

Review

Molecular basis of powdery mildew resistance in wheat (*Triticum aestivum* L.)

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Accepted 19 December, 2008

Powdery mildew is one of the most destructive foliar diseases of wheat worldwide. Improving wheat resistance to *Blumeria graminis* f. sp. *tritici* (*Bgt*) via modern bio-techniques to understand the molecular basis of powdery mildew resistance is very important. Powdery mildew resistance gene *Pm3b* has been isolated, and its alleles have been studied. Some other genes associated with resistance against *Bgt* were also studied. Wheat *TaMLO* genes, similar to barley powdery mildew resistance regulating gene *MLO*, were cloned by the authors. *TaEDR1*, similar to the *EDR1* gene associated with powdery mildew resistance in *Arabidopsis thaliana*, was also cloned. It has been demonstrated that *TaLRK*, *Ta-JA2*, *TaPR-1*, *TaPR-2* and *TaPR-5* genes play positive roles in powdery mildew resistance. However, no systemic signal pathways of powdery mildew resistance have been reported as yet. Therefore, this review is aimed particularly at the molecular basis of powdery mildew resistance in wheat.

Key words: Wheat, powdery mildew, resistance, molecular biology, signal pathway.

INTRODUCTION

Powdery mildew of wheat (*Triticum aestivum*), caused by the fungal pathogen *Blumeria graminis* f. sp. *tritici* (*Bgt*), is one of the most destructive foliar diseases in temperate climates and usually leads to 5 to 34% yield losses (Conner et al., 2003). Two types of resistance, qualitative and quantitative, are genetically classified. Qualitative powdery mildew resistance is major and controlled by powdery mildew (*Pm*) resistance (*R*) genes. Powdery mildew *R* gene-mediated resistance belongs to the category of "gene-for-gene" interaction (Flor, 1971). Up to now, there have been more than 55 powdery mildew resistant alleles designated at 39 loci (*Pm1* ~39) on wheat chromosomes (Huang and Röder, 2004; Miranda et al., 2007; Lillemo et al., 2008; He et al., 2009). At least five gene loci (*Pm1*, 3, 4, 5, and 8) have more than one resistance allele (Huang and Röder, 2004; Wicker et al., 2007). Powdery mildew resistance genes can be classified into dominant' and 'recessive' by their

hereditary 'characters. Among them, most are dominant. However, loci *Pm5*, 9, 26 and *PmLK906* are recessive (Bennett, 1984; Rong et al., 2000; Hsam et al., 2001; Huang et al., 2003; Niu et al., 2008). Recent studies showed that *Pm5a*, *5b* and *5c* were alleles at *Pm5*, but *Pm5e* as well as *Pm5d* and *Mlxbd* were closely linked *R* genes rather than *Pm5* alleles (Nematollahi et al., 2008). Moreover, a new resistance gene, *Pm2026*, in einkorn (*Triticum monococcum*) was also recessive (Xu et al., 2008). Most molecularly studied plant *R* genes encode proteins involved in host-pathogen recognition, but it still remains unknown what the dominant and recessive powdery mildew *R* genes encode and how the proteins work. Though several tens of wheat powdery mildew *R* genes have been genetically studied, only *Pm3b* was molecularly cloned (Yahiaoui et al., 2004). Besides *R* genes, some genes of other types possibly associated with powdery mildew resistance reactions were also isolated in wheat. However, the molecular studies on wheat powdery mildew resistance are limited and scattered. Therefore, it is important to provide an overall review of the related studies.

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POWDERY MILDEW RESISTANCE GENE AND RESISTANCE GENE ANALOGS

Up to now, more than 60 *R* genes in plant species have been isolated, of which the majority encode nucleotide-binding site (NBS) and leucine-rich-repeat (LRR) domains (Huang et al., 2003; Martin et al., 2003; Orgil et al., 2007). The NBS-LRR genes constituted the largest class of *R* genes and were abundant and ubiquitously expressed in all higher plants (Dangl and Jones, 2001; McHale et al., 2006). A less frequent class of *R* genes comprised members of extracellular LRR-containing receptor-like proteins (Jones et al., 1994) and receptor-like kinases (Song et al., 1995; Brueggeman et al., 2002; Sun et al., 2004). These two classes of LRR-containing *R* proteins were thought to be intracellular or cell-surface receptors detecting pathogen-derived virulence proteins through direct or indirect interaction (Dangl and Jones, 2001). The remaining characterized *R* genes encoded proteins that either resembled the overall structure or a domain of the two classes mentioned above, or had a novel protein structure not showing significant homology to any other *R* proteins (Büschges et al., 1997; Xiao et al., 2005; Orgil et al., 2007). Previously, coiled-coil nucleotide-binding site leucine-rich-repeat (CC-NBS-LRR) genes were identified only in monocotyledons other than dicotyledonous species (Ayliffe and Lagudah, 2004; Liu et al., 2007). Wheat *R* genes of *Lr10* and *Pm3b* also encoded this kind of protein (Feuillet et al., 2003; Yahiaoui et al., 2004). However, Rx in potato (*Solanum tuberosum*) was a CC-NBS-LRR resistance protein, which conferred resistance to *Potato virus X*. Functions of Rx conserved domains in pathogen recognition and signaling were systematically analyzed (Rairdan et al., 2008). These studies on plant *R* genes provide clues for studies on wheat *R* genes.

Molecular structure and evolution of *Pm3*

Pm3 is a dominant powdery mildew *R* gene locus on chromosome 1A with the most alleles in wheat. Ten *Pm3* alleles (*Pm3a* ~ *3j*) were identified genetically in wheat lines or cultivars (Zeller et al., 1993). Each conferred race-specific resistance to wheat powdery mildew. Yahiaoui et al. (2006) demonstrated that the amplified *Pm3* sequence of the lines carrying *Pm3h*, *3i* and *3j* (Huang et al., 2004) was identical to one of the previously cloned alleles *Pm3d*, *3c* and *3b*, so there were seven different active resistance alleles at the *Pm3* locus. Moreover, there was also a susceptible allele, *Pm3CS*, in the cultivar 'Chinese Spring'.

The *Pm3b* was identified by map-based cloning as a member of a cluster of genes encoding CC-NBS-LRR proteins (Yahiaoui et al., 2004). The coding sequences of the seven *Pm3* alleles (*Pm3a* ~ *3f*) showed an average sequence identity of 98% (Srichumpa et al., 2005; Yahiaoui et al., 2006). All the studied *Pm3* alleles had the

same gene structure with two exons and one intron of 200 bp at 86 bp upstream from the predicted stop codon. The 200-bp intron sequence is 100% identical among all alleles. *Pm3c*, *3d*, *3e* and *3g* coded for predicted proteins of 1,412 amino acids compared with 1,413 and 1,415 amino acids for *Pm3f* and for *Pm3a* and *3b*, respectively. All *Pm3* proteins had 28 LRR repeats each of which contained the LXXLXLXX motif (Yahiaoui et al., 2006).

Yahiaoui et al. (2006) reported that all *Pm3* resistance alleles were derived from *Pm3CS*, the susceptible allele widespread among common wheat lines. They classified *Pm3* alleles into two groups by the similarity of their amino acid sequences. The first group containing four *Pm3* resistance alleles showed few, delimited and polymorphic sequence blocks of an ancient origin, and was embedded in sequences identical to *Pm3CS* and possibly derived from gene conversion. The second group containing three alleles differed from *Pm3CS* in only two to five mutations in the LRR-encoding region. *Pm3* resistance specificities were based on change of one or just a few amino acids. This meant that change of a single amino acid could convert the susceptible *Pm3CS* protein to a resistance protein, suggesting that *Pm3* recognition specificity was controlled by a very limited number of amino acids in the LRR.

The *Pm3CS* allele was also found in wild tetraploid wheat (*Triticum dicoccoides* Korn.), one ancestor of common wheat. And the *Pm3* resistance alleles were proposed to have been generated from the agricultural ecosystems after domestication of wheat 10,000 years ago (Yahiaoui et al., 2006). Comparison of genomic sequences showed that wheat *Pm3* loci had an extremely dynamic evolution where sequence conservation was minimal between species and basically limited to very short sequences containing the genetic markers defining the orthology. The *Pm3*-like genes and their up- and downstream regions were reshuffled by multiple rearrangements, resulting in a complex mosaic of conserved and unique sequences (Wicker et al., 2007).

T. aestivum MLO-like genes (*TaMLO*)

Barley (*Hordeum vulgare*) *MLO* mutant confers broad-spectrum resistance to powdery mildew. The *MLO* gene was cloned by positional cloning. The deduced amino acid sequence of the gene revealed no homologies to any other characterized plant *R* proteins (Büschges et al., 1997). *MLO* proteins were localized in the plasma membrane and possessed seven transmembrane regions (Devoto et al., 1999). Homologs of *MLO* were cloned in rice (*Oryza sativa*), *Arabidopsis thaliana* and flax (*Linum usitatissimum*) (Devoto et al., 1999; 2003). Similar to that in barley, loss of *AtMLO2* (*A. thaliana MLO2*) conditioned resistance against multiple powdery mildew species that were able to successfully colonize in *A. thaliana* such as *Golovinomyces cichoracearum* and *Golovinomyces*

Table 1. Wheat TaMLO family members in GenBank.

Gene symbol	Accession no.	Aa*	Author
<i>TaMLO-A1a</i>	AF361933	435	Elliott C, Schulze-Lefert P
<i>TaMLO-A1b</i>	AX063298	534	Salmeron JM et al.
<i>TaMLO-A1c</i>	AF384144	534	Yu L et al.
<i>TaMLO-B1a</i>	AF361932	534	Elliott C, Schulze-Lefert P
<i>TaMLO-B1b</i>	AX063294	534	Salmeron JM et al.
<i>TaMLO-B1c</i>	AF384145	534	Yu L et al.
<i>TaMLO-B1d</i>	AY584534	419	Niu JS
<i>TaMLO-D1</i>	AX063296	534	Salmeron JM et al.

*Aa indicates amino acid number encoded by each isolated clone of the wheat *MLO*-like gene.

orontii (Consonni et al., 2006). Either HvMLO (*H. vulgare* MLO) or AtMLO2 interacted with the Ca²⁺ sensor calmodulin (Kim et al., 2002; Bhat et al., 2005) and appeared to inhibit vesicle-associated and SNARE protein-dependent defense reactions to powdery mildew fungi at the cell periphery (Collins et al., 2003; Schulze-Lefert, 2004; Panstruga, 2005). Barley epidermal cells require the actin cytoskeleton to function in basal defense against virulent powdery mildew pathogens, and for *mlo*-mediated resistance at the cell wall. Analysis on non-host resistance to two tested avirulent powdery mildews, *Bgt*, revealed that actin-dependent and actin-independent resistance pathways functioned at the cell periphery. These pathways acted synergistically and appeared to be under negative control by the plasma membrane-resident MLO protein (Opalski et al., 2005; Miklis et al., 2007).

Wheat *MLO*-like genes were reported first in 2002 and demonstrated to be associated with powdery mildew resistance (Elliott et al., 2002). Up to now, several *MLO*-like genes were reported (Table 1; Salmeron et al., 2000). We isolated a full-length cDNA from wheat, *TaMLO* (GenBank accession number: AF384144), highly similar to barley *MLO*. TaMLO protein was a membrane-bound protein as demonstrated by immunoblotting, and its molecular weight was about 60 kD (Büschges et al., 1997; Yu et al., 2005). The *TaMLO* gene was localized in regions of the 2AL, 2BL and 2DL chromosome arms by RFLP (restriction fragment length polymorphism) analysis using *T. aestivum*-*Haynaldia villosa* 6VS-6AL translocation line (Chen et al., 1995), Chinese Spring nullit-tetrasomic and deletion lines. One putative nuclear localization signal (K-K-K-VR), nine casein kinase II motifs, and seven protein kinase C motifs (S/T-X-R/K) were found in the deduced amino acid sequence of TaMLO. TaMLO was 89% identical to barley MLO, and the main domains were highly conserved.

The transcribing of *TaMLO* was enhanced slightly by *Bgt* infection, but the protein TaMLO could be detected in leaves only at 24 h after induction of *Bgt* (Yu et al., 2005). Structure-function analysis of *TaMLO-B1* provided strong evidence for co-operative loop-loop interplay either within the protein or between the MLO molecules (Elliott et al.,

2005). These data indicated that TaMLO function is similar to that of barley MLO protein.

GENES POSSIBLY ASSOCIATED WITH POWDERY MILDEW RESISTANCE SIGNALING

Despite the apparent diversity of cereal resistance mechanisms, some of the additional molecules required for R protein function are conserved among cereal and dicotyledonous species and even other eukaryotic species. Thus the derivation of functional homologues and interacting partner proteins from other species contributes to the understanding of resistance signaling (Ayliffe and Lagudah, 2004). *R* gene-mediated recognition triggers a diverse set of cellular responses. Signaling molecules such as reactive oxygen species, nitric oxide, jasmonic acid (JA), ethylene, and salicylic acid (SA) are produced, and defense-related genes (e.g., the pathogenesis-related [*PR*] genes) are transcriptionally activated (Lamb and Dixon, 1997). Some genes probably associated with powdery mildew resistance in wheat have been studied molecularly.

T. aestivum EDR1-like gene (*TaEDR1*)

In the past several years, it has become apparent that mitogen-activated protein kinase (MAPK) cascades play important roles in elicitor signal transduction in plants (Hirt, 2000; Ren et al., 2002; Chinnusamy et al., 2004; ; Agorio and Vera, 2007; Ge et al., 2007). The *enhanced disease resistance 1* (*EDR1*) mutation of *A. thaliana* resulted in resistance to powdery mildew caused by the fungus *G. cichoracearum* (Frye and Innes, 1998; Tang and Innes, 2002). The *EDR1* gene was isolated by positional cloning and found to encode a putative MAP kinase kinase kinase (MAPKKK) similar to CTR1 (constitutive triple response), a negative regulator of ethylene responses in *A. thaliana* (Frye et al., 2001). Putative orthologs of EDR1 were present in monocots such as rice and barley, indicating that EDR1 may

regulate defense responses in a wide range of crop species. It was suggested that the EDR1 pathway was conserved in crops (Frye et al., 2001). EDR1 might function as a negative regulator at the top of a MAPK cascade in wild-type plants (Suzuki, 2002). EDR1 exerted a negative regulation on hypersensitive response (HR) cell death and powdery mildew resistance by limiting the transcriptional amplification of *RPW8.1* and *RPW8.2* (Xiao et al., 2005). EDR1 was also involved in stress response signaling, and functioned at a point of cross talk between ethylene and SA signaling impinging on senescence and cell death (Tang et al., 2005).

Based upon the cDNA sequences of *EDR1* and its homologs, we cloned a full-length cDNA sequence of *EDR1*-like gene in wheat, *TaEDR1* (*T. aestivum EDR1*; GenBank accession number: AY743662) (Niu et al., 2005). The cDNA sequence of *TaEDR1* was 3,050 bp long, and encoded a polypeptide consisting of 959 amino acid residues. The amino acid sequence of *TaEDR1* showed 92% identity to that of barley *HvEDR1* (*H. vulgare EDR1*). There was a highly conserved catalytic domain of serine/threonine protein kinases at the C-terminus of *TaEDR1*. Because it had a putative nuclear localization motif, this protein was considered to function in the nucleus. High similarity in structure of *TaEDR1* with *EDR1* and *HvEDR1* suggested that there also existed an *EDR1* pathway in wheat, and the pathway might play a role in regulating defense responses (Tang et al., 2005; Xiao et al., 2005).

The transcribing of *TaEDR1* was enhanced by *Bgt* infection. *TaEDR1* was expressed in leaves, stems, spikes, and roots. The transcription level was relatively lower in roots than in other organs (Niu et al., 2005). The lower conserved cDNA fragments at the N-terminus were selected and inserted into plant expression vectors by anti-RNA and RNAi (RNA interference) strategies (Jana et al., 2004; Fu et al., 2007). The primary result of the transgenic study suggested *TaEDR1* might play a role in regulating wheat powdery mildew resistance. However, molecular functions of *TaEDR1* in wheat are mainly unknown.

***T. aestivum* Leaf rust kinase like gene (*TaLRK*)**

By screening a set of near-isogenic lines carrying different leaf rust resistance genes with a wheat probe encoding a serine/threonine protein kinase, Feuillet et al. (1997) detected a polymorphic DNA fragment in a line having the *Lr10* resistance gene. This fragment was mapped to the *Lr10* disease resistance locus and encoded a receptor-like protein kinase called LRK10. LRK10 contained a new type of extracellular domain not found in any known plant or animal receptor kinase. Several conserved amino acids in S-domain glycoproteins and receptor-like kinases were also found in LRK10. Afterwards, Feuillet et al. (1998) described *WLRK* (wheat leaf rust kinase), a *RLK* gene family in wheat with a new type

of extracellular domain. *LRK10* was reported to be an important gene involved in wheat disease resistance reactions (Feuillet et al., 2003).

We cloned a 2,255 bp full-length cDNA sequence *TaLRK* (*T. aestivum LRK*; GenBank accession number: AY584533), a member of *WLRK*, from a powdery mildew resistance wheat line (Niu et al., 2006). *TaLRK* encoded a polypeptide consisting of 637 amino acid residues. Protein *TaLRK* had five distinct domains: a hydrophobic signal sequence at the amino-terminus, a putative extracellular domain, a transmembrane domain, a highly charged sequence, and a serine/threonine kinase domain at the carboxy-terminus. The transcribing of *TaLRK* in leaves was significantly enhanced by *Bgt* infection. *TaLRK* was specifically expressed in leaves, with only few transcripts detected in stems. These results indicated that it probably plays a role in wheat powdery mildew resistance.

***T. aestivum* jasmonate-regulated protein gene (*Ta-JA*)**

In response to both exogenous and endogenous cues, plants synthesize various fatty acid derivatives that act as signaling molecules. Among them, JA and methyl jasmonate (MeJA), collectively known as jasmonates (JAs), are the best characterized fatty acid-derived cyclopentanone signals. JAs modulate a number of vital physiological processes including defense against pathogens and insects, wound responses, secondary metabolite biosynthesis, and flower development and fertility (Cheong and Choi, 2003; Pozo et al., 2005; Shah, 2005; Dombrecht et al., 2007). JA pathway is a major signal pathway in plant defense responses. For example, it played a predominant role in the resistance to the oomycete pathogen *Pythium irregulare* in *A. thaliana* (Adie et al., 2007).

JAs distribute throughout higher plants, induce the transcriptional activation of plant defense genes, and produce jasmonate-regulated proteins (JRP). One class of 32 kD JRP, JRP-32, was present in Gramineae. However, functions of these proteins are still unclear. Wang and Ma (2005) cloned *Ta-JA1* encoding a JRP-32 protein in wheat. We used gene chip hybridization combined with bulked segregating analysis to identify ESTs (expression sequence tags) involved in powdery mildew resistance or linked to the *R* gene *PmLK906* in wheat line 'Lankao 90(6)' (Niu et al., 2008b). Gene chip hybridization showed that the JA-induced protein gene was expressed sixteen-fold higher in the resistant bulk than in the susceptible bulk. Subsequently, a new jacalin gene *Ta-JA2* (GenBank accession number: EU035635) was isolated from 'Chinese Spring' (Niu et al., 2008a). The cDNA sequences of *Ta-JA1* and *Ta-JA2* showed 99% identity. *Ta-JA2* encoded a 304 amino acid constituted peptide. *Ta-JA2* protein had two typical domains, one for plant disease response dirigent-like proteins, and the other for jacalin-like lectins. *Ta-JA2* is expressed in leaves and stems, but

hardly in roots and young spikes. The expression level of *Ta-JA2* increased sequentially from young leaves, to strong leaves and then flag leaves. The transcribing was enhanced by *Bgt* in seedling leaves of 'Chinese Spring' and a *T. dicoccoides* line. The expression level of *Ta-JA2* was steady and relatively higher in seedling leaves of powdery mildew resistant wheat line 'Lankao 90(6)21-12'. These data indicated that JA signal pathway played a role in powdery mildew resistance reaction in wheat.

PATHOGENESIS RELATED PROTEIN GENES

Active disease resistance in plant species includes *R* gene-mediated protection and induced resistance (IR). IR can be divided into local acquired resistance (LAR), systemic acquired resistance (SAR), and induced systemic resistance (ISR) (Conrath et al., 2001). Among them, *R* gene-mediated protection and SAR are important active types, and both are associated with *PR* gene activation.

Molecular mechanism of plant disease resistance was widely studied in model plant *A. thaliana*. The most intensively studied IR was SAR that was activated by a pathogen and led to high-level expression of SAR related genes (e.g., *PRs*) (Ryals et al., 1997). SAR was not only against the initial pathogen but also against subsequent infection by a variety of other viral, fungal, and bacterial pathogens (Ryals et al., 1997). *PR* genes activated in SAR such as *PR-1*, *PR-2* and *PR-5* were often used as markers for SAR in different plant species (Kim and Delaney, 2002). Both SA and NPR1 (nonexpresser of *PR* gene I) protein were required for SAR and *R* gene-mediated resistance (Weigel et al., 2001, 2005). At least in *A. thaliana*, SA accumulation was necessary for most *R*-gene-mediated resistance (Rairdan and Delaney, 2002). In plant species, there are 14 distinct groups of *PRs* designated so far, and almost all classes of *PRs* are present in wheat (Yun et al., 1997; Van Loon and Van Strien, 1999).

Differential expression gene cloning techniques were applied to clone *Bgt*-upregulated genes in wheat. By cDNA library differential screening, Schweizer et al. (1989) isolated six cDNA clones of *Bgt* induced genes. Among them, WIR3 encoded a truncated peroxidase. The WIR3 cDNA clone was used to screen a Bluescript leaf cDNA library of *T. aestivum* 'Cheyenne' 12 to 14 h after *Bgt* infection. A full-length cDNA clone encoding a pathogen-induced putative peroxidase was isolated in wheat (Rebmann et al., 1991a). Båga et al. (1995) used a PCR-based screening approach to isolate genomic clones from wheat encoding peroxidase isozymes. Three complete genes (*pox1*, *pox2* and *pox4*) and one truncated gene (*pox3*) were characterized. The *pox1*, *pox2* and *pox4* genes predominantly expressed in roots. Lower levels of expression were found for *pox4* and *pox3* in leaves. *Bgt* infection selectively induced expression of *pox2* in leaves. These results suggested that some of the

peroxidase genes (*PR-9*) had a positive function in powdery mildew resistance.

The WIR2 cDNA clone (Schweizer et al., 1989) was used to screen a Bluescript cDNA library prepared from mRNA extracted from leaves of 'Cheyenne' 14 h after infected with *B. graminis* f. sp. *hordei* (*Bgh*). A full-length cDNA clone pWIR232 encoding a thaumatin-like protein was isolated (Rebmann et al., 1991b). We also cloned a thaumatin-like protein gene (*TaTLP1*; GenBank accession number: AF384146) from a powdery mildew resistance wheat line. The transcribing of *TaTLP1* gene was enhanced significantly by *Bgt*. These data indicated thaumatin-like protein gene (*PR-5*) played a role in wheat powdery mildew resistance.

We isolated a cDNA clone encoding *TaPR-1* (GenBank accession number: AF384143) from wheat leaves after *Bgt* infection (Yu et al., 2001). *TaPR-1* was a 164 amino acid constituted peptide with 24 amino acids in the putative signal peptide, and the mature peptide comprised 140 amino acids (15.1 kD). The deduced amino acid sequence showed close homology to *PR-1* like proteins isolated from many plant species. The mRNA of *TaPR-1* accumulated dramatically in wheat leaves upon inoculation with *Bgt*, indicating that *TaPR-1* played a role in powdery mildew resistance.

By tissue-specific cDNA-AFLP (amplified fragment length polymorphism) and microarray hybridization analysis, Bruggmann et al. (2005) found 141 wheat transcripts upregulated by *Bgh*. Among them, 44 transcripts accumulated predominantly in the epidermis whereas 76 did so in the mesophyll. Genes induced in the mesophyll included defense-related genes encoding homologs of the rice Pir7 esterases, superoxide dismutase, and well-known *PR* proteins such as *PR-2* (β -1,3-glucanases) and *PR-5* (thaumatin-like proteins; TLPs).

The expression patterns of *PR-1*, *PR-2* and *PR-5* in seedling leaves of susceptible and resistant wheat cultivars or lines were studied by semi-quantitative RT-PCR after *Bgt* infection or SA treatment. We found significant enhancement of transcribing of *PR-1*, *PR-2* or *PR-5* by *Bgt* infection in susceptible wheat cultivar 'Zhoumai 18'. The expression of *PR-1* and *PR-5* was activated more quickly and strongly in resistant than in susceptible wheat lines. SA significantly activated the transcribing of *PR-1* and *PR-5*, but had less effect on *PR-2*. Both *Bgt* and SA significantly upregulated the expression of *PR-1* and *PR-5*, but the effect of *Bgt* was stronger than that of SA. These results indicated that *PR-1* and *PR-5* played an important role in wheat powdery mildew resistance, and they were once used as marker genes for SAR (Niu et al., 2007).

Transgenic plants of *PR* genes can enhance disease resistance (Datta et al., 1999; Yamamoto et al., 2000; Anand et al., 2003b; Takahashi et al., 2005). Over-expression of a *H. villosa* glutathione reductase gene (*Hv-GR*) in powdery mildew susceptible wheat cultivar 'Yangmai 158' resulted in enhanced resistance to *Bgt*.

Table 2. *Bgt*-upregulated genes and their functions.

Gene type	Genes	Functions
I	Glutathione-S-transferase, cytochrome P450, superoxide dismutase, catalase, superoxide dismutase, and alternative oxidase	Detoxification and redox
II	Rab family of small G-proteins	Vesicle docking
III	Lectin-like kinase, LRR-RLK, Myb-related transcription factor, putative histidine kinase, wall-associated kinases, MAP kinase kinase, GTP-binding protein, jasmonate-induced protein, and calreticulins	Signal transduction
IV	SAR related genes as <i>PRs</i>	Disease resistance
V	Glucosyltransferases, Gigantea (Gl)-like gene, a putative UDP-galactose/UDP- glucose transporter, a ubiquitin-conjugating enzyme, a prohibitin	Metabolic activities such as glucose transportation

Transformation with *Hv-GR* induced transcription accumulation of *PR-1a* and *PR-5* (Chen et al., 2007). In the course of gene coexpression for PR proteins for a class IV chitinase and an acidic glucanase in transgenic wheat plants, Anand et al. (2003a) regenerated a wheat line developing necrotic lesions with dead cells in T₂ and subsequent generations. Lesion development was demonstrated to be associated with accumulation of host-encoded PR proteins such as chitinases, β -1,3-glucanases and thaumatin-like proteins. These data suggested close correlations of transgene-induced lesion-mimic phenotypes with enhanced SA biosynthesis. Current studies showed that the rice thaumatin-like protein (*Rtlp1*) promoter was induced within 6 h after infection with *Magnaporthe grisea*. Also, the *Rtlp1* promoter was induced by SA, MeJA, wounding, or an elicitor from a rice blast fungus. W-box elements were verified to be required for response of the *Rtlp1* promoter to fungal elicitors (Hiroyuki and Terauchi, 2008). TGA transcription factors and their cofactor NPR1 regulated the expression of *PR* genes (Ryals et al., 1997; Kesarwani et al., 2007). Furthermore, many *PR* genes have been mapped at quantitative powdery mildew resistance loci (Li et al., 1999). All these data suggested that PR proteins contributed to wheat powdery mildew resistance.

Conclusions

Common wheat is an allohexaploid ($2n = 6x = 42$) species with three genomes (A, B and D) and has an extremely large genome with over 80% repetitive DNA. Traditional gene isolation approaches such as map-based cloning and T-DNA/transposon-tagging are difficult or even impossible to apply to wheat. Therefore, studies on wheat *R* gene cloning and molecular mechanism of resistance are limited. Comparatively, pathogen-upregulated genes are easy to clone. Thus cDNA library differential screening (Schweizer et al., 1989), differential display reverse transcription-PCR (DDRT-PCR; Niu et al., 2002a, 2002b), cDNA-AFLP (Bruggmann et al., 2005),

suppression subtractive hybridization (SSH) cDNA library (Luo et al., 2002), and gene-chip hybridization (Niu et al., 2008a) were all applied to study *Bgt*-upregulated genes. Homology gene cloning was another approach applied for wheat, since studies on the molecular mechanism of powdery mildew resistance in *A. thaliana* and barley were more thorough. Powdery mildew symptom and resistance in barley and wheat are almost the same. And barley powdery mildew has been well studied and can be regarded as a model for wheat powdery mildew.

The molecular structure of Pm3 protein indicated that it functioned in host-pathogen interaction similar to many plant R proteins. Like its homolog in barley, TaMLO was a powdery mildew resistance-controlling element. Many PR proteins have antifungal activities and played positive roles in powdery mildew resistance. SA, JA and H₂O₂ (Li et al., 2005) were important in diverse wheat-*Bgt* interactions.

Results obtained by high throughput techniques such as cDNA-AFLP, SSH library and gene chip hybridization provided useful information for wheat powdery mildew resistance, but they largely remained to be explored in detail. Some *Bgt*-upregulated genes obtained by high throughput techniques were listed in Table 2. These data suggest that wheat powdery mildew resistance is rather complex. SA, JA and MAP-related signal transduction pathways are involved in powdery mildew resistance in wheat, and SAR genes play positive roles. However, studies on the molecular mechanism of powdery mildew resistance in wheat lag far behind those in barley.

ACKNOWLEDGEMENTS

The authors are grateful to the Innovation Foundation for Outstanding Scholars of Henan Province, P. R. China (0621001700) and the Science and Technology Commission Foundation of Henan Province, P. R. China (05220010300). They also wish to express their great appreciation to Dr. Andre Jagendorf, professor of plant biology at Cornell University, USA, for his technical

suggestions and English grammar checking, and to Dr. Cankui Zhang, a postdoctorate research associate in the Department of Plant Biology at Cornell University, for his kind assistance in revising the MS.

Abbreviations

AFLP, amplified fragment length polymorphism; **AR**, acquired resistance; **Bgh**, *Blumeria graminis* f. sp. *hordei*; **Bgt**, *Blumeria graminis* f. sp. *tritici*; **BSA**, bulked segregating analysis; **CC**, coiled-coil; **CTR**, constitutive triple response; **DDRT-PCR**, differential display reverse transcription-PCR; **EDR1**, enhanced disease resistance 1; **EST**, expression sequence tag; **HR**: hypersensitive response; **IR**: induced resistance; **ISR**: induced systemic resistance; **JA**, jasmonic acid; **JRP**, jasmonate-regulated protein; **LAR**, local acquired resistance; **LRR**, leucine-rich repeat; **MAPK**, mitogen-activated protein kinase; **MeJA**, methyl jasmonate; **NBS**, nucleotide-binding site; **NLS**, nuclear localization motif; **NPR1**, nonexpresser of PR gene I; **PR**, pathogenesis-related; **R**, resistance; **RFLP**, restriction fragment length polymorphism; **RGA**, resistance gene analog; **RNAi**, RNA interference; **SA**, salicylic acid; **SAR**, systemic acquired resistance; **SSH**, suppression subtractive hybridization; **WLRK**, wheat leaf rust kinase.

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