



# A review of approaches to control bacterial leaf blight in rice

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## Abstract

The Gram-negative bacteria *Xanthomonas oryzae pv. oryzae*, the causative agent of bacterial leaf blight (BLB), received attention for being an economically damaging pathogen of rice worldwide. This damage prompted efforts to better understand the molecular mechanisms governing BLB disease progression. This research revealed numerous virulence factors that are employed by this vascular pathogen to invade the host, outcompete host defence mechanisms, and cause disease. In this review, we emphasize the virulence factors and molecular mechanisms that *X. oryzae pv. oryzae* uses to impair host defences, recent insights into the cellular and molecular mechanisms underlying host-pathogen interactions and components of pathogenicity, methods for developing *X. oryzae pv. oryzae*-resistant rice cultivars, strategies to mitigate disease outbreaks, and newly discovered genes and tools for disease management. We conclude that the implementation and application of cutting-edge technologies and tools are crucial to avoid yield losses from BLB and ensure food security.

**Keywords** *Xanthomonas oryzae pv. oryzae* · Host-pathogen interaction · Antimicrobials · Rice · Virulence factors

## Introduction

Rice feeds almost half of humanity and thus is one of the most important crops on the planet. However, in recent years, rice production worldwide has experienced enormous

economic losses from bacterial leaf blight (BLB), a deadly bacterial disease caused by the Gram-negative proteobacterium *Xanthomonas oryzae pv. oryzae* (Qian et al. 2013; Tian et al. 2014). BLB causes serious disease on most popular commercial rice strains (Duy et al. 2021), and is one of the three main pests of rice, challenging both *Oryza sativa* (*Os*) subsp. *japonica* and *Oryza sativa* subsp. *indica* (Ji et al. 2016).

Bacterial leaf blight causes a variety of symptoms in rice. *Xanthomonas oryzae pv. oryzae* infection initially induces streaks on rice leaves that spread from the tips and margins. These streaks become larger and eventually release a milky fluid that dries yellow. Late stages of infections are characterized by grayish white lesions on the leaves, eventually resulting in the leaves drying out and dying. In seedlings, BLB causes the leaves to dry out and wilt, usually killing the seedling within two to three weeks. Although adult plants may survive the infection, yield and quality are diminished.

Controlling BLB has proven challenging, and consequently, BLB poses a threat to global food security. Chemical control, such as the use of antibiotics, has been restricted partly because of concerns over safety, practicality, and bacterial resistance. Biological control methods have also been limited. Given the obstacles posed by chemical and biological control, researchers have mainly focused on discovering

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the molecular mechanisms underlying BLB transmission and pathogenicity, as well as the factors determining host susceptibility or resistance to BLB – major foci of this review. Indeed, researchers have discovered more than 30 genes that confer resistance to *X. oryzae pv. oryzae*, some of which are now integrated into the genomes of commercial rice strains.

Research has revealed that the pathogenicity of *X. oryzae pv. oryzae* is a function of several compounds and mechanisms employed by the pathogen. Much of the pathogenicity of *X. oryzae pv. oryzae* is a function of its type III secretion system (T3SS) that translocates effector proteins into eukaryotic host cells to overcome host defences. The transcription activator-like (TAL) effectors constitute a major family of effector proteins that suppress host defences. This family targets the host susceptibility genes SWEET, which stands for Sugars Will Eventually be Exported Transporters (e.g. *SWEET11*, *SWEET13* or *SWEET14*, Oliva et al. 2019). *Xanthomonas oryzae pv. oryzae* is also endowed with some non-TAL effectors (e.g., XopR) that hijack and subvert the host defence system (Sun et al. 2021). *Xanthomonas oryzae pv. oryzae* pathogenicity is also influenced by the O-antigen component of the bacterium's lipopolysaccharide (LPS). The LPS of the bacterium triggers callose deposition (Girija et al. 2017; Wang et al. 2018), which is a plant xyloglucan polysaccharide that can act as a barrier against pathogens. However, *Xanthomonas* bacteria possess xyloglucan depolymerization machinery that breaks down this barrier and facilitates plant invasion and pathogenesis (Vieira et al. 2021). Another important compound affecting *X. oryzae pv. oryzae* pathogenicity is putative phytase A (phyA), which is used to pump out phosphate from the plant tissue to improve the nutritional status of the bacterium (Blüher et al. 2017). Finally, amino acids can also play essential roles in *X. oryzae pv. oryzae* pathogenicity. A recent report established that leucine, isoleucine, valine, histidine, threonine, arginine, tryptophan, and cysteine are key players in both *X. oryzae pv. oryzae* growth and virulence in rice host (Li et al. 2019a).

Although there have been previous reviews of BLB in rice (Jiang et al. 2020b), this review highlight three topics that have not been thoroughly addressed by other reviews: (i) the mechanisms and speed by which T3SS transfers effector proteins into host cells without molecule leakage, (ii) the molecular system by which a component of the type-III effectors (T3Es) remodel actin cytoskeleton to subvert host immune responses, and (iii) important new rice resistance genes and antimicrobial peptides against *X. oryzae pv. oryzae* infection.

## Contributions of various biological systems to *X. oryzae pv. oryzae* infection

Various biological sensing systems contribute to the pathogenicity of *X. oryzae pv. oryzae*. For example, it is crucial for *X. oryzae pv. oryzae* to integrate photo-sensing with intracellular signaling. More specifically, by using light-sensing photoreceptors and bacteriophytochrome to detect changes in wavelengths of light, *X. oryzae pv. oryzae* fine-tunes intracellular levels of c-di-GMP [(bis-(3'-5')-cyclic di-guanosine monophosphate)] that modulates the secretion of virulence factors, iron metabolism, and the transition from a sessile to motile life stages of the pathogen (Verma et al. 2020). *Xanthomonas oryzae pv. oryzae* also employs chemotactic systems to improve fitness. For example, *X. oryzae pv. oryzae* uses chemoreceptors Mcp2 of its chemotaxis signal transduction system to sense xylem sap, components of xylem exudate (methionine, serine, histidine), and initiate epiphytic entry into the host plant (Kumar et al. 2018). To sense and adapt to external stimuli during pathogenesis, *X. oryzae pv. oryzae* employs a regulatory system with two known components, a histidine protein kinase (HK) sensor and a response regulator (Antar et al. 2020). For example, *X. oryzae pv. oryzae* reacts to osmotically stressful conditions by regulating the activity of the HK sensor VgrS via a periplasmic, PDZ-domain-containing protease that cleaves the N-terminal sensor region of VgrS (Deng et al. 2018). Hence, the use of molecules that interfere with these various sensing systems employed by *X. oryzae pv. oryzae* might represent promising ways to control BLB.

Upon initial contact with rice, genes related to cell motility, inorganic ion transport, and protein effectors are among the first set of genes to be upregulated in *X. oryzae pv. oryzae* (Kim et al. 2021). The delivery of bacterial effector proteins directly into rice cells is one of the most important first steps to bacterial establishment and pathogenicity. The most abundant virulence proteins produced by *X. oryzae pv. oryzae* during its initial interaction with rice include outer membrane proteins, T3SS proteins, TonB-dependent receptors, and TAL effectors (Zhang et al. 2020).

Type III secretion system mediates not only the release of TAL effector proteins into eukaryotic cells but also regulates the production of *Xanthomonas*-induced small RNAs, non-coding small RNAs (sRNA) involved in gene silencing, plant growth regulation, and plant development and stress responses (Reshetnyak et al. 2021). Therefore, thorough knowledge of the biological function of sRNA can be vital for developing effective management methods to control BLB. Further, Hüsing et al. (2021) noticed that the delivery of T3SS core proteins occurred at a high rate without leakage of small molecules. They discovered that a deformable gasket (M-gasket), in cooperation with a plug

domain (R-plug) and a network of salt-bridges, maintain membrane integrity during high-speed protein translocation by the T3SS. The T3SS also mediates the transfer of non-TAL effectors. The mechanism of transfer of the type III non-TAL effector *Xanthomonas* outer protein R (XopR) has been described by Sun et al. (2021). Once translocated into host cells, XopR forms a macromolecular complex with actin-binding proteins at the cell cortex and competes for actin-depolymerizing factors to progressively manipulate multiple steps of actin assembly, including formin-mediated nucleation, crosslinking of F-actin, and actin depolymerization (Sun et al. 2021). This process allows for *Xanthomonas* species to subvert the host’s actin cytoskeleton defence system. Additional bacterial factors that contribute to *X. oryzae pv. oryzae* pathogenesis include newly described proteins, such as phosphohexose mutase (XanA) and inositol monophosphatase (Imp) (Wu et al. 2021).

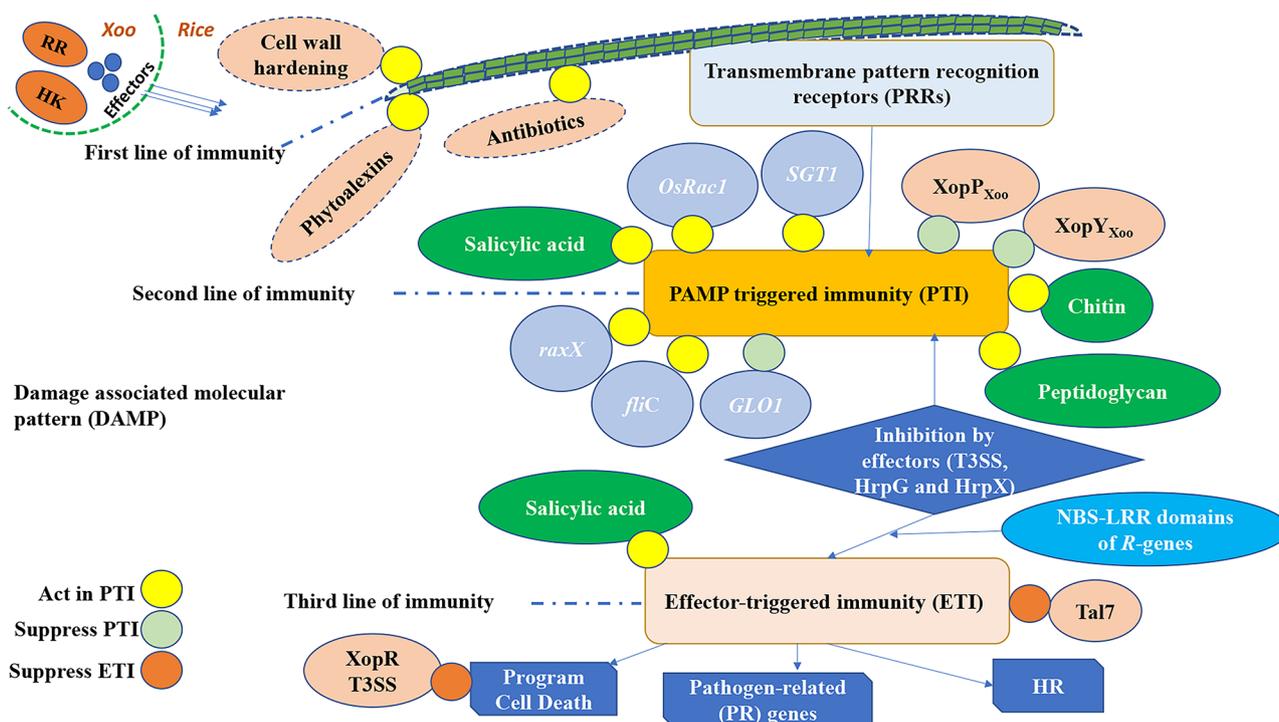
### Typical mechanisms of disease resistance in most rice plants

A recently identified glycerol kinase (GK)-encoding gene, *OsNHO1*, and a class II small heat shock protein gene, *OsHsp18.0* (which acts in nucleo-cytoplasmic trafficking),

were both shown to be upregulated in rice plants resistant to multiple *X. oryzae pv. oryzae* strains (Kuang et al. 2017; Xiao et al. 2022), implicating their importance in BLB resistance. The pathways associated with these genes also implicate monothiol glutaredoxin proteins in resistance, as the *OsGRXS15* gene that drive expression of monothiol glutaredoxin in the mitochondria and nucleus confers resistance to *X. oryzae pv. oryzae* (Son et al. 2020).

The presence of receptors that can translate upstream molecular events into downstream immune reactions associated with successive layers of passive and active barriers is critical to provide resistance to pathogens. It is conventionally thought that nucleotide-binding leucine-rich repeat (NLR) immune receptor activation required specific cognate effectors delivered from pathogens; nevertheless, a recent study uncovered a type of NLR, so-called autoactive NLRs, that do not need cognate effectors to confer broad-spectrum resistance to *X. oryzae pv. oryzae* (Li et al. 2019b). This finding illustrated the powerful potential that could provide autoactive NLRs in broad-spectrum resistance.

It is conventionally thought that this NLRs activations required a specific cognate effectors delivered from pathogens; nevertheless, recent study has uncovered a type of NLRs, so-called autoactive NLRs, that do not need cognate effectors to confer broad-spectrum resistance to Xoo.



**Fig. 1** Plant-immunity-defense mechanisms implicated pathogenic bacteria. These schematic designs are based on Antar et al. (2020); Ishikawa et al. (2014); Yamaguchi et al. (2013); Cheng et al. (2016); Midha et al. (2017); Verma et al. (2019); Jiang et al. (2020a) descriptions. Gene (blue), protein activator (Green), protein suppressor (Brown). Hypersensitive response : HR, Nucleotide-binding site-leucine-rich repeat : NBS-LRR domain

The cuticle and cell wall are the key passive barriers to pathogens in rice plants, whereas active barriers encompass secondary metabolites with antimicrobial activity, callose deposition, lignification of the cell wall, and cell death. The cell wall is subjected to a reinforcement mechanism with superoxide production and this step is accompanied by phytoalexins, antibiotic compounds, peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase syntheses, and leaf senescence-associated mechanisms (Zulfugarov et al. 2016; Sun et al. 2017; Hunjan et al. 2021). Cell wall architecture is importantly also defined by polygalacturonase proteins, which depolymerize pectin by hydrolysis and activate cell wall immune responses (Cao et al. 2021).

In addition to passive defence mechanisms and antimicrobial compounds, pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) in rice facilitate the production of defence metabolites that orchestrate immune responses to *X. oryzae pv. oryzae* (Wang et al. 2017; Hong et al. 2017). During ETI responses, a hypersensitive immune reaction (Kong et al. 2020) occurs that is prone to impairment by XopR T3SS effector from *X. oryzae pv. oryzae*, contributing to its pathogenesis (Verma et al. 2019). Components involved in PTI and ETI responses are highlighted in Fig. 1.

The regulation of some defence hormones is also connected to rice immune response mechanisms. Phytohormone signaling pathways, such as salicylic acid, jasmonic acid, and ethylene are enriched in *Oryza meyeriana* in response to *X. oryzae pv. oryzae* infection (Cheng et al. 2016). It should be stressed that jasmonic acid biosynthesis in rice tends to reduce *X. oryzae pv. oryzae* virulence (Hou et al. 2019). Expression of the Class III acyl-CoA-binding gene, *OsACBP5*, which upregulates salicylic acid-mediated defence pathways, has also been shown to be important in conferring resistance to *X. oryzae pv. oryzae* (Panthapulakkal et al. 2020).

## Strategies for controlling *X. oryzae pv. oryzae* infections

Pyramiding of genes, or the process of combining two or more genes from multiple parents to develop elite lines and varieties, is recognized as a promising strategy to enhance resistance to BLB (Pradhan et al. 2020). Several BLB-resistance genes have been discovered that can be exploited in rice breeding programs. These include *Xa1-2*, *Xa14*, and *Xa31(t)*, which confer resistance by encoding for atypical NLRs with unique central tandem repeats (CTRs), and *Xa46(t)* isolated from resistant rice mutant H120 (Zhang et al. 2020; Chen et al. 2020), *xa-45(t)* (recessive resistance genes) isolated from *Oryza glaberrima* accession IRGC

102600B (Neelam et al. 2020) and *xa44(t)* recovered from rice IR73571-3B-11-3-K3 (P6) (Kim 2018).

Furthermore, pyramiding of genes has also been found to be beneficial to developing rice cultivars that are resistant to *X. oryzae pv. oryzae* combined with other stressors. For example, the pyramided line IRBB67, carrying both *Xa4* and *Xa7* resistance genes, exhibited greater resistance to the combined stressors of high temperature and *X. oryzae pv. oryzae* than the monogenic line IRBB4, carrying only the *Xa4* R gene (Dossa et al. 2020). Given persistent climate change and disease emergence (Rohr et al. 2013; Rohr and Cohen 2020; Cohen et al. 2020), it is particularly crucial to use a transgenic line (e.g., IRBB 67) that can maintain its resistance to *X. oryzae pv. oryzae* under current and elevated temperatures (35/31°C) (Sahu et al. 2020; Dossa et al. 2020).

Another useful tool to confer resistance in rice varieties has been gene editing. For example, CRISPR/Cas9 was recently used to reduce rice susceptibility to *X. oryzae pv. oryzae* by inserting mutations into the effector binding elements of the susceptibility genes, *OsSWEET13*, *OsSWEET14*, and *OsSULTR3;6* (Ni et al. 2021; Zeng et al. 2020; Zafar et al. 2020; Moniruzzaman et al. 2020). CRISPR/Cas12a was used to effectively introduce site-specific mutations into transcription activator-like 1 effector box in the promoter region of the rice *Xa13* gene to generate transgenic BLB-resistant lines (Yu et al. 2021). Alternatives to CRISPR/Cas approaches, such as TALEN-based techniques, have also been used to reduce disease susceptibility. For example, TALEN-based techniques were used to enhance rice resistance by altering transcription factor protein-encoding genes (e.g. *TFIIAγ* encoded by *TFIIAγ5* gene, Han et al. 2020). Finally, the insertion of non-coding sRNAs has been successful in conferring a sulfate-mediated antibacterial defence to rice. Indeed, the rice microRNA miR395 impairs the virulence of *X. oryzae pv. oryzae* by exploiting *X. oryzae pv. oryzae*'s sensitivity to high levels of extracellular sulfate and reducing extracellular polysaccharide production and biofilm formation (Yang et al. 2021). In addition to breeding disease-resistant rice cultivars, it is critical to expand control methods against *X. oryzae pv. oryzae*, such as antibiotics effective against *X. oryzae pv. oryzae*.

## Antimicrobial strategies to circumvent *X. oryzae pv. oryzae* infection

Antibacterial molecules continue to be discovered that have new structural and/or functional features relevant to *X. oryzae pv. oryzae* control. As examples, fungal chitosan from *Aspergillus niger* and hamuramicins A (1) and B (2) or C15surfactin A produced by *Bacillus velezensis* HN-2 were

recently discovered and hold promise for reducing *X. oryzae pv. oryzae*. These latter three compounds induce a hypersensitive response via the mediation of antioxidant-related enzymes and have been exploited as protective agents against BLB (Stanley-Raja et al. 2021; Suga et al. 2018; Jin et al. 2020). Other antimicrobial compounds include the new natural plant-based product catechol that binds with the catalytic domain of XanA protein (controlling the production of xanthan and xanthomonadin in *X. oryzae pv. oryzae*) to inhibit biofilm formation of *X. oryzae pv. oryzae* (Vishakha et al. 2020). Anthranilamide from *Streptomyces spp.* also strongly impairs biofilm formation in *X. oryzae pv. oryzae* (Ham and Kim 2018). The recently discovered microbial enzyme chumacin-1/2 (produced by *Pseudomonas aeruginosa* strain CGK-KS-1) inhibits quorum-sensing factors (*cis*-11-methyl-2-dodecenoic acid) in *X. oryzae pv. oryzae* (Kanugala et al. 2019). Another promising antimicrobial compound is carbazomycin B, which is produced by *Streptomyces roseoverticillatus* 63 (Sr-63). It adversely impacts the cell membrane of *X. oryzae pv. oryzae*, reducing the production of xanthomonadin and EPS (Shi et al. 2021). Similarly, resveratrol inhibits *X. oryzae pv. oryzae* growth by inducing oxidative stress and perturbing its metabolic processes (Luo et al. 2020). Interestingly, a high-density conditioned medium containing the amoebae species *Acanthamoeba castellanii*, *Acanthamoeba lenticulata*, *Acanthamoeba polyphaga*, *Dictyostelium discoideum*, and *Vermamoeba vermiformis* displayed either bacteriostatic or bactericidal effects on *X. oryzae pv. oryzae* (Long et al. 2018). In a somewhat surprising discovery, niclosamide [5-chloro-N-(2-chloro-4-nitrophenyl)-2-hydroxybenzamide], which is traditionally an oral antihelminthic drug and molluscicide, has been used successfully to locally and systemically block rice leaf wilt caused by *X. oryzae pv. oryzae* without negatively affecting rice growth or yields (Kim et al. 2016). Finally, compounds that induce leakage of the cytoplasmic content of bacterial cells could serve as new sources of antibiotics against *X. oryzae pv. oryzae*. These compounds are listed in Table 1.

## Conclusion and future perspectives

Several solutions exploiting natural and synthetic compounds as well as engineering strategies exploiting synthetic biology have been implemented for counteracting or reducing the impact of *X. oryzae pv. oryzae* on rice production. We suggest that the combination of pyramiding methods with antimicrobial products will improve *X. oryzae pv. oryzae* control. A better understanding of the complex host–bacteria interactions may lead to the potential identification of new host surveillance systems deploy against effectors

**Table 1** Antimicrobial compounds identified during the studies focused on *Xanthomonas oryzae pv. oryzae*

Compounds	Antibacterial effects	References
Silver nanoparticles (AgNPs)	Antibacterial effect and significant inhibitory impact on <i>Xoo</i> biofilm formation	Mishra et al. (2020)
Niclosamide	Directly inhibited the growth of <i>Xoo</i> , increased the levels of salicylate and, induced the expression of the genes <i>OsPR1</i> and <i>OsWRKY45</i>	Kim et al. (2016)
Peptide melittin	Disrupted the cytoplasmic membrane of <i>Xoo</i> by making holes and channels	Shi et al. (2016)
Resveratrol	Growth inhibition of <i>Xoo</i>	Luo et al. (2020)
4 H-pyran-4-one,2,3-dihydro-3,5-dihydroxy-6-methyl- (DDMP)	Growth inhibition of <i>Xoo</i>	Syed Ab Rahman et al. 2014
(2Z)-2-butenedioic acid-2-(1-methylethenyl)-4-methyl ester	Fairly strong antagonistic activity	Jiang et al. (2019)
Dissolved zinc thiazole at 25 µg/ml	Enhanced the cell division and altered the cell wall integrity of <i>Xoo</i>	Chen et al. (2019)
4-((1E,4E)-5-(3-nitrophenyl)-3-oxopenta-1,4-dien-1-yl)phenylthiophene-2-sulfonate	Excellent antibacterial activities	Guo et al. (2020)
Allelochemical catechol	Antibacterial, anti-biofilm, and antivirulence potential	Vishakha et al. (2020)
18β-glycyrrhetic acid(GA) hydrazide 3 C	Curative and protective activities against <i>Xoo</i> at 200 µg/mL	Zhang et al. (2021)

that mediate phytobacterial infection. As the transition to

more suitable alternatives to enhance rice tolerance to rice bacterial leaf blight continues, more studies are needed to tap into the many unexploited potentials of amino acids metabolisms as well as newly discovered genes for broadening the immune system response of rice.

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## References

- Antar A, Lee MA, Yoo Y, Cho MH, Lee SW (2020) PXO\_RS20535, Encoding a Novel Response Regulator, Is Required for Chemotactic Motility, Biofilm Formation, and Tolerance to Oxidative Stress in *Xanthomonas oryzae pv. oryzae*. *Pathogens* (Basel Switzerland) 9(11). doi:<https://doi.org/10.3390/pathogens9110956>
- Blüher D, Laha D, Thieme S, Hofer A, Eschen-Lippold L, Masch A, Balcke G, Pavlovic I, Nagel O, Schonsky A, Hinkelmann R, Wörner J, Parvin N, Greiner R, Weber S, Tissier A, Schutkowski M, Lee J, Jessen H, Schaaf G, Bonas U (2017) A 1-phytase type III effector interferes with plant hormone signaling. *Nat Commun* 8(1):2159. doi:<https://doi.org/10.1038/s41467-017-02195-8>
- Cao Y, Zhang Y, Chen Y, Yu N, Liaqat S, Wu W, Chen D, Cheng S, Wei X, Cao L, Zhang Y, Liu Q (2021) *OsPGI* Encodes a Polygalacturonase that Determines Cell Wall Architecture and Affects Resistance to Bacterial Blight Pathogen in Rice. *Rice* 14, 36. <https://doi.org/10.1186/s12284-021-00478-9>
- Chen S, Wang C, Yang J, Chen B, Wang W, Su J, Feng A, Zeng L, Zhu X (2020) Identification of the novel bacterial blight resistance gene Xa46(t) by mapping and expression analysis of the rice mutant H120. *Sci Rep* 10(1):12642. doi:<https://doi.org/10.1038/s41598-020-69639-y>
- Chen X, Zhou L, Laborda P, Zhao Y, Li K, Liu F (2019) First method for dissolving zinc thiazole and re-evaluation of its antibacterial properties against rice bacterial blight disease. *Phytopathol Res* 1(1):30. doi:<https://doi.org/10.1186/s42483-019-0036-4>
- Cheng XJ, He B, Chen L, Xiao Sq, Fu J, Chen Y, Yu TQ, Cheng ZQ, Feng H (2016) Transcriptome analysis confers a complex disease resistance network in wild rice *Oryza meyeriana* against *Xanthomonas oryzae pv. oryzae*. *Sci Rep* 6(1):38215. doi:<https://doi.org/10.1038/srep38215>
- Cohen JM, Sauer EL, Santiago O, Spencer S, Rohr JR (2020) Divergent impacts of warming weather on wildlife disease risk across climates. *Science* 370:eabb1702
- Deng CY, Zhang H, Wu Y, Ding LL, Pan Y, Sun ST, Li YJ, Wang L, Qian W (2018) Proteolysis of histidine kinase VgrS inhibits its autophosphorylation and promotes osmotic stress resistance in *Xanthomonas campestris*. *Nat Commun* 9(1):4791. doi:<https://doi.org/10.1038/s41467-018-07228-4>
- Dossa GS, Quibod I, Atienza-Grande G, Oliva R, Maiss E, Vera CC, Wydra K (2020) Rice pyramided line IRBB67 (Xa4/Xa7) homeostasis under combined stress of high temperature and bacterial blight. *Sci Rep* 10(1):683. doi:<https://doi.org/10.1038/s41598-020-57499-5>
- Duy PN, Lan DT, Pham TH, Thi THP, Nguyen TH, Pham NP, Auguy F, Bui TTH, Manh TB, Cunnac S, Pham XH (2021) Improved bacterial leaf blight disease resistance in the major elite Vietnamese rice cultivar TBR225 via editing of the OsSWEET14 promoter. *PLoS ONE* 16(9):e0255470. doi:<https://doi.org/10.1371/journal.pone.0255470>
- Girija AM, Kinathi BK, Madhavi MB, Ramesh P, Vungarala S, Patel HK, Sonti RV (2017) Rice Leaf Transcriptional Profiling Suggests a Functional Interplay Between *Xanthomonas oryzae pv. oryzae* Lipopolysaccharide and Extracellular Polysaccharide in Modulation of Defense Responses During Infection. 30:16–27. <https://doi.org/10.1094/mpmi-08-16-0157-r.1>
- Guo T, Xia R, Chen M, Su S, He J, He M, Wang H, Xue W (2020) Biological activity evaluation and action mechanism of 1,4-Pentadien-3-one derivatives containing thiophene sulfonate. *Phosphorus, Sulfur, and Silicon and the Related Elements* 195(2):123–130. doi:<https://doi.org/10.1080/10426507.2019.1655418>
- Ham Y, Kim TJ (2018) Anthranilamide from *Streptomyces spp.* inhibited *Xanthomonas oryzae* biofilm formation without affecting cell growth. *Appl Biol Chem* 61(6):673–680. doi:<https://doi.org/10.1007/s13765-018-0405-1>
- Han J, Xia Z, Liu P, Li C, Wang Y, Guo L, Jiang G, Zhai W (2020) TALEN-based editing of TFIIA5 changes rice response to *Xanthomonas oryzae pv. oryzae*. *Sci Rep* 10(1):2036. doi:<https://doi.org/10.1038/s41598-020-59052-w>
- Hong Y, Yang Y, Zhang H, Huang L, Li D, Song F (2017) Overexpression of MoSM1, encoding for an immunity-inducing protein from *Magnaporthe oryzae*, in rice confers broad-spectrum resistance against fungal and bacterial diseases. *Sci Rep* 7:41037. doi:<https://doi.org/10.1038/srep41037>
- Hou Y, Wang Y, Tang L, Tong X, Wang L, Liu L, Huang S, Zhang J (2019) SAPK10-Mediated Phosphorylation on WRKY72 Releases Its Suppression on Jasmonic Acid Biosynthesis and Bacterial Blight Resistance. *iScience* 16:499–510. doi:<https://doi.org/10.1016/j.isci.2019.06.009>
- Hunjan MS, Kamboj I, Lore JS, Bhatia G, Pannu PPS (2021) Expression of defense related enzymes in rice near isogenic lines IRBB4 and IRBB7 challenged with *Xanthomonas oryzae pv. oryzae* at elevated temperature. *Indian Phytopathol* 74:33–43. <https://doi.org/10.1007/s42360-020-00304-0>
- Hüsing S, Halte M, van Guse LU, Gálvez A, Charpentier EJC, Blair E, Erhardt DF, Renault M TT (2021) Control of membrane barrier during bacterial type-III protein secretion. *Nat Commun* 12(1):3999. doi:<https://doi.org/10.1038/s41467-021-24226-1>
- Ishikawa K, Yamaguchi K, Sakamoto K, Yoshimura S, Inoue K, Tsuge S, Kojima C, Kawasaki T (2014) Bacterial effector modulation of host E3 ligase activity suppresses PAMP-triggered immunity

- in rice. *Nat Commun* 5(1):5430. doi:<https://doi.org/10.1038/ncomms6430>
- Ji ZJ, Yang SD, Zeng YX, Liang Y, Yang CD, Qian Q (2016) Pyramiding blast, bacterial blight and brown planthopper resistance genes in rice restorer lines. *J Integr Agric* 15(7):1432–1440. doi:[https://doi.org/10.1016/S2095-3119\(15\)61165-0](https://doi.org/10.1016/S2095-3119(15)61165-0)
- Jiang G, Liu D, Yin D, Zhou Z, Shi Y, Li C, Zhu L, Zhai W (2020a) A Rice NBS-ARC Gene Conferring Quantitative Resistance to Bacterial Blight Is Regulated by a Pathogen Effector-Inducible miRNA. <https://doi.org/10.1016/j.molp.2020a.09.015>. *Molecular Plant* doi:
- Jiang N, Yan J, Liang Y, Shi Y, He Z, Wu Y, Zeng Q, Liu X, Peng J (2020b) Resistance Genes and their Interactions with Bacterial Blight/Leaf Streak Pathogens (*Xanthomonas oryzae*) in Rice (*Oryza sativa* L.)—an Updated Review. *Rice (N Y)* 13(1):3. doi:10.1186/s12284-019-0358-y
- Jin P, Wang Y, Tan Z, Liu W, Miao W (2020) Antibacterial activity and rice-induced resistance, mediated by C15surfactin A, in controlling rice disease caused by *Xanthomonas oryzae pv. oryzae*. *Pestic Biochem Physiol* 169:104669. doi:<https://doi.org/10.1016/j.pestbp.2020.104669>
- Kanugala S, Kumar CG, Rachamalla HKR, Palakeeti B, Kallaganti VSR, Nimmu NV, Cheemalamarri C, Patel HK, Thipparapu G (2019) Chumacin-1 and Chumacin-2 from *Pseudomonas aeruginosa* strain CGK-KS-1 as novel quorum sensing signaling inhibitors for biocontrol of bacterial blight of rice. *Microbiol Res* 228:126301. doi:<https://doi.org/10.1016/j.micres.2019.126301>
- Kim S, Jang WE, Park J, Kim MS, Kim JG, Kang LW (2021) Combined Analysis of the Time-Resolved Transcriptome and Proteome of Plant Pathogen *Xanthomonas oryzae pv. oryzae*. 12. <https://doi.org/10.3389/fmicb.2021.664857>. 1354
- Kim SI, Song JT, Jeong JY, Seo HS (2016) Niclosamide inhibits leaf blight caused by *Xanthomonas oryzae* in rice. *Sci Rep* 6(1):21209. doi:<https://doi.org/10.1038/srep21209>
- Kim SM (2018) Identification of novel recessive gene *xa44(t)* conferring resistance to bacterial blight races in rice by QTL linkage analysis using an SNP chip. *Theor Appl Genet* 131:2733–2743. doi:<https://doi.org/10.1007/s00122-018-3187-2>
- Kong W, Ding L, Xia X (2020) Identification and characterization of genes frequently responsive to *Xanthomonas oryzae pv. oryzae* and *Magnaporthe oryzae* infections in rice. *BMC Genomics* 21(1):21. doi:<https://doi.org/10.1186/s12864-019-6438-y>
- Kuang J, Liu J, Mei J, Wang C, Hu H, Zhang Y, Sun M, Ning X, Xiao L, Yang L (2017) A Class II small heat shock protein OsHsp18.0 plays positive roles in both biotic and abiotic defense responses in rice. *Sci Rep* 7(1):11333. doi:<https://doi.org/10.1038/s41598-017-11882-x>
- Kumar VR, Samal B, Chatterjee S (2018) *Xanthomonas oryzae pv. oryzae* chemotaxis components and chemoreceptor Mep2 are involved in the sensing of constituents of xylem sap and contribute to the regulation of virulence-associated functions and entry into rice. *Mol Plant Pathol* 19(11):2397–2415. doi:<https://doi.org/10.1111/mpp.12718>
- Li T, Zhan Z, Lin Y, Lin M, Xie Q, Chen Y, He C, Tao J, Li C (2019a) Biosynthesis of Amino Acids in *Xanthomonas oryzae pv. oryzae* Is Essential to Its Pathogenicity. *Microorganisms* 7(12). doi:10.3390/microorganisms7120693
- Li Z, Huang J, Wang Z, Meng F, Zhang S, Wu X, Zhang Z, Gao Z (2019b) Overexpression of Arabidopsis Nucleotide-Binding and Leucine-Rich Repeat Genes RPS2 and RPM1(D505V) Confers Broad-Spectrum Disease Resistance in Rice. *Front Plant Sci* 10:417. doi:10.3389/fpls.2019b.00417
- Long JJ, Jahn CE, Sánchez-Hidalgo A, Wheat W, Jackson M, Gonzalez-Juarrero M, Leach JE (2018) Interactions of free-living amoebae with rice bacterial pathogens *Xanthomonas oryzae pathovars oryzae* and *oryzicola*. *PLoS ONE* 13(8):e0202941. doi:<https://doi.org/10.1371/journal.pone.0202941>
- Luo HZ, Guan Y, Yang R, Qian GL, Yang XH, Wang JS, Jia AQ (2020) Growth inhibition and metabolomic analysis of *Xanthomonas oryzae pv. oryzae* treated with resveratrol. *BMC Microbiol* 20(1):117. doi:<https://doi.org/10.1186/s12866-020-01803-w>
- Midha S, Bansal K, Kumar S, Girija AM, Mishra D, Brahma K, Laha GS, Sundaram RM, Sonti RV, Patil PB (2017) Population genomic insights into variation and evolution of *Xanthomonas oryzae pv. oryzae*. *Sci Rep* 7:40694–40694. doi:<https://doi.org/10.1038/srep40694>
- Mishra S, Yang X, Ray S, Fraceto LF, Singh HB (2020) Antibacterial and biofilm inhibition activity of biofabricated silver nanoparticles against *Xanthomonas oryzae pv. oryzae* causing blight disease of rice instigates disease suppression. *World J Microbiol Biotechnol* 36(4):55. doi:<https://doi.org/10.1007/s11274-020-02826-1>
- Moniruzzaman M, Zhong Y, Yan H, Yuanda L, Jiang B, Zhong G (2020) Exploration of Susceptible Genes with Clustered Regularly Interspaced Short Palindromic Repeats—Tissue-Specific Knockout (CRISPR-TSKO) to Enhance Host Resistance. *Crit Reviews Plant Sci* 39(5):387–417. doi:<https://doi.org/10.1080/07352689.2020.1810970>
- Neelam K, Mahajan R, Gupta V, Bhatia D, Gill BK, Komal R, Lore JS, Mangat GS, Singh K (2020) High-resolution genetic mapping of a novel bacterial blight resistance gene *xa-45(t)* identified from *Oryza glaberrima* and transferred to *Oryza sativa*. *Theor Appl Genet* 133, 689–705. <https://doi.org/10.1007/s00122-019-03501-2>
- Ni Z, Cao Y, Jin X, Fu Z, Li J, Mo X, He Y, Tang J, Huang S (2021) Engineering Resistance to Bacterial Blight and Bacterial Leaf Streak in Rice. *Rice* 14:38. <https://doi.org/10.1186/s12284-021-00482-z>
- Oliva R, Ji C, Atienza-Grande G, Hugueta-Tapia JC, Perez-Quintero A, Li T, Eom JS, Li C, Nguyen H, Liu B, Auguy F, Sciallano C, Luu VT, Dossa GS, Cunnac S, Schmidt SM, Slamet-Loedin IH, Vera CC, Szurek B, Frommer WB, White FF, Yang B (2019) Broad-spectrum resistance to bacterial blight in rice using genome editing. *Nat Biotechnol* 37(11):1344–1350. doi:<https://doi.org/10.1038/s41587-019-0267-z>
- Panthapulakkal NS, Lung SC, Liao P, Lo C, Chye ML (2020) The overexpression of OsACBP5 protects transgenic rice against necrotrophic, hemibiotrophic and biotrophic pathogens. *Sci Rep* 10(1):14918. doi:<https://doi.org/10.1038/s41598-020-71851-9>
- Pradhan SK, Barik SR, Nayak DK, Pradhan A, Pandit E, Nayak P, Das SR, Pathak H (2020) Genetics, Molecular Mechanisms and Deployment of Bacterial Blight Resistance Genes in Rice. *Crit Reviews Plant Sci* 39(4):360–385. doi:<https://doi.org/10.1080/07352689.2020.1801559>
- Qian G, Zhou Y, Zhao Y, Song Z, Wang S, Fan J, Hu B, Venturi V, Liu F (2013) Proteomic analysis reveals novel extracellular virulence-associated proteins and functions regulated by the diffusible signal factor (DSF) in *Xanthomonas oryzae pv. oryzicola*. *J Proteome Res* 12(7):3327–3341. doi:<https://doi.org/10.1021/pr4001543>
- Reshetnyak G, Jacobs JM, Auguy F, Sciallano C, Claude L, Medina C, Perez-Quintero AL, Comte A, Thomas E, Bogdanove A, Koebnik R, Szurek B, Dievart A, Brugidou C, Lacombe S, Cunnac S (2021) An atypical class of non-coding small RNAs is produced in rice leaves upon bacterial infection. *Sci Rep* 11(1):24141. doi:<https://doi.org/10.1038/s41598-021-03391-9>
- Rohr JR, Raffel TR, Blaustein AR, Johnson PTJ, Paull SH, Young S (2013) Using physiology to understand climate-driven changes in disease and their implications for conservation. *Conserv Physiol* 1. doi:<https://doi.org/10.1093/conphys/cot1022>
- Rohr JR, Cohen JM (2020) Understanding how temperature shifts could impact infectious disease. *PLoS Biol* 18:e3000938. <https://doi.org/10.1371/journal.pbio.3000938>

- Sahu A, Das A, Saikia K, Barah P (2020) Temperature differentially modulates the transcriptome response in *Oryza sativa* to *Xanthomonas oryzae* pv. *oryzae* infection. *Genomics* 112(6):4842–4852. doi:<https://doi.org/10.1016/j.ygeno.2020.08.028>
- Shi T, Guo X, Zhu J, Hu L, He Z, Jiang D (2021) Inhibitory Effects of Carbazomycin B Produced by *Streptomyces roseovorticillatus* 63 Against *Xanthomonas oryzae* pv. *oryzae*. 12. <https://doi.org/10.3389/fmicb.2021.616937>. 637
- Son S, Kim H, Lee KS, Kim S, Park SR (2020) Rice glutaredoxin GRXS15 confers broad-spectrum resistance to *Xanthomonas oryzae* pv. *oryzae* and *Fusarium fujikuroi*. *Biochem Biophys Res Commun* 533(4):1385–1392. doi:<https://doi.org/10.1016/j.bbrc.2020.10.027>
- Stanley-Raja V, Senthil-Nathan S, Chanthini KMP, Sivanesh H, Ramasubramanian R, Karthi S, Shyam-Sundar N, Vasanth-Srinivasan P, Kalaivani K (2021) Biological activity of chitosan inducing resistance efficiency of rice (*Oryza sativa* L.) after treatment with fungal based chitosan. *Sci Rep* 11(1):20488. doi:<https://doi.org/10.1038/s41598-021-99391-w>
- Suga T, Kimura T, Inahashi Y, Iwatsuki M, Nonaka K, Také A, Matsumoto A, Takahashi Y, Omura S, Nakashima T (2018) Hamuramicins A and B, 22-membered macrolides, produced by an endophytic actinomycete *Allostreptomyces* sp. K12-0794. *J Antibiot Res* 71(7):619–625. doi:<https://doi.org/10.1038/s41429-018-0055-x>
- Sun H, Zhu X, Li C, Ma Z, Han X, Luo Y, Yang L, Yu J, Miao Y (2021) *Xanthomonas* effector XopR hijacks host actin cytoskeleton via complex coacervation. *Nat Commun* 12(1):4064. doi:<https://doi.org/10.1038/s41467-021-24375-3>
- Sun L, Wang Y, Liu LL, Wang C, Gan T, Zhang Z, Wang Y, Wang D, Niu M, Long W, Li X, Zheng M, Jiang L, Wan J (2017) Isolation and characterization of a spotted leaf 32 mutant with early leaf senescence and enhanced defense response in rice. *Sci Rep* 7(1):41846. doi:<https://doi.org/10.1038/srep41846>
- Syed-Ab RSF, Sijam Kamaruzaman O, Dzolkhifli (2014) Chemical composition of *Piper sarmentosum* extracts and antibacterial activity against the plant pathogenic bacteria *Pseudomonas fuscovaginae* and *Xanthomonas oryzae* pv. *oryzae*. *J PLANT DIS PROTECT* 121(6):237–242. doi:<https://doi.org/10.1007/BF03356518>
- Tian Y, Zhao Y, Xu R, Liu F, Hu B, Walcott RR (2014) Simultaneous Detection of *Xanthomonas oryzae* pv. *oryzae* and *X. oryzae* pv. *oryzicola* in Rice Seed Using a Padlock Probe-Based Assay. *Phytopathology* 104(10):1130–1137. doi:<https://doi.org/10.1094/phyto-10-13-0274-r>
- Verma G, Mondal KK, Kulshreshtha A, Sharma M (2019) XopR T3SS-effector of *Xanthomonas oryzae* pv. *oryzae* suppresses cell death-mediated plant defense response during bacterial blight development in rice. *3 Biotech* 9(7):272. doi:<https://doi.org/10.1007/s13205-019-1802-9>
- Verma RK, Biswas A, Kakkar A, Lomada SK, Pradhan BB, Chatterjee S (2020) A Bacteriophytochrome Mediates Interplay between Light Sensing and the Second Messenger Cyclic Di-GMP to Control Social Behavior and Virulence. *Cell Rep* 32(13):108202. doi:<https://doi.org/10.1016/j.celrep.2020.108202>
- Vieira PS, Bonfim IM, Araujo EA, Melo RR, Lima AR, Fessel MR, Paixão DAA, Persinoti GF, Rocco SA, Lima TB, Pirolla RAS, Moraes MAB, Correa JBL, Zanphorlin LM, Diogo JA, Lima EA, Grandis A, Buckeridge MS, Gozzo FC, Benedetti CE, Polikarpov I, Giuseppe PO, Murakami MT (2021) Xyloglucan processing machinery in *Xanthomonas* pathogens and its role in the transcriptional activation of virulence factors. *Nat Commun* 12(1):4049. doi:<https://doi.org/10.1038/s41467-021-24277-4>
- Vishakha K, Das S, Banerjee S, Mondal S, Ganguli A (2020) Allelochemical catechol comprehensively impedes bacterial blight of rice caused by *Xanthomonas oryzae* pv. *oryzae*. *Microb Pathog* 149:104559. doi:<https://doi.org/10.1016/j.micpath.2020.104559>
- Wang B, Wu G, Zhang Y, Qian G, Liu F (2018) Dissecting the virulence-related functionality and cellular transcription mechanism of a conserved hypothetical protein in *Xanthomonas oryzae* pv. *oryzae*. *Mol Plant Pathol* 19(8):1859–1872. doi:<https://doi.org/10.1111/mpp.12664>
- Wang C, Wang G, Zhang C, Zhu P, Dai H, Yu N, He Z, Xu L, Wang E (2017) OsCERK1-Mediated Chitin Perception and Immune Signaling Requires Receptor-like Cytoplasmic Kinase 185 to Activate an MAPK Cascade in Rice. *Mol Plant* 10(4):619–633. doi:<https://doi.org/10.1016/j.molp.2017.01.006>
- Wu G, Zhang Y, Wang B, Li K, Lou Y, Zhao Y, Liu F (2021) Proteomic and Transcriptomic Analyses Provide Novel Insights into the Crucial Roles of Host-Induced Carbohydrate Metabolism Enzymes in *Xanthomonas oryzae* pv. *oryzae* Virulence and Rice-*Xoo* Interaction. *Rice* 14, 57. <https://doi.org/10.1186/s12284-021-00503-x>
- Xiao X, Wang R, Khaskhali S, Gao Z, Guo W, Wang H, Niu X, He C, Yu X, Chen Y (2022) A Novel Glycerol Kinase Gene OsNHO1 Regulates Resistance to Bacterial Blight and Blast Diseases in Rice. 12. <https://doi.org/10.3389/fpls.2021.800625>
- Yamaguchi K, Yamada K, Ishikawa K, Yoshimura S, Hayashi N, Uchihashi K, Ishihama N, Kishi-Kaboshi M, Takahashi A, Tsuge S, Ochiai H, Tada Y, Shimamoto K, Yoshioka H, Kawasaki T (2013) A receptor-like cytoplasmic kinase targeted by a plant pathogen effector is directly phosphorylated by the chitin receptor and mediates rice immunity. *Cell Host Microbe* 13(3):347–357. doi:<https://doi.org/10.1016/j.chom.2013.02.007>
- Yang Z, Hui S, Lv Y, Zhang M, Chen D, Tian J, Zhang H, Liu H, Cao J, Xie W, Wu C, Wang S, Yuan M (2021) miR395-regulated sulfate metabolism exploits pathogen sensitivity to sulfate to boost immunity in rice. *Mol Plant*. doi:<https://doi.org/10.1016/j.molp.2021.12.013>
- Yu K, Liu Z, Gui H, Geng L, Wei J, Liang D, Lv J, Xu J, Chen X (2021) Highly efficient generation of bacterial leaf blight-resistant and transgene-free rice using a genome editing and multiplexed selection system. *BMC Plant Biol* 21, 197 (2021). <https://doi.org/10.1186/s12870-021-02979-7>
- Zafar K, Khan MZ, Amin I, Mukhtar Z, Yasmin S, Arif M, Ejaz K, Mansoor S (2020) Precise CRISPR-Cas9 Mediated Genome Editing in Super Basmati Rice for Resistance Against Bacterial Blight by Targeting the Major Susceptibility Gene. *Front Plant Sci* 11:575. doi:<https://doi.org/10.3389/fpls.2020.00575>
- Zeng X, Luo Y, Vu NTQ, Shen S, Xia K, Zhang M (2020) CRISPR/Cas9-mediated mutation of OsSWEET14 in rice cv. Zhonghua11 confers resistance to *Xanthomonas oryzae* pv. *oryzae* without yield penalty. *BMC Plant Biol* 20(1):313. doi:<https://doi.org/10.1186/s12870-020-02524-y>
- Zhang B, Zhang H, Li F, Ouyang Y, Yuan M, Li X, Xiao J, Wang S (2020) Multiple Alleles Encoding Atypical NLRs with Unique Central Tandem Repeats in Rice Confer Resistance to *Xanthomonas oryzae* pv. *oryzae*. *Plant Commun* 1(4):100088. doi:<https://doi.org/10.1016/j.xplc.2020.100088>
- Zhang L, Fu Y, Ding Y, Meng J, Wang Z, Wang P (2021) Antibacterial Activity of Novel 1β-Glycyrrhetic Hydrazide or Amide Derivatives. *Chem Res Chin Univ* 37(3):662–667. doi:<https://doi.org/10.1007/s40242-021-0370-9>
- Zulfugarov IS, Tovuu A, Kim CY, Vo KTX, Ko SY, Hall M, Seok HY, Kim YK, Skogstrom O, Moon YH, Jansson S, Jeon JS, Lee CH (2016) Enhanced resistance of PsbS-deficient rice (*Oryza sativa* L.) to fungal and bacterial pathogens. *J Plant Biol* 59:616–626. <https://doi.org/10.1007/s12374-016-0068-6>

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