

Powdery Mildew Resistance Genes in Wheat: Identification and Genetic Analysis

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Abstract

Wheat powdery mildew, caused by *Blumeria graminis* f. sp. *Tritici* is one of the most devastating diseases of common wheat worldwide. To date, 41 loci (*Pm1* to *Pm45*, *Pm18*=*Pm1c*, *Pm22*=*Pm1e*, *Pm23*=*Pm4c*, *Pm31*=*Pm21*) with more than 60 genes/alleles for resistance to powdery mildew have been identified and located on 18 different chromosomes in bread wheat. 29 resistance genes/alleles have been tagged with molecular markers such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), sequence tagged sites (STS) and simple sequence repeats (SSRs), by using F_2 , back-cross populations, near-isogenic lines (NILs), doubled haploids (DH), recombinant inbred lines (RILs) or bulked segregant analysis (BSA). The detail information on chromosomal location, molecular markers linked to powdery mildew, mapping population and molecular mapping of powdery mildew resistance genes have been reviewed.

Keywords: *Blumeria graminis* f.sp. *tritici*, Molecular markers, Mapping population, Molecular mapping, Powdery mildew resistance gene, *Triticum aestivum*

1. Introduction

Wheat powdery mildew, caused by *Blumeria graminis* (DC.) E.O. Speer f. sp. *Tritici* Em. Marchal (*Bgt*) = *Erysiphe graminis* DC. *Ex Merat* f. sp. *Tritici* Em. Marchal, is one of the most devastating diseases of common wheat occurs in many areas, including China, Germany, Japan, Russia, United Kingdom, South and West Asia, North and East Africa, and the Southeastern United States (Bennett, 1984). Yield losses ranging from 13 to 34% due to this disease (Griffey *et al.*, 1993; Leath & Bowen, 1989). Growing of resistant cultivars offer effective, economically sound and environmentally safe approach to eliminate the use of fungicides and reducing crop losses caused by powdery mildew. There are two types of resistance to powdery mildew. One is called monogenic (vertical) or race specific resistance, which is effective for some isolates of powdery mildew, but ineffective for others. Race specific resistance is mainly via a hypersensitive foliar reaction directly involving single major R genes, designated as *Pm* (powdery mildew) genes, in a gene-for-gene interaction (Bennett, 1984;

Chen and Chelkowski, 1999; Hsam and Zeller, 2002). Race-specific resistance genes are expressed in seedlings and throughout the vegetative cycle of wheat. Though race-specific resistance have been extensively used in wheat breeding programs, selection pressure exerted by cultivars with race-specific resistance genes results in the rapid build-up of isolates with matching virulence genes. Afterward, race-specific resistance breaks down when confronted by pathogen isolates with matching virulence genes and, therefore, is ephemeral.

Another type of resistance to powdery mildew is called adult plant resistance (APR), which retards infection, growth and reproduction of the pathogen in adult plants but not in seedlings. It is also called “slow mildewing” (Shaner, 1973) and “partial resistance” (Hautea *et al.*, 1987). This type of resistance can be identified in cultivars with defeated race-specific genes or lacking known race-specific resistance genes. APR to powdery mildew is more durable than race-specific resistance. For example, APR in wheat cultivar Knox and its derivatives remained effective against powdery mildew infection during the 20 years in which these cultivars were grown commercially (Shaner, 1973). Massey, a derivative of Knox62, was released from Virginia Tech in 1981 (Starling *et al.* 1984), and still has effective powdery mildew resistance in adult plants. Up to now, 41 loci (*Pm1* to *Pm45*, *Pm18*=*Pm1c*, *Pm22*=*Pm1e*, *Pm23*=*Pm4c*, *Pm31*=*Pm21*) with more than 60 genes/alleles for resistance to powdery mildew have been identified and located on various chromosomes in bread wheat and its relatives (Ma *et al.*, 2011; McIntosh *et al.*, 2008; Luo *et al.*, 2009; Li *et al.*, 2009; Hua *et al.*, 2009; He *et al.*, 2009). However, resistances of genes are frequently overcome by new *Bgt* isolates, because the presence and frequency of virulence genes in the pathogen population changes continuously (Leath & Murphy, 1985; Menzies & MacNeil, 1986; Limpert *et al.* 1987; Namuco *et al.* 1987). The effective management strategy has been to replace cultivars when their resistance is no longer effective (Wolf, 1984; Leath & Heun, 1990).

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. The use of PCR based molecular markers to tag genomic regions are more efficient for marker assisted selection (MAS), due to the small amount of DNA template required and easy to handling of large population sizes. The identification of molecular markers of flanking disease resistance genes, simplifies breeding activities such as cultivar development (Bonnett *et al.*, 2005), near isogenic line development (Zhou *et al.*, 2005), and pyramiding resistance genes into single genotypes by marker assisted selection (MAS). Many of the recently reported of *Pm* genes have associated markers (Miranda *et al.*, 2006, 2007; Perugini *et al.*, 2008). Recently, molecular markers such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), sequence tagged sites (STS) and microsatellites, also termed simple sequence repeats (SSRs), have been widely used to tag and identify powdery mildew resistance genes in wheat by using F₂ and back-cross populations, near-isogenic lines (NILs), doubled haploids (DH), recombinant inbred lines (RILs) or bulked segregant analysis (BSA, Michelmore *et al.*, 1991).

2. Chromosomal Location of Identified *Pm* Genes

In recent years, wheat genomics research has increased the use of genetic maps to position a gene of interest between close flanking markers (Haley & Knott, 1992). The application of molecular markers in plant systems increases the efficiency of conventional plant breeding by carrying out indirect selection through molecular markers linked to the traits of interest (Gupta *et al.*, 1999). A linkage map gives information on the position of markers within a linkage group. The map positions are inferred from estimates of recombination frequencies between markers. The distance between these markers is expressed in centimorgan (cM) which represents the recombination rates between them (Jones *et al.*, 1997). Chromosomal positions of several mapped powdery mildew resistance gene loci are presented in Figure 1.

The presence of *Pm* resistant genes is vital not only for monogenic resistance but also the defeated *Pm* genes often confer oligogenic and quantitative type resistance when combined together (Royer *et al.*, 1984; Pedersen & Leath, 1988; Paillard *et al.*, 2000). Chromosomal locations, cultivars/lines, sources and references for the 64 known powdery mildew resistance genes/alleles have been identified as major genes for vertical resistance to powdery mildew in wheat (Ma *et al.*, 2011; McIntosh *et al.*, 2008; Luo *et al.*, 2009; Li *et al.*, 2009; Hua *et al.*, 2009; He *et al.*, 2009) (Table 1). Thirty *Pm* alleles at 25 loci have been nominated for wheat powdery mildew resistance (McIntosh *et al.* 1995). Twenty-five alleles at 19 loci from *Pm1* to *Pm19*, their locations at chromosomes, and their sources have been reviewed (McIntosh *et al.* 1995). Other *Pm* alleles such as *Pm20*, *Pm21*, and *Pm22* have been reported by Friebe *et al.*, 1994, Qi *et al.*, 1995, and Peusha *et al.*, 1996 and *Pm25* has been identified by Shi *et al.* 1998. Host-pathogen interactions analysis, chromosomal (cytogenesis) analysis and molecular marker techniques have been utilized for determining chromosomal locations of *Pm* genes. These powdery mildew resistance genes are non-randomly distributed in the genome (Table 3), but form clusters in gene-rich regions (Gill *et al.*, 1996a, b). The highest numbers of *Pm* loci are contained by each 6B and 7B chromosome with 5 known *Pm* loci. Chromosomes

without known *Pm* genes are 3A (*Pm44*), 4D, and 5A (according to Hsam & Zeller, 2002). Gene loci that contain more than one resistance allele are *Pm1* with 4 alleles, *Pm3* with 9 alleles, *Pm4* with 3 alleles, *Pm5* with 4 alleles (Chen & Chelkowski, 1999; Hsam & Zeller, 2002). Hsam and Zeller (2002) stated that loci *Pm10*, *Pm11*, *Pm14*, and *Pm15* contain individual genes for resistance to *Erysiphe graminis* f.sp. *agropyri* and are not effective against *Blumeria graminis* f. sp. *Tritici*. Eight gene loci were identified in homoeologous group 1, whereas only one gene (*Pm16*) was found in homoeologous group 4 (i.e. chromosome 4A; Reader & Miller, 1991).

Xue *et al.* (2009) reported that the Chinese landraces wheat line Xiaobaidong contained a new recessive gene, *mlxbd* which was located on chromosome 7BL and near the locus *Pm5*. Powdery mildew resistance gene *Mld* was located on chromosome 4B in the wheat lines, Halle 13471, H8810/47 and Maris Dove. It was transferred from *T. durum* (McIntosh *et al.*, 1995). Zeller *et al.* (1993b) reported that three wheat cultivars, Abo, Aristide and Courtot, contained a major gene, *Mlar*, for resistance to the German *Bgt* isolate no.2. Robe and Doussinault (1995) reported that the line RF714 contained a new recessive gene, *mlre*, for wheat powdery mildew resistance, which was derived from a cross between *Aegilops squarrosa* 33 and *Triticum dicoccum* 119. They postulated that *mlre* was derived from *T. dicoccum*. A new recessive gene, *pmTD1*, was identified in the wheat line NC92-8562 transferred from *Ae. Tauschii* ssp. *Tauschii* (Shi *et al.*, 1998). Liu *et al.* (1989) reported that the variety Kengua 1 contained a new gene, *KG*, for powdery mildew resistance, which was located on chromosome 6A.

3. Sources and Distribution of Resistance Genes

Common sources of *Pm* genes are different species within the primary, secondary and tertiary gene pools. Bread wheat is an allohexaploid species ($2n=6x=42$), with three distinct genomes (AABBDD). Many of the resistance genes were introduced from ancestral and other wild species related to common wheat such as *Triticum monococcum*, close relative of the A genome progenitor *Triticum uratu*, the B genome progenitor *Aegilops speltoides*, and the D genome progenitor *Ae. Tauschii* (Hsam & Zeller, 2002; Jiang *et al.*, 1994). Chen and Chelkowski (1999) and Hsam and Zeller (2002) reported a total of 22 resistance alleles at 10 loci including *Pm1*, *Pm2*, *Pm3* (3a, 3b, 3c, 3d, 3e, and 3f), *Pm9*, *Pm18*, *Pm22* and *Pm45* in *T. aestivum* indicating that *Pm* genes may still be found in cultivated wheat. Although Bennett (1984) reported that just a small number of *Pm* genes have been identified which originated in the cultivars *T. aestivum*. Mains (1933) identified that the wild wheat relatives *T. monococcum* (AA genomes), *T. dicoccum* (AABB), and *T. timopheevi* (AAGG) are the sources of resistance genes to powdery mildew as early as 1933. Screening of old wheat cultivars, land-races and related species for resistance to powdery mildew started in the 1930's (Hsam & Zeller, 2002). *Pm* genes were identified in many different, widely distributed wheat cultivars and landraces. *Pm5a* and *Pm5b*, followed by *Pm2*, *Pm6*, and *Pm8* are the most common in Europe, Asia and Mediterranean cultivars. *Pm3a* is commonly found in wheat cultivars grown in diverse geographical locations including the Balkans, Japan, china and the US. *Pm3c* was identified in Germany, while *Pm3d* was found in several European countries and China. *Pm4a* has been used in commercial wheat cultivars in Germany and China. A number of commercially grown cultivars have been found to have *Pm* gene combinations (Heun & Fischbeck, 1987). The best known cultivars are Normandie with *Pm1*, *Pm2*, and *Pm9*, Maris Huntsman with *Pm2* and *Pm6*, Kronjuvel with *Pm4b* and *Pm8*, and 623/65 with *Pm4b* and *Pm8* (Liu *et al.*, 1999). Gene transfer from species within the primary gene pool of *Triticum* that homologous chromosomes to wheat can be done directly by hybridization, recombination and backcrossing.

Diploid *Aegilops tauschii* Coss ($2n=2x=14$, DD) has proved to be a valuable relative for wheat breeding and diversifying disease resistance (Gill *et al.* 1986, Cox *et al.* 1992). For wheat powdery mildew resistance, Gill *et al.* (1986) reported on the reactions of 60 accessions of *A. tauschii* to four *Bgt* isolates. Among the 60 accessions, four showed an immune reaction, seven were highly resistant, and 20 were moderately resistant. Two resistance alleles, *Pm2* and *pm19*, were transferred into common wheat from *A. tauschii* (Hsam & Zeller, 2002). Although *Pm10* and *Pm15* are not effective against *Bgt*, they can be traced from *A. tauschii* (McIntosh *et al.*, 1995). Four new germplasm lines, NC96BGTD1, NC96BGTD2, were released with wheat powdery mildew resistance alleles, which were transferred from *A. tauschii* and two germplasm line NC96BGTD3 and NC97BGTD7 contain *Pm34* and *Pm35* (Murphy *et al.*, 1998; Mirinda *et al.*, 2006, 2007). Shi *et al.*, (1998) identified new allele(s) for powdery mildew resistance transferred from *Ae. Tauschii* ssp. *Tauschii* in NC92-8562 and NC109-2-1-G1-1; diploid einkorn wheat (*T. monococcum*) ($2n=2x=14$, AA genome) derivative common wheat germplasm NC96BGTA5 contain *Pm25* (Shi *et al.*, 1998; Murphy *et al.*, 1998).

Tetraploid wild emmer wheat (*T. dicoccoides*) ($2n=4x=28$, AABB), the progenitor of common tetraploid and hexaploid wheats (Liu *et al.*, 2002); and the source of *Pm16*, *Pm26*, *Pm3*, *Pm31*, *Pm36*, *Pm41* and *pm42* (Rong *et al.*, 2000; Liu *et al.*, 2002; Hsam & Zeller, 2002; Hua *et al.*, 2009). Krivchenko *et al.*, (1979) determined the reactions of 29 *T. dicoccoides* samples to wheat powdery mildew. Twenty-eight were resistant in the field, and fifteen were resistant in the seedling stage. Wang *et al.* (2007) reported that the temporary design powdery mildew resistance gene

PmAS846 derived from wild emmer (*T. dicoccoides*) accession As846. Moseman *et al.* (1984) reported on the reactions to powdery mildew of 233 *T. dicoccoides* *nti-infla*. Resistance to at least one isolate was found in 149 accessions, and 137 expressed intermediate to complete resistance to four *Bgt* isolates; tetraploid *T. dicoccum* ($2n=4x=28$, AABB), a source of genes for resistance to powdery mildew (Bennett, 1984; Navarro *et al.*, 2000; Hsam and Zeller, 2002) including *Pm4a* and *Pm5a*; tetraploid *T. durum* ($2n=4X=28$, AABB), a somewhat less valuable source of resistance to powdery mildew (Mains, 1934; Hsam & Zeller, 2002), although it contributed *Pm3h* (Zeller and Hsam, 1998); This species is highly regarded as a source for *Pm* and other resistance genes (Mains, 1934; Grechter-Amitai and Van Silfhout, 1984; Hsam & Zeller, 2002); tetraploid *T. carthlicum* ($2n=4x=28$, AABB genomes) was a donor of *Pm4b* and *Pm33* (Hsam & Zeller, 2002; Zhu *et al.*, 2005).

Polyploid *Triticum* and *Aegilops* genotypes sharing at least one common genome with *T. aestivum* belong to the secondary gene pool. If genes are on the homologous chromosomes, gene transfer may be by direct hybridization, or may require special cytogenetic techniques such as embryo rescue (Jiang *et al.*, 1994). Some diploid and tetraploid species belong to this group and some species have been used as sources of resistance genes such as; tetraploid cultivated *T. timopheevii* and its wild form, *T. araraticum*, ($2n=4x=28$, AAGG), contributed *Pm6*, *Pm27*, *Pm37* and contain at least one more *Pm* gene (Mains, 1934; Järve *et al.*, 2000; Hsam & Zeller, 2002; Murphy *et al.*, 2002; Perugini *et al.*, 2008); *Ae. Speltoides* ($2n=2x=14$, SS) was the donor of *Pm1d*, *Pm12* and *Pm32* (Hsam and Zeller, 2002; Hsam *et al.*, 2003); and *Ae. Longissima* ($2n=2x=14$, SS), was the donor of *Pm13* (Cenci *et al.*, 1999). *Ae. Speltoides* and *Ae. Longissima* are both diploid species with the S genome, which is closely related to the B genome of wheat and show co-linearity with at least five chromosomes with the wheat D genome (Zhang *et al.*, 2001; Hsam & Zeller, 2002). Other species such as Dasypyrum (*Hylandia*) ($2n=2x=14$, VV), cultivated rye (*Secale nti-i*) ($2n=2x=14$, RR), and some *Aegilops* species which do not share with common wheat genomes belong to the tertiary gene pool. A homologous recombination with such donor parents cannot be used for gene transfer. Genetic techniques such as induction of chromosome translocations radiated or induced mutation at *Ph1* locus on chromosome 5BL or lack of 5B chromosomal pair can be used to facilitate gene transfer (Jiang *et al.*, 1994). The products of these methods are wheat/alien chromosome translocation, or recombination lines. Four *Pm* (*Pm7*, *Pm8*, *Pm17*, and *Pm20*) genes were transferred from rye (*Secale nti-i*, $2n=14$, RR) into cultivated wheat (Hsam and Zeller, 2002). The 1RS chromosome arm from rye is the most widely incorporated alien chromatin in present wheat genomes (Hsam *et al.*, 2000). Wheat germplasm Transec contain *Pm7* as a 4BS.4BL-5RL translocation (Table 1). *Pm8* derived from rye cultivar Petkus (Ren *et al.*, 1997) and *Pm17* are both located on the short arm of the 1R chromosome in rye. *Pm8* and *Pm17* segregated independently from each other in Amigo wheat which indicated two distinct translocations. *Pm8* is located in T1BL.1RS, and *Pm17* is located in T1AL.1RS wheat-rye translocation lines (Heun *et al.*, 1990; Friebe *et al.*, 1994). *Pm20* was transferred from the 6RL rye chromosome into common wheat. *Aegilops nti-* ($2n=4X=28$, UUMM) was the donor of *Pm29* and the wild diploid *Hylandia vilosa* ($2n=2x=14$, VV) was the donor of *Pm21* (Zeller *et al.*, 2002). Other species with potentially useful powdery mildew resistance genes are *Ae. nti-in*, *Ae. Markgrafii*, *Ae. Umbelluata*, *Ae. Variabilis*, *Ae. Triuncalis*, and *Ae. Mutica*, as well as the perennial subspecies of *Triticae*, such as *Elymus*, *Leymus*, *Elytrigia* and *Thinopyrum*, (Jiang *et al.*, 1994; Eser, 1998; Hsam & Zeller, 2002; Luo *et al.*, 2009).

4. Molecular Markers Linked to Powdery Mildew Resistance Gene

Molecular markers are tools that help to locate and identify parts of DNA that are located near a gene or genes of interest. DNA markers identify locations where the sequences differ among varieties. These can be located within genes or in the DNA between genes, so long as they are unique sequences and differ between the plants of interest. Differences of this type are called polymorphisms, and there are a variety of ways to detect and use these signposts within the chromosomes (Suslow *et al.* 2002). Different molecular techniques have been used to characterize and manipulate resistance genes and to dissect different types of resistance. Molecular markers were used for mapping monogenic resistance, characterization of quantitative resistance in germplasms and marker-aided selection (Michelmore, 1995). Molecular identification of specific DNA sequences can be used to identify the presence or absence of *Pm* genes in a cultivar, their chromosomal location, the number of genes and the way in which they are transmitted to progeny (Chen & Chelkowski, 1999). With the help of molecular markers, more than 20 powdery mildew resistance genes, such as *Pm30* (Liu *et al.*, 2002), *Pm31* (Xie *et al.*, 2003), *Pm33* (Zhu *et al.*, 2005), *Pm34* (Miranda *et al.*, 2006), *Pm35* (Miranda *et al.*, 2007), *PmY39* (Zhu *et al.*, 2006), *PmY201* and *PmY212* (Sun *et al.*, 2006), *PmU* (Qiu *et al.*, 2005), *MIZec1* (Mohler *et al.*, 2005), *Mlm2033*, *Mlm80* and *pm2026* (Yao *et al.*, 2007; Xu *et al.*, 2008), *PmLK906* (Niu *et al.*, 2008) *Pm43* (He *et al.*, 2009) and *Pm45* (Ma *et al.*, 2011), have been discovered and mapped. Molecular marker techniques commonly used for identification and confirmation of *Pm* genes to powdery mildew are:

4.1 Restriction Fragment Length Polymorphisms (RFLP)

RFLPs were the first molecular markers that developed and used in genetic analysis, initially in humans (Botstein *et al.*, 1980), and later applied to plants (Weber & Helentjaris, 1989). Even though these markers were extensively used for mapping approaches in various plant species, they didn't fulfill the initial expectations as universal genotyping assays, since they require large amounts of DNA, are expensive and time consuming. Devos & Gale (1993) considered the RFLP technology too slow and too expensive to use for routine screening of the mapping populations. Thus, RFLPs have limited application in wheat breeding programs that require large-scale screening of progenies from intra-specific crosses in a short time period. A large number of identified powdery mildew resistance genes have been tagged with RFLP markers in wheat, such as: *Pm1*, *Pm2*, *Pm3b*, *Pm4a* (Ma *et al.*, 1994), *Pm1*, *Pm2*, and *Pm18* (Hartl *et al.*, 1995), *Pm1c* (Hartl *et al.*, 1999), *Pm2* (Mohler & Jahoor, 1996), *Pm2*, *Pm4a*, *Pm21* (Liu *et al.*, 2000), *Pm3a*, *Pm3b*, and *Pm3c* (Hartl *et al.*, 1993b), *Pm3g* (Sourdille *et al.*, 1999), *Pm6* (Tao *et al.*, 2000), *Pm12* (Jia *et al.*, 1996), *Pm13* (Cenci *et al.*, 1999), *Pm17* (Hsam *et al.*, 2000), *Pm21* (Liu *et al.*, 1999), *Pm26* (Rong *et al.*, 2000), *Pm27* (Järve *et al.*, 2000) and *Pm29* (Zeller *et al.*, 2002).

4.2 Random Amplified Polymorphisms (RAPD)

RAPD is based on the amplification of random DNA segments using a single primer of arbitrary nucleotide sequence. Sequence information and radioactivity are not required for RAPD analysis. It is economical and easy to use. Several powdery mildew resistance genes tagged with RAPD markers, such as: *Pm1* (Hu *et al.*, 1997), *Pm1*, *Pm2*, *Pm3*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm4a*, *Pm12* (Shi, 1997), *Pm13* (Cenci *et al.*, 1999), *Pm18* (Hartl *et al.*, 1995), *Pm21* (Qi *et al.*, 1996; Liu *et al.*, 1999), and *Pm25* (Shi *et al.*, 1998). More than forty RAPD markers and two RFLP markers have been identified to be associated with *Pm1*, *Pm2*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm4a*, and *Pm21* (Hartl *et al.*, 1993b, Ma *et al.*, 1994, Qi *et al.*, 1996). However, most RAPD markers are dominant, and sometimes the results are difficult to reproduce. Fortunately, RAPD markers can be converted to more reliable markers, such as SCARs (sequence characterized amplified regions). For example, the RAPD marker linked to the wheat powdery mildew resistance gene *Pm21* was converted to a SCAR marker (Liu *et al.*, 1996).

4.3 Amplified Fragment Length Polymorphisms (AFLP)

The AFLP technique is based on selectively amplifying a subset of restriction fragments from a complex mixture of DNA fragments obtained after digestion of genomic DNA with restriction endonucleases (Vos *et al.*, 1995). AFLP analysis is a reliable and efficient method and a powerful technique to generate large numbers of markers for the construction of high-density genetic maps (Becker *et al.*, 1995; Keim *et al.*, 1997), identifying specific genes (Kasuga *et al.*, 1997; Schwarz *et al.*, 1999) and map-based cloning of resistance genes (Buschges *et al.*, 1997; Wei *et al.*, 1999). Linked AFLP markers have already been found for *Pm1c* and *Pm4a* (Hartl *et al.*, 1999), *Pm17* (Hsam *et al.*, 2000), *Pm24* (Huang *et al.*, 2000b), *Pm29* (Zeller *et al.*, 2002) and *pm42* (Hua *et al.*, 2009).

4.4 Microsatellites (Simple Sequence Repeat, SSR)

Microsatellites or simple sequence repeats (SSRs) are an alternative type of codominant marker more suitable for screening large populations than RFLPs. They are simple sequence repeats of only a few base pairs (1-6) that are commonly found in eukaryotic genomes (Gupta *et al.*, 1999). Most of microsatellite markers are chromosome specific, thereby simplifying the assignment of linkage groups (Röder *et al.*, 1998; Gupta *et al.*, 1999). The genome specificity of microsatellite markers can also be used to recognize the arm and sub-arm localization of disease resistance genes using Chinese Spring ditelosomic and deletion stocks (Endo & Gill 1996). Gene-flanking microsatellite markers can be assigned to chromosome arms and interval breakpoints by examining their presence or absence in ditelosomic and deletion lines (Plaschke *et al.*, 1996; Sourdille *et al.*, 2004). Over 1000 microsatellites from wheat are currently available (Gupta *et al.*, 2002; Guyomarc'h *et al.*, 2002; Huang *et al.*, 2003b; Röder *et al.*, 2004; Song *et al.*, 2002; Stephenson *et al.*, 1998). Recently, using SSR markers, there are several powdery mildew resistance genes identified and mapped such as: *Pm24* (Huang *et al.*, 2000b), *Pm27* (Järve *et al.*, 2000), *Pm30* (Liu *et al.*, 2002), *Pm33* (Zhu *et al.*, 2005), *Pm34* (Miranda *et al.*, 2006), *Pm35* (Miranda *et al.*, 2007), *Pm36* (Blanco *et al.*, 2008), *Pm40* (Luo *et al.*, 2009), *Pm41* (Li *et al.*, 2009), *pm42* (Hua *et al.*, 2009), *Pm43* (He *et al.*, 2009) and *Pm45* (Ma *et al.*, 2011).

4.5 Sequence Tagged Site (STS)

STS markers are single copy sequence amplified using specific primers that match the nucleotide sequences at the ends of a DNA fragment of an RFLP probe (Olson *et al.*, 1989). This approach is extremely useful for studying the relationship between various species and linked to some specific traits (Bustos *et al.*, 1999; Hartl *et al.*, 1993a). RFLP probes specifically linked to a desired trait can be converted into PCR-based STS markers, based on nucleotide sequence of the probe giving polymorphic band pattern, to obtain specific amplification. Tedious hybridization

procedures involved in RFLP analysis can be overcome using this technique. Tagged STS markers have been identified for *Pm1* (Hu *et al.*, 1997), *Pm2* (Mohler & Jahoor, 1996), *Pm13* (Cenci *et al.*, 1999), *Pm41* (Li *et al.*, 2009) and *pm42* (Hua *et al.*, 2009).

5. Mapping Population

Both F_2 and backcross populations are easy to construct and can be produced within short time. F_2 is more powerful for detecting QTLs with additive effects, and can also be used to estimate the degree of dominance for detected QTLs. When dominance is present, backcrosses give biased estimates of the effects because additive and dominant effects are completely irritating in this design (Carbonell *et al.*, 1993). Many markers require to be analyzed for a large number of plants when F_2 or backcross populations are used for gene mapping. Besides, some traits are difficult to score on an individual plant basis. So, alternative strategies have been used to improve the efficiency of genetic mapping such as NILs (near-isogenic lines), BSA (bulk segregant analysis) and RILs (recombinant inbred lines) lines or DH (double haploid, Michelmore *et al.*, 1991).

NILs that differ by the presence or absence of the target gene and flanking a small region of DNA, are useful to identify markers linked with the target gene (Young *et al.*, 1988). Genetic markers are polymorphic between the NIL and its recurrent parent that are putatively linked to the target gene (Muehlbauer *et al.*, 1988). Many disease resistance genes have been mapped using NILs, including powdery mildew resistance in wheat and barley (Hinze *et al.*, 1991; Schuller *et al.*, 1992). *Pm2*, *Pm3*, *Pm4a* and *Pm6* have been mapped using NILs (Hartl *et al.*, 1995; Tao *et al.*, 2000).

Although NILs are helpful to construct gene map, often they are unavailable, and the development of NILs is time-consuming and laborious. To overcome the problems of NILs, Michelmore *et al.*, (1991) successfully used bulked segregant analysis (BSA) to identify RAPD markers tightly linked to genes for resistance to lettuce downy mildew. Many powdery mildew resistance gene/allele such as *Pm1*, *Pm4a*, *Pm8*, *Pm24*, *Pm25*, *Pm29*, *Pm30* and *Pm31* have been identified using BSA (Shi *et al.*, 1998). This strategy involves comparing two DNA samples pool of individuals from a segregating population. Within each pool, or bulk, the individuals are identical for the trait or gene of interest but are uninformed for all the other genes. All polymorphic markers between two DNA pools are putatively linked with the target gene.

Recombinant inbred lines or double haploid populations are permanent populations that can be used indefinitely for mapping. They can also be readily disseminated among labs and new data can be continuously added to a pre-existing map. Furthermore, RI lines or DH populations can be evaluated in many different environments. Since each genotype is represented by an inbred line, rather than by an individual plant, a more accurate assessment of the genetic component of variance can be made in studying quantitative traits (Burr *et al.*, 1988). Therefore, RI lines or DH populations are more useful for analysis of quantitative traits or traits that are difficult to characterize on an individual plant basis. DH lines have been used to screen molecular markers associated with genes, *Pm3a*, *Pm3g* and *Pm8* for powdery mildew resistance in wheat (Hartle *et al.*, 1993b; Sourdille *et al.*, 1999; Wricke *et al.*, 1996). *Pm13* has been mapped using RI lines (Donini *et al.*, 1995).

6. Mapping of Powdery Mildew Resistance Genes

The development of genetic maps of wheat is now adding a new dimension for identification of molecular markers associated with powdery mildew resistance genes. Screening markers can be conducted in the two parents, by selecting several markers on each chromosome of the genetic map, and then linkage between the allele for resistance and the polymorphic markers in the two parents can be estimated by use of QTL statistical analysis based on the data from a segregating population. In plants, molecular mapping and cloning of disease resistance genes will facilitate the study of molecular mechanisms underlying and evolution of resistance and will permit marker-assisted selection in breeding programs. Several powdery mildew resistance genes have been tagged with molecular markers (Table 2). Using cultivar Chancellor as the recurrent parent, Briggie (1969) developed NILs for powdery mildew resistance genes *Pm1*, *Pm2*, *Pm3* and *Pm4a*, respectively. Hartl *et al.* (1995) found that RFLP marker Whs178 was 3 cM away from gene *Pm1*. Hu *et al.* (1997) used RAPD markers to tag gene *Pm1*. RAPD markers UBC320420 and UBC638550 cosegregated with gene *Pm1* among 244 F_2 plants. Another RAPD marker OPF12650 was 5.4 cM away from gene *Pm1*. Recently, Hartl *et al.* (1999) have used AFLP markers to map gene *Pm1c*. Among 96 primer combinations, 31 polymorphic AFLP fragments between the resistant and susceptible pools were in accordance with the patterns of the parents. The eight most reliable polymorphic markers were analyzed in a segregating population for the gene *Pm1c*. Two of them cosegregated with the gene *Pm1c* and the other six markers were tightly linked with the gene. One AFLP marker, 18M2, was found to be highly specific for the *Pm1c* gene in diverse genetic backgrounds. RFLP analysis of NILs possessing the gene *Pm2* and the recurrent parent indicated that: 1) RFLP marker BCD1871 was 3.5 cM away from gene *Pm2* (Ma *et al.*, 1994); 2) RFLP marker Whs295 mapped 2.7 cM

away from the gene *Pm2* (Hartl *et al.*, 1995); and 3) the gene *Pm2* was also linked with RFLP marker Whs350 (Hartl *et al.*, 1995). Ma *et al.*, (2011) found that *Pm45* on chromosome 5DS which was flanked by Xgwm205 and Xmag6176, with a genetic distance of 8.3 cM and 2.8 cM, respectively. This gene was 3.3 cM from a locus mapped by the STS marker MAG6137, converted from the RFLP marker BCD1871, which was 3.5 cM from *Pm2*. Using RFLP analysis of NILs possessing the gene *Pm3* and the recurrent parent, Hartl *et al.* (1993b) found that RFLP marker Whs179 revealed polymorphism not only between the NILs with and without gene *Pm3*, but also among NILs possessing different alleles of the *Pm3* locus. The genetic distance between probe Whs179 and *Pm3* was 3.3 ± 1.9 cM. Ma *et al.* (1994) reported that RFLP marker BCD1434 was 1.3 cM away from *Pm3a* or *Pm3b*. Ma *et al.* (1994) also reported that *Pm4a* cosegregated with RFLP markers BCD1231-2A(2) and CDO678-2A, and was closely flanked by BCD1231-2A(1) and BCD292-2A. Xue *et al.* (2009) reported that SSR marker Xgwm577 was linked to powdery mildew resistance gene *mlxbd* with a distance of 3.5cM. Blanco *et al.*, (2008) found that *Pm36* linked on chromosome 5BL with five AFLP markers XP43M32 (250), XP46M31(410), XP41M37(100), XP41M39(250) and XP39M32(120), three genomic SSR markers (Xcfd07, Xwmc75, Xgwm408) and one EST-derived SSR marker (BJ261635). Using F₂ population Zhang *et al.* (2010) also found that the temporary design powdery mildew resistance gene *MI3D232* on chromosome 5BL which was flanked by Xgwm415 and Xwmc75. Zhang *et al.* (2009) also found temporary *Pm* design gene *MIW29* on 5BL chromosome and also flanked by Xgwm415 and Xwmc75, with a genetic distance of 2.5 cM and 17.6 cM, respectively.

7. Conclusion

Molecular markers tightly linked to economically important monogenic or oligogenic trait have potential for immediate utility in plant improvement. Efficient application of molecular markers in plant breeding will depend on the development cost-effective and automated diagnostic technologies. A major problem is when the linked marker used for selection is at a distance away from the gene of interest, leading to crossover between the marker and the gene. In future, the success of marker assisted selection may depend on the possibility of tagging the favorable alleles themselves.

Valuable lessons learnt from past research are likely to encourage more researchers to develop reliable markers and plant breeders to adopt MAS. PCR-based markers are more attractive for MAS, due to the small amount of template required and more efficient handling of large population sizes. PCR-based molecular markers are suitable for marker assisted selection (MAS), due to small amount of DNA require, more efficient managing of large population sizes and possible to map and tag almost any trait. DNA markers have facilitated the dissection of the genetic basis of complex traits and have helped in understanding their mode of action and how their functioning is modulated by the environment. AFLP, RAPD and STS markers can not be applied for differentiation of homozygous and heterozygous individuals in segregating population. Among the DNA marker systems of wheat, microsatellites are recently the optimal marker for MAS, because of their co-dominant inheritance, chromosome-specific and evenly distributed along chromosomes. A large numbers of microsatellite makers are available that offer identification and molecular mapping of powdery mildew resistance gene in wheat (Gupta *et al.*, 2002; Guyomarc'h *et al.*, 2002; Huang *et al.*, 2001; Roder *et al.*, 2004; Song *et al.*, 2002; Stephenson *et al.*, 1998). Already some *Pm* genes have been identified and mapped by specific microsatellite markers.

We believe that several other factors will greatly affect the efficiency and effectiveness of linkage mapping and MAS research in the future: new developments and improvements in marker technology, the integration of functional genomics with linkage mapping, and the availability of more high-density maps.

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Table 1. Chromosomal location, cultivar/line, source and Reference of identified powdery mildew resistance genes

Gene	Location	Cultivar/line	Source	Reference
<i>Pm1a</i>	7AL	Axminister	<i>T. aestivum</i>	Hsam <i>et al.</i> , 1998
<i>Pm1b</i>	7AL	MocZlatka	<i>T. monococcum</i>	Hsam <i>et al.</i> , 1998
<i>Pm1c(Pm18)</i>	7AL	Weihestephan M1N	<i>T. aestivum</i>	Hsam <i>et al.</i> , 1998
<i>Pm1d</i>	7AL	<i>T. spelta</i> var. <i>duhamelianum</i>	<i>T. spelta</i>	Hsam <i>et al.</i> , 1998
<i>Pm1e</i> (<i>Pm22</i>)	7AL	Virest	<i>T. aestivum</i>	Singrun <i>et al.</i> , 2003
<i>Pm2</i>	5DS	Ulka/XX 194	<i>T. aestivum/Ae. Tauschii</i>	McIntosh & Baker, 1970 and Lutz <i>et al.</i> , 1995
<i>Pm3a</i>	1AS	Asosan		Briggle & Sears, 1966
<i>Pm3b</i>	1AS	Chul	<i>T. aestivum</i>	Briggle, 1966
<i>Pm3c</i>	1AS	Sonora	<i>T. aestivum</i>	Briggle, 1966
<i>Pm3d</i>	1AS	Kolibri	<i>T. aestivum</i>	Zeller <i>et al.</i> , 1993a
<i>Pm3e</i>	1AS	W150	<i>T. aestivum</i>	Zeller <i>et al.</i> , 1993a
<i>Pm3f</i>	1AS	Michigan Amber	<i>T. aestivum</i>	Zeller <i>et al.</i> , 1993a
<i>Pm3g</i>	1AS	Aristide	<i>T. aestivum</i>	Zeller & Hsam, 1998
<i>Pm3h</i>	1AS	Abessi	<i>T. durum</i>	Zeller & Hsam, 1998
<i>Pm3i</i>	1AS	N324	<i>T. aestivum</i>	Zeller & Hsam, 1998
<i>Pm3j</i>	1AS	GUS 122	<i>T. aestivum</i>	Zeller & Hsam, 1998
<i>Pm4a</i>	2AL	Khapli	<i>T. dicoccum</i>	The <i>et al.</i> , 1979
<i>Pm4b</i>	2AL	Armada	<i>T. carthlicum</i>	The <i>et al.</i> , 1979
<i>Pm4d</i>	2AL	Tm27d2	<i>T. monococcum</i>	Schmolke <i>et al.</i> , 2011
<i>Pm5a</i>	7BL	Hope	<i>T. dicoccum</i>	Law & Wolfe, 1966
<i>Pm5b</i>	7BL	Ibis	<i>T. aestivum</i>	Hsam <i>et al.</i> , 2001
<i>Pm5c</i>	7BL	Kolandi	<i>T. aestivum ssp.</i> <i>Sphaerococcum</i>	Hsam <i>et al.</i> , 2001
<i>Pm5d</i>	7BL	IGV 1-455	<i>T. aestivum</i>	Hsam <i>et al.</i> , 2001
<i>Pm5e</i>	7BL	Fuzhuang 30	<i>T. aestivum</i>	Huang <i>et al.</i> 2003a
<i>mlxbd(Pm5)</i>	7BL	Xiaobaidong	<i>T. aestivum</i>	Huang <i>et al.</i> , 2000a
<i>Pm6</i>	2BL	TP 114	<i>T. timopheevii</i>	Jørgensen, 1973
<i>Pm7</i>	4BS.4BL-2RL	Transec	<i>S.cereale</i>	Friebe <i>et al.</i> , 1994
<i>Pm8</i>	1RS.1BL	Disponent	<i>S.cereale</i>	Hsam & Zeller, 1997
<i>Pm9</i>	7AL	N14	<i>T. aestivum</i>	Hsam <i>et al.</i> , 1998
<i>Pm10</i>	1D	Norin 26	<i>T. aestivum</i>	Tosa <i>et al.</i> , 1987
<i>Pm11</i>	6BS	Chinese Spring	<i>T. aestivum</i>	Tosa <i>et al.</i> , 1988
<i>Pm12</i>	6BS-6SS.6SL	Trans.line 31	<i>Ae.speltoides</i>	Jia <i>et al.</i> , 1996
<i>Pm13</i>	3BL.3SS-3S 3DL.3SS-3S	Cstrans.line	<i>Ae.longissima</i>	Ceoloni <i>et al.</i> , 1992

Gene	Location	Cultivar/line	Source	Reference
<i>Pm14</i>	6BS	Norin 10	<i>T. aestivum</i>	Tosa & Sakai, 1990
<i>Pm15</i>	7DS	Norin 26	<i>T. aestivum</i>	Tosa & Sakai, 1990
<i>Pm16</i>	4A	Norman rec. line	<i>T. dicoccoides</i>	Reader & Miller, 1991
<i>Pm17</i>	1RS.1AL	Amigo	<i>S.cereale</i>	Heun <i>et al.</i> , 1990
<i>Pm19</i>	7D	XX 186	<i>Ae. tauschii</i>	Lutz <i>et al.</i> , 1995
<i>Pm20</i>	6BS.6RL	KS93WGRC28	<i>S.cereale</i>	Friebe <i>et al.</i> , 1994
<i>Pm21</i>	6VS.6AL	Yangmai 5 line	<i>Haynaldia villosa</i>	Chen <i>et al.</i> , 1995
<i>Pm23(Pm4c)</i>	2AL	82-7241	<i>T. aestivum</i>	McIntosh <i>et al.</i> , 1998
<i>Pm24</i>	1DS	Chiyacao	<i>T. aestivum</i>	Huang <i>et al.</i> , 2000b
<i>Pm25</i>	1A	NC96BGTA5	<i>T. boeoticum</i>	Shi <i>et al.</i> , 1998
<i>Pm26</i>	2BS	TTD140	<i>T. dicoccoides</i>	Rong <i>et al.</i> , 2000
<i>Pm27</i>	6B-6G	146-155-T	<i>T. timopheevii</i>	Jarve <i>et al.</i> , 2000
<i>Pm28</i>	1B	Meri	<i>T. aestivum</i>	Peusha <i>et al.</i> , 2000
<i>Pm29</i>	7DL	Pova	<i>A. ovata</i>	Zeller <i>et al.</i> , 2002
<i>Pm30</i>	5BS	C20	<i>T. dicoccoides</i>	Liu <i>et al.</i> , 2002
<i>Pm31(MIG)</i> <i>cancel</i>	6AL	G-305-M/781//Jing411*3	<i>T. dicoccoides</i>	Xie <i>et al.</i> , 2003
<i>Pm32</i>	1BL.1SS	L501	<i>Ae. Speltoides</i>	Hsam <i>et al.</i> , 2003
<i>Pm33</i>	2BL	PS5	<i>T. carthlicum</i>	Zhu <i>et al.</i> , 2005
<i>Pm34</i>	5DL	NC97BGTD7	<i>Ae. Tauschii</i>	Miranda <i>et al.</i> , 2006
<i>Pm35</i>	5DL	NC96BGTD3	<i>Ae. Tauschii</i>	Miranda <i>et al.</i> , 2007
<i>Pm36</i>	5BL	MG29896	<i>T. dicoccoides</i>	Blanco <i>et al.</i> , 2008
<i>Pm37</i>	7AL	NC99BGTAG11	<i>T. timopheevii</i>	Perugini <i>et al.</i> , 2008
<i>Pm38</i>	7DS	RL6058	<i>T. aestivum</i>	Spielmeyer <i>et al.</i> , 2005
<i>Pm39</i>	1BL	Saar	<i>T. aestivum</i>	Lillemo <i>et al.</i> , 2008
<i>Pm40</i>	7BS	GRY19	<i>Elytrigia intermedium</i>	Luo <i>et al.</i> , 2009
<i>Pm41</i>	3BL	IW2	<i>T. dicoccoides</i>	Li <i>et al.</i> , 2009
<i>pm42</i>	2BS	G-303-1M	<i>T. dicoccoides</i>	Hua <i>et al.</i> , 2009
<i>Pm43</i>	2DL	CH5025	<i>Thinopyrum intermedium</i>	He <i>et al.</i> , 2009
<i>Pm44</i>	3AS	Hombar	<i>T. aestivum</i>	Chen <i>et al.</i> , 2011
<i>Pm45</i>	6DS	D57	<i>T. aestivum</i>	Ma <i>et al.</i> , 2011

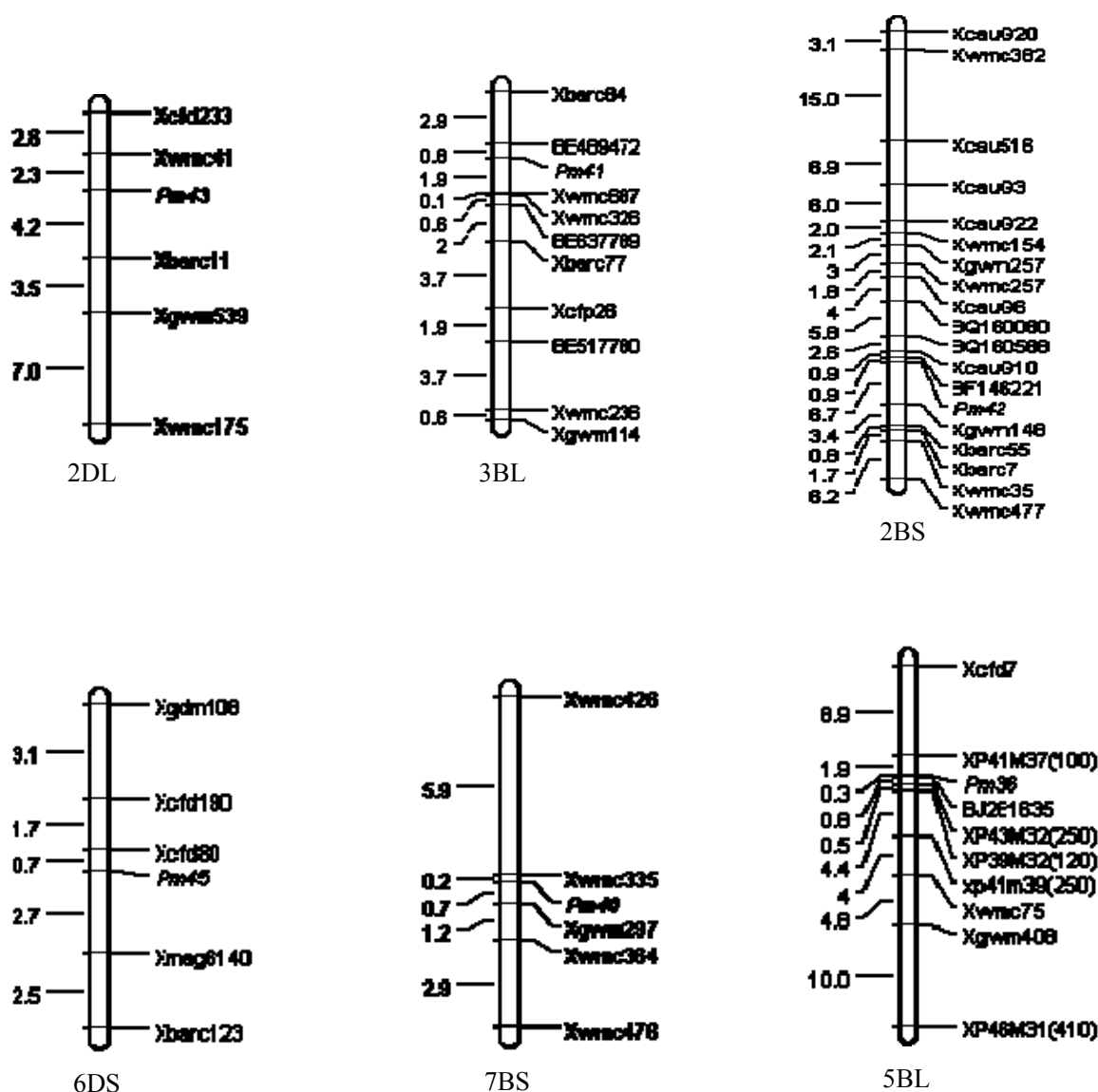
Table 2. Molecular markers linked to major powdery mildew resistance genes

Gene	Location	Type of markers	Closest/flanking marker	Linkage distance/contribution	Mapping population	Reference
<i>Pm1a</i>	7AL	RAPD, STS	UBC320420, UBC638550	Both co-segregate	F ₅ , F ₂ lines, BSA	Hu <i>et al.</i> , 1997
		RFLP	WHS178-9.4kb-EcoRI	2.8 ± 2.7cM	F ₂ lines, NILs	Hartl <i>et al.</i> , 1995
		RFLP	CDO347	Co-segregate	F ₂ lines, NILs	Ma <i>et al.</i> , 1994
		RFLP, STS	mwg2062, cdo347, psr121, psr148, psr680, psr687, wir148, C607, STS638542, ksh9	All Co-segregate	F ₂ lines	Neu <i>et al.</i> , 2002
<i>Pm1c</i>	7AL	RFLP, RAPD	WHS178-15kb-EcoRI, OPH-111900	4.4 ± 3.6cM, 13cM	F ₂ lines, BSA	Hartl <i>et al.</i> , 1995
		AFLP	S19M22-325/200	Co-segregate	F ₃ + F ₄ lines, BSA	Hartl <i>et al.</i> , 1999
			S14M20-137/138	Co-segregate		
<i>Pm1e</i>	7AL	SSR, AFLP	GWM344-null-S13M26-372	0.9cM, 0.2 cM	F _{2,3} lines, BSA	Singrun <i>et al.</i> , 2003
<i>Pm2</i>	5DS	RFLP	WHS350-6.5kb-EcoRV, WHS295	3.8cM, 2.7±2.6 cM	F ₂ lines, NILs	Hartl <i>et al.</i> , 1995
		RFLP	BCD1871	3.5cM	F ₂ lines, NILs	Ma <i>et al.</i> , 1994
		STS	STSwhs350	-	F ₂ lines, NILs	Mohler & Jahoor, 1996
<i>Pm3a</i>	1AS	RFLP	WHS179	3.3 ± 1.9cM	DH, NILs	Hartl <i>et al.</i> , 1993b
<i>Pm3b</i>	1AS	RFLP	BCD1434	1.3cM	F ₂ lines, NILs	Ma <i>et al.</i> , 1994
<i>Pm3g</i>	1AS	RFLP	Gli-A5	5.2cM	DH	Sourdille <i>et al.</i> , 1999
<i>Pm4a</i>	2AL	RFLP	BCD1231, CDO678	Co-segregate	F ₂ lines, NILs	Ma <i>et al.</i> , 1994
		AFLP	4aM1	3.5cM	F ₃ + F ₄ lines, BSA	Hartl <i>et al.</i> , 1999
		STS	STSbcd1231-1.7kb	Co-segregate	NILs	Liu <i>et al.</i> , 1998
<i>Pm5e</i>	7BL	SSR	GWM1267-136	6.6cM	F _{2,3} lines, BSA	Huang <i>et al.</i> , 2003a
<i>Pm6</i>	2BL	RFLP	BCD135-9kb-EcoRV	1.6 ± 1.5cM	F ₂ lines, NILs	Tao <i>et al.</i> , 2000
<i>Pm8</i>	1RS.1BL	RFLP	IAG95	Tightly linkage	F ₂ lines, BSA	Wricke <i>et al.</i> , 1996
		RAPD	OPJ07-1200, OPR19-1350	-	Translocation lines	Iqbal & Rayburn, 1995
		STS	SEC-1b-412bp	-	Translocation lines	deFroidmont, 1998
		STS	STSia95-1050	Co-segregate	DH, F _{2,3} lines	Mohler <i>et al.</i> , 2001
<i>Pm12</i>	6BS-6SS .6SL	RFLP	psr10, psr106, Nor-2, psr141, psr113, psr142, psr149, psr2	Co-segregate	F ₂ lines	Jia <i>et al.</i> , 1996
<i>Pm13</i>	3BL.3SS	RFLP	psr305, psr1196	-	Recombinant	Donini <i>et al.</i> , 1995

Gene	Location	Type of markers	Closest/flanking marker	Linkage distance/contribution	Mapping population	Reference
	-3S 3DL.3SS -3S				lines	
		RFLP, RAPD, STS	cdo460, utv135, OPV13800, UTV13, OPX12570, UTV14	-	Recombinant lines	Cenci <i>et al.</i> , 1999
<i>Pm17</i>	IRS.1A L	RFLP, AFLP	IAG95-CA/CT-355	1.5cM	F _{2,3} lines	Hsam <i>et al.</i> , 2000
<i>Pm21</i>	6VS.6A L	RAPD	OPH171900	Co-segregate	F ₂ lines	Qi <i>et al.</i> , 1996
		RAPD, SCAR	OPH171400, SCAR1265, SCAR1400	All co-segregate	F ₂ lines	Liu <i>et al.</i> , 1999
<i>Pm24</i>	1DS	AFLP, SSR	E34/M51-407, Xgwm337-204	Co-segregate, 2.4 ± 1.2cM	F _{2,3} lines, BSA	Huang <i>et al.</i> , 2000b
		SSR	Xgwm1291	Co-segregate	F _{2,3} lines	Huang & Roder, 2003
<i>Pm25</i>	1A	RAPD	OPA04950	12.8cM	BC ₁ F ₁ lines, BSA	Shi <i>et al.</i> , 1998
<i>Pm26</i>	2BS	RFLP	wg516	Co-segregate	RSLs	Rong <i>et al.</i> , 2000
<i>Pm27</i>	6B-6G	RFLP, SSR	psp3131	Co-segregate	F ₂ lines	Jarve <i>et al.</i> , 2000
<i>Pm29</i>	7DL	RFLP, AFLP	S24M13-233, S19M23-240, S22M26-192, S25M15-145, S13M23-442, S22M21-217, S17M25-226	Allco-segregate	F ₂ lines, BSA	Zeller <i>et al.</i> , 2002
<i>Pm30</i>	5BS	SSR	Xgwm159-460, Xgwm159-500	5–6cM	BC ₂ F ₂ lines, BSA	Liu <i>et al.</i> , 2002
<i>Pm31</i>	6AL	SSR	Xpsp3029	0.6cM	BC ₂ F ₂ lines, BSA	Xie <i>et al.</i> , 2003
<i>Pm36</i>	5BL	SSR	BJ261635	Co-segregate	BC ₅ F ₅	Blanco <i>et al.</i> , 2008
<i>Pm40</i>	7BS	SSR	Xgwm297	0.4cM	F ₂ lines	Luo <i>et al.</i> , 2009
<i>Pm41</i>	3BL	SSR, ISBP, STS	BE489472	Co-segregate	F ₂ lines	Li <i>et al.</i> (2009)
<i>Pm42</i>	2BS	SSR, FLP-SCAR, EST-STs, RFLP-STs	BF146221	Co-segregate	F ₂ lines	Hua <i>et al.</i> , 2009
<i>Pm43</i>	2DL	SSR	Xwmc41	2.3cM	F ₃ and BC ₁ lines	He <i>et al.</i> , 2009
<i>Pm45</i>	6DS	SSR, STS	Xmag6176	2.8cM	F ₂ lines	Ma <i>et al.</i> , 2011

Table 3. Distribution of powdery mildew resistance genes among homoeologous chromosomes in wheat and Rye

Homoeologous group	A	B	D	R
1	<i>Pm3</i> , <i>Pm25</i>	<i>Pm28</i> , <i>Pm32</i>	<i>Pm10</i> , <i>Pm24</i>	<i>Pm8</i> , <i>Pm17</i>
2	<i>Pm4</i> , <i>Pm23</i>	<i>Pm6</i> , <i>Pm26</i> , <i>Pm33</i> , <i>pm42</i>	<i>Pm43</i>	<i>Pm7</i>
3	<i>Pm44</i>	<i>Pm13</i> , <i>Pm38</i> , <i>Pm41</i>		
4	<i>Pm16</i>			
5		<i>Pm36</i> , <i>Pm16</i> , <i>Pm30</i>	<i>Pm2</i> , <i>Pm34</i> , <i>Pm35</i>	
6	<i>Pm21</i> , <i>Pm31</i>	<i>Pm11</i> , <i>Pm12</i> , <i>Pm14</i> , <i>Pm27</i>	<i>Pm45</i>	<i>Pm20</i>
7	<i>Pm1</i> , <i>Pm9</i> , <i>Pm18</i> , <i>Pm37</i>	<i>Pm5</i> , <i>Pm40</i>	<i>Pm15</i> , <i>Pm19</i> , <i>Pm29</i> , <i>Pm39</i>	

Figure 1. Genetic linkage maps of powdery mildew resistance gene- *Pm43* (He *et al.*, 2009), *Pm41* (Li *et al.*, 2009), *pm42* (Hua *et al.*, 2009), *Pm45* (Ma *et al.*, 2011), *Pm40* (Luo *et al.*, 2009) and *Pm36* (Blanco *et al.*, 2008)