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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 hectareage 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

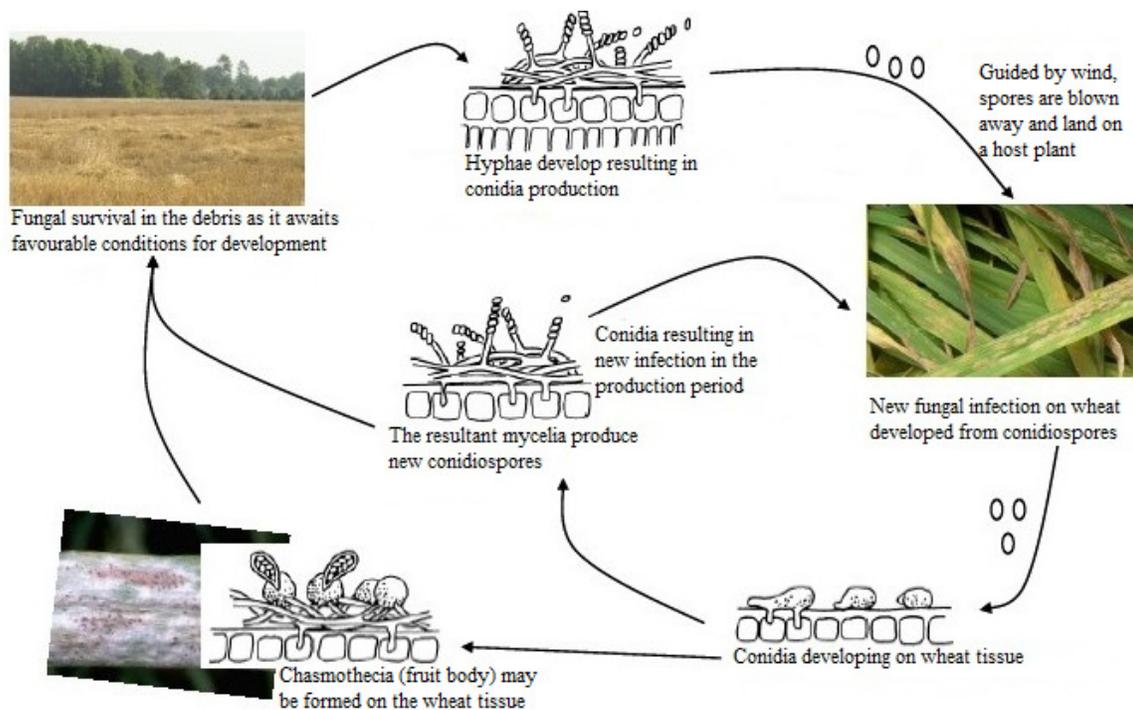


Figure 1. Wheat powdery mildew (*Blumeria graminis* f. sp. *tritici*) life cycle (modified from Perugini, 2007)

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

Table 1 continues

| | | | | |
|----------------------|-----|--------------|------------------------------|-------------------------|
| <i>Pm33</i> | 2BL | PS5 | <i>T. carthlicum</i> | Zhu et al., 2005 |
| <i>Pm34</i> | 5DL | NC97BGTD7 | <i>Ae. tauschii</i> | Miranda et al., 2006 |
| <i>Pm35</i> | 5DL | NC96BGTD3 | <i>Ae. tauschii</i> | Miranda et al., 2007 |
| <i>Pm36</i> | 5BL | MG29896 | <i>T. dicoccoides</i> | Blanco et al., 2008 |
| <i>Pm37</i> | 7AL | NC99BGTAG11 | <i>T. timopheevii</i> | Perugini et al., 2008 |
| <i>Pm38</i> | 7DS | RL6058 | <i>T. aestivum</i> | Spielmeier et al., 2005 |
| <i>Pm39</i> | 1BL | Saar | <i>T. aestivum</i> | Lillemo et al., 2008 |
| <i>Pm40</i> | 7BS | GRY19 | <i>Elytrigia intermedium</i> | Luo et al., 2009 |
| <i>Pm41</i> | 3BL | IW2 | <i>T. dicoccoides</i> | Li et al., 2009 |
| <i>Pm42</i> | 2BS | G-303-1M | <i>T. dicoccoides</i> | Hua et al., 2009 |
| <i>Pm43</i> | 2DL | CH5025 | <i>T. intermedium</i> | He et al., 2009 |
| <i>Pm44</i> | 3AS | Hombar | <i>T. aestivum</i> | Alam et al., 2011 |
| <i>Pm45</i> | 6DS | D57 | <i>T. aestivum</i> | Ma et al., 2011 |
| <i>Pm46</i> | 5DS | Tabasco | <i>T. aestivum</i> | Gao et al., 2012 |
| <i>Pm47</i> | 7BS | Hongyanglazi | <i>T. aestivum</i> | Xiao et al., 2013 |
| <i>Pm49 (MI5323)</i> | 2BS | MG5323 | <i>T. dicoccum</i> | Piarulli et al., 2012 |
| <i>Pm50</i> | 2AL | K2 | <i>T. dicoccum</i> | 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. longissima*, *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 Briggie, 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. *armeniicum* (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. timopheevii*, 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 |
|-----------------|----------|---|------------------------|------------------------|
| <i>Mld</i> | 4B | Maris Dove | <i>T. durum</i> | Bennet, 1984 |
| <i>MI-Ad</i> | - | Adlungs Alemannen | <i>T. aestivum</i> | Lutz et al., 1995 |
| <i>MI-Br</i> | - | Bretonischer | <i>T. aestivum</i> | Lutz et al., 1995 |
| <i>MI-Ga</i> | - | Garnet | <i>T. aestivum</i> | Lutz et al., 1995 |
| <i>MIRE</i> | 6AL | RE714 | <i>T. dicoccum</i> | Chantret et al., 2000 |
| <i>Mlly</i> | 7B | Jieyan 94-1-1 | <i>T. aestivum</i> | Huang et al., 2002 |
| <i>Mlsy</i> | 7B | Siyan 94-2-1 | <i>T. aestivum</i> | Huang et al., 2002 |
| <i>mlRD30</i> | 7AL | RD30 | <i>T. aestivum</i> | Singrun et al., 2004 |
| <i>PmDR147</i> | 2AL | DR147 | <i>T. durum</i> | Zhu et al., 2004 |
| <i>MIZec1</i> | 2BL | Zecoi 1 | <i>T. dicoccoides</i> | Mohler et al., 2005 |
| <i>PmPs5A</i> | 2AL | Am4 | <i>T. carthlicum</i> | Zhou et al., 2005 |
| <i>PmPs5B</i> | 2BL | Am9/3*Laizhou953 | <i>T. carthlicum</i> | Zhou et al., 2005 |
| <i>PmE</i> | 2AL | Xiaohan/4*Bainong3217 Xiaobing/3*Bainong 3217 | <i>Er. Orientale</i> | Zhou et al., 2005 |
| <i>PmP</i> | - | 3217 | Fuco/Agropyron | Zhou et al., 2005 |
| <i>PmY39</i> | 2U(2B) | 953*4/Am9 | <i>Ae. umbellulata</i> | Zhou et al., 2005 |
| <i>PmH</i> | 7BL | Hongquanmang <i>Ae. longissima</i> | <i>T. aestivum</i> | Zhou et al., 2005 |
| <i>PmY150</i> | 6B/6S | 3*Laizhou 953 | <i>Ae. longissima</i> | Zhou et al., 2005 |
| <i>PmM53</i> | 5DL | M53 | <i>Ae. tauschii</i> | Li et al., 2005 |
| <i>PmU</i> | 7AL | UR206/Laizhou | <i>T. urartu</i> | Qiu et al., 2005 |
| <i>PmY201</i> | 5DL | Y201 | <i>Ae. tauschii</i> | Sun et al., 2006 |
| <i>PmY212</i> | 5DL | Y212 | <i>Ae. tauschii</i> | Sun et al., 2006 |
| <i>Mlm2033</i> | 7AL | TA2033 | <i>T. monococcum</i> | Yao et al., 2007 |
| <i>Mlm80</i> | 7AL | M80 | <i>T. monococcum</i> | Yao et al., 2007 |
| <i>PmE</i> | 7BS | TAI7047 | <i>E. intermedium.</i> | Ma et al., 2007 |
| <i>PmYU25</i> | 2DL | TAI7047 | <i>E. intermedium.</i> | Ma et al., 2007 |
| <i>PmAS846</i> | 5BL | N9134 | <i>T. dicoccoides.</i> | Wang et al., 2007 |
| <i>PmAeY2</i> | 5DL | Y189 | <i>Ae. tauschii</i> | Zhang and Lang, 2007 |
| <i>PmY39-2</i> | 6AS | N9628-2 | <i>Ae. umbellulata</i> | Liu et al., 2008 |
| <i>Pm2026</i> | 5AL | TA2026 | <i>T. monococcum</i> | Xu et al., 2008 |
| <i>mlIW72</i> | 7AL | IW72 | <i>T. dicoccoides.</i> | Ji et al., 2008 |
| <i>PmTm4</i> | 7BL | Tangmai 4 | <i>T. aestivum</i> | Hu et al., 2008 |
| <i>PmLK906</i> | 2AL | Lankao 90(6) | <i>T. aestivum</i> | Niu et al., 2008 |
| <i>PmYm66</i> | 2AL | Yumai 66 | <i>T. aestivum</i> | Hu et al., 2008 |
| <i>MIWE18</i> | 7AL | 3D249 | <i>T. dicoccoides</i> | Han et al., 2009 |
| <i>MIAG12</i> | 7AL | NC06BGTAG12/ Jagger | <i>T. aestivum</i> | Maxwel et al., 2009 |
| <i>MIWE29</i> | 5BL | WE29 | <i>T. dicoccoides</i> | Zhang et al., 2009 |
| <i>TaAetPR5</i> | 2AL | EU082094 | <i>A. tauschii</i> | Niu et al., 2010 |
| <i>MI3D232</i> | 5BL | 3D232 | <i>T. dicoccoides</i> | Zhang et al., 2010 |
| <i>MIAB10</i> | 2BL | NC97BGTAB10 | <i>T. aestivum</i> | Maxwell et al., 2010 |
| <i>PmG16</i> | 7AL | G18-16 | <i>T. dicoccoides</i> | Ben-David et al., 2010 |
| <i>PmHnk</i> | 3BL | Zhoumai 22 | <i>T. aestivum</i> | Xu et al., 2010 |
| <i>Pm07J126</i> | - | 07jian126 | <i>T. aestivum</i> | Yu et al., 2012 |
| <i>PmAs846</i> | 5BL | N9134, N9738 | <i>T. dicoccoides</i> | Xue et al., 2012a |
| <i>PmTb7A.1</i> | 7AL | pau5088 | <i>T. boeoticum</i> | Chhuneja et al., 2012 |
| <i>PmTb7A.2</i> | 7AL | pau5088 | <i>T. boeoticum</i> | Chhuneja et al., 2012 |
| <i>PmLX66</i> | 5DS | Liangxing 66 | <i>T. aestivum</i> | Huang et al., 2012 |
| <i>PmG25</i> | 5BL | N0308 | <i>T. dicoccoides</i> | Alam et al., 2013 |
| <i>PmZB90</i> | 2AL | ZB90 | <i>T. aestivum</i> | 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 | <i>Pm3, Pm25</i> | <i>Pm28, Pm32,</i> | <i>Pm10, Pm24,</i> |
| 2 | <i>Pm4, Pm25, Pm50,</i> <i>PmDR147, PmPs5A, PmE,</i> <i>PmYm66, TaAetPR5,</i> <i>PmLK906, PmZB90</i> | <i>Pm6, Pm26, Pm33,</i> <i>Pm42, Pm49, MIZec1,</i> <i>PmY39, MIAB10,</i> <i>PmPs5B</i> | <i>Pm43, PmYU25</i> |
| 3 | <i>Pm44</i> | <i>Pm13, Pm38, Pm41,</i> <i>PmHMK</i> | |
| 4 | <i>Pm14</i> | <i>Mld</i> | |
| 5 | <i>Pm2026</i> | <i>Pm36, Pm16, Pm30,</i> <i>PmAS846, MI3D232,</i> <i>PmAs846, PmG25,</i> <i>MIWE29</i> | <i>Pm2, Pm34, Pm35, Pm46,</i> <i>PmM53, PmY201, PmY212,</i> <i>PmAeY2, PmLX66</i> |
| 6 | <i>Pm21, Pm31, MIRE,</i> <i>PmY39-2</i> | <i>Pm11, Pm12, Pm14,</i> <i>Pm27, PmY150</i> | <i>Pm45</i> |
| 7 | <i>Pm1, Pm9, Pm18, Pm37,</i> <i>mIRD30, PmU, MIm2033,</i> <i>MIm80, MIW72, PmTb7A.1,</i> <i>PmTb7A.2, MIAG12,</i> <i>PmG16, MIWE18</i> | <i>Pm5, Pm40, Pm47, Mlly,</i> <i>Mlsy, PmH, PmE,</i> <i>PmTm4</i> | <i>Pm15, Pm19, Pm29, Pm39</i> |

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; *MIZec1*, *PmY39*, *MIAB10*, *PmPs5B*, carry temporarily designated names (Table 2 and 3). Gene *MIZec1*, 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 F₁

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 *mIIW72* (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 *mIRD30* (Singrun et al., 2004), *MIZec1* (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), *MIAB10* (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 |
|-------------|----------------------------------|--|--|---|--|--|
| <i>Pm1a</i> | 7AL | RAPD, STS RFLP RFLP RFLP, STS | UBC320420, UBC638550 WHS178-9.4kb-EcoRI CDO347 mwg2062, cdo347, psr121, psr148, psr680, psr687, wir148, C607, STS638542, ksuh9 | Both co-segregate 2.8 ± 2.7 cM Co-segregate All Co-segregate | F ₅ , F ₂ lines, BSA F ₂ lines, NILs F ₂ lines, NILs F ₂ lines | Hu et al., 1997 Hartl et al., 1995 Ma et al., 1994 Neu et al., 2002 |
| <i>Pm1c</i> | 7AL | RFLP, RAPD AFLP | WHS178-15kb-EcoRI, OPH- 111900 S19M22-325/200 S14M20-137/138 | 4.4 ± 3.6 cM, 13 cM Co-segregate Co-segregate | F ₂ lines, BSA F ₃ + F ₄ lines, BSA | Hartl et al., 1995 Hartl et al., 1999 |
| <i>Pm1e</i> | 7AL | SSR, AFLP | GWM344-null-S13M26-372 | 0.9cM, 0.2 cM | F _{2:3} lines, BSA | Singrun et al., 2003 |
| <i>Pm2</i> | 5DS | RFLP RFLP STS | WHS350-6.5kb- EcoRV,WHS295 BCD1871 STSwhs350 | 3.8 cM, 2.7 ± 2.6 cM 3.5 cM | F ₂ lines, NILs F ₂ lines, NILs | Ma et al., 1994 Mohler and Jahoor, 1996 |
| <i>Pm3a</i> | 1AS | RFLP | WHS179 | 3.3 ± 1.9 cM | DH, NILs | Hartl et al., 1993 |
| <i>Pm3b</i> | 1AS | RFLP | BCD1434 | 1.3 cM | F ₂ lines, NILs | Ma et al., 1994 |
| <i>Pm3g</i> | 1AS | RFLP | Gli-A5 | 5.2 cM | DH | Sourdille et al., 1999 |
| <i>Pm4a</i> | 2AL | RFLP AFLP STS | BCD1231, CDO678 4aM1 STSbcd1231-1.7kb | Co-segregate 3.5 cM Co-segregate | F ₂ lines, NILs F ₃ +F ₄ lines, BSA NILs | Ma et al., 1994 Hartl et al., 1999 Liu et al., 1998 |
| <i>Pm4d</i> | 2AL | STS | Xbarc122, Xgwm526 | 1.0 cM; 3.4 cM | F _{2:3} lines | Schmolke et al., 2012 |
| <i>Pm5e</i> | 7BL | SSR | GWM1267-136 | 6.6 cM | F _{2:3} lines, BSA | Huang et al., 2003 |
| <i>Pm6</i> | 2BL | RFLP | BCD135-9kb-EcoRV | 1.6 ± 1.5 cM | F ₂ lines, NILs | Tao et al., 2000 |
| <i>Pm8</i> | 1RS.1BL | RFLP RAPD STS STS RFLP | IAG95 OPJ07-1200, OPR19-1350 SEC-1b-412bp STSiag95-1050 psr10, psr106, Nor-2, psr141, psr113, psr142, psr149, psr2 | Tightly linked | F ₂ lines, BSA Translocation lines Translocation lines DH, F _{2:3} lines F ₂ lines | Wricke et al., 1996 Iqbal and Rayburn, 1995 DeFroidmont, 1998 Mohler et al., 2001 Jia et al., 1996 |
| <i>Pm12</i> | 6BS- SS.6SL | RFLP | psr10, psr106, Nor-2, psr141, psr113, psr142, psr149, psr2 | Co-segregate Co-segregate | DH, F _{2:3} lines F ₂ lines | Mohler et al., 2001 Jia et al., 1996 |
| <i>Pm13</i> | 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 |
| <i>Pm17</i> | 1RS.1AL | RFLP, AFLP | IAG95-CA/CT-355 | 1.5 cM | F _{2:3} lines | Hsam et al., 2000 |
| <i>Pm21</i> | 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 |
| <i>Pm24a</i> | 1DS | AFLP, SSR | E34/M51-407, Xgwm337-204 | Co-segregate, 2.4 ± 1.2 cM | F _{2:3} lines, BSA | Huang et al., 2000b |
| <i>Pm24b</i> | 1DS | SSR SSR | Xgwm1291 Xgwm603/Xgwm789, Xbarc229 | Co-segregate 1.5 cM -1.0 cM | F _{2:3} lines F _{2:3} | Huang and Roder, 2004 Xue et al., 2012b |
| <i>Pm25</i> | 1A | RAPD | OPA04950 | 12.8 cM | BC ₁ F ₁ lines, BSA | Shi et al., 1998 |
| <i>Pm26</i> | 2BS | RFLP | wg516 | Co-segregate | RSLs | Rong et al., 2000 |
| <i>Pm27</i> | 6B-6G | RFLP, SSR | psp3131 | Co-segregate | F ₂ lines | Jarve et al., 2000 |
| <i>Pm29</i> | 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 |
| <i>Pm30</i> | 5BS | SSR | Xgwm159-460, Xgwm159-500 | 5 cM – 6 cM | BC ₂ F ₂ lines, BSA | Liu et al., 2002 |
| <i>Pm31</i> | 6AL | SSR | Xpsp3029 | 0.6 cM | BC ₂ F ₂ lines, BSA | Xie et al., 2003 |
| <i>Pm36</i> | 5BL | SSR | BJ261635 | Co-segregate | BC ₅ F ₅ | Blanco et al., 2008 |
| <i>Pm40</i> | 7BS | SSR | Xgwm297 | 0.4 cM | F ₂ lines | Luo et al., 2009 |
| <i>Pm41</i> | 3BL | SSR, ISBP, STS | BE489472 | Co-segregate | F ₂ lines | Li et al., 2009 |
| <i>Pm42</i> | 2BS | SSR, AFLP-SCAR, EST-STs, RFLP- STs | BF146221 | Co-segregate | F ₂ lines | Hua et al., 2009 |
| <i>Pm43</i> | 2DL | SSR | Xwmc41 | 2.3 cM | F ₃ and BC ₁ lines | He et al., 2009 |
| <i>Pm45</i> | 6DS | SSR, STS | Xmag6176 | 2.8 cM | F ₂ lines | Ma et al., 2011 |
| <i>Pm46</i> | 5DS | SSR | Xgwm205, Xcf81 | 18.9 cM | F ₂ and F _{2:3} lines | Gao et al., 2012 |
| <i>Pm47</i> | 7BS | SSR, EST | Xgwm46, BE606897 | 1.7 cM, 3.6 cM | F _{2:3} lines | Xiao et al., 2013 |
| <i>Pm49</i> | 2BS | EST-SSR | CA695634 | 0.84 cM-1.00 cM | F ₁ +F ₂ | Piarulli et al., 2012 |
| <i>Pm50</i> | 2AL | SSR | Xgwm294 | 2.9 cM | BC ₁ | Mohler et al., 2013 |
| <i>MIRE</i> | 6AL | SSR, RFLP SSR, AFLP | XksuD27 Xgwm344, XE33M62-392, XE39M58-414 | - | BSA, F ₃ BSA, F ₃ lines | Chantret et al., 2000 |
| <i>mIRD30</i> | 7AL | | | | | Singrun et al., 2004 |
| <i>PmDR147</i> | 2AL | SSR AFLP, SSR | Xgwm311, Xgwm382 E35M56-330, E35M57-56, E37M54-286, E38M54-207, | 5.9 cM, 4.9 cM 2.0 cM | BC ₃ F ₂ lines BSA, F ₃ lines | Zhu et al., 2004 |
| <i>MIZec1</i> | 2BL | | Xwmc356-2B | | | Mohler et al., 2005 |
| <i>PmPs5A</i> | 2AL | SSR SSR | Xgwm356, Xgwm111, Xgwm382, Xgwm526, Xwmc317 | 10.2 cM 1.1 cM | BC ₃ , BC ₄ lines F ₂ lines | Zhou et al., 2005 |
| <i>PmPs5B</i> | 2BL | SSR | Xgwm265, Xgwm311, Xgwm382 | 2.9 cM, 3.6 cM, 4.4 cM | F ₂ lines | Zhou et al., 2005 |
| <i>PmE</i> | 2AL | | | | | Zhou et al., 2005 |
| <i>PmH</i> | 7BL | SSR | Xgwm611, Xpsp3033 | 5.9 cM, 13.2 cM | BC ₅ F ₂ lines | Zhou et al., 2005 |

Table 4 continues

| | | | | | | |
|-----------------|--------|--------------------------|--|--|--|------------------------|
| <i>PmP</i> | | AFLP SSR | XM55P66, XM55P37 Xgwm257, Xgwm296, Xgwm319 | 0.8cM, 2.4 cM Co-segregate | F ₂ lines F ₂ lines | Zhou et al., 2005 |
| <i>PmY39</i> | 2U(2B) | SSR | Xgwm325, Xwmc382, Xwmc397 | | F ₂ lines | Zhou et al., 2005 |
| <i>PmY150</i> | 6B/6S | 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 | Zhou et al., 2005 |
| <i>PmM53</i> | 5DL | | | | | Li et al., 2005 |
| <i>PmU</i> | 7AL | SSR | Xgwm273, Xpsp3003 | 2.2 cM, 3.8 cM | F ₁ , F ₂ lines | Qiu et al., 2005 |
| <i>PmY201</i> | 5DL | SSR | Xgwm174 | 5.2 cM | F ₂ lines | Sun et al., 2006 |
| <i>PmY212</i> | 5DL | SSR | Cfd57 | 5.6 cM | F ₂ lines | Sun et al., 2006 |
| <i>Mlm2033</i> | 7AL | RFLP, STS, EST | Xgwm344, Xmag2185 | < 2 cM | F ₂ , F ₃ lines | Yao et al., 2007 |
| <i>Mlm80</i> | 7AL | RFLP, STS, EST | Xgwm344, Xmag2185 | < 2 cM | F ₂ , F ₃ lines | Yao et al., 2007 |
| <i>PmE</i> | 7BS | SSR | Xgwm297 | 13.0 cM | F ₂ lines | Ma et al., 2007 |
| <i>PmYU25</i> | 2DL | SSR | Xgwm210 | 16.6 cM | F ₂ lines | Ma et al., 2007 |
| <i>PmAS846</i> | 5BL | SSR SSR | Xgwm67 Xgwm583, Xgwm174, Xgwm182, Xgwm271 | 20.6 cM 25.7 cM, 16.7 cM, 9.1 cM, 7 cM | F ₁ , F ₂ lines F ₂ lines | Wang et al., 2007 |
| <i>PmAeY2</i> | 5DL | | | | | Zhang and Lang, 2007 |
| <i>PmY39-2</i> | 6AS | SSR SSR, STS, RFLP | Xwmc553, Xwmc684 Xcfd39, Xgwm126, MAG1491, MAG1493, MAG1494, MAG2170 | 10.99 cM, 7.43 cM 0.9 cM, Co-segregate | F ₂ , F ₃ lines F ₂ , F ₃ lines | Liu et al., 2008 |
| <i>Pm2026</i> | 5AL | SSR, EST, RFLP | Xgwm344, Xcfa2040, Xcfa2240, Xcfa2257, Xwmc525, MAG2185, MAG1759 | | F ₂ , F ₃ lines | Xu et al., 2008 |
| <i>mIIW72</i> | 7AL | SSR, EST-SSR, EST-STs | Xcau12, Xgwm611, PmTm4, XEST92, Xbarc1073, Xbarc82, Xwmc276 | | F ₂ , F ₃ lines, BSA | Ji et al., 2008 |
| <i>PmTm4</i> | 7BL | STS, SSR | EST48, EST83 (EST84), Xksum193, PmYm66 | | F ₂ , F ₃ lines | Hu et al., 2008 |
| <i>PmYm66</i> | 2AL | | | | | Hu et al., 2008 |
| <i>PmLK906</i> | 2AL | SSR | Xgwm265, Xgdm93 | 3.72 cM, 6.15cM | | Niu et al., 2008 |
| <i>MIAG12</i> | 7AL | SSR | Xwmc273, Xwmc346 | 8.3 cM, 6.6 cM | F ₂ , F ₃ lines, BSA | Maxwel et al., 2009 |
| <i>MIWE29</i> | 5BL | SSR | Xgwm415, Xwmc75 Xwmc525, Xcfa2040, Xwmc273, XE13-2, Xmag1759, MIWE18, Xcfa2240 | 2.5 cM, 17.6 cM | F ₂ , F ₃ lines F ₁ , F ₂ , lines | Zhang et al., 2009 |
| <i>MIWE18</i> | 7AL | SSR, STS, EST- STS | | | | Han et al., 2009 |
| <i>MI3D232</i> | 5BL | SSR, EST, STS | | 0.8 cM | F ₂ , F ₃ lines | Zhang et al., 2010 |
| <i>TaAetPR5</i> | 2AL | STS | p9-7p1, p9-7p2 | 7.62 cM | BSA | Niu et al., 2010 |
| <i>MIAB10</i> | 2BL | SSR | Xwmc445 | 7 cM | F _{2,3} lines | Maxwell et al., 2010 |
| <i>PmG16</i> | 7AL | SSR, STS, DAiT, CAPS | Xgwm344, wPt-9217, wPt- 1424, wPt-6019 | 3.6 cM | Recombinant, F _{2,3} lines | Ben-David et al., 2010 |
| <i>PmHnk</i> | 3BL | SSR | Xwmc291, Xgwm108 | 3.8 cM, 10.3 cM | BC ₁ , F ₂ , F ₃ lines | Xu et al., 2010 |

Table 4 continues

| | | | | | | |
|-----------------|-----|--------------------------------|--|---|--|-----------------------|
| <i>PmAs846</i> | 5BL | STS SSR, RFLP, STS, DArT | BJ261635, CJ840011 wPt4553, Xcfa2019 | Co-segregate 4.3 cM | F ₂ , F _{2:3} lines Recombinant lines | Xue et al., 2012a |
| <i>PmTb7A.1</i> | 7AL | SSR, RFLP, STS, DArT | MAG2185, MAG1759 | | Recombinant lines | Chhuneja et al., 2012 |
| <i>PmTb7A.2</i> | 7AL | DArT | | | | Chhuneja et al., 2012 |
| <i>PmLX66</i> | 5DS | SSR, SSR | SCAR203, Xcfd81 | 0.4, 2.8 cM | F ₂ , F _{2:3} lines | Huang et al., 2012 |
| <i>Pm07J126</i> | | SSR SSR | Xbarc183 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 F ₂ lines | Yu et al., 2012 |
| <i>PmG25</i> | 5BL | SRAP, RGA | Me5/Em5-650, Me8/Em16- 600 | 12.9 cM, 9.7 cM | F ₂ lines | Alam et al., 2013 |
| <i>PmZB90</i> | 2AL | | | | | 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.

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