Chapter 9
Endophytic *Bacillus* Species Induce Systemic Resistance to Plant Diseases

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9.1 Introduction

Plants have evolved a myriad of types of defense mechanisms against pathogens depending on the respective pathogen and their interaction with the microbes in the host plant. These kinds of plant-microbe interactions rely on the different pathways of resistance induction in the host cells. Some endophytic rhizobacteria are directly involved in inducing the systemic resistance during their interactions with host plants and pathogens. This systemic resistance induced in plants by nonpathogenic-antagonistic rhizobacteria is known as ISR (induced systemic resistance) against pathogens (Ryu et al. 2004a, b; Walters et al. 2005). It is one of the resistance mechanisms by the rhizobacteria or other root-colonizing nonpathogenic endophytic bacteria. Thus, these bacteria trigger the resistance induction to the plants against pathogens. But, the interaction between the pathogen and any other root-colonizing nonpathogenic microbe would be an indirect counterpart, i.e., pathogenic rhizobacteria are not directly involved to pathogen (Pieterse et al. 2009). Detailed studies of the immune-related mechanisms through the plant-microbe interaction have been executed in *Arabidopsis* and rice plants (Jones and Dangl 2006). In the monocot model plant rice, a devastating fungal pathogen, *Fusarium fujikuroi* Nirenberg (anamorph), which causes bakanae disease has been controlled successfully by the *Bacillus oryzicola* YC7007 (Hossain et al. 2016). Some other endophytic bacteria were reported to suppress rice diseases by inducing the "ISR" against bacterial and fungal pathogens and also to promoted rice growth. Endophytic

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Gluconacetobacter diazotrophicus strain PAL5 also controls the pathogen by enhancing the resistance through the JA signaling pathway (Alqueres et al. 2013; Hossain et al. 2016). Of the many endophytic bacteria, several *Bacillus* species stimulate the plant immune system and utilize the JA signaling pathway in the ISR to control plant diseases (Kloepper et al. 2004; McSpadden Gardener 2010). *Bacillus oryzicola* YC7007 and YC7010^T, which are two novel endophytic strains isolated from rice roots, were reported to induce systemic resistance against *F. fujikuroi*, *Burkholderia glumae*, and *Xanthomonas oryzae* pv. *oryzae* in rice (Chung et al. 2015). By inducing the expression of *OsLOS-L2* and *OsAOC* genes via the JA signaling pathway, strain *B. oryzicola* YC7007 successfully controlled rice bakanae disease (Hossain et al. 2016). In the dicot model plant *Arabidopsis*, endophytic *Bacillus* species such as *B. subtilis* GB03 and *B. amyloliquefaciens* IN937 against *Erwinia carotovora* subsp. *carotovora* and *B. cereus* AR156 and *B. subtilis* against *Pseudomonas syringae* pv. *tomato* DC3000 were also reported to switch on the defensive signaling network for the induction of systemic resistance in *Arabidopsis* (Kloepper et al. 2004; Kumar et al. 2012; Niu et al. 2011).

For controlling the diseases, chemical fungicides have been widely used during the past decades, but the efficacy of chemical pesticides has decreased recently due to the occurrence of resistance (Yang et al. 2012). Furthermore, application of some chemical fungicides encourages the fungus to produce more mycotoxins (D'Mello et al. 1998). So, the approach of alternative control measures like ISR using antagonistic microorganisms with the underlying defensive mechanisms would be a breakthrough for controlling plant diseases.

9.2 Biological Control Agents

According to Pal and McSpadden Gardener (2006), biological control can be defined as the use of antagonist microbes to suppress the pathogens and finally control diseases. According to the US National Research Council, biological control refers to "the use of natural or modified organisms, formulated product, genes, or gene products, to reduce the effects of undesirable organisms and to favor desirable organisms such as crops, beneficial insects, and microorganisms" (Anon. 1996). Biological agents, therefore, must be environmentally sound as a trigger bio-agent for controlling plant disease. It has a vast network of living organisms interacting in their natural environment. The presence of an organism is determined by favorable environment; presence of associated organisms (symbionts) for its development, or of organisms required for its survival (e.g., hosts for parasites); and the inhibition or absence of organisms (disease organisms, antagonistic, predators) to cause the extinction of pathogen. Thus, interaction is the essence of a population, and this continued existence would be evidence of biological balance. Mutualism, protocooperation, commensalism, antagonisms, competition, and neutralism to the nature are the principle for biological agents. Many mutualistic rhizobacteria, fungus, and yeasts are well reported as biological agents. Fungi, *Piriformospora indica* against the *Fusarium culmorum* (Harrach et al. 2013), *Talaromyces* sp. KNB-422, and *Trichoderma* isolates against bakanae (Bhramaramba and Nagamani 2013; Kato et al. 2012), and yeasts, *Metschnikowia pulcherrima* and *Pichia guilliermondii* against bakanae (Matic et al. 2014), have been reported as biological agents. Additionally, bacterial genera such as *Bacillus*, *Burkholderia*, *Lysobacter*, *Pantoea*, *Pseudomonas*, and *Streptomyces* have been used as biocontrol agents for controlling diseases of many crops. In recent years, much research has been done on biological agents for different crops using the *Bacillus* species. However, biological control of diseases of agricultural crops, especially rice, is still in its infancy compared with chemical pesticides. Meanwhile, there is a public demand for healthier foods free of contamination from chemical residues.

9.3 The Genus *Bacillus* Is the Good Source for Biological Control

The genus *Bacillus* was first described by Cohn in 1872 (Claus and Berkeley 1986). Numerous *Bacillus* strains have been reported as biocontrol agents for plant pathogens. They can lead to suppression of plant diseases as well as to stimulate plant growth directly (Niu et al. 2011). Many *Bacillus* species produce different types of antibiotic compounds, such as phenazines, pyrrolnitrin, and pyoluteorins, as well as lipopeptides, such as fengycin, iturin, or surfactin, which inhibit the growth of plant pathogens. Some of these species also produce phytohormones, including auxin indole acetic acid (IAA), cytokinin, and gibberellins that actively promote the plant growth (Arkhipova et al. 2005; Bais et al. 2004). A greater understanding of this genus with their many uses will help to accelerate the development and improvement of crop quality and yields. Recently, one endophytic *Bacillus oryzicola* YC7007 has been reported as a novel species that successfully controlled the rice bakanae and bacterial blast diseases (Chung et al. 2015; Hossain et al. 2016). The *Bacillus* species which are widely used for biological control of many plant diseases in different hosts include *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* (Kloepper et al. 2004; McSpadden Gardener 2010; Niu et al. 2011). *B. subtilis* GB03 and *B. amyloliquefaciens* IN937 were demonstrated to control the bacterial pathogen, *Erwinia carotovora* subsp. *carotovora* in *Arabidopsis* (Ryu et al. 2004b). *B. cereus* AR156 and *B. subtilis* were also demonstrated to control *Pseudomonas syringae* pv. *tomato* DC3000 successfully in *Arabidopsis* by inducing resistance (Niu et al. 2011). Some of these *Bacillus* species have been well characterized in terms of their anti-fungal, antibacterial, plant growth-promoting, and resistance-inducing activities in host plants (Park et al. 2009; Ryu 2013). Among the diverse antagonistic bacteria, several *Bacillus* species have been developed as commercial biopesticides because they can produce endospores and persist successfully in natural environments for a long period after treatment (Hu et al. 2011). *Bacillus* species have been reported as strong biological agents showing the dramatic action against the rice pathogens. Diverse species of

Table 9.1 *Bacillus* species used for controlling the major rice diseases

Bacillus species	Pathogen (disease)	Mechanism	References
Bacillus oryzicola YC7007	*B. glumae* (panicle blight), *F. fujikuroi* (bakanae)	ISR	Chung et al. (2015)
B. polymyxa	*Magnaporthe oryzae* (blast of rice)	ISR	Gnanamanickam and Mew (1992) and Kavitha (2002)
B. pumilus	*Magnaporthe oryzae* (blast of rice)	ISR	Gnanamanickam and Mew (1992) and Kavitha (2002)
B. coagulans	*Magnaporthe oryzae* (blast of rice)	ISR	Gnanamanickam and Mew (1992) and Kavitha (2002)
B. polymyxa	*Rhizoctonia solani* (sheath blight)	ISR	Gnanamanickam and Mew (1992)
B. cereus	*X. oryzae* pv. *oryzae* (bacterial blight)	ISR	Velusamy and Gnanamanickam (2003)

Bacillus have been isolated from various terrestrial and halophytic plants, and some of them have been shown to be endophytic (Bibi et al. 2012; Bibi et al. 2011) (Table 9.1).

9.4 History of Resistance Induction

History of resistance induction is not very precisely denoted in the literature. Many scientists have documented their opinions about the history of resistance induction. Biological control that encompasses resistance induction is a more interesting research topic compared with only biological control measures. From the beginning, in the 1970s to the 1980s, biological control research consisted screening of antagonistic microorganisms for their biological activity (Ryu 2013). However, mechanisms were not elucidated in many cases. Through the study of plant-microbe interactions it is revealed how microbes work in the defense signaling pathways such as induced systemic resistance (ISR), systemic acquired resistance (SAR), and primed induced resistance (PIS) against phytopathogens is an interesting subject in the biocontrol measures. Resistance induction, therefore, is called a safe fungicide (Walters et al. 2005). Resistance induction was first proposed as the "acquired physiological immunity" by Chester (1933). Systemic acquired resistance was first proposed by Ross (1961). Pathogen-related gene *PR* was discovered by Van loon (1982). Since then, the plant-microbe interaction was implemented in agriculture. When ISR was first proposed by Van Peer and Schippers (1992), resistance induction by the plant growth-promoting rhizobacteria (PGPR) was shown to be more protective against phytopathogens with indirect interaction. Since then, many scientists were involved in the ISR mechanisms for controlling plant diseases.

9.5 Resistance Induction by the Microbe-Associated Molecular Patterns

Plants have well-organized varieties of physical cell wall (cellular) and hormonal defense mechanisms to defend themselves against microbial pathogens. Cellular defense, innate immunity of plants, can be regulated through phytoalexin, camalexin, callose deposition, cell wall reinforcements, and hydrogen peroxide (H_2O_2) accumulation (Ahn et al. 2007; De Vleesschauwer et al. 2008). These types of innate immunity lead to pattern recognition receptors (PRRs) that are indicators for the receptor response of the molecules from the beneficiary microbes. Plants recognize chemically diverse molecules patenting from microbes (pathogen-/microbe-associated molecular patterns, PAMPs/MAMPs) through pattern recognition receptors (PRRs), inducing a set of defense responses known as pattern-triggered immunity (PTI) (Jones and Dangl 2006). This PTI also encodes PAMP-triggered immunity. In plants, pattern recognition receptors (PRRs) are all membrane-associated receptor-like kinases or receptor-like proteins. PRRs confer robustness to the whole PTI system in plant in which different PRRs are simultaneously involved with microbial attacks (Saijo et al. 2018). The functional significance of PRR-mediated microbe recognition with beneficial microbes is an important era for the plant immune system. MAMPs, viz., fungal chitin, glycans, and, their glycoconjugates, lipopolysaccharides (LPSs), flagellin, and peptidoglycan, are molecules derived from microbes that must be detected by receptors of the host cell to suppress the pathogen. MAMPs of root-associated microbiota can trigger defenses and promote the expense of plant growth. However, beneficial rhizobacteria, such as *Pseudomonas simiae* WCS417, *Martellela endophytica* YC6887, and *B. oryzicola* YC7007, promote plant growth and induce systemic resistance (Hossain et al. 2016; Khan et al. 2016; Stringlis et al. 2018). Recent studies point to a role for host PTI in the selection and management of plant-associated microbial communities that actually enhance the resistance induction and promotion (Hossain et al. 2019; Hacquard et al. 2017). These findings are consistent with the idea that PTI plays a central role in the establishment and maintenance of plant-associated microbiomes for resistance induction. Recently, elicitors of plant defenses such as bacterial flagellin have emerged as a novel generation of plant protection products. Expression of a number of defensive genes has been associated with plant defense transcriptomes and can be induced by MAMPs, ethylene (ET) and jasmonic acid (JA) or SA signaling pathways (Huffaker et al. 2013). Hormonal defense mechanisms are fulfilled by plant hormones salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), cytokinins (CKs), and brassinosteroids (BR) in molding plant-pathogen interaction in the plant immune system. These types of hormonal inductions, which are regulated by hormonal networks of cross talks or interconnected by transductional signals, depend on the lifestyles of pathogens. Hormonal defense to control the diseases with SA or JA/ET, which is mainly involved with biotrophic or necrotrophic pathogens, respectively, is predominantly associated with those respective signaling molecules (Pieterse et al. 2009; Robert-Seilaniantz et al. 2011). Biotrophic pathogen is mainly associated with SA-dependent defense which leads to systemic acquired resistance (SAR) having a long-lasting plant immunity. The role of SA in plant immunity was maintained by the exogenous application of SA or endogenous accumulation of transcription levels and expressed in the network signaling against the biotrophic pathogen. The transcriptional levels of *PATHOGENESIS-RELATED* (*PR*) genes such as *PR1*, *PR2*, and *PR5* under the SA pathways protect the *Pst* DC3000 (Niu et al. 2011). Consistent with these *PR* genes in the SA pathway, three upregulating biosynthesis genes such as *Enhanced Disease Susceptibility* (*EDS1*, *EDS5)*, *Phytoalexin Deficient (PAD4)*, and *Salicylic Acid Induction Deficient* (*SID2)* are also essential against biotrophic pathogen responses (Brodersen et al. 2006; Wang et al. 2010). On the contrary, some receptors and signal molecules, which are required for defense responses against necrotrophic pathogens such as *Alternaria brassicicola* and *Botrytis cinerea*, are regulated through the JA and ET pathways. The transcription levels of *Plant Defensin1.2* (*PDF1*.2) and *PR* genes such as *PR3* and *PR4* were elevated in *Arabidopsis* against the necrotrophic pathogen infection (Thomma et al. 1998). Moreover, interactions between these two types of hormonal defenses based on SA or JA/ET are mostly antagonistic to one another. This multitude of defenses is performed or inducible through cellular reinforcement and hormonal defenses of SA or JA/ET signaling pathways that can be enhanced by biological agents or an abiotic inducer locally or systemically through subsequent pathogen infection or without attack. These hormonal inductions led by the endophytic *Bacillus* species are important for resistance induction against pathogens through PTI machineries.

9.6 Plant-Microbe Interaction by Resistance Induction

The beneficial rhizobacteria as biotic inducers play prominent roles in the defense system of the plant. These bacterial species produce phytohormones or convert the fixed nutrients to the available form for plant development and inhibit the phytopathogens by secreting various metabolites (Walters et al. 2005; Ryu et al. 2004b). These bacterial metabolites can assist in inducing hormonal and cellular defenses, and thus, some rhizobacteria can elicit the plant resistance induction by induced systemic resistance (ISR) or priming induced resistance depending on the lifestyle of pathogens (Ahn et al. 2007; De Vleesschauwer et al. 2012; Niu et al. 2011). Some nonpathogenic rhizobacteria elicited an ISR response through JA or ET pathways or JA and SA simultaneously via *NPR1* dependent and suppress the disease by expressing the specific defense genes (Niu et al. 2011; Ryu et al. 2004a, Thomma et al. 1998). Some plant growth-promoting rhizobacteria (PGPR)-mediated ISR was also switched on by the lipopolysaccharides, siderophores, and SA (Pieterse et al. 1996). On the contrary, some *Bacillus* species can activate the plant's defense system by enhancing the different hormonal pathways of either salicylic acid (SA) or ethylene/jasmonic (ET/JA) acid or, simultaneously, both pathways (Niu et al. 2011). Therefore, it is really interesting to induce the signaling molecules in the plant defense system by the PGPR strains. Several signaling molecules, such as SA, JA, ET, abscisic acid (ABA), cytokinins (CKs), brassinosteroids (BRs), and reactive oxygen species, have been implicated in inducible defense systems involving rhizobacterial interaction (Koornneef and Pieterse 2008). Most of these defense-related hormonal pathways are activated by rhizobacteria, *Bacillus*, and *Pseudomonas* species, which can elicit an induced systemic resistance (ISR) response through the JA or ET pathway or both pathways in a *NPR1*-dependent process (Niu et al. 2011). This phenomenon is well-defined in the *Arabidopsis*. ISR triggered by rhizobacteria suppresses the diseases by expressing the specific defense-related genes during the interaction (Bakker et al. 2007; Doornbos et al. 2011; Niu et al. 2011; Ton et al. 1999).

9.7 Conclusion and Future Trends

The genus *Bacillus* could be more effective in controlling rice disease than current chemical pesticides. The PGPR strains, especially *Bacillus* species, could turn on different signaling pathways against pathogens. Endophytic *Bacillus* species are superior bioactive agents against pathogens, induce systemic resistance, and make a good symbiotic relationship with the plant host. Their MAMP-mediated defense enhances the PTI and ultimately controls the plant disease with resistance induction.

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