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REVIEW

Genes responsible for powdery mildew resistance and improvement in wheat using molecular marker-assisted selection

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Abstract Plants have the capability to protect themselves from attacks by several types of fungal pathogens. Several powdery mildew resistance genes have been reported at different loci, and most of them have been originated from progenitors of wheat or wild accessions. Powdery mildew resistance is deliberated to be quantitative traits (QTLs), also considered as complex traits, because they are measured by several genes and are affected by fungal pathogens. Numerous researchers have been studied such traits in the past periods for the development of genetic markers, which could be used in several wheat breeding studies mainly encompassing simple sequence repeat, restriction fragment length polymorphism, random amplified polymorphic DNA, single nucleotide polymorphism, and amplified fragment length polymorphism. The discovery of molecular markers and related technologies, such as marker-assisted selection (MAS), has led to the appearance of a new genetic background in plant breeding. MAS would be exceedingly valuable in the cases of polygenic or quantitative disease resistance, in which the individual quantitative trait loci (QTL) would have minute effects on disease development. This review elaborately describes the availability of many molecular markers that recognize the locus of gene mapping for an understanding of the genetic background of disease resistance.

Keywords Resistance genes · Molecular markers · Gene location · Powdery mildew

Introduction

Cultivation of disease-resistant cultivars/varieties is an efficient factor in both experimental and commercial breeding, and disease control performed by the management of resistance genes might enhance the stability of the variety. Such resistance durability might be exceedingly beneficial to farmers as it leads to increase in yield, reduces the costs, and is environmentally friendly (Shah et al. 2017a). So far, 82 PM resistance genes have been formally cataloged on 54 loci (McIntosh et al. 2017), but most of them are race specific and are easily overcome by new Bgt isolates (Li et al. 2014). Among them, the *Pm3* resistance alleles have been well categorized (Yahiaoui et al. 2004; 2006); likewise, four other genes named as *Pm1*, *Pm3*, *Pm4*, and *Pm5* have more than one allele contributing to the resistance to powdery mildew (Yahiaoui et al. 2006). The A-genome progenitor is *Triticum urartu* (Ling et al. 2013). Wheat gene pool of the diploid ''A'' genome progenitor containing three closely related species, for instance, *Triticum monococcum*, *Triticum boeoticum*, and *T. urartu*, has valuable variability for several economically significant genes, coding resistance to powdery mildew (Singh et al. 2007; Hussien et al. 1997). Similarly, several other genes including *Pm4a, Pm4b, Pm5a, Pm6, Pm16, Pm26, Pm27, Pm30, Pm31*, and *Pm33* have been introduced from tetraploid wheat (McIntosh et al. 2007); two

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new alleles of *Pm1* have been introgressed from two different accessions of *T. monococcum*, conferring defense response to powdery mildew. Several molecular markers, including RAPD, RFLP, AFLP, expressed sequence tags (EST), and STS, have been found to be associated with more than 29 powdery mildew resistance genes on wheat chromosomes (McIntosh et al. 2007; Alam et al. 2011). Some of the above reported markers have been effectively applied in gene map-based cloning (Yahiaoui et al. 2004), MAS and gene pyramiding against powdery mildew (Liu et al. 2001). Molecular markers might help selection in the early developmental stages and might be assessed for high yield with high heritability and they can easily be found by the genetic linkage of the desirable gene group on the chromosome associated with disease resistance (Hua et al. 2009).

Sources of resistance to powdery mildew in wheat

In a report published by Marone et al. (2013), several resistance genes were transferred from diploid and tetraploid relatives of wheat, such as *Triticum carthlicum* Nevski (*Pm6* and *Pm33*), *Triticum timopheevii* (*Pm27, Pm37, PmNCAG11, and MlAG12*), *Triticum turgidum* var. dicoccoides (*MlIW170, Pm42, MlAB10, MlZec1, Pm41, Pm16, Ml3D232, PmAS846, Pm36, PmG3M, PmG16*, and *MlIW72*), *T. monococcum* (*Pm4d, Pm2026, NCA6Pm, Mlm2033*, and *PmNCA4*), *T. boeoticum* (Boiss) (*PmTb7A.1, PmTb7A.2*, and *Mlm80*), *T. urartu* (Tum.) (*PmU*) and several *Aegilops* spp. (*PmY212, Pm35, PmY201, Pm34, and Pm12*) or from related genera, such as Elytrigia (*Pm40*), *Secale* (*PmHNK54* and *PmTm4*), and *Thinopyrum intermedium* (Host) (*Pm43)*. The confluence in the same region of QTL and the genes that derive from diverse species is the most exemplified instance along the chromosomes of the wheat genome, which leads to the hypothesis that diverse sources of resistance might have contributed to these regions. Chromosome 1A was characterized in *Triticum militinae*, which contains the marker *Xpsp2999* (47.2 cM) (Jakobson et al. 2012), where a gene-rich region resulting *MQTL4* was recognized on chromosome 2A. This region appears to have been subjected to multiple events of introgression from wild species as genes and QTL that derive from different sources were mapped (*T. monococcum*, *Triticum aestivum*, *Triticum dicoccum*, *T. timopheevii*, and *T. carthilicum*). There are other convergence regions in which different origins of resistance have contributed to the same chromosomal region on chromosomes 2B (*T. carthlicum*, *T. aestivum*, and *Triticum dicoccoides*), 5B (*T. dicoccoides*, *T. aestivum*), 5A (*T. aestivum*, *T. monococcum*, and *T. militinae*), and 6B (*T. aestivum*, *T. timopheevi*, and *T. dicoccoides*, *Aegilops speltoides*) (Marone et al. 2013).

So far, approximately 82 designated powdery mildew-resistant genes have been identified at 54 loci (*Pm1-Pm54*), including *Pm1a-Pm1e* at *Pm1*, *Pm3a-Pm3g* at *Pm3*, *Pm4a-Pm4d* at *Pm4, Pm5e-Pm5, Pm8, Pm17*, and *Pm24a-Pm24b at Pm24* (Table 1, Hao et al. 2015). Another published report Zeller et al. (1993) stated that *Pm3d, Pm3e*, and *Pm3f* were identified on short arm of wheat chromosome 1A. In other report, The et al. (1979) stated that *Pm4a* and *Pm4b* have been recognized on long arm of *T. dicoccum* and *T. carthlicum* chromosome 2A, respectively. Reportedly, most of the designated host defense genes have been originated from *T. aestivum* and wild plants. For example, the sources of resistance genes including *Pm1b* and *Pm25* were introduced to common wheat from *T. monococcum*; *Pm16*, *Pm26*, and *Pm30* genes were introduced from *T. turgidum* sub sp. *dicoccoides*; *Pm6* and *Pm27* genes from *T. timopheevii*; *Pm4a* and *Pm5a* genes from *T. turgidum* sp. *Dicoccum*; *Pm4b* gene was introduced from *T. turgidum* subsp. *Carthlicum*; *Pm5*c was introduced from *T. aestivum* subspp. *sphaerococcu*; *Pm7, Pm8, Pm17*, and *Pm20* genes were transferred from *Secale cereale*; *Pm2* and *Pm19* genes were introduced from *Aegilops tauschii*, *Pm21* gene was transferred from *Dasypyrum villosum*; *Pm12* and *Pm32* genes were transferred from *A. speltoides*; and *Pm29* gene was introduced from *Aegilops ovate* to wheat plant as described by Hsam et al. (2003). Resistance gene *Pm10* to powdery mildew was recognized on wheat chromosome 1D (Tosa et al. 1987). Similarly, resistance genes *Pm11, Pm14*, and *Pm15* to powdery mildew were recognized on small arm of wheat chromosome 6B (Table 1, Tosa and Sakai 1990; Tosa et al. 1988). Extensive molecular studies for the identification of the sources of host resistance to virulent pathogens are needed to allow effective utilization of disease resistance in wheat breeding populations for commercial use (Ma et al. 2014). Li et al. (2011) and Song et al. (2012) evaluated a large number of powdery mildew isolates in China and reported that some wheat cultivars have resistance genes to powdery mildew genes: *PmYm66* linked to *Ksum193* and *PmHNK54* flanked by *Barc5* and *Gwm312* that were identified on chromosome arm 2AL in Yumai 66 and Zheng 9754, respectively (Xu et al. 2011). Powdery mildew resistance gene *PmTm4* is flanked by *Gwm611* and *EST92* in Tangmai 4 on chromosomal arm 7BL (Tie-Zhu et al. 2008), where *Pm2* was the first powdery mildew gene found on chromosomal arm 5DS and was designated as *Pm2a*, while the new allele *Pm2b* at the same locus was already reported earlier (Ma et al. 2015). The another powdery mildew resistance gene, *Pm48*, was observed to be located in the multi-allelic *Pm2* region of the chromosome of the German cultivar Tabasco (Gao et al. 2012), which is consistent with the findings of

Table 1 Genes associated with powdery mildew resistance, source of identification, and their chromosomal location

Gene/allele	Location	Source	References
Pm1a	7AL	*T. aestivum*	Briggle and Sears (1966)
Pm1b	7AL	*T. monococcum*	Hsam et al. (1998)
Pm1c (formerly *Pm18*)	7AL	*T. aestivum*	Hsam et al. (1998)
Pm1d	7AL	*T. spelta*	Hsam et al. (1998)
Pm1e (*Pm22*)	7AL	*T. aestivum*	Ch et al. (2003)
Pm2	5DS	*T. aestivum/Ae. tauschii*	Mclntosh and Baker (1970) and Briggle and Sears (1966)
Pm3a	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3b	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3c	1AS	*T. aestivum*	Briggle and Sears (1966)
Pm3d	1AS	*T. aestivum*	Zeller et al. (1993)
Pm3e	1AS	*T. aestivum*	Zeller et al. (1993)
Pm3f	1AS	*T. aestivum*	Zeller et al. (1993)
Pm4a	2AL	*T. dicoccum*	The et al. (1979)
Pm4b	2AL	*T. carthlicum*	The et al. (1979)
Pm5a	7BL	*T. dicoccum*	Law and Wolfe (1966)
Pm5b	7BL	*T. aestivum*	Hsam et al. (2001)
Pm5c	7BL	*T. aestivum* ssp. *sphaerococcum*	Hsam et al. (2001)
Pm5d	7BL	*T. aestivum*	Hsam et al. (2001)
Pm5e	7BL	*T. aestivum*	Huang et al. (2003)
mlxbd (*Pm5* allele)	7BL	*T. aestivum*	Huang et al. (2000)
Pm6	2BL	*T. timopheevii*	Marone et al. (2013) and Helmsj∅rgensen and Jensen (1973)
Pm7	4BS·4BL-2RL	*S. cereale*	Hsam et al. (2003) and Friebe et al. (1994)
Pm8	1RS·1BL	*S. cereale*	Hsam et al. (1998)
Pm9	7AL	*T. aestivum*	Hsam et al. (1998)
Pm10	1D	*T. aestivum*	Tosa et al. (1987)
Pm11	6BS	*T. aestivum*	Tosa et al. (1988)
Pm12	6BS-6SS·6SL	*Ae. speltoides*	Jia et al. (1996)
Pm13	3BL·3SS-3S,3DL·3SS-3S	*Ae. longissima*	Ceoloni et al. (1992)
Pm14	6BS	*T. aestivum*	Tosa and Sakai (1990)
Pm15	6BS	*T. aestivum*	Tosa and Sakai (1990)
Pm16	4A	*T. dicoccoides*	McIntosh et al. (2007) and Reader and Miller (1991)
Pm17	1RS·1AL	*S. cereale*	Hao et al. (2015), Heun et al. (1990) and Hsam et al. (1998)
Pm19	7D	*Ae. tauschii*	Hsam et al. (2003) and Lutz et al. (1995)
Pm20	6BS·6RL	*S. cereale*	Friebe et al. (1994)
Pm21	6VS·6AL	*Haynaldia villosa*	Chen et al. (1995)
Pm23	5A	*T. aestivum*	Hao et al. (2008) and Mcintosh (1998)
Pm24	1DS	*T. aestivum*	Huang et al. (2000)
Pm25	1A	*T. boeoticum*	Shi et al. (1998)
Pm26	2BS	*T. dicoccoides*	Rong et al. (2000)
Pm27	6B-6G	*T. timopheevii*	Järve et al. (2000)
Pm28	1B	*T. aestivum*	Peusha et al. (2000)
Pm29	7DL	*A. ovata*	Hsam et al. (2003) and Zeller et al. (2002)
Pm30	5BS	*T. dicoccoides*	Liu et al. (2002)
Pm31 (*MlG*)	6AL	*T. dicoccoides*	Xie et al. (2003)
Pm32	1BL·1SS	*Ae. speltoides*	Hsam et al. (2003)

Table 1 continued

Gene/allele	Location	Source	References
Pm33	2BL	*T. carthlicum*	Zhu et al. (2005)
Pm34	5DL	*Ae. tauschii*	Miranda et al. (2006)
Pm33	2BL	*T. carthlicum*	Zhu et al. (2005)
Pm34	5DL	*Ae. tauschii*	Miranda et al. (2006)
Pm35	5DL	*Ae. tauschii*	Miranda et al. (2007)
Pm36	5BL	*T. dicoccoides*	Blanco et al. (2008)
Pm37	7AL	*T. timopheevii*	Perugini et al. (2008)
Pm38	7DS	*T. aestivum*	Lillemo et al. (2005)
Pm39	1BL	*T. aestivum*	Lillemo et al. (2008)
Pm40	7BS	*Elytrigia intermedium*	Marone et al. (2013) and Luo et al. (2009)
Pm41	3BL	*T. dicoccoides*	Li et al. (2009)
Pm42	2BS	*T. dicoccoides*	Hua et al. (2009)
Pm43	2DL	*T. intermedium*	Marone et al. (2013) and He et al. (2009)
Pm44	3AS	*T. aestivum*	Alam et al. (2011)
Pm45	6DS	*T. aestivum*	Ma et al. (2011)
Pm46	5DS	*T. aestivum*	Gao et al. (2012)
Pm47	7BS	*T. aestivum*	Xiao et al. (2013)
Pm49 (Ml5323)	2BS	*T. dicoccum*	Piarulli et al. (2012)
Pm50	2AL	*T. dicoccum*	Mohler et al. (2013)
Pm51	2BL	*Thinopyrum ponticum*	Zhan et al. (2014)
Pm54	6BL	*T. aestivum*	Hao et al. (2015)
Pm55	5VS	*Dasypyrum villosum*	Zhang et al. (2016)
Pm57	T2BS.2BL-2S	*Ae. searsii*	Liu et al. (2017)

(Mcintosh et al. 2011) who reported that it was initially designated as *Pm46* and then formally re-designated as *Pm48*. The commonly used wheat resistance line Lankao 906, introduced from a cross between wheat and rye (Mzalenod Beer) and Xuanxi (Baofeng), was found to carry a recessive powdery mildew resistance gene located on wheat chromosome 2AL that was temporarily named *PmLK906* (Niu et al. 2008). Likewise, one more temporarily named gene (*TacsAetPR5*) was recognized on chromosomal arm 2AL at *Pm4* locus in cultivar Lankao 906 and was designated as *PmLK906*. Similarly, other temporary genes (*PmPS5A*) were introduced from *T. carthlicum* to common wheat (Zhu et al. 2005), and *PmYm66* was introduced from common wheat (Yumai 66) (Tie-Zhu et al. 2008). Nine powdery mildew resistance genes were mapped on chromosome 2B, and four of them were designated as *MlZec1, PmY39, MlAB10*, and *MlIw170*. *PmY39* was converged by hybridization between the population of Am9 and Laizhou 953. Resistance gene *Pm38* was identified on wheat chromosome 7DS (Spielmeyer et al. 2005), whereas *Pm39* was recognized on wheat chromosome 1BL (Table 1, Lillemo et al. 2008). Likewise, resistance gene *Pm51* was identified on chromosome 2BL in wild plant *Dasypyrum villosum* (Zhan et al. 2014), whereas *Pm57* was recognized on chromosome 2BL in *Ae. searsii* (Table 1, Liu et al. 2017).

Adult plant resistance

Race-specific resistance is easily recognized in the field by its qualitative monogenic inheritance and is easy to integrate into the genome of receptive plant cells. Unfortunately, this type of resistance is easily influenced by emergence of new races. The traits related to quantitative trait loci (QTL), for example, adult plant resistance (APR), are widespread in plant breeding due to their stability over a wide geographic range and time. Plant defense responses may be induced at the different stages of host development, varying with plant age or tissue ripeness, and are extremely closely associated with plant and pathogen interactions (Shah et al. 2017c; Develey-Rivière and Galiana 2007). For instance, Cowger et al. (2012) reported that APR to powdery mildew in numerous widely cultivated cultivars has an effective durability of more than four decades. Slow fungus infections and multiplication of fungal pathogens have been observed at adult plant stages (Shaner 2003). CIMMYT wheat (*T. aestivum* L.) lines Francolin#1 and Quaiu#3 displayed effective and stable adult plant resistance to Chinese *Blumeria graminis* f. sp. *tritici* isolates in the field (Ren et al. 2017). Other researchers, Hsam et al. (2003) found that *Pm5* gene acts as a source of APR to wheat powdery mildew. Das and Griffey (1994) identified 14 chromosomes involved in the expression of APR in monosomic wheat varieties (Chinese Spring and Caribo). They also investigated the winter wheat cultivars Knox 62, Massey, and Redcoat and concluded that two to three genes with moderate to high heritability controlled APR. Similarly, the resistance to fungal development was observed on seven chromosomes at the adult plant stage of the wheat cultivar Knox 62. For example, chromosomes 5A, 7A, 4B, and 5D displayed a higher association with the resistance to fungal infections at the adult plant stage (Lan et al. 2009). In addition, powdery mildew resistance gene (*MlRE*) was reported to have a significant defense response to pathogen infections during the adult stage of the winter wheat cultivar RE714 because of dominant residual effects (Chantret et al. 1999). Ren et al. (2017) detected six QTL conferring APR to powdery mildew across environments, including *QPm.heau-1BL* (*Pm39*), *QPm.heau-1DL, QPm.heau-2DL, QPm.heau-4BL, QPm.heau-5BL, and QPm.heau-6BS. QPm.heau-1DL* is likely to be a novel QTL for resistance to powdery mildew. Besides *Pm39, QPm.heau-2DL* might be another co-located/pleotropic resistance gene in wheat, which maps to same position as *Yr54*.

Another published report revealed that *Pm12*, *Pm16*, and *Pm20* genes confer most effective defense response against powdery mildew inoculation in adult plant stage (Wang et al. 2007). Based on phenotype variation only, it is hard to recognize plants with both race-specific resistance and APR to powdery mildew. However, some molecular markers associated with genes encompassing *Pm1* (Hu et al. 1997); *Pm2* and *Pm3* (Ma et al. 1994); *Pm4* (Hartl et al. 1999); *Pm12* (Jia et al. 1996); *Pm13* (Cenci et al. 1999); *Pm21* (Qi et al. 1996) and *Pm25* (Shi et al. 1998) have been reported with both race-specific resistance and APR to powdery mildew. With MAS, it is also probable to choose plants with both race-specific resistance, and APR to powdery mildew. Some molecular markers, such as SSR and SNP, were utilized for the identification of adult plant resistance genes against powdery mildew infection (Zhang et al. 2010). QTLs associated with the defense response were mapped at *Pm4* locus (Muranty et al. 2009), which exhibited most influential defense response to powdery mildew infection during the adult plant stage. Zhao et al. (2013) and Purnhauser et al. (2011) identified markers that were tightly linked to *Pm6* for APR. QTL associated with resistance against powdery mildew was mapped near the *Pm1* locus (Chantret et al. 2001), and another QTL related to the *Pm3a* locus was identified for adult plant resistance (Liang et al. 2006). In addition, QTLs associated with *Pm5* and *Pm13* loci were mapped for APR (Chen et al. 2009). In their investigations, Muranty et al. (2009) and Lan et al. (2009) recognized and mapped QTLs for wheat adult plant resistance at or near the *Pm3*5 and *Pm43* loci, respectively.

Marker-assisted selection

Wheat molecular markers that are strongly linked to the resistance genes can be used for MAS to improve the efficacy of assortment in early generations (Gupta et al. 2010). For example, in wheat breeding programs, *T. intermedium*-derived barley yellow dwarf virus resistance gene *Bdv2* has been transferred into commercial cultivars by using MAS (Zhang et al. 2004), but a small alien segment was found to be present. The alien-derived leaf rust resistance genes, e.g., *Lr9, Lr24* and *Lr47*, have been introduced from *Aegilops umbellulata*, *Thinopyrum ponticum*, and *A. speltoides*, respectively, into other common wheat cultivars by the use of genetic markers (Nocente et al. 2007). As a result, these genes functioned as ‘perfect’ markers or were linked to wheat-derived markers.

Using the BC_2F_1 population of the cross KM2939/3*Shimai 15, seven molecular markers were recognized that were closely linked to the *Pm2b* resistance gene. Similarly, three RAPD markers associated with *Pm25* could not detect the existence of *Pm25* in some genetic circumstances because of the large genetic distances between the markers and *Pm25* (Shi et al. 1998). Twenty years ago, it was challenging to identify all cultivars possessing *Pm1* and *Pm2a* by the use of closely linked RFLP markers (Hartl et al. 1995), while a similar report from that time detected the presence of *Pm2a* using an STS marker that was converted from the corresponding RFLP marker linked to *Pm2a* (Mohler and Jahoor 1996). Later, Gupta et al. (2010) stated that for MAS it was essential to check the accessibility of the closely associated markers in various genetic backgrounds. Introducing *Pm2b* into various vulnerable cultivars by MAS has been performed for many years, and an advanced line has been attained, and several transgenic lines showed resistance to powdery mildew at both the seedling and adult stages (Gupta et al. 2010).

Molecular markers

The following molecular markers can be useful for the detection of disease resistance genes: (a) restriction fragment length polymorphisms (RFLPs); (b) simple-sequence repeats (SSRs); (c) amplified fragment length polymorphisms (AFLPs); and (d) single nucleotide polymorphism (SNP). The above reported markers provide a polymorphic detection platform; they are easily applicable for disease resistance detection in a population, while owing to co-dominant inheritance, these molecular markers are commonly used in molecular breeding for genetic mapping (Shah et al. 2017b). For example, using wheat cultivar Chancellor as a recurrent parent, Briggle and Sears (1966) developed NILs for the assembling of powdery mildew resistance genes, including *Pm1*, *Pm2, Pm3*, and *Pm4a*, which was confirmed by using RFLP markers. An RFLP marker (*Whs179*) was associated with the *Pm3* locus and mapped at the distance of 1.9 cM (Hartl et al. 1993), and RFLP marker (*BCD1434*) was mapped at a distance of 1.3 cM from the *Pm3b* locus (Ma et al. 1994). Likewise, they also reported that the RFLP markers *BCD1231-2A* and *CDO678-2A* were associated with the *Pm4a* gene and mapped at a distance of 1.5 cM.

The RAPD marker *OPF12650* was mapped at a distance of 5.4 cM from the *Pm1* locus (Hu et al. 1997). Likewise, the *Pm21* gene was recognized and mapped by using the RAPD marker *OPH17-1900* on chromosome arm 6VS in common wheat (Qi et al. 1996). Two *Dasypyrum villosum* accessions, D.v#2 and No. 1026 from England and Russia, respectively, contain *Pm21* on chromosome 6V#2S and *PmV* on chromosome 6V#4S (Li et al. 2017). These both genes confer high resistance to powdery mildew in wheat. Even though several molecular markers have been developed to detect *Pm21* and *PmV*, only the MBH1 marker can simultaneously detect both *Pm21* and *PmV*. It is noteworthy that Neu et al. (2002) converted the RAPD marker *UBC638* into a dominant SCAR marker (*STS638*) and used for the identification of the *Pm1* resistance locus on wheat chromosome. However, RAPDs technology was not used frequently due to the limited influence of the genetic background for powdery mildew resistance as well as due to the minor levels of polymorphism among the populations.

In this respect, simple-sequence repeats (SSR)-based markers are a convenient and commonly used technique as due to the detection of high levels of polymorphism among the populations. The microsatellite marker (*PSP2999*) was found to be linked with the *Pm3* locus that conferring defense response to powdery mildew (Bougot et al. 2002). Later, Huang et al. (2003) mapped *Pm5e* on chromosome 7BL using SSR marker *Xgwm1267*. Another example is the study of Hua et al. (2009), in which the authors used two SSR markers (*Xbarc7* and *Xbarc55*) that were strongly associated with *Pm42* gene, with distances of 10.9 and 10.1 cM, respectively. Two genes (*Pm42* and *MlIW170*) were identified by using two SSR markers, *Xbarc7* and *Xbarc55* (Liu et al. 2012), and these two genes can be related to the same gene clusters (Marone et al. 2013). Two reported genes including *PmHNK54* and *PmYm66* were detected by the SSR markers *Gwm312* and *Barc5* on chromosome 2AL in Zheng 9754 and Yumai 66, respectively (Xu et al. 2011). The defense responses of several wheat cultivars to powdery mildew were established in China (Song et al. 2012; Li et al. 2011). *PmLX66, PmW14*, and *PmZ155* genes on chromosome 5DS in wheat (Liangxing 66) were found to be responsible for the defense against powdery mildew (Song et al. 2014; Huang et al. 2012; Sun et al. 2015). Successful transfer of *PmTb7A.1* and *PmTb7A.2* resistance genes is possible by using susceptible *T. durum* as a backcross linking species, and the obtained F_1 can be crossed with hexaploid wheat for the transfer of the two powdery mildew resistance genes (*PmTb7A.1* and *PmTb7A.2*) into breed wheat (Chhuneja et al. 2012).

For example, associations of *Pm34* with *Barc144* and *Barc177* (Fig. 3, Miranda et al. 2006), of *Pm-M53* with *Gwm292* and *Wmc289* (Li et al. 2011), and of *Pm35* with *Xcfd26* at a distance of 11.9 cM (Miranda et al. 2007) have been revealed on chromosome arm 5DL, which, according to the published maps, are positioned at the distances of approximately 92, 55, and 41 cM from *Pm2b*, respectively (Somers et al. 2004). *Pm2a* was found to be associated with *Xcfd81* (SSR marker) with a genetic distance of 2.0 cM on chromosome 5DS in the wheat landrace Ulka and at a distance of 3.3 cM from *Pm2b* (Qiu et al. 2006). Temporarily designated powdery mildew resistance genes were identified on chromosome arm 5DS containing MlBrock, which is co-segregated with *Cfd81* in the Brock cultivar (Li et al. 2009). Several genes, such as *PmLX66*, were mapped by *Cfd81* and *SCAR203* in the Chinese wheat cultivar/variety Liangxing 66 (Huang et al. 2012), *PmD57-5D* was identified and mapped by *Mag6176* and *Gwm205* in line D57 (Ma et al. 2011), *PmX3986-2* was identified by Cfd81 and SCAR112 in an indigenous germplasm (Ma et al. 2014), and *Pm46* was recognized by *Mp510* and *Gwm205* in the German cultivar/variety Tabasco (Gao et al. 2012). The resistance genes *Mlbrock* and *PmD57-5D* are same in comparison with *Pm2a* (Li et al. 2009; Ma et al. 2011), *PmX3986-2, Pm46*, and *PmLX66* are at distances of 0.7, 1.8, and 4.1 cM, respectively, from *Pm2b* based on the maps published (Gao et al. 2012; Huang et al. 2012). To clarify the associations between the above-mentioned genes, wheat genotypes, including *KM2939*, Ulka/8*Cc (with *Pm2a*), Tabasco (with *Pm46*), Liangxing 66 (with

PmLX66), and *X3986-2* (with *PmX3986-2*) were verified by 27 Bgt isolates (Ma et al. 2015). Their inoculation results showed that KM2939 conferred a response pattern that is dissimilar from that of lines with *Pm2a, PmLX66, Pm46*, and *PmX3986-2* (Ma et al. 2015). Hence, reportedly, *Pm2b* showed an association, which was different from that of *Pm2a, Pm46, PmLX66,* and *PmX3986-2*. It is noteworthy that they developed a near-isogenic line (NIL) using the susceptible wheat cultivar Shimai (recurrent parent) and applied 284 SSR markers across the population to measure the genetic polymorphism of selected lines to the backcross parent. According to the findings of a published report, the SSR marker *Xgwm337* and the AFLP marker locus *XE35M59-407* and *XE34/M51-346* was found to be linked to *Pm24* (Fig. 1, Huang et al. 2000) in Egyptian wheat cultivars, whereas two SSR markers (*Xgwm332* and *Xwmc790*) were noted to be linked to *Pm37* (Fig. 3, Perugini et al. 2008). Four other SSR markers (*Xbarc7, Xbarc13, Xbarc55,* and *Xwmc441*) were associated with the *Pm5055* gene with the genetic distances of 23, 23, 23.9, and 10.6 cM, respectively (Saidou et al. 2016). On the other hand, *PmAF7DS* was mapped on the short arm of chromosome 7D with a distance to a 14.6 cM interval and was flanked by the SSR markers *Xgwm350a* and *Xbarc184* on its distal and proximal sides (Reddy et al. 2016). Reportedly, two genes including *PmTb7A.1* and *PmTb7A.2* were established to be associated between *wPt4553* and *Xcfa2019* markers at a distance of 4.3 cM (Elkot et al. 2015).

Powdery mildew resistance loci were mapped with the utilization of high-density SNP markers in the RILs of Shanghai3/Catbird x Naxos and confirmed the consequences in a various genetic background; Soru#1 × Naxos (Susanne et al. 2017). They genotyped both populations with the Illumina iSelect 90 K wheat chip, and unified linkage maps developed by addition of previously genotyped DArT and SSR markers. In their reports, they identified a sum of 12 QTL with the novel linkage maps by utilizing SNP and DArT markers for powdery mildew resistance in the RILs of Shanghai3/Catbird x Naxos, of which eight were introduced from Naxos. A report published by Lu et al. (2012) stated that using SSR and DArT markers in the mapping population Shanghai3/Catbird x Naxos, discovered numerous important powdery mildew-resistant QTLs from Naxos. Similarly, they reported that several QTLs on chromosome 1AS and 2BL were more accurately mapped by utilizing SNP markers that facilitated finding of novel QTL on chromosome 1AL, 2AL, 5AL, and 5AS. Likewise, recently four powdery mildew resistance QTLs were recognized in the Soru#1 × Naxos population performed by Susanne et al. (2017), of which three had resistance to powdery mildew from Naxos. By using SNP-derived markers Bwm20, Bwm21, and Bwm25, Ma et al. (2016) flanked a temporarily designated gene (PmFG) at genetic distances of only 0.3, 0.3, and 0.5 cM, respectively, in the F_2 population. Genetic analysis confirmed that a qualitative gene designated as PmFG, deliberated resistance to powdery mildew in FG-1 population at the seedling stage.

Numerous AFLP markers were found to be very nearly associated with *Pm1c*, and among them one AFLP marker XS19M22-325/200 was specific for *Pm1c* (Hartl et al. 1999), whereas in two wheat crosses segregating population, AFLP markers *XE39M58-77* and *XE34M53-439* on chromosome 7A for *Pm22* (Fig. 2) and *Pm1c* (Fig. 1), respectively, specified that *Pm22* gene, which had previously been consigned to chromosome 1D in the Italian wheat variety (Virest) (Peusha et al. 1996), was an allele of the complex *Pm1* locus. *Pm22* was therefore re-designated as *Pm1e* (Singrun et al. 2003). Two AFLP markers, *XAG/AG-228* and *XCA/CT-355*, were linked to *Pm17* with genetic distances of 2.4 and 1.5 cM, respectively (Fig. 1, Hsam et al. 2000). In double-haploid wheat population, *Pm3g* was mapped by using RFLP markers XGli-A5 at distance of 5.2 cM from *Pm3g* gene to the distal region of the short arm of chromosome 1AS (Sourdille et al. 1999), whereas using SSR marker *Xgwm905, Pm3h* was nearly linked on short arm of wheat chromosome 1A at distance of 3.7 cM from the gene (Fig. 1, Huang and Roder 2004). A report published by Liu et al. (1998) stated that fragment using STS primers developed from the sequence of the RFLP probe BCD1231 produced a particular band which was existing in all 11 tested 214 varieties/cultivars and lines encompassing the *Pm4a* and *Pm4b* alleles, whereas using microsatellite marker *Xbarc122, Pm4b* was nearly associated with wheat chromosome 2AL at distance of 2.0 cM from the gene (Hao et al. 2015). *Pm6* has been extensively and effectively used in wheat powdery mildew resistance breeding as described by Bennett (1984). It was transferred to wheat from wild plant (*T. timopheevii)* by recombination between the B genome of hexaploid wheat and the G genome of *T. timopheevii*. RFLP marker *xbcd135* was mapped at a distance of 1.6 ± 1.5 cM from *Pm6*, whereas two RFLP markers *Xbcd307* and *Xbcd266* were mapped at a distance of 1.6 ± 1.5 and 4.8 ± 2.6 cM from *Pm6*, respectively (Tao et al. 2000). Three SSR markers associated with *Pm16* on short arm of wheat chromosome 5BS in F_2 population (Chancellor'(susceptible) × '70,281'(resistant)) (Chen et al. 2005), whereas *Pm17* was nearly mapped with RFLP marker *Xiag95* on short arm of *Secale cereale* chromosome 1RS (Hsam et al. 2000). *Pm23* gene was recognized in the hexaploid wheat line from 81 to 7241 and originally assigned to wheat chromosome 5A and was repositioned on long arm of chromosome 2A with the help of microsatellite markers (Fig. 1, Hao et al. 2008). Three genes encompassing *Pm12*,

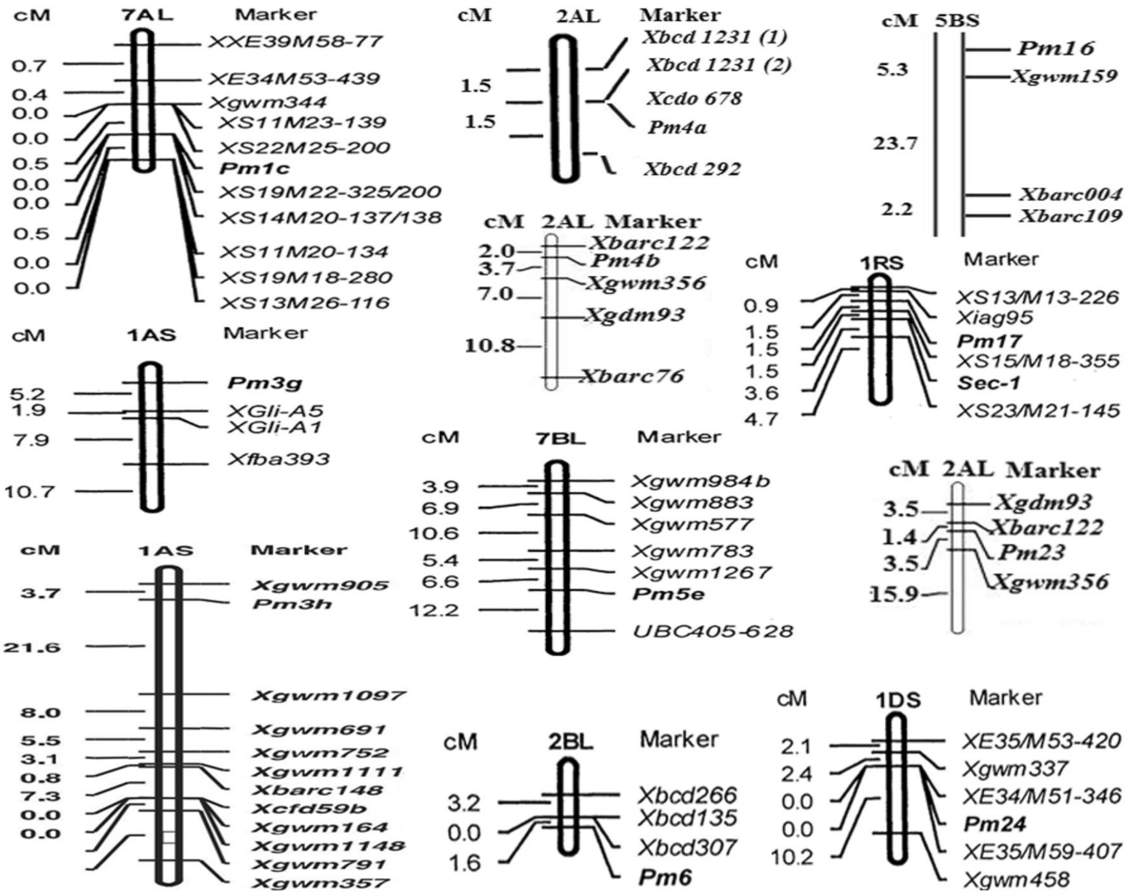

Fig. 1 Various powdery mildew resistance genes were mapped by different type of molecular markers. *Pm1C: Pm1C* gene was detected on long arm of wheat chromosome 7A with a marker interval of XS22M25-200–XS19M22-325/200 (Singrun et al. 2003), *Pm3g*: *Pm3g* was mapped by RFLP markers to the distal region of the short arm of chromosome 1A (Sourdille et al. 1999), *Pm3h*: Microsatellite marker *Xgwm905* was nearly linked at a distill end on short arm of wheat chromosome 1A at distance of 3.7 cM from the gene (Huang and Roder 2004), *Pm4a*: This gene was closely flanked by three RFLP markers on chromosome 2AL at distance of 1.5 cM from the gene (Ma et al. 1994), *Pm4b*: Microsatellite marker *Xbarc122* was nearly associated on at a distill end on wheat chromosome 2AL at distance of 2.0 cM from the gene (Hao et al. 2015). *Pm5e*: *Pm5e* was closely linked with SSR marker *Xgwm1267* on long arm of wheat chromosome 7BL at distance of 6.6 cM from the gene (Hao et al. 2015). *Pm6:* RFLP marker *xbcd135* was mapped at a distance of 1.6 ± 1.5 cM from *Pm6*, whereas two RFLP markers *Xbcd307* and *Xbcd266* were mapped at a distance of 1.6 ± 1.5 and 4.8 ± 2.6 cM from *Pm6*, respectively (Tao et al. 2000). *Pm16:* Genetic map created with three SSR markers associated with *Pm16* on short arm of wheat chromosome 5BS (Chen et al. 2005), *Pm17*: *Pm17* was nearly mapped with RFLP marker *Xiag95* on short arm of *S. cereale* chromosome 1RS (Hsam et al. 2000). *Pm23* were located with the interval of microsatellite markers *Xbarc122-Xgwm356* on long arm of wheat chromosome 2AL (Hao et al. 2008), *Pm24*: Two AFLP markers associated in coupling with *Pm24* and the AFLP marker locus *XE35M59-407* and *XE34/M51-346* were co-segregated with the *Pm24* allele and *XE35M53-420* mapped at distance of 4.5 cM from *Pm24* gene (Huang et al. 2000b)

Pm20, and *Pm27* and one temporarily designated gene such as *PmG3M* were found to be recognized on chromosome 6B. *Pm12* was accumulated into line #31 from *A. speltoides*, and was positioned on the chromosome 6BS-6SS.6SL (Jia et al. 1996). Likewise *Pm27* was introduced from *T. timopheevii* to hexaploid wheat, and positioned on a translocation fragment close the centromeric region of chromosome 6B (Järve et al. 2000). Nevertheless, two other genes, e.g., *PmG3M* and *Pm20*, were assigned to the same deletion bin as *PmA2K* (Fig. 2, Jia et al. 1996). *PmG3M* was located at the distance of 23.3 cM to the marker *Xbarc134* (Xie et al. 2012), while *PmA2K* was located to proximal to the marker at the distance of 1.2 cM; hence, the linkage distance between the two genes is about 24.5 cM. However, *PmG3M* was introduced from wild emmer *T. dicoccoides*, while *PmA2K* derived from hexaploid wheat. *Pm26* gene was accumulated from wild emmer (*T. turgidum*) to common wheat and co-segregated with a polymorphic locus detected by the RFLP marker *Xwg516*, 49.4 cM from the terminal marker *Xcdo456* (Rong et al. 2000). Linkage analysis exhibited that the *Pm29* in Pova was particularly located on chromosome 7DL nearly associated with one RFLP and three SSR markers. Three microsatellite markers on the long arm of

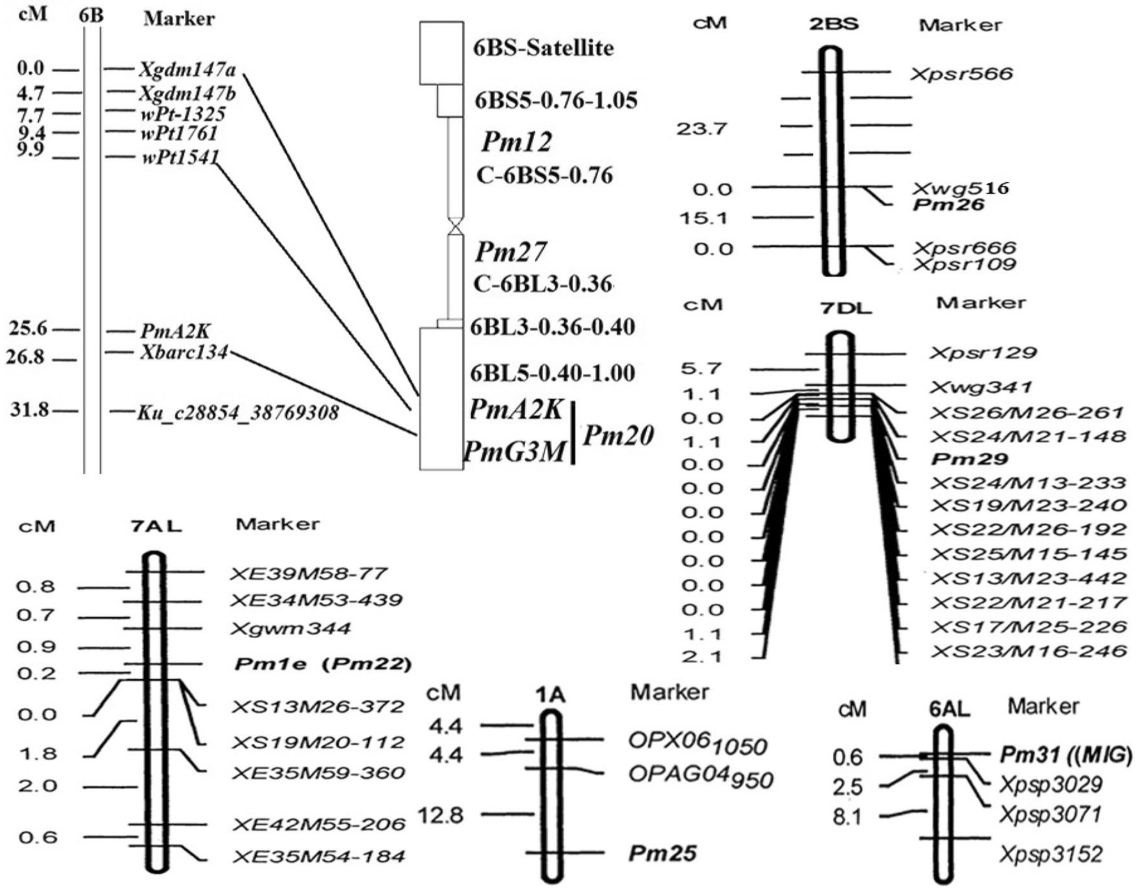

Fig. 2 Various powdery mildew resistance genes were mapped by different type of molecular markers. *Pm20*: QTL *PmA2K* was detected on the long arm of wheat chromosome 6B, whereas deletion bins were showed as intervals on the genetic and physical map (e.g., 0.40–1.00). *Pm20* gene was detected on the distal third of the long arm of from *S. cereale* L (Hao et al. 2015). chromosome 6R in a T6BS.6RL translocation, *Pm22*: Genetic maps and physical position on long arm of wheat chromosome 7A surrounding the wheat powdery mildew resistance alleles *Pm22* (*Pm1e*) were mapped by using SSR and RFLP markers (Singrun et al. 2003), *Pm25:* Two RAPD markers, OPX061050 and OPAG04950, were reported to be associated with *Pm25* situated on chromosome 1A (Shi et al. 1998), *Pm26:* This gene co-segregated with a polymorphic locus recognized by the RFLP marker *Xwg516* on short of chromosome 2B (Rong et al. 2000), *Pm29*: *Pm29* was closely linked to flanking AFLP markers *XS26M26-261* and *XS23M16-246* at distance of 1.1 cM, respectively (Zeller et al. 2002), *Pm31*: Microsatellite markers from long of wheat chromosome 6A were mapped in a BC$_2$F$_3$ population, in which the SSR locus *Xpsp3029-6A* was nearly (0.6 cM) associated with *Pm31* gene (Xie et al. 2003)

chromosome 6A were linked in a BC$_2$F$_3$ population, in which the SSR locus *Xpsp3029-6A* was closely linked (0.6 cM) to *Pm31* (Fig. 2, Xie et al. 2003), whereas two RAPD markers, *OPX06105*0 and *OPAG04950* were found to be linked to *Pm25* located on chromosome 1A (Shi et al. 1998). The SSR marker *Xgwm159/500* were reported to be associated with the powdery mildew resistance gene *Pm30* on short arm of wheat chromosome 5BS with a genetic distance of 5–6 cM (Fig. 3, Liu et al. 2002), whereas *Pm36* came from *T.turgidum* in durum wheat and the genetic association of the five AFLP markers were linked with *XP43M32*(*250*) at the distance of 1.1 cM from *Pm36* (Blanco et al. 2008).

Conclusions and future prospects

Phylogeny of mapmaking programs along with the improvement or development of high-density SNP chips also make it practicable to build integrated maps with various marker types, giving an even enhanced map resolution and making it probable to exchange formerly used DArT, SSR, and RFLP with SNP markers. The SNP markers are easygoing to use in genotyping with today's technology platforms, for example, KASP (Semagn et al. 2014). Significant breakthrough in the genomic of wheat research was established in 2012 with the achievement of *de novo* sequencing of common wheat, Chinese Spring variety (CS42), enabling improvements in genomic research into the genus *Triticum* and giving visions into the polyploidization of wheat. A report published by Brenchley

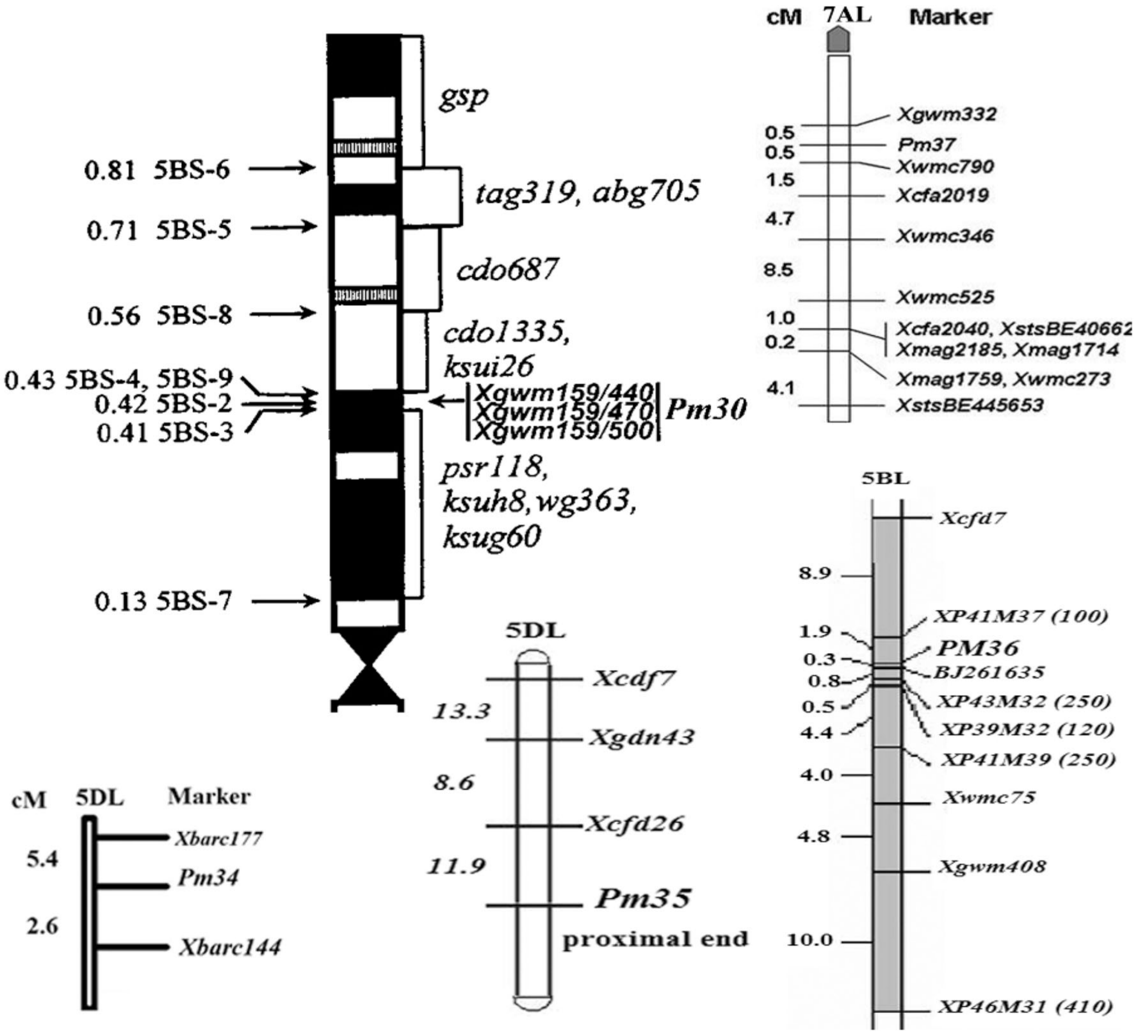

Fig. 3 Various polymorphic or microsatellite markers *Xgwm159/430, Xgwm159/460*, and *Xgwm159/500* were reported to be associated with the powdery mildew resistance gene *Pm30* on short arm of wheat chromosome 5BS (Liu et al. 2002), *Pm34:* Two co-dominant SSR markers *Xbarc177-Xbarc144* were found to be associated with *Pm34* on long arm of wheat chromosome 5DL (Miranda et al. 2006), *Pm35*: Microsatellite markers were found to be associated with *Pm35* gene and their most likely order was *Xcfd7*, 10.3 cM, *Xgdm43*, 8.6 cM, *Xcfd26*, 11.9 cM, *Pm35* gene on long of wheat chromosome 5DL (Miranda et al. 2007), *Pm36*: Five AFLPs markers (*XP43M32*(*250*), *XP46M31*(*410*), *XP41M37*(*100*), *XP41M39*(*250*), *XP39M32*(*120*)) were assigned to long arm of wheat chromosome and were identified to be linked to powdery mildew resistance gene *Pm36* (Blanco et al. 2008). *Pm37*: Microsatellite markers *Xgwm332* and *Xwmc790* were associated with the distance of 0.5 cM on long of wheat chromosome 7AL (Perugini et al. 2008)

et al. (2012) stated that genome of wheat was sequenced by utilizing Roche 454 pyro-sequencing technology, e.g., GS FLX Titanium and GS FLX + Platforms.

One of the most important targets for a breeder is to develop a cultivar which is potentially resistance to disease infection. Substantial advancements have been made during the last two decades in detecting marker–trait associations and their use in MAS for wheat improvement. So far, most of the characters used for the development through MAS are simple and confer the disease defense response and these marker–trait associations will be the key object of attention in prospects wheat breeding efforts, including those by the use of MAS. The application and development of genetic markers will remain an effective approach in the classification or selection of target genes and the detection of their locus on the chromosome. In addition, the use of such markers of gene sequences will enable the recognition and distribution of innovative genes for the development of wheat disease resistance traits. The most efficient factor in the future achievements of wheat breeding will be the strategies and novelties that come through the utilization of molecular approaches and the plant breeders will easily gain targets and recognize effective germplasm for analysis by using advanced molecular technologies. These molecular technologies will support the further development, and it seems feasible that novelties in breeding approaches will be effective factors to the future role of MAS. There are several hurdles in wheat development due to the difficulties of working with three genomes; however, these challenges can be overcome, and improved genetic traits can be obtained by the utilization and development of strongly associated genetic markers for the recognition of new resistance genes to diseases. A large set of SNPs (132,000 SNPs) in A, B, and D genes will enhance future studies aimed at identifying QTLs and discovering associations of traits.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The authors state that this review has good novelty for the control of powdery mildew disease.

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