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Qualitative and quantitative resistance against powdery mildew in wheat

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Abstract. Bread and durum wheats are among the most important cultivated crop plants worldwide. Powdery mildew caused by *Blumeria graminis* f. sp. *tritici* is one of the most destructive foliar diseases of wheat, affecting yield and end-use quality, especially in areas with a cool or maritime climate. Breeding for resistance using diversified disease resistance genes is the most promising approach to prevent outbreaks of powdery mildew. To date, more than 60 genes/alleles have been identified and mapped on the wheat chromosomes, and many of these genes have been extensively used in breeding. Very few have been cloned, but most of them have been tagged with molecular markers, especially microsatellites, useful for marker-assisted selection, allowing selection for resistance in the absence of the pathogen. The details about most of the resistance genes mapped on the wheat genome, the source of resistance and molecular markers tightly associated to them have been reviewed.

Keywords. Wheat – Resistance to powdery mildew – Pm genes – Marker-assisted selection.

Résistance qualitative et quantitative contre l'oïdium du blé

Résumé. *Les blés tendre et dur sont parmi les principales espèces végétales cultivées dans le monde entier. L'oïdium causé par Blumeria graminis f. sp. tritici est l'une des maladies foliaires du blé les plus destructrices, affectant le rendement et la qualité d'utilisation finale, notamment dans les régions à climat froid ou océanique. La sélection pour la résistance utilisant différents gènes de résistance aux maladies est l'approche la plus prometteuse pour prévenir l'apparition de l'oïdium. À ce jour, plus de 60 gènes/allèles ont été identifiés et cartographiés sur les chromosomes du blé, et beaucoup d'entre eux ont été largement utilisés dans la sélection. Un petit nombre de ces gènes ont été clonés, mais la plupart d'entre eux ont été marqués avec des marqueurs moléculaires, en particulier des microsatellites, utiles pour la sélection assistée par marqueurs, permettant la sélection pour la résistance en l'absence de l'agent pathogène. Dans ce travail, nous allons focaliser l'attention sur la plupart des gènes de résistance cartographiés sur le génome du blé, la source de résistance et les marqueurs moléculaires qui leur sont étroitement liés.*

Mots-clés. *Blé – Résistance à l'oïdium – Gènes Pm – Sélection assistée par marqueurs.*

I – Introduction

Bread and durum wheat are among the most important cultivated crops worldwide in terms of cultivated area and food source. Powdery mildew of wheat, caused by the biotrophic pathogen *Blumeria graminis* f.sp *tritici*, is one of the most devastating foliar diseases in temperate climates and usually leads to yield losses ranging from 5 to 34% and affects end-use quality (Conner *et al*., 2003). The disease is favoured by intensive cultivation methods associated with modern agriculture such as the use of semi-dwarf and high-yielding cultivars in combination with high levels of nitrogen fertilization. Growing resistant cultivars is the most economical and environmentally sound method to decrease the use of fungicides and to reduce crop losses due to this disease. This approach, however, requires comprehensive exploration of potential genetic resources and an in-depth understanding of their resistance mechanisms.

II – Scientific evidence

Two types of powdery mildew resistance exist in wheat: qualitatively and quantitatively inherited resistances. Qualitative resistance, also called “monogenic” or “vertical” or “race-specific”, is controlled by major race-specific genes that are generally effective only against some isolates of powdery mildew, providing a complete protection of the crop. The resistance (R) gene-mediated resistance belongs to the category of “gene-for-gene” interaction (Bennett *et a*l., 1984; Hsam and Zeller, 2002). Unfortunately, qualitative resistance is usually of short durability due to frequent changes in the pathogen population (Hsam and Zeller, 2002). Consequently, new resistance genes are continuously needed to replace the defeated ones. To date, more than 60 powdery mildew resistance genes/alleles have been reported in common and durum wheat (Alam *et al*., 2011) and some of these genes have been cloned, supported by the genome sequence information of wheat species with lower ploidy levels. In particular, *Pm3b* from hexaploid wheat is a member of the coiled-coil nucleotide binding site leucine-rich repeat (NBS-LRR) class of disease resistance genes (Yahiaoui *et al*., 2004). A putative serine/threonine protein kinase gene (*Stpk-V*) was also characterized conferring the durable resistance in the *Pm21* locus, located on the chromosome 6V of *Dasypyrum villosum* [syn. *Haynaldia villosa*] and transferred to wheat as a 6VS·6AL translocation (Cao *et al*., 2011).

The second type of powdery mildew resistance is represented by adult plant resistance (APR), also called “slow-mildewing” or “partial resistance” (Alam *et al*., 2011). It can be identified in cultivars with defeated race-specific genes or lacking known resistance genes and allows the plants to be infected with the pathogen, but significantly retards the development of disease in adult plants (Hautea *et al*., 1987). Even if it has been shown to be more durable, the quantitative nature of partial resistance to powdery mildew makes it more complicated to handle in a breeding program compared to race-specific resistance. Examples with good levels of partial resistance include the winter wheat cultivar Knox (Shaner, 1973) and the derived cultivar Massey (Liu *et al*., 2001), which have provided effective resistance against powdery mildew in the southeastern United States for half a century. Breeding for resistance has been greatly enhanced by the use of molecular markers. Many reports about high-density linkage maps used to map *Pm* genes and quantitative trait loci (QTL) governing this trait are available in literature (i.e Zhang *et al*., 2008; Lan *et al*., 2010; Muranty *et al*., 2010). Very often the partial resistance is controlled by a number of genes, but this is not always the case. An example of monogenic partial resistance is the gene *Mlo*. Homologs of barley gene *Mlo* were found in syntenic positions in the three genomes of hexaploid wheat (Elliot *et a*l., 2002; Salmeron *et al*., 2000; Niu and He, 2009; Konishi *et al*., 2010). The gene *Mlo*, isolated by positional cloning, consists of an integral membrane protein with seven transmembrane helices and two casein kinase II motifs (Büschges *et al*., 1997). Chromosomal positions of the main mapped powdery mildew resistance loci are reported in Table 1. The powdery mildew resistance genes are not equally distributed in the genome, but often form clusters of genes. Particularly reach of genes of resistance to powdery mildew are the chromosomes 7A and 2B (Table 1). The D genome seems to be the one with the lowest number of mapped genes, except for the chromosome 5D. As reported in Table 1, some genes were transferred from wild relatives, such as *T. turgidum* var. *dicoccoides* and var. *dicoccum*, *T. timopheevii*, *T. monococcum*, *T. tauschii*, *Ae. speltoides*, or from more distant species, like *Secale cereale*. It is well established that the genetic diversity of crop plants has been eroded with respect to their wild relatives as a result of the genetic bottleneck associated with the domestication process and subsequent modern breeding processes (Ladizinsky, 1998). This genetic erosion had far-reaching agronomic consequences limiting our ability to protect crop plants from biotic and abiotic stress factors and to meet future global challenges (e.g., Harlan, 1972; Zamir, 2001). Using crosses between domesticated and wild species of inbreeding plants, alleles that were “left behind” during domestication may be reintroduced into the domesticated gene-pool. Nevertheless, other genes have been identified in *T. aestivum*, and this permits to hypothesize that cultivated wheats can be even explored to identified new alleles.

Table 1. Chromosomal location, source and reference of the most mapped *Pm* genes.

Gene	Chromosome	Source	Reference
Pm3g	1A	*T.aestivum*	Bougot *et al*., 2002
Pm3e	1A	*T. aestivum*	Mohler *et al*., 2011
Mlar	1A	*T. aestivum*	Sourdille *et al*., 1999
Pm3a	1A	*NA*	Chen *et al*., 2009
Pm24	1DS	*T. aestivum*	Huang *et al*., 2000
Pm24b	1DS	*T. aestivum*	Xue *et al*., 2012
Pm4d	2A	*T. monococcum*	Schmolke *et al*., 2012
Pm23 (Pm4c)	2AL	*T. aestivum*	Hao *et al*., 2008
Pm4b	2AL	*T. dicoccum*	Mingeot *et al*., 2002
PmHNK54	2AL	*Secale cereale*	Xu *et al*., 2011
MlIW70	2B	*T. dicoccoides*	Liu *et al*., 2011
MlZec1	2BL	*T. dicoccoides*	Mohler *et al*., 2005
PmJM22	2BL	*T. aestivum*	Yin *et al*., 2009
PmPS5B (Pm33)	2BL	*T. carthlicum*	Zhu *et al*., 2005
Pm6	2BL	*T. carthlicum*	Zhu *et al*., 2005
MlAB10	2BL	*T. dicoccoides*	Maxwell *et al*., 2010
Pm42	2BS	*T. dicoccoides*	Hua *et al*., 2009
Ml5323	2BS	*T. dicoccum*	Piarulli *et al*., 2012
Pm43	2DL	*Th. intermedium*	He *et al*., 2009
Pm41	3BL	*T. dicoccoides*	Li *et al*., 2009
Pm2026	5A	*T. monococcum*	Xu *et al*., 2008
Pm36	5BL	*T. dicoccoides*	Blanco *et al*., 2008
Ml3D232	5BL	*T. dicoccoides*	Zhang *et al*., 2010
Pm16	5BS	*T. dicoccoides*	Chen et al., 2005
PmD57-5D	5D	*T. aestivum*	Ma *et al*., 2011
Pm46	5DS	*T. aestivum*	Gao *et al*., 2012
Pm34	5DL	*Ae. Tauschii*	Miranda *et al*., 2006
Pm35	5DL	*Ae. Tauschii*	Miranda *et al*., 2007
PmY201	5DL	*Aegilops tauschii*	Sun *et al*., 2006
PmY212	5DL	*Aegilops tauschii*	Sun *et al*., 2006
MlRE	6AL	*T. dicoccum*	Chantret *et al*., 2000
Pm12	6B	*Ae. spelotides*	Song *et al*., 2007
Pm27	6B	*T. timopheevii*	Jarve *et al*., 2000
PmG3M	6B	*T. dicoccoides*	Xie *et al*., 2011
PmD57 (Pm45)	6DS	*T. aestivum*	Ma *et al*., 2011
MlAG12	7A	*T. timopheevii*	Maxwell *et al*., 2009
Pm37	7A	*T. timopheevii*	Perugini *et al*., 2008
PmNCAG11	7A	*T. timopheevii*	Srnic´ *et al*., 2005
PmNCA4	7A	*T.monococcum*	Srnic´ *et al*., 2005
Mlm80	7A	*T. monococcum*	Yao *et al*., 2007
Mlm2033	7A	*T. monococcum*	Yao *et al*., 2007
PmG16	7AL	*T. dicoccoides*	Ben-David *et al*., 2010
MlIW72	7AL	*T. dicoccoides*	Ji *et al*., 2008
NCA6Pm	7AL	*T. monococcum*	Miranda *et al*., 2007
Pm1a	7AL	*T. aestivum*	Neu *et al*., 2002
PmU	7AL	*T. urartu*	Qiu *et al*., 2005
Pm22(Pm1e)	7AL	*T. aestivum*	Singrun *et al*., 2003
MlRD30	7AL	*T. aestivum*	Singrun *et al*., 2004
PmTm4	7BL	*Secale cereale* L.	Hu *et al*., 2008
Pm5e	7BL	*T. aestivum*	Huang *et al*., 2003
Pm5d	7BL	*T. aestivum*	Nematollahi *et al*., 2008
mlxbd	7BL	*T. aestivum*	Xue *et al*., 2009
Pm40	7BS	*Elytrigia intermedium*	Luo *et al*., 2009
Lr34/Yr18/Pm	7D	*T.aestivum*	Spielmeyer *et al*., 2005

NA: Not Available.

Molecular markers have been largely used for mapping to specific chromosomes or chromosome regions a number of these genes (Zhang *et al*., 2010). Currently, SSRs are the markers of choice for mapping in wheat and numerous microsatellites have been found to be associated to *Pm* resistance genes, such as *Ml3D232* on chromosome 5BL that is flanked by *Xgwm415* and *Xwmc75* (Zhang *et al*., 2010) or *Pm37* on chromosome 7AL for which two markers *Xgwm332* and *Xwmc790* have been found tightly linked to the gene (Perugini *et al*., 2008). Molecular markers have also been used to map quantitative trait loci (QTL) for partial resistance to powdery mildew in several wheat cultivars, including the Swiss winter wheat Forno (Keller *et al*., 1999), the French winter wheats RE714 (Chantret *et* al., 2000, 2001; Mingeot *et al*., 2002) and RE9001 (Bougot *et al*., 2006), the North American winter wheats Massey (Liu *et al*., 2001) and USG3209 (Tucker *et al*., 2007) and the Japanese cultivar Fukuho-komugi (Liang *et al*., 2006).

Molecular markers tightly associated to resistance QTL/genes have a great potential for utility in plant improvement and for breeders to adopt marker-assisted selection (MAS). As an example, in publicly financed wheat breeding programs in the USA, Australia and Canada, about 50 genes are used in MAS for resistance to the main wheat diseases, which include powdery mildew, rusts, cereal cyst nematode, and viruses, and similar numbers of resistance genes are available in barley (Marone *et al*., 2013). In particular on the MAS wheat website (ttp://maswheat.ucdavis.edu) in which MAS protocols to incorporate valuable genes for many traits of interest into the best wheat breeding lines are described, a MAS protocol is available for the gene *Pm34*, derived from *Ae. tauschii* and carried by the North Carolina germplasm line NC97BGTD7, and for *Pm35*, present in germplasm line NC96BGTD3, with the closely linked SSR *Xcfd26*. The knowledge of the gene sequences linked to the resistance is very important, as this allows the design of perfect molecular markers that are not subject to the risk of recombination between the marker and the R gene. A functional marker has been developed by Qin *et al*., (2012) for the gene *Pm6*, localized on chromosome 2B, which has been introduced from the tetraploid wheat *T. timopheevii* into the hexaploid common wheat. The sequence of the barley RFLP probe BCD135 found to be closely linked with the powdery mildew resistance gene *Pm6,* corresponded to a putative receptor-like protein kinase gene (*HvRPK*) in barley, a protein implicated in diverse signaling pathways such as the disease response.

III – Conclusions

A great number of resistance genes to powdery mildew have been identified and mapped in bread and durum wheat. Most of them are race-specific and therefore characterized by a short durability. To prolong and enhance the effectiveness of race-specific resistance, gene pyramiding, multi-lines, and cultivar mixtures have been proposed and used in wheat breeding programs. The availability of molecular markers, co-dominant and PCR-based, facilitates the wheat breeders in marker assisted selection (MAS). Near-complete resistance in a wheat cultivar is expected to be obtained by pyramiding the major and minor resistance genes to reach a more complete level of resistance.

References

Alam A., Xue F., Wang C., Ji C., 2011. Powdery Mildew Resistance Genes in Wheat: Identification and Genetic Analysis. *J. Mol. Biol. Res.,* 1, pp. 20-39.

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

Bennett F.G.A., 1984. Resistance to powdery mildew in wheat: a review of its use in agriculture and breeding programmes. *Plant Pathol.,* 33, pp. 279–300.

Blanco A., Gadaleta A., Cenci A., Carluccio A.V., Abdelbacki A.M.M., Simeone R., 2008.. Molecular mapping of the novel powdery mildew resistance gene Pm36 introgressed from *Triticum turgidum* var. *dicoccoides* in durum wheat. *Theor. Appl. Genet.,* 117, pp. 135–142.

Bougot Y., Lemoine J., Pavoine M.T., Barloy D., Doussinault G., 2002. Identification of a microsatellite marker associated with Pm3 resistance alleles to powdery mildew in wheat. *Plant Breeding,* 121, pp. 325-329.

Bougot Y., Lemoine J., Pavoine M.T., Guyomarch H., Gautier V., Muranty H., Barloy D., 2006. A major QTL effect controlling resistance to powdery mildew in winter wheat at the adult plant stage. *Plant Breeding,* 125, pp. 550-556.

Büschges R., Hollricher K., Panstruga R., Simons G., Wolter M., Frijters A., van Daelen R., van der lee T., Diergaarde P., Groenendijk J., Töpsch S., Vos P., Salamini F., Schulze-Lefert P., 1997. The barley Mlo gene: a novel control element of plant pathogen resistance. *Cell,* 88, pp. 695–705.

Cao A., Xing L., Wang X., Yang X., Wang W., Sun Y., Qian C., Ni J., Chen Y., Liu D., Wang X., Chen P., 2011. Serine/threonine kinase gene Stpk-V, a key member of powdery mildew resistance gene Pm21, confers powdery mildew resistance in wheat. *Proc. Nat. Acad. Sci. USA,* 108, 19, pp. 7727–7732.

Chantret N., Mingeot D., Sourdille P., Bernard M., Jacquemin J.M., Doussinault G., 2001. A major QTL for powdery mildew resistance is stable over time and at two development stages in winter wheat. *Theor. Appl. Genet.,* 103, pp. 962–971.

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

Chen X.M., Luo H., Xia X.C., Xia L.Q., Chen X., Ren Z.L., He Z.H., Jia .ZJ., 2005. Chromosomal location of powdery mildew resistance gene Pml6 in wheat using SSR marker analysis. *Plant Breeding,* 124, pp. 225-228.

Chen Y., Hunger R.M., Carver B.F., Zhang H., Yan L., 2009. Genetic characterization of powdery mildew resistance in U.S. hard winter wheat. *Mol. Breeding,* 24, pp. 141–152.

Conner R.L., Kuzyk A.D., Su H., 2003. Impact of powdery mildew on the yield of soft white spring wheat cultivars. *Canadian J. Plant Sci.,* 83, pp. 725-728.

Elliott C., Zhou F., Spielmeyer W., Panstruga R., Schulze-Lefert P., 2002. Functional Conservation of Wheat and Rice Mlo Orthologs in Defense Modulation to the Powdery Mildew Fungus. *M.P.M.I.* 15(10), pp. 1069–1077.

Gao H., Zhu F., Jiang Y., Wu J., Yan W., Zhang Q., Jacobi A., Cai S., 2012. Genetic analysis and molecular mapping of a new powdery mildew resistant gene *Pm46* in common wheat. *Theor. Appl. Genet.,* 125(5), pp. 967-73.

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

Harlan J.R., 1972. Breeding success brings a peril. *Crops and Soils,* 72, pp. 5-6.

Hautea R.A., Coffman W.R., Sorrells M.E., Bergstrom G.C., 1987. Inheritance of partial resistance to powdery mildew in spring wheat. *Theor. Appl. Genet.,* 73, pp. 609–615.

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

Hsam S.L.K., Zeller .FJ., 2002. Breeding for powdery mildew resistance in common wheat *Triticum aestivum* L.). In: *The powdery mildews: A comprehensive treatise*. Berlanger R.R. *et al*. (eds). Am. Phytopath. Soc., St. Paul, MN. , pp. 219–238

Hu T.Z., Li H.J., Xie C.J., You M.S., Yang Z.M., Sun Q.X., Liu Z.Y., 2008. Molecular Mapping and Chromosomal Location of the Powdery Mildew Resistance Gene in Wheat Cultivar Tangmai 4. *Acta Agronomica Sinica,* 34(7), pp. 1193−1198.

Hua W., Liu Z., Zhu J., Xie C., Yang T., Zhou Y., Duan X., Sun Q., Liu Z., 2009. Identification and genetic mapping of pm42, a new recessive wheat powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). *Theor. Appl. Genet.,* 119, pp. 223–230.

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

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

Jarve K., Peusha H.O., Tsymbalova J., Tamm S., Devos K.M., Enno T.M., 2000. Chromosomal location of a *Triticum timopheevii* - derived powdery mildew resistance gene transferred to common wheat. *Genome,* 43, pp. 377–381.

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

Jing H.C., Bayon C., Kanyuka K., Berry S., Wenzl P., Huttner E., Kilian A., Hammond-Kosack K.E., 2009. DArT markers: diversity analyses, genomes comparison, mapping and integration with SSR markers in *Triticum monococcum*. *BMC Genomics,* 10, pp. 458.

Keller M., Keller B., Schachermayr G., Winzeler M., Schmid J.E., Stamp P., Messmer M.M., 1999. Quantitative trait loci for resistance against powdery mildew in a segregating wheat x spelt population. *Theor. Appl. Genet.* 98, pp. 903-912.

Konishi S., Sasakuma T., Sasanuma T., 2010. Identification of novel Mlo family members in wheat and their genetic characterization. *Genes & Genetic Systems,* 85(3), pp. 167-175.

Ladizinsky G., 1998. Plant evolution under domestication. Dordrecht: Kluwer Academic Press, pp. 262.

Lan C., Ni X., Yan J., Zhang Y., Xia X., Chen X., He Z., 2010. Quantitative trait loci mapping of adult-plant resistance to powdery mildew in Chinese wheat cultivar Lumai 21. *Mol. Breeding,* 25, pp. 615–622.

Li G., Fang T., Zhang H., Xie C., Li H., Yang T., Nevo E., Fahima T., Sun Q., Liu Z., 2009. Molecular identification of a new powdery mildew resistance gene Pm41 on chromosome 3BL derived from wild emmer (*Triticum turgidum* var. *dicoccoides*). *Theor. Appl. Genet.,* 119, pp. 531–539.

Liang S.S., Suenaga K., He Z.H., Wang Z.L., Liu H.Y., Wang D.S., Singh R.P., Sourdille P., Xia X.C., 2006. Quantitative trait loci mapping for adult-plant resistance to powdery mildew in bread wheat. *Phytopathology,* 96, pp. 784-789.

Liu C.J., Devos K.M., Chinoy C.N., Atkinson M.D., Gale M.D., 1992. Non-homoeologous translocations between group 4, 5 and 7 chromosomes in wheat and rye. *Theor. Appl. Genet.,* 83, pp. 305–312.

Liu S.X., Griffey C.A., Maroof M.A.S., 2001. Identification of molecular markers associated with adult plant resistance to powdery mildew in common wheat cultivar Massey. *Crop Sci.,* 41, pp. 1268–1275.

Liu Z., Zhu J., Cui Y., Liang Y., Wu H., Song W., Liu Q., Yang T., Sun Q., Liu Z., 2012. Identification and comparative mapping of a powdery mildew resistance gene derived from wild emmer (*Triticum turgidum* var. *dicoccoides*) on chromosome 2BS. *Theor. Appl. Genet.,* 124(6), pp. 1041-9.

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

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

Marone D., Russo M.A., Laidò G., De Leonardis A.M., Mastrangelo A.M., 2013. Plant Nucleotide Binding Site–Leucine-Rich Repeat (NBS-LRR) Genes: Active Guardians in Host Defense Responses. *Int. J. Mol. Sci.,* 14, pp. 7302-7326.

Maxwell J.J., Lyerly J.H., Cowger C., Marshall D., Brown-Guedira G., Murphy J.P. 2009. MlAG12: a *Triticum timopheevii*-derived powdery mildew resistance gene in common wheat on chromosome 7AL. *Theor. Appl. Genet.,* 119, pp. 1489–1495.

Maxwell J.J., Lyerly J.H., Srnic G., Parks R., Cowger C., Marshall D., Brown-Guedira G., Murphy J.P., 2010. MlAB10: A *Triticum turgidum* Subsp. *dicoccoides* Derived Powdery Mildew Resistance Gene Identified in Common Wheat. *Crop Sci.,* 50, pp. 2261-67.

Mingeot D., Chantret N., Baret P.V., Dekeyser A., Boukhatem N., Sourdille P., Doussinault G., Jacquemin J.M., 2002. Mapping QTL involved in adult plant resistance to powdery mildew in the winter wheat line RE714 in two susceptible genetic backgrounds. *Plant Breeding,* 121, pp. 133-140.

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

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

Mohler V., Bauer A., Bauer C., Flath K., Schweizer G., Hartl L., 2011. Genetic analysis of powdery mildew resistance in German winter wheat cultivar Cortez. *Plant Breeding,*130, pp. 35-40.

Mohler V., Zeller F.J., Wenzel G., Hsamet S.L.K., 2005. Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.). 9. Gene MlZec1 from the *Triticum dicoccoides*-derived wheat line Zecoi-1. *Euphytica,* 142 , pp. 161–167.

Muranty H., Pavoine M.T., Doussinault G., Barloy D., 2010. Origin of powdery mildew resistance factors in RE714, a wheat breeding line obtained from two interspecific crosses. *Plant Breeding.* 129, pp. 465-471.

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

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

Niu J., He D., 2009. Molecular basis of powdery mildew resistance in wheat (*Triticum aestivum* L.). *African Journal of Biotechnology,* 8 19, pp. 4708-4716.

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

Piarulli L., Gadaleta A., Mangini G., Signorile M.A., Pasquini M., Blanco A., Simeone R., 2012. Molecular identification of a new powdery mildew resistance gene on chromosome 2BS from *Triticum turgidum* ssp. *dicoccum. Plant Sci.,* 196, pp. 101– 106.

Qin B., Chen T., Cao A., Wang H., Xing L., Ling H., Wang D., Yu C., Xiao J., Ji J., Chen X., Chen P., Liu D., Wang X., 2012. Cloning of a Conserved Receptor-Like Protein Kinase Gene and Its Use as a Functional Marker for Homoeologous Group-2 Chromosomes of the *Triticeae* Species. *PLoS ONE,* 7(12): e49718.

Qiu Y.C., Zhou R.H., Kong X.Y., Zhang S.S., Jia J.Z., 2005. Microsatellite mapping of a *Triticum urartu* Tum. derived powdery mildew resistance gene transferred to common wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.,* 111, pp. 1524–1531.

Salmeron J.M., Weislo L.J., Strawn L.J., Kramer C.M., Wang H.X., Vernooij B.T., Levin J.Z., Heifetz P.B., Patton D.A., Que Q., 2000. Mlo-genes controlling diseases. U.S. Patent WO 0078799-A 3.

Schmolke M., Mohler V., Hartl L., Zeller F.J., Hsam S.L.K., 2012. A new powdery mildew resistance allele at the Pm4 wheat locus transferred from einkorn (*Triticum monococcum*). *Mol. Breeding,* 29, pp. 449–456.

Shaner G., 1973. Evaluation of slow-mildewing resistance of Knox wheat in the field. *Phytopathology,* 63, pp. 867–872

Singrun Ch., Hsam S.L.K., Hartl L., Zeller F.J., Mohler V., 2003. Powdery mildew resistance gene Pm22 in cultivar Virest is a member of the complex Pm1 locus in common wheat (*Triticum aestivum* L. em Thell.). *Theor. Appl. Genet.* 106, pp. 1420–1424.

Singrun Ch., Hsam S.L.K., Zeller F.J., Wenzel G., Mohler V., 2004. Localization of a novel recessive powdery mildew resistance gene from common wheat line RD30 in the terminal region of chromosome 7AL. *Theor. Appl. Genet.,* 109, pp. 210–214.

Song W., Xie H., Liu Q., Xie C., Ni Z., Yang T., Sun Q., Liu Z., 2007. Molecular identification of Pm12-carrying introgression lines in wheat using genomic and EST-SSR markers. *Euphytica,* 158, pp. 95–102.

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

Spielmeyer W., McIntosh R.A., Kolmer J., Lagudah E.S., 2005. Powdery mildew resistance and Lr34 / Yr18 genes for durable resistance to leaf and stripe rust cosegregate at a locus on the short arm of chromosome 7D of wheat. *Theor. Appl. Genet.,* 111, pp. 731–735.

Srnic´ G., Murphy J.P., Lyerly J.H., Leath S., Marshall D.S., 2005. Inheritance and Chromosomal Assignment of Powdery Mildew Resistance Genes in Two Winter Wheat Germplasm Lines. *Crop Sci,* 45, pp. 1578–1586.

Sun X.L., Liu D., Zhang H.Q., Huo N.X., Zhou R.H., Jia J.Z., 2006. Identification and Mapping of Two New Genes Conferring Resistance to Powdery Mildew from *Aegilops tauschii* (Coss.) Schmal. *J. Integrative Plant Biology,* 48(10) , pp. 1204−1209.

Tucker D.M., Griffey C.A., Liu S., Brown-Guedira G., Marshall D.S., Saghai Maroof M.A., 2007. Confirmation of Three Quantitative Trait Loci Conferring Adult Plant Resistance to Powdery Mildew in Two Winter Wheat Populations. *Euphytica,* 155, pp. 1–13.

Xie W., Ben-David R., Zeng B., Distelfeld A., Ro¨der M.S., Dinoor A., Fahima T., 2011. Identification and characterization of a novel powdery mildew resistance gene PmG3M derived from wild emmer wheat, *Triticum dicoccoides*. *Theor. Appl. Genet.,* 124(5), pp. 911-22.

Xu H., Yao G., Xiong L., Yang L., Jiang Y., Fu B., Zhao W., Zhang Z., Zhang C., Ma Z., 2008. Identification and mapping of pm2026: a recessive powdery mildew resistance gene in an einkorn (*Triticum monococcum* L.) accession. *Theor. Appl. Genet.,* 117, pp. 471–477.

Xu W., Li C., Hu L., Wang H., Dong H., Zhang J., Zan X., 2011. Identification and molecular mapping of PmHNK54: a novel powdery mildew resistance gene in common wheat. *Plant Breeding,* 130(6), pp. 603–607.

Xue F., Wang C., Li C., Duan X., Zhou Y., Zhao N., Wang Y., Ji W., 2012. Molecular mapping of a powdery mildew resistance gene in common wheat landrace Baihulu and its allelism with Pm24. *Theor. Appl. Genet.,* 125(7), pp.1425-32.

Xue F., Zhai W.W., Duan X.Y., Zhou Y.L., Ji W.Q., 2009. Microsatellite Mapping of Powdery Mildew Resistance Gene in Wheat Landrace Xiaobaidong. *Acta Agronomica Sinica,* 35(10), pp. 1806−1811.

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

Yao G., Zhang J., Yang L., Xu H., Jiang Y., Xiong L., Zhang C., Zhang Z., Ma Z., Sorrells M.E., 2007. Genetic mapping of two powdery mildew resistance genes in einkorn (*Triticum monococcum* L.) accessions. *Theor. Appl. Genet.,* 114, pp. 351–358.

Yin G.H., Li G.Y., He Z.H., Liu J.J., Wang H., Xia X.C., 2009. Molecular Mapping of Powdery Mildew Resistance Gene in Wheat Cultivar Jimai 22. *Acta Agronomica Sinica,* 35(8), pp. 1425−1431.

Zamir D., 2001. Improving plant breeding with exotic genetic libraries. *Nat. Rev. Genet.,* 2, pp. 983–989.

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

Zhang K.P., Zhao L., Hai Y., Chen G.F., Tian J.C., 2008. QTL Mapping for Adult-Plant Resistance to Powdery Mildew, Lodging Resistance and Internode Length below Spike in Wheat. *Acta Agronomica Sinica,* 34(8), pp. 1350−1357.

Zhu Z., Zhou R., Kong X., Dong Y., Jia J., 2005. Microsatellite markers linked to 2 powdery mildew resistance genes introgressed from *Triticum carthlicum* accession PS5 into common wheat. *Genome,* 48, pp. 585–590.