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REVIEW

Fighting wheat powdery mildew: from genes to fields

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Abstract

Key message **Host resistance conferred by *Pm* genes provides an effective strategy to control powdery mildew. The study of *Pm* genes helps modern breeding develop toward more intelligent and customized.**

Abstract Powdery mildew of wheat is one of the most destructive diseases seriously threatening the crop yield and quality worldwide. The genetic research on powdery mildew (*Pm*) resistance has entered a new era. Many *Pm* genes from wheat and its wild and domesticated relatives have been mined and cloned. Meanwhile, modern breeding strategies based on high-throughput sequencing and genome editing are emerging and developing toward more intelligent and customized. This review highlights mining and cloning of *Pm* genes, molecular mechanism studies on the resistance and avirulence genes, and prospects for genomic-assisted breeding for powdery mildew resistance in wheat.

Introduction

Wheat (*Triticum aestivum* L.) is an important staple food crops worldwide. With the increasing population and the improving standard of living, demand for wheat yield and quality has been increasing annually. However, wheat grain yield and quality are seriously threatened by nearly 50 diseases and pests (Singh et al. 2016). Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is one of the most destructive foliar diseases, which generally decreases wheat yield by 10–15%, and up to 50% in severe cases (Juroszek and von Tiedemann 2012). Traditional strategies for controlling this disease include the use of host resistance, application of fungicides, and integrated disease managements. Compared with other methods, host resistance has been demonstrated as the most effective and environmentally friendly strategy to control or slow epidemics of powdery mildew.

To date, more than 100 formally and/or temporarily designated wheat powdery mildew (*Pm*) resistance genes/alleles have been identified (Zhu et al. 2022). However, most of them confer race-specific resistance. New virulent *Bgt* isolates can easily defeat such type of *Pm* genes. For example, *Pm1*, *Pm2*, *Pm3*, *Pm4*, *Pm5*, and *Pm8* are losing or have almost lost their resistance to *Bgt* isolates currently prevalent in many wheat production regions in China (Wang et al. 2005; Xiao et al. 2022; Zeng et al. 2014). Even the most effective gene *Pm21*, derived from *Dasypyrum villosum*, is also undergoing strong selection pressure and the risk of losing its resistance (He et al. 2020). Currently, efficient utilization of disease resistance genes and rapid pyramiding of major genes are effective means to develop new disease resistance wheat varieties.

Wheat *Pm* genes can be divided into two categories: race-specific and non-race-specific resistance genes. The former usually confers qualitative resistance, which follows the Mendel's Law of Segregation, and accounts for most of the documented *Pm* genes, especially those of nucleotide-binding site leucine-rich repeat (NBS-LRR) receptor protein-encoding genes (Wu et al. 2022a). The latter confers mostly partial quantitative resistance. Multiple fungal pathogen resistance genes *Pm38/Yr18/Lr34/Sr57*, *Pm39/Lr46/Yr29/Sr58*, and *Pm46/Yr46/Lr67/Sr55* also provide the quantitative resistance (Krattinger et al. 2009; Lillemo et al. 2008; Moore et al. 2015). Qualitative and quantitative resistance genes together constitute the genetic basis against powdery mildew. The qualitative resistance

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genes endow plants with resistance in a manner of 'gene for gene,' which are generally believed to provide a relatively high level of resistance but the limited species of pathogens (Alemu et al. 2021; Limpert et al. 1987). Quantitatively inherited genes usually provide more durable but general levels of resistance, and they often deliver partial resistance to adult plants, and the genetic analysis is more complicated (Spielmeyer et al. 2005). Besides, according to the stages that the resistance expresses, *Pm* genes could be categorized as all-stage resistance (ASR) genes and adult-plant resistance (APR) genes. Most of the *Pm* genes confer ASR, except for *Pm38*, *Pm39*, *Pm46*, and *Pm62*; *Pm6* exhibits a moderate immunity at the seedling stage and high resistance from the fourth leaf stage onward. In addition, two wheat-*D. villosum* translocation lines harboring *Pm55* and *Pm67* confer the tissue-differentiated ASR resistance (Fig. 1).

Exploration and location of *Pm* genes

From the early genetic research in the 1930s to the modern gene mining based on high-quality genomes of common wheat and its relatives in the last decade, mining of wheat *Pm* genes has entered a new era (Avni et al. 2017; IWGSC 2014, 2018; Li et al. 2022b; Ling et al. 2018; Luo et al. 2017; Waterhouse 1930; Xiao et al. 2022). *Pm* genes or alleles have been identified from species in genera *Triticum*, *Thinopyrum*, *Secale*, *Aegilops*, and *Dasypyrum*. Most *Pm* genes were derived from common wheat. Besides, wheat relatives also contribute a large proportion of these *Pm* genes. For instance, *Pm40* and *Pm43* and other three temporarily named *Pm* genes are derived from *Thinopyrum* spp.; five *Pm* genes (*Pm7*, *Pm8*, *Pm17*, *Pm20*, and *Pm56*) are identified from *S. cereale*; *Ae. tauschii* is the diploid progenitor of hexaploid wheat providing the D subgenome, and 10 *Pm* genes originate from four *Aegilops* species; *D. villosum* is another excellent resistance resource, and *Pm21*/*PmV*, *Pm55*/*Pm5V*, *Pm62*, and *Pm67* have been introgressed from this species into common wheat in forms of compensating Robertsonian translocations (Chen et al. 1995, 2006; Zhang et al. 2016, 2018b, 2021b). Modern genomic and genetic techniques have greatly accelerated mining of the *Pm* genes in the last years. Research progresses of the *Pm* genes in Triticeae crops are introduced in the following (Fig. 2).

(1) ***Pm* genes on the homoeologous group 1 chromosomes**. These *Pm* genes include the *Pm3* alleles (Bourras et al. 2019; Zeller et al. 1993), *Pm10* (Tosa et al. 1987), *Pm24*, *Pm25* (Shi et al. 1998), *Pm28* (Peusha et al. 2000), *Pm39* (Lillemo et al. 2008), and *MlHLT* (Wang et al. 2015) from *Triticum* Spp., *Pm8* (Hurni et al. 2014), *Pm17* (Singh et al. 2018) and *PmSESY* (He et al. 2021a) from *Secale* spp., *Pm32* (Hsam et al. 2003) from *Ae. speltoides*, and *Pm67* (Zhang et al. 2021b) from *D. villosum*. *Pm67*, a dominant *Pm* resistant gene, is derived from a wheat-*D. villosum* introgression line and physically located in the distal bin (FL 0.70–1.00) of 1VS#5. The introgression line harboring *Pm67* is immune to powdery mildew at the seedling stage and sheaths, stems, and spikes at the adult-plant stage and meanwhile a low level of susceptibility without the formation of conidiophores although a spot of colonies in leaves at adult-plant stage. Another wheat-*D. villosum*

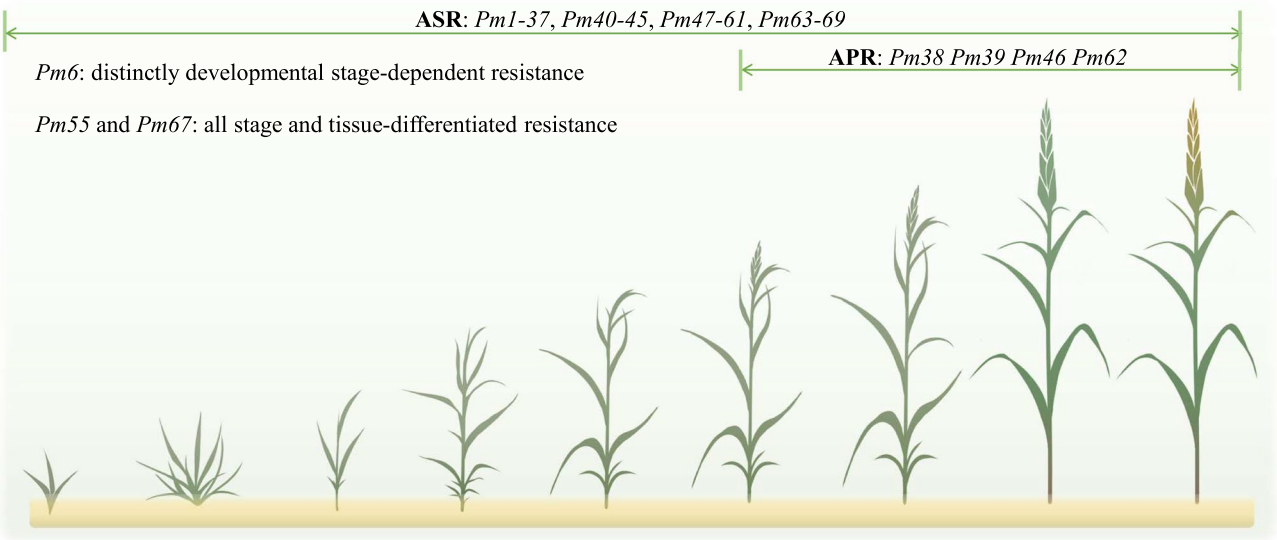

Fig. 1 Resistance stages of *Pm* genes. This figure shows the resistance period of the officially named *Pm* gene. ASR: all-stage resistance; APR: adult-plant resistance

Fig. 2 The distribution, position, origin, and existence form of the wheat powdery mildew resistance genes. The chromosomes of common wheat are represented by a cylindrical shape with black border, and the chromosomes from other wheat relatives are represented by a cylindrical shape with blue border. The black dot in the middle of cylindrical shape represents the centromere. The orange rectangles on chromosomes represent the genetic distance between *Pm* genes and the closely flanking marker. The number on the left side of chromosomes represents the physical location, and the number on the right side represents genetic distance. *: *Pm* genes encoding NBS-LRR protein; △: *Pm* genes encoding kinase; and ○: *Pm* genes encoding transporter. The map was performed based on the information from Chinese Spring RefSeq v1.0 chromosomes, The International Wheat Genome Sequencing Consortium (IWGSC)

translocation line T5V#4S·5DL harboring *Pm55* shows a nearly different immune reaction at the adult-plant stage from *Pm67* (Zhang et al. 2016). When the *Pm55* translocation line was crossed to the *Pm67* donor, all the F_1 plants showed immunity at the adult-plant stage. This suggested that the combination of the two genes might provide comprehensive powdery mildew resistance in wheat, and these two genes could become the valuable germplasms for adult-plant resistance to powdery mildew. *PmSESY*, derived from the rare rye wild species *S. sylvestre*, is identified as a dominant *Pm* gene and confers a broad-spectrum resistance to different *Bgt* isolates. He et al. (2021a) mapped *PmSESY* to the 1.88-cM genetic interval at the end of chromosome 1RL.

(2) ***Pm* genes on the homoeologous group 2 chromosomes**. The second homoeologous chromosome group has the largest number of *Pm* genes, including *Pm4a* (Mcintosh and Bennett 1979), *pm50* (Mohler et al. 2013), and *Pm49* (*Ml5323*) (Piarulli et al. 2012) from *T. turgidum* ssp. *dicoccum*, *Pm4b* (Mcintosh and Ben-

nett 1979), *Pm33*, and *PmPS5A* (Zhu et al. 2005) from *T. carthlicum*, *Pm4c* (Hao et al. 2008), *Pm4e* (Li et al. 2017), *Pm52* (Zhao et al. 2013), *Pm63* (Tan et al. 2019), *Pm65* (Li et al. 2019), *PmHNK54* (Xu et al. 2011), *pmX* (Fu et al. 2013), *pmQ* (Li et al. 2020e), *PmKN0816* (Wang et al. 2021), *PmLS5082* (Wu et al. 2022a), *PmCG15-009* (Zhang et al. 2023), and *PmYN99102* (Mu et al. 2022) from *T. aestivum*, *Pm4d* from einkorn wheat *T. monococcum* (Schmolke et al. 2012), *Pm6* from *T. timopheevii* (Helmsjϕrgensen and Jensen 1973), *pm26* (Rong et al. 2000), *pm42* (Hua et al. 2009), *Pm64* (Zhang et al. 2019), *MlIW170* (Liu et al. 2012), *MlWE74* (Zhu et al. 2022), *MLZec1* (Mohler et al. 2005), and *MlIW39* (Qiu et al. 2021) from wild emmer wheat *T. turgidum* var. *dicoccoides*, *Pm43* (He et al. 2009), *PmL962* (Shen et al. 2015), and *PmWE99* (Ma et al. 2016) from *Th. intermedium*, *Pm51* from *Th. ponticum* (Zhan et al. 2014), *Pm57* from *Ae. searsii* (Liu et al. 2017), *Pm58* from *Ae. tauschii* (Wiersma et al. 2017; Xue et al. 2022), *Pm62* from *D. villosum* (Zhang et al. 2018b), *Pm68* from *T. durum* (He et al. 2021b), and *MlHubel* from *T. aestivum* ssp. *spelta* (syn. *T. spelta*) (Peng et al. 2014).

Among these *Pm* genes, six were mapped on the chromosome arm 2AL, including three formally named genes *Pm4*, *pm50*, and *Pm65*, and the other three temporally named genes *PmPS5A*, *PmHNK54*, and *pmX*. *pm50* is located in the distal end of the marker *Xgwm294*, and the *pm50* donor maintains high level of powdery mildew resistance at the adult-plant stage (Mohler et al. 2013); *Pm65* is a dominant gene located between the markers *Xstars355* and *Xstars356* (Li et al. 2019); *PmPS5A* and *pmX* may be allelic to *Pm4* (Fu et al. 2013; Zhu et al. 2005); *PmHNK54* is located on chromosome 2AL-1-0.85 and tightly linked to markers *Xbarc5* and *Xgwm312* (Xu et al. 2011).

Nine *Pm* genes were identified on the chromosome arm 2BS, including the formally named genes *pm26*, *pm42*, and *Pm68* and the temporarily named genes *Ml5323*, *MlIW170*, *PmL962*, *PmWE99*, *MlWE74*, and *MlIW39*. *Pm68* was identified from resistant Greek durum wheat TRI 1796 and flanked by markers *Xdw04* and *Xdw12/Xdw13* with the corresponding physical region of 16.2–24.8 Mb (He et al. 2021b); *pm26* and *pm42* were recessive genes derived from wild emmer wheat (WEW) and molecular marker analysis indicated that they were not located at the same locus (Hua et al. 2009); *MlIW170* is located in 2BS3-0.84–1.00 and *pm26* and *MlIW170* appear to be allelic (Liu et al. 2012); *MlWE74* is located in the genomic region of 799.9 kb of the Zavitan reference sequence (Zhu et al. 2022). Whether comparing the resistant spectrum of *pm26*, *MlIW170*, *MlWE74*, or using the alleles of co-segregated marker *WGGBD425* and flanking markers *WGGBD412* and *WGGBH346*, it is difficult to identify their positional relationship, and therefore, it needs further evidence to distinguish them.

The chromosome arm 2BL harbors the largest number of *Pm* genes, including *Pm6*, *Pm33*, *Pm51*, *Pm52*, *Pm63*, *Pm64*, *pmQ*, *MlZec*, *PmKN0816*, *PmLS5082*, *PmCG15-009*, and *PmYN99102*. *Pm6* was located on the wheat-*T. timopheevii* 2B/2G introgression. In 2016, *TaRLK* was first considered to be the candidate gene of *Pm6*; however, the follow-up study indicated that it was not located on the 2G segment in the introgression line IGV1-465, which was excluded (Chen et al. 2016). Due to severe recombination inhibition between chromosomes 2B and 2G, genetically mapping *Pm6* was very difficult, and *Pm6* was mapped and flanked by markers *CIT02g-20* and *CIT02g-18* (Wan et al. 2020); *Pm52*, derived from the wheat cultivar Liangxing 99, was initially localized in the 2BL2-0.36–0.50 region and later narrowed to the interval between the markers *Xicssl326* and *Xicscl795* (Wu et al. 2019); *pmQ* is a recessive gene located between markers *Xicsq405* and *WGGBH913*, and its physical interval overlapped those of *Pm51* and *Pm63*, which needs to be distinguished from each other (Li et al. 2020e).

A few *Pm* genes were identified on chromosome 2D. *MlHubel* is the first recessive *Pm* gene identified on the chromosome arm 2DL, and *Pm43* is another *Pm* gene on this chromosome arm with the dominant inheritance and located between markers *Xwmc41* and *Xbarc11* (He et al. 2009; Peng et al. 2014). *Pm58* is located on the chromosome arm 2DS and has been narrowed to a 0.22-cM interval between markers *Xsts20220* and *Xkasp61553*. *AET2Gv20068500* is considered to be the candidate gene for *Pm58*, which encodes a typical NLR protein (Wiersma et al. 2017; Xue et al. 2022).

In addition, *Pm57* was derived from *Ae. searsii* and transferred into common wheat in the form of T2BS·2BL-2S^{S}#1L translocation. *Pm57* was then mapped in a 5.13-Mb physical region between markers *X67593* (773.72 Mb) and *X62492* (778.85 Mb) (Dong et al. 2020; Liu et al. 2017). *Pm62* was derived from *D. villosum* and transferred into the common wheat in the form of T2BS·2 V#5L translocation, and it was a novel adult-plant resistance gene (Zhang et al. 2018b).

In summary, many formally and/or tentatively named *Pm* genes have been found on the second homoeologous chromosome group, suggesting that it is most likely an enrichment region for the *Pm* genes. Cloning these genes and exemplary genomic assembly of this homoeologous group could clarify this issue.

(C) ***Pm* genes on the homoeologous group 3 chromosomes**. The third homoeologous chromosome group contains fewer *Pm* genes, including *Pm44* on chromosome 3A (Alam et al. 2011), *Pm13* from the translocated chromosome 3S of *Ae. longissima* (Ceoloni et al. 1992), and *Pm41* on chromosome 3BL (Li et al.

2009); besides, *TaRPP13L1-3D* on chromosome 3D was reported to respond to powdery mildew (Zhang et al. 2021a). *Pm41* is derived from wild emmer accession IW2, encoding a typical NBS-LRR protein, and the other *Pm* genes on the third homoeologous chromosome group have not been cloned (Li et al. 2020c). Recent studies showed that *TaRPP13L1-3D* is a truncated CC-NB-ARC gene, and its overexpression enhances the resistance to *Bgt* isolates and up-regulates the expression of defense-related genes. Interestingly, *TaRPP13L1-3D* is located in the plasma membrane and nucleus, and migration was detected from the plasma membrane to the nucleus (Zhang et al. 2022). The RanGAP2-WPP complex is the plant-specific nuclear pore complex mediating the connection between nucleoplasm and cytoplasm (Zhou et al. 2012). TaRPP13L1 directly interacts with the WPP domain-containing protein 1 (TaWPP1), while it does not interact with RanGAP2L in the yeast two-hybrid (Y2H) system (Zhang et al. 2022). This implies the variable interaction in NBS-LRR proteins conserved domains. So, *TaRPP13L1* should be an essential component for plant basal defense, probably via migration from the plasma membrane to the nucleus, although the molecular function remains to be elucidated.

(D) ***Pm* genes on the homoeologous group 4 chromosomes**. The fourth homoeologous chromosome group contains several *Pm* genes, including *pm61*, *MLIW30*, and *PmPBDH* on the chromosome arm 4AL (Geng et al. 2016; Liang et al. 2022; Sun et al. 2018); *Pm66* on the translocation chromosome T4S^{l}S·4BL of *Ae. longissima* (Li et al. 2020a); and *Lr67/Yr46/Sr55/Pm46/Ltn3*, a multi-resistance locus on the chromosome arm 4DL (Herrera-Foessel et al. 2014; Moore et al. 2015). *QPm.osu-4A*, *QPm.uga-4A*, and *QPm.tut-4A* were reported in the same interval as *MLIW30*, but they were distinct loci (Chen et al. 2009; Geng et al. 2016; Hao et al. 2015; Jakobson et al. 2012). The recessive gene *pm61* from Chinese wheat landrace Xuxusanyuehuang (XXSYH) is also located on 4AL-0.8–1.00 as *MLIW30* and *QPm.uga-4A*, but they should be different from each other (Hao et al. 2015; Jakobson et al. 2012; Sun et al. 2018). Further studies revealed that *pm61* is localized at a genetic interval of 0.71 cM, corresponding to the Chinese Spring reference genome of 0.61 Mb, between *MlIW30* and *QPm.tut-4A* (Hu et al. 2019). In addition, a wheat-rye line WR41-1 carrying T4BL·4RL and T7AS·4RS translocations is resistant to powdery mildew, which implies that WR41-1 may contain a new *Pm* gene (An et al. 2013).

(E) ***Pm* genes on the homoeologous group 5 chromosomes**. Many *Pm* genes are located on the fifth homoeologous chromosome group, including *pm2026* on the chromosome arm 5AL (Xu et al. 2008); *Pm36* (Blanco et al. 2008), *Pm53* (Petersen et al. 2015), *MIWE4* (Zhang et al. 2015), *MI3D232* (Zhang et al. 2010), and *PmAS846* (Xue et al. 2012a) on the chromosome arm 5BL; *Pm16* (Chen et al. 2005; Reader and Miller 1991) and *Pm30* (Liu et al. 2002) on the chromosome arm 5BS; *Pm34* and *Pm35* on the chromosome arm 5DL (Miranda et al. 2007, 2006); *Pm48* (reconfirmed as *Pm2*) (Wu et al. 2023), *Pm2* and its alleles on the chromosome arm 5DS of common wheat and *Ae. tauschii* (Briggle 1969; Fu et al. 2017; Ma et al. 2015a; Ma et al. 2014; Ma et al. 2015b; Sun et al. 2015a; Sun et al. 2015b; We, 2014; Xu et al. 2015); *Pm7* on the translocated chromosome T4BS·4BL-5RL (Heun and Friebe 1990); and *Pm55* on the chromosome arm 5VS of *D. villosum* (Zhang et al. 2016).

Pm2 is one of the most widely used *Pm* genes in wheat production. Many *Pm2* alleles have been reported in wheat cultivars, but they are all the *Pm2a* allele (Jin et al. 2022; Ma et al. 2015a; Yu et al. 2022). To identify the new *Pm2* allele, a large number of *Ae. tauschii* accessions were screened, and *Pm2d–Pm2j* were then identified (Manser et al. 2021). *pm2026* is a recessive *Pm* gene and the first tentatively named resistance gene on chromosome 5A from *T. monococcum* (Xu et al. 2008). WEW is an essential germplasm for wheat powdery mildew resistance, and *Pm16, Pm30*, *Pm36*, *PmAS846*, *Ml3D232*, and *MIWE4* are all derived from WEW. Recently, *Pm36* was finely mapped and located in the genetic interval of 1.5 cM. Thirteen protein-coding genes were found in the *Pm36* region, and three of them had no homologous components in the WEW Zavitan v2.0 reference genome. Among the remaining 10 protein-coding genes, six encode the BTB/POZ (broad-complex, tram track, and bric-abrac/poxvirus and zinc finger) protein. Recent studies indicate that BTB/POZ plays an essential role in plant growth and development, and the gene encoding BTB/POZ protein may be a potential candidate gene for *Pm36* (Nigro et al. 2022; Shalmani et al. 2021). In addition, by comparing the physical interval of *Pm36* and *Ml3D232*, it was found that they were not the same gene, but it was difficult to determine whether *Pm36*, *PmAS846*, and *MlWE4* were alleles. *PmAS846* is located in bin 5BL14 (0.75–0.76) (Xue et al. 2012a). Using weighted gene correlation network analysis (WGCNA), specific genes induced by *Bgt* invasion were divided into three modules (black module, darkolivegreen4 module, and plum1 module) (Hu et al. 2020). Candidate genes in the *PmAS846* region and protein–protein interaction networks were also constructed. This study provided the new idea and methods for the discovery of *Pm* genes.

(F) ***Pm* genes on the homoeologous group 6 chromosomes**. Several *Pm* genes are found on chromosome

of this homoeologous group, including *PmGZ1* on chromosome 6A (Li et al. 2022a); *Pm54* and *Pm69* (*PmG3M*) on 6BL (Hao et al. 2015; Xie et al. 2012b); *Pm11* and *Pm14* on 6BS (Tosa and Sakai 1990; Tosa et al. 1988); and *Pm45* (Ma et al. 2011) and *Pm07J126* (Yu et al. 2012) on 6DS. In addition, there are five *Pm* genes from relative species in forms of chromosome translocations: *Pm12* (T6BS-6SS·6SL) (Jia et al. 1996), *Pm20* (T6BS·6RL) (Friebe et al. 1994), *Pm21* (T6AL·6 V#4S) (Chen et al. 1995), *Pm27* (6B/6G) (Järve et al. 2000), and *Pm56* (T6AL·6RS) (Hao et al. 2018). Among these genes, *Pm11*, *Pm14*, *Pm45*, *Pm54*, and *PmGZ1* are all derived from *T. aestivum. PmGZ1* was found in the wheat cultivar Guizi 1 (GZ1). By genotyping-by-sequencing (GBS) and QTL analysis, *PmGZ1* was localized on chromosome 6A, within the confidence interval of chr6a-307802221 and chr6a-309885836, corresponding to the genetic interval of Chinese spring 58.6–60.9 cM (2.3 cM) (Li et al. 2022a). *Pm56* was derived from Qinling rye. Chromosomes 6A and 6R dimonomer individuals are developed by infiltrating the rye 6R chromosome into wheat. Further analysis of hybrid line harboring incomplete forms of 6R revealed that *Pm* gene(s) is present on both arms of chromosome 6R; meanwhile, the presence of a short arm can give complete immunity, but the presence of the long arm can only confer a moderately to highly resistant level (Hao et al. 2018).

(G) ***Pm* genes on the homoeologous group 7 chromosomes**. Many *Pm* genes have been reported on the chromosome in this homoeologous group, including *Pm1* (and its alleles) (Hsam et al. 1998), *pm9* (Fiona 1984), *Pm37* (Perugini et al. 2008), *Pm59* (Tan et al. 2018), *Pm60* (and its alleles) (Ji et al. 2008; Li et al. 2021b; Wu et al. 2022b, 2021a; Zou et al. 2022, 2018), *Mlm80* and *Mlm2033* (Yao et al. 2007) on the chromosome arm 7AL; *Pm5* (and its alleles) on the chromosome arm 7BL (Heun and Fischbeck 1987; Hsam et al. 2001; Huang et al. 2003; Lebsock and Briggle 1974); *Pm40* (Luo et al. 2009) and *pm47* (Xiao et al. 2013) on the chromosome arm 7BS; *PmH* on the chromosome 7B (Zhou et al. 2005); *Pm29* on the chromosome arm 7DL (Zeller et al. 2002); and *Pm15* (Tosa and Sakai 1990), *Pm19* (Lutz et al. 1995), and *Pm38* (Dyck 1977) on the chromosome arm 7DS.

Pm15, *pm9*, *Pm29*, *pm47*, *Pm59*, and *PmH* are all derived from *T. aestivum*. Among the rest, *pm47* is a gene on a new unique locus by marker correlation alignment with *Pm40* on 7BS and *Pm5e*, *mlxbd*, *PmH*, and *Mlmz* on 7BL. The EST marker *BE606897* and the microsatellite marker *Xgwm46* were located on both sides of the single intransigent gene *pm47*, and the genetic distances were 1.7 cM and 3.6 cM, respectively (Xiao et al. 2013). *Pm59*, a dominant gene, was mapped between STS markers *Xmag1759* and *Xmag1714*, with genetic distances of 0.4 cM and 5.7 cM, respectively (Tan et al. 2018).

Pm40 is derived from a wheat-*Elytrigia intermedium* translocation line. After twice gene mapping, a full-length *TraesCS7B01G164000* encoding an NBS-LRR protein was cloned in the *Pm40* region by analyzing transcriptional data and identifying gene expression differences between the resistant donor and the susceptible line (Luo et al. 2009; Zhong et al. 2016). Co-isolation analysis by SNP of *TraesCS7B01G164000* in L658- and L958-based markers and qRT-PCR analysis both suggested that this gene is a candidate for *Pm40* (Yang et al. 2021).

Cloning and functional analysis of the *Pm* genes

Understanding the molecular nature of the *Pm* genes is a prerequisite for rational application of them to fight powdery mildew. Although more than 100 *Pm* genes/alleles have been documented, only a dozen of them have been cloned so far, and most of the cloned *Pm* genes encoded NBS-LRR proteins, including *Pm1a*, *Pm2*, *Pm3b*, *Pm5e*, *Pm8*, *Pm12*, *Pm17*, *Pm21*, *Pm41*, *Pm60*, and *Pm69*. *Pm4b* and *Pm24* encode kinase-MTC and tandem kinase, respectively, and both *Pm38* and *Pm46* encode transporters conferring a quantitative resistance.

At present, methods for cloning *Pm* genes mainly include map-based cloning, target sequence enrichment sequencing (TEnSeq) including mutagenesis chromosome flow sorting and short-read sequencing (MutChromSeq) and mutagenesis and resistance gene enrichment sequencing (MutRenSeq), homologous-based cloning, core genome targeting sequencing, re-sequencing, and genome-wide association study (GWAS). Most cloned *Pm* genes used the map-based cloning strategy, including *Pm1a*, *Pm2b*, *Pm3*, *Pm5e*, *Pm21*, *Pm24*, *Pm38*, *Pm41*, and *Pm60*. However, the map-based cloning relies on a large segregation population and acceptable mapping interval, often needs extensive efforts, and spends many years. Moreover, common wheat is an allohexaploid species, with a large genome (exceeding 16 Gb) and a large number of repetitive sequences, which increases the difficulty of map-based cloning. In recent years, target sequence enrichment and re-sequencing techniques emerged, which accelerated cloning of wheat *Pm* genes. MutChromSeq was applied to the cloning of *Pm2* and *Pm4b*. MutChromSeq is independent of recombination and based on the purification of individual chromosomes from susceptible mutants, making it convenient, fast, and highly accurate. MutRenSeq is based on the precise capture of NLR-targeted sequences and therefore is only available for NLR resistance genes. *Pm1a* and *Pm21* are identified by MutRenSeq. Homologous cloning is according to the reference genome of related species

to design target gene primers for amplifying the target gene, which have resulted in the isolation of *Pm8* and *Pm17*. In addition, more precise genome sequencing technology, such as long-read Oxford nanopore technology (ONT) and core genome-targeted sequencing (CGT-Seq), combined with bulked segregant RNA sequencing (BSR-Seq) or short-read transcriptome sequencing (RNA-Seq), facilitates cloning of the *Pm* genes, which has been used in isolating *Pm69* and *MlWE18*.

Here, we provide an overview of the *Pm* genes that have been cloned, summarize their discovery, location, cloning, and functional analysis, and highlight the recent advances in the molecular function analysis of these *Pm* genes.

NBS-LRR protein

Plant NBS-LRR receptors are typical plant pathogen-resistant proteins that can recognize the pathogen effectors inducing effector-triggered immunity (ETI). NBS-LRR protein consists of a carboxyl-terminal LRR domain, a central NB domain that binds ATP or ADP, and an amino-terminal Toll, interleukin-1 receptor, resistance protein domain (TIR), or coiled-coil (CC) domain (Dodds and Rathjen 2010). However, in monocot plants, including wheat, the N-terminal domain of NBS-LRR proteins appears to be restricted to the CC domain, but not the TIR domain (Araújo et al. 2019). According to the resistant genes that have been identified in cereal crops at present, 85% of wheat race-specific resistance genes encode NLRs (Sánchez-Martín and Keller 2021). As follows, we will introduce the progress of *Pm* genes that belong to the NLR family and propose the further research direction of NLR protein and its application in resistance breeding.

Pm1

Pm1 is the first officially cataloged *Pm* gene in wheat, and it has been studied since the 1950s, combined with the leaf rust and stem rust resistance genes *Lr20* and *Sr15* (Waterhouse 1952; Watson and Luig 1966). More *Pm1* alleles, including *Pm1a–e*, were identified in *T. aestivum*, *T. monococcum*, and *T. spelta*; and *Pm18* and *Pm22* were also identified as a member of the *Pm1* cluster and identical to *Pm1c* and *Pm1e*, respectively (Hsam et al. 1998; Singrun et al. 2003). For decades, great efforts have been made to finely map and clone the *Pm1* locus (Alam et al. 2011; Worthington et al. 2014; Yao et al. 2007). In 2021, *Pm1a* was successfully cloned using MutRenSeq, and its avirulence gene *AvrPm1* was also isolated simultaneously using the strategy of map-based cloning combined with whole-genome re-sequencing (Hewitt et al. 2021). Stable transformation of *Pm1a* confers a strong resistance in susceptible cv. Fielder and heterologous co-expression of *Pm1a* and *AvrPm1* proved their receptor–effector relation. Interestingly, through phylogenetic analysis and the terminal chromosome arm 7AL rearrangement, *Pm1a* is closer to *D. villosum*-derived *Pm21* at the evolutionary level.

After long-term popularization in production, a dozen of hypothetical *Pm1* alleles were reported, including *Pm1a–1e*, *MlAG12*, *Mlm2033*, *Mlm80*, *PmTb7A.2*, *HSM1*, *MlUM15*, *PmU*, *Pm37*, *Pm59*, *pm9*, and *mlRD30*; however, whether allelic or distinct should be questioned because of the suppressed recombination in this region (Hewitt et al. 2021; Liang et al. 2016; Perugini et al. 2008; Tan et al. 2018). The cloning and identification of *Pm1a* in a highly chromosome-rearranged region provide a new strategy for the isolation of heterologous resistance genes. Moreover, we speculate that it could be possible to explore more *Pm* genes in this region with the ancient resistance cluster.

Pm2

Pm2 was officially named in the 1950s (Briggle 1966; Pugsley and Carter 1953) and then located on the chromosome arm 5DS in the 1970s (McIntosh and Baker 1970). Later, molecular markers linked to *Pm2* were continuously developed and utilized, including the RFLP marker *Xbcd1871*, SSR markers *Xcfd81*, *Xgwm190*, *Xcfd18*, and *Xgwm114*, and the RAPD marker OPP15(900) (Ma et al. 1994; Qiu et al. 2006; Wang et al. 2004). It is also a multi-allelic locus including several alleles, such as *Pm2a–2j*. Through MutChromSeq, *Pm2a* was cloned and encoded a typical NLR protein (Sánchez-Martín et al. 2016). Through further homologous sequence analysis, the *Pm2* alleles in the common wheat were all *Pm2a* haplotype (Chen et al. 2019), but in the *Ae. tauschii*, several new alleles were identified, including *Pm2d–2j* (Manser et al. 2021). Among the new *Pm2* alleles, *Pm2e*, *Pm2f*, *Pm2i*, and *Pm2j* have higher similarity with *Pm2a*, while *Pm2d*, *Pm2g*, and *Pm2h* have considerable variation compared with *Pm2a*. Recently, the function of *Pm2b* was further verified by barley stripe mosaic virus-induced gene silencing, and PM2b could self-associate and interact with the transcription factor TaWRKY76-D, which was proven to regulate wheat powdery mildew resistance negatively (Jin et al. 2022).

Among the documented *Pm* genes, *Pm2* is one of the most widely used *Pm* genes in wheat breeding. Only in our lab, 33 wheat cultivars/breeding lines were identified to carry *Pm2* alleles from 641 wheat genotypes. Unfortunately, these alleles were also confirmed to be the *Pm2a* haplotype, which implies a serious simplification trend of *Pm2* alleles in wheat production. We have reasons to believe the new alleles *Pm2d–2j* could enrich the genetic diversity of this locus and have high breeding value once they were introgressed in wheat background.

Pm3/8/17

Pm3, located on the chromosome arm 1AS, formed the largest allelic series of *Pm* genes, which include about 17 alleles (*Pm3a–g*; *Pm3k–Pm3t*) (Bhullar et al. 2010a; Bourras et al. 2019; Yahiaoui et al. 2006). *Pm3* is the first cloned *Pm* gene, and it also encodes an NBS-LRR protein. According to the sequence conservation of the A genome among the diploid *T. monococcum* (A^mA^m genome), the tetraploid *T. durum* (AABB genome), and the hexaploid wheat, *Pm3b* was the first cloned allele in locus *Pm3* (Yahiaoui et al. 2004). The molecular approaches used for the *Pm3b* candidate gene confirmation contained bacterial artificial chromosome (BAC) libraries-based physical mapping from diploid and tetraploid wheats, genetic mapping in hexaploid wheat, γ-ray mutagenized population sequencing, southern blot analysis, chromosome walking, and 3'RACE-PCR. Functional validation of the candidate gene was also carried out. Infection with a fungal isolate followed by transient co-bombarding into epidermal cells of pUbi:GUS and the wild-type or mutant *Pm3b* concluded that the candidate *Pm3b* confers the *AvrPm3b*-dependent resistance (Yahiaoui et al. 2004).

The successful identification of *Pm3* benefits from the conversion and difference among Triticeae genomes. Although all *Pm3* alleles showed sequence similarity and CC/NBS-domain conservatism, if other *Pm3* alleles are true or encoded by other resistance gene-like sequences closely linked on chromosome 1A is remained to be determined (Bhullar et al. 2010b). It is reported that the combination of different *Pm3* alleles will suppress the *Pm3*-mediated resistance (Stirnweis et al. 2014). Different *Pm3* alleles usually display different polymorphisms in the NBS and/or the LRR domains, thus determining various signaling activities and recognition spectra (Stirnweis et al. 2014). For example, only two polymorphic residues are sufficient to convert susceptible PM3CS to the functional PM3E; similarly, a single residue shared in PM3B and PM3C also plays a decisive role in the powdery mildew resistance (Brunner et al. 2010). A recent study demonstrated the importance of naturally occurring polymorphic residues in the LRR domain to the PM3 function in protein abundance, AVR recognition, and immune response activities (Lindner et al. 2020). In summary, a better understanding of molecular structure and function will support the artificial NLR receptor improvement and molecular breeding in agricultural application like the *Pm3* locus.

Pm8 and *Pm17* are located on chromosome arm 1RS of rye. It has been confirmed that *Pm8* is a homoeologous gene of *Pm3*, and the homoeologous relationship between these two genes has been conformed (Hurni et al. 2013). According to the genetic analysis, *Pm17* also proved to be an allele of *Pm8*, and the similarity between *Pm17* and *Pm8* was as high as 87% (Hsam and Zeller 1997; Singh et al. 2018). Furthermore, the dominant inhibitory effect of *Pm3CS* against the disease resistance of *Pm8* was directly confirmed using the single-cell transient expression determination. The transgenic lines (*Pm3a*, *Pm3f*, and *Pm3b*) were separately crossed with the *Pm8* transgenic lines, confirming that these three *Pm3* alleles also suppressed the resistance of *Pm8* to the avirulent *Bgt* isolates (Hurni et al. 2014).

Based on the homologous relationship with *Pm3*, *Pm8*, and *Pm17* were cloned. The cloning and functional validation of *Pm8* were performed via the *Pm3* gene sequence (Hurni et al. 2013). The PCR marker *aIAG95* facilitates the identification of *Pm17* (Mohler et al. 2001). Functional analyses of southern blot, transient expression technology, and transgene demonstrated that *Pm17* encodes an NLR-type R protein (Singh et al. 2018).

Pm5

Pm5 is located on chromosome arm 7BL. Five alleles (*Pm5a–5e*) were identified (Heun and Fischbeck 1987; Hsam et al. 2001; Lebsock and Briggle 1974). Recently, *Pm5e* was finely mapped to a 0.04-cM region, corresponding to a 13.5-kb genomic region, within which there are three protein-coding genes. DNA sequencing, EMS mutation, and transgene experiments showed that *Pm5e* encodes an NLR resistance protein. The allelic association analysis of *Pm5e* showed that a mutation of Met to Ile in the C-terminal LRR domain conferred its powdery mildew resistance (Xie et al. 2020).

Pm5e was initially genetically identified from the Chinese wheat cultivar Fuzhuang 30 (FZ30), which maintained powdery mildew resistance for over 80 years (Huang et al. 2003). Multiple *Pm5* alleles were found in Chinese wheat landraces; however, the resistance *Pm5e* allele (NLR^A) is rare. It is inferred that natural point mutation in the susceptible NLR^G allele and disease screening pressure is the main reason for the acquisition of disease resistance in *Pm5e*. The mutation of Met to Ile in the *Pm5e* LRR domain represents powdery mildew resistance obtained, and the concomitant change in recognition and interaction with the AVR in *Bgt* is still nebulous. Uncovering the molecular mechanism of *Pm5e*-mediated resistance will contribute to enriching the genetic source of powdery mildew resistance for wheat improvement.

In addition to the multi-allelic *Pm5* (*Pm5a–Pm5e*), several hypothetical *Pm5* alleles were also reported. The *mlxbd* was located between markers *7BLSSR49* and *WGGC5746*, with genetic distances of 0.4 and 0.3 cM, respectively (Jin et al. 2020). The *pmDHT* was located in the region between *Xwmc526/XBE443877* and *Xgwmm611/Xwmc511*, with a genetic distance of 0.8 and 0.3 cM, respectively (Qie et al. 2019). *PmBYYT* was located between SNP markers *W7BL-8* and *W7BL-15*, with genetic distances of 3.0 and 2.9 cM,

respectively. Gene allelic analysis has shown that *pmDHT*, *mlxbd*, *PmBYYT*, and *Pm5e* are alleles or tightly linked (Qie et al. 2019; Xu et al. 2018). Recently, *PmAL11* was mapped in the *Pm5* locus and sequenced to be identical to recessive *Pm5e*, although it was mediated by a dominant inheritance pattern (Han et al. 2023). The relationship between *PmAL11* and *Pm5* needs further determination.

Pm12/Pm21

Pm12 was derived from *Ae. speltoides* and transferred to wheat cv. Wembley, generating highly resistant common wheat Line#31 (Wembley Line#31, WL31). As early as 1991–1992, an RFLP molecular marker for the *Pm12* gene was developed in an F_2 generation segregating population, and it was clarified that the chromosome carrying *Pm12* is a T6BS-6SS·6SL translocation. Meanwhile, there was serious recombination suppression between the alien chromosome segment from *Ae. speltoides* and the corresponding segment of common wheat (Jia et al. 1996). An EST-SSR marker *Xcau127* that co-segregated with *Pm12* was found, and this marker can detect both *Pm12* and *Pm21* in different genomes, which firstly implied the potential homologous relationship between *Pm12* and *Pm21* (Song et al. 2007, 2009).

Pm21, originating from the chromosome arm 6VS of *D. villosum*, is a highly effective resistance gene against almost all the tested *Bgt* isolates (Chen et al. 1995; Zhu et al. 2023). However, it is challenging to isolate *Pm21* due to the recombination inhibition between the chromosome arm 6VS and the homoeologous wheat chromosome arms. In 2018, two groups of scientists simultaneously cloned *Pm21* and confirmed that it encodes an NBS-LRR protein using different strategies (He et al. 2018; Xing et al. 2018). He et al. (2018) used a map-based cloning strategy based on the segregation population between resistant and susceptible *D. villosum* accessions. Xing et al. (2018) used a distinct-different MutRenSeq strategy to clone this gene. In addition, three *D. villosum*-derived *Pm21*(*#4*), *Pm21*(*#4*)-*H*, and *PmV* were also confirmed to be allelic to *Pm21* (Li et al. 2005, 2020d; Zhao et al. 2019). Recently, a resistance *Pm21* haplotype *Pm21*(*8#*) from a new wheat-*H. villosa* translocation T6DL·6 V#8S was cloned and showed dramatic sequence polymorphism, variable transcriptional patterns, and different resistance performance from other *Pm21* alleles. The *Pm* resistance conferred by *Pm21* was challenged by rapid evolution of *Bgt* population in wheat production; diverse resistance mechanism among *Pm21* haplotypes will help increase the utilization of *Pm21* cultivars in breeding process (Huang et al. 2023).

Pm12 was then cloned using deletion mutation and physical positioning, and the homologous relationship between *Pm12* and *Pm21* was finally determined (Zhu et al. 2023). The coding sequence of *Pm12* shares 89.9% identity with that of *Pm21*. It is worth noting that these two orthologous genes differed in their resistance to *Bgt* isolates. We found that different intramolecular interactions may be the reason for the differences in cell death-inducing activity. *Pm12* and *Pm21* are ancient genes with abundant evolutionary dynamics, and transposable elements (TEs) insertion in the second intron of *Pm12/Pm21* orthologs may be the reason for the loss of function in Chinese Spring. The cloning of *Pm12* and *Pm21* provides an excellent promotion for their rational and durable breeding use. Further studies on amino acid variations between *Pm12/Pm21* and their orthologs may reveal the molecular mechanism of effector recognition and the interaction network in the disease resistance mediated by *Pm12/Pm21*.

Pm41

Pm41 was identified on chromosome arm 3BL. It was first mapped in the 2.7-cM region and then finely narrowed to a region of 0.6 cM (Li et al. 2009; Song et al. 2014). A NLR disease resistance gene was then identified as the *Pm41a* candidate by map-based cloning (Li et al. 2020c). Strikingly, haplotype analysis indicated that *Pm41b* and other *Pm41* haplotypes were silent alleles of *pm41a*, probably due to transposon insertions. This result represents an unexplored hidden variation of *Pm* resistance in modern wheat breeding (Li et al. 2020c). Recently, a similar phenomenon was also reported. Sixteen wheat accessions containing *Pm41* were detected among 332 wheat varieties, whereas all are susceptible to *Bgt* isolate at the seedling stage, unlike in IW2 (Cheng et al. 2022). It is implied that natural mutants frequently happened in *Pm41*, and more accurate molecular markers are required to distinguish the resistant and susceptible versions. *Pm41* is the first cloned *Pm* gene from the WEW accession IW2 and confers the all-stage resistance. It is reported that *Pm41* is only limitedly distributed among minority populations but harbors a high resistance to *Bgt* in the hexaploid Fielder and the tetraploid WEW IW2. Consequently, it is expected that *Pm41* could be exploited as a valuable powdery mildew resistance resource and plays a vital role in wheat genetic improvement after introgression into cultivated wheat.

Pm60

Pm60 was isolated recently from *T. urartu*. Molecular markers locked the *Pm60* in a 356-kb region of the *T. urartu* genome; cloning and sequence analysis identified two candidate genes, *PmR1* and *Pm60*, both encoding NBS-LRR proteins. By gene silencing, single-cell transient expression, and stable transformation analysis, *Pm60* was functionally validated. The *Pm60* alleles *Pm60a* and *Pm60b*

were then obtained by homologous cloning in *T. urartu* accessions PI428210 and PI428215, respectively (Zou et al. 2022). *Pm60a* showed sensitivity to *Bgt* isolate E18, whereas *Pm60* and *Pm60b* were resistant. Further analysis showed no inhibition of allelic resistance function among these three alleles. This indicated that the amino acid deletion in *Pm60a* narrowed the resistance spectrum. PI428210 (*Pm60a*) was found to carry other uncharacterized resistance genes through hybridization analysis (Zou et al. 2022). Also, a non-functional allele of *Pm60a* named *Pm60a'* was identified from *T. urartu* accession PI662227, and two molecular markers, *M-Pm60-S1* and *M-Pm60-S2*, were developed to distinguish *Pm60a* from *Pm60a'* (Zhao et al. 2020). Except for *Pm60a*, *Pm60b*, and *Pm60a'*, several other alleles were also described from different wheat genotypes and related species, including *MlWE18*, *PmG16*, *MlIW72*, and *MlIW172* (Ben-David et al. 2010; Ji et al. 2008; Ouyang et al. 2014; Zhao et al. 2020; Zou et al. 2018). The dominant gene *PmU* was also located on chromosome arm 7AL, which was later considered to be *Pm60* (Qiu et al. 2005; Zhang et al. 2018a).

MlWE18 was mapped in the common wheat line 3D249 to a 0.09-cM genetic interval between markers *WGGC4660* and *WGGC4657*, corresponding to a 334-kb physical region. Using RT-PCR, it was found that *resk36_3047604* (NLR^{WE18}) was highly homologous to the protein encoded by *Pm60*. Sequencing and transgenic technology showed that NLR^{WE18} was the allele *MlWE18* (Wu et al. 2021a). A high-density SNP genetic map of the G18-16 × LDN RIL population (147 strains) was conducted to locate *PmG16* in the 1.4-cM genetic interval between markers *uhw386* and *uhw390*, in which the NLR gene *TRIDC7AG077150.1* with high sequence similarity with *Pm60* was found. Marker *M-Pm60-S1* showed separation from *PmG16*, indicating that *TRIDC7AG077150.1* was a candidate gene of *PmG16* and named *TdPm60* (Ben-David et al. 2010; Li et al. 2021b; Zhao et al. 2020). It is found that *MlIW72* and *MlIW172* also contain *TdPm60* alleles (Li et al. 2021b). Using molecular markers associated with *Pm1a*, *Pm60 MlWE18*, *Mlm2033*, as well as polymorphic markers of Mo75, *MlIW172* was mapped to the 0.048-cM interval between markers *M405* and *WGGC4656* (Hewitt et al. 2021; Yao et al. 2007). There were four CGT-Seq markers in IW172, and NLR^{IW172} was expressed after inoculating with E09. The subsequent function validation proved NLR^{IW172} as a new allele of *Pm60* (Wu et al. 2022b).

Pm69

Pm69, derived from WEW, was mapped on chromosome arm 6BL, a complex genomic region with structural variations and suppressed recombination. So, it is difficult to clone it by the conventional positional cloning method. Recently, *Pm69* was cloned and confirmed to encode an NLR protein using a long-read sequencing strategy Oxford Nanopore Technology (ONT) (Li et al. 2022d). High polymorphism was detected in the *Pm69* region among different Triticeae genomes, implying a rapidly evolution event in this NLR cluster. This implied that we could mine more functional *Pm69* alleles with different reaction patterns to the *Bgt* isolates. *Pm69* was a rare NLR only found in individual WEW accessions and hence was expected as an undeveloped and valuable genetic resource for resistance breeding.

Kinase

Pm4 and *Pm24* are the only two cloned *Pm* genes that encode kinases. *Pm4* is located on the chromosome arm 2AL and has several alleles, including *Pm4a*, *Pm4b* (*Mle*), *Pm4c*, *Pm4d*, and *Pm4e* (Hao et al. 2008; Li et al. 2017; Mcintosh and Bennett 1979; Schmolke et al. 2012; Ullah et al. 2018; Wu et al. 2018; Yao et al. 2022). *Pm4b* proved to play a vital role in powdery mildew resistance in many wheat cultivars (Vincent et al. 2017). After confirming the precise physical localization of these alleles, *AET2Gv21296200* was identified as *Pm4b*, which encodes the chimeric kinase-MCTP (multiple C2 domains and transmembrane region protein) (Sánchez-Martín et al. 2021). Firstly, EMS-mutant lines were obtained from the *Fed-Pm4b* wheat lines, and the chromosome 2A carrying *Pm4b* was flow-sorted and sequenced by the MutChromSeq approach. Interestingly, it is proven that only the existence of two spliceosomes, *Pm4b_V1* and *Pm4b_V2*, could confer powdery mildew resistance by the transgenic and VIGS analyses. Furthermore, subcellular localization and in vitro and in vivo interaction analysis demonstrated that *Pm4b_V2* interacts with and recruits *Pm4b_V1* from cytosol to endoplasmic reticulum to form an ER-associated complex. This study revealed a new notion of race-specific powdery mildew resistance conducted by receptor-like cytoplasmic kinases. However, the downstream signal molecules and interacting partners are not clear, and the exposition of how the *Pm4*-ER complex detects and manipulates pathogen effectors will help understand *Pm4*-mediated resistance at the mechanistic level.

Pm24 and its alleles *Pm24b*, *PmDTM*, and *MlHLT* are localized on the chromosome arm 1DS, and they were confirmed as the identical alleles responsible for the resistance to powdery mildew (Huang et al. 2000; Lu et al. 2020a, 2020b; Wang et al. 2015; Xue et al. 2012b). In 2020, *Pm24* from Chinese wheat landrace Hulutou was identified as *TraesCS1D02G058900* according to the IWGSC CS RefSeq, and a 6-bp natural deletion of lysine–glycine is critical for the powdery mildew resistance (Lu et al. 2020b). Another team owned the same result from Datoumai (Lu et al. 2020a). *TraesCS1D02G058900* encoded a receptor-like serine/threonine protein kinase. Receptor-like cytoplasmic kinases usually act as the preliminary defense in pattern

recognition receptor-mediated immunity and have been reported and well described to confer pathogen resistance in *Arabidopsis* (Bi et al. 2018; Liu et al. 2019).

Transporter

Pm38/Yr18/Lr34/Sr57 from bread wheat acts as one of the few genes with durable disease against multiple fungal diseases for over 50 years. To understand the molecular nature of this resistance gene, great efforts have been made for decades.

At first, *Lr34* was localized between the two markers *gwm1220* and *SWM10* on the chromosome arm 7DS and then locked in a 363-kb physical interval (Bossolini et al. 2006; Spielmeyer et al. 2008). Eight open reading frames were identified in this candidate region. Further molecular marker assays, consistent sequence polymorphism in the alleles, and candidate DNA sequencing analysis in loss of function of the *Lr34* mutants limited the candidate to an ABC transporter consisting of 24 exons (Krattinger et al. 2009). *Lr34* sequencing comparison between Chinese Spring (+*Lr34*) and Renan (a French winter cultivar, -*Lr34*) indicated only three polymorphisms, among which two were located in exons containing one deletion of a phenylalanine residue and a tyrosine to a histidine in Chinese Spring (Krattinger et al. 2011). However, both amino acid changes were found only in domesticated bread wheat (*Lr34res*), but not in the wild wheat progenitors and susceptible wheat cultivars (Krattinger et al. 2016). It is presumed that the conservative phenylalanine residue plays a pivotal role in *Pm38*-resistance. A study on barley (*Hordeum vulgare* L.) cultivar Golden Promise showed that a deletion of a single phenylalanine codon in the D genome is sufficient to convert the *lr34*-susceptible allele to a functional *Lr34* resistance gene (Chauhan et al. 2015). These data demonstrated that *Lr34/Pm38* encodes an ABC-type transporter conferring a single origin and durable fungal diseases resistance to which the domesticated phenylalanine residue absence is critical.

To explore the molecular mechanism of *Pm38*, the *Lr34/Pm38* transgenic wheat was generated, and resistance assays confirmed that a minimum transcriptional threshold of *Lr34* was required. This evidence explained the discrepant resistance between adult plants and field-grown seedlings and between hexaploid wheat and durum wheat or barley (Rinaldo et al. 2017). It revealed a transcription mechanism in the *Pm38*-regulated resistance.

In *Lr34*-expressing rice, transcriptomics, physiology, genetics, and in vitro and in vivo transport assays clarified that LR34 transports ABA and alters the ABA-regulated gene expression and biological processes (Krattinger et al. 2019). A similar result showed that the redistribution of plant hormone abscisic acid and a series of phenotypes of increasing ABA signaling, including reduced stomatal conductance or leaf tip necrosis, was shown in *Lr34*-expressing wheat and barley (Braunlich et al. 2021). It is worth noting that *Lr34* was found to interact with other rust resistance genes, including *Lr13*, *Lr37*, and *Lr46*, to maintain durable and effective plant resistance (McCallum and Hiebert 2022); however, the interaction mechanism in *Pm38*-mediated powdery mildew resistance has not been studied.

Pm38, acting as an almost 'all-around' resistance gene in cereal crops, plays a pivotal role in wheat breeding. The molecular essence and action mechanism have been investigated preliminarily; nevertheless, the intracellular interaction network conferring the pathogen resistance needs to be further explored.

Like *Pm38*, *Pm46/Yr46/Lr67/Sr55* also confers multiple pathogen resistance in adult plants. In 2015, *Lr67* was identified as a hexose transporter. At first, a wheat bacterial artificial chromosome (BAC) clone carrying a closely linked (0.4 cM) marker with *Lr67* on chromosome 4DL was isolated in the near-isogenic wheat cultivar Thatcher + *Lr67* line, RL6077. In the BAC clone, two conservative genes were predicted, and then, more markers were designed to distinguish the resistant and susceptible lines. After scoring these markers and sequence analysis in susceptible EMS mutants of RL6007, a predicted sugar transporter (*STP*) was preliminarily identified. Amino acid changes resulting from nucleotide transitions or fragment deletions in *STP* were found in all EMS mutants. In addition, *STP*-transgenic wheat and barley conferred the adult-plant resistance to stripe rust or leaf rust. Conclusively, the sugar transporter gene was identified to confer the *Lr67* multi-pathogen resistance (Moore et al. 2015). Functional analysis of *Lr67* was also carried out. Conservative Gly144 and Val387 residues were mutated to Arg and Leu in *Lr67*-resistant alleles. Using hexose transport deficient yeast mutant, [^{14}C] glucose uptake assay was conducted. Resistant LR67 protein was incapable of glucose import, whereas the replacement of Arg144 with Gly restored the transport activity, but Leu387 could not. Kinetic assay and inhibitor treatment suggested that LR67sus functions as an H^+/hexose symporter. Bimolecular fluorescence complementation (BiFC) assay in LR67 ectopic expressed *Nicotiana benthamiana* indicated that LR67 can form homo- and heterodimers. According to the dimerization-mediated dominant-negative interference on transporter activity in other plant sugar transporter families, it is inferred that LR67res reduced hexose transport by forming inactive heteromultimeric protein complexes. Together, LR67-mediated pathogen resistance has proven to be closely related to hexose transportation; however, more evidence, especially in wheat, is still needed to illuminate the specific mechanism and regulation network of LR67 during plant defense responses.

Pm38 and *Pm46* are both pleiotropic APR genes that confer a broad spectrum of powdery mildew resistance.

However, they are usually difficult to be selected by conventional breeding methods because they are always pyramided with other resistance genes or QTL. Therefore, precision breeding utilizing modern molecular biology may be a better choice; and the in-depth study of the molecular mechanism and interaction network of *Pm38* and *Pm46* will significantly accelerate this process.

Various *Pm* genes that may be effective against single or multiple races of *Bgt* isolates have been characterized. Notably, most of the cloned *Pm* genes encoded NBS-LRR protein that belongs to the typical pathogen resistance factors; and other *Pm* genes are identified as kinase or transporter. Undoubtedly, these resistance genes possess diverse acting mechanisms and form huge molecular interaction networks. Pathogen perception, effector identification, defense signaling, variable splicing, transcription regulation and other resistance response mechanism will further be explored and discovered to expand our knowledge of wheat powdery mildew resistance at the molecular level.

Powdery mildew avirulent genes and the interaction mechanism with resistance genes

Upon the interaction between plants and pathogens, effectors are secreted by pathogens and then recognized by plant NBS-LRR proteins, therefore activating the ETI immune response. Most *Pm* resistance genes identified in wheat encode NBS-LRR immune receptors that conform gene-for-gene hypothesis and correspond to avirulent effectors (encoded by *Avr* gene) in pathogens. Identification of avirulent gene diversity in pathogen populations is a critical factor that may be related to the durable resistance in wheat production. In recent years, many insights about the *AvrPm* genes are obtained using the map-based cloning, GWAS, RNA sequence, BAC sequence, and other technologies. At present, several *AvrPm* genes have been described, including *AvrPm1a*, *AvrPm2*, $AvrPm3^{a2/f2}$, $AvrPm3^{b2/c2}$, $AvrPm3^{d3}$, *AvrPm4, AvrPm8*, and *AvrPm17* (Hewitt et al. 2021; Müller et al. 2022; Praz et al. 2017).

AvrPm1a is identified as *BgtE-5612_THUN12*, and the RNase-like folding was found in the *AvrPm1a* structural modeling. Utilizing transient co-expression assay in the *N. benthamiana* system, specific recognition between *Pm1a* and *AvrPm1a* has confirmed and led to a hypersensitive (HR) response. However, further physiological and biochemical evidence is still needed to analyze the interaction mechanism between *AvrPm1a* and *Pm1a*. *AvrPm2* encoding as *BgtE-5845* belongs to the family of RNase-like effectors, and RNase effectors play an essential role in controlling powdery mildew virulence and pathogen race specificity. *AvrPm2* also shares a structural homology with known RNase-like ribonuclease, which is required for haustorium formation (Pedersen et al. 2012; Pennington et al. 2016; Pliego et al. 2013). Therefore, it was hypothesized that *AvrPm2* could not only interact with *Pm2* to trigger the HR response in hosts and participate in the defense process but also participate in haustorial formation and inhibit the defense response of plant cells. In the study on the specific resistance mechanism of *Pm4*, it is suggested that *AvrPm4* could directly interact with *Pm4* during haustorial formation to elicit a defense response. *AvrPm4* can bind to any *Pm4* variant, and the heterologous complex can result in kinase activation and disease resistance (Sánchez-Martín et al. 2021).

The diversification of *AvrPm3* is inseparable from the diversification of *Pm3* alleles. It can be predicted that *AvrPm3* will continue to evolve to avoid *R* gene recognition (Sela et al. 2014). At present, the research on *AvrPm3* is relatively comprehensive. $AvrPm3^{a2/f2}$ and its alleles $AvrPm3^{b2/c2}$ and $AvrPm3^{d3}$ were described; meanwhile, a specific suppressor gene has been identified in the pathogen. $AvrPm3^{a2/f2}$ corresponding to *Pm3a* and *Pm3f* was cloned, and it could specifically recognize these two alleles (Bourras et al. 2019). Furthermore, it was found that $Bcg\text{-}1^{vir}$ from the pathogen inhibited the resistance mediated by $AvrPm3^{a2/f2}$-$Pm3^{a/f}$. A new model Avr-R-Svr was proposed and confirmed by the addition of the third interaction element 'suppressor of avirulence (Svr)' (Bourras et al. 2015, 2019). $SvrPm^{3a1/f1}$ involved in this model may inhibit the expression of *AvrPm3* or *Pm3*, impede the recognition of *AvrPm3*, and lead to the reduction of the HR phenotype. Another study implied that *Pm3f* is controlled by a single locus *AvrPm3f*, while the *AvrPm3c* has two independent loci, and *AvrPm3c1* is epistatic to *AvrPm3c2* (Parlange et al. 2015). The interaction mechanism of *AvrPm3-Pm3* is complex. It has been shown that $SvrPm^{3a1/f1}$ can not only inhibit $AvrPm3^{a2/f2}$ and reduce the intensity of HR but also have the same effect on $AvrPm3^{b2/c2}$ (Bourras et al. 2019). The interaction between other *Pm3* alleles can also inhibit the interaction of *AvrPm3-Pm3* (Bourras et al. 2015; Stirnweis et al. 2014). *Svr*, an avirulent inhibitor encoded by pathogens, also plays a role in the AVR-R-SVR model. However, many isolates are not suitable for the AVR-R-SVR model, which further indicates the complexity of the molecular mechanism of *Pm3* avirulence genes.

Pm8 and *Pm17* are the homologous versions of *Pm3* in rye. *AvrPm17* is encoded by a gene pair of *BgTH12-04537* and *BgTH12-04538* and functionally validated recently. Co-expression and protein detection showed that *Pm17* could recognize *AvrPm17*_THUN12 and *AvrPm17*_96224. According to the sequence analysis, effector expansion occurred in wheat powdery mildew after the divergence from the barley mildew lineage, and *AvrPm17* is encoded in an expanded gene cluster. It is supposed that effector expansion is coevolution with the host immune system and is important for resistance durability in introgression species.

AvrPm17 mutation occurred earlier than the time when *Pm17* entered wheat, which indicated that ancient variation in the *AvrPm17* limits the effectiveness of rye *Pm17* resistance genes in wheat (Müller et al. 2022). *AvrPm8* was identified by GWAS and functionally validated in *N. benthamiana*. Multiple unique gain-of-virulence mutations of *AvrPm8* were sequenced from a global collection of 219 *Bgt* isolates. According to the statistical analysis between the worldwide distribution of these mutants of *AvrPm8* and the avirulent variant, Kuna et al (2023) inferred that the high prevalence of *Pm8* wheat results in continual gain-of-virulence mutations. On the contrary, *AvrPm3* and *AvrPm17* gain-of-virulence mutations were relatively more conservative and relied on single amino acid polymorphisms meanwhile preserving at least one functional ORF (Bourras et al. 2019; McNally et al. 2018; Muller et al. 2022). Regional breeding programs impact the immune escape ability from *Avr* effector mutant; perhaps, only the ancient genetic variation that occurred before introgression to wheat could allow the more durable resistance like in *AvrPm17*. The ultimate approach to breeding is to continue to track the avirulence gene mutations and then manipulate them by molecular means.

Although many potential avirulence genes are predicted to exist in the powdery mildew fungi, only a few *Avrs* have been cloned or described. Further studies on their composition and function are needed for the remaining undiscovered *Avrs*. The identification and cloning of *Avr* genes can provide new ideas and help understand the molecular mechanism during wheat resistance to powdery mildew. In addition, specific markers for *Avr* genes allow easy determination of their presence and evolution, which contributes to the practical analysis of pathogen avirulence patterns and rational deployment of resistance genes in specific agricultural events. Furthermore, breeders will benefit from the precise selection of specific *Avr* proteins and lower risks for pathogen adaptability. Predictably, breeding strategies that integrate with pathogen molecular biology will make great improvement in powdery mildew resistance breeding and assist agricultural development.

Genomic-assisted breeding for powdery mildew resistance

Conventional breeding has a long history and still plays a key role in modern crop improvement. This approach involves the use of natural germplasm collection, hybridization and integration of complementary genetic sources, and extensive screening of excellent traits in the different generations. Using conventional breeding approaches, many elite cultivars have been produced, bringing a significant promotion in wheat production. However, conventional breeding requires multiple generations of screening and is easily affected by complex environmental and climatic conditions; hence, it is time-consuming, labor-intensive, and inefficient.

Molecular breeding provides means and possibilities for accelerating the conventional breeding process. Understanding the performance of parents, especially the main genes, can predict the performance of hybrid combinations, providing the possibility for purposeful variety cultivation. With the help of molecular breeding technology, the breeding process should be more effective and reasonable.

Molecular markers are complementary tools to conventional breeding since they are easy to assay, highly heritable, more accurate, cheaper, faster, and not affected by environments. Marker-assisted selection (MAS) transfers phenotype screening in the breeding process to the molecular detection. In recent years, 'speed breeding' combined with the molecular selection tools has been used to transfer and pyramid *R* genes into elite susceptible cultivars, which greatly shortens breeding cycle. By extending the photopericycle, common wheat and durum wheat could breed six generations per year. Speed breeding accelerates the growth and development of normal plants without affecting the excellent phenotype (Watson et al. 2018). Recently, a new comprehensive speed breeding for long-day crops was also proposed (Song et al. 2022). Furthermore, integration of precise MAS tools, high-throughput genotyping, and speeding breeding may efficiently accelerate the breeding use of *Pm* genes, increase the wheat genetic variation, and help fight with powdery mildew (Fig. 3).

Development and utilization of breeding markers for *Pm* genes

Due to the continuous variation of virulent *Bgt* isolates and the high barrier in introducing resistant cultivars, the current situation of high-quality wheat cultivars with high yield and *Pm* resistance is worrying. Therefore, the introduction of diversified *Pm* genes and the enhancement of germplasm innovation are urgent and practical approaches for the high-yield and multi-resistance breeding of wheat (Fig. 4).

Molecular markers have been widely used to detect *Pm* genes. For example, 659 resistant accessions to *Bgt* isolate E09 were screened from 2978 wheat accessions, and specific molecular markers closely linked to *Pm2*, *Pm4*, *Pm5*, *Pm6*, *Pm8*, *Pm21*, and *Pm24* were used to test the 659 resistant accessions, 328 resistance accessions may carry single *Pm* gene and 191 accessions carry combined *Pm* genes consequently (Jin et al. 2021). Similarly, six accessions carrying *Pm3*, 18 accessions carrying *Pm8*, five accessions carrying *Pm16*, and three accessions carrying *Pm21* were identified in the germplasms from Yunnan Province, China (Wu et al. 2021b). In summary, molecular markers screening reveals resistance information of local wheat cultivars and provides

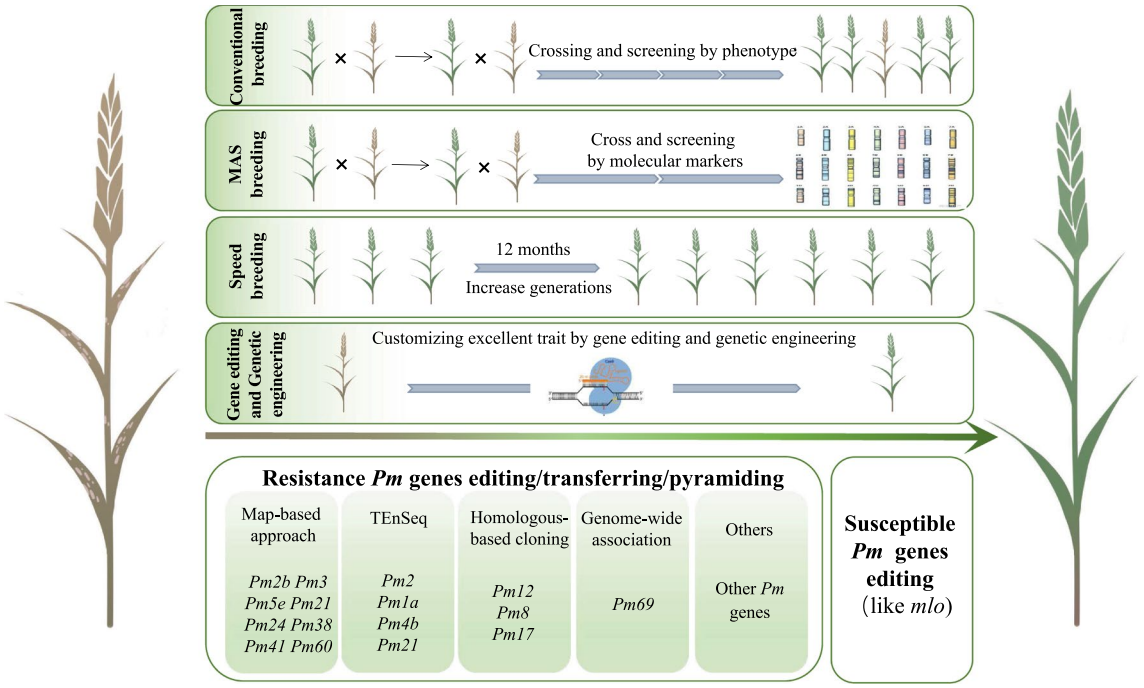

Fig. 3 Comparison of four breeding strategies and utilization of *Pm* genes in modern breeding approach. Four breeding strategies including conventional breeding, MAS breeding, speed breeding, and gene editing and genetic engineering are displayed above the arrow. The bottom represents modern breeding methods based on powdery mildew- resistant and susceptible genes

a favorable reference for the rational planting of different resistant cultivars in the production process (Table 1).

In addition, MAS technology can help transfer or pyramid different *Pm* genes for developing broad-spectrum germplasms, which has been the mainstream direction of breeding in recent years. For example, KASP markers that can simultaneously diagnose *Pm12*, *PmV*, and *Pm21* are developed, which help pyramid these genes to other genotypes (Zhang et al. 2021c). Based on SLAF-Seq, 404 PCR and 14 KASP rye-specific markers on a large scale were developed, of which two KASP markers, *SWK5282* and *SWK252224*, were successfully applied in rye molecular breeding, which will help the detection and transfer of rye chromosomes 1RS and 2RL in the wheat background (Han et al. 2020a). Four new varieties with elite agronomic traits are developed using molecular markers linked to *Pm40* (Tang et al. 2018). Using MAS and phenotypic identification, *Pm2b* was introduced into three elite susceptible cultivars, and *Pm2b* near-isogenic lines (NLRs) with improved agronomic performance were developed (Xu et al. 2017). The combination of MAS technology and genetic engineering will make the breeding process more efficient and predictable, and there will be important breakthroughs in molecular mark-assisted breeding.

As a simple and low-cost technique, molecular markers also play an essential role in the molecular identification of distant hybridization materials between wheat and its relatives. Wheat-rye T1RS·1BL translation line harbors many disease resistance genes, including *Pm8*, *Yr9*, *Lr26*, and *Sr31*. Although *Pm8* and *Lr26* have lost its resistance due to the pathogen evolution, T1RS·1BL is still widely used in wheat breeding because of its yield potential and extensive environmental adaptability. By molecular markers analysis of rye chromosome arm 1RS, R2207 was confirmed as a cytogenetically stable T1RS·1BL translocation line with highly resistant to stripe rust and powdery mildew with superior agronomic traits (Han et al. 2020b).

At present, molecular markers have made large contribution in the wheat powdery mildew breeding process; however, it is still an urgent task to develop more efficient molecular markers for *Pm* resistance screening. In the breeding process, it is also necessary to select high-quality genes for pyramiding according to the immunization periods and tissues for different genes. In future, the combination of MAS technology with transgenic and gene editing technologies will significantly improve the accuracy and effective utilization of *Pm* resistance and other key agronomic traits.

Gene editing and intelligent breeding

With the innovation of molecular sequencing and cloning technologies, more and more *Pm* genes will be revealed. However, there is still a massive gap between gene cloning and the actual production application. The integration

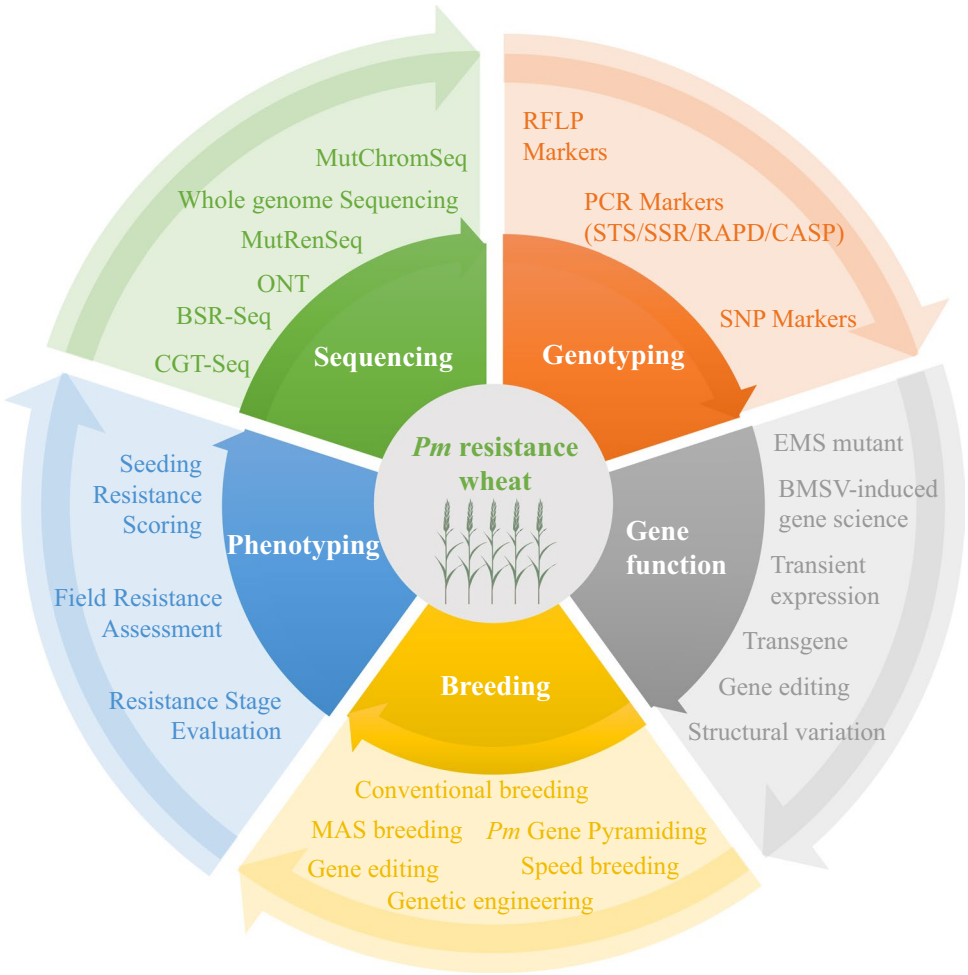

Fig. 4 Turnaround of wheat powdery mildew resistance research. The main aspects of wheat powdery mildew resistance research include phenotyping, sequencing, genotyping, gene function, and breeding. These aspects complement and depend on each other

and introgression of resistance genes from wild relatives to wheat landraces and local cultivars have attracted widespread attention. Genetic engineering is available only for the cloned *Pm* genes; introgressive hybridization is an alternative method, but the rearrangement of wheat genetic material, distance incompatibility, and undesirable agricultural traits are always accompanied and resulting in a low efficiency.

Increasing studies demonstrated that structural variation, including alternative splicing, fragment deletion or insertion, and resistance-determined SNP play vital roles in resistance gene-mediated defense reactions (Andersen et al. 2020; Jin et al. 2022; Lu et al. 2020b). CRISPR/Cas9, a powerful gene editing tool, makes it possible to artificially modify the molecular structure in susceptible alleles to a resistant version. CRISPR/Cas9 has been used to edit multiple genes in wheat to alter morphogenesis, create male sterile mutant, analyze the gene function, and improve *Pm* resistance (Hyde et al. 2023; Li et al. 2020b; Liu et al. 2020; Zhang et al. 2017). A notable breakthrough has been reported that the targeted deletion of susceptible *Pm* gene *Mlo* by Crispr generates broad resistance to powdery mildew without yield penalty (Li et al. 2022c). However, the bottleneck imposed by tissue culture and regeneration restricts the promotion of wheat genetic transformation. Recently, a *Barley stripe mosaic virus*-based sgRNA (BSMV-sg) delivery system was developed and helps achieve culture-free and heritable genome editing in wheat plants (Chen et al. 2022; Li et al. 2021a). Consequently, basic researches on *Pm* genes structural variation combined with powerful genome editing tools may provide new and more intelligent breeding strategies to promote broad-spectrum powdery mildew resistance.

Perspective

Mining *Pm* resistance genes is the foundation for exploring host resistance. However, the process is long, complex, and full of uncertainty. For instance, wheat cultivars harboring *Pm2* are widely used in wheat production worldwide. We identified 33 wheat cultivars/breeding lines carrying *Pm2* alleles. These alleles were all confirmed to be *Pm2a* haplotype by sequencing although these genotypes showed different reaction patterns to different *Bgt* isolates. It is supposed

Table 1 List of officially named *Pm* genes in wheat resource bank

Location	Gene/allele	Source	Markers	Type	References
1A	*Pm25*	*T. monococcum*	*OPX06*$_{1050}$, *OPAG4*$_{950}$, *OPAI14*$_{600}$	RAPD	(Shi et al. 1998)
1AS	*Pm3* and alleles	*T. aestivum*	*294D11-31*, *294D11-22*	RFLP	(Yahiaoui et al. 2004)
1B	*Pm28*	*T. aestivum*			(Peusha et al. 2000)
1BL	*Pm39*	*T. aestivum*	*Ucw.k34*, *Ucw.k18*	SSR	(Cobo et al. 2019)
1D	*Pm10*	*T. aestivum*			(Tosa et al. 1987)
1DS	*Pm24*	*T. aestivum*	*WGGB241*, *WGGB244*	STS, SNP	(Lu et al. 2020b)
T1RS·1BL	*Pm8*	*S. cereale*			(Hurni et al. 2013)
T1RS·1AL	*Pm17*	*S. cereale*			(Singh et al. 2018)
T1BL·1SS	*Pm32*	*Ae. speltoides*			(Hsam et al. 2003)
T1DL·1 V#5S	*Pm67*	*D. villosum*	*1 V-253*	STS	(Zhang et al. 2021b)
2AL	*Pm4a*	*T. dicoccum*	*Xgwm356*	SSR	(Ma et al. 2004)
2AL	*Pm4b*	*T. carthlicum*	*Xics13*, *Xics43*	SNP	(Wu et al. 2018)
2AL	*Pm4c* (*Pm23*)	*T. aestivum*	*Xbarc122*, *Xgwm356*	SSR	(Hao et al. 2008)
2AL	*Pm4e*	*T. aestivum*	*Xwgrc763*, *Xwgrc865*	SSR	(Ullah et al. 2018)
2AL	*Pm50*	*T. dicoccum*	*Xgwm294*	SSR	(Mohler et al. 2013)
2AL	*Pm65*	*T. aestivum*	*Xstars355*, *Xstars356*	SSR	(Li et al. 2019)
2BL	*Pm6*	*T. timopheevi*	*CIT02g-20*, *CIT02g-18*		(Wan et al. 2020)
2BL	*Pm33*	*T. carthlicum*	*Xwmc317*, *Xgwm526*	SSR	(Zhu et al. 2005)
2BL	*Pm51*	*Th. ponticum*	*Xwmc332*, *BQ246670*	SSR, EST	(Zhan et al. 2014)
2BL	*Pm52*	*T. aestivum*	*Xicsl795*, *Xicsl326*	SSR	(Wu et al. 2019)
2BL	*Pm63*	*T. aestivum*	*Xbcd135-2*, *Xstars419*	STS, SSR	(Tan et al. 2019)
2BL	*Pm64*	*T. dicoccoides*	*WGGBH1364*, *WGGBH612*	STS, SSR	(Zhang et al. 2019)
2BS	*pm26*	*T. dicoccoides*	*WGGC1323*, *WGGC9140*	SSR, SNP	(Liang et al. 2015)
2BS	*pm42*	*T. dicoccoides*	*Xgwm148*, *BF146221*	SSR, EST-STS	(Hua et al. 2009)
2BS	*Pm49 (Ml5323)*	*T. dicoccum*	*Xcau516*, *CA695634*	STS, EST-SSR	(Piarulli et al. 2012)
2BS	*Pm68*	*T. durum*	*Xdw04*, *Xdw12 /Xdw13*	SNP, InDel	(He et al. 2021b)
2DL	*Pm43*	*Th. intermedium*	*Xwmc41*, *Xbarc11*	SSR	(He et al. 2009)
2DS	*Pm58*	*Ae. tauschii*	*Xsts20220*, *Xkasp61553*	KASP, STS	(Xue et al. 2022)
T2BS·2BL-2S^{S}#1L	*Pm57*	*Ae. searsii*	*X67593*, *X62492*	SSR	(Dong et al. 2020)
T2BS·2 V#5L	*Pm62*	*D. villosum*	*XCINAU1025*	STS	(Zhang et al. 2018b)
3AS	*Pm44*	*T. aestivum*			(Alam et al. 2011)
3BL	*Pm41*	*T. dicoccoides*	*M171*, *M160*	SNP	(Li et al. 2020c)
T3S^{1}S-3DS·3DL	*Pm13*	*Ae. longissima*	*BE398268*, *wmc674*	SSR	(Zhang et al. 2014)
4AL	*Pm61*	*T. aestivum*	*Xicsx79*, *Xgwm160*	SNP, SSR	(Hu et al. 2019)
T4BS·4BL-5RL	*Pm7*	*S. cereale L*			(Heun and Friebe 1990)
T4S^{1}S·4BL	*Pm66*	*Ae. longissima*			(Li et al. 2020a)
5BL	*Pm36*	*T. dicoccoides*	*IWB7454*, *IWB22904*	SNP	(Nigro et al. 2022)
5BL	*Pm53*	*Ae. speltoides*	*IWA6024*, *IWA2454*	SNP	(Petersen et al. 2015)
4A·5BS	*Pm16*	*T. dicoccoides*	*Xgwm159*	SSR	(Chen et al. 2005)
5BS	*Pm30*	*T. dicoccoides*	*Xgwm159*	SSR	(Liu et al. 2002)
5DL	*Pm34*	*Ae. tauschii*	*Xbarc177*, *Xbarc144*	SSR	(Miranda et al. 2006)
5DL	*Pm35*	*Ae. tauschii*	*Xcfd26*	SSR	(Miranda et al. 2007)
T5V#4S·5DL	*Pm55*	*D. villosum*	*5EST237*	STS	(Zhang et al. 2016)
5DS	*Pm2* and alleles	*T. aestivum*	*Xcfd81*, *Xcfd78*, *SCAR112*, *SCAR203*	SSR, SCAR	(Sanchez-Martin et al. 2016)
5DS	*Pm48*	*T. aestivum*	*Xmp510*, *Xmp1112*	SSR	(Fu et al. 2017)
6BL	*Pm54*	*T. aestivum*	*Xbarc134*	SSR	(Hao et al. 2015)
6BL	*Pm69*	*T. dicoccoides*	*uhw367*, *uhwk389*		(Li et al. 2022d)
6BS	*Pm11*	*T. aestivum*			(Tosa et al. 1988)

Table 1 (continued)

Location	Gene/allele	Source	Markers	Type	References
6BS	*Pm14*	*T. aestivum*			(Tosa and Sakai 1990)
6DS	*Pm45*	*T. aestivum*	*Xmag6140, Xcfd80*	EST-STS	(Ma et al. 2011)
T6AL·6RS	*Pm56*	*S. cereale*			(Hao et al. 2018)
T6BS-6SS·6SL	*Pm12*	*Ae. speltoides*	6SS-04		(Zhu et al. 2023)
T6BS·6RL	*Pm20*	*S. cereal*			(Friebe et al. 1994)
T6AL·6 V#4S	*Pm21* = *Pm31*	*D. villosum*	*CINAU1692* / *CINAU1716*	SNP	(Xing et al. 2018)
T6B·6G	*Pm27*	*T. timopheevi*	*Xpsp964* / *Xpsr8* (6BS), *Xpsr154* / *Xpsr546* (6BL)	RFLP	(Järve et al. 2000)
7AL	*Pm1a*	*T. aestivum*	*Pm1aSTS1*	STS	(Hewitt et al. 2021)
7AL	*Pm1c* = *Pm18*	*T. aestivum*	*xWhs178*, *18M2*	RFLP / AFLP	(Hartl et al. 1999)
7AL	*Pm1e* = *Pm22*	*T. aestivum*	*Xgem344*, *XS13M26-372*	SSR/AFLP	(Singrun et al. 2003)
7AL	*Pm9*	*T. aestivum*			(Schneider et al. 1991)
7AL	*Pm37*	*T. timopheevi*	*Xgwm332*, *Xwmc790*	SSR	(Perugini et al. 2008)
7AL	*Pm59*	*T. aestivum*	*Xmag1714*, *Xmag1759*	STS	(Tan et al. 2018)
7AL	*Pm60*	*T. urartu*	*scaf12-6.30*, *scaf14-6.30*	dCAPS	(Zou et al. 2018)
7BL	*Pm5a, b, d, e*	*T. dicoccoides*	*Xgwm1267*, *UBC405-628*, *WGGC6892*, *WGGC11541*	SSR SNP	(Huang et al. 2003; Xie et al. 2020)
7BL	*Pm5c*	*T. sphaerococcum*			(Hsam et al. 2001)
7BS	*Pm40*	*Th. intermedium*	*Xwmc335*, *BF291338*	SSR/EST-STS	(Zhong et al. 2016)
7BS	*Pm47*	*T. aestivum*	*Xgwm46*, *BE606897*	SSR / EST-STS	(Xiao et al. 2013)
7D	*Pm19*	*Ae. tauschii*			(Lutz et al. 1995)
7DL	*Pm29*	*T. aestivum*	*S24M26-261*, *S23M16-246*	AFLP	(Zeller et al. 2002)
7DS	*Pm15*	*T. aestivum*			(Tosa and Sakai 1990)
7DS	*Pm38*	*T. aestivum*	*csLVMS1*, *BF473324*	SSR/EST	(Spielmeyer et al. 2008)

that the various resistance phenotypes in these wheat cultivars are influenced by different genetic backgrounds. Another possibility is that *Pm2* does not function alone in these wheat cultivars/breeding lines. There may exist other factors or enhancers closely linked with *Pm2*, which form a genetic unit to function together with *Pm2*. In addition, the heterozygous or mixed population of isolates may increase diversity of *Avr* genes and uncertainty in the phenotype identification. Therefore, further and deep evidence are needed to clarify the genetic and/or molecular mechanisms of *Pm2*-mediated resistance.

The ideal *Pm* resistance is a broad-spectrum and durable resistance in the whole growth period, but most of the *Pm* genes only show partial resistance. Pyramiding multiple *Pm* genes into a same genetic background may be the best option for achieving ideal *Pm* resistance. However, not all *Pm* genes are suitable for pyramiding. For example, the combination of *Pm3* and *Pm8* does not have a good breeding effect. Moreover, two quality resistance genes with high resistance may over allocate photosynthetic energy, leading to a decrease in yield. Therefore, a better choice is to pyramid different types of *Pm* genes, such as a major gene and an adult resistance gene or a QTL, which may bring better resistance without losing excellent agronomic traits. Furthermore, the combination of different germplasms with tissue-differentiated resistance may provide new ideas for resistance breeding. For example, *Pm67* showed seedling and sheaths, stems, and spikes at the adult-plant stage immunity, but a low level of susceptibility on adult-plant leaves. In contrast, *Pm55* conferred a near immunity response on leaves after 5-leaf stage but susceptibility on sheaths and spikes. The F_1 hybrid plants between *Pm55* and *Pm67* harboring lines exhibited complete immune across all tissues (Zhang et al. 2021b). Therefore, pyramiding these two genes may conduct a different resistance mechanism and could become the novel and potential valuable germplasms for adult-plant powdery mildew resistance.

Pm genes from wild relatives usually confer a high-level resistance. However, linkage drags are usually difficult to overcome, which impede the effective and rapid utilization of most alien *Pm* genes in breeding. To make use of these *Pm* genes in the actual breeding process, the best way is to clone them and directly transfer these genes to wheat background using transgenic technology. Alternatively, some strategies, such as creating smaller translocation fragment, multigenerational backcrossing, mutagenesis treatment, or cutting the linkage drags by gene editing, could also accelerate their application in breeding.

Author contribution statement PM conceived the review. BW, TM, and BX drafted the manuscript. BX and TY drafted the figures. TY and YJ revised the manuscript.

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Declarations

Conflict of interest There are no conflicts of interest to declare.

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