Wheat powdery mildew (*Blumeria graminis* f. sp. *tritici)*: Damage effects and genetic resistance developed in wheat (*Triticum aestivum*)

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Abstract

Wheat powdery mildew caused by fungus *Blumeria graminis* f. sp. *tritici* is one of the most prevalent wheat diseases in the world. Damages ranging from 13% to 34% when low or moderate infestation and 50% to 100% under severe infestation, could be recorded in a field. Understanding of the disease damaging trend as well as host resistance to the fungus is vital for successful control. Molecular studies on host resistance to powdery mildew are continuously being conducted resulting in identification and mapping of resistant genes in wheat. Currently, 50 resistant genes (*Pm1* to *Pm50*) in more than 64 alleles of wheat cultivars have been located and designated. More than 50 resistance genes have been located but carry temporarily designated names. Use of molecular markers such as Simple Sequence Repeat (SSR), Amplified Fragment Length Polymorphism (AFLP), Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNAs (RAPD) and Sequence Tagged Sites (STS) has contributed to identification and mapping of more than 33 resistant genes. Damages caused by wheat powdery mildew, major resistance genes and molecular markers flanking the resistant genes have been reviewed.

Keywords: *Blumeria graminis* f.sp. *tritici*, *Triticum aestivum*, molecular markers, plant resistance, *Pm* genes.

INTRODUCTION

Common wheat (*Triticum aestivum* L.) is one of the most important crops currently being grown in most parts of the world. The crop is among the three world's major cereal export earners with others including maize and rice (Tong et al., 2003). It forms more than 40% of the world's staple food and 95% of people in the developing countries eat wheat or maize in form of flour as a main staple food source (Akhtar et al., 2011; Coventry et al., 2011). Common bread wheat (*T. aestivum*) and durum wheat (*Triticum durum* Desf.) contribute a total of 90% of the world's wheat production and they are grown on approximately 17% of the world's cultivatable land, covering over 200 million hectares (Jones, 2005; Xin et al., 2012).

Despite the increment in hectarage of wheat production worldwide, the cereal crop faces disease challenges which hinder its expansion. Wheat powdery mildew is one of the most devastating plant fungal diseases in the world. The disease is caused by fungus *Blumeria graminis* f.sp. *tritici* (syn. *Erysiphe graminis* (DC) f.sp. *tritici*). It is a highly specialized haustorium-forming parasite, classified in the phylum Ascomycota in the order of Erysiphales and depends on living tissue to survive seldom killing its host. It is regarded as an obligate biotrophic pathogen due to its reliance on a living plant for growth and propagation (Both and Spanu, 2004; Oberhaensli et al., 2011).

Damages caused by wheat powdery mildew

The disease damage range from 13% to 34% when low

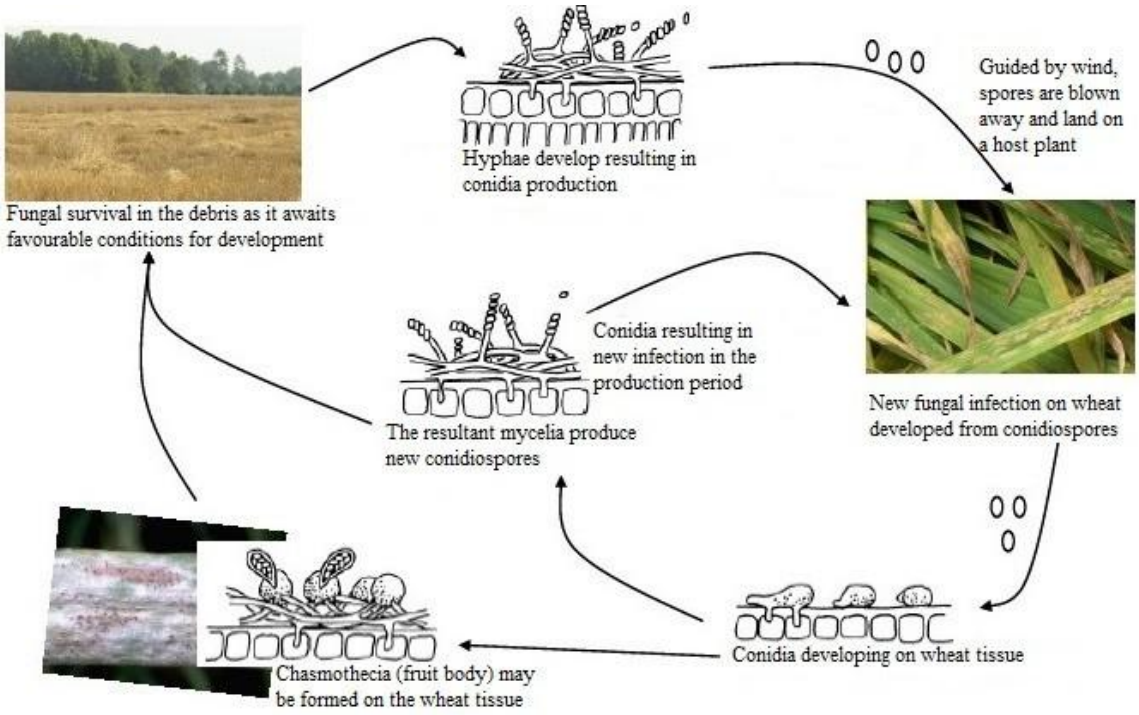

Figure 1. Wheat powdery mildew (*Blumeria graminis* f. sp*. tritici)* life cycle (modified from Perugini, 2007)

infestation but 50% to 100% under severe infestation could be recorded in a field (Alam et al., 2013; Li et al., 2011; Zhang et al., 2008). Disease symptoms may be evident at any time after plant emergence. Signs of powdery mildew are most common on leaves but they may develop on all aerial parts of the plant (Piarulli et al., 2012). The fungus grows almost entirely superficially over the surfaces of the host plants and penetrates host cells forming intracellular haustoria. The disease is characterized by white, cottony patches or colonies of mycelium and conidia. The white colonies later turn dull gray-brown and when severe infections occur, stunting growth of wheat plants becomes evident. Individual patches often merge and cover large areas of the stem, leaf surface, or head. Leaf tissues on the opposite side of the mildew pustules become yellow, later turning tan or brown (Agrios, 2005). Multiple races of the fungus currently exist and many more new ones continue to be produced as a result of mutation as well as genetic recombination due to sexual reproduction (Perugini, 2007; Li et al., 2012).

The fungus spreads mainly through the wind and may infect some fields distant from the initial field where infection occurred (Green et al., 2002; Liu et al., 2012). The infection develops an appressorium on the epidermal surface from which a hyphal filament grows and penetrates the cell wall of the host. The distal end of the hyphal filament is called the haustorial neck and enlarges to produce the haustorial body (Figure 1). The entire haustorium is surrounded by a sheath, which is enclosed by the invaginated host plasma membrane and even though the haustoria are intracellular they lie outside the host protoplast. The body and neck region are delimited by a septum (Agrios, 2005).

The fungus critical survival periods may be either during cold winter or hot summer, surviving as conidia or mycelium on infected plants during warm period (Liu et al., 2012). In an environment where survival of host plant is limited, the fungus develops sexual ascospores, which develop in groups of eight per ascus inside a closed ascocarp also called chasmothesium, a fungal fruiting body (Figure 1). The chasmothesium appears as black pinheaded spherical containers interwoven with the secondary mycelium and are produced towards the end of the growing season after reduction of conidial production (Agrios, 2005; Perugini, 2007).

Liu et al. (2012) reported that the fungus relies on the chasmothesium left together on plant debris to over-summer and release ascospores in winter which can form one of the potential sources of disease inocula during winter wheat cultivation; the main wheat crop grown in most regions of China. Other wheat crops planted during summer become the most likely hosts for the pathogen surviving vegetative as dormant mycelium. In some cases, infections come from volunteer seedlings, infected from chasmothesium on debris or conidia on late ripe wheat.

Table 1. Designated names, chromosomal positions, cultivar/line and sources of identified resistance genes to powdery mildew in wheat

Gene	Position	Cultivar/ line	Source	Reference
Pm1a	7AL	Axminster	*T. aestivum*	Sears and Briggle, 1969
Pm1b	7AL	MocZlatka	*T. monococcum*	Hsam et al., 1998
Pm1c (Pm18)	7AL	Weihestephan M1N	*T. aestivum*	Hsam et al., 1998
Pm1d	7AL	*T. spelta* var. *Duhamelianum*	*T. spelta*	Hsam et al., 1998
Pm1e (Pm22)	7AL	Virest	*T. aestivum*	Singrun et al., 2003
Pm2	5DS	Ulka/XX 194	*T.aestivum/ Ae. tauschii*	Lutz et al., 1995
Pm3a	1AS	Asosan	-	Briggle and Sears, 1966
Pm3b	1AS	Chul	*T. aestivum*	Briggle, 1969
Pm3c	1AS	Sonora	*T. aestivum*	Briggle, 1969
Pm3d	1AS	Kolibri	*T. aestivum*	Zeller et al., 1993
Pm3e	1AS	W150	*T. aestivum*	Zeller et al., 1993
Pm3f	1AS	Michigan Amber	*T. aestivum*	Zeller et al., 1993
Pm3g	1AS	Aristide	*T. aestivum*	Zeller and Hsam, 1998
Pm3h	1AS	Abessi	*T. durum*	Zeller and Hsam, 1998
Pm3i	1AS	N324	*T. aestivum*	Zeller and Hsam, 1998
Pm3j	1AS	GUS 122	*T. aestivum*	Zeller and Hsam, 1998
Pm3k	1AS	IG46439	*T. dicoccoides*	Yahiaoui et al., 2006
Pm4a	2AL	Khapli	*T. dicoccum*	The et al., 1979
Pm4b	2AL	Armada	*T. carthlicum*	The et al., 1979
Pm4c (*Pm23*)	2AL	81-7241	*T. aestivum*	Hao et al., 2008
Pm4d	2AL	Tm27d2	*T. monococcum*	Schmolke et al., 2012
Pm5	7BL	Xiaobaidong	*T. aestivum*	Huang et al., 2000b
Pm5a	7BL	Hope	*T. dicoccum*	Law and Wolfe, 1966
Pm5b	7BL	Ibis	*T. aestivum*	Hsam et al., 2001
Pm5c	7BL	Kolandi	*T. aestivum* ssp. *T. aestivum spp. sphaerococcum*	Hsam et al., 2001
Pm5d	7BL	IGV 1-455	*T. aestivum*	Hsam et al., 2001
Pm5e	7BL	Fuzhuang 30	*T. aestivum*	Huang et al., 2003
Pm6	2BL	TP 114	*T. timopheevii*	Jørgensen, 1973
Pm7	4BS.4BL-2RL	Transec	*S. cereal*	Friebe et al., 1994
Pm8	1RS.1BL	Disponent	*S. cereal*	Hsam and Zeller, 1997
Pm9	7AL	N14	*T. aestivum*	Hsam et al., 1998
Pm10	1D	Norin 26	*T. aestivum*	Tosa et al., 1987
Pm11	6BS	Chinese Spring	*T. aestivum*	Tosa et al., 1988
Pm12	6BS-6SS.6SL	Trans. Line 31	*Ae. speltoides*	Jia et al., 1996
Pm13	3BL.3SS-3S 3DL.3SS-3S	C strans. Line	*Ae. longissima*	Ceoloni et al., 1992
Pm14	6BS	Norin 10	*T. aestivum*	Tosa and Sakai, 1990
Pm15	7DS	Norin 26	*T. aestivum*	Tosa and Sakai, 1990
Pm16	4A	Norman rec. line	*T. dicoccoides*	Reader and Miller, 1991
Pm17	1RS.1AL	Amigo	*S. cereal*	Heun et al., 1990
Pm19	7D	XX 186	*Ae. tauschii*	Lutz et al., 1995
Pm20	6BS.6RL	KS93WGRC28	*S. cereal*	Friebe et al., 1994
Pm21(Pm31)	6VS.6AL	Yangmai 5 line	*Haynaldia villosa*	Chen et al., 1995
Pm23 (Pm4c)	2AL	82-7241	*T. aestivum*	McIntosh et al., 1998
Pm24a	1DS	Chiyacao	*T. aestivum*	Huang et al., 2000b
Pm24b (mlbhl)	1DS	Baihulu	*T. aestivum*	Xue et al., 2012b
Pm25	1A	NC96BGTA5	*T. boeoticum*	Shi et al., 1998
Pm26	2BS	TTD140	*T. dicoccoides*	Rong et al., 2000
Pm27	6B-6G	146-155-T	*T. timopheevii*	Järve et al., 2000
Pm28	1B	Meri	*T. aestivum*	Peusha et al., 2000
Pm29	7DL	Pova	*A. ovate*	Zeller et al., 2002
Pm30	5BS	C20	*T. dicoccoides*	Liu et al., 2002
Pm31 (Pm21)	6AL	G-305-M/781	*T. dicoccoides*	Xie et al., 2003
Pm32	1BL.1SS	L501	*Ae. speltoides*	Hsam et al., 2003

Table 1 continues

Pm33	2BL	PS5	*T. carthlicum*	Zhu et al., 2005
Pm34	5DL	NC97BGTD7	*Ae. tauschii*	Miranda et al., 2006
Pm35	5DL	NC96BGTD3	*Ae. tauschii*	Miranda et al., 2007
Pm36	5BL	MG29896	*T. dicoccoides*	Blanco et al., 2008
Pm37	7AL	NC99BGTAG11	*T. timopheevii*	Perugini et al., 2008
Pm38	7DS	RL6058	*T. aestivum*	Spielmeyer et al., 2005
Pm39	1BL	Saar	*T. aestivum*	Lillemo et al., 2008
Pm40	7BS	GRY19	*Elytrigia intermedium*	Luo et al., 2009
Pm41	3BL	IW2	*T. dicoccoides*	Li et al., 2009
Pm42	2BS	G-303-1M	*T. dicoccoides*	Hua et al., 2009
Pm43	2DL	CH5025	*T. intermedium*	He et al., 2009
Pm44	3AS	Hombar	*T. aestivum*	Alam et al., 2011
Pm45	6DS	D57	*T. aestivum*	Ma et al., 2011
Pm46	5DS	Tabasco	*T. aestivum*	Gao et al., 2012
Pm47	7BS	Hongyanglazi	*T. aestivum*	Xiao et al., 2013
Pm49 (MI5323)	2BS	MG5323	*T. dicoccum*	Piarulli et al., 2012
Pm50	2AL	K2	*T. dicoccum*	Mohler et al., 2013

Conidia are produced on the mycelium and serve as secondary inoculum. Liu et al. (2012) reported that three infection incidences of powdery mildew occur in wheat. Firstly, chasmothesium release ascospores to infect volunteer wheat, which produces conidia that are carried by air currents to infect volunteer wheat plants in the same and different regions, affecting generation after generation. Secondly, few chasmothesium survive high temperatures in the summer until the next generation seedling stage, and then release ascospores to infect the sown wheat plants. This occurs rarely under natural conditions because the ascus does not carry out meiosis nor differentiate into ascospores until it absorbs water. This means as long as it rains, chasmothecia discharge ascospores readily and they do not wait until autumn seedlings come out. Thirdly, conidia that are wind-blown from other places affect volunteer wheat or main wheat crop, in turn infecting seedlings in season. Most of the processes for the fungal invasion occur in the dark but formation of conidia and subsequent host penetration require light.

Environmental conditions are very crucial for successful colonization of the fungus (Costamilan, 2005; Hau and De Vallavieille-Pope 2006; Luck et al., 2011). Cool, humid weather with temperatures between 15 °C – 20 °C form the best conducive environment for fungal invasion but infection can take place between 5 °C and 30 °C. With availability of favorable developing conditions, the fungus can complete a repeating cycle in 7-10 days thereby providing a high possibility of rapid conidia production, which results in development of new virulent powdery mildew races through increased mutation frequency of the fungus (Piarulli et al., 2012).

Genetic resistance to wheat powdery mildew

Control of wheat powdery mildew is one of the vital components required for successful global wheat production. With the continuous mutation of wheat powdery mildew fungus resulting in production of more virulent strains, the development of wheat cultivars resistant or tolerant to the powdery mildew pathogens has become one effective control method widely adopted by scientists. Several susceptible wheat cultivars have been crossed with identified resistant wheat cultivars either from the wild compatible cereal members or from the known resistant cultivars found in other part of the world. This has resulted in location and mapping of the responsible genes on wheat chromosomes.

So far, over 64 resistance genes or alleles have been designated on 50 loci (*Pm1– Pm50*). Six of these loci (*Pm1a* to *Pm1e* at *Pm1*, *Pm3a* to *Pm3r* at *Pm3*, *Pm4a* to *Pm4d* at *Pm4*, *Pm5a* to *Pm5e* at *Pm5*, *Pm8/Pm17, Pm24a* and *Pm24b* at *Pm24*) have multiple resistant alleles (Table 1).

Sources of these genes for powdery mildew disease resistance have emerged from landraces, common wheat cultivars and related species and genera. 33 designated powdery mildew resistant genes were derived from *T. aestivum*. Among others, they include genes *Pm44, Pm45, Pm46, Pm47* identified from cultivars Hombar, D57, Tabasco and Hongyanglazi, respectively. Other genes originated either from species closely related to common wheat such as *T. monococcum*, *T. turgidum*, *T. timopheevii, Aegilops speltoides, Ae. tauschii*, *Ae. longissina*, *Ae. vate*, and *Ae. umbellulata* or more distant relatives such as *Secale* cereal, *Elytrigia intermedium* and *Dasypyrum villosum* (Chen and Chelkowski 1999; Zeller et al., 2002; Perugini, 2007; Xue et al., 2009; Xue et al., 2012b).

The first gene to be identified was *Pm1* in the Canadian wheat cultivar Axminster and was located to the long arm of chromosome 7A and designated as *Pm1a* (Sears and Briggle, 1969). At present, five alleles

at the locus *Pm1* of chromosome 7A have been identified and designated. Hsam et al., (1998) reported availability of allele *Pm1b* in wheat from *Triticum monococcum* while allele *Pm1c*, initially called *Pm18* was also introgressed from the same species (*T. monococcum*). They also reported the presence of allele *Pm1d* in *T. spelta* (Table 1). Peusha et al. (1996) initially identified gene *Pm22* as located on the wheat chromosome 1D but it was later re-located to the long arm of chromosome 7A and attained the name *Pm1e* (Singrun et al., 2003; Perugini, 2007). Srnic et al. (2005) also identified and introgressed a resistant gene to powdery mildew from *T. timopheevii* subsp. *armeniacum* (2n = 28, AtAtGG) to the susceptible wheat cultivar Saluda and mapped on the long arm of chromosome 7AL.

Briggle (1969) developed near-isogenic lines (NILs) in the genetic background of the susceptible wheat cultivar Chancellor (Cc) carrying the *Pm3a* allele from the Japanese 'Asosan', *Pm3b* from the Russian 'Chul' and *Pm3c* from the Mexican 'Sonora' (Table 1). Seven more alleles at the *Pm3* locus were reported by Zeller et al. (1993). Through monosomic analysis and allelism tests, Zeller et al. (1993) described three *Pm3* alleles: *Pm3d* in the German spring wheat 'Kolibri', *Pm3e* in the Australian wheat strain W150, and *Pm3f* in the NIL Michigan Amber. Four alleles, *Pm3g*, *Pm3h*, *Pm3i,* and *Pm3j*, were identified, respectively, in the French wheat 'Aristide', lines Abessi (whose resistance was derived from an Ethiopian durum wheat), N324 from Nepal and GUS 122 from Russia (Sourdille et al., 1999; Huang et al., 2004).

Bhullar et al. (2009) and Yahiaoui et al. (2009) reported the discovery of 7 additional alleles from *Pm3k* to *Pm3r* with *Pm3r* being the only allele isolated from tetraploid wheat while the rest of the functional *Pm3* alleles were isolated from hexaploid wheat. They also reported that from this group, *Pm3l* up to *Pm3r* have been successfully cloned as a result of allele mining study that led to the rapid isolation of the seven alleles. This followed another successful cloning of allele *Pm3d* (Yahiaoui et al., 2004). Further findings on *Pm3* allele resulted in identification of 8 new alleles namely *Pm3_11150*, *Pm3_15011*, *Pm3_2616*, *Pm3_2816*, *Pm3_7524*, *Pm3_8152, Pm3_3220* and *Pm3_4650* (Bhullar et al., 2010). The alleles were isolated from wheat accessions collected from China and Nepal and were identified out of the eight cloned *Pm3* sequences. The findings resulted in *Pm3* locus being one of the largest allelic series of plant resistance genes. *Pm4a* and *Pm4b* on chromosome 2AL were first reported by The et al. (1979) on cultivars Khapli (*T. dicoccum*) and Armada (*T. carthlicum*) respectively and subsequently reviewed by Huang and Roder (2004) and Alam et al. (2011). The *Pm4* locus also contains *Pm4c*, an allele which was initially mapped on wheat chromosome 5A (McIntosh et al., 1998) as *Pm23* but Hao et al. (2008) found that the gene was allelic to *Pm4b* and it was re- located to chromosome 2A as allele of *Pm4* locus. *Pm4d* is another latest gene located on *Pm4* locus, which was found in Tm27d2 cultivar of *T. monococcum* (Schmolke et al., 2012).

Alleles of resistant powdery mildew *Pm5* were identified and mapped on wheat chromosome 7BL. These include gene *Pm5a* in the wheat cultivar Hope, a recessive gene that originated from *T. dicoccum* L. The Germany cultivar Ibis carrying *Pm5b* (*Mli*) displayed similar infection type as *Pm5a*. Both *Pm5a* and *Pm5b* are susceptible to the major Chinese *B. graminis* f. sp. *tritici* isolates. *Pm5c* was derived from *T. sphaerococcum* var. *rotundatum* (Hu et al., 2008). *Pm5d* was derived from CI 10904, which was introduced from Nanjing, China to USA in 1929. *Pm5e* in Fuzhuang 30 is a recessive or partial recessive allele. Fuzhuang 30 was developed from Jingyang 30 and was resistant to the prevalent Chinese powdery mildew isolates (Huang et al., 2000a; Nematollahi et al., 2008; Hu et al., 2008) (Table 1). Several other powdery mildew resistant genes, their locations and sources of resistance have also been reviewed by Alam et al. (2011).

Wild relatives of wheat have been exploited as sources of new resistance genes. Wild emmer (*Triticum turgidum* var. *dicoccoides*), the immediate progenitor of cultivated durum and bread wheat, is a source of most designated powdery mildew resistance genes. These genes are expressed in both seedling and adult plants while others are expressed only in adult plants. For instance, the genes *Pm26,* located on chromosome 2BS (Rong et al., 2000), *Pm42* (Hua et al., 2009) and *Pm49*, another dominant gene controlling resistance at the seedling stage located on chromosome 2BS, were originated from ssp. *dicoccoides.* Other resistance genes; *Pm16, Pm30*, *Pm31, Pm36*, *Pm41*, *Pm42, Pm49* and *Pm50,* located on chromosomes 4A, 5B, 6A, 5B, 3B, 2B and 2A respectively, were also transferred from ssp. *dicoccoides* to cultivated wheat (Piarulli et al., 2012; Mohler et al., 2013).

Other wild relatives found to carry designated resistant genes include *T. timopheevi*, which carries genes *Pm6, Pm27, Pm37* and *Pm33*. *Pm6* is originated from the 2G chromosome of *T. timopheevii* and was introgressed into chromosome 2BL of common wheat (Tao et al., 2000). *T. carthlicum* is another wild relative source of powdery mildew resistance genes. They include genes *Pm4b* and *Pm33*, the latter having originated from accession PS5 and transferred into common wheat (Zhu et al., 2005). *Pm1b* and *Pm4d* originated from *T. monococcum* (Hsam et al., 1998; Schmolke et al., 2012). Powdery mildew genes *Pm12, Pm13, Pm19, Pm29, Pm32, Pm34, and Pm35* were transferred from *Aegilops* (Miranda et al., 2007; Xue et al., 2012b). *Pm7, Pm8, Pm17* and *Pm20* originated from *Secale*, a distant relation of common wheat (McIntosh et al., 2011). Two designated genes *Pm40* and *Pm43* were introgressed into common wheat from *Elytrigia intermedium* (He et al., 2009; Luo et al., 2009) while

Table 2. Chromosomal position, cultivars/lines, sources and references of the temporarily designated powdery mildew resistance genes in wheat

Gene	Position	Cultivar/ line	Source	Reference
Mld	4B	Maris Dove	*T. durum*	Bennet, 1984
Ml-Ad	-	Adlungs Alemannen	*T. aestivum*	Lutz et al., 1995
Ml-Br	-	Bretonischer	*T. aestivum*	Lutz et al., 1995
Ml-Ga	-	Garnet	*T.aestivum*	Lutz et al., 1995
MIRE	6AL	RE714	*T. dicoccum*	Chantret et al., 2000
Mljy	7B	Jieyan 94-1-1	*T.aestivum*	Huang et al., 2002
Mlsy	7B	Siyan 94-2-1	*T. aestivum*	Huang et al., 2002
mlRD30	7AL	RD30	*T. aestivum*	Singrun et al., 2004
PmDR147	2AL	DR147	*T. durum*	Zhu et al., 2004
MlZec1	2BL	Zecoi 1	*T. dicoccoides*	Mohler et al., 2005
PmPs5A	2AL	Am4	*T. carthlicum*	Zhou et al., 2005
PmPs5B	2BL	Am9/3*Laizhou953	*T. carthlicum*	Zhou et al., 2005
PmE	2AL	Xiaohan/4*Bainong3217	*Er. Orientale*	Zhou et al., 2005
PmP	-	Xiaobing/3*Bainong 3217	Fuco/*Agropyron*	Zhou et al., 2005
PmY39	2U(2B)	953*4/Am9	*Ae. umbellulata*	Zhou et al., 2005
PmH	7BL	Hongquanmang	*T. aestivum*	Zhou et al., 2005
PmY150	6B/6S	*Ae. longissima*/ 3*Laizhou 953	*Ae. longissima*	Zhou et al., 2005
PmM53	5DL	M53	*Ae. tauschii*	Li et al., 2005
PmU	7AL	UR206/Laizhou	*T .urartu*	Qiu et al., 2005
PmY201	5DL	Y201	*Ae. tauschii*	Sun et al., 2006
PmY212	5DL	Y212	*Ae. tauschii*	Sun et al., 2006
Mlm2033	7AL	TA2033	*T. monococcum*	Yao et al., 2007
Mlm80	7AL	M80	*T. monococcum*	Yao et al., 2007
PmE	7BS	TAI7047	*E. intermedium.*	Ma et al., 2007
PmYU25	2DL	TAI7047	*E. intermedium.*	Ma et al., 2007
PmAS846	5BL	N9134	*T. dicoccoides.*	Wang et al., 2007
PmAeY2	5DL	Y189	*Ae. tauschii*	Zhang and Lang, 2007
PmY39-2	6AS	N9628-2	*Ae. umbellulata*	Liu et al., 2008
Pm2026	5AL	TA2026	*T. monococcum*	Xu et al., 2008
mlIW72	7AL	IW72	*T. dicoccoides.*	Ji et al., 2008
PmTm4	7BL	Tangmai 4	*T. aestivum*	Hu et al., 2008
PmLK906	2AL	Lankao 90(6)	*T .aestivum*	Niu et al., 2008
PmYm66	2AL	Yumai 66	*T. aestivum*	Hu et al., 2008
MlWE18	7AL	3D249	*T. dicoccoides*	Han et al., 2009
MlAG12	7AL	NC06BGTAG12/ Jagger	*T. aestivum*	Maxwel et al., 2009
MlWE29	5BL	WE29	*T. dicoccoides*	Zhang et al., 2009
TaAetPR5	2AL	EU082094	*A. tauschii*	Niu et al., 2010
Ml3D232	5BL	3D232	*T. dicoccoides*	Zhang et al., 2010
MlAB10	2BL	NC97BGTAB10	*T. aestivum*	Maxwell et al., 2010
PmG16	7AL	G18-16	*T. dicoccoides*	Ben-David et al., 2010
PmHNK	3BL	Zhoumai 22	*T. aestivum*	Xu et al., 2010
Pm07J126	-	07jian126	*T. aestivum*	Yu et al., 2012
PmAs846	5BL	N9134, N9738	*T. dicoccoides*	Xue et al., 2012a
PmTb7A.1	7AL	pau5088	*T. boeoticum*	Chhuneja et al., 2012
PmTb7A.2	7AL	pau5088	*T. boeoticum*	Chhuneja et al., 2012
PmLX66	5DS	Liangxing 66	*T. aestivum*	Huang et al., 2012
PmG25	5BL	N0308	*T. dicoccoides*	Alam et al., 2013
PmZB90	2AL	ZB90	*T. aestivum*	Yi et al., 2013

Pm21 originated from *Haynaldia villosum* (Chen et al., 1995; Piarulli et al., 2012; Xiao et al., 2013).

Wheat powdery mildew temporarily designated resistance genes

Several studies have identified and located more than fifty resistance wheat powdery mildew genes but up to now they carry temporarily designated names. Table 2 shows some of these powdery mildew resistance genes located on different chromosomes originating from known resistant wheat cultivars as well as wild relatives of wheat. These genes have both recessive as well as dominant characteristics.

Niu et al. (2008) reported that wheat (*Triticum aestivum*) line Lankao 90(6) originating from a cross

Table 3. Distribution of powdery mildew resistance genes on homologous wheat chromosomes

Homologous chromosome	A	B	D
1	*Pm3, Pm25*	*Pm28, Pm32,*	*Pm10, Pm24,*
2	*Pm4, Pm25, Pm50, PmDR147, PmPs5A, PmE, PmYm66, TaAetPR5, PmLK906, PmZB90*	*Pm6, Pm26, Pm33, Pm42, Pm49, MlZec1, PmY39, MIAB10, PmPs5B*	*Pm43, PmYU25*
3	*Pm44*	*Pm13, Pm38, Pm41, PmHNK*	
4	*Pm14*	*Mld*	
5	*Pm2026*	*Pm36, Pm16, Pm30, PmAS846, Ml3D232, PmAs846, PmG25, MIWE29*	*Pm2, Pm34, Pm35, Pm46, PmM53, PmY201, PmY212, PmAeY2, PmLX66*
6	*Pm21, Pm31, MIRE, PmY39-2*	*Pm11, Pm12, Pm14, Pm27, PmY150*	*Pm45*
7	*Pm1, Pm9, Pm18, Pm37, mlRD30, PmU, Mlm2033, Mlm80, MlIW72, PmTb7A.1, PmTb7A.2, MlAG12, PmG16, MlWE18*	*Pm5, Pm40, Pm47, Mljy, Mlsy, PmH, PmE, PmTm4*	*Pm15, Pm19, Pm29, Pm39*

between 'Mzalenod Beer' (hexaploid triticale)/ 'Baofeng 7228'// '90 Xuanxi', carry a recessive powdery mildew resistance gene temporarily named *PmLK906* located on chromosome 2AL of wheat. The gene appeared different from the known dominant alleles found on *Pm4* locus located on the same chromosome. Another gene, temporarily designated as *TaAetPR5* was identified in the same Lankao 90(6) cultivar on chromosome 2AL where *Pm4* locus and *PmLK906* were located. The gene was found to be tightly linked to *PmLK906* (Niu et al., 2010). Other resistant powdery mildew genes/alleles located on the chromosome 2A include *PmDR147* identified from wheat (*T. durum*) line DR147 (Zhu et al., 2004), *PmPS5A,* which originated from *T. carthlicum* (Zhou et al., 2005), *PmE* from a cross between Xiaohan/4*Bainong3217 (Zhou et al., 2005), *PmYm66* originating from wheat (*Triticum aestivum*) line Yumai 66 (Hu et al. 2008) and *PmZB90* originating from wheat (*T. aestivum*) line ZB90 (Yi et al., 2013) (Table 2).

On chromosome 2B, nine powdery mildew resistance genes have been mapped and four of these genes; *MlZec1, PmY39, MIAB10, PmPs5B*, carry temporarily designated names (Table 2 and 3). Gene *MlZec1*, a single dominant gene, originated from wheat (*Triticum turgidum* ssp. *dicoccoides*) line Zecoi-1. The line was a cross between *T. dicoccoides* line Mo49 and German spring wheat cultivar Ralle carrying *Pm3d* gene (Mohler et al., 2005). Powdery mildew gene *PmY39* was located following a cross between Am9 and 3*Laizhou 953. Am9 was an amphidiploid synthesized with *T. carthlicum* acc. PS5 and *Ae. umbellulata* acc. Y39. The derivative between the cross of the two parents (Am9/3*Laizhou 953-2) resulted in location of the resistant gene on chromosome 2U/2B of the substitution line. The resistance gene identification was the first successful transfer of powdery mildew resistance gene from *Ae. umbellulata* to cultivated wheat (Zhou et al., 2005). Another dominant gene was identified from the same Am9 when it was crossed with 3*Laizhou 953-1. The gene was temporarily designated as *PmPs5B* and was mapped 30 cM apart with another already known gene *Pm6* located on the same chromosome (Zhou et al., 2005). Other temporarily designated genes reported on similar study by Zhou et al. 2005 include *PmPs5A*, *PmH, PmP* and *PmY150* (Table 2).

Chhuneja et al., (2012) reported the presence of two temporarily designated genes *PmTb7A.1* and *PmTb7A.2* in accession pau5088, a diploid A^bA^b genome progenitor accession of *T. boeoticum*, which was crossed with *T. monococcum* accession pau14087 to produce Recombinant In-bred Line (RIL) population. The population contained other important features such as disease resistance to stripe rust and cereal cyst nematode resistance (Singh et al., 2007a, 2010; Chhuneja et al., 2008) apart from expression of resistance to wheat powdery mildew. The two genes were located and mapped on chromosome 7AL where 10 other temporary designated genes are also mapped (Table 2 and 3). Since the source of resistance was from a diploid A^bA^b genome of *T. boeoticum* and this genome combines freely with the A genome of wheat, Chhuneja et al. (2012) suggested that successful transfer of the identified genes would be possible by using susceptible *T. durum* as a backcross bridging species where the F_1

would be crossed with hexaploid wheat for the transfer of the two (*PmTb7A.1* and *PmTb7A.2*) powdery mildew resistance genes into wheat.

Resistance genes distribution on wheat chromosomes

In this review, distribution of mapped powdery mildew genes on wheat chromosomes show that some chromosomes contains more *Pm* genes than others while two chromosomes do not have mapped powdery mildew genes. For example, apart from the chromosome 1A, which contains a heavy cluster of alleles for *Pm3* locus and *Pm25* gene, chromosome 7A contains 14 powdery mildew resistance genes namely; *Pm1*, *Pm9, Pm18, Pm37* and 10 temporary named genes (Table 3). Chromosome 2A contains 10 mapped powdery mildew resistance genes; *Pm4* (comprising of multiple alleles), *Pm25, Pm50* and 7 others non-designated genes carrying temporarily names. Chromosomes 3A, 4A, 4B, 5A and 6D carry one mapped powdery mildew resistance gene each namely *Pm44*, *Pm14*, *Mld*, *Pm2026* and *Pm45*, respectively while chromosomes 3D and 4D do not carry any known powdery mildew resistance gene (Table 3).

Molecular markers linked to powdery mildew resistance genes

Molecular markers are tools that help to locate and identify parts of DNA positioned near a gene or genes of interest (Alam et al., 2011). The markers are important in locating and identifying positions with different sequences among varieties or cultivars. These differences may occur within genes or between genes in the DNA strand as long as unique sequences varying between the plants of interest can be recorded. Differences of this type are referred to as polymorphisms and can be detected through a variety of methods. Molecular identification of specific DNA sequences can be used to identify the presence or absence of wheat powdery mildew (*Pm*) genes in wheat cultivars, their chromosomal location, the number of genes and the way in which they are transmitted to progeny (Chen and Chelkowski, 1999).

In location and mapping of these genes, one or more markers may be used to increase the precision and accurate positioning of the identified genes. Since the markers are associated with a particular wheat chromosome and region where polymorphism may occur, it becomes easier to map the identified gene following polymorphisms of a marker using preferred gene mapping software. By using these molecular markers, over thirty three designated powdery mildew resistance genes have been located and mapped in wheat (Table 4). Also, over forty two wheat powdery mildew resistance genes have been located and mapped on wheat chromosomes but they currently carry temporary designated gene names.

Molecular marker techniques used for identification and confirmation of *Pm* genes to powdery mildew include Restriction Fragment Length Polymorphisms (RFLP). It was the first molecular marker to be developed and first tried in humans before being used in plants (Weber and Helentjaris, 1989). Due to their requirement of a large amount of DNA, these markers are not popularly used though some studies continue to use them for Quantitative Traits Loci (QTL) mapping as well as gene identifications. Genes such as *Pm1a*, *Pm1c*, *Pm2*, *Pm6*, *Pm13*, *Pm26* have been mapped using this marker (Huang and Roder, 2004; Alam et al., 2011). Also temporary designated genes such as *MIRE* (Chantret et al., 2000), *Mlm2033* and *Mlm80* (Yao et al., 2007), *Pm2026* (Xu et al., 2008) and *mlIW72* (Ji et al., 2008) were located and mapped using RFLP in combination with other known markers (Table 4).

Random Amplified Polymorphic DNA (RAPD) is another molecular tool developed for genetic studies. The technique is based on the amplification of random DNA segments using a single primer of arbitrary nucleotide sequence. It is economical and easy to use and several designated powdery mildew resistance genes, which among others include *Pm1a* (Hu et al., 1997), *Pm6* (Wricke et al., 1996), *Pm13* (Cenci et al., 1999) and *Pm25* (Shi et al., 1998) were mapped using the technique (Table 4).

Amplified Fragment Length Polymorphisms (AFLP), a powerful technique, reliable and efficient in generating large numbers of markers for the construction of high-density genetic maps (Keim et al., 1997) was developed and helped in mapping powdery mildew genes *Pm1c* and *Pm4a* (Hartl et al., 1999), *Pm17* (Hsam et al., 2000), *Pm24a* (Huang et al., 2000b) and *Pm29* (Zeller et al., 2002). Several other temporary designated genes including *mlRD30* (Singrun et al., 2004), *MlZec1* (Mohler et al., 2005), *PmP* (Zhou et al., 2005) and *PmM53* (Li et al., 2005) were located and mapped using AFLP molecular marker in combination with other markers.

Simple Sequence Repeats (SSR) also known as microsatellite is one other important molecular technique developed for locating and mapping genes. It remains one of the most popular markers to-date and the latest designated powdery mildew resistant genes; *Pm 46* (Gao et al., 2012), *Pm 47* (Xiao et al., 2013), *Pm49* (Piarulli et al., 2012) and *Pm50* (Mohler et al., 2013) have been identified and mapped using this technique. Several other genes including *Pm1e, Pm5e, Pm24a, Pm24b, Pm27, Pm30, Pm31, Pm36, Pm40, Pm42, Pm43* and *Pm45* were also located and mapped using microsatellite or Simple Sequence Repeat (SSR) markers (Table 4). Temporary designated gene such as *PmU* (Qiu et al., 2005), *PmY201*, *PmY212* (Sun et al., 2006), *MlAB10* (Maxwel et al., 2010), *Pm07J126* (Yu et al., 2012),

Table 4. Molecular markers linked to powdery mildew resistance genes in wheat

Gene	Position	Type of markers	Closest/ flanking marker	Linkage distance/ contribution	Mapping population	Reference
Pm1a	7AL	RAPD, STS	UBC320420, UBC638550	Both co-segregate	F_5, F_2 lines, BSA	Hu et al., 1997
		RFLP	WHS178-9.4kb-EcoRI	2.8 ± 2.7 cM	F_2 lines, NILs	Hartl et al., 1995
		RFLP	CDO347	Co-segregate	F_2 lines, NILs	Ma et al., 1994
		RFLP, STS	mwg2062, cdo347, psr121, psr148, psr680, psr687, wir148, C607, STS638542, ksuh9	All Co-segregate	F_2 lines	Neu et al., 2002
Pm1c	7AL	RFLP, RAPD	WHS178-15kb-EcoRI, OPH-111900	4.4 ±3.6 cM, 13 cM	F_2 lines, BSA	Hartl et al., 1995
		AFLP	S19M22-325/200	Co-segregate	F_3 + F_4 lines, BSA	Hartl et al., 1999
			S14M20-137/138	Co-segregate		
Pm1e	7AL	SSR, AFLP	GWM344-null-S13M26-372	0.9cM, 0.2 cM	$F_{2:3}$ lines, BSA	Singrun et al., 2003
Pm2	5DS	RFLP	WHS350-6.5kb-EcoRV,WHS295	3.8 cM, 2.7 ±2.6 cM	F_2 lines, NILs	Hartl et al., 1995
		RFLP	BCD1871	3.5 cM	F_2 lines, NILs	Ma et al., 1994
		STS	STSwhs350		F_2 lines, NILs	Mohler and Jahoor, 1996
Pm3a	1AS	RFLP	WHS179	3.3 ± 1.9 cM	DH, NILs	Hartl et al., 1993
Pm3b	1AS	RFLP	BCD1434	1.3 cM	F_2 lines, NILs	Ma et al., 1994
Pm3g	1AS	RFLP	Gli-A5	5.2 cM	DH	Sourdille et al.,1999
Pm4a	2AL	RFLP	BCD1231, CDO678	Co-segregate	F_2 lines, NILs	Ma et al., 1994
		AFLP	4aM1	3.5 cM	F_3+F_4 lines, BSA	Hartl et al., 1999
		STS	STSbcd1231-1.7kb	Co-segregate	NILs	Liu et al., 1998
Pm4d	2AL	STS	Xbarc122, Xgwm526	1.0 cM; 3.4 cM	$F_{2:3}$ lines	Schmolke et al., 2012
Pm5e	7BL	SSR	GWM1267-136	6.6 cM	$F_{2:3}$ lines, BSA	Huang et al., 2003
Pm6	2BL	RFLP	BCD135-9kb-EcoRV	1.6 ± 1.5 cM	F_2 lines, NILs	Tao et al., 2000
Pm8	1RS.1BL	RFLP	IAG95	Tightly linked	F_2 lines, BSA	Wricke et al., 1996
		RAPD	OPJ07-1200, OPR19-1350		Translocation lines	Iqbal and Rayburn, 1995
		STS	SEC-1b-412bp		Translocation lines	DeFroidmont, 1998
		STS	STSiag95-1050	Co-segregate	DH, $F_{2:3}$ lines	Mohler et al., 2001
Pm12	6BS-SS.6SL	RFLP	psr10, psr106, Nor-2, psr141, psr113, psr142, psr149, psr2	Co-segregate	F_2 lines	Jia et al., 1996
Pm13	3BL.3SS-3S 3DL.3SS-3S	RFLP	psr305, psr1196		Recombinant	Donini et al., 1995
		RFLP, RAPD, STS	cdo460, utv135, OPV13800, UTV13, OPX12570, UTV14		Recombinant lines	Cenci et al., 1999
Pm17	1RS.1AL	RFLP, AFLP	IAG95-CA/CT-355	1.5 cM	$F_{2:3}$ lines	Hsam et al., 2000
Pm21	6VS.6AL	RAPD	OPH171900	Co-segregate	F_2 lines	Qi et al., 1996

Table 4 continues

		RAPD, SCAR	OPH171400, SCAR1265, SCAR1400	All co-segregate	F_2 lines	Liu et al., 1999
Pm24a	1DS	AFLP, SSR	E34/M51-407, Xgwm337-204	Co-segregate, 2.4 ± 1.2 cM	$F_{2:3}$ lines, BSA	Huang et al., 2000b
		SSR	Xgwm1291	Co-segregate	$F_{2:3}$ lines	Huang and Roder, 2004
Pm24b	1DS	SSR	Xgwm603/Xgwm789, Xbarc229	1.5 cM -1.0 cM	$F_{2:3}$	Xue et al., 2012b
Pm25	1A	RAPD	OPA04950	12.8 cM	BC_1F_1 lines, BSA	Shi et al., 1998
Pm26	2BS	RFLP	wg516	Co-segregate	RSLs	Rong et al., 2000
Pm27	6B-6G	RFLP, SSR	psp3131	Co-segregate	F_2 lines	Jarve et al., 2000
Pm29	7DL	RFLP, AFLP	S24M13-233, S19M23-240, S22M26-192, S25M15-145, S13M23-442, S22M21-217, S17M25-226	All co-segregate	F_2 lines, BSA	Zeller et al., 2002
Pm30	5BS	SSR	Xgwm159-460, Xgwm159-500	5 cM – 6 cM	BC_2F_2 lines, BSA	Liu et al., 2002
Pm31	6AL	SSR	Xpsp3029	0.6 cM	BC_2F_2 lines, BSA	Xie et al., 2003
Pm36	5BL	SSR	BJ261635	Co-segregate	BC_5F_5	Blanco et al., 2008
Pm40	7BS	SSR	Xgwm297	0.4 cM	F_2 lines	Luo et al., 2009
Pm41	3BL	SSR, ISBP, STS	BE489472	Co-segregate	F_2 lines	Li et al., 2009
Pm42	2BS	SSR, AFLP-SCAR, EST-STS, RFLP-STS	BF146221	Co-segregate	F_2 lines	Hua et al., 2009
Pm43	2DL	SSR	Xwmc41	2.3 cM	F_3 and BC_1 lines	He et al., 2009
Pm45	6DS	SSR, STS	Xmag6176	2.8 cM	F_2 lines	Ma et al., 2011
Pm46	5DS	SSR	Xgwm205, Xcf81	18.9 cM	F_2 and $F_{2,3}$ lines	Gao et al., 2012
Pm47	7BS	SSR, EST	Xgwm46, *BE606897*	1.7 cM, 3.6 cM	$F_{2,3}$ lines	Xiao et al., 2013
Pm49	2BS	EST-SSR	CA695634	0.84 cM-1.00 cM	F_1+F_2	Piarulli et al., 2012
Pm50	2AL	SSR	Xgwm294	2.9 cM	BC_1	Mohler et al., 2013
MlRE	6AL	SSR, RFLP	XksuD27	-	BSA, F_3	Chantret et al., 2000
		SSR, AFLP	Xgwm344, XE33M62-392, XE39M58-414		BSA, F_3 lines	
mlRD30	7AL					Singrun et al., 2004
PmDR147	2AL	SSR	Xgwm311, Xgwm382	5.9 cM, 4.9 cM	BC_3F_2 lines	Zhu et al., 2004
		AFLP, SSR	E35M56-330, E35M57-56, E37M54-286, E38M54-207, Xwmc356-2B	2.0 cM	BSA, F_3 lines	
MlZec1	2BL					Mohler et al., 2005
PmPs5A	2AL	SSR	Xgwm356,	10.2 cM	BC_3, BC_4 lines	Zhou et al., 2005
		SSR	Xgwm111, Xgwm382, Xgwm526, Xwmc317	1.1 cM	F_2 lines	
PmPs5B	2BL					Zhou et al., 2005
		SSR	Xgwm265, Xgwm311, Xgwm382	2.9 cM, 3.6 cM, 4.4 cM	F_2 lines	
PmE	2AL					Zhou et al., 2005
PmH	7BL	SSR	Xgwm611, Xpsp3033	5.9 cM, 13.2 cM	BC_5F_2 lines	Zhou et al., 2005

Table 4 continues

PmP		AFLP	XM55P66, XM55P37	0.8cM, 2.4 cM	F_2 lines	Zhou et al., 2005
PmY39	2U(2B)	SSR	Xgwm257, Xgwm296, Xgwm319	Co-segregate	F_2 lines	Zhou et al., 2005
PmY150	6B/6S	SSR	Xgwm325, Xwmc382, Xwmc397		F_2 lines	Zhou et al., 2005
PmM53	5DL	AFLP, SSR	$P16M16_{-109}$, $P5M16_{-161}$, Xwmc289b, Xgwm583, Xgwm292	1.0 cM, 3.0 cM, 20.0 cM, 33.0 cM, 24.0 cM	F_2, F_3 lines	Li et al., 2005
PmU	7AL	SSR	Xgwm273, Xpsp3003	2.2 cM, 3.8 cM	F_1, F_2 lines	Qiu et al., 2005
PmY201	5DL	SSR	Xgwm174	5.2 cM	F_2 lines	Sun et al., 2006
PmY212	5DL	SSR	Cfd57	5.6 cM	F_2 lines	Sun et al., 2006
Mlm2033	7AL	RFLP, STS, EST	Xgwm344, Xmag2185	< 2 cM	F_2, F_3 lines	Yao et al., 2007
Mlm80	7AL	RFLP, STS, EST	Xgwm344, Xmag2185	< 2 cM	F_2, F_3 lines	Yao et al., 2007
PmE	7BS	SSR	Xgwm297	13.0 cM	F_2 lines	Ma et al., 2007
PmYU25	2DL	SSR	Xgwm210	16.6 cM	F_2 lines	Ma et al., 2007
PmAS846	5BL	SSR	Xgwm67	20.6 cM	F_1, F_2 lines	Wang et al., 2007
PmAeY2	5DL	SSR	Xgwm583, Xgwm174, Xgwm182, Xgwm271	25.7 cM, 16.7 cM, 9.1 cM, 7 cM	F_2 lines	Zhang and Lang, 2007
PmY39-2	6AS	SSR	Xwmc553, Xwmc684	10.99 cM, 7.43 cM	F_2, F_3 lines	Liu et al., 2008
Pm2026	5AL	SSR, STS, RFLP	Xcfd39, Xgwm126, MAG1491, MAG1493, MAG1494, MAG2170	0.9 cM, Co-segregate	F_2, F_3 lines	Xu et al., 2008
mlIW72	7AL	SSR, EST, RFLP	Xgwm344, Xcfa2040, Xcfa2240, Xcfa2257, Xwmc525, MAG2185, MAG1759		F_2, F_3 lines	Ji et al., 2008
PmTm4	7BL	SSR, EST-SSR, EST-STS	Xcau12, Xgwm611, PmTm4, XEST92, Xbarc1073, Xbarc82, Xwmc276		F_2, F_3 lines, BSA	Hu et al., 2008
PmYm66	2AL	STS, SSR	EST48, EST83 (EST84), Xksum193, PmYm66		F_2, F_3 lines	Hu et al., 2008
PmLK906	2AL	SSR	Xgwm265, Xgdm93	3.72 cM, 6.15cM		Niu et al., 2008
MlAG12	7AL	SSR	Xwmc273, Xwmc346	8.3 cM, 6.6 cM	F_2, F_3 lines, BSA	Maxwel et al., 2009
MlWE29	5BL	SSR	Xgwm415, Xwmc75	2.5 cM, 17.6 cM	F_2, F_3 lines	Zhang et al., 2009
MlWE18	7AL	SSR, STS, EST-STS	Xwmc525, Xcfa2040, Xwmc273, XE13-2, Xmag1759, MlWE18, Xcfa2240		F_1, F_2, lines	Han et al., 2009
Ml3D232	5BL	SSR, EST, STS		0.8 cM	F_2, F_3 lines	Zhang et al., 2010
TaAetPR5	2AL	STS	p9-7p1, p9-7p2	7.62 cM	BSA	Niu et al., 2010
MlAB10	2BL	SSR	Xwmc445	7 cM	$F_{2:3}$ lines	Maxwell et al., 2010
PmG16	7AL	SSR, STS, DArT, CAPS	Xgwm344, wPt-9217, wPt-1424, wPt-6019	3.6 cM	Recombinant, $F_{2:3}$ lines	Ben-David et al., 2010
PmHNK	3BL	SSR	Xwmc291, Xgwm108	3.8 cM, 10.3 cM	BC_1, F_2, F_3 lines	Xu et al., 2010

Table 4 continues

PmAs846	5BL	STS	BJ261635, CJ840011	Co-segregate	F_2, $F_{2:3}$ lines	Xue et al., 2012a
PmTb7A.1	7AL	SSR, RFLP, STS, DArT	wPt4553, Xcfa2019	4.3 cM	Recombinant lines	Chhuneja et al., 2012
PmTb7A.2	7AL	SSR, RFLP, STS, DArT	MAG2185, MAG1759		Recombinant lines	Chhuneja et al., 2012
PmLX66	5DS	SCAR, SSR	SCAR203, Xcfd81	0.4, 2.8 cM	F_2, $F_{2:3}$ lines	Huang et al., 2012
Pm07J126		SSR	Xbarc183		F_2 lines	Yu et al., 2012
PmG25	5BL	SSR	Xgpw7425, Xwmc75, Xgwm408, Xwmc810, Xbarc232, Xbarc142	7.4cM, 9.4 cM, 11.2 cM, 22.3 cM, 25.4 cM, 29.3 cM	F_2 lines	Alam et al., 2013
PmZB90	2AL	SRAP, RGA	Me5/Em5-650, Me8/Em16-600	12.9 cM, 9.7 cM	F_2 lines	Yi et al., 2013

PmG25 (Alam et al., 2013) among several others (Table 4) were located and mapped using SSR markers. In many instances, the mapping was conducted in combination with other molecular markers.

Identification of *Pm* genes is also done using Sequence Tagged Site (STS) markers. These are single copy sequences, which are amplified by specific primers matching the nucleotide sequences at DNA fragment endings of an RFLP probe (Olson et al., 1989). The method is very useful for studying the relationship between various species and linked to some specific traits (Bustos et al., 1999). Powdery mildew resistance genes namely *Pm1a, Pm2, Pm4a, Pm6, Pm13, Pm41, Pm42* and *Pm45* were tagged and mapped using STS markers apart from other molecular markers used to identify and locate genes (Table 4).

CONCLUSION

Wheat powdery mildew caused by *B. graminis* f. sp. *tritici* is still challenging to wheat producers around the world as crop damage levels are enormously high. A proper understanding of the damaging trend, including aspects covered in this review, may benefit scientists to come up with more research ideas to counter the disease. Research studies on genetic resistance have resulted in identification and mapping of new genes on wheat chromosomes. The discovery of fifty designated genes (*Pm1 - Pm50*) as well as over fifty additional non-designated genes is helping in development of more resistant wheat varieties suitable in overcoming many virulent pathogen races. The use of molecular markers such as Simple Sequence Repeat (SSR), Amplified Fragment Length Polymorphism (AFLP), Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNAs (RAPD) and Sequence Tagged Sites (STS) has led to successful gene identification and mapping for over 33 resistant genes to wheat powdery mildew including the recently designated *Pm46* to *Pm50* genes and over 42 temporarily designated powdery mildew resistance genes.

REFERENCES

Agrios G (2005). Plant Pathology, 5th ed Burlington MA USA: Elsevier Academic Press.

Ahmad H, Moore K (2007). Inheritance of chromosomal location of powdery mildew resistance gene in wild wheat *Triticum turgidum* var. *dicoccoides*. Plant Pathol. J. 6(2): 164 -168.

Akhtar S, Anjum FM, Anjum MA (2011). Micronutrient fortification of wheat flour: Recent development and strategies. F. Res. Int. 44: 652–659.

Alam MA, Mandal MSN, Wang C, Ji W (2013). Chromosomal location and SSR markers of a powdery mildew resistance gene in common wheat line N0308. Afric. J. Micro. Res. 7(6) 477-482.

Alam MA, Xue F, Wang C, Ji W (2011). Powdery Mildew Resistance Genes in Wheat: Identification and Genetic Analysis. J. Mol. Bio. Res. 1 (1): 20-39.

Ben-David R, Xie W, Peleg Z, Saranga Y, Dinoor A, Fahima T (2010). Identification and mapping of *PmG16*, a powdery mildew resistance gene derived from wild emmer wheat. Theor. Appl. Genet. 121: 499-510.

Bennett FGA (1984). Resistance to powdery mildew in wheat: a review of its use in agriculture and breeding programmes. Plant Pathol 33(3): 279-300.

Bhullar NK, Zhang Z, Wicker T, Keller B (2010). Wheat gene bank accessions as a source of new alleles of the powdery mildew resistance gene *Pm3*: a large scale allele mining project. BMC Plant Bio 10(88): 1471-2229.

Bhullar NK, Street K, Mackay M, Yahiaoui N, Keller B (2009). Unlocking wheat genetic resources for the molecular identification of previously undescribed functional alleles at the *Pm3* resistance locus. Proc. Natl. Acad. Sci. 106:9519-9524.

Blanco A, Gadaleta Cenci AA, Carluccio AV, Abdelbacki AMM, Simeone R (2008). Molecular mapping of the novel powdery mildew resistance gene *Pm36* introgressed from *Triticum turgidum* var. *dicoccoides* in durum wheat. Theor. Appl. Genet. 116: 417-425.

Both M, Spanu PD (2004). *Blumeria graminis* f. sp. *hordei*, an obligate pathogen of barley. In: Talbot NJ (Ed) Plant Pathogen Interactions. Blackwell Publishing Oxford pp. 202- 218.

Briggle LW (1969). Near-isogenic lines of wheat with genes for resistance to *Erysiphe graminis* f. sp. *tritici*. Crop Sci., 9:70-72.

Briggle LW, Sears ER (1966). Linkage of resistance to *Erysiphe graminis* f.sp. *tritici* (*Pm3*) and hairy glume (*Hg*) on chromosome 1A of wheat. Crop Sci. 6: 559-561.

Bustos A, Soler C, Jouve N (1999). Analysis by PCR-based markers using designed primers to study relationships between species of *Hordeum* (Poaceae). Genome 42: 129-38.

Cenci A, D'Ovidio R, Tanzarella OA, Ceoloni C, Porceddu E (1999). Identification of molecular markers linked to *Pm13*, an *Aegilops longissima* gene conferring resistance to powdery mildew in wheat. Theor. Appl. Genet. 98: 448-454.

Ceoloni C, DelSignore G, Ercoli L, Donini P (1992). Locating the alien chromatin segment in common wheat- *Aegilops longissima* mildew resistance transfers. Hereditas 116: 239-245.

Chantret N, Sourdille P, Röder M, Tavaud M, Bernard G, Doussinault G (2000). Location and mapping of the powdery mildew resistance gene *MlRE* and detection of a resistance QTL by bulked segregant analysis (BSA) with microsatellites in wheat. Theor. Appl. Genet. 100(8): 1217-1224.

Chen PD, Qi LL, Zhou B, Zhang SZ, Liu DJ (1995). Development and molecular cytogenetic analysis of wheat-Haynaldia villosa 6VS/6AL translocation lines specifying resistance to powdery mildew. Theor. Appl. Genet. 91: 1125-1129.

Chen Y, Chelkowski J (1999). Genes for resistance to wheat powdery mildew. J. Appl. Genet. 40:317-334.

Chhuneja P, Kaur S, Garg T, Ghai M, Kaur S, Prashar M, Bains NS, Goel RK, Keller B, Dhaliwal HS, Singh K (2008). Mapping of adult plant stripe rust resistance genes in diploid A genome wheat species and their transfer to bread wheat. Theor. Appl. Genet. 116:313–324.

Chhuneja P, Kumar K, Stirnweis D, Hurni S, Keller B, Dhaliwal H, Singh K (2012). Identification and mapping of two powdery mildew resistance genes in *Triticum boeoticum* L. Theor. Appl. Genet. 124:1051–1058.

Costamilan LM (2005). Variability of the wheat powdery mildew pathogen *Blumeria graminis* f. sp. *tritici* in the 2003 crop season. Fitopatol. Bras. 4: 102-103.

Coventry DR, Gupta RK, Yadav A, Poswal RS, Chhokar RS, Sharma RK, Yadav VK, Gill SC, Kumar A, Mehta A, Kleemann SGL, Bonamano A, Cummins JA (2011). Wheat quality and productivity as affected by varieties and sowing time in Haryana. India F. Cr. Res. 123: 214–225.

DeFroidmont D (1998). A co-dominant marker for the 1BL/1RS wheat-rye translocation via multiplex PCR. J. Cereal Sci. 27: 229-232.

Donini P, Koebner RMD, Ceoloni C (1995). Cytogenetic and molecular mapping of the wheat-*Aegilops longissima* chromatin break points in powdery mildew resistant introgression lines. Theor. Appl. Genet. 91: 738-743.

Friebe B, Heun M, Tuleen N, Zeller FJ, Gill BS (1994). Cytogenetically monitored transfer of powdery mildew resistance from rye into wheat. Crop Sci. 34: 621-625.

Gao H, Zhu F, Jiang Y, Wu J, Yan W, Zhang Q, Jacobi A, Cai S (2012). Genetic analysis and molecular mapping of a new powdery mildew resistant gene *Pm46* in common wheat. Theor. Appl. Genet. 125 (5): 967-973.

Green JR, Carver TLW, Gurr SJ, (2002). The formation and function of infection and feeding structures. In: Belanger RR, Dik AJ, Bushnell, WR (Eds.). The Powdery Mildews APS Press, St Paul pp. 66 -82.

Han J, Zhang L, Li G, Zhang H, Xie C, Yang Z, Sun Q, Liu Z (2009). Molecular mapping of powdery mildew resistance gene *MlWE18* in wheat originated from wild emmer (*Triticum turgidum* var. *dicoccoides*). Acta Agronomica Sinica 35(10): 1791–1797 (in Chinese).

Hao Y, Liu A, Wang Y, Feng D, Gao J, Li X, Liu S, Wang H (2008) *Pm23*: a new allele of *Pm4* located on chromosome 2AL in wheat. Theor. Appl. Genet. 117: 1205–1212.

Hartl L, Mohler V, Zeller FJ, Hsam SKL, Schweizer G (1999). Identification of AFLP markers closely linked to the powdery mildew resistance genes *Pm1c* and *Pm4a* in common wheat. Genome 42: 322-329.

Hartl L, Weiss H, Stephan U, Zeller FJ, Jahoor A (1995). Molecular identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 90: 601-606.

Hartl L, Weiss H, Zeller FJ, Jahoor A (1993) Use of RFLP markers for the identification of alleles of the *Pm3* locus conferring powdery mildew resistance in wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 86: 959-963.

Hau B, De Vallavieille-Pope C (2006). Wind-dispersed diseases. Plant Dis. Epidemiol. 2: 387- 416.

He R, Chang Z, Yang Z, Yuan Z, Zhan H, Zhang X, Liu J (2009) Inheritance and mapping of powdery mildew resistance gene *Pm43* introgressed from *Thinopyrum intermedium* into wheat. Theor. Appl. Genet. 118: 1173–1180.

Heun M, Friebe B, Bushuk W (1990). Chromosomal location of the powdery mildew resistance gene of Amigo wheat. Phytopath. 80: 1129-1133.

Hsam SLK, Huang XQ, Ernst F, Hartl L, Zeller FJ (1998). Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 5. Alleles at the *Pm1* locus. Theor. Appl. Genet. 96:1129-1134.

Hsam SLK, Huang XQ, Zeller FJ (2001) Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.) 6. Alleles at the *Pm5* locus. Theor. Appl. Genet. 102: 127-133.

Hsam SLK, Mohler V, Hartl L, Wenzel G, Zeller FJ (2000). Mapping of powdery mildew and leaf rust resistance genes on the wheat-rye translocated chromosome T1BL.1RS using molecular and biochemical markers. Plant Breed. 119: 87-89.

Hsam SLK, Lapochkina IF, Zeller FJ (2003). Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 8. Gene *Pm32* in a wheat *Aegilops speltoides* translocation line. Euphytica 133: 367-370.

Hsam SLK, Zeller FJ (1997). Evidence of allelism between genes *Pm8* and *Pm17* and chromosomal location of powdery mildew and leaf rust resistance genes in the common wheat cultivar 'Amigo'. Plant Breed. 116: 119-122.

Huang J, Zhao Z, Song F, Wang X, Xu H, Huang Y, An D, Li H (2012). Molecular detection of a gene effective against powdery mildew in the wheat cultivar Liangxing 66. Mol. Breeding 30: 1737–1745.

Huang XQ, Coster H, Ganal MW, Roder MS (2003). Advanced backcross QTL analysis for the identification of quantitative trait loci alleles from wild relatives of wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 106: 1379-1389.

Huang XQ, Hsam SLK, Mohler V, Röder MS, Zeller FJ (2004). Genetic mapping of three alleles at the *Pm3* locus conferring powdery mildew resistance in common wheat (*Triticum aestivum* L.) Genome 47: 1130–1136.

Huang X Q, Hsam S L K, Zeller F J, Wenzel G, Mohler V (2000b). Molecular mapping of the wheat powdery mildew resistance gene *Pm24* and marker validation for molecular breeding. Theor Appl Genet 101: 407–414.

Huang X, Hsam SLK, Zeller FJ (2002). Chromosomal location of genes for resistance to powdery mildew in Chinese wheat lines Jieyan 94-1-1 and Siyan 94-1-2. Hereditas 136: 212–218.

Huang X Q, Hsam S L K, Zeller F J (2000a). Chromosomal location of powdery mildew resistance genes in Chinese wheat (*Triticum aestivum* L. em Thell.) landraces Xiaobaidong and Fuzhuang 30. J. Genet. Breed. 54: 311–317.

Huang X Q, Röder M S (2004). Molecular mapping of powdery mildew resistance genes in wheat: a review. Euphytica 137: 203–223.

Huang X Q, Wang L X, Xu M X, Röder M S (2003). Microsatellite mapping of the powdery mildew resistance gene *Pm5e* in common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 106: 858–865.

Hua W, Liu Z, Zhu J, Xie C, Yang T, Zhou Y, Duan X, Sun Q, Liu Z (2009). Identification and genetic mapping of *Pm42*, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor. Appl. Genet. 119, 223-230.

Hu T, Li H, Xie C, You M, Yang Z, Sun Q, Liu Z (2008). Molecular Mapping and Chromosomal Location of Powdery Mildew Resistance Gene in Wheat Cultivar Tangmai 4. Acta Agron. Sin. 34(7): 1193–1198.

Hu XY, Ohm HW, Dweikat I (1997). Identification of RAPD markers linked to the gene *Pm1* for resistance to powdery mildew in wheat. Theor. Appl. Genet. 94: 832-840.

Iqbal M J, Rayburn AL (1995). Identification of the 1RS rye chromosomal segment in wheat by RAPD analysis. Theor. Appl. Genet. 91: 1048-1053.

Järve K, Peusha HO, Tsymbalova J, Tamm S, Devos KM, Eno TM (2000). Chromosomal location of a *Triticum timopheevii*-derived powdery mildew resistance gene transferred to common wheat. Genome 43:377-381.

Jia J, Devos KM, Chao S, Miller TE, Reader SM, Gale MD (1996). RFLP-based maps of the homologous group-6 chromosomes of wheat and their application in the tagging of *Pm12*, a powdery mildew resistance gene transferred from *Aegilops speltoides* to wheat. Theor. Appl. Genet. 92, 559-565.

Ji X, Xie C, Ni Z, Yang T, Nevo E, Fahima T, Liu Z, Sun Q (2008). Identification and genetic mapping of a powdery mildew resistance gene in wild emmer (*Triticum dicoccoides*) accession IW72 from Israel. Euphytica 159, 385-390.

Jones HD (2005). Wheat transformation: current technology and applications to grain development and composition. J. Cr. Sci. 41, 137–147.

Jørgensen, JH (1973). Gene *Pm6* for resistance to powdery mildew in wheat. Euphytica 22: 43.

Keim P, Schupp JM, Travis SE, Clayton K, Zhu T, Shi L, Ferreira A, Webb DM (1997). A high-density soybean genetic map based on AFLP markers. Crop Sci., 37, 537-543.

Law C N, Wolfe M S (1966). Location for genetic factors for mildew resistance and ear emergence time on chromosome 7B of wheat. Can. J. Genet. Cytol. 8, 462-470.

Li G, Fang T, Zhang H (2009) Molecular identification of a new powdery mildew resistance gene *Pm41* on chromosome 3BL derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). Theor. Appl. Genet. 119, 531-539.

Li H, Wang X, Song F, Wu C, Wu X, Zhang N, Zhou Y, Zhang X (2011). Response to Powdery Mildew and Detection of Resistance Genes in Wheat Cultivars from China. Acta Agron. Sin. 37(6), 943–954.

Li N, Jia S, Wang X, Duan X, Zhou Y, Wang Z, Lu G (2012). The effect of wheat mixtures on the powdery mildew disease and some yield components. J. Integrated Agric. 11(4): 611-620 (in Chinese).

Li T, Zhang Z, Lin Z, Chen X, Gao S, Xin ZY (2005). Mapping of a novel gene conferring resistance to wheat powdery mildew using AFLP and SSR markers. Acta Agronomica Sinica 31 (9): 1105-1109 (in Chinese).

Lillemo M, Asalf B, Singh R P, Huerta-Espino J, Chen X M, He Z H, Bjørnstad Å (2008). The adult plant rust resistance loci Lr34/Yr18 and Lr46/Yr29 are important determinants of partial resistance to powdery mildew in bread wheat line Saar. Theor. Appl. Genet. 116: 1155–1166.

Liu DJ, Liu JY, Tao WJ, Chen PD (1998). Molecular markers and breeding wheat for powdery mildew resistance. In: Slinkard AE (Ed) Proceedings of the 9th International Wheat Genet Symposium, University Extension Press, Saskatoon, Canada 3: 128-131.

Liu N, Gong G, Zhang M, Zhou Y, Chen Z, Yang J, Chen H, Wang X, Lei Y, Liu K (2012). Over-summering of wheat powdery mildew in Sichuan Province, China. Crop Prot. 34: 112 -118.

Liu S, Wang C, Wang Q, Ji W (2008). SSR analysis of powdery mildew resistance gene in a new germplasm N9628-2 of *Triticum aestivum* L. Acta Agronomica Sinica 34(1): 84–88 (in Chinese).

Liu Z, Sun Q, Ni Z, Nevo E, Yang T (2002). Molecular characterization of a novel powdery mildew resistance gene *Pm30* in wheat originating from wild emmer. Euphytica 123: 21-29.

Liu Z, Sun Q, Yang T (1999). Development of SCAR markers linked to the *Pm21* gene conferring resistance to powdery mildew in common wheat. Plant Breed. 118: 215-219.

Luck J, Spackman M, Freeman A (2011). Climate change and diseases of food crops. Plant Pathol. 1: 113- 121.

Luo P G, Luo H Y, Chang Z J, Zhang H Y, Zhang M, Ren Z L (2009). Characterization and chromosomal location of *Pm40* in common wheat: a new gene for resistance to powdery mildew derived from *Elytrigia intermedium*. Theor. Appl. Genet. 118: 1059–1064.

Lutz J, Hsam SLK, Limpert E, Zeller FJ (1995). Chromosomal location of powdery mildew resistance genes in *Triticum aestivum* L. (common wheat) Genes *Pm2* and *Pm19* from *Aegilops squarrosa* L. Heredity 74: 152-156.

Lutz J, Katzhammer M, Stephan U, Felsenstein FG, Oppitz K, Zeller FJ (1995). Identification of powdery mildew resistance genes in common wheat (*Triticum aestivum* L. em. Thell.). V. Old German cultivars and cultivars released in the former GDR. Plant Breed. 114(1): 29-33.

Ma Q, Luo PG, Ren ZL, Jiang HR, Yang ZJ (2007). Genetic analysis and chromosomal location of two new genes for resistance to powdery mildew in wheat (*Triticum aestivum* L.). Acta Agronomica Sinica 33(1): 335-338 (in Chinese).

Ma H, Kong Z, Fu B, Li N, Zhang L, Jia H, Ma Z (2011). Identification and mapping of a new powdery mildew resistance gene on chromosome 6D of common wheat. Theor. Appl. Genet. 123: 1099-1106.

Ma ZQ, Sorrells ME, Tanksley SD (1994). RFLP markers linked to powdery mildew resistance genes *Pm 1*, *Pm2*, *Pm3*, and *Pm4* in wheat. Genome 37: 871-875.

Maxwell JJ, Lyerly H, Srnic G, Parks R, Cowger C, Marshall D, Brown-Guedira G, Murphy JP (2010). *MlAB10*: A *Triticum turgidum* subsp. *dicoccoides* derived powdery mildew resistance gene identified in common wheat. Crop Sci 50: 2261-2267.

Maxwell JJ, Lyerly JH, Cowger C, Marshall D, Brown-Guedira G, Murphy JP (2009). *MlAG12*: a *Triticum timopheevii*-derived powdery mildew resistance gene in common wheat on chromosome 7AL. Theor. Appl. Genet. 119: 1489-1495.

McIntosh RA, Zhang P, Cowger C, Parks R, Lagudah ES, Hoxha S (2011). Rye-derived powdery mildew resistance gene Pm8 in wheat is suppressed by the Pm3 locus. Theor. Appl. Genet. 123:359–367.

McIntosh RA, Hart GE, Gale MD, Rogers WJ (1998). Catalogue of gene symbols for wheat. In: Slinkard AE (Ed.), Proceedings of the 9th International Wheat Genet Symposium, University Extension Press, University of Saskatchewan, Saskatoon, Canada. 5: 1-235

Miranda LM, Murphy J, Marshall PD, Leath S (2006). *Pm34*: A new powdery mildew resistance gene transferred from *Aegilops tauschii* Coss. to common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 113, 1497-1504.

Miranda LM, Murphy J, Marshall PD, Cowger C, Leath S (2007). Chromosomal location of *Pm35*, a novel *Aegilops tauschii* derived powdery mildew resistance gene introgressed into common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 114: 1451-1456.

Mohler V, Bauer C, Schweizer G, Kempf H, Hartl L (2013). *Pm50*: a new powdery mildew resistance gene in common wheat derived from cultivated emmer. J. Appl. Genet. 54 (3): 259-263.

Mohler V, Hsam SLK, Zeller FJ, Wenzel G (2001). An STS marker distinguishing the rye-derived powdery mildew resistance alleles at the *Pm8/Pm17* locus of common wheat. Plant Breed. 120: 448-450.

Mohler V, Jahoor A (1996). Allele specific amplification of polymorphic sites for the detection of powdery mildew resistance loci in cereals. Theor. Appl. Genet. 93: 1078-1082.

Mohler V, Zeller FJ, Wenzel G, Hsam SLK (2005). Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.), gene *MlZec1* from the *Triticum dicoccoides*-derived wheat line Zecoi-1. Euphytica 142: 161–167.

Nematollahi G, Mohler V, Wenzel G, Zeller F J, Hsam S L K (2008). Microsatellite mapping of powdery mildew resistance allele *Pm5d* from common wheat line IGV1-455. Euphytica 159: 307–313.

Neu C, Stein N, Keller B (2002). Genetic mapping of the *Lr20– Pm1* resistance locus reveals suppressed recombination on chromosome arm 7AL in hexaploid wheat. Genome 45: 737-744.

Niu J, Jia H, Yin J, Wang B, Ma Z, Shen T (2010). Development of an STS Marker Linked to Powdery Mildew Resistance Genes *PmLK906* and *Pm4a* by Gene Chip Hybridization. Agric. Sci. Cn. 9(3): 331-336.

Niu JS, Wang BQ, Wang YH, Cao AZ, Qi ZJ, Shen TM (2008). Chromosome location and microsatellite markers linked to a powdery mildew resistance gene in wheat line 'Lankao 90(6). Plant Breed. 127(4): 346-349.

Oberhaensli S, Parlange F, Buchmann JP, Jenny FH, Abbott JC, Burgis TA, Spanu PD, Keller B, Wicker T (2011). Comparative sequence analysis of wheat and barley powdery mildew fungi reveals gene colinearity, dates divergence and indicates host-pathogen co-evolution. Fungal Genet. Bio. 48: 327–334.

Olson M, Hood L, Cantor C, Doststein D (1989). A common language for physical mapping of the human genome. Science 254: 1434-1435.

Perugini LD (2007). Genetic Characterization of Wheat Germplasm with Resistance to Fusarium Head Blight (FHB) and Powdery Mildew. A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. pp. 2- 123.

Perugini, L. D. Murphy, J. P. Marshall, D. & Brown-Guedira, G. (2008) *Pm37*, a new broadly effective powdery mildew resistance gene from *Triticum timopheevii*. Theor. Appl. Genet. 116: 417-425.

Peusha H, Enno T, Priilinn O (2000). Chromosome location of powdery mildew resistance genes and cytogenetic analysis of meiosis in common wheat cultivar Meri. Hereditas 132: 29-34.

Peusha H, Hsam SLK, Zeller FJ (1996). Chromosomal location of powdery mildew resistance genes in common wheat (*Triticum aestivum* L. em Thell.). Gene *Pm22* in cultivar Virest. Euphytica 91:149-152.

Piarulli L, Gadaletaa A, Manginia G, Signorilea MA, Pasquinib M, Blancoa A, Simeone R (2012). Molecular identification of a new powdery mildew resistance gene on chromosome 2BS from *Triticum turgidum* ssp. *dicoccum*. Plant Sci. 196: 101– 106.

Qi LL, Cao MS, Chen PD, Li WL, Liu DJ (1996). Identification, mapping, and application of polymorphic DNA associated with resistance gene *Pm21* of wheat. Genome 39: 191-197.

Qiu YC, Zhou RH, Kong XY, Zhang SS, Jia JZ (2005). Microsatellite mapping of a *Triticum urartu* Tum. derived powdery mildew resistance gene transferred to common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 111(8): 1524-1531.

Reader SM, Miller TE (1991). The introduction into breed wheat of a major gene for resistance to powdery mildew from wild emmer wheat. Euphytica 53(1): 57-60.

Rong JK, Millet E, Manisterski J, Feldman M (2000). A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP based mapping. Euphytica 115: 121–126.

Schmolke M, Mohler V, Hartl L, Zeller FJ, Hsam SLK (2012). A novel powdery mildew resistance allele at the *Pm4* locus from einkorn wheat (*Triticum monococcum*). Mol. Breeding 29(2): 449-456.

Sears ER, Briggle LW (1969). Mapping the gene *Pm1* for resistance to *Erysiphe graminis* f. sp. *tritici* on chromosome 7A of wheat. Crop Sci 9:96-97.

Shi AN, Leath S, Murphy, JP (1998). A major gene for powdery mildew resistance transferred to common wheat from wild eikorn wheat. Phytopath. 88(2): 144-147.

Singh K, Chhuneja P, Ghai M, Kaur S, Goel RK, Bains NS, Keller B, Dhaliwal HS (2007a). Molecular mapping of leaf and stripe rust resistance genes in Triticum monococcum and their transfer to hexaploid wheat. In: Buck H, Nisi JE, Solomon N (eds) Wheat production in stressed environments. Springer, Netherlands, pp 779–786.

Singh K, Chhuneja P, Singh I, Sharma SK, Garg T, Garg M, Keller B, Dhaliwal HS (2010). Molecular mapping of cereal cyst nematode resistance in *Triticum monococcum* L. and its transfer to the genetic background of cultivated wheat. Euphytica 176:213–222.

Singrün C, Hsam SLK, Zeller FJ, Wenzel G, Mohler V (2004). Localization of a novel recessive powdery mildew resistance gene from common wheat line RD30 in the terminal region of chromosome 7AL. Theor. Appl. Genet. 109(1): 210-214.

Singrun C, Hsam SLK, Hartl L, Zeller FJ (2003). Powdery mildew resistance gene *Pm22* in cultivar Virest is a member of the complex *Pm1* locus in common wheat (*Triticum aestivum* L. em Thell.). Theor. Appl. Genet. 106:1420-1424.

Sourdille P, Robe P, Tixier MH, Doussinault G, Pavoine MT, Bernard M (1999). Location of *Pm3g*, a powdery mildew resistance allele in wheat, by using a monosomic analysis and by identifying associated molecular markers. Euphytica 110:193–198.

Spielmeyer W, McIntosh RA, Kolmer J, Lagudahe S (2005). Powdery mildew resistance and *Lr34/Yr18* genes for durable resistance to leaf and stripe rust co-segregate at a locus on the short arm of chromosome 7D of wheat. Theor. Appl. Genet. 111: 731-735.

Srnic G, Murphy JP, Lyerly JH, Leath S, Marshall DS (2005). Inheritance and chromosomal assignment of powdery mildew resistance genes in two winter wheat germplasm lines. Crop Sci. 45:1578-1586.

Sun X, Liu D, Zhang H, Hou X, Zhou R, Jia J (2006). Identification and Mapping of Two New Genes Conferring Resistance to Powdery Mildew from *Aegilops tauschii* (Coss.) Schmal. J. Integrative Plant Bio. 48(10): 1204-1209 (in Chinese).

Tao W, Liu D, Liu J, Feng Y, Chen P (2000). Genetic mapping of the powdery mildew resistance gene *Pm6* in wheat by RFLP analysis. Theor. Appl. Genet. 100: 564–568.

The TT, McIntosh RA, Bennett FGA (1979). Cytogenetical studies in wheat. Monosomic analysis, telocentric mapping and linkage relationship of gene *Sr21*, *Pm4* and *Mle*. Aust J. Biol. Sci. 32: 115-125.

Tong C, Hall CAS, Wang H (2003). Land use change in rice, wheat and maize production in China (1961–1998). Agric. Eco. Environ. 95: 523–536.

Tosa Y, Sakai K (1990). The genetics of resistance of hexaploid wheat to the wheat grass powdery mildew fungus. Genome 33: 225-230.

Tosa Y, Tokunaga H, Ogura H (1988). Identification of a gene for resistance to wheat grass powdery mildew fungus in the common wheat cultivar Chinese Spring. Genome 30: 612-614.

Tosa Y, Tsujimoto H, Ogura H (1987). A gene involved in the resistance of wheat to wheat grass powdery mildew fungus. Genome 29: 850-852.

Wang CY, Ji WQ, Zhang GS, Wang QY, Cai DM, Xue XZ (2007). SSR markers and preliminary chromosomal location of a powdery mildew resistance gene in common wheat germplasm N9134. Acta Agronomica Sinica 33(1):163-166 (in Chinese).

Weber D, Helentjaris T (1989). Mapping RFLP loci in maize using B-A translocations. Genetics 121: 583-590.

Wricke G, Dill P, Senft P (1996). Linkage between a major gene for powdery mildew resistance and an RFLP marker on chromosome *1R* of rye. Plant Breed. 115: 71-73.

Xiao M, Song F, Jiao J, Wang X, Xu H, Li H (2013). Identification of the gene *Pm47* on chromosome 7BS conferring resistance to powdery mildew in the Chinese wheat landrace Hongyanglazi. Theor. Appl. Genet. 126 (5): 1397-1403.

Xie C, Sun Q, Ni Z, Yang T, Nevo E, Fahima T (2003). Chromosomal location of a *Triticum dicoccoides*-derived powdery mildew resistance gene in common wheat by using microsatellite markers. Theor. Appl. Genet. 106: 341-345.

Xin M, Wang X, Peng H, Yao Y, Xie C, Han Y, Ni Z, Sun Q (2012). Transcriptome comparison of susceptible and resistant wheat in response to powdery mildew infection. Genom. Prote. Bioinfo. 10: 94–106.

Xue F, Ji WQ, Wang CY, Zhang H, Yang B (2012a). High-density mapping and marker development for the powdery mildew resistance gene *PmAS846* derived from wild emmer wheat (*Triticum turgidum* var. *dicoccoides*). Theor. Appl. Genet. 124:1549-1560.

Xue F, Wang C, Li C, Duan X, Zhou Y, Zhao N, Wang Y, Ji W (2012b). Molecular mapping of a powdery mildew resistant gene in common wheat landrace Baihulu and its allelism with *Pm24*. Theor. Appl. Genet. 125(7): 1425-1432.

Xue F, Zhai W, Duan X, Zhou Y, Ji W (2009). Microsatellite Mapping of a Powdery Mildew Resistance Gene in Wheat Landrace Xiaobaidong. Acta Agron. Sin. 35(10): 1806–1811.

Xu H, Yao G, Xiong L, Yang L, Jiang Y, Fu B, Zhao W, Zhang Z, Zhang C, Ma Z (2008). Identification and mapping of Pm2026: a recessive powdery mildew resistance gene in an einkorn (*Triticum monococcum* L.) accession. Theor. Appl. Genet. 117(4): 471-477.

Xu WG, Li CX, Hu L, Zhang L, Zhang JZ, Dong HB, Wang GS (2010). Molecular mapping of powdery mildew resistance gene *PmHNK* in winter wheat (*Triticum aestivum* L.) cultivar Zhoumai 22. Mol. breeding 26: 31-38.

Yahiaoui N, Kaur N, Keller B (2009). Independent evolution of functional *Pm3* resistance genes in wild tetraploid wheat and domesticated bread wheat. Plant J. 57: 846-856.

Yahiaoui N, Brunner S, Keller B (2006). Rapid generation of new powdery mildew resistance genes after wheat domestication. Plant J. 47:85-98.

Yahiaoui N, Srichumpa P, Dudler R, Keller B (2004). Genome analysis at different ploidy levels allows cloning of the powdery mildew resistance gene *Pm3b* from hexaploid wheat. Plant. J. 37: 528–538.

Yao GQ, Zhang JL, Yang LL, Xu HX, Jiang YM, Xiong L, Zhang CQ, Zhang ZZ, Ma ZQ, Sorrells ME (2007). Genetic mapping of two powdery mildew resistance genes in einkorn (*Triticum monococcum* L.) accessions. Theor. Appl. Genet. 114(2): 351-358.

Yi Y, Li R, Xu H, Wu X, Li S, Zhang J, Yin Y (2013). Identification of SRAP and RGA markers linked to powdery mildew (*Blumeria graminis*) resistance gene *PmZB90* in common wheat. Aust J. Crop Sci. 7(3):454-459.

Yu S, Long H, Yang H, Zhang J, Deng G, Pan Z, Zhang E, Yu M (2012). Molecular detection of rye (*Secale cereale* L.) chromatin in wheat line 07jian126 (*Triticum aestivum* L.) and its association to wheat powdery mildew resistance Euphytica 186:247–255.

Zeller FJ, Hsam SLK (1998). Progress in breeding for resistance to powdery mildew in common wheat (*Triticum aestivum* L.) pp. 178-180. In Slinkard AE (ed) Proceedings of the 9th International Wheat Genetics Symposium. Vol. 1, University of Saskatchewan, Saskatoon, Canada.

Zeller FJ, Kong L, Hartl L, Mohler V, Hsam SLK (2002). Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 7. Gene *Pm29* in line Pova. Euphytica 123:187-194.

Zeller FJ, Lutz J, Stephan U (1993). Chromosome location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L.) *Mlk* and other alleles at the *Pm3* locus. Euphytica 68: 223–229.

Zhang H, Guan H, Li J, Zhu J, Xie C, Zhou Y, Duan X, Yang T, Sun Q, Liu Z (2010). Genetic and comparative genomics mapping reveals that a powdery mildew resistance gene *Ml3D232* originating from wild emmer co-segregates with an NBS-LRR analog in common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 121:1613-1621.

Zhang H, Lang J (2007). Studies on SSR marker of powdery mildew resistance genes of *Ae. tauschii.* Hubei Agric. Scie. 46: 335-338 (in Chinese).

Zhang K, Zhao L, Hai Y, Chen G, Tian J (2008). QTL Mapping for Adult-Plant Resistance to Powdery Mildew, Lodging Resistance, and Internode Length Below Spike in Wheat. Acta Agron. Sin. 34(8): 1350-1357.

Zhang L, Hua W, Guan H, Li G, Xie C, Yang Z, Sun Q, Liu Z (2009). Molecular mapping of powdery mildew resistance gene *MlWE29* in wheat originated from wild emmer (*Triticum turgidum* var. *dicoccoides*). Acta Agronomica Sinica 35 (6): 998-1005 (in Chinese).

Zhou R, Zhu Z, Kong X, Huo N, Tian Q, Li P, Jin C, Dong Y, Jia J (2005). Development of wheat near-isogenic lines for powdery mildew resistance. Theor. Appl. Genet. 110: 640–648.

Zhu Z, Kong X, Zhou R Jia J (2004). Identification and Microsatellite Marker of a Resistance Gene to Powdery Mildew in Common Wheat Introgressed from *Triticum durum*. J. Integrative Plant Bio. 46(7): 867-872 (in Chinese).

Zhu Z, Zhou R, Kong X, Dong Y, Jia J (2006). Microsatellite Marker Identification of a *Triticum aestivum-Aegilops umbellulata* Substitution Line with Powdery Mildew Resistance. Euphytica 150(1): 149-153.

Zhu ZD, Zhou RH, Kong XY, Dong YC, Jia JZ (2005). Microsatellite markers linked to two genes conferring resistance to powdery mildew in common wheat introgressed from *Triticum carthlicum* acc. PS5. Genome 48: 585 -590.