
Plant Growth-Promoting Rhizobacteria: Key Mechanisms of Action

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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

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-

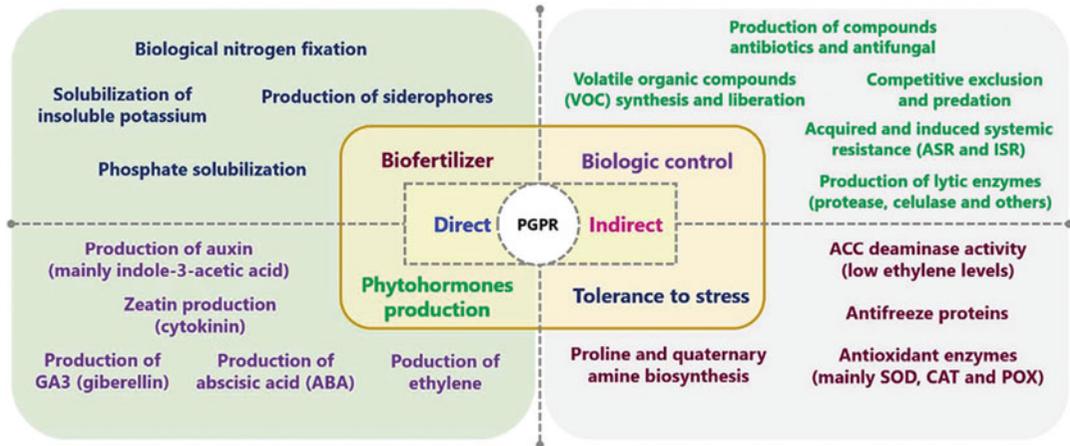


Fig. 3.1 Direct and indirect mechanisms mediated by plant growth-promoting rhizobacteria (PGPR) with beneficial effects on host plants (Chauhan et al. 2015; Pii et al. 2015)

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 synthesized 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 bio-control 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 (Grobela 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 nitrogen-

limited 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 (myo-inositol 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 (Ögüt 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 (Ögüt 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

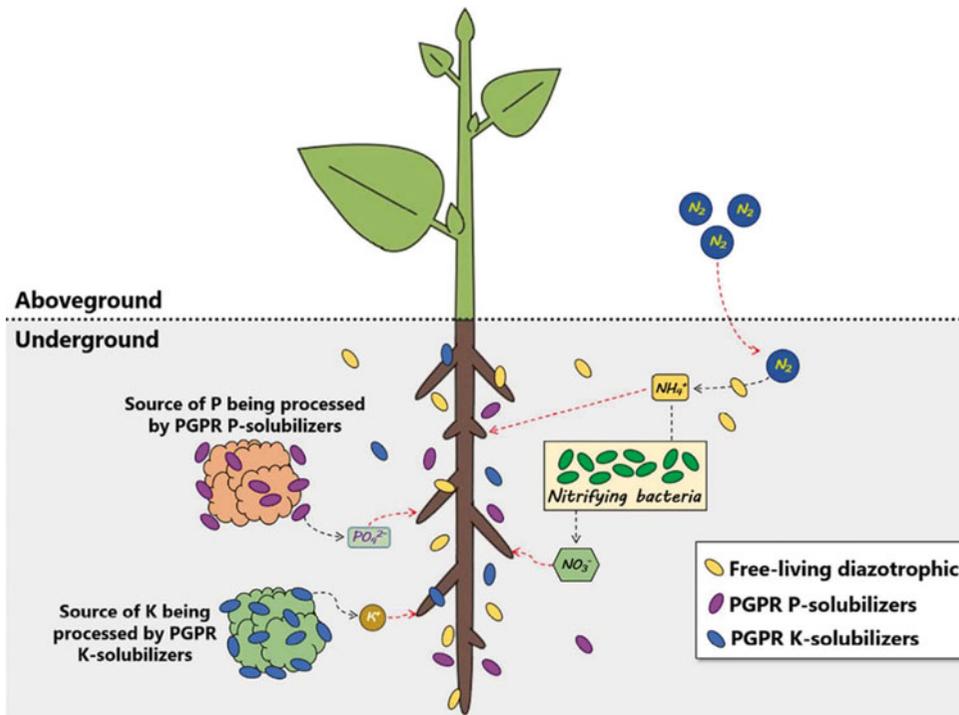


Fig. 3.2 Modes of nitrogen (N), phosphorus (P), and potassium (K) improvement for soil and plants mediated by plant growth-promoting rhizobacteria (PGPR). Free-living diazotrophic bacteria are able to capture nitrogen

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 synthesize 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 Schmölling 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

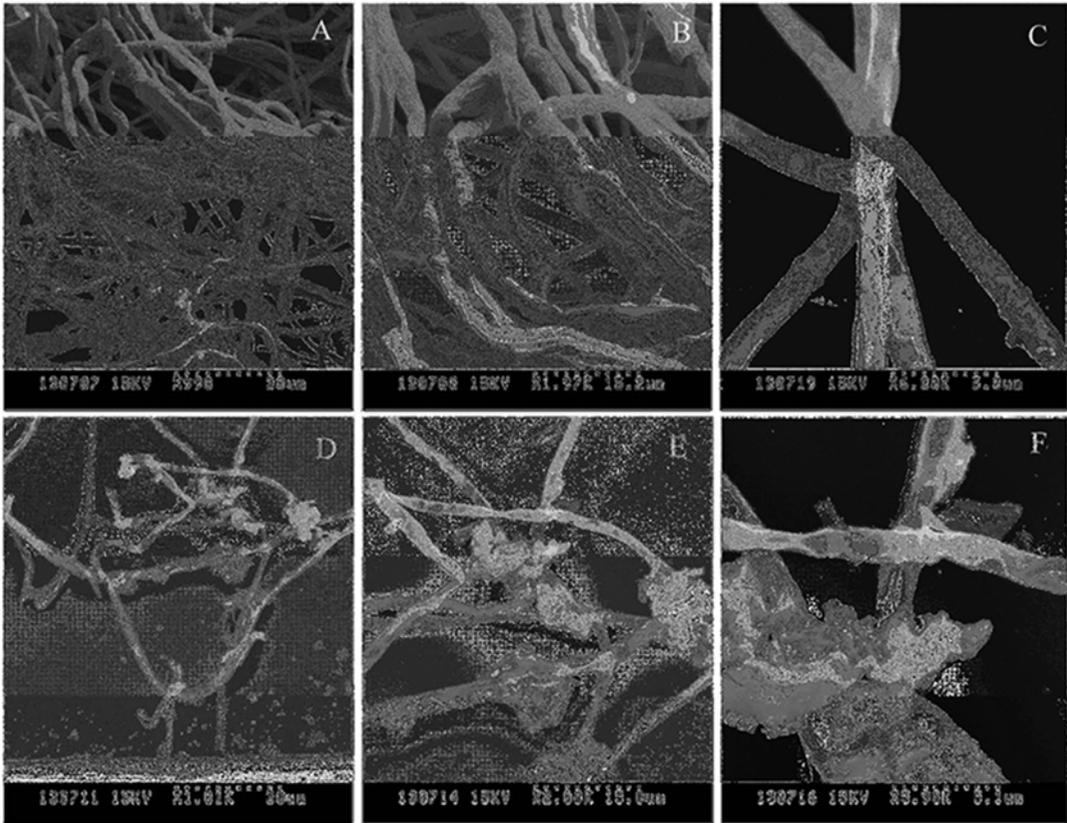


Fig. 3.3 Scanning electron microscope analysis of antagonistic bacteria interacting with hyphae of pathogens on PDA medium on the fifth day after incubation at

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.

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