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Bacterial Blight Resistance Genes and Strategies for Engineering Broad-spectrum Resistance in Rice

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Abstract

Bacterial Blight (BB), caused by gram-negative bacteria *Xanthomonas oryzae pv. oryzae (Xoo)*, is one of the major constraints for rice production across the world. For decades, a series of rice resistance *(R)* genes against BB have been identified and extensively used in breeding for resistance. However, the existence and emergence of new virulent *Xoo* populations or strains always make the resistant varieties short-lived. Deep understanding of the molecular mechanisms of *R* gene-mediated resistance is important for effective deployment of *R* genes. In this mini review, we summarized the advances in identification and characterization of BB *R* genes, molecular interactions between rice and *Xoo*, and the strategies for developing varieties with Broad-Spectrum Resistance (BSR) to BB. The future challenges are also discussed.

Keywords: Rice; Bacterial blight; *R* gene; Transcription-Activator like Effector (TALE); Broad-spectrum resistance

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Introduction

As an ancient domesticated crop, rice (*Oryza sativa L.*) is the staple food and source of daily calories for nearly half of the global population [1]. Sustainable rice production is important for safeguarding world food security. However, diseases caused by diverse pathogens pose a significant threat for rice production worldwide [2]. The bacteria *specific BB resistance (R) genes oryzae pv. oryzae (Xoo)* caused rice bacterial blight (BB), is one of the most devastating diseases in rice, which can lead to huge yield loss [3,4]. *Xoo* invades rice leaves typically through hydathodes and/or wounds and multiply in leaf veins and xylem causing blockage and plant wilting [5]. At the cellular and molecular level, *Xoo* is capable of injecting Transcription-Activator Like Effector (TALE) proteins into the host plant cells depending on the type III (T3S) secretion system like other plant pathogenic bacteria of the genus *Xanthomonas* [6]. Once in the plant cell, TALEs enter the nucleus and bind to Effector Binding Elements (EBEs) in a sequence-specific manner and transcriptionally activate host genes, leading to susceptibility or resistance [7]. Due to its scientific and economic importance, *Xoo* has been ranged as top 10 plant bacterial pathogens [8]. Over the last two decades, rice genetic resistance to BB and rice-*Xoo* interactions have been extensively studied. To date, nearly 46 race-specific BB resistance *(R)* genes to different *Xoo* races derived from cultivated, wild rice and mutants were identified, and fifteen were molecularly cloned and characterized [9-13]. Based on structural features of the encoding proteins, these *R genes* can be categorized into five groups, including Receptor-Like Kinase (RLK) genes (*Xa21, Xa3/Xa26 and Xa4*), Nucleotide-binding Leucine-rich Repeat (*NLR*) (*Xa1, Xa2/Xa31, Xa14, Xa45 and CGS-Xo1*$_{11}$) genes, sugar will eventually be exported transporter (Sweet) genes (*Xa13, Xa25 and Xa41*), executor genes (*Xa10, Xa23 and Xa27*) and a variant of the transcription factor gamma subunit gene (*Xa5***(Table 1).**

Table 1: List of the cloned rice *R genes* against bacterial blight.

Gene	Encoded protein	Chromosome
Xa3/Xa26	RLK	11
Xa21		11
Xa4		11
Xa13 (OsSWEET11)	SWEET-type protein	8
Xa25 (OsSWEET13)		12
Xa41 (OsSWEET14)		11
Xa10	Executor R protein	11
Xa23		11
Xa27		6
Xa1	*NLR*	4
Xa2/Xa31		4
Xa14		4
Xa45		4
CGS-Xo111		4
Xa5	TFIIA transcription factor	5

RLK Genes

As the primary level of immune system in plants, sensing of the diverse Pathogen Associated Molecular Patterns (PAMPs) by the cell surface-localized Pattern Recognition Receptors (PRRs), is critical for triggering downstream signaling and immune responses. Most of the reported plant PRRs are either transmembrane Receptor-Like Kinases (RLKs) or Receptor-Like Proteins (RLPs) [14]. Compared with RLKs, RLPs lack an intracellular kinase domain [15]. In rice, more than 1100 candidate RLKs/RLPs were identified [16]. The first cloned *R gene Xa21* against BB originated from the wild rice species Oryza longistaminata encodes a Leucine-Rich Repeat-Like Kinase (LRR-RLK), representing the largest subfamily of plant RLK [17,18]. It was found that *Xa21* recognizes the tyrosine-sulfated peptide RaxX (required for activation of *Xa21*-mediated immunity *X*) secreted by *Xoo* by direct binding with high affinity and activates host defense responses [19,20,21]. Additionally, *Xa21* functions in a complex with several *XBs* (*Xa21* binding proteins) for its stability and signaling [10]. *Xa3* and *Xa26*, identified from an *indica* restorer line Minghui 63 and a japonica variety Wase Aaikoku 3, respectively, were found to be the identical gene encoding LRR-RLK [22,23]. The cognate avirulence (*Avr*) gene to *Xa3/Xa26, AvrXa3*, has also been isolated, but how it is recognized by *Xa3/Xa26* and initiates host resistance is still largely unknown [24]. Similar to *Xa21*, other components were found to be involved in *Xa3/Xa26*-meditaed resistance [25,26]. *Xa4* encodes a cell Wall-Associated Kinase (WAK), another subfamily of RLK. In contrast to the developmentally controlled resistance mediated by *Xa21* and *Xa3/Xa26*, *Xa4* confers a race-specific resistance to *Xoo* at all growth stages [27]. A boost of jasmonic acid-isoleucine and an accumulation of phytoalexins, sakuranetin and momilactone A, are likely to be associated with *Xa4*-mediated resistance [28]. In addition, it could improve the lodging resistance by strengthening the cell wall via promoting cellulose synthesis and suppressing cell wall loosening.

NLR Genes

Among all typedfs of plant *R* genes, *NLR* is the largest group and accounts for more than 60% of the *R* genes [29]. Around 480 *NLR* genes have been found in rice genome [30]. *Xa1* was the first cloned *NLR* gene against *Xoo* and confers race-specific resistance by recognizing multiple TALEs [31-33]. However, a group of atypical TALE variants lacking the C-terminal transcription activation domains, termed as interfering TALEs (iTALEs), could suppress *Xa1*-mediated resistance. Most recently, several *Xa1* alleles including *Xa2/Xa31, Xa14, CGS-Xo1*$_{11}$, and *Xa45* were isolated by two research groups [12,13]. Like *Xa1*, the resistance of these newly cloned *R* genes were also suppressed by *Xoo* strains carrying iTALEs. A genome-wide survey indicated that iTALE genes are prevalent in Asian strains, accounting for over 95% of the tested strains, but not African strains [13]. It is probably that iTALEs function as decoys interfering with the interaction between intact TALEs and *Xa1* allelic members, and block immune signaling in rice [33].

Sweet Genes

Sweet genes constitute a family of sugar efflux transporters involved in a variety of functions, such as senescence, pollen development and plant-microbe interactions [34-37]. Interestingly, plant pathogens are able to hijack these Sweet genes for their nutrition supply that is essential for pathogens growth and infection. Although rice genome contains 22 Sweet genes which is phylogenetically divided into four clades, only five Sweet genes belonging to clade III can function as susceptibility (S) genes targeted by *Xoo*. Three of them including *OsSWEET11 (Xa13), OsSWEET13 (Xa25), OsSWEET14 (Xa41)*, are known as S genes to be targeted by natural TALEs. TALEs were found to induce the genes expression by binding to the EBEs in the promoter of *Xa*13, X25 and *Xa*41. However, mutations in the EBEs of the recessive alleles *Xa13, Xa25 and Xa41* could prevent *Xoo*-mediated activation of these genes, leading to host resistance to *Xoo* [38-48].

Executor Genes

Three executor genes, including *Xa27, Xa10* and *Xa23*, confer dominant and TALEs-dependent transcriptional based resistance [49-51]. *Xa27* was originated from the wild rice *O. minuta* Acc. 101141 and specifically induced by *Xoo* stains containing the TALE *AvrXa27* [49]. Increased expression of *Xa27* showed the thickened vascular bundle elements, even in absence of the *Xoo* infection. *Xa27* is localized to apoplast relying on the

N-terminal signal-anchor-like sequence, which is crucial for its resistance to *Xoo* [52]. Similarly, *Xa10*, first identified from rice cultivar Cas 209, was specifically induced by the TALE *AvrXa10* by direct binding to *Xa10* promoter [53,54]. Transgenic plants constitutively and weakly expressed *Xa10* displayed lesion mimic phenotype. *Xa10* was found to localize in the Endoplasmic Reticulum (ER) membrane of plant and HeLa cells in the form of hexamers, and induces ER Ca^{2+} depletion, which is consistent with some processes of Programmed Cell Death (PCD) [50,55]. *Xa23*, another executor gene originated from a wild rice (*Oryza rufipogon*), confers broad-spectrum resistance to *Xoo* strains depending on the transcriptional activation of *Xa23* by the TALE *AvrXa23*. *Xa23* shares 50% identity with *Xa10*. An identical Open Reading Frame (ORF) is shared by the susceptible *Xa23* allele and a 7-bp polymorphism in the promoter regions accounts for the failure of *Xa23* induction by *AvrXa23* [51]. *AvrXa23* was found to be highly conserved in all tested *Xoo* strains [56].

Transcription Factor Gamma Subunit Gene

The recessive gene *Xa5* with broad-spectrum resistance against *Xoo* encodes a mutated *OsTFIIAγ5* in which Valine (V) is changed to glutamic acid (E) at the 39th amino acid residue (V39E) [57]. *TFIIAγ5* is hijacked by TALEs by direct physical interaction with a Transcription Factor Binding (TFB) region, which is required for TALE-regulated transcriptional activation of host S or *R* genes [58]. However, the induction of host genes is attenuated in the *Xa5* background or *TFIIAγ5-RNAi* transgenic plants. [58,59]. The other *OsTFIIAγ* gene in rice, *OsTFIIAγ1*, plays a compensatory role in the absence of *Xa5*. *OsTFIIAγ1* is activated by TALE PthXo7, which increases the expression of the TALEs targeted host genes [60].

Engineering BSR against BB

Five *R* genes with relatively broad spectra of resistance against *Xoo*, including *Xa5, Xa7, Xa13, Xa21* and *Xa23* are more frequently used by rice breeders. However, rapid adaption of pathogens usually makes the monogenic resistance short-lived. Marker-assisted (MAS) pyramiding of *R* genes is an efficient route to achieve durable and broad-spectrum resistance. There have been many successful cases for enhancing BB resistance by pyramiding *R* genes [10].

Genome-editing technologies, particularly the clustered regularly interspaced short palindromic repeats (CRISPR)/Cas9 (CRISPR-associated protein-9 nuclease) with its simplicity, versatility and high precision, have revolutionized the field of agriculture and plant science. [61-63]. The powerful tools have great potential in improving the plant disease resistance. Editing EBEs of S genes or adding EBEs to the promoters of executor R genes could enhance the resistance to BB. Two recent studies reported that CRISPR/Cas9-mediated mutations in the promoters of *OsSWEET* genes provide BSR to the tested *Xoo* strains [45,64]. In another report, EBEs corresponding three TALEs, were inserted into the promoter of *Xa27*, leading to broad-spectrum resistance [65].

Future Perspectives

Rice-*Xoo* patho-system is a powerful model for research toward solutions in disease control. Tremendous progress has been made in the two decades, but there are still

many queries and challenges:

- The cognate *Avr* genes to *Xa4* is still not isolated.
- How *R* genes activate downstream signaling components and trigger host immune defense responses needs to be elucidated.
- The underlying mechanism of TALEs’ translocation into host cell nucleus remains unknown.
- How iTALEs interfere with the resistance activated by the recognition of TALEs by *Xa1* or its alleles remains unclear. Are there direct physical interactions between iTALEs (or TALEs) and *Xa1* or *Xa1*-like *NLR*s?
- After the above-listed queries or challenges are elucidated, the *R* genes against BB should be well understood in breeding and scientifically deployed in production. The yield loss of rice caused by BB endemic will thus be greatly controlled.

Competing Interests

The authors declare no competing interests.

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