletion lines on a hypothetical chromosome drawn to scale on the basis of the mean length of group-6 chromosomes. The deletion mapping data of each marker on the three homoeologous chromosomes was then combined to position the marker to the shortest chromosome interval.

Results

Genetic analysis of powdery mildew resistance gene *Pm12*

Line #31 and its derivatives remained highly resistant to race E09 (no symptoms or hypersensitive reaction was observed), after crossing and backcrossing with Chinese common wheat lines. The Line #31/3*Jin 207 BC_3F_2 population segregated 206 resistant (IT 0 or 0;) and 99 susceptible (IT 4) ($\chi^2_{3:1} = 9.27$, $P < 0.01$) and the BC_3F_3 progenies segregated 54 homozygous resistant, 152 heterozygous resistant and 99 homozygous susceptible ($\chi^2_{1:2:1} = 15.92$, $P < 0.01$). The significant deviations from 3:1 and 1:2:1 ratios reflected probable low male transmission of the 6B-6S alien translocation chromosome carrying *Pm12*.

Identification of genomic SSR and EST-SSR markers linked to the resistance gene

Of 182 genomic SSR and EST-SSR markers for homoeologous group-6 chromosomes, 18 SSR markers were polymorphic and linked to *Pm12*. These markers included: *Xbarc198, Xbarc247, Xbarc1030, Xbarc1169, Xcau24, Xcau44, Xcau127, Xcau186, Xcau196, Xcfd13, Xcfd80, Xcfd190, Xgwm361, Xgwm570, Xgdm127, Xksum102, Xpk69* and *Xwmc105* (Fig. 1). Four markers, *Xbarc198*, *Xcfd80, Xcfd190*, and *Xgdm127*, co-segregated with the resistance locus. *Xcfd13* mapped 3.7 cM distal to *Pm12*, whereas the remaining markers were tightly linked to *Pm12*, revealing minimal recombination between wheat chromosome 6B and the *Aegilops speltoides* segment.

Physical mapping of the resistance gene *Pm12* and its linked SSR markers

Among the genomic and EST SSR markers, *Xcfd13, Xcfd190, Xbarc198* and *Xwmc105* were physically

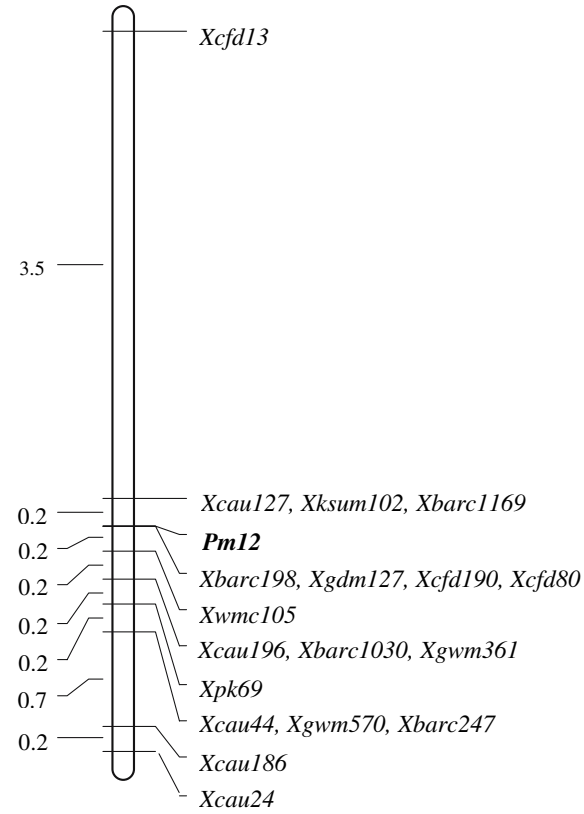

Fig. 1 Linkage map of *Pm12* and its linked microsatellite markers. The numbers on the left indicated the genetic distances (cM) between adjacent loci

mapped to the short arm; *Xbarc1030* and *Xgwm361* were assigned to the long arms of homoeologous group 6 chromosomes (Sourdille et al. 2004). Based on the amplification patterns in Chinese Spring and its nullisomic-tetrasomics, ditelosomics and deletion lines, the rest of the *Pm12*-linked genomic SSR and EST-SSR markers were mapped to chromosome 6B and physically assigned to specific bins. For example, *Xcau127* amplified 3 DNA fragments in Chinese Spring and susceptible plants, but only 2 DNA fragments in Chinese Spring N6AT6B, N6BT6A, N6DT6A, Line #31 and resistant plants (Fig. 2). The absence of a 153 bp DNA fragment in Chinese Spring N6BT6A, Line #31 and resistant plants indicated that the *Pm12* translocation involved chromosome 6B. Six microsatellite loci, *Xcau44*, *Xcau127*, *Xcau186*, *Xcfd13*, *Xcfd190* and *Xgwm570*, were detected loci on all three homoeologous chromosomes 6A, 6B and 6D. *Xcau196* and *Xpk69* amplified loci on 6A and 6B, *Xcau24* and *Xbarc1169* detected loci on 6B and 6D,

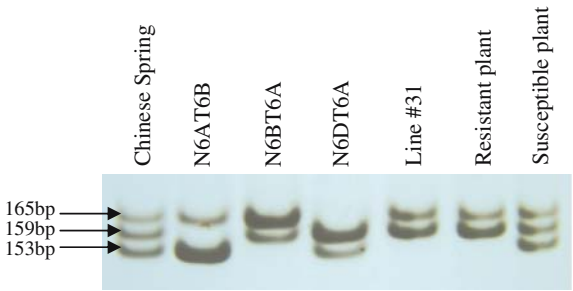

Fig. 2 Amplification patterns of CAU127 on 8% non-denaturing polyacrylamide gel. The fragments *Xcau127/153*, *Xcau127/159* and *Xcau127/165* are indicated with arrows

Xcfd80 detected loci on 6A and 6D. However, *Xbarc1030* and *Xgdm127* identified loci only on chromosome 6D and *Xbarc198*, *Xbarc247*, *Xgwm361*, *Xksum102*, and *Xwmc105* detected loci only on chromosome 6B. Overall, of 18 polymorphic loci, 18, 16, 11 and 9 loci were located on 6S, 6B, 6A and 6D, respectively, indicating a relative closer relationship between 6S and 6B than between 6S and 6A or 6S and 6D. After combining the deletion mapping results from three homoeologous chromosomes, a consensus physical mapping of *Pm12*-linked microsatellite markers was constructed and each marker was assigned to the shortest possible chromosome interval (Fig. 3). *Xcfd13*, *Xbarc1169* and *Xksum102* were physically mapped to the distal telomeric region, along with *Xcau127*, *Xbarc198*, *Xcfd190*, *Xgdm127* to the middle region, and *Xwmc105* and *Xcfd80* to the proximal region of the short arm. It was also shown that *Xcau196*, *Xcau186*, *Xcau24*, *Xbarc247*, *Xcau44*, *Xgwm570 and Xpk69* were located on the distal telomeric region, along with *Xbarc1030* and *Xgwm361* to the middle part of the long arm.

Recombination between wheat 6B and *Ae. speltoides* 6S chromosomes

The telomeric physical locations of *Xcfd13* and *Xcau24* and their close genetic distances to *Pm12* (3.7 cM and 1.7 cM, respectively) revealed severe recombination suppression between wheat chromosome 6B and *Ae. spelotides* chromosome 6S as expected for a large alien translocation. However, eight recombination breakpoints were observed between wheat chromosome 6B and *Ae. speltoides*

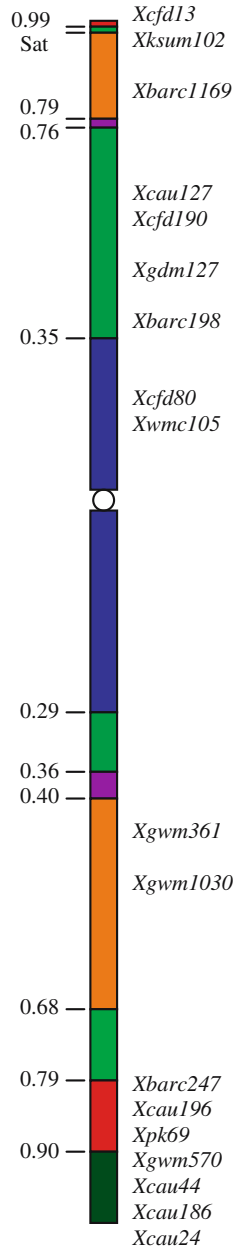

Fig. 3 Physical mapping of *Pm12* linked SSR markers on the consensus homoeologous group 6 chromosomes. Deletion breakpoints were indicated with lines and fraction length (FL) values were on the left. SSR markers, on the right, were assigned to the corresponding deletion bin

chromosome 6S, resulting in 28 recombinants divided into eight classes. Three breakpoints close to markers *Xcfd13, Xcau127* and *Xwmc105* were located on the short arm while another 5 breakpoints were assigned to the long arm (Fig. 4). Among the

recombination events, 18 occurred near *Xcfd13*; 4 close to *Xcau186*; and single recombinations were observed beside *Xcau24, Xcau44, Xcau127, Xbarc1030*, *Xbarc1169*, *Xksum102, Xpk69* and *Xwmc105* (Fig. 4). One heterozygous resistant plant, 1338-8, lacked the entire long arm of chromosome 6S. This plant was self-pollinated to obtain 4 homozygous resistant plants containing a much shorter segment of chromosome 6S with the aid of genomic and EST SSR markers.

Genomic and EST SSR markers linked to *Pm12* were validated using 5 resistant and 5 susceptible plants selected from crosses Line #31/8*Jing 411, Line #31/6*87-1, Line #31/3*Nongda 101 and Line #31/3*Jin 190. No recombinants were found between the marker loci and *Pm12* among this set of materials. The lack of recombination was attributed to the small numbers of plants used in backcrossing and progeny testing.

Discussion

Genetic and physical mapping of powdery mildew resistance gene *Pm12*

Gene *Pm12* was introduced into common wheat by crossing variety Wembley and *Ae. speltoides* and backcrossing 5 times with Wembley. The resistance gene was initially located on chromosome 6A by monosomic analysis (Miller et al. 1988). Using RFLPs, however, *Pm12* was mapped to a 6BS-6SS.6SL translocation chromosome with the breakpoint proximal to *Xpsr551-6B* (Jia et al. 1996). SSR mapping confirmed that the translocation involved wheat chromosome 6B. Four SSR markers, *Xbarc198, Xgdm127, Xcfd190*, and *Xcfd80*, co-segregated with *Pm12*. However, the physical bins with these markers span most of the 6SS chromosome arm (76%). *Xwmc105* was located on group 6 close to the centromere (Sourdille et al 2004). A recombination between *Xwmc105* and *Pm12* was identified in the mapping population. Hence the likely physical position of *Pm12* is between *Xwmc105* and *Xcau127* on 6SS (Fig. 4).

Recombination between the wheat 6B and *Ae. speltoides* 6S chromosomes

It has been suggested that *Ae. speltoides* (SS genome) contributed the B genome to tetraploid and hexaploid wheats (Sarkar and Stebbins 1956; Riley et al. 1969); other researchers argued against *Ae. speltoides* as the likely donor (Kimber and Athwal 1972; Dvorak and Zhang 1990; Huang et al. 2002). In any case, no recombination was observed between wheat chromosome 6B and the 6S segment in Line #31 by Jia et al. (1996) and a very low frequency of recombination

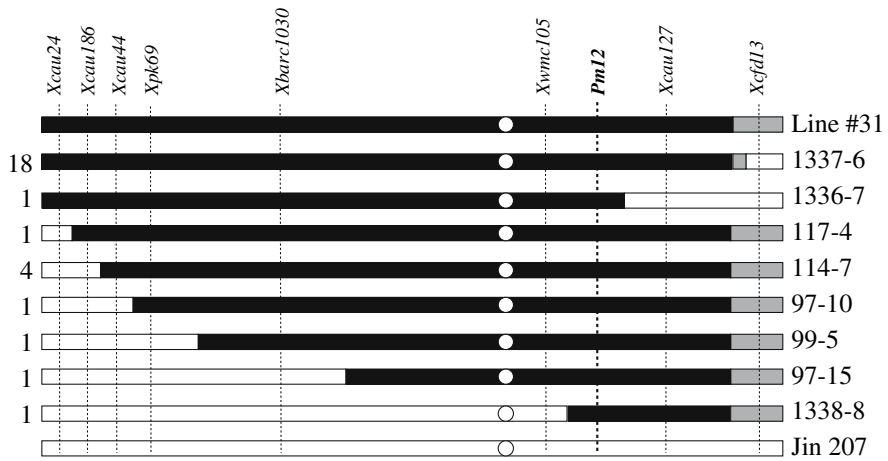

Fig. 4 Comparative organization of recombinants between chromosomes T6BS-6SS.6SL and 6B. The extent of 6B chromosome segments in Jin 207 (*blank*) and Line# 31 (*gray*) and 6S chromosome segments (*black*) in Line #31 and each recombinant is shown. *Blank circles* represent the centromeres. The breakpoint positions may lie anywhere between two adjacent SSR marker loci. The numbers on the left and right sides of chromosomes represent numbers and names of recombinants, respectively. The *Pm12* gene lies between *Xcau127* and *Xwmc105*

(5.4 cM) between distally located markers in group 6 chromosomes was detected in the present work (Fig. 1). Only 28 recombinants were identified in 305 plants (610 gametes); 18 involved *Xcfd13* and this polymorphism probably represented a difference between Wembley (the original wheat parent) and Jin 207. Unfortunately Wembley was not included in the study. Because of their ordered groupings, it appears likely that the other 10 recombinants involved 6B-6S recombination events.

Pm12 is highly effective and confers powdery mildew resistance worldwide (Duan et al. 1998; Niewoehner and Leath 1998; Huang and Röder 2004). However, it has not been used in any cultivar because of poor agronomic traits probably associated with the alien segment. A smaller alien segment should be achieved by crossing recombinants 1336-7 and 1338-8 and selecting *Pm12* and wheat alleles at *Xcau127* and *Xwmc105* as was done with rye and wheat recombinants by Lukaszewski (2000).

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