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REVIEW ARTICLE

# Endophytic bacteria as biocontrol agents against plant pathogens: current state-of-the-art

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**Abstract** Most plants co-exist with fungal and bacterial endophytes. Generally, endophytes are beneficial microorganisms that colonize the internal tissues of their host plants. Plants derive several advantages from endophytic colonization, such as the biocontrol of phytopathogens and growth-promoting factors. In this review, we discuss the current knowledge of endophytic bacteria and their potential as natural biocontrol agents for plants.

**Keywords** Biocontrol agents · Endophytic bacteria · Genome sequencing analysis · Leaf-colonizing bacteria

## Introduction

Plants have evolved complex mechanisms that mediate defense responses and communication with their environment (Lee et al. 2015). Endophytes are plant-associated microorganisms that live in plant tissues without causing any detrimental effects to their hosts (Ryan et al. 2008; Schulz and Boyle 2006). Due to the various benefits of endophytes, the interest in endophytes has been growing in recent years, and many results have been published. Endophytes are known to enhance plant nitrogen fixation or secrete plant hormone-like substances to promote growth (Hurek and Reinhold-Hurek 2003; Iniguez et al. 2004; Sevilla et al. 2001), and also to produce versatile secondary metabolites, which have medical and industrial applications (Hardoim et al. 2015; Ryan et al. 2008). In addition, plant disease control by endophytes is one of the useful properties because endophytes can support sustainable agriculture and they do not cause environmental pollution or harmful toxic effects unlike chemical pesticides.

## Diversity and localization of endophytic bacteria

Approximately 300,000 plant species have one or more endophytes (Strobel et al. 2004). Endophytic bacteria have been observed inside plant tissues such as leaves, roots, seeds, stems, fruits, ovules, and tubers (Benhizia et al. 2004; Hallmann et al. 1997; Sturz et al. 1997), and they are commonly localized in intercellular spaces and xylem vessels (Reinhold-Hurek and Hurek 1998; Sprent and James 1995). The most extensively studied endophytes occur in three major phyla: Firmicutes, Proteobacteria, and Actinobacteria. Important endophytic genera include members of *Bacillus*, *Pseudomonas*, *Burkholderia*, *Azoarcus*, *Herbaspirillum*, *Gluconobacter*, and *Klebsiella* (James 2000).

Rosenblueth and Martínez-Romero (2004) reported that roots contain larger endophyte populations compared with those of aerial tissues (Rosenblueth and Martínez-Romero 2004). The population sizes of endophytic and epiphytic bacteria are highly variable and depend on the bacterial species, inoculum density, environmental conditions, and host genotype and developmental stage (Pillay and Nowak 1997; Tan et al. 2003). Hallmann et al. (1997) observed that the development of an individual endophytic population depended on the physiological status of the host plant.

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For example, diazotrophic endophytes of the *Azoarcus* genus have been restored from nitrogen-deficient soil and used to support the cultivation of salt-tolerant Kallar grass in Pakistan (Reinhold-Hurek et al. 1993). Endophytic and rhizospheric microbial populations are regulated by biotic and abiotic conditions (Rosenblueth and Martínez-Romero 2006). However, endophytic bacteria are more protected from biotic and abiotic stresses than rhizospheric bacteria due to their residence in plant internal tissues (Rosenblueth and Martínez-Romero 2006). There is still some debate about whether the benefits derived from endophytic bacteria are more valuable for plants than those derived from rhizobacteria and whether it is more advantageous for bacteria to have an endophytic or rhizospheric lifestyle. Further research on molecular mechanisms involved in plant–microbe interactions will be needed to answer these questions.

## Biocontrol activity of endophytic bacteria

Endophytic bacteria inhabit plant internal tissues in a similar niche as phytopathogens, and they may compete with bacterial pathogens as biocontrol agents (Berg et al. 2005; Hallmann et al. 1997). Inoculation of plants with beneficial endophytes can inhibit disease symptoms caused by viral, insect, fungal, and bacterial pathogens (Berg and Hallmann 2006; Kerry 2000; Ping and Boland 2004; Sturz et al. 2000). The beneficial effects derived from endophytic bacteria are similar to those from rhizosphere bacteria (Ryan et al. 2008); however, it is anticipated that endophytic bacteria are more suitable as biocontrol agents because they sustainably transmit to the next generation. The endophytic fungus *Taxomyces andreanae* synthesizes the valuable compound taxol, which is a well-known antitumor agent (Strobel et al. 1993). The Bt toxin synthesized by *B. thuringiensis* is currently one of the most effective, commercially available bioinsecticides (Jeong et al. 2016). *Streptomyces* spp., *Pseudomonas viridiflava*, *Serratia marcescens*, and *Paenibacillus polymyxa* are endophytic bacteria that produce active metabolites with antimicrobial and antifungal activities (Beck et al. 2003; Castillo et al. 2002; Guan et al. 2005; Li et al. 2007; Miller et al. 1998; Strobel et al. 1993, 2004). Moreover endophytic bacteria with biocontrol activities have been isolated from various plant species (Table 1). We recently reported that the leaf-inhabiting endophytic KB strains isolated from *Arabidopsis* suppressed phytopathogen-induced disease symptoms (Hong et al. 2016a; Hong et al. 2015). The *B. thuringiensis* KB1 strain displayed antagonistic activities against *Fusarium oxysporum* and *P. syringae* pv. *tomato* DC3000 in vitro and/or *in planta* (Hong et al. 2015). We found that *Rhodococcus* sp. KB6 strain reduced symptoms of black rot disease in sweet potato leaves caused by the fungal pathogen *Ceratocystis fimbriata* (Hong et al. 2016b). These results support the hypothesis that endophytic bacteria act as biocontrol agents in plants. Although the biocontrol activity of endophytic bacteria has been studied, the complex mechanisms and inter-species signaling pathways involved in biocontrol activities have not been elucidated (Rosenblueth and Martinez-Romero 2006). Further research is required for the development of practical biocontrol agents using endophytic bacteria.

## Endophytic bacterial genomes

Genomic analyses have identified beneficial traits related to biocontrol activities in the genome sequences of several endophytic bacterial species, including *Azoarcus* sp. BH72, *Azospirillum* sp. B510, *Bacillus subtilis* BSn5, *Burkholderia phytofirmans* PsJN, *Enterobacter* sp. 638, *Gluconacetobacter diazotrophicus* Pal5, *Herbaspirillum seropedicae* SmR1, *Klebsiella pneumoniae* 342, *Pseudomonas putida* W619, *Pseudomonas stutzeri* A1501, *Serratia proteamaculans* 568, and *Stenotrophomonas maltophilia* R551-3 (Bertalan et al. 2009; Deng et al. 2011; Fouts et al. 2008; Han et al. 2011; Kaneko et al. 2010; Krause et al. 2006; Malfanova et al. 2013; Pedrosa et al. 2011; Taghavi et al. 2009; Taghavi et al. 2010; Weilharter et al. 2011; Yan et al. 2008). We recently published a draft genome sequence of endophytic KB strains and predicted beneficial secondary metabolites of *B. thuringiensis* KB1 and *Rhodococcus* sp. KB6 (Hong et al. 2016a; Jeong et al. 2016). Genomic analysis showed that most of these endophytes had gene clusters that could synthesize metabolites that helped the plant to absorb nitrogen or increase disease resistance. Interestingly, in the case of KB1, the gene group generating the toxin was deleted. In the future, further genome sequencing analysis of endophytic bacteria will provide deeper insights into their biochemical functions and the interactions with plants.

## Concluding remarks

Endophytic bacteria provide important benefits to plants, such as directly and indirectly promoting plant growth through nutrient acquisition and phytopathogen suppression. It is expected that control of plant diseases using endophyte will be a great help to future agriculture in the situation where environmental pollution and destruction caused by agrochemicals are a big problem today. In this review, we discussed the current state of knowledge regarding endophytic bacteria as biocontrol agents for plants. In recent years, the endophyte studies have been

Table 1 List of reported endophytic bacteria showing biocontrol activities

| Endophytic bacteria | Host plants | Target pathogens | References |
|---|---|---|---|
| *P. polymyxa* GS01 | *Panax ginseng* | *Rhizoctonia solani* | Cho et al. (2007) |
| *Bacillus* sp. GS07 | *Panax ginseng* | *R. solani* | Cho et al. (2007) |
| *Pseudomonas poae* JA01 | *Panax ginseng* | *R. solani* | Cho et al. (2007) |
| *B. amyloliquefaciens* subsp. *plantarum* | *Panax notoginseng* | *Fusarium oxysporum*, *Ralstonia* sp., *Meloidogyne hapla* | Ma et al. (2013) |
| *B. methylotrophicus* | *Panax notoginseng* | *F. oxysporum*, *Ralstonia* sp., *M. hapla* | Ma et al. (2013) |
| *B. subtilis* | *Triticum aestivum* L. | *Gaeumannomyces graminis* var. tritici | Liu et al. (2009) |
| *B. licheniformis* | *Platycodon grandiflorum* | *Phytophthora capsici*, *F. oxysporum*, *R. solani*, *Pythium ultimum* | Asraful Islam et al. (2010) |
| *B. pumilus* | *Platycodon grandiflorum*, *Codonopsis lanceolata* | *P. capsici*, *F. oxysporum*, *R. solani*, *P. ultimum* | Asraful Islam et al. (2010), Kang et al. (2013) |
| *Paenibacillus* sp. | *Manihot esculenta* | *R. solani* | Canova et al. (2010) |
| *P. aeruginosa* | *Piper nigrum L* | *P. capsici* | Aravind et al. (2009) |
| *P. putida* | *Piper nigrum L* | *P. capsici* | Aravind et al. (2009) |
| *B. megaterium* | *Piper nigrum L* | *P. capsici* | Aravind et al. (2009) |
| *B. thuringiensis* KB1 | *A. thaliana* | *F. oxysporum*, *P. syringae* pv. *tomato* DC3000 | Hong et al. (2015) |
| *Rhodococcus* sp. KB6 | *A. thaliana* | *Ceratocystis fimbriata*, *P. syringae* pv. *tomato* DC3000 | Hong et al. (2016a) |
| *P. polymyxa* AC-1 | *Capsicum annuum* | *P. capsici*, *C. fimbriata*, *P. syringae* pv. *tomato* DC3000 | Hong et al. (2016b) |

carried out deeply through the metagenomics in the model plants, *Arabidopsis*, and these results have increased our understanding of interactions between plants and endophyte (Bai et al. 2015). However, we still do not know how a plant accepts endophytes, how to keep them in the internal side, and how to use them to fight pathogens. To address this, we need to establish an understanding of the interactions of environments, plants, endophytes, and phytopathogens.

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