Plant Growth-Promoting Rhizobacteria: Key Mechanisms of Action

3

Márcia do Vale Barreto Figueiredo,
Aurenívia Bonifacio,
Artenisa Cerqueira Rodrigues,
and Fabio Fernando de Araujo

Abstract

Plant growth-promoting rhizobacteria (PGPR) have gained worldwide importance and acceptance for their agricultural benefits through the application of combinations of different mechanisms of action, which allows increases in crop yield. This is due to the emerging demand for reduced dependence on synthetic chemical products and to the growing necessity of sustainable agriculture within a holistic vision of development and environmental protection. The use of selected plant-beneficial rhizobacteria may represent an important biotechnological approach to alleviate the negative effects of stress and to optimize nutrient cycling in different crops. Recent progress in our understanding of their action mechanisms, diversity, colonization ability, formulation, and application should facilitate their development as reliable components in the management of sustainable agricultural systems. In addition, numerous studies indicate increased crop performance with the use of these microorganisms. In this chapter, an understanding of the direct and indirect mechanisms of action of PGPR and their various benefits to plants are summarized and discussed.

Keywords

PGPR • Phytohormones • Effectiveness • Crop • ISR • Catabolic enzymes

---

M.d.V.B. Figueiredo (✉)
National Research and Technological Development,
Agronomical Institute of Pernambuco, IPA/SEAGRI,
1371, Gen. San Martin Avenue, Recife, PE, Brazil,
50761-000
e-mail: mbarreto@elogica.com.br

A. Bonifacio
Department of Exact Science and Biotechnology,
Gurupi, Federal University of Tocantins,
Gurupi, TO, Brazil
e-mail: bonifacio.a@live.com

A.C. Rodrigues
Department of Agricultural Engineering and Soil
Science, Federal University of Piaui,
Campus of Socopo, Teresina, PI, Brazil
e-mail: artenisacerqueira@ufpi.edu.br

F.F. de Araujo
Agrarian Sciences, University of West Paulista
(UNOESTE), Presidente Prudente, SP, Brazil
e-mail: fabio@unoeste.br

D.K. Choudhary, A. Varma (eds.), *Microbial-mediated Induced Systemic Resistance in Plants*,
DOI 10.1007/978-981-10-0388-2_3

3.1 Introduction

During the past couple of decades, the use of plant growth-promoting rhizobacteria (PGPR) for sustainable agriculture has increased tremendously in various parts of the world. Significant increases in the growth and yield of agronomically important crops in response to inoculation with PGPR have been repeatedly reported (Kloepper et al. 1980; Chanway 1997; Vessey 2003; Gray and Smith 2005; Araujo 2008; Figueiredo et al. 2010; Kang et al. 2010; Rodrigues et al. 2013; Chauhan et al. 2015). Studies have also shown that the growth-promoting ability of some bacteria may be highly specific to certain plant species, cultivars, and genotypes (Bashan 1998).

PGPR can affect plant growth by various direct and indirect mechanisms (Kloepper and Schroth 1978; Glick et al. 1995; Cattelan et al. 1999; Gupta et al. 2000; Li et al. 2000; Hayat et al. 2010; Saraf et al. 2011; Minaxi et al. 2012; Kavamura et al. 2013; Ahemad and Kibret 2014). These mechanisms can probably be active simultaneously or sequentially at different stages of plant growth (Chaparro et al. 2013). Some examples of these mechanisms are (a) increased mineral nutrient solubilization and nitrogen fixation, making nutrients available to the plant; (b) phytohormone production, such as indole–3–acetic acid, abscisic acid, gibberellin, cytokinins, and ethylene; (c) antagonism against phytopathogenic bacteria by producing siderophores, β-1,3-glucanase, chitinases, antibiotics, fluorescent pigments, and cyanide; (d) the ability to produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, a vital enzyme that reduces ethylene levels in the roots of developing plants, thereby increasing root length and growth; and (e) improving plant stress tolerance to salinity, metal toxicity, and drought through the production of exopolysaccharides (EPSs), biofilm formation, and osmolyte reduction to avoid cell water loss.

The modes of action of the PGPR and their various benefits to plants range from the simple occupation of empty biological spaces to ecological relationships such as antibiosis, competition, predation, and symbiosis, among others (Kloepper et al. 2004; Avis et al. 2008). The use of selected microorganisms may represent an important biotechnological approach to decrease the deleterious effects of stress in crops (Egamberdieva et al. 2013; Nadeem et al. 2014). An effective strategy to alleviate the negative effects of stress in plants is the co-inoculation of seeds with different PGPR species, such as *Rhizobium* and *Azospirillum* (Figueiredo et al. 2008; Bashan and de-Bashan 2015). The presence of *Azospirillum* sp. in the rhizosphere was reported to elicit or activate the hydrolysis of conjugated phytohormones and flavonoids in the root tissue, thus bringing about the release of compounds in their active forms (Saikia et al. 2010).

Overall, the ability of microbes to confer stress tolerance to plants may provide an eco-friendly strategy for mitigating the impacts of global climate change on agricultural and native plant communities, as well as provide excellent models for understanding stress tolerance mechanisms that can be subsequently engineered into crop plants (Choudhary 2012).

3.2 PGPR: Current Perspective

In search of more sustainable agriculture, PGPR have been used extensively worldwide (Choudhary et al. 2011). PGPR benefit plant growth and development when present in the rhizo- and endosphere (Lugtenberg and Kamilova 2009; Compant et al. 2010; Choudhary et al. 2011; Duca et al. 2014). In an effort to elucidate the concept of PGPR, Bashan and Holguin have proposed to divide them into two groups: PGPB and biocontrol-PGPB. According to this classification, PGPB would encompass bacteria capable of synthesizing growth-promoting substances; fixing atmospheric nitrogen; providing phosphate, potassium, iron, and other nutrients; and mitigating the deleterious effects of abiotic stresses, whereas biocontrol-PGPB are able to decrease or prevent the deleterious effects of soil plant pathogens (Bashan and Holguin 1998). Gray and Smith (2005) have shown that PGPR associations depend on the degree of bacterial proximity to the root and the intimacy of the association. In general, these associations can be separated into two categories: (1) extracellular (ePGPR) associations, which exist in the rhizosphere, on the rhizoplane, or in the spaces between the cells of the root cortex, and (2) intracellular (iPGPR) associations, which exist inside root cells in specialized nodular structures. Most of rhizobacteria belonging to this group are Gram-negative rods with a lower proportion being Gram-positive rods, cocci or pleomorphic (Bhattacharyya and Jha 2012).

PGPR are widely distributed in the Bacteria domain, mainly in the phyla *Actinobacteria*, *Bacteroidetes*, *Cyanobacteria*, *Firmicutes*, and *Proteobacteria* (Figueiredo et al. 2010). When present in soil (cultivated or noncultivated), these bacteria are responsive to chemical attractants—a diverse group of compounds that are synthesized, accumulated, and secreted by plant roots; these compounds are generically referred to as root exudates (Huang et al. 2014). The root exudates modify the chemical and physical properties of the soil and regulate the bacterial community that is present in the area surrounding the root surface (Dakora and Phillips 2002). In fact, the chemicals present in root exudates act as substrates and chemotactic or signaling molecules and mediate the selection of the microbial community that will interact with the plant (Chaparro et al. 2014).

In addition to root exudates, quorum-sensing molecules are increased in response to bacteria present in the rhizo- and endosphere (Compant et al. 2010; Chaparro et al. 2013). Quorum-sensing molecules, which are defined as a group of molecules responsible for cell-to-cell communication between plants and bacteria, allow bacteria to share information about their cell density (Badri et al. 2009). This sharing of information regulates the expression of various genes (mainly in the roots) that are linked to plant development (Badri et al. 2008). *N*-Acyl-homoserine lactone (AHL) is the most important quorum-sensing molecule and is generally found in Gram-negative bacteria that live in association with plants (Babalola 2010). Interestingly, AHL has a differential influence on the interaction between *Methylobacterium mesophilicum* and rice and *Eucalyptus*, using different metabolic routes for each plant host (Dourado et al. 2013). In *Azospirillum lipoferum*, quorum-sensing molecules are associated with rhizosphere competence and adaptation during the plant-host interaction (Boyer et al. 2008).

Once near the roots, PGPR can stimulate plant performance and development through direct or indirect mechanism (Ahemad and Kibret 2014). The direct mechanisms involve nutrient acquisition and the synthesis of phytohormones (Compant et al. 2010). Bacterial populations present at high density in the rhizosphere stimulate nutrient uptake by plant roots; this has been observed for *Azospirillum*, *Bacillus*, and *Rhizobium* (van Loon 2007). The most studied and longest exploited PGPR are the rhizobia (including the *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium*) for their ability to fix N in their legume hosts (Vessey 2003). Furthermore, the free-living diazotrophic *Azospirillum* supplies its host plant, mainly maize, wheat, and sugarcane, with nitrogen through nitrogen atmospheric fixation and positively affects plant growth (Bashan and de-Bashan 2010, 2015; Duca et al. 2014).

Nitrogen, phosphorus, and potassium are most important macronutrients for plant development and their deficiencies reduce plant yield. Similar to nitrogen, the uptake of potassium and phosphorus may be mediated by PGPR when interacting with their host plant (Lugtenberg and Kamilova 2009; Richardson and Simpson 2011). Co-inoculation of pepper and cucumber plants with *Bacillus megaterium* var. *phosphaticum*, a phosphate-solubilizing bacterium, substantially increased the availability of phosphorus for these plants, whereas co-inoculation with *B. mucilaginosus*, a bacterium that solubilizes potassium, significantly improved the availability of potassium to both pepper and cucumber (Han et al. 2006). As a result, the increased phosphorus and potassium availability improved the growth of pepper and cucumber plants. Consequently, the use of phosphate and potassium PGPR solubilizers as a biofertilizer source represents an ecologi-

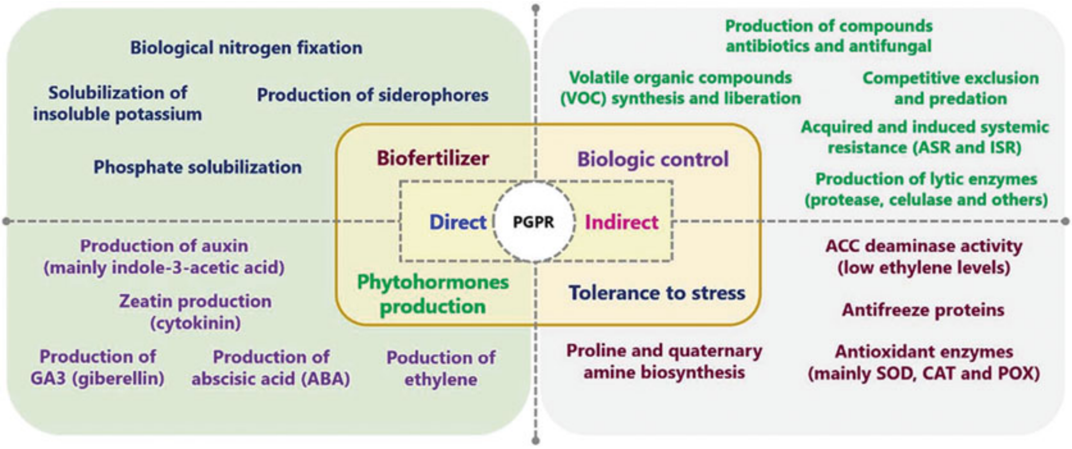

Fig. 3.1 Direct and indirect mechanisms mediated by plant growth-promoting rhizobacteria (PGPR) with beneficial effects on host plants (Chauhan et al. 2015; Pii et al. 2015)

cal solution for soil fertilization and the improvement of plant nutrition and production (Vessey 2003).

PGPR can produce or modulate phytohormone levels and thereby affect the hormonal balance of the host plant (Duca et al. 2014; Glick 2014). Auxin, gibberellin, cytokinins, ethylene, abscisic acid, and brassinosteroids are classical phytohormones with key roles in plant development (Huang et al. 2014). Phytohormone synthesis and release by *Azospirillum* strains present in the rhizosphere are considered the major mechanisms for the modification of root architecture and the increase in nutrient uptake by plants (Cohen et al. 2008; Cassan et al. 2014). Auxins are the most important phytohormone produced by *Azospirillum*, *Bacillus*, *Paenibacillus*, and *Pseudomonas*, while gibberellins are strongly synthetized by *Acetobacter*, *Azospirillum*, *Bacillus*, *Herbaspirillum*, and *Rhizobium* (Babalola 2010; Cassan et al. 2014). *Burkholderia* and *Paenibacillus* exhibited ethylene production and secretion linked with plant growth and biocontrol activity (Vacheron et al. 2013).

The improvement of plant development is often related to the presence of rhizobacteria responsible for fixing atmospheric nitrogen, solubilizing potassium and phosphate, or producing phytohormones (Fig. 3.1). Moreover, the production and secretion of lytic enzymes and antibiotics as well as iron sequestration are indirect mechanisms mediated by rhizobacteria that result in plant growth promotion (Badri et al. 2009; Huang et al. 2014). Under iron-deficient conditions, bacteria synthesize siderophores and can supply the host plant with chelated iron (Saha et al. 2013). Iron-chelating siderophores produced by PGPR in the rhizo- and endosphere may suppress soilborne plant pathogens (Compant et al. 2010). Species of *Bacillus*, *Paenibacillus*, *Serratia*, *Enterobacter*, and *Pantoea* use lytic enzymes, such as amylase, chitinase, β-1,3-glucanase, and protease, to destroy the cell walls of soilborne pathogens (Backman and Sikora 2008; Nimnoi et al. 2010; Jha et al. 2013; Chauhan et al. 2015).

The stimulation of plant development by PGPR can probably be activated at different stages of plant growth (Figueiredo et al. 2010). The plant-microbe interaction specific to each plant age can be useful to combat pathogenic microorganisms or to improve nutrient uptake by plants (Chaparro et al. 2014). Species of *Azospirillum*, *Bacillus*, *Burkholderia*, *Herbaspirillum*, *Nitrobacter*, and other nitrogen-fixing bacteria, which directly or indirectly provide nitrogen to plants, are mainly attracted by root exudates released by plants in later stages of development, e.g., when greater quantities of nitrogen are required for flowering and grain filling (Franche et al. 2009). The roots of *Arabidopsis* plants released more defense-related compounds at later stages of life; these compounds attracted rhizobacteria that were antagonistic to many plant pathogens (Chaparro et al. 2013; Ahemad and Kibret 2014).

In addition to preventing deleterious effects caused by phytopathogens, the use of PGPR can positively affect plant growth and development under stressful situations (Yang et al. 2009; Hayat et al. 2010; Carmen and Roberto 2011). Under drought or salt stress, strains of *Azospirillum* change plant development and behavior to cope with these stressful environments (Arzanesh et al. 2011). Under limiting conditions, plants often adjust their endogenous phytohormone levels to decrease the negative effects of environmental stressors (Hayat et al. 2010; Glick 2015). The co-inoculation of common bean plants with *Paenibacillus polymyxa* and rhizobia alleviated the adverse effects of drought stress and maintained plant growth and development (Figueiredo et al. 2008). These findings indicate that the use of PGPR in association with plants represents an effective and promising tool to increase plant yield worldwide.

3.3 PGPR: Direct Mechanisms of Action

PGPR directly affect plant metabolism by providing nutrients that are usually scarce in the rhizosphere, such as nitrogen (Ahmad et al. 2008; Babalola 2010). The capture and subsequent release of nitrogen to plants is carried out by bacteria present in the rhizo- and endosphere through a diverse set of processes. PGPR may convert nitrogen trapped in the molecular or atmospheric form (N_2) into biologically useful forms in a process known as biological nitrogen fixation (BNF). Only diazotrophic bacteria execute BNF, as the nitrogenase enzyme is present only in these organisms (Bhattacharjee et al. 2008). Members of the genera *Anabaena*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Clostridium*, *Klebsiella*, *Nostoc*, *Paenibacillus*, and *Rhodobacter* are examples of free-living diazotrophic bacteria that provide available nitrogen to several plants (Grobelak et al. 2015).

Nitrogen is the nutrient that is required in the highest amount, and its availability is a major factor that limits plant development (Courty et al. 2015). Globally, considerable attention has been given to the shortage of nitrogen in agricultural soils, which reduces plant yield capacity, and new technologies have been developed and tested to prevent the use of chemical fertilizers in cultivated areas (Bhattacharjee et al. 2008; Figueiredo et al. 2013). The combination of species of *Anabaena*, a free-living diazotrophic bacterium that fixes nitrogen, and *Azolla* is a natural means of providing nitrogen to waterlogged rice plants (Bhuvaneshwari and Kumar 2013; Fosu-Mensah et al. 2015). In this case, the free-living diazotrophic *Anabaena* may be referred to as a "biofertilizer," i.e., a beneficial microorganism that helps to maintain soil quality and plant health through its biological activity. Biofertilization of rice with *Anabaena* contributes high nitrogen amounts (up to 50 kg ha^{-1}), reduces nitrogen loss via ammonia volatilization, and stimulates plant growth (Bhuvaneshwari and Kumar 2013).

Various *Azospirillum* species enhance plant growth, mainly those with the C4 photosynthetic pathway, through atmospheric nitrogen fixation (Bhattacharyya and Jha 2012). Additionally, the biosynthesis and liberation of ammonium ions, nitric oxide (NO), and phytohormones in soil solution are other mechanisms that are activated by *Azospirillum* and which have positive impacts on plant growth (Molina-Favero et al. 2008; Pii et al. 2015). *A. brasilense* and *A. lipoferum* are the major *Azospirillum* species studied worldwide and are frequently used for the inoculation of rice, maize, and sugarcane (Bashan and de-Bashan 2010). *A. brasilense* is able to alter plant root architecture by increasing the formation of lateral and adventitious roots and root hairs (Bashan et al. 2014; Bashan and de-Bashan 2015) and displays the ability to synthesize NO by different pathways (Molina-Favero et al. 2008). NO is required for root organogenesis, root hair formation, and the growth of adventitious and lateral roots (Molina-Favero et al. 2008; Pii et al. 2015), which enhance nitrogen uptake by plants.

In a study conducted on *Arabidopsis* inoculated with *A. brasilense* Sp7 under nitrogenlimited conditions, a significant increase in plant gene expression of high-affinity transport systems (HATSs) was observed (Ahmed 2010). Inorganic nitrogen may be taken up by HATSs localized in root cells (Courty et al. 2015). These systems, which are predominant in the micromolar range, are able to capture ammonium or nitrate ions, resulting in more effective nitrogen capture by the host plants (Pii et al. 2015). The modulation of HATS function is linked to alterations in plant growth and development (Richardson et al. 2009; Ahmed 2010). Furthermore, through an active process that occurs in the root cell wall, plants may absorb nitrate ions generated by nitrifying bacteria after the release of ammonium produced by *Azospirillum* (Marulanda et al. 2010; Courty et al. 2015; Pii et al. 2015).

In addition to nitrogen, phosphorus and potassium are important nutrients provided to plants by PGPR under nutrient-limited conditions (Babalola 2010; Sharma et al. 2013; Courty et al. 2015). The mechanisms involved in phosphorus uptake by PGPR remain poorly understood (Pii et al. 2015). Phosphorus is found in soil mainly in an organic form, principally phytate or insoluble inorganic phosphate, and is commonly found as calcium phosphate, hydroxyapatite, and/or rock phosphate (Richardson et al. 2009). PGPR act as phosphate solubilizers and convert inaccessible phosphorus into forms that can be absorbed by plants through phytase action or the production of organic acids (Sharma et al. 2013). Phytase (myoinositol hexakisphosphate phosphohydrolase) is an enzyme that is active in *Bacillus*, *Enterobacter*, *Klebsiella*, and *Pseudomonas* (Jorquera et al. 2011; Sharma et al. 2013; Vacheron et al. 2013). For this reason, these PGPR are collectively referred to as phosphate-solubilizing or phytase-producing bacteria (PPB).

The capacity to mineralize phytate in combination with other PGPR qualities, e.g., siderophore and phytohormone production, increases the potential use of PGPR in soils with high organic phosphate contents (Pii et al. 2015). Moreover, phosphate-solubilizing PGPR that provide phosphates through the release of organic acids are important in modern agriculture (Sharma et al. 2013). *Bacillus*, *Burkholderia*, *Erwinia*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, and *Serratia* are described in literature as possessing phosphate-solubilizing ability through the release of organic acids (Öğüt et al. 2011). The release of organic acids, mainly acetate, oxalate, and citrate, by PGPR enhances proton efflux and acidifies the rhizosphere; consequently, inorganic phosphate is solubilized from mineral sources (Bhattacharyya and Jha 2012). The use of phosphate-solubilizing PGPR is considered an environmentally friendly alternative to phosphorus supplementation and improves plant growth (Fig. 3.2).

PGPR can effectively promote the absorption of other nutrients, in addition to nitrogen and phosphorus, as well as promote plant growth (Ahmad et al. 2008). The inoculation of wheat with *Pseudomonas* sp. or *Bacillus* sp. resulted in significant increases in potassium, calcium, and magnesium uptake in a calcareous soil without fertilization (Öğüt et al. 2011). These PGPR species deliver potassium through the solubilization of insoluble potassium sources through the production and liberation of organic acids (oxalate, succinate, and citrate) in the rhizosphere, similar to PGPR phosphate solubilizers (Sharma et al. 2013). The solubilization of potassium by PGPR improves soil fertility and the bioavailability of soluble potassium to plants and is thus considered an important plant growth-promotion mechanism under field conditions (Sharma et al. 2013).

Bacillus megaterium increased calcium, phosphorus, boron, copper, iron, manganese, and zinc uptake and increased biomass in trefoil plants under water-limited conditions (Marulanda et al. 2010). Iron is a micronutrient that is involved in various metabolic pathways, and its deficiency disrupts essential processes in plant metabolism, such as respiration or photosynthesis (Radzki et al. 2013). Under iron-limiting conditions, *Bacillus*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhodococcus*, and other rhizobacteria produced siderophores, small iron chelator molecules that enable the transport of iron to the root cells (Raza and Shen 2010). This process helps to maintain plant growth and creates an unfavorable environment for phytopathogens that cannot grow under

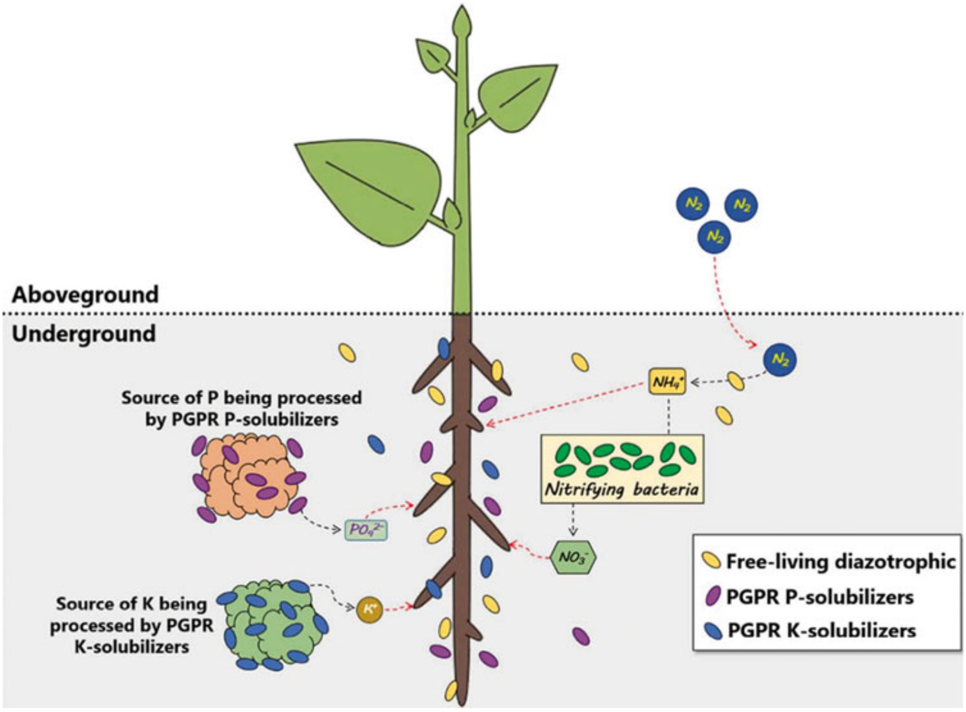

Fig. 3.2 Modes of nitrogen (N), phosphorus (P), and potassium (K) improvement for soil and plants mediated by plant growth-promoting rhizobacteria (PGPR). Free-living diazotrophic bacteria are able to capture nitrogen from the atmosphere (aboveground) and release it to plants as ammonium (NH_4^+) or nitrate (NO_3^-). Other PGPR act as K or P solubilizers and release K or P in forms that can be absorbed by plants

iron-deficient conditions (Pii et al. 2015). The multi-facets of PGPR provide effective uptake of macro- and micronutrients associated with phytohormone production, which enables plant growth under various environmental conditions.

In addition to improved plant nutrition, the biosynthesis of phytohormones is also considered to directly stimulate plant growth (Hayat et al. 2010; Spence and Bais 2015). Auxin, gibberellin, cytokinin, ethylene, and abscisic acid are examples of phytohormones produced and released by numerous members of the genera *Alcaligenes*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Brevibacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Mycobacterium*, *Pseudomonas*, *Rhizobium*, and *Serratia* (Egorshina et al. 2012; Spence and Bais 2015). Among the phytohormones produced by PGPR, the effects of auxin are the most commonly studied and described in the literature. Auxins are produced in meristematic areas and regulate numerous plant processes linked to cell elongation. Alteration in root morphology and development is the most modified trait in plants inoculated with PGPR auxin producers (Glick 2014; Spence and Bais 2015).

Wheat seedlings treated with spores of *Bacillus subtilis* 11BM exhibited growth stimulation as well as a transient increase in indole–3–acetic acid (IAA), the auxin that is most commonly studied worldwide (Egorshina et al. 2012). *Azospirillum brasilense* Az39 and *Bradyrhizobium japonicum* E109 synthetize IAA in concentrations that are adequate to induce morphological changes and promote growth in maize and soybean (Cassan et al. 2009). IAA production by *Mesorhizobium* sp. and/or *Pseudomonas aeruginosa* positively stimulated potassium and phosphorus uptake by chickpea inoculated with these microorganisms (Verma et al. 2013). These increases in nutrient uptake are related to better access to soil nutrients as a consequence of the increase in the root surface or intensifications in root exudation that provide additional nutrients for plants and maintain the growth of PGPR in the rhizosphere (Hayat et al. 2010).

A considerable number of PGPR secrete phytohormones in the rhizosphere; however, among these, PGPR gibberellin producers remain poorly understood (Pii et al. 2015). Gibberellins (GAs) are a group of phytohormones associated with alterations in plant morphology, mainly in stem and root tissues (Spence and Bais 2015). *Acinetobacter calcoaceticus*, *Bacillus pumilus*, *Bacillus licheniformis*, *Burkholderia cepacia*, *Herbaspirillum seropedicae*, and *Promicromonospora* sp. are examples of bacteria that produce gibberellins and result in positive effects in the endogenous GA of their host plants (Richardson et al. 2009; Figueiredo et al. 2010; Vacheron et al. 2013).

B. siamensis is a bacilli species that is able to produce GA and promote increases in the growth of banana plants (Ambawade and Pathade 2015). Different types of GA are produced by PGPR (Ahemad and Kibret 2014). In *Azospirillum*, GA3 is the major GA type identified and appears to be involved in promoting plant growth (Cassan et al. 2009).

Phytohormones are involved in practically all steps of plant growth. *Pseudomonas fluorescens* is a PGPR proficient in synthesizing the phytohormone cytokinin and solubilizing organic phosphorus, and their association with *Azospirillum brasilense* is able to improve the biomass and grain yield of wheat (Naiman et al. 2009). *Bacillus megaterium* induces the genes linked to cytokinin receptors in *Arabidopsis* before specifically initiating growth stimulation (Ortíz-Castro et al. 2008). These authors showed that growth promotion by *B. megaterium* is strongly related to three cytokinin receptors that are necessary for normal *Arabidopsis* growth. The production and elongation of root hairs are cytokinin-regulated growth responses (Werner and Schmülling 2009), and root system architecture of *Arabidopsis* elicited by *B. megaterium* is probably also linked to other phytohormones, such as auxin and ethylene (López-Bucio et al. 2007).

1-aminocyclopropane-1-carboxylate (ACC) is a direct ethylene precursor exuded by roots. ACC may be metabolized by PGPR that possess ACC deaminase, an enzyme that converts ACC in α-ketobutyrate and ammonium and therefore reduces ethylene amounts (Hayat et al. 2010; Glick 2014). At low concentrations, ethylene facilitates root elongation in plants under normal and stressful conditions. Considering that bacterial ACC deaminase reduces ethylene levels, the modulation of ACC levels in hosts may mitigate detrimental effects of biotic and abiotic stresses (Glick 2014). In addition to ethylene, abscisic acid (ABA) also modulates plant development under stressful conditions (Glick 2015; Spence and Bais 2015). *Achromobacter xylosoxidans*, *Bacillus licheniformis*, *B. pumilus*, *B. subtilis*, *Brevibacterium halotolerans*, *Lysinibacillus fusiformis*, and *Pseudomonas putida* are ABA-producing bacteria that positively influence plant homeostasis (Sgroy et al. 2009; Glick 2014).

Currently, there is a growing need to increase food production and minimize applications of chemical fertilizers; in this context, the employment of sustainable agriculture is extremely important (Bhattacharyya and Jha 2012). For sustainable agriculture, different cropping systems can be employed, among which the use of PGPR is promising. Nutrient uptake and phytohormone production are considered as direct mechanisms of PGPR (Ahemad and Kibret 2014).

3.4 PGPR: Indirect Mechanisms of Action

Several lines of evidence indicate that rhizospheric microorganisms are protective agents against soil pathogens (Melo 1991; Kloepper 1999). Rhizobacteria can suppress diseases that develop through various mechanisms of action, e.g., antagonism related to the production of antifungal antibiotics such as iturin by *B. subtilis* (Araujo et al. 2005); competition for space and nutrients with phytopathogens and other harmful microorganisms in the rhizosphere (Robin et al. 2008); production of volatile organic molecules, such as hydrogen cyanide (HCN) and ammonia

(Kai et al. 2009); production of molecules that can degrade cell walls such as chitinases and biosurfactants (Zhao et al. 2014); and induced resistance (Wall and Sanchez 1993).

Recent studies have indicated that biofilm formation in the rhizosphere is of considerable importance in the mechanisms of action of rhizobacteria on root pathogens. The presence of high concentrations of bacterial cells in biofilms results in the release of various metabolites such as toxins and antibiotics in their periphery, which has an inhibitory effect on phytopathogens in the soil. The biofilm of *Bacillus subtilis* is composed of compounds of a family of surfactins, i.e., cyclic molecules with amino acids and lipids, which act as powerful biosurfactants with antifungal and antibacterial activity. Moreover, biofilm of *B. subtilis* can participate in the induction of resistance in plants (Kwon and Kim 2014).

Catabolic enzymes (proteases, β-1,3-glucanase, and chitinases) and small molecules can be secreted by various microbial species and can contribute to the suppression of soilborne plant pathogens. Studies using electron microscopy show details of the antagonist effect on *Fusarium* hyphae (Fig. 3.3), highlighting the obvious abnormality of the mycelial growth, which can be attributed to the effect of cell wall-degrading enzymes such as chitinases, produced by rhizobacteria (Zhao et al. 2014). In addition, antibiotics and various compounds toxic to phytopathogens have been recovered from the metabolites of *Bacillus* strains (Esikova et al. 2002). *B. subtilis* produces lipopeptide antibiotics of the iturin and surfactin group that can suppress several plant diseases. Antagonism involving competition for space and nutrients within an ecological niche also plays an important role in the rhizosphere. This was proven in studies on *B. megaterium*, which can competently colonize roots and suppress *Rhizoctonia solani* (Zheng and Sinclair 2000).

The research conducted on the *Bacillus* genus has contributed significantly to the biological control of diseases especially that conducted on certain species of this genus, such as *B. subtilis* (Araujo 2008). It has been reported that *B. subtilis* can produce 66 different types of antibiotics (Katz and Demain 1977), mostly polypeptides with inhibitory effect against pathogenic bacteria and fungi. Side effects related to the biological control of fungi have been highlighted in recent years, such as the reduction of toxic metabolites in food and the production of enzymes such as chitinases, which can degrade the cell wall of fungi (Zhao et al. 2014).

The production of siderophores is a secondary effect of rhizobacteria. These molecules have the ability to sequester Fe^{3+} ions, which are considered essential for metabolism and cell growth. In this sense, the bacteria that colonize plant roots can compete for available iron in the soil and may inhibit the growth of other microorganisms in the rhizosphere. Siderophore-producing rhizobacteria can prevent the proliferation of pathogenic microorganisms around the root (Kumar et al. 2015).

Plants have a natural basal defense system against phytopathogens, but other systems that increase the resistance of plants can be activated or induced (Bonas and Lahaye 2002). The two commonly studied forms of resistance induction are acquired systemic resistance (ASR) and induced systemic resistance (ISR). ASR occurs when plants are exposed to an inducer agent (such as a pathogenic organism), resulting in the activation of defense mechanisms at the induction site, which displays alterations (necrosis), as well as other distant sites, resulting in the plant being systemically protected against subsequent infections caused by a broad spectrum of pathogens (Romeiro 2000). ASR is accompanied by an increase in the concentration of salicylic acid and the accumulation of proteins related to pathogenesis (PRPs), which are mechanisms involved in plant defense (Moraes 1998). ISR can be triggered by nonpathogenic microorganisms in the rhizosphere and does not involve the signaling pathway of salicylic acid or the induction of PRPs; rather, this type of resistance is activated by resistance-signaling pathway of jasmonic acid and ethylene (Pieterse et al. 1998).

When rhizobacteria colonize the root system, the constituent molecules of the bacterial cell or those synthesized by the bacteria act as elicitors of a biochemical signal. This signal is translocated to sites that are distant from the original

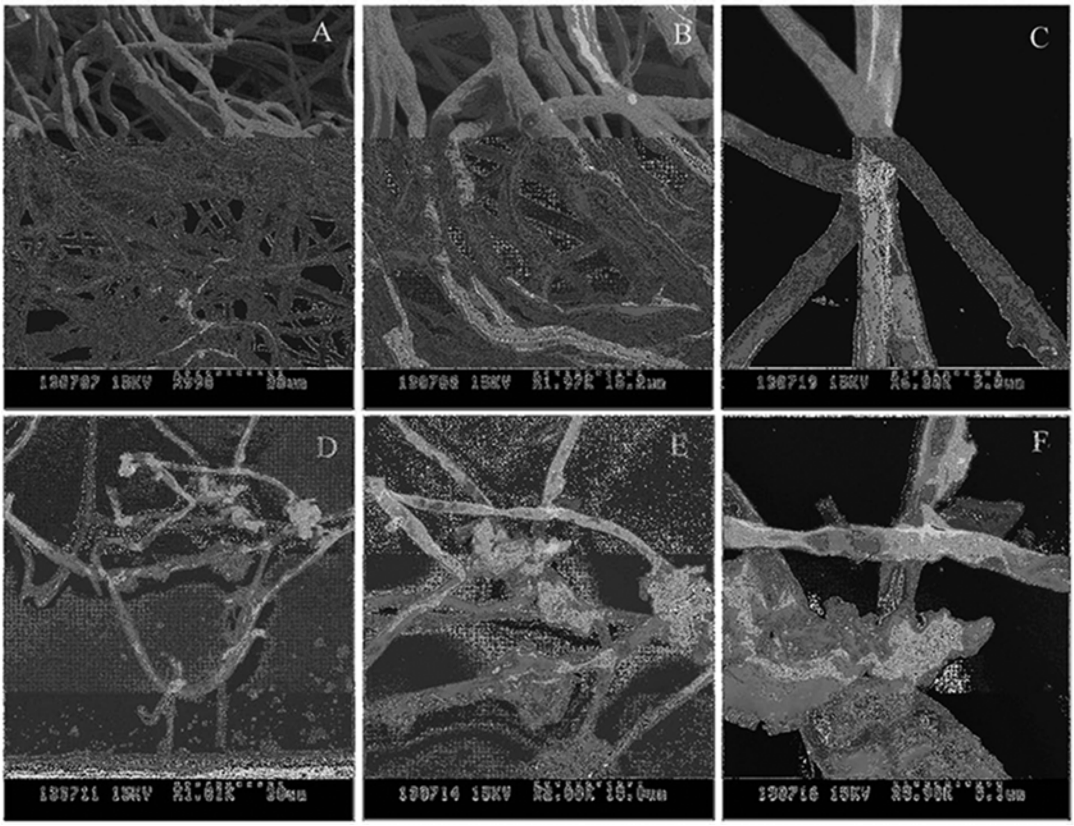

Fig. 3.3 Scanning electron microscope analysis of antagonistic bacteria interacting with hyphae of pathogens on PDA medium on the fifth day after incubation at 28 °C. Normal hyphae of *Fusarium graminearum* are depicted in (**a**–**c**), while abnormal hyphae of *F. graminearum* are shown in (**d**–**f**) (Zhao et al. 2014)

location, resulting in the activation of genes that dynamically code for the synthesis of resistant components and, consequently, the expression of induced systemic resistance (Romeiro 2000). Recent studies aimed to identify these elicitor molecules, which are components of the cell wall, such as lipopolysaccharides, or are released during the energy metabolism of cells. Of these, the most studied are the volatile organic compounds, such as butanediol and acetoin, which are released during anaerobic fermentation and actively participate as elicitors in induced systemic resistance (Choudhary et al. 2008). To confirm the role of butanediol in *Arabidopsis* growth promotion under biological conditions, mutant strains of *B. subtilis* genetically blocked in the production of butanediol were compared with their parental to examine the effect on plant-growth promotion. In this case, the butanediol-synthesis mutants reduced plant growth, whereas the controls did not (Ryu et al. 2003).

The identification of compounds produced by *B. subtilis* during its secondary metabolism is important to clarify the beneficial effects that the bacteria provide to plants (Phae and Shoda 1991). The large number of mechanisms involved in producing these compounds may be the reason why *B. subtilis* has been assessed in a wide range of agricultural crops under different conditions (Kilian et al. 2000). Within the major metabolic pathways studied and those involving the participation of rhizobacteria, stands out the metabolism involved in the production of phytohormones in the rhizosphere environment (Araujo et al. 2005), and the induction of resistance to biotic and abiotic stresses (Kang et al. 2010) has been reported. The accumulation of proline in plants acts as an osmoprotectant, maintaining the water potential under deficit conditions and facilitating water uptake from the soil (Hanson et al. 1979). Rampazzo (2013) observed that proline accumulation in sugarcane was affected by inoculation with rhizobacteria: plants inoculated and subjected to water stress had a 2.2-fold increase in the concentration of proline in leaves compared with plants inoculated in the absence of stress.

Plants produce a range of antioxidant enzymes such as catalases, peroxidases, and superoxide dismutases involved in scavenging free radicals (Simova-Stoilova et al. 2008). The introduction of growth-promoting bacteria to the rhizosphere can greatly contribute to the production of antioxidant enzymes in plants. Inoculation with *Bacillus subtilis* increased the concentration of detoxification enzymes in plants, which is characterized as another beneficial effect resulting from the inoculation of these bacteria (Li et al. 2008). In tomato, the inoculation of *B. subtilis* was reflected as an increase in the peroxidase activity in plants (Araujo and Menezes 2009). Similarly, in corn plants inoculated with *Piriformospora indica*, the activity of catalase and superoxide dismutase was increased, and the effect of biotic stress was reduced (Kumar et al. 2009).

The presence of antioxidant enzymes in food is beneficial to the health of consumers because antioxidants are nutraceutical molecular components of functional foods, according to Andlauer and Fürst (2002). The term nutraceutical defines a wide variety of foods and food components with medical or health benefits. Nutraceutical action ranges from the supply of essential minerals and vitamins to protection against various infectious diseases (Hungenholtz and Smid 2002). Antioxidants can act directly in neutralizing the action of free radicals or can indirectly participate in enzymatic systems involved in this function (Moraes and Colla 2006). The main antioxidant compounds with nutraceutical characteristics in plants are flavonoids, which act as potent antioxidants and metal chelators, and are also well known for their anti-inflammatory, antiallergic, antiviral, and anticarcinogenic properties (Tapas et al. 2008).

3.5 Concluding Remarks

There is an urgent need for research to clearly define what bacterial traits are useful and necessary for different environmental conditions and plants so that optimal bacterial strains can be selected. Different compounds related to the presence of these microorganisms confer benefits to protect plants against pathogens and stressful conditions that may occur during cultivation. Foods derived from these plants can have a healthier chemistry for consumers. Due to direct and indirect mechanisms used by PGPR, the use of microbes in the cultivation of plants of agronomic interest is considered a useful tool in modern agriculture and therefore represents the core of eco-friendly agricultural practices. In this context, the increased use of PGPR is one of the major pathways to maintain or increase yield as well as reduce the environmental footprint via elucidation of different mechanisms involved that will help to make these plant-beneficial rhizobacteria a valuable partner in agriculture to develop future insights.

References

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. J King Saud Univ Sci 26(1):1–20

Ahmad F, Ahmad I, Khan MS (2008) Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. Microbiol Res 163(2):173–181

Ahmed N (2010) Physiological and molecular basis of *Azospirillum-Arabidopsis* interaction. Dissertation, Universitätsbibliothek der Universität Würzburg

Ambawade MS, Pathade GR (2015) Production of gibberellic acid by *Bacillus siamensis* BE 76 isolated from banana plant (*Musa* spp.). Int J Sci Res 4(7):394–398

Andlauer W, Fürst P (2002) Nutraceuticals: a piece of history, present status and outlook. Food Res Int 35:171–176

Araujo FF (2008) Seed inoculation with *Bacillus subtilis*, formulated with oyster meal and growth of corn, soybean and cotton. Ciênc Agrotech 32(2):456–462

Araujo FF, Menezes D (2009) Induction of resistance in tomato by biotic (*Bacillus subtilis*) and abiotic (Acibenzolar-S-Metil) inducers. Summa Phytopathol 35:163–166

Araujo FF, Henning AA, Hungria M (2005) Phytohormones and antibiotics produced by *Bacillus subtilis* and their effects on seed pathogenic fungi and on soybean root development. World J Microbiol Biotechnol 21:1639–1645

Arzanesh MH, Alikhani HA, Khavazi K, Rahimian HA, Miransari M (2011) Wheat (*Triticum aestivum* L.) growth enhancement by *Azospirillum* sp. under drought stress. World J Microbiol Biotechnol 27:197–205

Avis TJ, Gravel V, Antoun H, Tweddell RJ (2008) Multifaceted beneficial effects of rhizosphere microorganisms on plant health and productivity. Soil Biol Biochem 40:1733–1740

Babalola OO (2010) Beneficial bacteria of agricultural importance. Biotech Lett 32(11):1559–1570

Backman PA, Sikora RA (2008) Endophytes: an emerging tool for biological control. Biol Cont 46(1):1–3

Badri DV, Loyola-Vargas VM, Du J, Stermitz FR, Broeckling CD, Iglesias-Andreu L, Vivanco JM (2008) Transcriptome analysis of *Arabidopsis* roots treated with signaling compounds: a focus on signal transduction, metabolic regulation and secretion. New Phytol 179:209–223

Badri DV, Weir TL, van der Lelie D, Vivanco JM (2009) Rhizosphere chemical dialogues: plant-microbe interactions. Curr Opin Biotech 20(6):642–650

Bashan Y (1998) Inoculants of plant growth-promoting bacteria for use in agriculture. Biotechnol Adv 16:729–770

Bashan Y, de-Bashan LE (2010) How the plant growth-promoting bacterium *Azospirillum* promotes plant growth -a critical assessment. Adv Agron 108:77–136

Bashan Y, de-Bashan LE (2015) Inoculant preparation and formulations for *Azospirillum* spp. In: Cassán FD, Okon Y, Creus CM (eds) Handbook for *Azospirillum*: technical issues and protocols. Springer, Cham, pp 469–485

Bashan Y, Holguin G (1998) Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. Soil Biol Biochem 30(8):1225–1228

Bashan Y, De-Bashan LE, Prabhu SR, Hernandez JP (2014) Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). Plant Soil 378:1–33

Bhattacharjee RB, Singh A, Mukhopadhyay SN (2008) Use of nitrogen-fixing bacteria as biofertilizer for non-legumes: prospects and challenges. Appl Microbiol Biotech 80(2):199–209

Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World J Microbiol Biotechnol 28(4):1327–1350

Bhuvaneshwari K, Kumar A (2013) Agronomic potential of the association *Azolla-Anabaena*. Sci Res Report 3(1):78–82

Bonas U, Lahaye T (2002) Plant disease resistance triggered by pathogen-derived molecules: refined models of specific recognition. Curr Opin Microbiol 5:44–50

Boyer M, Bally R, Perrotto S, Chaintreuil C, Wisniewski-Dye F (2008) A quorum-quenching approach to identify quorum-sensing-regulated functions in *Azospirillum lipoferum*. Res Microbiol 159(9–10):699–708

Carmen B, Roberto D (2011) Soil bacteria support and protect plants against abiotic stresses. In: Shanker A, Venkateswarlu B (eds) Abiotic stress in plants mechanisms and adaptations. InTech, doi:10.5772/23310

Cassan F, Perrig D, Sgroy V, Masciarelli O, Penna C, Luna V (2009) *Azospirillum brasilense* Az39 and *Bradyrhizobium japonicum* E109, inoculated singly or in combination, promote seed germination and early seedling growth in corn (*Zea mays* L.) and soybean (*Glycine max* L.). Eur J Soil Biol 45(1):28–35

Cassan F, Vanderleyden J, Spaepen S (2014) Physiological and agronomical aspects of phytohormone production by model plant-growth-promoting rhizobacteria (PGPR) belonging to the genus *Azospirillum*. J Plant Growth Reg 33(2):440–459

Cattelan AJ, Hartel PG, Fuhrmann JJ (1999) Screening for plant growth rhizobacteria to promote early soybean growth. Soil Sci Soc Am J 63:1670–1680

Chanway CP (1997) Inoculation of tree roots with plant growth promoting rhizobacteria: an emerging technology for reforestation. For Sci 43:99–112

Chaparro JM, Badri DV, Bakker MG, Sugiyama A, Manter DK, Vivanco JM (2013) Root exudation of phytochemicals in *Arabidopsis* follows specific patterns that are developmentally programmed and correlate with soil microbial functions. PLoS One 8(2):e55731

Chaparro JM, Badri DV, Vivanco JM (2014) Rhizosphere microbiome assemblage is affected by plant development. ISME J 8(4):790–803

Chauhan H, Bagyaraj DJ, Selvakumar G, Sundaram SP (2015) Novel plant growth promoting rhizobacteria -prospects and potential. Appl Soil Ecol 95:38–53

Choudhary DK (2012) Microbial rescue to plant under habitat-imposed abiotic and biotic stresses. Appl Microbiol Biotechnol 96:1137–1155

Choudhary DK, Bhavdish NJ, Prakash A (2008) Volatiles as priming agents that initiate plant growth and defense responses. Curr Sci 94:595–604

Choudhary DK, Sharma KP, Gaur RK (2011) Biotechnological perspectives of microbes in agro-ecosystems. Biotechnol Lett 33(10):1905–1910

Cohen A, Bottini R, Piccoli P (2008) *Azospirillum brasilense* Sp 245 produces ABA in chemically-defined culture medium and increases ABA content in *Arabidopsis* plants. Plant Growth Regul 54:97–103

Compant S, Clément C, Sessitsch A (2010) Plant growth-promoting bacteria in the rhizo-and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol Biochem 42(5):669–678

Courty P, Smith P, Koegel S, Redecker D, Wipf D (2015) Inorganic nitrogen uptake and transport in beneficial plant root-microbe interactions. Cr Rev Plant Sci 34:4–16

Dakora FD, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245:35–47

Dourado MN, Bogas AC, Pomini AM, Andreote FD, Quecine MC, Marsaioli AJ, Araújo WL (2013) *Methylobacterium*-plant interaction genes regulated by plant exudate and quorum sensing molecules. Braz J Microbiol 44(4):1331–1339

Duca D, Lorv J, Patten CL, Rose D, Glick BR (2014) Indole-3-acetic acid in plant– microbe interactions. A Van Leeuw J Microb 106:85–125

Egamberdieva D, Berg G, Lindström K, Räsänen LA (2013) Alleviation of salt stress of symbiotic *Galega officinalis* L. (goat's rue) by co-inoculation of *Rhizobium* with root-colonizing Pseudomonas. Plant Soil 369:453–465

Egorshina AA, Khairullin R, Sakhabutdinova AR, Luk'yantsev MA (2012) Involvement of phytohormones in the development of interaction between wheat seedlings and endophytic *Bacillus subtilis* strain 11BM. Russ J Plant Phys 59(1):134

Esikova TZ, Temirov YV, Sokolov SL, Alakhov YB (2002) Secondary antimicrobial metabolites produced by thermophilic *Bacillus* spp. strains VK2 and VK21. Appl Bioch Micro 38:226–231

Figueiredo MVB, Burity HA, Martínez CR, Chanway CP (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. Appl Soil Ecol 40:182–188

Figueiredo MVB, Seldin L, Araujo FF, Mariano RLR (2010) Plant growth promoting rhizobacteria: fundamentals and applications. In: Maheshwari DK (ed) Plant growth and health promoting bacteria. Springer, Heidelberg, pp 21–43

Figueiredo MVB, Mergulhão ACES, Kuklinsky-Sobral J, Lira Junior MA, Araujo ASF (2013) Biological nitrogen fixation: importance, associated diversity, and estimates. In: Arora NK (ed) Plant microbe symbiosis: fundamentals and advances. Springer, New Delhi, pp 267–289

Fosu-Mensah BY, Vlek PL, Manske G, Mensah M (2015) The influence of *Azolla pinnata* on floodwater chemistry, grain yield and nitrogen uptake of rice in Dano, Southwestern Burkina Faso. J Agr Sci 7(8):118–130

Franche C, Lindstrom K, Elmerich C (2009) Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. Plant Soil 321:35–59

Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169(1):30–39

Glick BR (2015) Beneficial plant-bacterial interactions. Springer, Cham

Glick BR, Karaturovic DM, Newell PC (1995) A novel procedure for rapid isolation of plant growth promoting *Pseudomonas*. Can J Microbiol 41:533–536

Gray EJ, Smith DL (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. Soil Biol Biochem 37:395–412

Grobelak A, Napora A, Kacprzak M (2015) Using plant growth-promoting rhizobacteria (PGPR) to improve plant growth. Ecol Eng 84:22–28

Gupta A, Gopal M, Tilak KV (2000) Mechanism of plant growth promotion by rhizobacteria. Indian J Exp Biol 38:856–862

Han HS, Supanjani, Lee KD (2006) Effect of co-inoculation with phosphate and potassium solubilizing bacteria on mineral uptake and growth of pepper and cucumber. Plant Soil Environ 52(3):130–136

Hanson AD, Nelsen CE, Pedersen AR, Everson EH (1979) Capacity for proline accumulation during water stress in barley and its implications for breeding for drought resistance. Crop Sci 19(4):489–493

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60(4):579–598

Huang XF, Chaparro JM, Reardon KF, Zhang R, Shen Q, Vivanco JM (2014) Rhizosphere interactions: root exudates, microbes, and microbial communities. Botany 92(4):267–275

Hungenholtz J, Smid EJ (2002) Nutraceutical production with food-grade microorganisms. Curr Opin Biotech 13:497–507

Jha PN, Gupta G, Jha P, Mehrotra R (2013) Association of rhizospheric/endophytic bacteria with plants: a potential gateway to sustainable agriculture. Greener J Agri Sc 3(2):73–84

Jorquera MA, Crowley DE, Marschner P, Greiner R, Fernández MT, Romero D, Menezes-Blackburn D, Mora MDL (2011) Identification of β-propeller phytase-encoding genes in culturable *Paenibacillus* and *Bacillus* spp. from the rhizosphere of pasture plants on volcanic soils. FEMS Microbiol Ecol 75(1):163–172

Kai M, Haustein MF, Petri A, Scholz B, Piechulla B (2009) Bacterial volatiles and their action potential. Appl Microbiol Biotechnol 81:1001–1012

Kang BG, Kim WT, Yun H, Chang S (2010) Use of plant growth-promoting rhizobacteria to control stress responses of plant roots. Plant Biotechnol Rep 4:179–183

Katz E, Demain AL (1977) The peptide antibiotics of *Bacillus*: chemistry, biogenesis and possible functions. Bacteriol Rev 41:449–474

Kavamura VN, Santos SN, Silva JL, Parma MM, Ávila LA, Visconti A, Zucchi TD, Taketani RG, Andreote F, Melo IS (2013) Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. Microbiol Res 168:183–191

Kilian M, Steiner U, Krebs B, Junge H, Schmiedeknecht G, Hain R (2000) Fzb24 *Bacillus subtilis*: mode of action of a microbial agent enhancing plant vitality. Pflanzenschutz-Nachr Bayer 1:72–93

Kloepper JW (1999) Plant root-bacterial interactions in biological control of soil borne diseases and potential extension to systemic and foliar diseases. Australas Plant Pathol 28:21–26

Kloepper JW, Schroth MN (1978) Plant growth-promoting rhizobacteria on radishes. In: Abstract of the 4th international conference on plant pathogenic bacteria, Station de pathologie végétale et phytobactériologie, Angers, p 27, 2 Aug Sept, 1978

Kloepper JW, Schroth MN, Miller TD (1980) Effects of rhizosphere colonization by plant growth-promoting rhizobacteria on potato plant development and yield. Phytopathology 70:1078–1082

Kloepper JW, Ryu CM, Zhang S (2004) Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94:1259–1226

Kumar M, Yadav V, Tuteja N, Johri AK (2009) Antioxidant enzyme activities in maize plants colonized with *Piriformospora indica*. Microbiology 155:780–790

Kumar A, Bahadur I, Maurya BR, Raghuwanshi R, Meena VS, Singh DK, Dixit J (2015) Does a plant growth promoting rhizobacteria enhance agricultural sustainability? J Pur Appl Microbiol 9:715–724

Kwon JW, Kim SD (2014) Characterization of an Antibiotic Produced by *Bacillus subtilis* JW-1 that suppresses *Ralstonia solanacearum*. J Microbiol Biotechnol 24:13–18

Li J, Ovakin DH, Charles TC, Glick BR (2000) An ACC deaminase minus mutant of *Enterobacter cloacae* UW4 no longer promotes root elongation. Curr Microbiol 41:101–105

Li S, Hua G, Liu H, Guo J (2008) Analysis of defense enzymes induced by antagonistic bacterium Bacillus subtilis strain AR12 towards *Ralstonia solanacearum* in tomato. Ann Microbiol 58:573–578

López-Bucio J, Campos-Cuevas JC, Hernández-Calderón E, Velásquez-Becerra C, Farías-Rodríguez R, Macías-Rodríguez LI, Valencia-Cantero E (2007) *Bacillus megaterium* rhizobacteria promote growth and alter root-system architecture through an auxin-and ethylene-independent signaling mechanism in *Arabidopsis* thaliana. Mol Plant Microbe In 20(2):207–217

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Ann Rev Microbiol 63:541–556

Marulanda A, Azcón R, Chaumont F, Ruiz-Lozano JM, Aroca R (2010) Regulation of plasma membrane aquaporins by inoculation with a *Bacillus megaterium* strain in maize (Zea mays L.) plants under unstressed and salt-stressed conditions. Planta 232(2):533–543

Melo IS (1991) Potentiality of uses of *Trichoderma* spp. in biological control of plant diseases. In: Bettiol W (ed) Biological control of plant diseases. Embrapa, Campinas, pp 135–156

Minaxi LN, Yadav RC, Saxena J (2012) Characterization of multifaceted *Bacillus* sp. RM-2 for its use as plant growth promoting bioinoculant for crops grown in semi arid deserts. Appl Soil Ecol 59:124–135

Molina-Favero C, Creus CM, Simontacchi M, Puntarulo S, Lamattina L (2008) Aerobic nitric oxide production by *Azospirillum brasilense* Sp245 and its influence on root architecture in tomato. Mol Plant Microbe In 21(7):1001–1009

Moraes MG (1998) Mechanisms of acquired systemic resistance in plants. Revis Anu Patol Plantas 6:261–284

Moraes FP, Colla LM (2006) Functional foods and nutraceuticals: definition, legislation and health benefits. Rev Eletrôn Farm 3:109–122

Nadeem SM, Ahmad M, Zahir ZA, Javaid A, Ashraf M (2014) The role of mycorrhizae and plant growth promoting rhizobacteria (PGPR) in improving crop productivity under stressful environments. Biotech Adv 32(2):429–448

Naiman AD, Latrónico A, De Salamone IEG (2009) Inoculation of wheat with *Azospirillum brasilense* and *Pseudomonas fluorescens*: impact on the production and culturable rhizosphere microflora. Eur J Soil Biol 45(1):44–51

Nimnoi P, Pongsilp N, Lumyong S (2010) Endophytic actinomycetes isolated from *Aquilaria crassna* Pierre ex Lec and screening of plant growth promoters production. World J Microbiol Biotech 26(2):193–203

Öğüt M, Er F, Neumann G (2011) Increased proton extrusion of wheat roots by inoculation with phosphorus solubilizing microorganism. Plant Soil 339:285–297

Ortíz-Castro R, Valencia-Cantero E, López-Bucio J (2008) Plant growth promotion by *Bacillus megaterium* involves cytokinin signaling. Plant Signal Behav 3(4):263–265

Phae C, Shoda M (1991) Investigation of optimal conditions for separation of iturin an antifungal peptide produced by *Bacillus subtilis*. J Ferment Bioengineer 71:118–121

Pieterse CMJ, van Pelt JA, Knoester M, Laan R, Gerrits H, Weisbeek PJ, van Loon LC (1998) Novel signaling pathway controlling induced systemic resistance in *Arabidopsis*. Plant Cell 10:1571–1580

Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C (2015) Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process: a review. Biol Fert Soils 51(4):403–415

Radzki W, Manero FG, Algar E, García JL, García-Villaraco A, Solano BR (2013) Bacterial siderophores efficiently provide iron to iron-starved tomato plants in hydroponics culture. A Van Leeuw J Microb 104(3):321–330

Rampazzo PE (2013) Interaction between rhizobacteria and sugarcane under different conditions of substrate moisture: growth, photosynthesis and water relations. Dissertation, Institute Agronomic of Campinas, Campinas

Raza W, Shen Q (2010) Growth, Fe^{3+} reductase activity, and siderophore production by *Paenibacillus poly-*

myxa SQR-21 under differential iron conditions. Curr Microbiol 61(5):390–395

Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability update on microbial phosphorus. Plant Physiol 156(3):989–996

Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C (2009) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321:305–339

Robin A, Vansuyt G, Hinsinger P, Meyer JM, Briat JF, Lemanceau P (2008) Iron dynamics in the rhizosphere: consequences for plant health and nutrition. Adv Agron 99:183–225

Rodrigues AC, Bonifacio A, Antunes JEL, Silveira JAG, Figueiredo MVB (2013) Minimization of oxidative stress in cowpea nodules by the interrelationship between *Bradyrhizobium* sp. and plant growth-promoting bacteria. Appl Soil Ecol 64:245–251

Romeiro RS (2000) PGPR and systemic induction of resistance against plant pathogens. Summa Phytopathol 26:177–184

Ryu C, Farag MA, Hu C, Reddy MS, Wei H, Pare PA, Kloepper JW (2003) Bacterial volatiles promote growth in *Arabidopsis*. Proc Natl Acad Sci U S A 100:4927–4932

Saha R, Saha N, Donofrio RS, Bestervelt LL (2013) Microbial siderophores: a mini review. J Basic Microbiol 53:303–317

Saikia SP, Dutta SP, Goswami A, Bhau BS, Kanjilal PB (2010) Role of *Azospirillum* in the improvement of legumes. Springer, Vienna

Saraf M, Rajkumar S, Saha T (2011) Perspectives of PGPR in agri-ecosystems. In: Maheshwari DK (ed) Bacteria in agrobiology: crop ecosystems. Springer, Heidelberg, pp 361–385

Sgroy V, Cassán F, Masciarelli O, Del Papa MF, Lagares A, Luna V (2009) Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. Appl Microbiol Biotechnol 85(2):371–381

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA (2013) Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. Springer Plus 2:587

Simova-Stoilova L, Demirevska K, Petrova T, Tsenov N, Feller U (2008) Antioxidative protection in wheat varieties under severe recoverable drought at seedling stage. Plant Soil Environ 54:529–536

Spence C, Bais H (2015) Role of plant growth regulators as chemical signals in plant-microbe interactions: a double edged sword. Curr Opin Plant Biol 27:52–58

Tapas AR, Sakarkar DM, Kakde RB (2008) Flavonoids as nutraceuticals: a review. Trop J Pharm Res 7:1089–1099

Vacheron J, Desbrosses G, Bouffaud ML, Touraine B, Moënne-Loccoz Y, Muller D, Legendre L, Wisniewski-Dyé F, Prigent-Combaret C (2013) Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci 4:356

van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. Eur J Plant Pathol 119(3):243–254

Verma JP, Yadav J, Tiwari KN, Kumar A (2013) Effect of indigenous *Mesorhizobium* spp. and plant growth promoting rhizobacteria on yields and nutrients uptake of chickpea (*Cicer arietinum* L.) under sustainable agriculture. Ecol Engin 51:282–286

Vessey JK (2003) Plant growth-promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Wall GC, Sanchez JL (1993) A biocontrol agent for *Pseudomonas solanacearum*. In: Hatman GL, Hayward AC (eds) Proceedings of international conference held at Kaohsiung, Taiwan, 1993

Werner T, Schmülling T (2009) Cytokinin action in plant development. Curr Opin Plant Biol 12:527–538

Yang J, Kloepper JW, Ryu CM (2009) Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci 14:1–4

Zhao Y, Selvaraj JN, Xing F, Zhou L, Wang Y, Song H (2014) Antagonistic action of *Bacillus subtilis* Strain SG6 on *Fusarium graminearum*. PLoS One 9:e92486

Zheng XY, Sinclair JB (2000) The effects of traits of *Bacillus megaterium* on seed and root colonization and their correlation with the suppression of *Rhizoctonia* root rot of soybean. BioControl 45:223–243