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Research Status and Prospect of *Burkholderia glumae*, the Pathogen Causing Bacterial Panicle Blight

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Abstract: Bacterial panicle blight caused by *Burkholderia glumae* is one of the most severe seed-borne bacterial diseases of rice in the world. Currently, this disease has affected many countries of Asia, Africa, South and North America. It is a typical example of the shifting from minor plant disease to major disease due to the changes of environmental conditions. Some virulent factors of *B. glumae* have been identified, including toxoflavins and lipases, whose productions are dependent on the TofI/TofR quorum-sensing system, and type III effectors. In spite of its economic significance, neither effective control measure for this disease nor resistant rice variety is currently available. In recent years, genomics, transcriptomics and other molecular methods have provided useful information for better understanding the molecular mechanisms underlying *B. glumae* virulence and the rice defence mechanisms against pathogens. For the prevention of this pathogen, our laboratory has developed a rapid and sensitive multiplex PCR assay for detecting and distinguishing *B. glumae* from other *Burkholderia* species. This improved understanding of *B. glumae* will shed new light on bacterial panicle blight disease management.

Key words: bacterial panicle blight; *Burkholderia glumae*; pathogenesis; genomics; transcriptomics; rice

Bacterial panicle blight (BPB) of rice is firstly reported in Japan in the 1950s, and since then it has become one of the most serious rice diseases in the world (Xie et al, 2003). Up to now, BPB has been reported in many rice growing countries in South and Central America (Dominican Republic, Venezuela, Ecuador, Brazil, Panama, Colombia, Nicaragua and Costarica), Africa (countries of South Africa and Tanzania) and Asia (Japan, Korea, Vietnam, the Philippines, India, Indonesia, Malaysia, Sri Lanka, Thailand and China) (Tsushima, 1996; Nandakumar et al, 2005, 2007; Wang et al, 2006; Kim et al, 2010; Quesada-González and García-Santamaría, 2014; Riera-Ruiz et al, 2014; Zhou, 2014; Mondal et al, 2015).

Burkholderia glumae is a seed-borne rice pathogen, and BPB caused by *B. glumae* can induce 75% yield loss in severely infested fields (Trung et al, 1993). Many countries, especially the tropical and subtropical countries, consider BPB as a potential high-risk bacterial disease of rice (Ham et al, 2011). Luo et al (2007) reported that *B. glumae* is a potential high-risk pest in China based on their pest risk analysis (PRA). Because of its quarantine importance, *B. glumae* is listed in the entry plant quarantine pest list of the People's Republic of China in 2007. In this paper, we present an overview of the recent progresses on *B. glumae* research, especially the molecular biology and molecular genetic studies.

Characteristics of *B. glumae*

In 1967, Kurita firstly named the bacterial pathogen

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causing rice grain rot as *Pseudomonas glumae*. Since 1992, based on the 16S rRNA sequences, DNA-DNA homology, cellular lipid and fatty acid compositions, and phenotypic characteristics, the non-fluorescent bacteria in *Pseudomonas* are classified as genus *Burkholderia* and the others. And therefore, *Pseudomonas glumae* is renamed as *Burkholderia glumae* in 1992 (Yabuuchi et al, 1992).

B. glumae is a gram-negative, non-fluorescent, rod-shaped bacterium with a polar flagella (Cho et al, 2007). Its optimum growth temperature is around 30 °C, but it can grow even at 41 °C (Saddler, 1994). This pathogen infects seeds and invades plumules through stomata and wounds, and proliferates in the intercellular spaces of parenchyma during seed germination (Zhu et al, 2010). The proliferation of *B. glumae* in plumules leads to the production of toxic materials, such as toxoflavin, which then results in rice seedling rot.

Epidemiology of BPB

B. glumae favors warm night and high humidity conditions which always occur during the rice-growing season (Cha et al, 2001). BPB appears during the rice heading stage when it has high night temperature and frequent rainfalls which are the important environmental conditions predisposing rice to disease outbreak. Under appropriate environmental conditions, the serious epidemics of BPB can be spread and increased rapidly. Xie et al (2003) discovered that *B. glumae* can cause spikelet sterility and the discoloration of emerging grains. *B. glumae* has also been found to be responsible for the decrease of grain weight, floret sterility, inhibition of seed germination and reduction of stands in rice seedlings (Jeong et al, 2003).

Bacterial wilt differs from fungal wilt in which fungi remain in vascular tissues until plant death, whereas bacteria often destroy parts of the cell wall in xylem vessels. When suffered from bacterial wilt, the vascular tissues of diseased stems and roots turn brown, and bacterial ooze flows in cross-sections (Jeong et al, 2003; Nandakumar et al, 2009). However, bacterial blight or wilt caused by *B. glumae* is symptomatically indistinguishable from that caused by *Ralstonia solanacearum*. Besides rice, *B. glumae* has also been reported to be capable of causing wilting in pepper, eggplant, sesame and tomato plants in Korea (Jeong et al, 2003). As BPB is highly dependent on weather conditions, the ecological aspects of its occurrence and the relationship between *B. glumae* survival and the environmental factors, such as temperature and drought, need to be studied in order to effectively manage BPB.

Virulent factors of *B. glumae*

The pathogenesis of *B. glumae* is a complex process that involves multiple virulent factors. The molecular genetics studies performed by several research groups have identified the major pathogenic determinants of *B. glumae*. Among them, the most important factors are phytotoxins and lipases. Additional virulent factors known to contribute to the full virulence of *B. glumae* include PehA and PehB polygalacturonases (Degrassi et al, 2008), KatG catalase (Chun et al, 2009) and the Hrp type III secretion system (Hrp-T3SS) (Kang et al, 2008). Endopolygalacturonase and exopolysaccharides are also good candidates that may have roles in *B. glumae* pathogenesis (Jeong et al, 2003).

Phytotoxins

The most important phytotoxins produced by *B. glumae* are the bright yellow pigments toxoflavin and fervenulin which are isomerides (Kim et al, 2004). To date, most research focuses on toxoflavin. The production of toxoflavin is dependent on growth temperature and reaches the maximal level at 37 °C, and no detectable toxoflavin is produced at 25 °C to 28 °C (Matsuda and Sato, 1988). Toxoflavin and fervenulin are essential for the pathogenicity of rice seedling and grain rot which result in the reduced growth of leaves and roots in rice seedlings, and also lead to chlorotic symptoms on rice panicles (Jeong et al, 2003).

The modes of toxoflavin biosynthesis and transportation are relatively well characterized (Kim et al, 2004; Shingu and Yoneyama, 2004; Suzuki et al, 2004). The Tox operons responsible for toxoflavin biosynthesis and transportation are polycistronic, and consist of five genes (*toxA*, *toxB*, *toxC*, *toxD* and *toxE*) and four genes (*toxF*, *toxH* and *I*), respectively. The LysR-type regulator ToxR regulates the expression of both *toxABCDE* operon and *toxFGHI* operon. These results indicate that toxoflavin can be synthesized via a common biosynthetic pathway for riboflavin synthesis, starting with the precursor GTP (Suzuki et al, 2004). In addition, the expression of both operons requires the transcriptional activator ToxJ whose expression is regulated by quorum sensing (QS). TofI, a LuxI-family protein, is responsible for the biosynthesis of

N-octanoyl homoserine lactone (C8-HSL). C8-HSL and its cognate receptor TofR (a LuxR-family protein) can activate *toxJ* expression (Goo et al, 2015). However, it is notable that very little is known about how *B. glumae* cells transport toxoflavin and protect themselves against this toxin.

Jung et al (2013) reported that the toxoflavin produced by *B. glumae* is not only responsible for the pathogenesis of BPB, but also can be used to control some fungal diseases in rice, such as those caused by *Fusarium graminearum.* In addition, some unique pigments produced by *B. glumae* also have the capacity of inhibiting the growth of some fungal pathogens, such as *Collectotrichum orbiculare* (Karki et al, 2012), or may act as the scavengers of reactive oxygen species generated from the oxidative burse responses of host cells (Zughaier et al, 1999). Recently, the enzymes related to the biosynthesis of these unique pigments have been reported. They are involved in the growth, UV resistance and virulence of *B. glumae* (Karki and Ham, 2014). The research has provided some clues to take the advantages of *B. glumae* as useful tools for biological control.

Lipases

Lipases have a high capacity to hydrolyze a wide range of triacylglycerols and synthesize acylglycerol esters. Microbial lipases have many important industrial applications because of their superior enzymatic properties, stability, selectivity and substrate specificity. During the last decade, the lipases produced by *B. glumae PG1* are found to be superior in improving overall detergency and have become the subject of most intense research. The complete genome sequence of *B. glumae PG1* has been reported recently (Voget et al, 2015).

Lipases have also been reported to be involved in the pathogenicity of *B. glumae*. The most important virulent-relative lipase is LipA, which is an active extracellular lipase (Frenken et al, 1993). Another important lipase is LipB, which is involved in the biosynthesis of LipA and essential for obtaining active LipA, and has a profound influence on the stability of the proteins for proteolytic degradation (Frenken et al, 1993; El Khattabi et al, 2000). Ca^{2+} plays an active structural role in stabilizing the lipase of *B. glumae* under detrimental conditions (Devescovi et al, 2007).

Other virulent factors

A previous study indicates that toxoflavin and lipase are not sufficient for causing grain rot because the flagellar motility system, secretion system and QS in bacteria appear to be required for efficiently infecting plant tissues.

The movement driven by flagella is important for pathogenic bacteria. It allows them to arrive at the infection sites in a potential host and confers a significant selective advantage during the initial establishment phase of infection (Davey and O'Toole, 2000). In addition, the flagellar function is coordinately regulated in response to certain environmental factors (such as QS, temperature, osmolarity and pH) and global regulatory proteins (such as H-NS and the cAMP-CAP complex) (Kim et al, 2007; Jang et al, 2014).

The type III secretion system (T3SS) plays a central role in the virulence of many gram-negative bacterial pathogens, but the function and underlying mechanism of T3SS in *B. glumae* are less characterized. A proteomic study of *B. glumae* has revealed that the *B. glumae* T3SS is encompassed of 34 proteins which accumulate in a HrpB-dependent manner. Most of these proteins are secreted through the type II protein secretion system (T2SS) (Kang et al, 2008). The less virulence in T3SS-deficient *B. glumae* mutant suggests that the effectors of T3SS are required for *B. glumae* virulence, and even none of them has been reported in *B. glumae*.

QS may be the most important environmental factor for *B. glumae* because various bacterial biological processes can be under the control of the QS regulon, particularly the systems involved in the secondary metabolite production, virulence and symbiosis (Barnard et al, 2007). Toxoflavin biosynthesis, lipase production and secretion, as well as the bacterial motility are all controlled by QS system (Devescovi et al, 2007; Goo et al, 2015). Only one QS system exists in *B. glumae*, and it is composed of a LuxI-family acyl-homoserine lactone synthase TofI, a LuxR-family acyl-homoserine lactone receptor and TofR (Kim et al, 2004). An et al (2014) discovered that QS can down-regulate glucose uptake, substrate level, oxidative phosphorylation and *de novo* nucleotide biosynthesis in *B. glumae*, and may function to modulate and coordinate nutrient utilization and the homeostatic primary metabolism of individual cells. However, QS is just one component of the extremely complicated regulatory hierarchy that allows bacteria to titrate and respond to external signals. The current challenge is to determine which position QS occupies in the global regulatory hierarchy and to elucidate its

true physiological and evolutionary functions.

Strain diversity of *B. glumae*

Previous studies have identified abundant strains of *B. glumae*, and more than 400 strains are isolated in the rice-production regions of the United States (Nandakumar et al, 2009). Some high virulent strains have been characterized and confirmed, and they can cause 50% to 75% yield reduction (Francis et al, 2013; Karki and Ham, 2014). It has also been noted that some avirulent strains isolated from infected rice grains in blighted panicles and sheath lesions do not produce toxoflavin and induce neither obvious symptom nor significant yield reduction. However, they can produce additional antifungal compounds against some fungi, such as *Magnaporthe grisea* and *Rhizoctonia solani*, which indicates that the avirulent strains with antifungal activities may be useful tools for biological control (Karki et al, 2012). According to the studies of Seo et al (2015), the diversity of *B. glumae* may related to its rapid genome rearrangements or deletions in response to hosts. The unique features of rice pathogenic *Burkholderia* species have also been clarified.

Weinberg et al (2007) reported that *B. glumae* causes human infecting chronic granulomatous disease which is rarely induced by plant bacterial pathogens. In the clinic, the physical examination of an 8-month-old patient continuously suffered from fevers reveals decreased breath sounds in the middle left and upper right lung fields with heterogeneous, multifocal, and certain nodular opacities that are the most confluent in the right upper and left lower lobes. Based on the analysis of cell wall fatty acid composition, the first isolated organism after 2 d of incubation using blood cultures is *Burkholderia cepacia*. Later, it is identified as *Burkholderia gladioli* based on its 16S rRNA sequence and polymerase chain reaction (PCR) based assay. Finally, this causal agent is determined as *B. glumae* by comparing its whole-cell protein profile with those of several reference strains, and then it is named as strain AU6208 (Weinberg et al, 2007). Some studies have reported that the *B. glumae* AU6208 is more virulent than the other *B. glumae* strains when inoculated to rice plants (Devescovi et al, 2007; Costa et al, 2011).

Omics study of *B. glumae*

With the development of high-throughput sequencing and bioinformatics, there is an increasing trend in exploring the pathogenesis, signal transduction, the interaction between *B. glumae* and host through genomics, transcriptomics and proteomics analysis. Lim et al (2009) firstly reported the genome sequence of the standard strain *B. glumae* BGR1 from a rice variety in Korea. This strain has two chromosomes and four plasmids. In 2012, our labaratory uploaded the draft genome of a high virulence rice strain LMG2196. Francis et al (2013) performed the comparative genomic analysis of the strain BGR1 and the high virulence strain 336gr-1 isolated from the United States. Their results reveal the unique regions of the two strains in mobile elements, phage-related genes and some predicted genomic islands, but little variations are detected in known and potential virulence genes. Later, Kim et al (2014) discovered that most genes related to bacterial chemotaxis-mediated motility, ascorbate and trehalose metabolisms, and sugar transporters (including *L*-arabinose and *D*-xylose) are highly enriched in *B. glumae* under *in vivo* condition. These omics studies on *B. glumae* will facilitate the elucidation of unknown plant-pathogenic bacteria interactions and the overall infection process of *B. glumae*.

Another study has shown that *B. gladioli* can induce similar symptoms as *B. glumae* in rice, although *B. glumae* strains are generally more aggressive and can cause more severe symptoms than *B. gladioli* (Nandakumar et al, 2009). In addition, the virulent strains of both species produce toxoflavin and have similar growth responses to temperature (Nandakumar et al, 2009). However, besides the genotypic differences between these two strains that can contribute to phenotypic differences of disease, comparative genomics analysis indicates that *B. glumae* and *B. gladioli* contain distinct groups of genes for encoding the type VI secretion systems, transcriptional regulators, and membrane sensing proteins (Fory et al, 2014). In addition, some researchers have enriched the model of gene locus for rice resistance to *B. glumae* (Magbanua et al, 2014; Mizobuchi et al, 2015).

Detection and control of *B. glumae*

With the gradually increasing of the BPB disease, many rice growing countries, especially the tropical and subtropical areas, now pay more attentions to restrict the entry of the seed-borne pathogen *B. glumae* into their agroecosystems during international

trade. Therefore, the phytosanitary regulations of these countries perhaps improve the most critical need of accurate and reliable diagnostic tools for *B. glumae*. The identification of bacterial pathogens *B. glumae* based on colony morphology or disease symptoms is difficult and time-consuming because of the high similarity among *Burkholderia* spp. Rapid detection and accurate identification of pathogens are critical steps to prevent pathogens.

To date, most research on bacteria detection is mainly based on conventional biochemical and molecular methods. Maeda et al (2006) have distinguished *B. glumae* from different *Burkholderia* spp. by using PCR and the specific primers designed for *gyrB* and *rpoD*. Sayler et al (2007) have developed a real-time PCR (RT-PCR) method for detecting the *B. glumae* isolated from the United States using the specific primers designed for internal transcribed spacer sequence. Fang et al (2009) have also developed a RT-PCR method for detecting *B. glumae* using SYBR Green dye and the specific primers designed for ITS sequence. In our laboratory, Luo et al (2008) have isolated and identified six *B. glumae* strains from the non-symptom rice seed samples in China based on physiological characteristics, colony morphology, pathogenicity test, biology, fatty acid methylester analysis and random amplified polymorphic DNA. Li et al (2010) have also developed a RT-PCR method for detecting *B. glumae* using the TaqMan probe designed for *gyrB*. Kim et al (2012) set up a Bio-PCR method to detect *B. glumae* using the specific primers designed for *rhs* gene family.

Molecular methods, such as RT-PCR, are highly sensitive techniques for the identification and quantification of plant pathogens. However, the *B. glumae* strains in different rice-production regions have some differences in their genome and virulence. Therefore, it is important to consider both local and reference *B. glumae* strains when developing diagnostic method. In addition, *B. glumae* can co-invade with other bacterial pathogens (such as *B. gladioli*) on the same tissue of rice (Nandakumar et al, 2009). The co-invasion bacteria will not induce symptom in latent infections or appear to be symptomless, but they may outbreak and become predominate in suitable environmental conditions, resulting in epidemics. It is difficult for farmers to detect or control bacterial pathogens. Moreover, it is so difficult to predict multi-pathogen epidemics in different rice-production countries due to their different environmental conditions, which is a potential threat to rice yield and quality.

Based on previous studies (Luo et al, 2008; Fang et al, 2009) and other data, our laboratory has recently developed a multiplex PCR (mPCR) method for the simultaneous detection of six common rice bacterial pathogens, including *B. glumae*, *B. gladioli*, *Xanthomonas oryzae* pv. *oryzae*, *Xanthomonas oryzae* pv. *oryzicola*, *Pseudomonas fuscovaginae* and *Acidovorax avenae* subsp. *avenae*. To ensure its efficacy and reliability, this mPCR method has been evaluated using 150 target and non-target bacterial strains from different rice-production regions worldwide. This method can use tissue extracts or DNA, which is cost-effective and time-saving. After applying the mPCR method in 44 symptomatic or asymptomatic natural rice samples, we have observed six target pathogens causing the bacterial diseases of rice in the same paddy field at the same time, but some of them are asymptomatic on rice. The result shows that 3–4 target pathogens are detected for the individual bacterial disease of the samples. From asymptomatic samples, 2–3 target pathogens can be detected. These results indicate that the mPCR method is sensitive in detecting pathogens for early diagnosis and can be of flexible applications according to the local disease symptoms, which may play a crucial role in effective disease prevention and management (unpublished data).

BPB is a severe disease not only due to the diverse of pathogens, but also because of the lack of effective methods to control this disease. Raising disease-resistant varieties may be the best option, but only partially resistant varieties are currently available and they lack desired commercial characteristics (Sayler et al, 2006; Ham and Groth, 2011; Karki et al, 2012). Oxolinic acid can be used in seed treatment or foliar application, and is the only chemical that can control BPB by now. However, it is not commercially available in some countries. Additionally, the occurrence of oxolinic acid-resistant *B. glumae* strains will limit the use of this chemical (Maeda et al, 2004; Ham and Groth, 2011). Cui et al (2014) reported that *B. glumae* exhibits multi-drug resistance to ampicillin and kanamycin, and discovered that both copper compounds and Cu^{2+} have antibacterial activity against *B. glumae* isolated from patients and rice plants. However, it is still very hard to explore an efficient and low-toxic bactericide to control this disease.

Challenges and perspectives

BPB is one of the most severe rice bacterial diseases with rapid spread in the world, and it tends to be more serious in recent years. In particular, significant yield loss from BPB have been experienced in the rice-producing regions of southeastern United States, including Louisiana, Texas and Arkansas in 1996, 1997, 2000, and most recently, in 2010 (Ham et al, 2011). The occurrence of many plant diseases has the characteristic of geographical or climate limitation but the BPB caused by *B. glumae* can be widely distributed in Asia, Africa, South and North America just in a few years, which is a notable issue. The high yield loss caused by *B. glumae* in rice is due to the lack of effective BPB prevention and control measures for susceptible rice cultures (Nandakumar et al, 2009). Moreover, the pathogenically/genetically diverse strains of *B. glumae* have been isolated from asymptomatic rice plants and those with BPB symptoms, which indicates the rapid evolution of *B. glumae*. Seo et al (2015) pointed out that it may result from the rapid genome rearrangements or deletion of *B. glumae* in response to hosts. Based on the above studies, the pathogen-host interaction may depend on environmental factors, such as temperature and humidity, the local rice cultivar grown in different rice-production regions and *B. glumae* strains. Therefore, Magbanua et al (2014) have analyzed the differences in gene expression among the resistant and susceptible rice cultivars interacted with *B. glumae*, which may provide a good clue for preventing BPB.

The identification of human pathogenic *B. glumae* strains presents a new challenge for the clinical research on the chronic granulomatous disease caused by *B. glumae* which is primarily an immunodeficiency disease, ultimately leading to the increased risk of invasive human infections. In addition, BPB is an emerging rice disease in the major rice-production regions worldwide in recent years. However, it has not been well understood, especially in China. Moreover, the bacterial wilt caused by *B. glumae* is symptomatically indistinguishable from the bacterial wilt caused by *R. solanacearum* in many field crops. Furthermore, the ecological conditions favor the development of BPB disease in some countries, such as China. Better understanding the molecular mechanisms of virulence in *B. glumae* and its interaction with rice will largely contribute to the development of efficient methods to control BPB.

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