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REVIEW

The emergence of *Pantoea* species as a future threat to global rice production

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Abstract

Pantoea species (*Pantoea* spp.) is a diverse group of Gram-negative bacteria in the Enterobacteriaceae family that leads to devastating diseases in rice plants, thus affecting significant economic losses of rice production worldwide. Most critical rice diseases such as grain discoloration, bacterial leaf blight, stem necrosis and inhibition of seed germination have been reported to be caused by this pathogen. To date, 20 *Pantoea* spp. have been identified and recognized as having similar phenotypic and diverse characteristics. Detection via phenotypic and molecular-based approaches, for example the polymerase chain reaction (PCR) and multiplex PCR give us a better understanding of the diversity of *Pantoea* genus and helps to improve effective disease control strategies against this emergent bacterial pathogen of rice. In this review, we focused on the significance of rice diseases caused by *Pantoea* spp. and insights on the taxonomy and characteristics of this destructive pathogen via phenotypic and molecular identification.

Keywords: bacterial leaf blight, grain discoloration, inhibition of seed germination, molecular approaches, *Pantoea* species

The *Pantoea* genus is a diverse group in the Enterobacteriaceae family, since it has been isolated from various ecological niches and hosts involving plants, animals, insects and humans (Muraschi *et al.* 1965; Ewing and Fife 1972; Brady *et al.* 2008; Völksch *et al.* 2009; Nandrasah and Stavrinides 2014). *Pantoea* species (*Pantoea* spp.) is commonly associated with plants as epiphytes or pathogens (Delétoile *et al.* 2009). In addition, several *Pantoea* strains can have plant growth-promoting traits or they can act as biological control agents against plant pathogens. The ability of microbes such as *Pantoea* to synthesize antibiotic compounds can confer significant advantages in competition with other microorganisms in specific ecological habitats (Raaijmakers and Mazzola 2012). Therefore, plant microbiologists used this theory for the production of biocontrol agents against plant diseases. *Pantoea ananatis* was reported as an epiphyte of rice (Watanabe *et al.* 1996) that may be beneficial to host plants by protecting them against infection by other pathogenic fungi and bacteria. *Pantoea agglomerans* has been described as an antagonist of several bacterial and fungal plant pathogens that are associated with the development of antibiotics or other mechanisms. It is a safe and environmentally friendly process that can be used as a biocontrol since it reduced pesticide doses, or even eliminates the use of chemicals (Morales *et al.* 2008). For instance, *P. ananatis* strain, *Serratia marcescens,* has been used to successfully control rice blast disease caused by *Pyricularia oryzae* (Simeya *et al.* 2003). *Pantoea agglomerans* has also demonstrated an inhibitory activity against a broad range of large fungal pathogens including *Pyricularia grisea*, a rice blast fungus causing a serious disease of rice. This bacteria produced indole-acetic acid (IAA) to promote rice growth *in vitro* (Kim and Lee 2019). *Pantoea agglomerans* strains that occur in the the rhizosphere (root-soil interface) of cultivable plants can promote the growth of rice through various mechanisms. Lakshmanan *et al.* (2015) confirmed that *Pantoea* spp. strain EA106, a natural rice rhizospheric isolate, reduces a high arsenic absorption in rice siderophore (iron binding) activity, which leads to increased Fe plaque on the roots of rice. This promotes rice development, and prevents toxic arsenic accumulation in plant tissue. Khalimi *et al.* 2012 revealed that rice seed treated with a bacterial suspension of two *P. agglomerans* strains isolated from the rhizosphere of groundnut, significantly increased plant growth and rice yield in Bali, Indonesia. However, in most previous research, *Pantoea* spp. was also paradoxically identified as a phytopathogenic species that has the ability to colonize and interact with members of both the plant and animal kingdoms. Some *Pantoea* spp. are recognized as the causative agent of bacterial diseases in various plant hosts such as maize, melon, cotton and onion (Gitaitis and Gay 1997; Walcott *et al.* 2002; Medrano and Bell 2007; Kido *et al.* 2008; Brady *et al.* 2011). The most recognized phytopathogenic *Pantoea* spp. are *P. ananatis*, *P. agglomerans* and *Pantoea stewartii* that affect economically important crops including vegetables, cereals and fruits (Brady *et al.* 2008; Coutinho and Venter 2009; Morin 2014). Over the years, *Pantoea* spp. was reported as one of the pathogenic bacteria that caused devastation to rice crops worldwide, resulting in serious economic losses. It has been reported that the current outbreaks of this species have caused more than 80% of plant diseases (Kini *et al.* 2019). The *Pantoea* genus was initially reported to cause destructive diseases on rice, such as palea browning and grain discoloration in Japan (Azegami 1983; Tabei *et al.* 1988), stem necrosis (Cother *et al.* 2004), bacterial leaf blight disease in Korea (Lee *et al.* 2010) and germplasm of rice seeds (Carrer Filho *et al.* 2018). Diseases caused by this pathogen can be a devastating threat to rice production worldwide, thus leading to significant losses in rice productivity and quality. In this review, relevant literature on taxonomy, characteristics, rice diseases and detection via molecular methods on *Pantoea* spp. will be overviewed to serve as guidelines for a better understanding on the diversity of this pathogen in global rice production.

History and taxonomy of *Pantoea* species

The genus *Pantoea,* derived from the Greek word "Pantoios", is defined as "of all sorts or sources". This indicates the diversity of the bacteria that can be isolated from various geographical and ecological niches (Kini *et al.* 2018). Originally, before it was well established, the taxonomy of *Pantoea* was complex and confusing. *Pantoea* genus was first introduced by Gavini *et al.* (1989), where some of the *Pantoea* members were classified as *Bacillus agglomerans* (Beijerinck 1888) and *Enterobacter agglomerans* (Beijerinck 1888; Tindall 2014).

Other names associated with group members of *Pantoea* were also created including *Bacterium herbicola*, *Pseudomonas herbicola*, *Erwinia herbicola* and *Erwinia milletiae.* Three groups were later classified as *P. agglomerans.* In 1992, bacterial strains that were isolated from soils and fruit samples were found to be shared by the general characteristics of the Enterobacteriaceae family. Based on DNA hybridization, three new species were introduced and classified in the genus *Pantoea* as *P. punctata, P. citrea* and *P. terrea* (Kageyama *et al.* 1992). Later, *Erwinia uredovora* and *E. ananas* were grouped into similar species based on DNA-related studies and fatty acid analysis, creating two subsequent species, namely *P. ananatis* and *P. stewartii.* Two subspecies were created within *P. stewartii*, known as *P. stewartii* spp. *stewartii* (*Pnss*) and *P. stewartii* spp. *indologenes* (*Pnsi*) (Mergaert *et al.* 1993).

Presently the *Pantoea* genus consists of 20 recognized species that are similar phenotypically and are comprised of 13 hybridization groups (Brady *et al.* 2008, 2009a, b; Popp *et al.* 2010; Walterson and Stavrinides 2015). The relationships between the established *Pantoea* groups were explained and constructed using *atpD*, *gyrB*, *infB* and *rpoB* genes (Fig. 1).

Etiology and symptoms of rice diseases

Numerous pathogens, including fungi, bacteria, viruses and nematodes are the causative agents of many rice diseases worldwide (Séré *et al.* 2013; Kini *et al.* 2019). Since rice is a crucial source of food for the human population worldwide, information about *Pantoea* spp. as one of the causal agents of rice diseases is essential. In Malaysia, three pathogenic *Pantoea* spp., *P. ananatis*, *P. stewartii* subsp. *indologenes*, and *P. dispersa,* were reported to have caused bacterial leaf blight (BLB) disease of rice (Azizi *et al.* 2019a, b; Toh *et al.* 2019).

Bacterial leaf blight disease is commonly caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), which

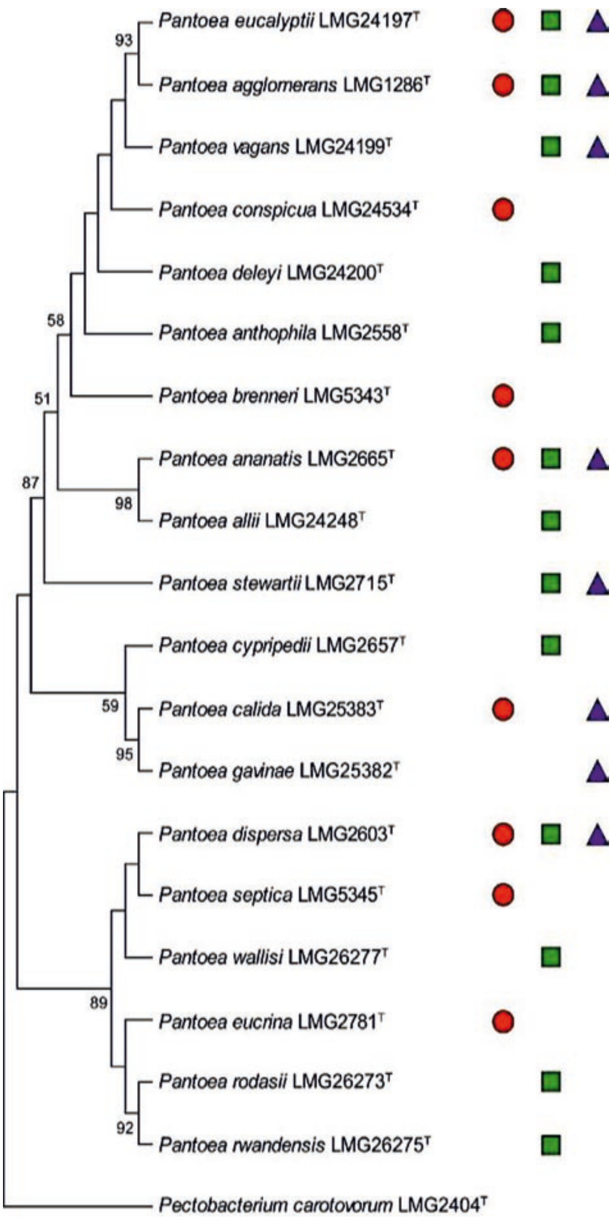

Fig. 1. Neighbor-joining phylogenetic tree of *Pantoea* strains using maximum-likelihood based on partial *rpoB*, *gyrB*, *atpD* and 16S rRNA genes. Nodes result showed 1,000 bootstrap replicates with values >50%. Symbols adjacent to each representative type strains indicated a setting where strains were isolated from (red circle), from plant hosts either as an epiphyte or a pathogen (green square), or from the natural environment (purple triangle) (adapted from Walterson *et al.* 2015)

was first described by Japanese growers in 1884 (Tagami 1962). The disease caused by *Xoo* is critical and it is the oldest bacterial disease of rice in Asia (Naqvi *et al.* 2014). Yield losses of 10–20% under moderate conditions and severe losses of up to 50% have been recorded in several Asian and Southeast Asian countries (Mew 1993; Kala *et al.* 2015; Ilsan *et al.* 2016). However, in 2010, BLB was first described to be caused by *P. agglomerans* in South Korea (Lee *et al.* 2010). BLB outbreaks were also reported in different regions including India (Mondal *et al.* 2011), Venezuela (Gonzalez *et al.* 2015), Russia (Egorova *et al.* 2015), Benin and Togo (Kini *et al.* 2017a, b), southern districts of Tamil Nadu (Vinodhini *et al.* 2017), and Malaysia (Azizi *et al.* 2019a, b; Toh *et al.* 2019).

Based on symptomatic leaves exhibiting typical blight characteristics as *Xoo* (Kini *et al.* 2017a) it is not possible to differentiate between *Pantoea* and *Xoo* as the causal agent of BLB disease. Therefore, BLB caused by *Xoo* is also caused by *Pantoea* due to similar symptoms (Lee *et al.* 2010; Mondal *et al.* 2011). However, the coloration symptoms exhibited by different *Pantoea* spp. varies slightly in infected rice plants (Doni *et al.* 2019). In Russia, BLB symptoms caused by *P. ananatis* were reported as water-soaked lesions, light and rusty on leaves which later turned brown (Egorova *et al.* 2015) (Fig. 2E). Symptoms were also characterized by Kini *et al.* (2017a) as orange to brown stripes on the leaf blade that expanded to the entire leaf, the leaf tip and along the margins.

Grain discoloration is also considered as a severe rice disease caused by certain microorganisms on the kernel, glumes or both. The disease is known to be caused by fungal pathogens such as *Bipolaris oryzae*, *Alternaria padwickii*, *Pyricularia oryzae*, *Fusarium moniliforme*, *Fusarium graminearum* and *Nigrosporaoryzae* (Ou 1983), and bacteria such as *Pseudomonas fuscovaginae*, *P. (Acidovorax) avenae*, *P. syringae* pv. *syringae* and *Burkholderia glumae* (Zeigler and Alvarez 1990). This disease has been described as an independent disease that contributes to significant losses in rice production (Mew *et al.* 2004; Arshad *et al.* 2009; Prabhu *et al.* 2012; Ashfaq *et al.* 2013; Chandramani and Awadhiya 2014). The *Pantoea* genus has also been described as the causative agent of grain discoloration since 1983, when it was first reported in Japan (Azegami 1983) and China (Xie 2001; Hong *et al.* 2002; Yan *et al.* 2010). The disease contributed to severe losses in rice production, as much as 75%, due to grain weight reduction, floret sterility, strands reduction, inhibition of seed germination and year-to-year transmission on account of the seed borne pathogen (Trung *et al.* 1993). Symptoms initially include light, rusty, water-soaked lesions on the lemma or palea, which later turn brown, causing grain discoloration and abortion (Yan *et al.* 2010).

In 2003, *P. ananatis,* which causes stem necrosis symptoms in rice, was reported in Australia (Cother *et al.* 2004). However, there has been no recent report of the disease caused by *Pantoea* spp. from other countries. Typically, the stems of rice which exhibited necrosis produced discoloration that extended from within the rachis down to the stem. Discoloration of the stem stopped near the flag leaf collar. However, in a few cases, discoloration extended into the sheath and ended

Fig. 2. Symptoms appeared on rice caused by *Pantoea* species: A – lesions on stem caused by *Pantoea ananatis*; B – necrotic stems caused by *P. ananatis*; C – light brown and moist lesions caused by *P. ananatis*; D – necrotic stems exhibiting blackened top nodes and lesion on flag sheath caused by *P. ananatis* (adapted from Cother *et al.* 2004); E – leaf blight on rice leaves (adapted from Egorova *et al.* 2015)

at the second node of the rice stem. A dark lesion was also visible at the panicle base. Meanwhile, the side of the top node turned black, displaying a severely affected stem (Fig. 2A, B, C, and D). Unseasonable conditions, such as hot, dry and windy weather, might be some of the important factors that aggravate the severity of the disease (Cother *et al.* 2004). Cother *et al.* (2004) have dissected infected samples and found a conspicuous amount of fine dust particles present between the flag leaf sheath as well as the stem. The situation occurred together with highly windy conditions, causing abrasion of surrounding tissue and allowing the entry of *P. ananatis* as well as its colonization. As the leaves age, the population of *P. ananatis* increases within the leaves and rapidly proliferates (Watanabe *et al.* 1996). *Pantoea ananatis* which lives epiphytically (Watanabe *et al.* 1996) on rice is able to multiply within rice plants infested with brown planthopper (*Nilaparvata lugens*), thus promoting the development of hopperburn symptoms (Cother *et al.* 2014).

In 2008 in Brazil, *P. agglomerans* was reported to be associated with germplasm of rice seeds (Carrer Filho *et al.* 2018). The disease was noticed when rice seeds showed little to no germination. The infected seed coat of 10 seeds was removed aseptically and cultured on media to obtain a bacterial colony. A hypersensitive test on tobacco seedlings and pathogenicity on 'Caloro' rice cultivar showed positive results for bacterial isolates. Symptoms displayed light brown spots on the leaf part which caused leaf browning and drying. Aksoy and Bulok (2018) also described a similar disease caused by *P. ananatis* which infected Japonica rice seeds during the 2016 and 2017 growing seasons. Table 1 shows a summary of rice diseases caused by *Pantoea* spp. from various countries.

Phenotype characteristics

Isolation

In general, the *Enterobacteriaceae* bacteria are isolated onto media such as nutrient agar, tryptic soy and blood agar. Specific media can also be employed for the isolation of the *Enterobacteriaceae* e.g. MacConkey and Hektoen media that are specifically designed for *P. ananatis* isolation (Grimont and Grimont 2015). In general, isolation of bacteria from infected plants is mainly carried out using nutrient agar (Bruton *et al.* 1991; Gitaitis and Gay 1997; Schaad 2001; Countinho *et al.* 2002). Based on previous studies, *Pantoea* spp., isolated from diseased rice plants, were streaked onto NSCV selective medium (Hasegawa *et al.* 2003), onto sucrose-phosphate-glutamate (S-PG) medium, King's medium B (Cother *et al.* 2004), yeast dextrose carbonate agar (Egorova *et al.* 2015), semi-selective peptone-sucrose-agar medium (Kini *et al.* 2017a) and Wakimoto's potato semi-synthetic medium (Vinodhini *et al.* 2017). All the media that was used to isolate bacteria displayed similar morphological characteristics with *Pantoea* spp. where the bacterial colonies produced were straw- to yellow-colored, round in shape and had smooth margins (Cother *et al.* 2004; Mondal *et al.* 2011; Egorova *et al.* 2014; Kini *et al.* 2017a, b; Vinodhini *et al.* 2017).

Recently, an inexpensive semi-selective medium called *Pantoea* genus-specific agar (PGSA) was developed by Kini *et al.* (2019) using halophilic properties. It is a selective and specific medium that allows only *Pantoea* isolates to grow without contamination of other bacteria and fungi. Based on the experiment conducted by Kini *et al.* (2019), 20 *Pantoea* spp. which included *P. ananatis, P. stewartii* and *P. agglomerans* isolates were cultured on PGSA medium and incubated for 48 h. Colonies of all isolates were characterized as being yellow with purple borders for 48 h. Cultures were continuously incubated till 72 h when floury and highly viscous pale-yellow colonies of *P. ananatis* and *P. agglomerans* were coalesced. In comparison, *P. agglomerans* was not floury, while *P. stewartii* was coalesced and sticky, but not highly viscous.

Table 1. Summary of rice diseases caused by *Pantoea* species from reported countries

State/Province	Disease	Causal agent	Reference
Japan	grain discoloration	*P. agglomerans*	Azegami *et al.* (1983)
South Korea	leaf blight	*P. agglomerans*	Lee *et al.* (2010)
China	grain discoloration	*P. ananatis*	Xie (2001) Hong *et al.* (2002) Yan *et al.* (2010)
Australia	stem necrosis	*P. ananatis*	Cother *et al.* (2004)
India	leaf blight	*P. ananatis*	Mondal *et al.* (2011)
Russia	leaf blight	*P. ananatis*	Egorova *et al.* (2015)
Venezuela	leaf blight	*P. ananatis*	González *et al.* (2015)
Togo	leaf blight	*P. ananatis* and *P. stewartii*	Kini *et al.* (2017b)
Benin	leaf blight	*P. ananatis* and *P. stewartii*	Kini *et al.* (2017a)
Southern Districts of Tamil Nadu	leaf blight	*P. stewartii* subsp. *indologenes*	Vinodhini *et al.* (2017)
Brazil	inhibition of rice seeds germination	*P. agglomerans*	Filho *et al.* (2018)
Turkey	inhibition of rice seeds germination	*P. ananatis*	Aksoy and Bulok (2018)
Malaysia	leaf blight	*P. stewartii* subsp. *indologenes*, *P. ananatis* and *P. dispersa*	Azizi *et al.* (2019a, b) Toh *et al.* (2019)

Identification of *Pantoea* species associated with rice diseases via phenotypic characteristics

A biochemical test is a traditional method that is used to routinely identify and characterize bacteria depending on the source of material, diversity of the bacteria encountered and purpose of experiment. Gram-staining is performed at an early stage of investigation to reveal the size, shape and arrangement of bacteria cells from morphological observation (Holding and Collee 1971). Table 2 shows the biochemical tests performed on three different *Pantoea* spp. of rice plants.

Molecular identification of *Pantoea* species associated with rice diseases

Identification of bacterial pathogens using molecular approaches is increasingly often used by most researchers since it is faster, more specific, accurate and can be performed without taxonomical expertise. In general, *Pantoea* strains isolated from diseased rice were identified based on universal 16S rDNA fragment amplification performed by conventional polymerase chain reaction (PCR). The 16S (small subunit) rDNA gene was the most frequently selected by researchers since it is present in all organisms, contains conserved regions and sufficient size bases which supplies abundant information for identification and phylogenetic analyses (Spratt 2004).

Specific primer designs have also been used in order to amplify the specific gene that provides better information for identification of bacteria. Carrer Filho *et al.* (2018) tested three different sets of primers to amplify *P. agglomerans*-specific based on cytokinin biosynthesis gene (*etz* gene), *P. ananatis*-specific ice nucleation active gene (*ina* gene) and the *P. stewartii*-specific *pstS-glmS* gene. New *gyrB*-specific PCR primers were designed by Kini *et al.* (2017a) based on *Pantoea* genome sequences. The *gaIE* gene amplification which encodes for UDP-glucose 4-epimerase (Gehring *et al.* 2004) was used to differentiate *P. stewartii* of subspecies *stewartii* and subspecies *indologenes* related to leaf blight disease of rice in Malaysia (Azizi *et al.* 2019a). Moreover, the *gaIE* gene is able to discriminate the single nucleotide polymorphism (SNP) variants, thus it was developed to characterize all related pathogens into species and subspecies levels (Achtman 2008).

A multiplex PCR (mPCR) was developed by Kini *et al.* (2018) as a diagnostic tool for accurate detection of pathogenic *Pantoea* spp. (e.g. *P. ananatis, P. stewartii* and *P. agglomerans*) that caused blight disease of rice. This method provides information on detection since it is robust, sensitive, specific and cost-efficient, hence useful for studies on the epidemiology of crop-threatening pathogens. Thirty-four whole genome sequences of three major pathogenic *Pantoea* spp. strains were used to design specific primers of three *Pantoea* spp. based on multilocus sequence analyses (MLSA) that were performed using complete coding sequences of four housekeeping genes (e.g. *atpD*, *gyrB*, *Infb* and *rpoB*) (Brady *et al.* 2008). Detection of three *Pantoea* spp. and other *Pantoea* members diagnosed via mPCR revealed a total of 609 *Pantoea* spp. strains from 11 different African countries (Kini *et al.* 2018). Table 3 shows a list of primers used for the amplification of *Pantoea* spp. from infected rice plants.

Challenges and future directions

Invasion of *Pantoea* spp. will affect sustainability of rice production and reduce commercial and economic activities in rice producing countries. From this review of the published literature, a better understanding on the taxonomy and identification of this pathogen via phenotypic and molecular-based approaches will help to improve and develop appropriate control strategies against *Pantoea* spp. The effectiveness and efficacy of disease management including chemical and biological controls is indeed, necessary to prevent disease transmission.

Very little is known about the virulence mechanisms and the most important phases of the pathogen cycle

Table 2. Biochemical tests of *Pantoea* species associated with rice plants

Tests	*Pantoea stewartii* subsp. *indologenes*	*Pantoea agglomerans*	*Pantoea ananatis*
Gram-staining	–	–	–
Motility	+	+	+
Indole production	+	–	+
Hydrogen sulphide production	–	–	–
Catalase test	+	+	+
Citrate utilization test	+	–	–

(+) – positive result; (–) – negative result
[Adapted from: Lee *et al.* (2010); Mondal *et al.* (2011); Egorova *et al.* (2015); Vinodhini *et al.* (2017); Aksoy and Bulok (2018)]

Table 3. List of primers used for sequencing of *Pantoea* species

Primer name	Sequence (5′-3′)	Expressed gene	References
27F 1429R	AGAGTTTGATCATGGCTCAG AAGGAGGTGATCCAACCGCA	16S rDNA	Turner *et al.* (1999)
PANsp_gyrB-F PANsp_gyrB-R	TTCCAGGARAAYATYTACTGCTT CGGTCATGATRATRATGCTGTG	*gyrB* of *Pantoea* genome	Kini *et al.* (2017a)
*etz*Fow *etz*Rev	GAGAGGTCTGGCTGATGGG CTTCTGGCAAGGATAGCACTC	*etz*	Manulis *et al.* (1998)
*ina*F *ina*R	GGGATCGCAAGCAAGCTCTGG GCGATTATTCTTCGGGTTT	*ina*	Kido *et al.* (2008)
galE 3614galE 3614galEc	CGACCTGTTTGCCTCTCACT CATCAGCTTGGAGGTGCCA	housekeeping genes *galE* of *P. stewartii* subsp. *stewartii*	Gehring *et al.* (2014) Azizi *et al.* (2019a)

of diseases. A method known as RNA-Seq has been extensively applied for expression profiling of transcripts between resistant and susceptible host plants against infection by pathogenic microbes. Thus, investigation on the interaction between rice-*Pantoea* strains associated with rice diseases using bacterial whole genome transcriptome and bioinformatic pipelines will facilitate elucidation of unknown host-pathogen interactions, as well as the overall infection processes.

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