Chapter 7
Biofertilizers Based on Bacterial Endophytes Isolated from Cereals: Potential Solution to Enhance These Crops

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Abstract Due to the increasing demand for the use of agricultural products, along with new and more restrictive policies regarding the application of fertilizers, the search for alternative ways to increase crop production in a responsible way with respect to the environment is necessary, especially considering that the use of nitrogen-based fertilizers are both very costly and polluting. As regards this chapter focuses on the production of cereals because they represent the most important source of total food consumption, particularly in developing countries with diets based mainly on these types of crops. One possible solution is the application of microbial-based fertilizers (biofertilizers) to enhance crop production. In the literature, bacteria that not only promote plant growth but are also capable of colonizing the interior of plants, known as endophytic bacteria, have been described. Several studies have characterized the different ways of locating these bacteria inside plants, as well as the effects of their colonization. In addition, some entophytes are able to fix nitrogen for their hosts, produce phytohormones (auxins, cytokinins, gibberellins), degrade harmful compounds, decrease the effects of saline stress and improve seed germination, among others benefits. Several companies have attempted to

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V. S. Meena (ed.), *Role of Rhizospheric Microbes in Soil*,
https://doi.org/10.1007/978-981-10-8402-7_7

exploit the positive effects caused by endophytic bacteria on their hosts by developing different products, used worldwide (e.g. Inogro®, QuickRoots®), that are based on these types of bacteria. The application of these products occurs despite the governing legislation of the different countries where it is used, and there are usually no specific regulations controlling the process of production, security and marketing of these biofertilizers.

Keywords PGPBEs · Biofertilization · Maize · *Azospirillum* · Bioinoculants

7.1 Introduction

The United Nations Food and Agriculture Organization (FAO) estimates that the total demand for agricultural products will be ~60% higher in 2030 than it is today. Remarkably, developing countries comprise ~85% of the global food demand. For over half a century, the world population has relied on modern agriculture for enhancing crop yields. Cereals are the most important source of total food consumption, especially in developing countries, where diets are based mainly on these types of crops. World cereal production has significantly increased during the last two decades, and during this time, the grain yields of several cereal crops has increased to ~122% all over the world, responding to this ever-increasing demand for food. However, this trend in grain production cannot be maintained due to the decrease in the number of hectares of cultivable land, which has been dedicated to rapidly growing urbanization (Mia and Shamsuddin 2010; Meena et al. 2013a, 2016a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016; Parewa et al. 2014; Prakash and Verma 2016).

One of the most important factors in obtaining high-yield cereal crops is the application of nitrogen-based fertilizers, which is why farmers apply high amounts of these types of fertilizers that are both very costly and hazardous to the environment, especially when used indiscriminately. In addition, ~50% of applied N-fertilizers are somehow lost through different bio-geological processes, which not only represent an economical loss but also pollute the environment (Ladha et al. 1998). Thus, crop scientists all over the world are facing this alarming situation and searching for cost-effective and biosafe alternatives (Jeyabal and Kupuswamy 2001). With this aim in mind, the scientific community needs to investigate ways to increase crop production and at the same time to avoid the problems associated with the overuse of fertilizers (García-Fraile et al. 2015).

Therefore, it is necessary to enhance crop productivity in a sustainable manner, which does not exacerbate the problem of pollution. Furthermore, farmers need to be open to the idea of using other kinds of fertilizing schemes, such as biofertilizers. The application of plant growth-promoting bacteria, such as those used as biofertilizers, for sustainable agriculture may provide a solution to this problem (Meena et al. 2015a, b, f, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2016a, 2017; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016).

The development of a proper biofertilizer requires: (i) isolation and selection of bacteria, (ii) effective carrier selection, (iii) observation of modes of entry of endophytic bacteria into the host plant, (iv) determining the mechanisms involved in plant growth promotion, (v) verifying the effectiveness of inoculants, and (vi) to check the biosafety of these strains for the environment and health (Berg and Smalla 2009; Chauhan et al. 2015). In addition, it is necessary to understand the nature of the microorganisms before their use as biofertilizers in order to utilize only microorganisms safe for human health; this includes not only the consumer or end user but also those handling the biofertilizers during their production (Meena et al. 2017). Strains belonging to the genera *Azospirillum*, *Gluconacetobacter*, *Bacillus* or *Azotobacter*, among others, are currently commercialized as biofertilizers for nonlegumes without any adverse effects being reported to date (Bashan 2014). In this chapter, we revise the available data regarding plant growth promotion by bacterial endophytes isolated from different cereals and focus on their possible use in biofertilization. Moreover, we will specifically focus on the culturomics approach, analysing the role of cultivable microorganisms since they are essential for agriculture and very important in the movement and availability of the minerals required for plant growth (Yasin et al. 2016; Meena et al. 2016c, d; Saha et al. 2016a; Yadav and Sidhu 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016). Ultimately, these microorganisms are essential for the partial or total reduction of synthetic fertilizers (Malusá and Vassilev 2014).

7.2 Endophytic Bacteria: Definition, Importance and Mechanisms of Action

For many years, scientists from all around the world have developed and published several studies reporting on the great potential that some bacterial strains have in the promotion of plant growth, namely, plant growth-promoting bacteria or PGPB, through several mechanisms (García-Fraile et al. 2015). Many of these bacteria are endophytes, which are defined as bacteria living inside a plant tissue (“endo”, inside; “phyte”, plant). Some of them can influence plant growth and pertain to a subset of the endophytic population called PGPBEs (Gaiero et al. 2013).The potential of PGPBEs to improve plant health has led to a great number of studies examining their applied use as inoculants, primarily in agricultural crops (Kuklinsky-Sobral et al. 2004; García-Fraile et al. 2015). Because of these qualities, PGPBEs are important candidates to be used as inoculants to reduce the need for chemicals, such as pesticides and fertilizers, becoming important in the development of sustainable agricultural practices (Saha et al. 2016b; Verma et al. 2014, 2015a, b; Meena et al. 2014a, 2015e; Sharma et al. 2016; Bahadur et al. 2016b).

In general, endophytes are more likely to show plant growth-promoting effects than bacteria exclusively colonizing the rhizosphere (Conn et al. 1997; Chanway et al. 2000). Also, some endophytes are better colonizers and are capable of outcompeting others present in the surroundings (Verma et al. 2004).Therefore, endophytes (single or forming consortia) found in a particular plant species can be considered as more competent and suitable for their reinoculation in the same plant crop from which they were isolated.

7.2.1 Plant Root Colonization

Colonization and infection processes in cereals by endophytic bacteria differ from leguminous plants. The infection process can take place at cracks, such as those occurring at root emergence sites or those created by deleterious microorganisms, as well as through cells situated at root tips (Reinhold-Hurek and Hurek 2011). To successfully colonize the host plant, endophytic bacteria have specific traits, such as flagella, cell wall degrading enzymes (CWDEs) or twitching motility, among others (Lodewychx et al. 2002). Due to endophytic bacteria being able to penetrate into the root of the host, they are better candidates than the bacteria found in the rhizosphere for use as PGPB in plants (Meena et al. 2013b, 2015c, 2016e; Shrivastava et al. 2016; Velazquez et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016; Teotia et al. 2016).

Active and passive mechanisms have been reported for the translocation processes of endophytic bacteria inside their plant hosts, allowing them to progress from the rhizoplane to the cortex of the root system (Fig. 7.1). Once a bacterium reaches the root cortical zone, a barrier such as the endodermis can block further colonization of the inner tissues; only few bacteria are able to pass through the endodermis (Gregory 2006). It is likely that endophytes able to pass through the endodermis can secrete CWDEs allowing them to continue colonization through the inner roots (James et al. 2002). Alternatively, some bacteria may passively enter as a portion of this endodermal cell layer is often disrupted, such as during the growth of secondary roots, which derive from the pericycle situated just below the endodermis barrier (Gregory 2006). Under natural conditions, some deleterious bacteria can also disrupt the endodermis, allowing endophytic bacteria at the same time to pass into the central cylinder to further reach the root xylem vessels of their hosts (Compant et al. 2010).

For example, *Azorhizobium caulinodans* are able to enter rice roots at emerging lateral roots (lateral root cracks) by crack entry and move into intercellular space within the cortical cell layer or roots (Goormachtig et al. 2004). Lateral root crack colonization of rice was also observed with similar frequency following inoculation with *Azospirillum brasilense*, where colonization was stimulated by naringenin and other flavonoids (Jain and Gupta 2003).

In addition, some strains may have the ability to infect rice root tissues via root hairs located at the emerging lateral roots and to spread extensively throughout the

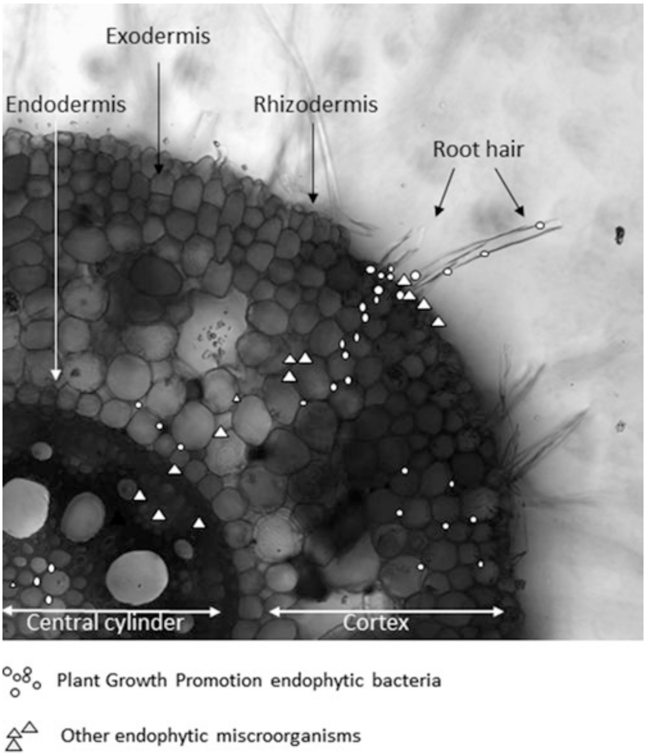

Fig. 7.1 Sites of plant colonization by endophytic bacteria. Plant growth-promoting endophytic bacteria (PGPBE), white circles; other endophytic microorganisms, black triangles

rice root (Ladha et al. 1996; Francine et al. 2007). Some naturally occurring rhizobia can invade the emerging lateral roots of rice, wheat, maize and oilseed rape (Cocking 2003; Bashan 2014; Yanni et al. 2016).

7.2.2 *How to Localize Endophytic Bacteria Inside Plants*

Colonization by these bacterial endophytes can be confirmed through multiple methods. These methods include fluorescent-tagging, immunological detection, fluorescence/confocal microscopy or scanning and transmission electron microscopy. Bacterial entry routes into the host plant have been traced and scored in many cases by using these approaches (Prayitno et al. 1999; Chaintreuil et al. 2000; Verma et al. 2004; Perrine-Walker et al. 2007a). Otherwise, specific primers could be of use to analyse bacteria inside plants (Hartmann et al. 2000).

Other authors like Bulgarelli et al. (2015) combine 16S rRNA gene profiling and shotgun metagenomic analysis to investigate the structure and function of the bacterial root microbiota in wild and domesticated barley (*Hordeum vulgare*). Moreover, Stets et al. (2013) used matrix-assisted laser desorption ionization time-of-flight mass spectrometry (MALDI-TOF MS) to assess the diversity of wheat-associated bacterial isolates. Also, they validated their results by using 16S rRNA gene sequence analyses, which correlated with the clusterization of the mass spectra profiles. The results obtained demonstrated that this technique had the potential to classify bacteria at different levels.

Several authors have previously demonstrated the potential of in situ visualization of specific *gfp*-tagged bacteria in plant roots (Chelius and Triplett 2000; Ramos et al. 2002). GFP-tagged *B. subtilis* CB-R05 strain was studied to monitor its interaction in *Oryza sativa* under axenic conditions by using confocal laser scanning microscope (CLSM). CB-R05 cells penetrate through the rhizoplane, especially in the elongation and differentiation zones of the rice roots and, also, are able to colonize it intracellularly (Ji et al. 2014).

Moreover, Chi et al. (2005) examined the colonization and infection of rice plant tissues by different species of *gfp*-tagged rhizobia and their influence on the growth physiology of rice. Other studies aim to evaluate the potential of *Rhizobium* sp. to colonize the roots of a wide variety of cereals by tagging bacteria with fluorescent proteins (Mitra 2014). Results derived from these studies showed that in the first days of the rhizobia-plant root interaction, bacteria predominantly colonized the elongation zone of the roots, the root surfaces and, interestingly, root hairs. Also, other studies reported the inoculation of rice seedlings with a GFP-tagged strain of *Rhizobium*, displaying some phenotypes similar to those seen in the infection process that occurs in leguminous plants. Results suggest that some strains may have the ability to infect rice root tissues via root hairs located at the emerging lateral roots and to spread extensively throughout the rice roots (Perrine-Walker et al. 2007b).

Quadt-Hallmann and Kloepper (1996) used antibodies coupled to fluorophores to study the colonization of internal tissues of different plant species by the endophytic bacteria *Enterobacter asburiae* JM22. Polyclonal and monoclonal antibodies applied in enzyme-linked immunosorbent assay (ELISA), dot blot assay, tissue printing, or immunogold labelling was sensitive and specific enough to detect JM22 in plant tissues.

Thomas and Reddy (2013) used the fluorophore Syto9 (S9), which binds nucleic acids in bacteria, in combination with propidium iodide (PI) to localize endophytic bacteria in the inner tissues of *Musa acuminate* (banana) by epifluorescence and confocal laser scanning microscopy (CLSM). Their results showed an extensive bacterial colonization of banana tissues. Rothballer et al. (2003) examined the endophytic potential of two strains of *A. brasilense*, Sp245 and Sp7, on roots of different wheat cultivars using fluorescent in situ hybridization (FISH) in combination with confocal laser scanning microscopy. The results obtained revealed which strain was able to grow better in contact with wheat roots.

The location of bacteria inside the plants reveals information about the preferences of colonization of internal tissues by the endophytic bacteria. We can also distinguish if they perform an intra- or extracellular colonization. However, these techniques just give us a qualitative idea of the colonization. To quantify and give an accurate result of bacterial colonization, techniques based on fluorescence should be combined with other techniques, such as bioinformatic tools. In this sense, Liu et al. (2001) developed a computer-aided interactive system called "CMEIAS" (Center for Microbial Ecology Image Analysis System) to analyse the high degree of morphological diversity in growing microbial communities associated or not to a substrate, which might be the plant root surface.

7.2.3 Plant Responses to Endophytic Bacterial Colonization

Once bacteria enter into the plant, different defence reactions have often been described. For example, the strengthening of cell walls, the production of antibiotics, growth-stimulating substances or enzymes and gum formation inside vessels have been observed (James et al. 2002; Compant et al. 2005; Miché et al. 2006). However, in contrast to the plant response to phytopathogens, few defence mechanisms have been described in plant response to PGPBEs. Moreover, certain plants have been shown to change their chemical responses when interacting with PGPBEs compared with non-beneficial bacteria, indicating that the plant does not recognize the PGPBEs as harmful agents (Miché et al. 2006; Rocha et al. 2007). It has also been reported that plants may show defence reactions controlling endophytic colonization, involving the production of salicylic acid (SA), jasmonic acid (JA) or ethylene, among other molecules. For example, dicotyledonous plants are known to use salicylic acid (SA) and ethylene as signalling molecules, which control colonization by some endophytes (Iniguez et al. 2005).

In monocotyledonous plants such as rice, the addition of jasmonic acid (JA), but not ethylene, was shown to interfere with the colonization of the diazotroph *Azoarcus* sp., suggesting that plant defence responses involving the JA signalling pathway may also control endophytic colonization inside the root system. However, in a compatible endophytic association, JA-associated plant responses were less pronounced and did not restrict endophytic colonization (Miché et al. 2006).

For example, rhizobial inoculation in cereal plants, especially rice, is associated with an increased accumulation of phenolic substances such as gallic, tannic, ferulic and cinnamic acids in plant leaves (Mirza et al. 2001). Such increases in phenolic acids are a pathogenic stress-related phenomenon in plants (Pieterse et al. 2002). Defence reactions triggered in response to rhizobial invasions are termed as rhizobacteria-mediated induced systemic resistance. However, this systemic resistance is not enough to prevent the entry of the *Rhizobium* inside the plant. Thus, rhizobia successfully colonize and disseminate throughout the inner host plant without evoking an observable defence reaction in the plant (Mia and Shamsuddin 2010).

7.3 Nitrogen-Fixing Bacterial Endophytes

Several studies have shown that endophytic bacteria are able to enter the inner tissues of plants, successfully colonize them and cause benefits. Therefore, it is inevitable that the use of these endophytic bacteriaasan alternatives to chemical fertilizers as a means to aid in the demand for food will receive support. According to FAO, the main cereal crops in terms of global production are maize, rice and wheat. In 2011, their production was more than 833, 723 and 704 Mt., respectively (Perez-Montaño et al. 2014). In order to maintain high production levels, there is a massive use of N-based fertilizers, and ~60% of the total synthetic nitrogen fertilizers produced worldwide is currently used in cereal crops (Dobermann 2007; Westhoff 2009). As nitrogen continues to be a serious problem for agriculture, due to the lack of available forms for plants or due to the excess of N-based fertilizers, the formulation of biofertilizers based in nitrogen-fixing endophytic bacteria presents itself as the more suitable solution to overcome these problems. In this section, we focus on endophytic bacteria that are able to fix nitrogen for these cereal crops with higher yields worldwide (Mia and Shamsuddin 2010; Sindhu et al. 2016; Meena et al. 2013c, 2014b, 2015d; Singh et al. 2016, 2015).

Bacteria responsible for nitrogen fixation are called diazotrophs, which harbour nitrogenase, the enzyme complex that catalyses the conversion of N_2 gas to ammonia, a form that can be used by plants (Santi et al. 2013). Some of these diazotrophic bacteria are also PGPBEs. They have been detected inside the plant, causing beneficial effects such as plant growth promoters and nitrogen fixation. These bacteria, found in close association with roots, are usually designated "associative" nitrogen-fixing bacteria. However, the frontier between associative and endophytic plant colonization is not always clear since associative bacteria can also be observed in plant tissues; although, they are less abundant than strains originally classified as endophytes (Elmerich 2007). In contrast to what occurs in endosymbiosis, these bacteria do not induce differentiated structures in the roots, and although endophytic bacteria invade plant tissues, they cannot be regarded as endosymbionts that reside intracellularly in living plant cells. Endophytic diazotrophs may have an advantage over root-surface associative diazotrophs as they colonize the interior of plant roots and can establish themselves in niches that provide more appropriate conditions for effective nitrogen fixation and subsequent transfer of the fixed nitrogen to the host plant (Reinhold-Hurek and Hurek 2011). Some of the main bacteria that can live in association with maize, rice and wheat and contribute to improve plant growth are presented in Table 7.1. Some bacterial genera, such as *Azospirillum*, *Azoarcus*, *Herbaspirillum* and *Gluconacetobacter*, which promote growth, fix nitrogen and have more efficiency in colonization, were isolated in a plant species and were more competent in the reinoculation in the same plant.

The use of the bacterial genus *Azospirillum* as inoculants and the discovery of the high acetylene reduction (AR) activity associated with the roots of cereals immediately attracted much interest among agronomists and soil microbiologists. Many studies were performed on the inoculation of these crops with *Azospirillum* sp.,

Table 7.1 Association of cereals and nitrogen-fixing PGP bacteria

Cereals	Diazotroph inoculant	Benefits (% increase)	References
Rice	*Azoarcus* sp.	16 (total dry weight)[b]	Reinhold-Hurek and Hurek (1997), Engelhard et al. (2000)
Maize	*Burkholderia* sp.	68 (shoot biomass)[b]	Baldani et al. (2000)
		19 (seed biomass)[b]	
	B. vietnamiensis	13–22 (yield)[a]	Van et al. (2000)
	Gluconacetobacter diazotrophicus	30 (total dry weight)[b]	Muthukumarasamy et al. (2005)
	Herbaspirillum seropedicae	37.6 (plant dry weight)[b]	James et al. (2002)
	Serratia marcescens	23 (total dry weight)[b]	Gyaneshwar et al. (2001)
	Burkholderia sp.	5.9–6.3 (yield)[a]	Estrada et al. (2005)
	Azospirillum brasilense	13–25 (yield)[b]	Riggs et al. (2001), Dobbelaere et al. (2001)
		33 (grain yield)[a]	
	Pseudomonas protegens	44 (total dry weight)[b]	Fox et al. (2016)
Wheat	*H. seropedicae*	19.5 (yield)[a]	Riggs et al. (2001)
	Pseudomonas sp.	11.7 (total biomass)[b]	Shaharoona et al. (2006)
	H. seropedicae	49–82 (total biomass)[b]	Riggs et al. (2001)
	P. protegens	47 (total dry weight)[b]	Fox et al. (2016)
Pearl millet	*A.brasilense*	12.05 (fresh weight of roots)[b]	Tien et al. (1979)
Soybean	*A.brasilense*	9.19 (total root length)[b]	Molla et al. (2001)
Sorghum	*A. brasilense*	33–40 (total number of length)[b]	Sarig et al. (1992)

Modified from Santi et al. (2013)
Experiments in fields ([a]) or in controlled conditions ([b])

particularly the *Azospirillum brasilense* type strain Sp7 originally isolated from the rhizosphere soil of *Digitaria decumbens* (and the closely related strain Cd) (Bashan and Levanony 1990). Boddey and Dobereiner (1995) showed that *Azospirillum* strains isolated from surface-sterilized roots of a certain cereal showed a greater aptitude to reinfect the same cereal and to promote responses in crop yield and/or N accumulation when these "homologous" strains were inoculated. In this respect, several studies showed that the *A. brasilense* strain Sp 245, isolated from surface-sterilized wheat roots, repeatedly increased grain yield and N accumulation in wheat in both field and pot experiments, where Sp 7 and/or Cd promoted little or no plant response (Baldani et al. 2002). Similar results have been obtained with maize, wheat and pearl millet by other authors (Couillerot et al. 2013; Masciarelli et al. 2013; Piccinin et al. 2013; Morley 2013; Lakhani et al. 2014).

The genus *Azoarcus* is a group of gram-negative, endorhizospheric diazotrophic bacteria, originally isolated from roots of the grass *Leptochloa fusca* (L.), namely, Kallar grass, which are able to invade plant tissues due to their cellulolytic enzymes (Reinhold-Hurek et al. 1993). Reinhold-Hurek et al. (1993) observed that *Azoarcus* is able to colonize the interior of sorghum plants by means of its cellulolytic enzymes. Therefore, *Azoarcus* sp. strain BH72 is not specific to its original host plant, Kallar grass, and maybe used as inoculum for other members of the Gramineae family. To evaluate its contribution of biological nitrogen fixation (BNF), the total nitrogen content in the whole system was analysed. After 28 days of cultivation, a sevenfold increase of total *N* was measured, from which the majority (72.6%) was located in the growth medium.

Gluconacetobacter diazotrophicus, a N_2-fixing bacterium has been originally isolated from sugarcane roots and inside stems collected in various sites of Brazil (Cavalcante and Dobereiner 1988) and of Australia (Li and Macrae 1992). This endophytic bacterium is able to fix N_2 even in the presence of nitrates and seems to be best adapted to the environment for growing sugarcane (Cavalcante and Dobereiner 1988). This bacterium could have more economic importance compared with other diazotrophs associated with sugarcane (Fuentes-Ramirez et al. 1993).

Moreover, some studies have shown its ability to act as a PGPBE (Fuentes-Ramirez et al. 1993; Saravanan et al. 2008; Mehnaz and Lazarovits 2006; Sahai et al. 2015). Fuentes-Ramirez et al. isolated 18 strains belonging to this species that produce different concentrations of indoleacetic acid (IAA). Thus, considering that *G. diazotrophicus* was found within the plant tissue, the biosynthesis of IAA suggests that these strains could promote root formation and improve sugarcane growth by direct effects on metabolic processes, in addition to their role in N_2 fixation. *G. diazotrophicus* has been isolated from other plant hosts, such as wetland rice, pineapples, tea, coffee, etc. (Saravanan et al. 2008). Mehnaz and Lazarovits (2006) showed the inoculation effects of *G. diazotrophicus* in maize provided significant plant growth promotion expressed as increased root and shoot weight when compared to uninoculated plants.

Species from the genus *Herbaspirillum*, which are classified as plant growth-promoting rhizobacteria (PGPR), can produce biological nitrogen fixation (BNF) for plants, as well as present *P*-solubilization and siderophore production (Richardson et al. 2009). In a recent study, Alves et al. (2015) showed the plant growth promotion effect of 21 strains of *Herbaspirillum* species on maize plants. In this trial, the grain yield was evaluated as well as the contribution of biological nitrogen fixation (BNF). This study showed that *H. seropedicae* ZAE94 was the best strain under controlled conditions, and its application as a field inoculant increased maize yield up to ~34%, depending on the plant genotype.

All these nitrogen-fixing endophytic bacteria also improve root development by the production of different classes of growth regulators that influence primary root growth and increase the number and length of lateral roots and elongating root hairs, which in turn results in an increase in the field productivity of crops (Dobbelaere et al. 1999; Contesto et al. 2008; Combes-Meynet et al. 2011; Walker et al. 2012).

7.4 Bacterial Endophytes from Cereals Used as Plant Probiotics

Many bacterial endophytes able to promote plant growth have been isolated from within the cereals, as shown in Table 7.2. Nevertheless, we can observe that these same isolates are then used to reinoculate the same plant host. It may be due to adaptation that the bacteria have to colonize the plant. This kind of bacteria has a potential to interact with cereals, due to the effects and benefits produced. In this part of the chapter, we focus on the description of various mechanisms used by endophytes to enhance plant growth, improve agronomic characteristics and solve problems of pollution.

Currently, there are a huge number of studies published that report the use of endophytic bacteria as PGPR inoculants (some of them summarized in Table 7.2). Commonly, plant growth promotion occurs due to a combination of different action modes, such as the improvement of the host's nutrient status, promoting root surface area and increasing the availability of nutrients to the plants (Perez-Montaño et al. 2014 (Fig. 7.2). Every bacterial strain may use one or several mechanisms, depending on the phase of plant's life cycle (Long et al. 2008).

According to Govindarajan et al. (2008), rice yield production was increased with respect to a control treatment when a bacterial inoculant was applied. Moreover, the effect of the inoculation caused rice seedlings to grow better under *N*-deficient conditions. Mäder et al. (2011) showed an increase in wheat grain yield (~31%) after the inoculation with *Pseudomonas jessenii* R62 and *Pseudomonas synxantha* R81, in comparison to uninoculated control plants.

Recently, the potential of endophytic bacteria to degrade pollutants in order to allow plants to emerge as the natural vegetation at a contaminated site or to decrease contaminant concentration is being analysed (Syranidou et al. 2016). Although many number of studies focus on the degradation of compounds, such as herbicides, pesticides and hazardous organic compounds, in many occasions, these benefits and effects are also related and associated with an improvement of plant development. Sorty et al. (2016) reported that endophytic bacteria could alleviate the harmful effects of salt stress and enhance seed germination in wheat, as well as to promote plant growth and to increase dry biomass and total soluble sugars. Wheat seedlings are able to germinate under different salinity regimes after co-inoculation with *Bacillus subtilis* SU47 and *Arthrobacter* sp. SU18 (Upadhyay et al. 2012).

Under stress conditions, plants increase their ethylene levels causing important cell damage (Argueso et al. 2007; Hardoim et al. 2015; Perez-Montaño et al. 2014). Thus, the role of ACC deaminase production by endophytic bacteria and the ability to decrease ethylene levels have been also analysed (Glick 2014; Etesami et al. 2014; Gamalero and Glick 2015; Khan et al. 2016). Ethylene is a plant hormone, which is also the key regulator of plant colonization by endophytic bacteria. According to Etesami et al. (2014), the endophytic strain *P. fluorescens* REN1, selected for its high ACC deaminase production, significantly colonized rice seedling roots in comparison with other ACC deaminase-producing isolates in controlled

Table 7.2 Bacterial endophytes isolated from cereals used as plant growth promoters

Bacterial endophytes isolated from cereals	Reinfection tests in cereals	Effect (% increase)	References
Wheat			
Arthrobacter sp. and *Bacillus subtilis*	Wheat	26 (total dry weight)	Upadhyay et al. (2012)
Pseudomonas jessenii (R62) and *Pseudomonas synxantha* (R81)	Wheat	41 (grain yield)	Mäder et al. (2011)
Rhizobium leguminosarum bv. *trifolii*	Wheat	24 (wheat shoot dry matter and grain yield)	Hilali et al. (2001)
Maize			
A. brasilense	Maize	45 and 82 (grain yield and total N accumulation, respectively)	de Salamone et al. (1996)
Rhizobium etli bv. *phaseoli*	Maize	20–45 (total biomass)	Gutierrez-Zamora and Martınez-Romero (2001)
Serratia liquefaciens, *Bacillus* sp. *Pseudomonas* sp.	Maize	14 (dry weight)	Lalande et al. (1989)
Rice			
R. leguminosarum bv. *trifolii* E11	Rice	8–22 (grain yield)	Biswas et al. (2000)
R. leguminosarum bv. *trifolii* ARC100 and ARC101	Rice	19.7 and 6.31 (grain weight and grain yield, respectively)	Yanni et al. (1997)
Pantoea agglomerans	Rice	63.5 (total biomass)	Verma et al. (2001)
B. vietnamiensis MGK3	Rice	9.36 (grain yield)	Govindarajan et al. (2008)
Herbaspirillum seropedicae LMG6513	Rice	2.6 (grain yield)	Govindarajan et al. (2008)
B. vietnamiensis LMG10929	Rice	5.4 (grain yield)	Govindarajan et al. (2008)
H. seropedicae LMG6513	Rice	2.6 (grain yield)	Govindarajan et al. (2008)
Bradyrhizobium sp. ORS278	Rice	20 (total biomass)	Chaintreuil et al. (2000)
Gluconacetobacter diazotrophicus	Rice	30 (total dry weight)	Muthukumarasamy et al. (2005)
H. seropedicae	Rice	38–54 (root biomass)	Elbeltagy et al. (2001)
	Rice	22–50 (shoot biomass)	Gyaneshwar et al. (2002)
	Rice	37.6 (plant dry weight)	James et al. (2002)
	Rice	52–112, 71 (fresh and dry weight)	Baldani et al. (2000)

(continued)

Table 7.2 (continued)

Bacterial endophytes isolated from cereals	Reinfection tests in cereals	Effect (% increase)	References
Serratia marcescens	Rice	23 (total dry weight)	Gyaneshwar et al. (2001)
R. leguminosarum bv. trifolii	Rice	15–22, 8–22 (grain yield)	Yanni et al. (1997), (2001)
Pantoea agglomerans	Rice	63.5 (total biomass)	Verma et al. (2001)
B. vietnamiensis LMG10929T	Sugarcane	19.5 (yield)	Govindarajan et al. (2006)
H. seropedicae	Sugarcane	5–12 (yield)	Govindarajan et al. (2008)
Sugarcane			
Enterobacter cloacae	Sugarcane	55 and 70 (root and shoot biomass)	Mirza et al. (2001)
Klebsiella pneumoniae	Sugarcane	13–19.5 (total biomass)	Govindarajan et al. (2007)
G. diazotrophicus BR 11281	Sugarcane	(Mixture of five species) 23.5 stalk fresh weight and 27.4 dry matter	Oliveira et al. (2002)
H. seropedicae BR 11335			
Herbaspirillum rubrisubalbicans BR 11504			
Azospirillum amazonense BR 11115			
Burkholderia sp. BR 11366			
G. diazotrophicus LMG7603	Sugarcane	13–16 (yield)	Govindarajan et al. (2007)
H. seropedicae		26 (plant dry weight)	Muñoz-Rojas and Caballero-Mellado (2003)
		18.83–49.86 (total biomass)	Suman et al. (2005)
		35 (dry matter)	Oliveira et al. (2002)
H. rubrisubalbicans	Rice	6.6 (grain yield)	Govindarajan et al. (2008)
G. diazotrophicus LMG7603			
Leptochloa fusca	Rice	16 (total dry weight)	Reinhold-Hurek and Hurek (1997)
Azoarcus			

conditions. This result supports the idea of the use of ACC deaminase activity as a powerful tool to select effective endophytic bacteria with plant growth-promoting capabilities.

Another key factor to be analysed in the plant-endophytes association is phytohormone production (auxins, gibberellins and cytokinins), which is one of the most well-studied mechanisms in relation to plant growth promotion (Hardoim et al. 2015). Auxins are a class of *plant growth regulators*, known to stimulate cell elongation in plants, and their production by endophytic strains has been reported (Long et al. 2008; Shi et al. 2009). Merzaeva and Shirokikh (2010) presented an

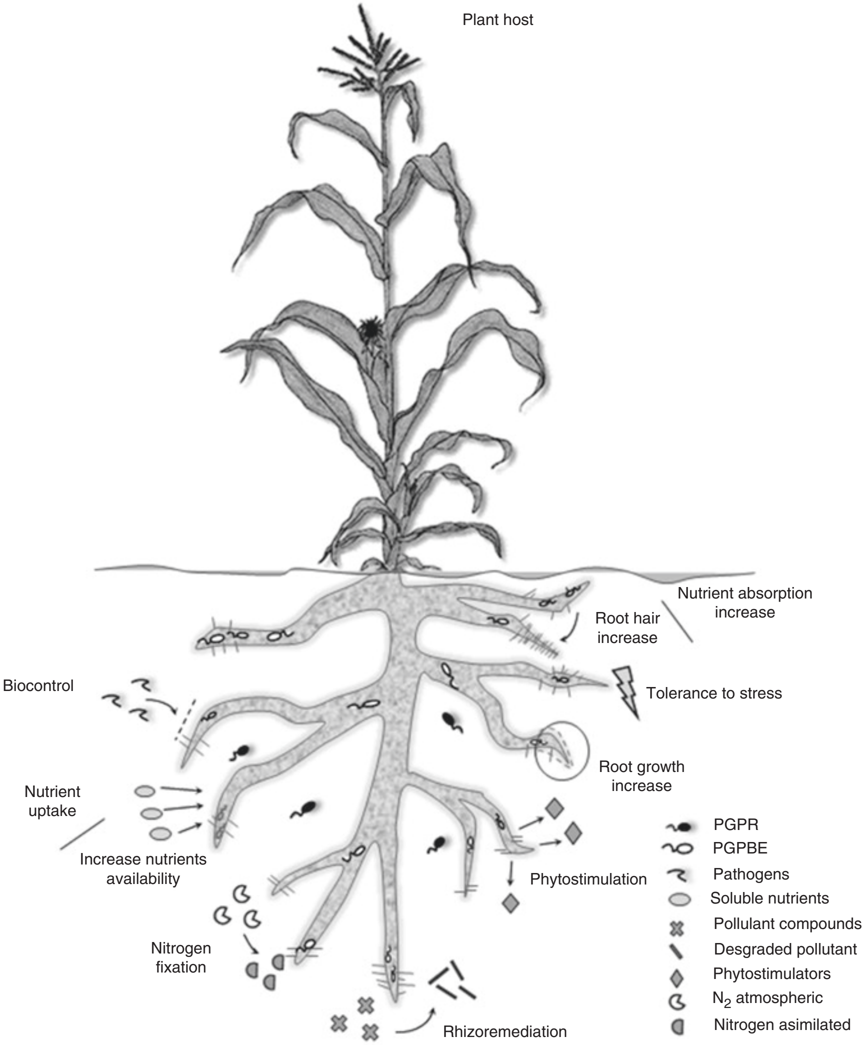

Fig. 7.2 Schematic representation of plant growth-promoting mechanisms of bacterial endophytes

increase in the germination capacity of rye seedlings, which were treated with auxins produced by endophytic bacteria.

Apart from being typical trait of root-associated endophytes, gibberellins production elicits various metabolic functions of plant growth (Macmillan 2001), and the production by endophytes is currently described worldwide (Khan et al. 2014; Shahzad et al. 2016). Cytokinin production by bacterial endophytes is commonly analysed and reported in relation to plant growth promotion. According to the data presented by Kudoyarova et al. (2014), *Bacillus subtilis* IB-22 increased amino acid rhizodeposition in wheat roots due to its ability to produce cytokinins. Apart from the fact that most of the described endophytes present the mechanisms explained above, some endophytes are also inoculated as biocontrol agents (Díaz-Herrera et al. 2016; Xu et al. 2017). According to Pan et al. (2015) *B. megaterium* BM1 (entophytic strain isolated from wheat) significantly reduces the incidence and severity of infection by *Fusarium graminearum* in wheat crops.

7.5 Current Situation of Commercial Products Based on Endophytic Bacteria

In order to satisfy the increase in food demand and environmental concerns, new ways of fertilization and the production of agronomic commercial products are being developed with the principal aim of creating a more sustainable agriculture. According to the new restrictive laws and some programmes and initiatives (e.g. Horizon 2020) concerning the use of chemical fertilizers, the creation and commercialization of new green products is expanding worldwide, and several companies are developing a wide range of products based on different bacterial inoculants. Researchers and companies must consider the introduction and use of endophytes for the formulation of these products, where the full understanding of their behaviour under different conditions is probably the key aspect for developing an application system that assures continuity and efficacy.

Despite the simplicity of production technologies and the low-cost industrial procedures of biofertilizer production, in comparison to the chemical fertilizer industry, there are big differences among the number of companies and the products they produce (Table 7.3), which are currently on sale globally (Naveed et al. 2015).

Europe is one of the areas that have developed more governmental policies for controlling the biofertilizer market (Garcia-Fraile et al. 2015). However, there are no existing specific regulations or a single process to regulate the quality for newly produced biofertilizers, and the already established laws are very different among the European Union member states. Some EU countries, such as the United Kingdom and Ireland, do not have specific regulations regarding the use of microbial inoculants.

Since 1998, the European company "Xurian Environnement" has been analysing and producing a wide range of commercial green products. The team of technical experts provide personalized assistance to increase the biomass of cereal and oilseed crops. One of the bestselling products is Ovalis Rhizofertil®, a microbial inoculant based on the strain *P. putida* I-4613. Another company, currently in expansion, is Symborg, which commercializes a product called VitaSoil®, a mix of rhizospheric microorganisms specific for the growth promotion of cereal crops and soil regeneration.

According to the Food and Agricultural Organization (FAO), Asia and the Pacific zone are the largest users of fertilizers in the world and import the three major nutrients (nitrogen, phosphate and potassium) in large amounts. However, regional gov-

Table 7.3 Current commercial products for cereal crops based on endophytic bacteria

Company	Product	Crop type
Xurian Environnement	Ovalis Rhizofertil®	Cereal and oilseed
Symborg	VitaSoil®	Cereal
Ajay Bio-tech	Ajay Azo®	Wheat, paddy and cotton
Ajay Bio-tech	Ajay Azospirillum®	Cash
JSC Industrial Innovations	Azotobacterin®	Wheat, barley, maize, among other cereals
China Bio-Fertilizer AG	CBF®	Cash
Monsanto	QuickRoots®	Wheat and corn
Flozyme Corporation	Inogro®	Rice
Laboratorios BioAgro S.A.	Liquid PSA®	Wheat
Semillera Guasch SRL	Zadpirillum®	Maize
Gujarat State Fertilizers and Chemicals LTD	Azotobacter®	Cereal, cash and horticultural
Gujarat State Fertilizers and Chemicals LTD	Azopirillum®	Cereal, cash and horticultural
Gujarat State Fertilizers and Chemicals LTD	Phosphate Solubilizing Bacteria®	All kind of crops
INTERMAG	BACTRIM STRAW®	Maize and oilseed
Prabhat Fertilizer & Chemical Works	Azoto ®	Cereals
Criyagen Agri	Azospirillum Biofertilizer®	Paddy, sugarcane, maize, wheat, sorghum, Bajra, cotton and sunflower among others
Criyagen Agri	PSB fertilizer®	Maize, wheat, paddy
Abiosa	BONASEED®	Cereals
Criyagen Agri	Bumper Crop Fertilizer®	Cereals

ernments promote the development of the biofertilizer market in order to contribute to a more sustainable agriculture in these countries. The most important companies in terms of sales and production are Agri Life and Ajay Bio-tech (India) LTD. Some of the products sold by these companies are suitable for cereal crops, such as Ajay Azo/Rhizo/Azospirillum® (different biofertilizers based on *Azotobacter*, *Rhizobium* and *Azospirillum* species, respectively) and Agri Life Nitrofix® (biological fertilizer based on the strain *A. chroococcum* MTCC 3853), among others. These biofertilizers are based on single or combined efficient nitrogen-fixing bacteria (NFB) or phosphate-solubilizing bacteria (PSB) that help plant uptake of nutrients when applied to seed or through the soil. Moreover, the company "JSC Industrial Innovations" commercializes Azotobacterin®, which produces up to a ~20% increase in yield of crops such as wheat, barley and maize, among other cereals. This product contains the diazotrophic bacterial strain *A. brasilense* B-4485. According to Garcia-Fraile et al. (2015), this product is one of the most frequently used in Russia.

In China, the company "China Bio-Fertilizer AG" sells a product called "CBF", which is formed by a mix of two bacterial species of the genus *Bacillus* (*B. muci-*

laginosus and *B. subtilis*) that are able to solubilize phosphorus and potassium, resulting in an increase in crop yields (up to ~30% depending on plant species).

In America, farmers are expected to use an additional 300,000 tonnes of nitrogen fertilizers in 2018, which will be mainly applied to agricultural surface crops (wheat, corn and forage crops). This continent has the biggest worldwide biofertilizer company, Monsanto, which currently belongs to the company Bayer. Monsanto focuses on empowering farmers to produce more from their land while conserving natural resources such as water and energy. Also, they produce "QuickRoots®", a microbial seed inoculant based on a bacteria-fungi mixture, mainly *B. amyloliquefaciens* and *T. virens*, to enhance nutrient uptake in wheat and corn crops, which results in an enhanced yield potential. Monsanto, as well as other companies such as Novozymes and BASF, also operates worldwide.

Also in the USA, the Flozyme Corporation, a company that has been testing new technologies designed to increase crop production and reduce or eliminate the need for fertilizers, produces and commercializes "Inogro". This product is a mix of more than 30 microbial species selected for their plant growth promotion abilities. Independent tests showed a significant increase in rice yields under greenhouse conditions (www.flozyme.com/agriculture/).

Since 1984, the company "Laboratorios Bioagro S.A. (Argentina)" has focused on the research and development of highly environmental friendly products to help satisfy the farmers' needs. One of their most famous products is "Liquid PSA", which contains *P. aurantiaca* SR1 and is registered by the national service for agricultural health of Argentina, due to its promotion of wheat growth. Moreover, in the same country, the company Semillera Guasch SRL launched a brand named Zaden Agrotecnologias®, which produces a biological inoculant called Zadpirillum® that is based on the plant growth-promoting strain *A. brasilense* AZ39 and enhances maize yields.

Even Africa will require 4 million tonnes of nitrogen fertilizers in 2018, and the use of biofertilizers varies widely among countries due to the farmers' reticence to apply microbial biofertilizers. Therefore, the experts recommend a combination between using local technological knowledge and microbial fertilizers (Babalola and Glick 2012) as the only way to satisfy the increasing food demand that will continue to exist over the next decades. As regards there are projects searching for solutions, such as Engineering Nitrogen Symbiosis for Africa project (ENSA) or N2Africa project, led by two of the most important European research centres, John Innes Centre and Wageningen University, respectively, which have received funding from the Bill and Melinda Gates Foundation and aim to help African farmers to enhance their crop yields by engineering nonleguminous plants for fixing nitrogen and to improve inoculants based on microbial strains.

In this context, the collaboration between researchers and industries becomes a key aspect for the development of microbial-based biofertilizers. The underlying mechanisms of the interaction of plants with bacterial endophytes is still unknown, and there are also bio safety issues that need to be addressed; for example, strains forming part of biofertilization schemes must be tested in order to avoid damages. The comprehensive research of bacterial endophytic populations will allow more efficient biofertilizers to be made. Moreover, it is very important that the efforts to develop biofertilizers must be approved and accepted by farmers around the world, where they are provided the proper education and simplified procedures for using the products correctly. These measures would be positive steps to encourage the commercialization and production of biofertilizers by companies worldwide.

7.6 Conclusion and Future Perspectives

Enhanced cereal crop production by the application of PGPBE-based biofertilizers is the necessary breakthrough to underpin a more sustainable food production for feeding the global population and to overcome the environmental issues derived from the abuse of chemical fertilizers. In this chapter, we have presented the great diversity of bacterial endophytic strains isolated from several cereal crops and their potential as plant growth promoters when inoculated onto their isolation source or other types of crops. These PGPBEs are able to establish a more intimate relationship with cereals crops, showing a better colonization of the inner tissues of these plants and performing their beneficial actions in a close interaction with their hosts. Hence, the progressive understanding of microbial populations that are applicable as inoculants for different crops is absolutely necessary in order to ensure higher yields in a sustainable way.

The Food and Agriculture Organization (FAO) promotes the use of biofertilizers in both developed and developing countries, and many have employed them to a greater or lesser extent (FAO 1991). Moreover, most countries have developed policies to reduce the use of chemical fertilizers due to the consumer demands for more organic food. Thus, the commercialization and application of bacterial fertilizers on agricultural crops are increasing year by year. In the near future, more efforts will be needed regarding the development of proper inoculants that enhance cereal growth and yields. Based on this premise, the Horizon 2020 Programme strongly supports European research dedicated to the biotechnological processes and products. Also, Latin America is one of the world's largest fertilizer consumers, particularly Mexico, and a programme to support the introduction of *N*-fixing biofertilizers based on *Azospirillum* was carried on ~1.5 M ha (Fuentes-Ramirez and Caballero-Mellado 2005). India has the most complete legal framework in the world related to biofertilizers, and ~350–500 t of biofertilizers are requested form the Indian National Biofertilizer Development Center (NBDC) and the Bio-Tech Consortium of India Ltd. (BCIL) for agricultural purposes in India (Dewasthale and Bondre 2008). In addition, Japan has long since begun to include nitrogen-fixing bacteria in the formulation of biofertilizers, and the Tokachi Federation of Agricultural Cooperatives (TFAC) is the largest producer and marketer of rhizobial biofertilizers since 1953. This company uses PGPR as biofertilizers and as biocontrol agents, among others. The Forum for Nuclear Cooperation in Asia (FNCA) is also located in Japan and actively develops biofertilizers in Asian countries (Naveed et al. 2015). According to Masso et al. 2014, in Africa, regulatory frameworks are required since biofertilizers are of poor quality and consequently cause economic loss. For this reason, Babalola and Glick (2012) suggest the combined use of traditional techniques together with microbial fertilizers.

Therefore, we propose that more work is needed in order to development better biofertilizers and to ensure their proper use. This also includes the establishment of specific legislation that regulates biofertilizers in order to facilitate the processes of production and commercialization. Governments should support the use of biofertilizers and provide proper funding for research and the creation of companies in the field of biofertilizers. To reduce the farmer's reticence towards these types of products, specific programmes and initiatives are needed to train farmers in the use of biofertilizers. Due to the increasing demand for fertilizers worldwide, more research efforts are needed to elucidate the inner mechanisms affecting the interaction between cereal crops and beneficial bacteria.

Acknowledgements The authors acknowledge financial support provided by the Spanish Government (Ministerio de Economía y Competitividad; MINECO) through the projects AGL2011-29227 and AGL2015-70510-R, by the Junta de Castilla y León (regional government) through the project JCyL SA169U14 and by the Diputación de Salamanca (local government) through the project V113/463AC06. AJG is thankful to a PhD grant from the Spanish Government (Ministerio de Educación, Cultura y Deporte). The authors are grateful to Emma Jane Keck for correcting English style.

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