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Plant beneficial endophytic bacteria: Mechanisms, diversity, host range and genetic determinants

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ABSTRACT

Endophytic bacteria are the plant beneficial bacteria that thrive inside plants and can improve plant growth under normal and challenging conditions. They can benefit host plants directly by improving plant nutrient uptake and by modulating growth and stress related phytohormones. Indirectly, endophytic bacteria can improve plant health by targeting pests and pathogens with antibiotics, hydrolytic enzymes, nutrient limitation, and by priming plant defenses. To confer these benefits, the bacteria have to colonize the plant endosphere after colonizing the rhizosphere. The colonization is achieved using a battery of traits involving motility, attachment, plant-polymer degradation, and evasion of plant defenses. The diversity of endophytic colonizers depends on several bacteria, plant and environment specific factors. Some endophytic bacteria can have a broad host range and can be used as bioinoculants in developing a safe and sustainable agriculture system. This review elaborates the factors affecting diversity of bacterial endophytes, their host specificity and mechanisms of plant growth promotion. The review also accentuates various methods used to study endophytic communities, wild plants as a source of novel endophytic bacteria, and innovative approaches that may improve plant-endophyte association. Moreover, bacterial genes expressed *in planta* and challenges to study them are also discussed.

1. Introduction

Plants can develop associations with members of their ecosystem to thrive in their natural environments. Microorganisms are one of the most important organisms that can develop beneficial associations with plants (Santoyo et al., 2016). Such plant-beneficial bacteria are a class of bacteria that provide numerous benefits to their host plants, helping them in tolerating various biotic and abiotic stresses that can challenge their growth (Miliute et al., 2015). These bacteria can live both externally or internally in their host plant. Bacteria that live outside their host plants are either epiphytic, those living on the plant leaf surfaces, or rhizospheric, those inhabiting plant roots within the soil (Compant et al., 2010). While, bacteria that live and thrive inside their host plant are called endophytic bacteria (Hardoim et al., 2008). All these classes of bacteria share numerous characteristics essential for host plant growth promotion (Compant et al., 2010).

Endophytic bacteria are considered a subclass of rhizospheric bacteria, commonly called as plant growth promoting rhizobacteria (PGPR). These are in fact a specialized group of rhizobacteria that have acquired the ability to invade their plant host (Reinhold-Hurek and Hurek, 1998). They share all the important traits consistent with the host plant growth promotion found in rhizobacteria. However, the beneficial effects provided by the endophytic bacteria to host plants are usually greater than those provided by many rhizospheric bacteria. Such effects may exacerbate when plants are challenged by stress conditions (Chanway et al., 2000; Hardoim et al., 2008).

In 1926, endophytic growth was described as a particular stage of bacterial growth, where bacteria infect and develop a close mutualistic relation with plants (Perotti, 1926). Thus, endophytic bacteria are now described as the bacteria that are isolated from surface sterilized plant tissues and do not cause any noticeably harm to their host plants (Santoyo et al., 2016). These bacteria can exists within the plant host, including aboveground and underground plant parts and even seeds, thereby positively affecting plant development (Chebotar et al., 2015). The bacteria use the plant endosphere as a unique protective ecological niche that provides a safe and consistent environment unperturbed by the fluctuating environmental conditions that affect rhizospheric and epiphytic bacteria (Senthilkumar et al., 2011). Moreover, most endophytic bacteria have a biphasic life cycle that alternates between plant and soil environments.

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Nearly 300,000 plant species that exist on earth are thought to be a host to one or more endophytes (Ryan et al., 2008). Theses endophytes can be both fungi and bacteria (Reinhold-Hurek and Hurek, 2011; Singh et al., 2011). The endophytic bacteria can not only promote growth of the host plant, but also help the host in tolerating stress conditions, and produce allelopathic effects against other competing plant species (Cipollini et al., 2012; Mei and Flinn, 2010; Rosenblueth and Martönez-Romero, 2006). Thus, they enable their host to have a better survival against biotic and abiotic challenges and competition by other plants.

Endophytic bacteria have been isolated and characterized from diverse type of plant hosts. These include agronomic crops, prairie plants, plants growing in extreme environments, and wild and perennial plants (Nair and Padmavathy, 2014; Yuan et al., 2014; Zinniel et al., 2002). Endophytic bacteria have been isolated from different plant parts that are above and below ground (Senthilkumar et al., 2011). These include roots, stems, leaves, seeds, fruits, tubers, ovules and nodules, where roots have the greatest number of bacterial endophytes as compared to above ground tissues (Rosenblueth and Martínez-Romero, 2006).

Numerous studies have reported endophytic bacteria that can promote growth of plants like wheat, rice, canola, potato, tomato, and many more (Mei and Flinn, 2010; Sturz and Nowak, 2000). Most of these studies demonstrated the possible growth promotion potential of endophytes isolated from the same plants. However, other studies have reported the growth promoting effects of endophytic bacteria on non-host plants (Sessitsch et al., 2005). There have been contrasting reports about the host specificity of endophytes. Some researchers have indicated that endophytes are only able to promote growth of plants that are very closely related to their natural host (Long et al., 2008). Conversely, there have been reports of endophytes promoting growth of diverse plant hosts (Ma et al., 2011b; Sessitsch et al., 2005). Nevertheless, the broad host range of endophytes makes them a powerful tool in agricultural biotechnology. Therefore, endophytes have a great potential to be used as biofertilizers and biopesticides in developing a sustainable, safe and effective agriculture system.

2. Colonization of plants by the endophytic bacteria

Endophytic bacteria can be considered a subset of rhizospheric bacteria (Marquez-Santacruz et al., 2010; Misko and Germida, 2002). However, compared to rhizobacteria, endophytic growth has an added advantage over rhizospheric growth. Living within plant tissues allows endophytic bacteria to be in close contact with the plant host to readily exert a direct beneficial effect in return for consistent supply of nutrients. In fact, endophytic bacteria represent a class of specialized rhizobacteria that have acquired the ability to invade plant roots after establishing a rhizospheric population (Compant et al., 2010).

Endophytic colonization of host by the bacteria is determined by a battery of different bacterial traits. These traits are collectively referred to as colonization traits and regulate the entire process of plant colonization. The colonization process involves complex communication between the two partners. The process usually starts from the roots, and requires recognition of specific compounds in the root exudates by the endophytic bacteria (de Weert et al., 2002; Rosenblueth and Martínez-Romero, 2006). Plants produce these root exudates to interact with the beneficial bacteria for their own ecological advantage (Compant et al., 2005). Moreover, it has been observed that endophytic bacteria colonize the plant interior in a sequence of events similar to rhizosphere colonization by rhizobacteria (Hallmann et al., 1997). However, endophytic colonization involves a suite of environmental and genetic factors that allow a bacterium to enter plant endosphere (Compant et al., 2010). Although, endophytic bacteria usually enter the plants through the root zone, the aerial parts of the plants, including stems, leaves, flowers and cotyledons, may also be used (Zinniel et al., 2002). Once inside the roots, endophytic bacteria can now systemically infect the adjacent plant tissues.

2.1. Rhizosphere colonization by the endophytic bacteria

The rhizosphere colonization is a highly competitive task for the endophytic bacteria to occupy spaces and get nutrients (Raaijmakers et al., 2002). Only those bacteria, either beneficial or pathogenic, that can competitively colonize plant rhizosphere will thrive in this environment and have an effect on plant growth and development (Haas and Keel, 2003). Bacterial traits like motility and polysaccharide production are important in the colonization of plant rhizosphere, as demonstrated for endophytic *Alcaligenes faecalis* and *Azospirillum brasilense* (Santoyo et al., 2016).

Bacterial rhizosphere population can range between 10^7-10^9 cfu/g of the rhizosphere soil (Benizri et al., 2001); rhizoplane population ranges from 10^5 to 10^7 cfu/g fresh weight (Bais et al., 2006; Benizri et al., 2001). Bacterial detection systems based on *gfp/gusA* labelled strains, immunomarkers, and fluorescence *in situ* hybridization (FISH) have revealed that bacterial cells first colonize the rhizosphere after they have been inoculated into the soil (Gamalero et al., 2003). The bacterial cells then attach to the root surfaces forming a string of cells (Hansen et al., 1997). The bacteria can then colonize the entire root surface and some rhizodermal cells, leading to the establishment of micro-colonies or biofilms by the bacteria (Benizri et al., 2001). Rhizoplane colonization has been investigated in both plants growing *in vitro* and plants growing in natural soils (Compant et al., 2010).

To confer beneficial effects on host plant, the bacteria have to competently colonize the plant rhizosphere and rhizoplane (Compant et al., 2005). They also have to compete with other rhizospheric members while colonizing the host plant (Whipps, 2001). Moreover, the bacteria do not colonize the host plant root system in a uniform manner. For example, Gamalero et al. (2003) reported that while colonizing tomato plants, distribution and density of *Pseudomonas fluorescens* strain A6RI varied according to the root zone. This non-uniform colonization of plant root by the bacteria is a result of different factors controlling the process of root colonization. These factors include root exudation patterns, bacterial attachment and motility, bacterial quorum sensing, bacterial growth rate, minimizing competition by producing antagonistic substances and acquiring nutrients efficiently (Compant et al., 2010). Moreover, to be successful, the bacteria need to metabolically adapt to the range of nutrients available in the plant root exudates. This was demonstrated by Matilla et al. (2007) in the gene expression analysis of *Pseudomonas putida* KT2440 competently colonizing corn rhizosphere, where the bacterial genes involved in metabolism and oxidative stress were upregulated.

2.2. Root colonization by the endophytic bacteria

After establishing themselves in the rhizosphere and rhizoplane, bacterial endophytes are known to make their way inside the plant root and colonize themselves with sub-populations ranging from 10^5-10^7 cfu/g fresh weight (Hallmann, 2001). This involves bacterial adhesion to cell surface structures, which is mediated by polysaccharides, pili and bacterial adhesins (Hori and Matsumoto, 2010). Once on the root surface, the bacteria might reach the root entry sites, like lateral root emergence and wounds, using type IV pili mediated twitching motility. Importance of this feature was demonstrated in diazotrophic endophyte *Azoarcus* sp. BH72 colonizing rice roots, where mutant defective in pilus retraction showed decreased root surface colonization compared to the wild-type bacteria (Böhm et al., 2007). Nevertheless, every endophytic bacterium has its own distinct colonization pattern and colonization site preferences (Zachow et al., 2010). Once these bacteria have established themselves on the roots surfaces, they start to penetrate into the root interior using specialized mechanisms.

The process of penetration into the host can be passive or active. Passive penetration can occur at cracks present at root emergence areas, root tips, or those created by deleterious organisms (Hardoim et al., 2008). Active penetration by the competent endophytic bacteria is

achieved by means of dedicated machinery of attachment and proliferation. This involves presence of lipopolysaccharides, flagella, pili, twitching motility, and quorum sensing, which can affect endophytic colonization and bacterial movement inside the host plants (Böhm et al., 2007; Dörr et al., 1998; Duijff et al., 1997; Suárez-Moreno et al., 2010). In addition, the secretion of cell-wall degrading enzymes, mainly pectinases and cellulases are known to be involved in bacterial penetration and spreading within the plant (Compant et al., 2005). Although not experimentally proven, it has been proposed that endophytic bacteria produce low levels of cell-wall degrading enzymes, as compared to phytopathogens that produce deleteriously high levels of these enzymes, and can thus avoid triggering plant defense systems (Elbeltagy et al., 2000). Furthermore, another way by which endophytic bacteria avoid being detected as a pathogen by the plant is by maintaining low cell densities (2–6 log cfu/gfw) as compared to pathogenic bacteria (7–10 log cfu/gfw) (Zinniel et al., 2002). Hence, the endophytic presence of bacteria is determined by chance factors and bacterial genetic determinants that enable bacterial-plant crosstalk, leading to an active endophytic colonization process (Hardoim et al., 2008). The plant host also plays a critical role in selecting an endophytic partner, where secretion of specific root exudates and a selective plant defense response are considered important factors in the selection of specific endophytes (Rosenblueth and Martönez-Romero, 2006).

2.3. Systemic colonization of aerial plant tissues by the endophytic bacteria

After entry into the roots, the endophytic bacteria can spread systemically to colonize above ground tissues. They can establish stem and leaf population densities between 10^3–10^4 cfu/gfw under natural conditions (Compant et al., 2010). It is not clear whether bacterial colonization of higher plant tissues confer similar beneficial effects on plant host as those seen with root colonization. Nevertheless, only few bacteria can colonize aerial vegetative parts of their host plants due to the physiological requirements needed to occupy these plant niches (Hallmann, 2001). Thus, the bacteria that migrate to the above ground plant tissue are well adapted to this particular endophytic niche. Bacterial movement inside plant is supported by bacterial flagella and plant transpiration stream (Compant et al., 2005; James et al., 2002). Migration along intercellular spaces requires the secretion of cell-wall degrading enzymes like cellulases and pectinases (Compant et al., 2010). However, movement through xylem element occurs through perforated plates that allow movement of bacteria through large pores without requiring cell-wall degrading enzymes (Sapers et al., 2005). The final sink for these specialized endophytic bacteria is leaf tissue. Endophytic bacteria mostly colonize the leaf tissues from plant roots, but just like phytopathogenic bacteria, endophytic bacteria can gain entry into the leaves from the phyllosphere *via* leaf stomata (Senthilkumar et al., 2011).

3. Diversity of endophytic bacteria

Bacterial endophytes have been found in every plant species that has been studied. Thus, an endophyte-free plant is a rare exception in the natural environment (Partida-Martinez and Heil, 2011). In fact, a plant without the associated beneficial bacteria would be less fit to deal with phytopathogens and more susceptible to the stress conditions (Timmusk et al., 2011). The type of endophytic diversity present in a plant can depend on several factors which are discussed below and summarized in Fig. 1.

3.1. Factors affecting endophytic bacterial diversity of a plant

Apart from bacterial competence to colonize plants as endophytes, the host plant and environmental factors can strongly influence the endophytic diversity of a particular plant. Host plant age, genotype, geographical location, and even the tissue being analyzed can determine the type of endophytic bacteria it harbors (Hallmann and Berg, 2006). Moreover, host plant growth stages can also determine the endophytic diversity of a plant, where plant stages enriched in nutrient availability tend to have increased bacterial diversity (Shi et al., 2014). Not only that, the climatic conditions can also influence the endophytic colonizers of a plant species. Penuelas et al. (2012) observed that changes in climate significantly altered the abundance and composition of endophytic bacteria within the leaf tissues.

Another important factor affecting the observable endophytic diversity of a plant is the method used to study these bacteria. The spectrum of bacteria recovered from a plant can depend on the nature, concentration and even length of the treatment time for a sterilizing agent used to recover bacteria (Hallmann and Berg, 2006; Hallmann et al., 1997).

The type of endophytic community of a plant is strongly influenced by the nature of plant host species (Ding and Melcher, 2016). Different plant species growing in the same soil can have distinctly different endophytic diversity. Germida et al. (1998) reported that canola and wheat plants grown in the same field had very different spectrum of bacterial species as endophytes. This observation was supported by Ding et al. (2013) who identified the host species being the most important determinant in selecting its endophytic community, followed by the sampling dates and the sampling locations. In fact, different cultivars of a plant species grown in the same soil can also differ in their endophytic diversity, as reported by Granér et al. (2003) for four different cultivars of *Brassica napus* having different endophytic bacterial inhabitants. Thus, the host plant species strongly governs the type of endophytic bacteria colonizing it.

More interestingly, the type of soil used to grow a plant can also determine its endophytic community. Thus, the same plant cultivar growing in different agricultural soils can have very different endophytic bacteria. This was observed by Song et al. (1999) who reported significantly different endophytic bacterial diversity for a peanut cultivar grown in different fields. Moreover, Rashid et al. (2012) isolated different types of endophytic bacteria by growing one cultivar of tomato in 15 different agricultural soils. Collectively, these findings indicate that occurrence of different endophytes is due to the diverse nature of soil samples.

The difference in endophytic community can also result by the preference imposed by the plant host in response to soil and stress conditions. Siciliano et al. (2001) reported that plants, while growing in the petroleum hydrocarbon contaminated soil, recruited those endophytic bacteria which had the necessary contaminant-degrading genes. Moreover, the genes encoding for nitro-aromatic compound degradation were more prevalent in endophytic strains selected by the plants than within rhizospheric or soil microbial communities. Similarly, Granér et al. (2003) reported that wilt resistant cultivar of oilseed rape contained a higher proportion of endophytic bacteria antagonistic to the wilt causing *Verticillium longisporum* than the susceptible cultivar. Presence of phytopathogens in plants has been considered an important factor in the restructuring of endophytic bacterial communities. This was noticed by Bogas et al. (2015) for their work on the restructured endophytic communities of asymptomatic and symptomatic *Paullinia cupana* plants challenged by *Colletotrichum* spp. Hence, the selection of endophytic bacterial communities is a dynamic process that is tightly controlled by the host plant (Berg and Hallmann, 2006; Trivedi et al., 2010), where bacteria that favor plant host in a particular situation are preferred by the plant over other bacterial endophytes.

3.2. Methods for studying endophytic bacterial diversity

Endophytic bacterial communities are conventionally studied using culture-based methods (Ding et al., 2013). However, to investigate the endophytic bacterial communities using these methods, the bacteria must be cultivable under laboratory conditions. Cultivation procedure relies on the isolation of endophytic bacteria from plant tissue. The

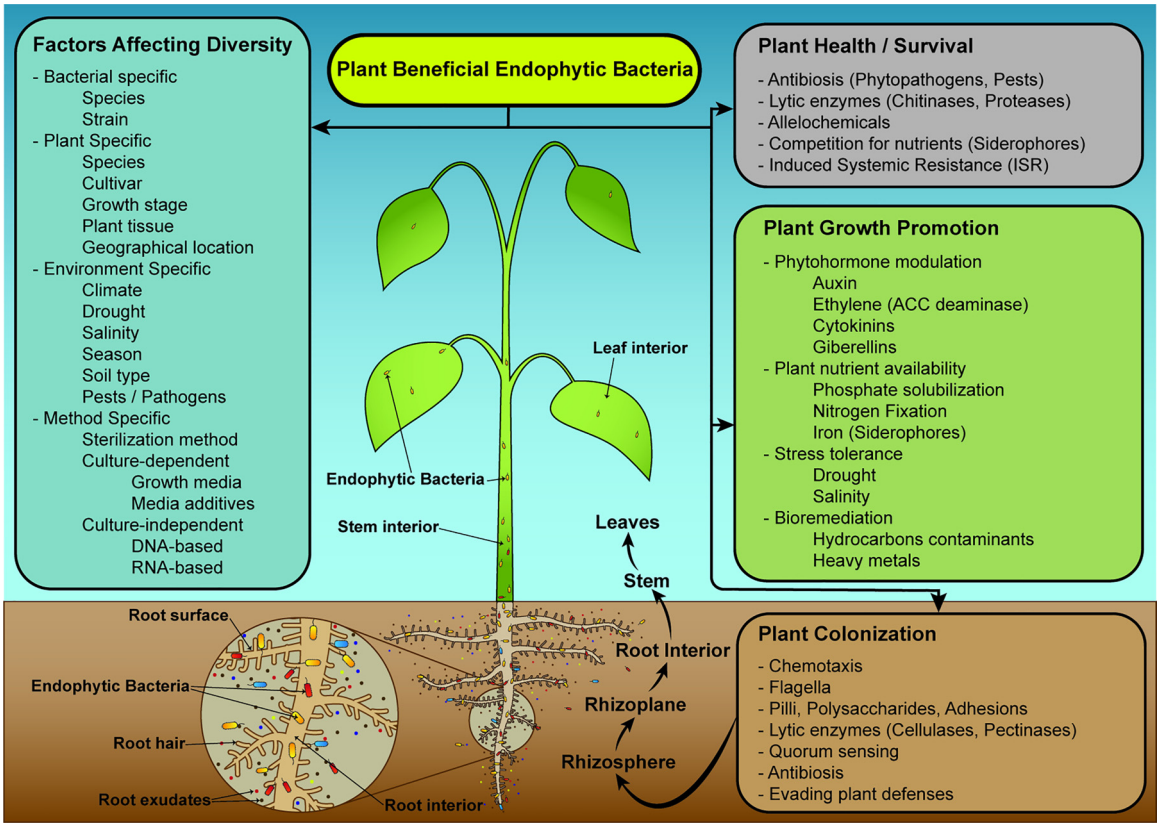

Fig. 1. Mechanisms of plant growth promotion, colonization, and factors affecting diversity of endophytic bacteria in host plant.
Endophytic bacteria can benefit their host both directly, by improving nutrient uptake and by modulating growth/stress related phytohormones (Green box), and indirectly, by targeting pest/pathogens and antagonizing competing plants (Grey box). To confer benefits, these bacteria have to competitively colonize the plant interior, achieved using a battery of colonization traits (Brown box). The colonization is a sequential process, starting from the plant rhizosphere (bacteria respond to plant root exudates), followed by rhizoplane (root surfaces) and root interior colonization. Once inside, the competent endophytes can move to the aerial parts of the plants (stem and leaves). The diversity of endophytic colonizers is affected by various bacteria, plant and environment related factors (Blue box). The type of method used can also affect the bacterial diversity analysis.

isolation procedure should be sensitive enough to recover most of the cultivable endophytic bacteria, but should be strong enough to eliminate epiphytes and other contaminating bacteria from the plant tissues being processed. Commonly, isolation protocol requires surface sterilization of plant tissues followed by their maceration, serial dilution and plating on the bacterial growth medium (Barac et al., 2004). Sterilizing agents like sodium hypochlorite, ethanol and hydrogen peroxide are commonly used to achieve surface sterilization, and usually these chemicals are used in a series to improve the effectiveness of the sterilization procedure (Lodewyckx et al., 2002; Romero et al., 2001; Schulz et al., 1993). The sterilized tissue is washed with sterile distilled water several times to remove the residual chemicals. The sterilization is confirmed by plating small amount of distilled water from the last wash on the culture media, where absence of bacteria confirms the effectiveness of sterilization procedure. Moreover, surface sterilization producing high numbers of endophytic bacterial growth on agar media indicates minimum damage to the endophytic population by the sterilization procedure (Eevers et al., 2015). This is desired as any damage to the endophytic community by the sterilizing agent can comprise the authenticity of the bacterial diversity analysis. These cultivable bacteria are then identified using morphological, physiological, biochemical and molecular approaches, where molecular approaches being the most accurate of all (Ma et al., 2011b). A number of molecular markers have been identified that permit the identification of specific microbial taxa and their phylogenetic classification. Among these molecular markers, 16S rRNA is most commonly employed to identify bacteria and determine their phylogenetic relatedness (Srinivasan et al., 2015).

Total population estimates of endophytic bacteria in plants may vary. These estimates can depend on the type of growth media used for isolation, growth conditions of the host plant, and method used to sterilize plant tissue (Eevers et al., 2015; Hallmann et al., 1997; Lodewyckx et al., 2002; Romero et al., 2001). For example, a successful surface sterilization can result in the penetration of these sterilizing chemicals in to the interior tissues, sometimes killing the endophytic colonizers and compromising the correct bacterial estimates (Hallmann et al., 1997; Lodewyckx et al., 2002). Similarly, selection of growth medium also affects the numbers and diversity of endophytes that can be isolated from a specific plant tissue, as no medium can meet the nutritional and growth requirements of all the bacteria (Eevers et al., 2015; Reiter et al., 2002). Growth media are not always the reason for the inability to culture bacteria as some bacteria can enter viable but nonculturable (VNC) state and are unable to divide (Sessitsch et al., 2002). Moreover, even when endophytic bacteria have been successfully isolated, maintaining them on growth media can sometimes prove to be difficult (Eevers et al., 2015; Trivedi et al., 2011). Nevertheless, it is recommended that endophytic bacteria are isolated using more than one type of growth media, and supplementing these media with plant extracts can increase the overall diversity of bacterial isolates (Eevers et al., 2015; Hallmann et al., 1997). However, cultivation-dependent methods can strongly underestimate the number of bacteria present in plant tissues (Bogas et al., 2015), as cultivable bacteria usually represents only 0.001% to 1% of the actual endophyte counts (Alain and Querellou, 2009; Torsvik and Øvreås, 2002). Thus, the culture-based methods have been surpassed by culture-independent methods, which tend to be less biased in analyzing the true endophytic diversity.

Table 1
Some common endophytic bacterial genera isolated from agronomic plants reported in literature (Hallmann et al., 1997; Rosenblueth and Martínez-Romero, 2006; Miliute et al., 2015).

Plant	Endophytic bacterial genera
Alfalfa	*Bacillus, Erwinia, Microbacterium, Pseudomonas, Salmonella*
Banana	*Azospirillum, Burkholderia, Citrobacter, Herbaspirillum, Klebsiella*
Black pepper	*Arthrobacter, Bacillus, Curtobacterium, Micrococcus, Pseudomonas, Serratia*
Canola	*Acidovorax, Agrobacterium, Aureobacterium, Bacillus, Chryseobacterium, Cytophaga, Flavobacterium, Micrococcus, Pseudomonas, Rathayibacter,*
Carrot	*Agrobacterium, Bacillus, Klebsiella, Pseudomonas, Rhizobium, Salmonella, Staphylococcus*
Clover	*Agrobacterium, Bacillus, Methylobacterium, Pseudomonas, Rhizobium*
Cotton	*Bacillus, Burkholderia, Clavibacter, Erwinia, Phyllobacterium, Pseudomonas*
Cucumber	*Agrobacterium, Bacillus, Burkholderia, Chryseobacterium, Clavibacter, Curtobacterium, Enterobacter, Micrococcus, Paenibacillus, Phyllobacterium, Pseudomonas, Serratia, Stenotrophomonas*
Grapevine	*Comamonas, Enterobacter, Klebsiella, MoraxellaPantoea, Pseudomonas, Rahnella, Rhodococcus, Staphylococcus, Xanthomonas*
Maize	*Achromobacter, Agrobacterium, Arthrobacter, Bacillus, Burkholderia, Corynebacterium, Curtobacterium, Enterobacter, Erwinia, Herbaspirillum, MicrobacteriumMicrococcus, Paenibacillus, Phyllobacterium, Pseudomonas, Rhizobium, Serratia*
Pineapple	*Azospirillum, Burkholderia*
Potato	*Acidovorax, Acinetobacter, Actinomyces, Agrobacterium, Alcaligenes, Arthrobacter, Bacillus, Capnocytophaga, Chryseobacterium, Comamonas, Corynebacterium, Curtobacterium, Enterobacter, Erwinia, Klebsiella, Leuconostoc, Methylobacterium, Micrococcus, Paenibacillus, Pantoea, Pseudomonas, Psychrobacter, Serratia, Shewanella, Sphinogomonas, Stenotrophomonas, Streptomyces, Vibrio, Xanthomonas*
Radish	*Proteobacteria, Salmonella*
Red clover	*Acidovorax, Agrobacterium, Arthobacter, Bacillus, Bordetella, Cellulomonas, Comamonas, Curtobacterium, Escherichia, Klebsiella, Methylobacterium, Micrococcus, Pantoea, Pasteurella, Phyllobacterium, Pseudomonas, Psychrobacter, Rhizobium, Serratia, Sphingomonas, Variovorax, Xanthomonas*
Rice (wild and cultivated)	*Agrobacterium, Azoarcus, Azorhizobium, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia, Chromobacterium, Enterobacter, Herbaspirillum, Ideonella, Klebsiella, Micrococcus, Pantoea, Pseudomonas, Rhizobium, Serratia, Stenotrophomonas*
Soybean	*Erwinia, Agrobacterium, Pseudomonas, Klebsiella, Enterobacter, Pantoea, Bacillus*
Sugar cane	*Acetobacter, Gluconacetobacter, Herbaspirillum, Klebsiella*
Tomato	*Brevibacillus, Escherichia, Pseudomonas, Salmonella*
Wheat	*Bacillus, Burkholderia, Flavobacterium, Klebsiella, Microbispora, Micrococcus, Micromonospora, Mycobacterium, Nacardiodes, Rathayibacter, Streptomyces*

Culture-independent methods to study endophytic diversity mostly rely on the total bacterial genomic DNA extraction from plant tissues. The plant tissue is first processed to remove the surface bacteria. This is usually achieved using aseptic peeling technique to remove the surface layers, or by vigorously shaking the plant tissues with acid-washed glass beads in saline solutions to dislodge the surface bacteria, followed by washes with sterile distilled water. The processed plant tissues are then homogenized to extract the bacterial genomic DNA (Sessitsch et al., 2002). The genomic DNA can then be analyzed using a range of molecular fingerprinting techniques. Most commonly, the genomic DNA is used to amplify a marker gene, usually the 16S rRNA gene, to analyze the bacterial diversity (Garbeva et al., 2001). The variety of amplified gene fragments, representing the entire endophytic population of a plant, are then analyzed using community DNA fingerprinting techniques like Amplified rDNA Restriction Analysis (ARDRA), Denaturing Gradient Gel Electrophoresis (DGGE), Temperature Gradient Gel Electrophoresis (TGGE), and Terminal Restriction Fragment Length Polymorphism (T-RFLP) (Hallmann et al., 1997; Ma et al., 2016). Alternatively, the highly variable region between 16S and 23S rDNA can be analyzed using (Automated) Ribosomal Intergenic Spacer Analysis (ARISA) for the community fingerprinting (Saito et al., 2007). However, to be detected by these fingerprinting techniques, an endophytic population must represent about 1% of the total community (Smalla, 2004). Moreover, chances of detecting novel bacteria using these methods are low, as databases of fingerprinting methods are largely incomplete (Ding et al., 2013).

The DNA fingerprinting techniques have largely been superseded by more advance molecular techniques like metagenomics to study the microbial diversity. Metagenomics involves DNA extraction from the entire bacterial population for analysis of its gene content using next generation sequencing (Allan, 2014). The sequencing could be done for the entire DNA, which is then assembled and annotated, or it could be done for one particular gene or phylogenetic marker, like 16S rRNA. Thus, the metagenomics approaches allow full depth of endophytic diversity analysis in comparison to traditional fingerprinting. Using metagenomics approach, Sessitsch et al. (2012) uncovered the hidden community of rice endorhizosphere, and deciphered many traits shared by the endophytic inhabitants that might be crucial in their endophytic competence and success. However, the DNA-based community analysis cannot selectively analyze the viable or metabolically active bacterial cells. For this, RNA-based approaches are utilized, which can specifically determine the metabolically active population, as the amount of RNA can be correlated to the growth activity of the endophytic bacteria. Sharma et al. (2004) compared the rhizosphere bacterial communities of three related legume plants and observed that metabolic profiles of the three bacterial communities were more dissimilar (45–50% similarity) as compared to DNA-based profiling (70–90% similarity). Similarly, comparative mRNA-based and DNA-based analyses of root-associated communities in rice plants revealed that only a fraction of nitrogen fixing bacteria actively performed the activity (Demba Diallo et al., 2008; Knauth et al., 2005).

Endophytic bacterial populations can also be studied directly in their natural settings. Techniques like fluorescence *in situ* hybridization (FISH) have allowed studying the endophytic bacteria in the natural habitat (Piccolo et al., 2010). Moreover, by combing FISH with other DNA fingerprinting techniques, the dominant population of the endophytic community of a plant can also be identified (Sun et al., 2008). Such a polyphasic approach that combines different methods is indeed recommended when analyzing endophytic bacterial communities. In fact, combinatorial approaches, combining both culture-dependent and culture-independent methods, can increase the likelihood of completely analyzing the structure and function of endophytic bacterial community of a plant (Hallmann and Berg, 2006; Sessitsch et al., 2004).

3.3. Endophytic bacterial diversity of different plants

Endophytic bacterial diversity has been reported for a number of plant species. In general, Proteobacteria is the most predominant phylum frequently isolated from plants, including the classes α-, β-, and γ-Proteobacteria, where γ-Proteobacteria is the most diverse and dominant. (Miliute et al., 2015; Santoyo et al., 2016). Members of Actinobacteria, Bacteroidetes, and Firmicutes are also among the classes most commonly found as endophytes (Reinhold-Hurek and Hurek, 2011). Other classes such as Acidobacteria, Planctomycetes and

Table 2
Diversity of endophytic bacteria isolated from some wild plants.

Plant	Location	Endophytic bacteria	References
Alnus firma	Mine tailing	*Bacillus sp.*	(Shin et al., 2012)
Alyssum bertolonii	Serpentine outcrop	*Arthrobater* *Bacillus* *Curtobacterium* *Leifsonia* *Microbacterium* *Paenibacillus* *Pseudomonas* *Staphylococcus*	(Barzanti et al., 2007)
Calystegia soldanella	Sand dunes	*Acinetobacter* *Arthrobacter* *Chryseobacterium* *Curtobacterium* *Enterobacter* *Microbacterium* *Pantoea* *Pedobacter* *Pseudomonas* *Stenotrophomonas*	(Park et al., 2005)
Cannabis sativa	Wild habitat	*Acinetobacter gyllenbergii* *Acinetobacter nosocomialis* *Acinetobacter parvus* *Acinetobacter pittii* *Bacillus anthracis* *Chryseobacterium sp.* *Enterobacter asburiae* *Enterococcus casseliflavus* *Nocardioides albus* *Nocardioides kongjuensis* *Pantoea vagans* *Planomicrobium chinense* *Pseudomonas taiwanensis* *Rhizobium radiobacter* *Streptomyces eurocidicus* *Xanthomonas gardneri*	(Afzal et al., 2015)
Commelina communis	Mine wasteland	*Arthrobacter* *Arthrobacter* *Bacillus* *Bacillus pumilus* *Herbaspirillum* *Microbacterium* *Sphingomonas*	(Sun et al., 2010)
Cressa cretica, Salicornia brachiate, Suadea nudiflora, Sphaeranthus indicus	Coastlines	*Acinetobacter* *Arthrobacter* *Bacillus* *Kocuria* *Oceanobacillus* *Paenibacillus* *Pseudomononas* *Virgibacilus*	(Arora et al., 2014)
Dodonaea viscosa	Wild rocky habitat	*Agrococcus terreus* *Bacillus cereus* *Bacillus idriensis* *Bacillus simplex* *Bacillus subtilis* *Brevundimonas subvibrioides* *Inquilinus limosus* *Microbacterium trichothecenolyticum* *Pseudomonas geniculata* *Pseudomonas taiwanensis* *Rhizobium huautlense* *Streptomyces alboniger* *Streptomyces caeruleatus* *Xanthomonas sacchari*	(Afzal et al., 2017)
Elsholtzia Splendens	Mine wasteland	*Acinetobacter calcoaceticus* *Acinetobacter junii* *Bacillus* *Bacillus firmus* *Bacillus megaterium* *Burkholderia* *Exiguobacterium aurantiacum* *Micrococcus luteus* *Moraxella* *Paracoccus* *Serratia marcescens* *Xanthomonas translucens*	(Sun et al., 2010)
Elymus mollis	Sand dunes	*Acinetobacter* *Arthrobacter* *Chryseobacterium* *Enterobacter* *Exiguobacterium* *Flavobacterium* *Klebsiella* *Pedobacter* *Pseudomonas* *Stenotrophomonas*	(Park et al., 2005)
Halimione portulacoides	Salt marsh	*Altererythrobacter* *Hoeflea* *Labrenzia* *Marinilactibacillus* *Microbacterium* *Salinicola* *Vibrio*	(Fidalgo et al., 2016)
Mammillaria fraileana (cactus)	Wild rocky habitat	*Azotobacter vinelandii* *Bacillus megaterium* *Enterobacter sakazakii* *Pseudomonas putida*	(Lopez et al., 2011)
Miscanthus sinensis	Mine wasteland	*Pseudomonas koreensis*	(Babu et al., 2013)
Noccaea caerulescens	Metal contaminated site	*Agreia* *Arthrobater* *Bacillus* *Kocuria* *Microbacterium* *Sthenotrophomonas* *Variovorax*	(Visioli et al., 2014)
Pachycereus pringlei (cardon cactus)	Volcanic areas	*Acinetobacter* *Bacillus* *Citrobacter* *Klebsiella* *Paenibacillus* *Pseudomonas* *Staphylococcus*	(Puente et al., 2009b)
Pinus contorta (Lodgepole pine)	Sub-boreal Pine Spruce	*Bacillus* *Brevibacillus* *Brevundimonas* *Cellulomonas* *Kocuria* *Paenibacillus* *Pseudomonas*	(Bal et al., 2012)
Pinus sylvestris	Mine wasteland	*Bacillus thuringiensis*	(Babu et al., 2013)
Polygonum pubescens	Heavy metal contaminated soil	*Rahnella sp. JN6*	(He et al., 2013)
Prosopis strombulifera	Saline environment	*Achromobacter xylosoxidans* *Bacillus licheniformis* *Bacillus pumilus* *Bacillus subtilis* *Brevibacterium halotolerans* *Lysinibacillus fusiformis* *Pseudomonas putida*	(Sgroy et al., 2009)
Salix caprea		*Bacillus* *Frigoribacterium*	(Kuffner et al., 2010)

(*continued on next page*)

Table 2 (*continued*)

Plant	Location	Endophytic bacteria	References
	Heavy metal contaminated soil	*Frondihabitans* *Kocuria* *Leifsonia* *Massilia* *Methylobacterium* *Microbacterium* *Ochrobactrum* *Pedobacter* *Plantibacter* *Rhodococcus* *Sphingomonas* *Spirosoma* *Subtercola*	
Sedum alfredii Hance	Mining area	*Burkholderia* *Sphingomonas* *Variovorax*	(Zhang et al., 2013)
Thuja plicata (Red cedar)	Sub-boreal Pine Spruce	*Arthrobacter* *Bacillus* *Paenibacillus* *Pseudomonas* *Streptoverticillium*	(Bal et al., 2012)
Wild prairie plants	Prairie	*Cellulomonas* *Clavibacter* *Curtobacterium* *Microbacterium*	(Zinniel et al., 2002)

Verrucomicrobia are less commonly found (Santoyo et al., 2016). However, predominance of these phyla can vary with the type of host plant species (Bodenhausen et al., 2013; Ding and Melcher, 2016). Among the most commonly isolated bacterial genera are *Bacillus*, *Burkholderia*, *Microbacterium, Micrococcus*, *Pantoea*, *Pseudomonas* and *Stenotrophomonas*, where *Bacillus* and *Pseudomonas* are the predominant genera (Chaturvedi et al., 2016; Hallmann et al., 1997). A list of endophytic bacteria isolated from some agronomic crop plants and some wild plants is provided in Tables 1 and 2.

4. Mechanisms of host plant growth promotion

Endophytic bacteria have been shown to impart several beneficial effects on their plant host directly or indirectly. They can benefit plants directly by assisting plants in getting nutrients, and improve plant growth by modulating growth related hormones, which can help plants grow better under normal and stressed conditions (Ma et al., 2016). Indirectly, endophytic bacteria improve plant growth by discouraging phytopathogens using mechanisms like antibiotic and lytic enzyme production, nutrient unavailability for the pathogens, and priming plant defense mechanisms and thereby protecting the plants from future attacks by pathogens (Miliute et al., 2015). These beneficial processes are discussed below and summarized in Fig. 1.

4.1. Nutrient acquisition

Soils usually lack a sufficient quantity of one or more of the nutrient compounds necessary for plant growth. The endophytic bacteria can help their host plants in getting increased amounts of limiting plant nutrients, which include nitrogen, iron, and phosphorus (Glick, 2012). These mechanisms are discussed below.

4.1.1. Nitrogen availability

Endophytic bacteria can increase the nitrogen availability for their host plants. These bacteria can supply fixed atmospheric nitrogen to their host plants by expressing nitrogenase activity (Montanez et al., 2012). Nitrogenase is a highly conserved protein and all N_2 fixing bacteria have this enzyme, with ample evidence suggesting lateral gene transfer (Ivleva et al., 2016). Nitrogen fixing bacteria like *Azoarcus* sp. BH72, *Azospirillum brasilense*, *Burkholderia* spp., *Gluconacetobacter diazotrophicus*, and *Herbaspirillum seropedicae* have been reported to increase the host plant biomass by N_2 fixation under controlled conditions (Bhattacharjee et al., 2008). Associative nitrogen-fixing endophytes perform better than rhizosphere microorganisms in enabling plants to thrive in nitrogen limited soil environments and promote plant health and growth (Hurek and Reinhold-Hurek, 2003). Gupta et al. (2013) reported that endophytic nitrogen-fixing bacteria may also enhance the rate of nitrogen fixation and accumulation in plants residing in nitrogen limited soils. Endophytic bacteria are not as efficient as root nodule associated *Rhizobium* in Nitrogen-fixation ability. However, endophytic strains of *G. diazotrophicus* perform exceptionally well in this ability. Strains of *G. diazotrophicus* have been identified living in symbiosis with sugarcane and pine plants (Carrell and Frank, 2014; Dong et al., 1994). Similarly, Nitrogen-fixing endophyte *Paenibacillus* strain P22 has been found in poplar tree, which was shown to contribute to the total nitrogen pool of the host plant (Scherling et al., 2009).

4.1.2. Phosphorus availability

Phosphorous is another major micronutrient crucial for enzymatic reactions responsible for many plant physiological processes (Ahemad, 2015). Although present in ample quantities, most of the soil phosphorus is insoluble, and therefore cannot support the plant growth due to its unavailability. Moreover, almost 75% of phosphorus applied as fertilizer forms complexes with soil and becomes unavailable for the plants (Ezawa et al., 2002). Endophytic bacteria can increase the availability of phosphorus for the plants by solubilizing precipitated phosphates, using mechanisms like acidification, chelation, ion exchange and production of organic acids (Nautiyal et al., 2000). They can also increase phosphorus availability in the soil by secreting acid phosphatase that can mineralize organic phosphorus (Van Der Heijden et al., 2008). Moreover, endophytic bacteria can prevent phosphate adsorption and fixation under phosphate-limiting conditions by assimilating solubilized phosphorus (Khan and Joergensen, 2009). Thus, these bacteria can act as a sink to provide phosphorus to the plants when they need it. Phosphate solubilization feature is commonly found in endophytic bacteria. For instance, around 59–100% of endophytic populations from cactus, strawberry, sunflower, soybean and other legumes were mineral phosphate solubilizers (Dias et al., 2009; Forchetti et al., 2007; Kuklinsky-Sobral et al., 2004; Palaniappan et al., 2010; Puente et al., 2009a). Puente et al. (2009b) examined the role of phosphate solubilizing endophytic bacteria by growing bacteria-free cacti on mineral phosphate supplemented with either endophytes or nutrients, and compared them with plants grown under sterile conditions. The inoculated plants grew well without nutrient addition, and their growth was comparable to fertilized plants, whereas the bacteria-free unfertilized cacti failed to grow. This indicated that endophytic bacteria provided the developing plantlets with the limiting nutrient.

4.1.3. Iron availability

Iron is an important element of life required by most organisms. Iron is part of many iron-containing proteins controlling important physiological processes like transpiration and respiration (Ma et al., 2016). Iron usually occurs in the insoluble ferric (Fe_3) form that is unavailable to most plants, which includes carbonates, hydroxides, oxides and phosphates of iron. Endophytic bacteria produce iron chelating agents called siderophores that can bind insoluble ferric ions, and plants can acquire iron from these bound siderophores *via* root based chelate degradation or ligand exchange (Ma et al., 2016; Rajkumar et al., 2009). Hence, bacterial siderophores play a major role in providing iron to plants under iron limitation (Ma et al., 2011b). Marques et al. (2010) demonstrated that siderophore production by plant beneficial bacteria strongly correlated with maize plant growth traits including shoot and root biomass. Furthermore, Radzki et al. (2013) demonstrated that bacterial siderophores efficiently provided iron to tomato plants during growth in hydroponic culture. Iron acquisition is

not the only benefit provided to the plants by siderophore producing bacteria. Endophytic bacteria can also discourage the growth of phytopathogens by siderophore production, possibly by iron depletion (Ahmad et al., 2008). In fact, Calvente et al. (2001) demonstrated that bacterial siderophore containing spent medium inhibited the growth of phytopathogenic molds, and antifungal activity was correlated to siderophore concentration.

4.2. Phytohormone production and modulation

Endophytic bacteria can enhance nutrient accumulation and metabolism of host plants by producing growth regulating phytohormones. Recent studies examining the possible role of plant hormones released by endophytic bacteria have shown that endophytic colonization caused enhanced plant nutrient uptake and biomass (Gravel et al., 2007; Phetcharat and Duangpaeng, 2012; Shi et al., 2014). In general, there are five types of plant hormones, namely abscisic acid, cytokinins, ethylene, gibberellins and indole-3-acetic acid (IAA), where IAA and ethylene are the most important hormones in plant-bacterial interactions.

4.2.1. Modulating plant indole acetic acid levels

IAA is a major plant auxin that is involved in numerous plant physiological processes. These include cell-cell signaling, regulation of plant development, and induction of plant defense systems (Gravel et al., 2007; Navarro et al., 2006; Spaepen et al., 2007). IAA can also initiate lateral and adventitious root formation, mediate responses to stimuli, affect photosynthesis and biosynthesis of metabolites, and mediate resistance to stress conditions (Glick, 2012). Further, IAA can even control synthesis of other plant hormones like ethylene (Woodward and Bartel, 2005).

Modulating plant IAA pools is an important trait by which endophytic bacteria can enhance plant growth. IAA production by the endophytic bacteria can result in improved plant root biomass and surface area, and increased production of lateral roots in host plants (Dias et al., 2009; Kuklinsky-Sobral et al., 2004; Taghavi et al., 2009; Tsavkelova et al., 2007). Tsavkelova et al. (2007) reported that endophytic bacteria that were isolated from terrestrial orchids produced IAA. They noticed that the culture supernatant of the bacteria stimulated root formation of kidney beans by significantly increasing root length and the number of developing roots, indicating the possible role of bacterial IAA in the development of plant root system. A more direct evidence of the role of bacterial IAA in plant beneficial effects came from Patten and Glick (2002), who showed that *Pseudomonas putida* GR12-2 defective in IAA synthesis was unable to increase plant root growth and lateral root formation.

While lower amounts of IAA production by the bacteria can enhance plant root growth, higher quantities can cause stunted growth (Malik and Sindhu, 2011). In a continuation work to Patten and Glick (2002) to study the effects of IAA levels on plant growth, *Pseudomonas putida* GR12-2 mutant, that was modified to overproduce IAA, produced much shorter roots in mung bean compared to uninoculated control plants. This is not surprising as high IAA production is known to be the characteristic of plant pathogens (Rashid et al., 2012), and can cause increased production of ethylene, which is a plant stress hormone (Woodward and Bartel, 2005).

IAA production is not the only way by which endophytic bacteria can improve host plant growth. Indeed, the reverse activity, degradation of IAA, can also play a significant role in enhancing plant growth. This was demonstrated by Leveau and Lindow (2005) for the plant growth promoting and IAA degrading *Pseudomonas putida* Strain 1290, which completely abolished the inhibitory effects of exogenous IAA on the elongation of radish roots. The bacteria also produced IAA in the presence of tryptophan, which is a precursor of IAA. However, it was shown that IAA production by *Pseudomonas putida* Strain 1290 did not have the similar deleterious effects on radish roots as did the high IAA-producing strains. Thus, the authors suggested that this dual status, the ability to both produce and destroy IAA, enables this bacterium to finely control IAA levels to produce a net positive effect on the host plant. Similarly, Zúñiga et al. (2013) showed that mutant *Burkholderia phytofirmans* PsJN, which was defective in IAA mineralization, was unable to alleviate the inhibitory effects of exogenous IAA in the roots of *Arabidopsis thaliana* compared to wild type strain. Nevertheless, bacterial IAA production is considered a very important trait in selecting plant beneficial bacteria. Moreover, plant IAA levels can also determine whether bacterial IAA stimulates or suppresses plant growth, as bacterial IAA production usually benefits those plants that have low levels of endogenous IAA (Glick, 2012).

4.2.2. Control of ethylene levels

Ethylene is an important plant hormone that controls the plant response to abiotic and biotic stresses. It can control different developmental and physiological processes like root initiation, leaf senescence, root nodulation, abscission, cell elongation, fruit ripening and auxin transport (Sun et al., 2016). Biotic and abiotic stresses result in an increased ethylene production in plants that leads to inhibition of root elongation, development of lateral roots and formation of root hair. Endophytic bacteria produce an enzyme called 1-aminocyclopropane-1-carboxylate (ACC) deaminase that can hydrolyze ACC, which is a precursor of plant hormone ethylene. ACC degrading bacteria can bind to plant roots and cleave the exuded ACC into α-ketobutyrate and ammonia, and use it as a nitrogen source (Sun et al., 2009). Thus, hydrolysis of ACC can alleviate plant stress, thereby improving plant growth under stress conditions (Santoyo et al., 2016). A number of plant growth promoting endophytic bacteria have been reported to have ACC deaminase activity (Nikolic et al., 2011; Rashid et al., 2012; Zhang et al., 2011). In fact, the ability of these bacteria to benefit plant growth can be related to ACC deaminase production. This was demonstrated by Sun et al. (2009) who mutated the ACC deaminase gene of the canola growth promoting *B. phytofirmans* PsJN and observed that the mutant was no longer able to promote canola root growth. However, introduction of wild-type ACC deaminase gene restored the growth promoting ability of the mutant *B. phytofirmans* PsJN, indicating the crucial role this enzyme plays in growth promotion of host plants.

4.2.3. Production of plant cytokinins and gibberellins

Several studies have shown that many plant beneficial endophytic bacteria can produce cytokinins and gibberellins. Cohen et al. (2009) revealed the effects of *Azospirillum lipoferum* in maize plants treated with inhibitor of gibberellins synthesis, and plants were either subjected to drought stress or were well-watered. The gibberellin produced by the endophytic bacterium was important in plant stress alleviation. Similarly, Bhore et al. (2010) identified cytokinin-like compounds in the broth-extracts of two endophytic bacteria, isolated from *Gynura procumbens*, using cucumber cotyledon greening bioassay. The two bacteria were identified as *Psuedomonas resinovorans* and *Paenibacillus polymaxa*. More work is needed to elucidate the role of bacterial gibberellins and cytokinins in improving plant growth.

4.3. Indirect growth promotion by suppression of phytopathogens

Endophytic bacteria enhance the host plant growth indirectly by discouraging the growth of phytopathogens and plant pests. They can produce substances that can antagonize phytopathogens, like antibiotics, toxins, siderophores, hydrolytic enzymes and antimicrobial volatile organic compounds (Sheoran et al., 2015). Both bacterial and fungal pathogens can be targeted by endophytic bacteria (Lodewyckx et al., 2002). Bacteria belonging to *Actinobacteria, Bacillus, Enterobacteor, Paenibacillus, Pseudomonas* and *Serratia* are the most commonly reported genera for their antimicrobial activity against phytopathogens (Aktuganov et al., 2008; Liu et al., 2010; Lodewyckx et al., 2002). Endophytic bacteria have been demonstrated to successfully

Table 3
Selected bacterial genes involved in endosphere colonization, host interaction and promotion of plant growth.

Gene	Function	Technique	Bacteria	References
acds (ACC deaminase)	Stress reduction	Gene deletion, complementation; gene disruption	*Burkholderia phytofirmans PsJN*	(Sun et al., 2009; Zúñiga et al., 2013)
iacC	IAA degradation	Gene disruption	*Burkholderia phytofirmans PsJN*	(Zúñiga et al., 2013)
N-acyl-homoserine lactone synthase	Quorum Sensing	Gene disruption	*Burkholderia phytofirmans PsJN*	(Zúñiga et al., 2013)
nifH (nitrogenase)	Nitrogen fixation	Pnif: :gusA fusion reporter system; RT-PCR	*Herbaspirillum seropedicae; Bradyrhizobium, Pelomonas, Bacillus sp., Cyanobacteria*	(Roncato-Maccari et al., 2003; Terakado-Tonooka et al., 2008)
eglA; *eglS* (endoglucanse)	Systemic colonization	Transposon mutagenesis; gene disruption by homologous recombination	*Azoarcus sp. strain BH72; Bacillus amyloliquefaciens*	(Reinhold-Hurek et al., 2006; Fan et al., 2016)
Pectinase	Systemic colonization	Gene overexpression	*Bacillus*	(Fan et al., 2013)
alkB (alkane monooxygenase)	Diesel degradation	Real-time PCR	*Pseudomonas sp., Rhodococcus sp.*	(Andria et al., 2009)
carAB	Pathogen cell-cell signaling disruption	Gene disruption, complementation	*Pseudomonas sp. strain G*	(Newman et al., 2008)
aiiA (N-acyl-homoserine lactonase)	Pathogen quorum sensing disruption	Gene introduction by electroporation	*Burkholderia sp. KJ006*	(Cho et al., 2007)
Multiple genes	Stress response, chemotaxis, metabolism, and global regulation	*dapB*-Based *In Vivo* Expression Technology System	*Pseudomonas stutzeri A15*	(Rediers et al., 2003)
CYP153 genes (alkane degradation)	Petroleum hydrocarbon defradation	Real-time PCR	*Enterobacter ludwigii; Pseudomonas sp. strain ITRI53, Pantoea sp. strain BTRH7*	(Afzal et al., 2011; Yousaf et al., 2011)
pilT (type IV pili)	Endophytic colonization by Twitching Motility	Deletion mutation	*Azoarcus sp. Strain BH72*	(Böhm et al., 2007)
O-antigenic side chain	Attachment	Spontaneous phage-mediated mutant	*Pseudomonas fluorescens strain WCS417r*	(Duijff et al., 1997)
Multiple genes	Transcription regulation, general metabolism (sugars, amino acids, lipids, and nucleotides), energy production, cellular homeostasis, cell redox homeostasis, ECF group IV sigma factors	In-planta RNA-seq based transcriptome profile	*Burkholderia phytofirmans PsJN*	(Sheibani-Tezerji et al., 2015)
Ferritin	Iron storage	Real-time PCR	*Burkholderia phytofirmans PsJN*	(Zhao et al., 2016)
TonB-dependent siderophore receptor	Siderophore mediated iron uptake	Real-time PCR	*Burkholderia phytofirmans PsJN*	(Zhao et al., 2016)
L-ornithine5-monooxygenase	Siderophore synthesis	Real-time PCR	*Burkholderia phytofirmans PsJN*	(Zhao et al., 2016)

suppress fungal disease in plants like black pepper, potato and wheat (Aravind et al., 2009; Coombs et al., 2004; Sessitsch et al., 2004). The antimicrobial activities against fungi can result from the production of fungal cell-wall targeting enzymes chitinase, proteases and glucanases (Zarei et al., 2011; Zhang et al., 2012). Antimicrobial activity against bacterial pathogens has been reported for *Bacillus subtilis* BSn5 that targeted plant pathogen *Erwinia carotovora* subsp. *carotovora*. However, the exact mechanism of action against the pathogen is not known (Deng et al., 2011; Dong et al., 1994). Moreover, an endophytic bacteria *Pantoea vagans* C9-1 has been commercialized as a bacterial biocontrol agent for the fire blight (Smits et al., 2011). Activity against nematodes was reported by Aravind et al. (2009) for suppression of phytopathogenic burrowing nematode (*Radopholus similis* Thorne) by endophytic bacteria *Bacillus megaterium* BP17 and *Curtobacterium luteum* TC10. Endophytic bacteria active against plant pests have also been demonstrated, where genetically modified endophytic *Pseudomonas fluorescens* expressing *Bacillus thuringiensis* toxin and *Serratia marcescens* chitinase effectively targeted *Eldana saccharina* (Sugarcane Borer) larvae (Downing et al., 2000).

Plant beneficial bacteria can also use a mechanism called induced systemic resistance (ISR) to protect their host plants from phytopathogens. ISR induced by endophytic bacteria can protect host against fungal, bacterial and viral pathogens (Alvin et al., 2014). The ISR primes plant defense mechanisms, thereby protecting unexposed plant parts against future pathogenic attacks by microbes and herbivorous insects. Endophytic bacteria can initiate ISR using salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) mediated pathways, which are usually a network of interconnected signaling pathways involved in ISR induction (Pieterse et al., 2012). Endophytic bacteria of genus *Bacillus*, *Pseudomonas* and *Serratia* have been shown to protect plant hosts using defense priming by ISR (Kloepper and Ryu, 2006; Pieterse et al., 2012). The bacteria must also be able to overcome these host defense responses in order to colonize the host plant (Ma et al., 2016).

ISR may involve both SA and JA/ET pathways. Niu et al. (2011) showed that *Bacillus cereus* AR156 triggered both SA and JA/ET signaling pathways in *Arabidopsis* to induce ISR, which led to an additive effect of plant protection. Similarly, Conn et al. (2008) indicated that *A. thaliana* plants inoculated with endophytic *Actinobacteria* showed up-regulation of both defense pathways, thereby protecting against subsequent infection by phytopathogenic bacteria *Erwinia carotovora* and fungus *Fusarium oxysporum*. However, the primed defense pathways differed for the two pathogen types. The resistance to *E. carotovora* was by JA/ET pathway, while resistance towards *F. oxysporum* was by SA pathway. Thus, the same bacterium was able to prime two different pathways to confer resistance to two different pathogens (Conn et al., 2008).

5. Bacterial genes expressed in the endosphere

Endophytic bacteria colonize the plant endosphere and confer growth benefits to their host by using a wide variety of traits. Some of these traits have been confirmed using techniques like gene deletion/disruption and complementation (Sun et al., 2009; Zúñiga et al., 2013), real-time PCR (Yousaf et al., 2011; Zhao et al., 2016), *in vivo* expression technology (IVET) (Rediers et al., 2003), gusA fusion reporter system (Roncato-Maccari et al., 2003), gene overexpression (Fan et al., 2013), gene introduction (Cho et al., 2007), and RNA-seq based whole transcriptome profiling (Sheibani-Tezerji et al., 2015).

Most of these studies have been done on *B. phytofirmans* strain PsJN, a model endophytic bacterium, with the ability to competently colonize (both rhizosphere and endosphere) and promote growth of a variety of different plant hosts, including *Arabidopsis thaliana*, grape, maize, potato, switch-grass, tomato, and wheat (Sessitsch et al., 2005; Sheibani-Tezerji et al., 2015). Moreover, strain PsJN can also increase tolerance of host plants to abiotic stresses such as chilling and drought (Barka et al., 2006; Naveed et al., 2014), and biotic stresses like inhibiting growth of fungal phytopathogens (Barka et al., 2006; Sharma and Nowak, 1998). Strain PsJN have been shown to require IAA degradation, ACC deaminase, and quorum sensing to colonize host plants and produce beneficial effects (Sun et al., 2009; Zúñiga et al., 2013). Moreover, *in planta* gene expression profiling revealed that, during its growth inside host plants, the bacterium expresses a number of different traits related to cellular homeostasis, cell redox homeostasis, energy production, general metabolism (amino acids, lipids, nucleotides, sugars), and transcription regulation (Sheibani-Tezerji et al., 2015). The same study revealed that bacterium expresses enzymes related to oxidative stress when host plants are challenged with drought stress. Another study on strain PsJN indicated that bacterium expresses traits involving iron uptake and storage (Zhao et al., 2016). Nevertheless, more work is needed to elucidate the importance of different genes required by strain PsJN for its endophytic success. Other bacteria have also been studied for their endophytic gene expression and lifestyle, which have been summarized in Table 3. Collectively, these studies indicate that plants recruit those bacteria which benefit them in a certain niche or a situation. For example, plants growing in hydrocarbon contaminated areas prefer hydrocarbon degrading endophytic partners that actively express these traits during *in planta* growth (Afzal et al., 2011; Yousaf et al., 2011). Furthermore, these bacteria also readily express traits that allow active penetration and systemic colonization of host plants and allow competitive advantage over other plant endosphere dwelling bacteria.

6. Host specificity of growth promoting endophytic bacteria

The plant growth promoting ability of endophytic bacteria can be influenced by the genotype of plant host. Long et al. (2008) noticed that plant growth promoting bacteria of *Solanum nigrum* were highly host specific, where these bacteria were unable to produce growth enhancement in *Nicotiana attenuate*, a non-host plant. Similarly, Kim et al. (2012) reported that growth promotion of switch grass by *B. phytofirmans* PsJN is plant genotype dependent. However, many endophytic bacteria can have a broad host range, as has been demonstrated in the case of *B. phytofirmans* PsJN, isolated from onion roots (Pillay and Nowak, 1997), which can promote growth of *Arabidopsis thaliana*, grape, maize, potato, switch-grass, tomato, and wheat (Sessitsch et al., 2005; Sheibani-Tezerji et al., 2015).

Bacterial genotype can also strongly influence the growth promoting effects of bacterial endophytes on host plants. This was demonstrated by Trognitz et al. (2008), where different strains of *B. phytofirmans* differed markedly in their abilities to promote growth of the same potato cultivar. Similarly, Dong et al. (1994) reported that four strains of endophytic *Salmonella enterica* colonized alfalfa roots and hypocotyl differently. Hence, plant colonization and growth promotion by the endophytic bacteria appears to be an active process that is controlled by the genetic factors of both partners.

There are numerous reports of non-host plant growth promotion by the endophytic bacteria. Ma et al. (2011a) isolated Nickel resistant *Pseudomonas* sp. A3R3 from Nickel accumulating *Alyssum serpyllifolium*. The bacteria promoted the growth of host plant and non-host *Brassica juncea* under metal stress. Similarly, Sun et al. (2016) showed that copper-resistant *Burkholderia* sp. GL12 and *Bacillus megaterium* JL35 could significantly promote growth of host *Elsholtzia splendens* and a non-host *Brassica napus* grown in heavy metal-contaminated soils. Thomas and Upreti (2014) demonstrated that endophytic bacterial isolates of crop plants that could inhibit *Ralstonia solanacearum* (wilt pathogen) also mitigated the disease effects of *Ralstonia solanacearum* on a non-host tomato plant. Moreover, endophytic bacteria isolated from different agricultural soils using tomato plants were able to promote canola growth under gnotobiotic conditions (Rashid et al., 2012). Similar finding was reported by Afzal et al. (2015) for the endophytic bacteria selectively isolated from *Cannabis sativa* rhizosphere using canola. Collectively, these findings suggest that endophytic bacteria can

have a broad host range in terms of their plant growth promoting potential, a feature that could be exploited in the agriculture sector. The broad host range of these endophytic bacteria can be attributed to the general plant growth promoting and plant colonization traits expressed by them.

7. Conclusions and future perspectives

Plant beneficial endophytic bacteria have a great potential to be used as biofertilizers and biopesticides. Although many such bacteria have been identified, and they can also have a broad host range, these bacteria generally fail to give consistent results under field conditions. One reason for this is our poor understanding of the complex dynamics that control plant-endophyte association. We need to identify the subtleties that govern plant-endophyte relationship at the molecular level. This is only possible if we have a better understanding of the bacterial genes that are expressed in the plant endosphere. Although some studies have been conducted in this area, they remain limited in their scope. Thus, a comprehensive study on the bacterial transcriptome expressed *in planta* can shed light on the lifestyle these bacteria adopt in the plant endosphere. Achieving this is a challenge as getting high quality RNA transcripts from bacteria growing *in planta* is extremely difficult. This task is further complicated by the low cell densities these bacteria maintain in their host plants to avoid triggering plant defenses. Therefore, getting enough of the good quality RNA for a bacterial transcriptome analysis is arduous. Nevertheless, with the advent of techniques like RNA-seq, which can effectively identify both abundant and rare transcripts, such analyses are now possible. Moreover, a bacterial meta-transcriptome analysis, a community-wide global gene expression profiling, will be even better in revealing the activity of endophytic community that a plant recruits to get growth and health benefits.

Plant genotype is an important determinant in the development of positive plant-endophyte association. Therefore, to minimize the effect of host genotype in plant-bacterial interactions, techniques like micropropagation and vegetative growth can be used, which produce genetic clones of the host plants having the same genotype. This way, plant-endophyte associations can be pre-formed under controlled conditions before these plants are taken to the field conditions, thus giving us more consistent field trials.

Lastly, as the endophytic diversity has been poorly studied, the prospects of finding unique and interesting bacteria in the unexplored wild plants are great. Wild plants tend to survive the harshness of environment and fight the biotic and abiotic stresses, which could be assisted by the specialized endophytes that they harbor. Identifying these rare and promising bacterial endophytes with general plant beneficial characteristics would require a combination of culture-dependent and culture-independent techniques.

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