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Chromosomal location of a *Triticum dicoccoides*-derived powdery mildew resistance gene in common wheat by using microsatellite markers

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Abstract The powdery mildew resistance has been transferred from an Israeli wild emmer (*Triticum dicoccoides*) accession 'G-305-M' into common wheat by crossing and backcrossing (G-305-M/781//Jing 411*3). Genetic analysis showed that the resistance was controlled by a single dominant gene at the seedling stage. Among the 102 pairs of SSR primers tested, four polymorphic microsatellite markers (*Xpsp3029*, *Xpsp3071*, *Xpsp3152* and *Xgwm570*) from the long arm of chromosome 6A were mapped in a BC_2F_3 population segregating for powdery mildew resistance and consisting of 167 plants. The genetic distances between the resistance gene and these four markers were: 0.6 cM to *Xpsp3029*, 3.1 cM to *Xpsp3071*, 11.2 cM to *Xpsp3152* and 20.4 cM to *Xgwm570*, respectively. The order of these microsatellite loci agreed well with the established microsatellite map of chromosome arm 6AL. We concluded that the resistance gene was located on the long arm of chromosome 6AL. Based on the origin and chromosomal location of the gene, it is suggested that the resistance gene derived from 'G-305-M' is a novel powdery mildew resistance gene and is temporarily designated *MlG*.

Keywords Common wheat · Wild emmer (*Triticum dicoccoides*) · *Erysiphe graminis* f.sp. *tritici* · Powdery mildew resistance · Microsatellite · Chromosomal location

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Introduction

Powdery mildew, caused by *Erysiphe graminis* f.sp. *tritici*, is one of the most important wheat diseases in China and worldwide. Disease resistance has been proved one of the most effective and environmentally safe approaches to control it. However, the resistance is usually short-lived due to changes of the pathogen population (Zadoks 1993), especially when a single resistance gene is deployed over a wide area. Hence, it is necessary to search for novel resistance genes in wheat breeding. Up to now, 30 major wheat powdery mildew resistance genes (*Pm1–Pm30*) have been reported (McIntosh et al. 1998; Järve et al. 2000; Peusha et al. 2000; Rong et al. 2000; Liu et al. 2002), some of which were introduced from wheat relatives. Wild emmer, *Triticum dicoccoides* (2n = 4*x* = 28; genome AABB), is the progenitor of cultivated tetraploid and hexaploid wheat and has a great potential for wheat improvement (Nevo 1995; Nevo et al. 2002). Wild emmer has been reported to be highly resistant to yellow rust (Gerechter-Amitai and Stubbs 1970), leaf rust (Moseman et al. 1985), stem rust (Nevo et al. 1991) and powdery mildew (Moseman et al. 1984). Several disease resistance genes have already been introduced from wild emmer into cultivated wheat, such as *Pm16* (Reader and Miller 1991), *Pm26* (Rong et al. 2000), *Pm30* (Liu et al. 2002), *Yr15* (Gerechter-Amitai et al. 1989) and *YrH52* (Peng et al. 1999).

Molecular markers, such as restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP) and random amplified polymorphic DNA (RAPD), were used to map powdery mildew resistance genes in wheat. So far, RFLP markers for *Pm1, Pm2, Pm3, Pm4, Pm12, Pm13* and *Pm26* (Hartl et al. 1993, 1995; Ma et al. 1994; Donini et al. 1995; Jia et al. 1996; 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* and *Pm24* (Hartl et al. 1999; Huang et al. 2000) have been established.

Microsatellites, also known as simple sequence repeats (SSRs), have the advantages of being easy to handle, inexpensive and reliable. Such markers in wheat are chromosome-specific and can detect a high level of polymorphism. Microsatellite-based linkage maps have been established in rice (Wu and Tanksley 1993), maize (Taramino and Tingey 1996), barley (Liu et al. 1996), wheat (Röder et al. 1998) and wild emmer (Peng et al. 2000a). In wheat, microsatellite markers were successfully used to map *Pm24* (Huang et al. 2000), *Pm27* (Järve et al. 2000), *Yr15* (Chagué et al. 1999), *YrH52* (Peng et al. 1999, 2000b) and *Pm30* (Liu et al. 2002).

The present paper reports the identification and the chromosomal location of a new powdery mildew resistance gene derived from wild emmer by using wheat microsatellite markers.

Materials and methods

Plant materials

Wild emmer (*T. dicoccoides*) accession 'G-305-M', kindly provided by Dr. Z.K. Gerechter-Amitai (Agricultural Research Organization, Institute of Plant Protection, the Volcani Center, Israel), was used as the donor of the powdery mildew resistance gene. Susceptible common wheat line '781' and elite cultivar 'Jing 411' were used as recipients for crossing and backcrossing. Six segregating BC_2F_3 families derived from the cross 'G-305-M/781//Jing 411*3' were chosen for the genetic analysis of the powdery mildew resistance.

Powdery mildew test

One prevailing local isolate of *E. graminis* f.sp. *tritici*, Race No.15, virulent to *Pm1, Pm3, Pm5* and *Pm8* but avirulent to accession 'G-305-M' and its derivatives, was used for the powdery mildew test. Inoculations were performed by brushing conidia from neighboring sporulating susceptible seedlings of 'Yanda 1817' onto the test seedlings.

The test results were scored about 2 weeks after inoculation when 'Yanda 1817' was heavily infected, on a 0, 0;, and 1 to 4 scale, with 0 representing no visible symptoms, 0; for necrotic flecks, and 1, 2, 3, 4 for highly resistant, resistant, susceptible and highly susceptible reactions, respectively. In our test, all resistant plants had the infection type of 0; and all susceptible plants had the infection type of 4.

Microsatellite analysis

One BC_2F_3 family segregating for powdery mildew resistance and consisting of 167 plants was chosen for SSR analysis. Instead of bulked segregant analysis (BSA), DNA samples of one resistant plant and one susceptible plant from this segregating population were arbitrarily chosen for microsatellite polymorphism analysis, and the polymorphic primers were then tested in the segregating population for linkage analysis between the SSR markers and the resistance gene.

Total DNA was extracted from the seedling leaf by the cetyltrimethylammonium bromide (CTAB) method (Saghai-Maroof et al. 1984) with minor modifications.

Wheat microsatellite primers used were kindly provided by Dr. M.S. Röder [Institut fur Pflanzengenetik und Kulturpflanzenforschung (IPK), Gatersleben, Germany] and Dr. M.D. Gale (John Innes Centre, UK) (Bryan et al. 1997), or synthesized according to the sequences published by Röder et al. (1998). Each PCR reaction was conducted in a total volume of 20 µl containing 10 mM of Tris–HCl, pH 8.3, 50 mM of KCl, 1.5 mM of $MgCl_2$, 0.2 mM of dNTPs, 1.25 U of *Taq* DNA polymerase, 50 ng of each primer, and 50–100 ng of total DNA. The amplifications were performed in a PE 480 Thermal Cycler for 35 cycles at 95 °C for 10 s, 50–63 °C (depending upon the microsatellite primers) for 10 s and 72 °C for 30 s with a final extension at 72 °C for 10 min (Huang et al. 2000).

The samples of 1.5–3 µl PCR products were mixed with an equal volume of loading buffer (98% formamide, 0.3% of each bromophenol blue and xylene cyanol, and 10 mM of EDTA), denatured at 95 °C for 5 min and chilled on ice. Electrophoresis was carried out on a 4% denaturing polyacrylamide gel (0.4 mm thick) in 1 × TBE (90 mM Tris-borate, 2 mM EDTA) at 85 W and 45 °C for 45 min. Gels were then silver stained and photographed.

Linkage analysis

Linkage between markers and the resistance gene was analyzed by using MAPMAKER/Version 2.0 with a LOD threshold of 3.0 (Lander et al. 1987).

Results

Powdery mildew test

All the six segregating families tested showed a segregation ratio of 3 resistant to 1 susceptible (Table 1), suggesting that a single dominant gene is controlling the resistance. This result indicates that a single dominant resistance gene has been successfully introduced into common wheat from wild emmer wheat accession 'G-305-M'. This gene is temporarily designated *MlG*.

Identification of microsatellite markers linked to *MlG*

Ninety six wheat microsatellite primers were screened; only one primer pair WMS570 yielded polymorphic DNA fragments between the resistant and susceptible plants.

Table 1 Segregation analysis of BC_2F_3 families of the cross 'G-305-M/781//Jing 411*3' for reaction to powdery mildew Race No.15 at the seedling stage

F_3 families	No. of plants	Resistant	Susceptible	Expected ratio	χ^2	*P*
1	167	122	45	3:1	0.337	0.50–0.70
2	87	72	15	3:1	2.793	0.05–0.10
3	86	64	22	3:1	0.016	0.90
4	85	59	26	3:1	1.416	0.20–0.30
5	95	74	21	3:1	0.424	0.50–0.70
6	116	80	36	3:1	2.253	0.10–0.20

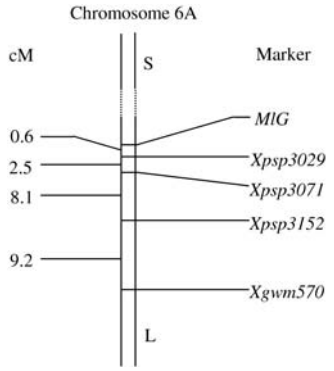

Fig. 1 An integrated genetic map of the *MlG* region. *S*, short arm; *L*, long arm

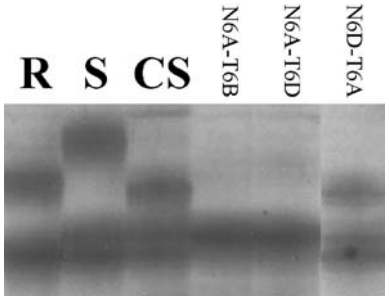

Fig. 2 The amplification of the resistant plant (*R*), the susceptible plant (*S*), Chinese spring (*CS*), and N6A-T6B, N6A-T6D and N6D-T6A lines with PSP3029, showing the chromosome location of *Xpsp3029* linked to *MIG*

After testing among 48 DNA samples of the BC_2F_3 segregating population (including 24 resistant plants and 24 susceptible plants), WMS570 amplified polymorphic amplicons *Xgwm570/135* and *Xgwm570/147*, which segregated with the resistance gene *MlG* and its susceptible allele, respectively, indicating that *Xgwm570* was linked to the *MlG* locus.

On the wheat microsatellite map constructed by Röder et al. (1998), *Xgwm570* was mapped on the long arm of chromosome 6A. Other primer pairs located on chromosome arm 6AL were tested to search for polymorphic markers. Three more primer pairs (PSP3152, PSP3071 and PSP3029, kindly provided by Dr. M.D. Gale, John Innes Centre, UK) detected polymorphism between the resistant and susceptible plants. The microsatellite loci *Xpsp3152*, *Xpsp3071* and *Xpsp3029* were also found to be linked to *MlG*. The polymorphic fragments amplified by three primer pairs were *Xpsp3152/210*, *Xpsp3071/160* and *Xpsp3029/175* for *MlG*, and *Xpsp3152/240*, *Xpsp3071/155* and *Xpsp3029/185* for the susceptibility allele, respectively.

Linkage alignment between *MlG* and the microsatellite markers

Linkage analysis (Table 2) indicated that the order of the four markers and the *MlG* locus was *MlG-Xpsp3029-Xpsp3071-Xpsp3152-Xgwm570*, with genetic distances of 0.6 cM, 2.5 cM, 8.1 cM and 9.2 cM for the four intervals. According to the microsatellite map of wheat published by Röder et al. (1998) and Stephenson et al. (1998), the genetic map of the *MlG* region was constructed (Fig. 1). The order of these microsatellite loci agreed well with the established maps of chromosome arm 6AL. Based on the analysis, we concluded that *MlG* is located on the long arm of chromosome 6A, close to the centromere.

Table 2 Linkage analysis of the powdery mildew resistance gene *MlG* and the microsatellite loci in one BC_2F_3 family with 167 plants derived from the cross 'G-305-M/781//Jing 411*3'

Microsatellite loci	122 Resistant plants Marker genotype[a]			45 Susceptible plants Marker genotype		
	AA	AB	BB	AA	AB	BB
Xgwm570	39	67	16	2	6	37
Xpsp3152	41	73	8	1	3	41
Xpsp3071	42	78	2	0	0	45
Xpsp3029	41	80	1	0	0	45

[a] Note: AA = homozygous for a marker of the resistant parent; BB = homozygous for a marker of the susceptible parent; AB = heterozygous marker

Discussion

Microsatellite loci, *Xpsp3029, Xpsp3071, Xpsp3152* and *Xgwm570*, all located on the long arm of chromosome 6A, were linked to the powdery mildew resistance gene *MlG* introgressed from wild emmer G-305-M. These results enabled the location of *MlG* on the long arm of chromosome 6A.

On the hexaploid wheat genetic map published by Stephenson et al. (1998), primer pair PSP3029 amplified DNA fragments from multiple loci, one locus on chromosome arm 2AS, one on chromosome arm 6AS, far from the centromere, and one on chromosome arm 6AL, close to the centromere. PSP3029 was used to amplify the Chinese Spring and a set of nulli-tetrasomic lines, and the *Xpsp3029* marker linked with *MlG* was located on chromosome 6A (Fig. 2). *Xpsp3071* and *Xpsp3152* were single-locus markers on chromosome arm 6AL. *Xgwm570* was mapped on the central part of chromosome arm 6AL (Röder et al. 1998). The *Xpsp3029* marker linked with *MlG* is linked to *Xpsp3071, Xpsp3152* and *Xgwm570*, and can therefore be the 6AL locus.

Two powdery mildew resistance genes have been mapped on chromosome 6A. *Pm21*, located on the short arm of chromosome 6V of *Haynaldia villosa*, was translocated to chromosome 6A of common wheat, forming a T6AL.6VS line (Qi et al. 1996). *MlRE*, introgressed from *T. dicoccum* 119, was mapped to the distal part of the long arm of chromosome 6A, linked with the microsatellite loci *Xgwm427* and *Xgwm617* (Chantret et al. 2000). The location of *MlG* on the long arm of chromo-

some 6A close to the centromere suggests that *MlG* differs from these two powdery mildew resistance genes on chromosome 6A.

Three powdery mildew resistance genes had already been introgressed from wild emmer into common wheat: *Pm16* located on chromosome 4A (Reader and Miller 1991), *Pm26* on chromosome arm 2BS (Rong et al. 2000), and *Pm30* on chromosome arm 5BS (Liu et al. 2002). Thus, the powdery mildew resistance gene *MlG* on chromosome arm 6AL, introgressed from wild emmer accession 'G-305-M', may be a novel powdery mildew resistance gene.

Although *Xpsp3029* is closely linked to *MlG* (Fig. 1), with a genetic distance of 0.6 cM, the physical size between *MlG* and *Xpsp3029* may be higher than expected because of a possible reduction of recombination rate that often occurs in distant crosses (Dvorak and McGuire 1981; Korol et al. 1994; Dubcovsky et al. 1997). Thus for the purpose of map-based cloning of the resistance gene, it is necessary to search for new molecular markers to map *MlG* further and more precisely.

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