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Microsatellite mapping of powdery mildew resistance allele *Pm5d* from common wheat line IGV1-455

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Abstract The powdery mildew resistance allele *Pm5d* in the backcross-derived wheat lines IGV1-455 (CI10904/7*Prins) and IGV1-556 (CI10904/7*Starke) shows a wide spectrum of resistance and virulent pathotypes have not yet been detected in Germany. Although this allele may be distinguished from the other documented *Pm5* alleles by employing a differential set of *Blumeria graminis tritici* isolates, the use of linked molecular markers could enhance selection, especially for gene pyramiding. *Pm5d* was genetically mapped relative to six microsatellite markers in the distal part of chromosome 7BL using 82 F_3 families of the cross Chinese Spring × IGV1-455. Microsatellite-based deletion line mapping placed *Pm5d* in the terminal 14% of chromosome 7BL. The closely linked microsatellite markers *Xgwm577* and *Xwmc581* showed useful variation for distinguishing the different *Pm5* alleles except the ones originating from Chinese wheat germplasm. Their use, however, would be limited to particular crosses because they are not functional markers. The occurrence of resistance genes closely linked to the *Pm5* locus is discussed.

Keywords Common wheat · Microsatellite markers · Powdery mildew · Resistance genes

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Introduction

Powdery mildew caused by *Blumeria graminis* f.sp. *tritici* is one of the most destructive foliar diseases of common wheat worldwide and is particularly prevalent in areas with cool or maritime climates. Breeding of resistant cultivars is the most economical and environmentally sound method to decrease the use of fungicides and to reduce crop losses due to this disease. Currently, 38 major host resistance genes are documented (Miranda et al. 2006; McIntosh personal communication). Five of these resistance gene loci (*Pm1*, *Pm3*, *Pm4*, *Pm5*, and *Pm8*) have more than one resistance allele making a total of 54 named *Pm* resistance genes.

The availability of different resistance genes allows their pyramiding into the same genotypes as a means of delaying a breakdown of resistance. Molecular markers tightly linked to disease resistance

genes allow selection for resistance in the absence of the pathogen. Various molecular marker types have been used for mapping powdery mildew resistance genes in wheat (Huang and Röder 2004). Microsatellites, also termed simple sequence repeats (SSR), reveal much higher polymorphisms in wheat than any other marker system and are now being preferentially used for genetic mapping. Linkage to microsatellites was recently described for *Pm33* (Zhu et al. 2005), *Pm34* (Miranda et al. 2006), and several tentatively designated genes, e.g. *MlZec1* (Mohler et al. 2005), *PmY201* and *PmY212* (Sun et al. 2006).

Among the 38 powdery mildew resistance loci, *Pm5* was located on the long arm of chromosome 7B (Law and Wolfe 1966; Lebsock and Briggle 1974). *Pm5* is widespread in cultivars and landraces of China and Europe (Huang et al. 1997; Zeller et al. 1998). Eight recessive resistance alleles at, or near, the *Pm5* locus have been reported (Hsam et al. 2001; Huang et al. 2000a, 2002), of which *Pm5e* was mapped relative to microsatellite markers (Huang et al. 2003). Line IGV1-455 carrying *Pm5d* provides resistance to all powdery mildew races in Germany and is, therefore, a valuable resistance source for the enhancement of wheat germplasm (Hsam et al. 2001). The major objectives of the present study were to construct a genetic linkage map around the powdery mildew resistance gene *Pm5d* using microsatellite markers, to determine the location of the resistance gene on the physical map of wheat chromosome 7B and to identify microsatellite markers which could be useful for marker-assisted selection (MAS).

Materials and methods

Plant materials

A total of 82 F_3 families originating from a cross between the powdery mildew-susceptible cultivar Chinese Spring (CS) and the resistant line IGV1-455 was used for linkage analysis of molecular markers and powdery mildew resistance allele *Pm5d*. Wheat genotypes Hope (*Pm5a*), Kormoran (*Pm5b*), *T. sphaerococcum* cv. Kolandi (*Pm5c*), IGV1-455 (*Pm5d*), IGV1-556 (*Pm5d*), Fuzhuang 30 (*Pm5e*), Xiaobaidong (*Mlxbd*, a recessive *Pm* gene on 7BL), Prins (nearly isogenic to IGV1-455), CS, and another 22 wheat genotypes (Table 2) were used for determining allele sizes of closely linked microsatellite markers. The backcross-derived wheat lines IGV1-455 (CI10904/7*Prins) and IGV1-556 (CI10904/7*Starke) were kindly provided by Dr. J. MacKey (Uppsala, Sweden). CS deletion lines 7BS-1, 7BL-14, 7BL-2, 7BL-9, 7BL-7, 7BL-10, 7BL-3, kindly provided by J. Raupp (Wheat Genetics Resource Centre, Kansas State University, USA), were used for physical mapping of powdery mildew resistance allele *Pm5d*. The fraction length (FL) value of a given deletion line identifies the breakpoint in the deleted chromosome and the length of the remaining chromosome arm from the centromere relative to the length of the complete arm (Endo and Gill 1996). Assignment of markers to bins was described in Werner et al. (1992).

Powdery mildew reaction tests

A set of up to 13 *Blumeria graminis tritici* (Bgt) pathotypes was used to test some of the cultivars and lines used in the present study (Table 1). These Bgt isolates possess the ability to differentiate known *Pm5* alleles (Hsam et al. 2001). To follow segregation of *Pm5d* in the mapping population, Bgt isolates 10 and 14, both avirulent to IGV1-455 and virulent to CS, were used. A minimum of 15 plants of each F_3 family was tested to identify the genotype of each corresponding F_2 plant. Reaction tests were conducted on agar-mounted detached primary leaf segments. The methods of inoculation, conditions of incubation and disease assessment were according to Hsam et al. (2001). χ^2 tests for goodness-of-fit were used to test for deviations of observed and expected segregation ratios.

Molecular mapping techniques

Nuclear DNA extraction from primary leaves followed the procedure described by Huang et al. (2000b). For genetic mapping of *Pm5d*, eight microsatellite markers from the distal half of chromosome 7BL (*Xgwm146*, *Xgwm611*, *Xgwm577*, *Xwmc70*, *Xwmc526*, *Xwmc581*, *Xwmc613* and *Xbarc1073*) were chosen from the GrainGenes database (http://wheat.pw.usda.gov). Microsatellite analysis was carried out according to Huang et al. (2000c). A partial linkage map around *Pm5d* was computed with the program JoinMap® 3.0 (Van Ooijen and

Table 1 Differential reaction of 21 wheat cultivars/lines after inoculation with 13 isolates of *Blumeria graminis* f.sp. *tritici*

Cultivar/line	*Blumeria graminis tritici* isolates													Gene
	2	5	9	10	12	13	14	15	16	17	71	77	E	
Hope	s	s	s	r	s	s	r	s	s	s	r, i	s	r	*Pm5a*
Spica	s	s	s	r	s	s	r	s	s	s	–	–	–	*Pm5a*
Kormoran	s	r, i	s, i	r	s	s	r	s	s	s	s	r, i	s	*Pm5b*
Dream	s	r, i	s, i	r	s	i	r	s	s	s	–	–	–	*Pm5b*
Kolandi	s, i	s	s	r	s	i	r	s	s	s	r	s	s	*Pm5c*
IGV1-455	r	r	r	r	r	r	r	r	r	r	r	r	r	*Pm5d*
IGV1-556	r	r	r	r	r	r	r	r	r	r	r	r	r	*Pm5d*
Fuzhuang 30	r	r	r	r	r	r	r	r	r	r	s	s	s	*Pm5e*
Xiaobaidong	r	r	r	r	r	r	r	r	r	r	s	s	r	*Mlxbd*
Chinese Spring	s	s	s	s	s	s	s	s	s	s	s	s	s	*None*
Prins	s	s	s	s	s	s	s	s	s	s	s	s	s	*None*
Renan	s	r	r	r	r	s	s	r	s	s	r	r	r	*Pm4b*
Atlantis	s	r	r	r	r	s	s	r	s	s	r	r	r	*Pm4b*
Solitär[a]	s	r, i	r	r, i	s	r, i	r, i	r, i	i	s	i	r	s	*Pm6*
Enorm[a]	r	r	r	r	r	r	r	s	r	i	s	r	s	*Pm3b + 5*
Petrus[a]	r	r	r	r	r	s	s	r	s	r	r	r	r	*Pm4b + 8*
Greif[a]	s	r, i	r	r	s	r, i	r	r, i	i	s	i	r	s	*Pm5 + 6*
Triso[a]	r	r	r	r	r	s	r	r	s	s	r	r	r	*Pm1 + 4b + 5*
Contra[a]	s	r, i	r	r	r	r, i	r, i	r	i	s	r	r	r	*Pm2 + 4b + 6*
Borneo[a]	s	r, i	r	r	r	r, i	r	r	i	s	r	r	r	*Pm4b + 5 + 6*
Centrum[a]	s	r, i	r	r	r	r, i	r	r	i	s	r	r	r	*Pm2 + 4b + 5 + 6*

r, resistant; s, susceptible; i, intermediate; –, not tested

[a] *Pm* gene classification according to the German Seed Board list (Anonymous 2006)

Voorrips 2001). Map distances were calculated using the Kosambi function (Kosambi 1944), which assumes cross-over interference. Charts of genetic linkage maps were drawn with the computer program MapChart 2.1 (Voorrips 2002).

Results

Powdery mildew reaction tests

The disease response patterns of 21 wheat cultivars and lines possessing either single resistance genes or gene combinations are given in Table 1. All wheats carrying a *Pm5* allele as the only resistance factor were resistant to Bgt pathotypes 10 and 14; however, a differential response to other isolates, especially 2, 5, 9, 13, 71, 77 and E, allowed identification of each allele by a unique reaction pattern. Lines IGV1-455 and IGV1-556 carrying *Pm5d* were resistant to all isolates. All other entries with known resistance genes and gene combinations showed differential responses. Cultivars Borneo, Centrum, Enorm, Greif and Triso were known to carry alleles at the *Pm5* locus (Anonymous 2006), but the specific alleles were undetermined. Clearly, none carried *Pm5d*. Segregation of F_3 lines in the CS × IGV1-455 mapping population with isolates 10 and 14 showed 26 homozygous resistant, 38 segregating and 18 homozygous susceptible lines ($\chi^2_{1:2:1}$ = 2.00, $P > 0.3$), indicating variation at a single locus.

Genetic and physical mapping

The powdery mildew resistance gene in line IGV1-455 was previously identified and designated *Pm5d* (Hsam et al. 2001). Eight microsatellite markers

from the distal half of chromosome 7BL were assayed on DNA from the nearly isogenic lines (NILs), IGV1-455 and Prins, and the parental lines of the mapping population. Microsatellite markers *Xbarc1073*, *Xgwm146*, *Xgwm577*, *Xgwm611*, *Xwmc526*, *Xwmc581* and *Xwmc613* showed polymorphism between IGV1-455 and Prins, whereas *Xwmc70* was null-allelic for both. In the parental survey, polymorphism was revealed for *Xgwm146*, *Xgwm577*, *Xgwm611*, *Xwmc70*, *Xwmc581* and *Xwmc613*. These six markers were used to generate a genetic map of the target region in the cross CS × IGV1-455. *Xgwm146*, *Xwmc581* and *Xwmc613* showed co-dominant inheritance, whereas the other three were dominant in repulsion phase. SSR marker *Xwmc581* was duplicated in both parental lines and showed fragment sizes of 125 bp and 141 bp in CS and 127 bp and 145 bp in IGV1-455. These duplicated bands were inherited together. Due to extreme stutter combined with the small size difference between the marker alleles of the parents, *Xwmc613* could be scored only as a dominant marker linked in repulsion with *Pm5d*. The genetic map of the distal part of wheat chromosome 7BL spanned a distance of 32.5 cM (Fig. 1). *Pm5d* was flanked by loci *Xgwm611* and *Xgwm577* with linkage distances of 2.1 cM and 2.0 cM, respectively. A set of seven CS deletion lines, each line carrying a different deletion of chromosome 7B, was used for targeting resistance allele *Pm5d* to an individual breakpoint interval. While deletion line 7BS-1 showed amplification for the six markers linked to the disease resistance locus, no PCR products were obtained from the DNA of any of the other lines with 7BL deletions. This indicated that *Pm5* is located distal to breakpoint 0.86 of deletion line 7BL-3 (Fig. 1).

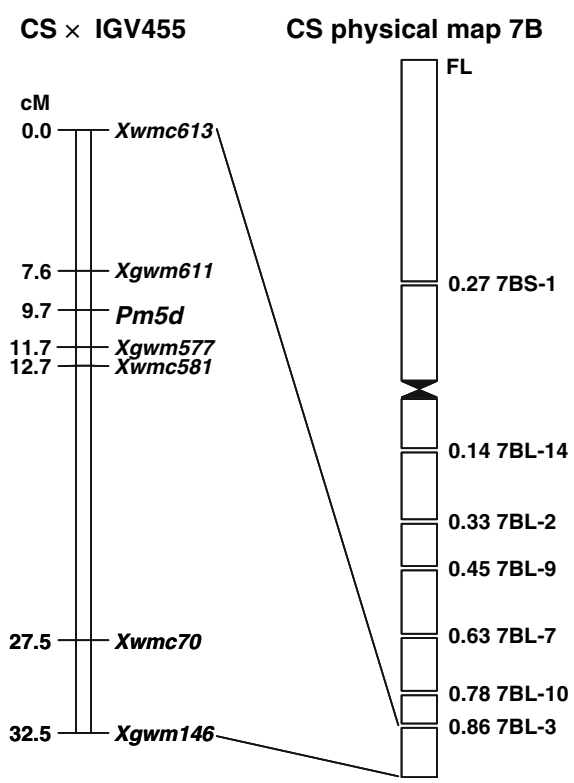

Fig. 1 Genetic and deletion-line maps showing the location of *Pm5d* on wheat chromosome 7BL. cM, centimorgans; FL, fraction length

Allelic sizes of linked microsatellite markers

None of the three closely linked markers could be used singly, or in combination, to distinguish between the different resistance alleles at the *Pm5* locus (Table 2). Wheat lines IGV1-455, IGV1-456 (*Pm5d*), Fuzhuang 30 (*Pm5e*) and Xiaobaidong (*Mlxbd*), all of Chinese origin, shared common marker haplotypes in the region of interest. Alleles of *Xgwm577* distinguished wheat lines carrying resistance alleles *Pm5a*, *Pm5b* or *Pm5c*. The marker size of wheat cultivar Spica was the same as cv. Hope confirming the likely presence of *Pm5a* previously indicated from the disease response pattern. Likewise, Dream had the same allele as the *Pm5b* reference line Kormoran. Chinese wheats with *Pm5* alleles shared a null allele in common with the German cv. Kolibri, carrying *Pm3d*. However, the marker sizes of susceptible CS and Prins and another 14 wheats with divergent *Pm* genes were clearly different from lines carrying *Pm5* alleles. Based on *Xgwm577* marker alleles, *Pm5a* was postulated for cv. Borneo, and *Pm5b* was postulated for Greif, Enorm, Centrum and Triso.

In addition to IGV1-455 and CS, *Xwmc581* was also duplicated in wheat genotypes Hope, Spica and Prins and the Chinese wheats with resistance alleles at the *Pm5* locus. In the set of wheats tested, the 145 bp allele was unique to Chinese wheats possessing *Pm5* resistance alleles. Among *Pm5a*-carrying wheats, a 113 bp allele was present in

Table 2 SSR allelic sizes amplified using three markers linked to *Pm5d* in wheat lines and cultivars

Wheat line/cultivar	Fragment sizes (bp)		
	Xgwm577	*Xwmc581*	*Xgwm611*
Hope (*Pm5a*)	165	127, 131	Null
Spica (*Pm5a*)	165	127, 131	Null
Borneo (*Pm4b + 5a + 6*)	165	113	162
Kormoran (*Pm5b*)	139	123	Null
Dream (*Pm5b*)	139	123	Null
Greif (*Pm5b + 6*)	139	123	162
Enorm (*Pm3b + 5b*)	139	123	172
Centrum (*Pm2 + 4b + 5b + 6*)	139	123	162
Triso (*Pm1 + 4b + 5b*)	139	123	172
Kolandi (*Pm5c*)	137	123	Null
IGV1-455 (*Pm5d*)	Null	127, 145	Null
IGV1-556 (*Pm5d*)	Null	127, 145	Null
Fuzhuang 30 (*Pm5e*)	Null	127, 145	Null
Xiaobaidong (*Mlxbd*)	Null	127, 145	Null
Chinese Spring (None)	133	125, 141	168
Prins (None)	131	125, 141	Null
Axminster/8*Cc[a] (*Pm1a*)	163	127	Null
Weihenstephan M1N (*Pm1c*)	163	127	Null
Asosan/8*Cc[a] (*Pm3a*)	163	127	Null
Chul/8*Cc[a] (*Pm3b*)	163	127	Null
Sonora/8*Cc[a] (*Pm3c*)	163	127	Null
Kolibri (*Pm3d*)	Null	139	164
W150 (*Pm3e*)	169	119	Null
Michigan Amber/8*Cc[a] (*Pm3f*)	163	127	Null
Aristide (*Pm3g*)	163	127	Null
Renan (*Pm4b*)	147	127	Null
Atlantis (*Pm4b*)	135	121	162
Solitär (*Pm6*)	135	121	162
Chiyacao (*Pm24*)	133	127	162
Petrus (*Pm4b + 8*)	135	121	162
Contra (*Pm2 + 4b + 6*)	153	113	172

[a] Seven times backcrossed to Chancellor

Borneo distinguishing it from Hope and Spica. In addition, the non-*Pm5* cv. Contra had the same allele. All cultivars previously classified as carrying *Pm5b* had the same *Xwmc581* allele, but it was also found in *T. sphaerococcum* cv. Kolandi with gene *Pm5c*. Thus *Xwmc581* is only of limited use for MAS of all *Pm5* alleles.

SSR marker *Xgwm611* was not suitable for MAS of *Pm5* because the same marker alleles, or null alleles, were present in many genotypes irrespective of powdery mildew response.

Discussion

The majority of mapped powdery mildew resistance genes in wheat are located at the chromosome ends; for example, resistance gene *mlRD30* is distal to RFLP marker *Xmwg2062* (Singrün et al. 2004) which maps to the terminal 1% of chromosome 7AL (Hohmann et al. 1994). This is also evident for *Pm5* since it was located in the most terminal bin on the deletion map of chromosome 7BL.

All the named *Pm5* alleles can be distinguished based on their differential reactions (Table 1). In addition, their chromosomal location on wheat chromosme 7BL as well as allelism tests in the F_2 and F_3 generations indicated that *Pm5a* to *Pm5d* are alleles (Hsam et al. 2001). However, genuine allelism of some of the named *Pm5* genes appears doubtful. Huang et al. (2000a) observed one susceptible and two segregating lines among the 61 F_3 families of a cross between Hope (*Pm5a*) and Fuzhuang 30 (*Pm5e*), indicating that *Pm5e* is a closely linked resistance gene rather than a *Pm5* allele. Likewise, one susceptible and two segregating families were found in the F_3 progeny of the cross Xiaobaidong (*Mlxbd*) × Selpek (*Pm5*a), whereas no susceptible lines were detected in 277 F_2 progenies of the cross between Xiaobaidong and Fuzhuang 30 (Huang et al. 2000a). These results suggest that genes at, or near, the *Pm5* locus may be clustered as also reported for powdery mildew resistance genes on chromosomes 1A (*Pm3*, *Pm25*, and *Pm* genes from wheat lines Abessi, N324 and GUS122 (Shi et al. 1998; Yahiaoui et al. 2006)) and 7A (*Pm1*, *Pm9*, *mlRD30*, resistance genes in hexaploid germplasms NC96BGTA4 and NC99BGTAG11, and *Mlm2033* and *Mlm80* in einkorn (Singrün et al. 2004; Srnić et al. 2005; Yao et al. 2007)).

The different resistance alleles at the *Pm5* locus could be distinguished from the susceptible allele through the combined use of the closely linked SSR markers *Xgwm577* and *Xwmc581*. *Xgwm577* showed specific alleles for *Pm5a*, *Pm5b* and *Pm5c*, whereas a null allele was found for *Pm5d*, *Pm5e* and *Mlxbd*. Null markers are not as efficient as amplifiable

markers in MAS because they cannot be screened in heterozygotes and therefore require at least two generations for detecting plants carrying target alleles (Ishii and Yonezawa 2007). To circumvent this disadvantage, *Xwmc581* can be used in MAS for any of the three *Pm5* alleles of Chinese origin.

Based on *Xgwm577* alleles, cultivars Greif, Enorm, Centrum and Triso were considered likely to carry *Pm5b* and Borneo possibly possessed *Pm5a*. To our knowledge, only resistance alleles *Pm5a* and *Pm5b* have been distributed in European wheat germplasm. Based on the present reaction tests, specific *Pm5* alleles in complex *Pm* genotypes were difficult to predict. However, Bgt isolate E showing virulence for *Pm3b*, *Pm5b* and *Pm6*, but avirulence for *Pm5a*, supported the postulation of *Pm5b* in cultivars Enorm and Greif (Table 1). This was not possible for Borneo, Centrum and Triso since *Pm4b* which is common to these lines conferred resistance to Bgt isolate E.

In conclusion, the closely linked markers will assist gene postulation in complex *Pm* genotypes and permit MAS of resistance alleles at, or near, the *Pm5* locus in those crosses or populations that have appropriate polymorphisms.

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