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Review

Potential use of rhizobium for vegetable crops growth promotion

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The system of vegetable crops production required large amounts of mineral fertilizers. One of the possible alternatives to assure the economic and environmental sustainability of this production system would be the use of promoting growth plant rhizobacteria (PGPR). However, care is needed to select a microorganism to be used in crops that are usually consumed raw, so human health is not at risk. It was important to search for PGPR, as rhizobium, that already were broadly used as inoculants for leguminous plants for several decades, without risks to human health. PGPR can promote growth and development of plants through direct and indirect mechanisms, by production and secretion of chemical substances in the rhizosphere. The direct mechanisms were involved with the uptake of nutrients by the plants (nitrogen, phosphorus and essential minerals) through phosphate solubilization, production of siderophores and growth regulators. The indirect mechanisms were involved with the decrease of inhibitory effects from various pathogenic agents related with biological pest control, thereby favoring plant growth. Nevertheless, due to its ability to promote beneficial effects to plants, effective bacterial colonization was extremely important. Some bacteria that colonized the rhizoplane may penetrate the plant roots and some strains may move to the aerial part, with decreased bacterial density, compared with colonizing populations in the rhizosphere or roots. It can be concluded that Rhizobia promotes plant growth using different mechanisms as biological nitrogen fixation and production of different plant growth regulators (e.g. auxins). Therefore, new studies with Rhizobia characterization and observation about its different mechanisms of promoting plant growth should be performed. Such information would be useful for the identification of plants with potential to increase agricultural production due to the benefits of using plant growth promoter's rhizobia.

Key words: Growth promotion, vegetable crops, rhizobacteria, growth regulators.

INTRODUCTION

Rhizobium as plant growth promoters

Bacteria capable of colonizing the rhizosphere or plant roots and also assist direct or indirectly the crop growth and development are called promoting growth plant rhizobacteria (PGPR) (Kloepper et al., 1980; Abbasi et al., 2011). These rhizobacteria have the ability to stimulate crop growth through enrichment of soil nutrients,

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such as biological nitrogen fixation, phosphate solubilization, siderophores production and growth regulators. Furthermore, they may act as a biological control, producing defense substances for the plant, as cellulase, protease, lipase and β-1,3 glucanase (Ahmed et al., 2009; Bulgarelli et al., 2013; Gopalakrishnan et al., 2015).

In the search for a more sustainable agricultural production, the pant-rhizobacteria interactions are important when related to nutrients transformation, mobilization and solubilization, so the plant may absorb nutrients that would otherwise be unavailable for its development (Hayat et al., 2010; Gopalakrishnan et al., 2015). Agricultural production sustainability is based on biological approaches for enhancement of agricultural production, seeking alternatives to reduce fertilizers. Rhizobacteria may be an alternative for assisting cultivars growth and protection.

Several studies are being conducted with the objective of investigating the potential for rhizobacteria to promote plant growth through substances that regulate growth, tolerance of these bacteria to agrochemicals, abiotic stress, among others (Ahamad and Khan, 2012; GurURANI et al., 2013; Gopalakrishnan et al., 2015). However, most of the studies with plant growth promoting bacteria is related to the *Enterobacter*, *Burkholderia*, and *Bacillus* species. Although there are promising results with the use of rhizobium for growth promotion in several crop species as rice, wheat and corn (Hahn, 2013; Osório Filho, 2014), the mechanisms involved in those processes are not yet fully understood. Findings on the use of rhizobium for plant growth broaden the perspectives for its use on diverse agricultural systems and on the different crop species. Initially, when the term rhizobacteria was introduced, it was destined to non-symbiotic bacteria present in the rhizosphere with the ability to colonize the radicular system and favor plant growth (Kloepper and Schroth, 1978).

With the advances of studies on the plant-microbe interactions, new concepts were established. This includes bacteria that establish symbiotic relationships with the plant, in the group of the so called intracellular PGPR (iPGPR), which live inside of the root cells, form nodules and live in specialized structures. These new concepts also include bacteria that develops in the rhizosphere, rhizoplane or intercellular space, without the formation of nodules, but capable of crop growth promotion through the production of specific substances, which is the group called extracellular PGPR (ePGPR) (Gray and Smith, 2005).

Among the intracellular PGPR, the most studied are the rhizobium with leguminous plants symbiosis (Gray and Smith, 2005), and among the extracellular PGPR are the bacteria from the *Bacillus* and *Pseudomonas* genera (HarTEMAN et al., 2010; Rocha and Moura, 2013). There are, however, rhizobacteria that can stablish both in the interior and exterior of cells, belonging to both groups, that is, *Burkholderia* (Gray and Smith, 2005). The best studied example is the beneficial interaction between rhizobium and plants from the Fabaceae family (leguminous), and they are the most used agricultural inoculants in the world. In symbiosis, the rhizobium grows using the carbohydrates supplied by the host plant, and in exchange, provides fixed nitrogen for amino acid biosynthesis (Brencic and Winans, 2005; Gray and Smith, 2005). This symbiosis is an example of the intimal relationship between a soil bacteria and its host plant, and illustrates the concept of iPGPR for soils with nitrogen deficiency. Bacteria convert atmospheric nitrogen (N_2) to ammonia (NH_3), thus promoting leguminous plant growth through the supply of this nutrient (Van Loon, 2007). However, rizhobium may also be classified as ePGPR when associated with non-leguminous plants, being able to accommodate between the spaces among the plant cells or in the rhizosphere, on the roots surface. As such, they stimulate plant growth through several ways, such as: growth regulators production, phosphate solubilization, siderophores production, and more (Moreira et al., 2010; Garcia-Fraile et al., 2012; Flores-Félix et al., 2013).

MECHANISMS OF PLANT GROWTH PROMOTION

Plant-microbe interactions may affect the growth of the crops by direct or indirect mechanisms (Glick, 2012). Among the direct mechanisms, are the biological fixation of nitrogen (BFN); plant growth regulators production such as indolacetic acid (IAA), gibberellins, cytokinins and ethylene; phosphate solubilization; and siderophores production.

Biological nitrogen fixation

Microorganisms capable of atmospheric nitrogen fixation are called diazotrofic and are classified as: symbionts, e.g. rhizobium that establish relationships with leguminous plants or *Frankia* that establishes relationship with non-leguminous plants, free-living, associative and endophytic, as *Azospirillum, Azotobacter* and cyanobacteria (*Anabaena, Nostoc*) (Ahemad and Khan, 2012; Bhattacharyya and Jha, 2012).

Biological fixation of nitrogen (BFN) is the process by which the diazotrofic microorganisms in the soil convert atmospheric N_2 into NH_3, which is the form the plants can assimilate. This process is accomplished through an enzymatic complex called nitrogenase (Zehr et al., 2003; Stefan et al., 2008; Bulgarelli et al., 2013). Through BFN, the nitrogenated compounds are readily available to plants, by associative relations, or released to the environment, by the decomposition of the bacterial biomass (Lindermann and Glover, 2003; Gopalakrishnan et al., 2015).

The symbiotic relationship between rhizobium and leguminous plants is able to fix approximately 460 kg of nitrogen per year (Bulgarelli et al., 2013). Several studies have demonstrated the importance of BFN by rhizobium, not only because of the benefits for leguminous plants, but also through mixed intercropping, benefiting the species to be planted after the leguminous cultivar (Castro et al., 2004; Hayat et al., 2008). Several free-living bacteria, either associative and/or endophytic, promote the growth of several plants by BFN, that is, bacteria from the *Azospirillum, Burkholderia, Herbaspirillum, Klebsiella, Enterobacter,* and *Citrobacter* genera *(*James et al., 2000; Kennedy et al., 2004; Gholami et al., 2009).

Production of substances that regulate crop growth

Plant growth regulators are chemical compounds that influence and promote the growth and development of plants. The main classes are: auxins, cytokinins, gibberellins, abscisic acid and ethylene (Santner and EstELLE, 2009). Among the auxins, indolacetic acid (IAA) is the most abundant one and it is involved with several cellular processes and processes of crop growth and development. It is also the most physiological active auxin on crops and it is the focus of studies related with promoting growth plant rhizobacteria (Bulgarelli et al., 2013).

Several studies have demonstrated the involvement of rhizobacteria in the biosynthesis of IAA, both in culture and in the soil (Hameed et al., 2004; Khalid et al., 2004; Thakuria et al., 2004). One of the direct effects of IAA producing rhizobacteria is the proliferation of secondary rooting and radicular hairs, enhancing the nutrient absorption by the plants associated with these bacteria and, therefore, improving crop growth and development (Biswas et al., 200; Lambrecht et al., 2000; Machado, 2011).

The ability to produce indolacetic acid is one of the most studied mechanisms in the promotion of plant growth by rhizobacteria, and approximately 80% of bacteria isolated in the rhizosphere can produce IAA. Several studies have demonstrated that most rhizobium is able to produce IAA. It is involved with the processes of cell division and differentiation, which are essential for the nodule formation, when in symbiosis with the leguminous species (Ahemad and Khan, 2012; Hahn, 2013; Osório Filho, 2014; Machado, 2015).

Another growth regulator produced by PGPR are gibberellins, that were named after the compounds excreted from the fungus *Giberella fujikuroi*, which triggered exaggerated growth on rice plant height and suppressed the production of seeds. The first isolated compound from the fungus culture was called gibberellic acid (GA3), which is responsible for stem growth due to the stimuli that the gibberellins promote on cellular elongation rates and division (Taiz and Zeiger, 2013). On the other hand, gibberellins are never present in tissues with total lack of auxins, and the effects of gibberellins on growth might also depend on the acidification of the environment by auxins. Application of gibberellins is also responsible for parthenocarpy in fruits, by increasing the fruit size and the number of buttons and seed germination, more specifically over the production of α-amylase in the aleurone layer of cereals (Camili, 2007; Taiz and Zeiger, 2013). Gibberellins help in seeds germination, as is the case for lettuce and cereal, and control of flowering and sexual expression of flowers. Many PGPR are described as producing gibberellins (Dobbelaere et al., 2003), including *Rhizobium*, *Sinorhizobiu meliloti* (Boiero et al., 2007).

In the literature, few are the studies about the production of cytokinins by plant growth promoting bacteria. Ortiz-Castro et al. (2008) studied cytokinin signaling in the promotion of crop growth by *Bacillus megaterim*, and found that cytokinin receptors play a complementary role on crop growth promotion. This growth regulator has great capacity to promote cellular division, participating in the process of elongation and cellular differentiation, especially when interacting with auxins (Taiz and Zeiger, 2013).

Ethylene is a growth regulator produced by all plants, and is essential for proper growth and development. When in stressful situations, as drought, salinity, flooding, trace elements, and pathogens, the plant significantly increases production of this growth regulator, triggered by its defense response (Saleem et al., 2007; Bhattacharyya and Jha, 2012). But if the stress persists, the severe increase in ethylene concentration by the plant will trigger senescence processes, chlorosis and abscission, leading to inhibitory effects on growth and development (Stearns and Glick, 2005).

In relation to growth promotion involving ethylene, several studies have been made with bacteria capable to promote plant growth, related to the synthesis of the enzyme ACC (1-aminociclopropano-1-carboxilato) deaminase, which hydrolyses ACC, an immediate precursor of ethylene. Since high concentrations of ethylene act on radicular growth inhibition and senescence, ACC-deaminase regulates the levels of ethylene in order to assist the plant in its growth and development (Onofre-Lemus et al., 2009).

Rhizobacteria capable of producing the enzyme ACC deaminase belong to several genera, as *Bacillus, Burkholderia,* and *Rhizobium*, among others (Zahir et al., 2008; Onofre-Lemus et al., 2009; Kang et al., 2010). These bacteria associated with plants help regulate ethylene levels, acting as ACC sinks, reducing the deleterious effects of ethylene and promoting plant growth. The main effects of plant inoculation with ACC deaminase-producing rhizobacteria are increase in seed germination rates, radicular growth stimulation, enhancement in nutrient absorption, as nitrogen, phosphorus and potassium, and increase in nodulation on rhizobium (Zafar-Ul-Hye et al., 2007; Glick, 2012).

Phosphate solubilization

Phosphorus is the second limiting nutrient for vegetable growth after nitrogen, and is abundant in the soil both on organic and inorganic forms. However, in most soils this element is in low availability to plants, since they can only absorb it in the forms of the soluble ions $H_2PO_4^-$ and HPO_4^{-2} (Khan et al., 2009; Bhattacharyya and Jha, 2012). The search for strategies to enhance the availability of this mineral to plants can significantly improve crop growth and productivity, since the fraction of phosphorus that is available for plants is relatively low in soils (5% of total phosphorus) (Dobbelaere et al., 2003).

The use of microorganisms that solubilize phosphate may assist or substitute the use of phosphate fertilizers in agriculture (Khan et al., 2006). The mechanism used by bacteria to solubilize inorganic phosphorus is through the production of organic acids, while the mineralization of organic phosphorus is through the production of several phosphatases that result in the release of phosphoric acids (Bulgarelli et al., 2013; Glick, 2012). Rhizobacteria as *Rhizobium, Bacillus* and *Pseudomonas*, are efficient in the process of solubilization of inorganic phosphate, making it available for the plants. Studies show the positive effect of inoculation with bacteria that solubilize phosphate on the promotion of plant growth (Marra et al., 2011; Ahemad and Khan, 2012; VikRAM and Hamzehzarghani, 2008).

Production of siderophores

Iron, as well as phosphorus, is an abundant element in soil, but, due to the low solubility of iron oxides, little is available for plants (Rajkumar et al., 2010). Thus, plants need to use strategies to increase Fe availability through either the release of protons in order to reduce the pH of the soil and increase Fe, or the release of a Fe chelating agent, as siderophores, which will bind Fe, so it can be absorbed by the plant roots (Jeong and Guerinot, 2009).

Rhizobacteria, as well as plants, have the ability to produce iron chelating molecules, called siderophores, when there is low availability of Fe for their development. The release of siderophores by the rhizosphere bacteria assists the crop growth, inhibiting the proliferation of pathogens in the roots, due to the competition for Fe in the soil (Dobbelaere et al., 2003; Bulgarelli et al., 2013). Plants have the capacity to absorb the bacterial Fe-siderophores complex, and, once inside the plant, the Fe unbounds from the siderophore and this molecule is then recycled or destroyed (Rajkumar et al., 2010).

In studies with the plant *Arabidopsis thaliana*, it was found the presence of Fe-pyoverdines, a siderophore synthesized by *Pseudomonas fluorescens*, and an increase in Fe content inside the plant and also an increase in crop growth (Vansuyt et al., 2007).

Rhizobacteria also act on biological control by reducing fungus diseases in the plants, and thus promoting plant growth (Dey et al., 2004).

Sequestration and transport of iron on plant cells through siderophores from rhizobium is one of the ways to provide iron to the plants when in conditions of low iron availability in the environment. Several strains of rhizobium can synthesize siderophores, that will bind Fe^{3+}, reduce it to Fe^{2+}, making it available for the plant (Carson et al., 2000; Arora et al., 2001).

INDIRECT MECHANISMS

The main indirect mechanism of crop growth promotion is related to the use of rhizobacteria as agents of biological control against plant pathogens, by induction of resistance and production of antifungal substances. Many PGPR are capable of producing antifungal metabolites, as hydrogen cyanide and enzymes, such as chitinases and glucanases, that degrade the fungal cell wall (Persello-Cartieaux et al., 2003).

The interaction between plants and rhizobacteria stimulates crops to acquire resistance against some pathogenic microorganisms, as bacteria, fungi and viruses. This process is known as induced systemic resistance (ISR), which is caused by the release of some bacterial molecules that activate promoting genes of defensive compounds in the plant (Lugtenberg and Kamilova, 2009).

Strains of *Bacillus*, when used as a biocontrol agent against phytopathogens, use this mechanism of production of antibiotic substances (Kokalisburelle et al., 2006). *P. fluorescens* are bacteria known by the suppression of pathogenic fungi in the soil, by producing antifungal metabolites and releasing siderophores, by making the iron unavailable to the pathogens in the roots (Dwivedi and Johri, 2003). Several species of *Bacillus* and *Pseudomonas* are used in biologic control, such as in tomato plants when inoculated with bacteria from these genera, which leads to a reduction of wither symptoms caused by *Ralstonia solanacearum* and *Fusarium oxysporum f. sp. lycopersici* (Rocha and Moura, 2013).

Besides acting on control of bacteria, fungi and viruses, PGPR may also act on the control of nematodes. In studies with watermelon and melon, inoculation of rhizobacteria decreased nematode attacks to these plants (Kokalis-Burelle et al., 2003). In rice seeds inoculated with PGPR, the control of *Meloidogyne graminicola* associated with growth promotion in plants was found (Souza Junior et al., 2010).

BACTERIAL COLONIZATION

Colonization of plant roots by beneficial rhizobacteria is one important step towards interactions between plant and bacteria. However, it is a complex process that is influenced by several biotic and abiotic factors, such as quantity of bacteria and root exudation (Benizri et al., 2001). The success of root colonization by rhizobacteria, as its persistence in the rhizosphere, is a fundamental factor for exerting the beneficial effects to the plants. A minimal bacterial density is necessary for the establishment of the molecular, biochemical and physiological mechanisms of plant-microbe interaction, and this concept is called *quorum sensing* (QS) (Williams, 2007; Sanchez-Contreras et al., 2007).

The mechanism of QS depends on synthesis and release of chemical signals by the bacteria in the environment, and detection of these signals, as a function of the cellular population density (Camilli and Bassler, 2006). Such group behavior results in alteration of genetic expression, which drives the activity of the microorganisms in a coordinated manner (Williams, 2007). Among the chemical signs released, the more common used by Gram-negative bacteria are called homoserine lactones, originally called *N*-acyl homoserine lactones (AHLs). Biosynthesis and effects of self-inducers like AHLs rely especially on the activity of a protein family of LuxI and LuxR. After the AHLs are produced by AHL synthases enzymes, they spread across bacterial membranes and accumulate until they reach higher concentrations. In a certain concentration threshold (approximately 10 nM), AHL binds to the gene LuxR, forming a complex that regulates gene expression (Hanzelka and Greenberg, 1995).

Communication via *quorum sensing* by AHLs in rhizobium affects its metabolic and physiologic processes, including mobility, exopolysaccharide synthesis, biofilm formation, production of virulence factors, plasmid transfer, efficiency in root nodulation and efficiency of nitrogen fixation (González and Marketon, 2003; Sanchez-Contreras et al., 2007; Pierson and Pierson, 2007). Studies with rhizobacteria of the genus *Pseudomonas* tagged with fluorescent genes found that, as a consequence of the radicular colonization by these bacteria, there was an increase in the biosynthesis of siderophores, growth regulators, antibiotics and hydrolases (Compant et al., 2010).

CONCLUSION AND RECOMMENDATION

In the search for a more sustainable agricultural production, the interactions between plants and rhizobacteria are important for the plant to absorb nutrients that otherwise would be unavailable for its development. Rhizobium is already used for leguminous plants, with excellent results because of its ability to fix atmospheric nitrogen. They may act as growth promoters in oleraceous plants because they have direct and indirect mechanisms of plant growth promotion. Since most studies involving growth promoting bacteria for oleraceous plants are with the *Pseudomonas* and *Bacillu*s genera, it is important to seek other genera and species.

In the current literature, there are very few studies using rhizobium as growth promoters for oleraceous plants. However, there are various rhizobium species that need to be explored, as well as species and variety of crops, in which the effect of inoculation is poorly studied. Therefore, new studies with Rhizobia characterization and observation about its different mechanisms of promoting plant growth should be performed. Such information would be useful for the identification of plants with potential to increase agricultural production due to the benefits of using plant growth promoter’s rhizobia.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

REFERENCES

Abbasi MK, Sharif S, Kazmi M, Sultan T, Aslam M (2011). Isolation of plant growth promoting rhizobacteria from wheat rhizosphere and their effect on improving growth, yield and nutrient uptake of plants. Plant Biosystems 145:159-168.

Ahemad M, Khan MS (2012). Effects of pesticides on plant growth promoting traits of Mesorhizobium strain MRC4. Journal of the Saudi Society of Agricultural Sciences 11:63-71. Ahemad M, Khan MS (2012). Productivity of greengram intebuconazole-stressed soil, by using a tolerant and plant growth promoting Bradyrhizobium spp. MRM6 strain. Acta Physiol Planta 34:245-254.

Ahemad M, Khan MS, Zaidi A, Wani PA (2009). Remediation of herbicides contaminated soil using microbes. In: Khan, M.S.; Zaidi, A, Musarrat, J. (Eds.), Microbes in Sustainable Agriculture. New York: Nova Science Publisher.

Arora NK, Kang SC, Maheshwari DK (2001). Isolation of siderophore producing strains of *Rhizobium meliloti* and their biocontrol potential against *Macrophomina phaseolina* that causes charcoal rot of groundnut. Current Science 81:673-677.

Benizri E, Baudoin E, Guckert A (2001). Root colonization by inoculated plant growth promoting rhizobacteria. Biocontrol Science and Technology 11(5):557-574.

Bhattacharyya PN, Jha DK (2012). Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World Journal of Microbiology and Biotechnology 28:1327-1350.

Biswas JC, Ladha JK, Dazzo FB, Yanni YG, Rolfe BG (2000). Rhizobial inoculation influences seedling vigor and yield of rice. Agronomy Journal 92:880-886.

Boiero L, Perrig D, Masciarelli O, Penna C, Cassán F, Luna V (2007). Phytohormone production by three strains of *Bradyrhizobium japonicum* and possible physiological and technological implications. Applied Microbiology and Biotechnology 74:874-880.

Brencic A, Winans SC (2005). Detection of and response to signals in host-microbe interactions by plant-associated bacteria. Microbiology and Molecular Biology Reviews 69(1):155-94.

Bulgarelli D, Schlaeppi K, Spaepen S, Ver Loren van Themaat E, Schulze-Lefert P (2013). Structure and functions of the bacterial microbiota of plants. Annual Review of Plant Biology 64:807-838.

Camili EC (2007). Ação de biorreguladores na brotação, produção e algumas características físico-químicas de uva do cultivar superior seedless. Thesis (Doctorate in Agronomy)- Universidade Estadual Paulista, Botucatu.

Camilli A, Bassler BL (2006). Bacterial small-molecule signaling pathways. Science 311:1113-1116.

Carson KC, Meyer JM, Dilworth MJ (2000). Hydroxamate siderophores of root nodule bacteria. Soil Biology and Biochemistry 32:11-21.

Castro CM, Alves BJR, Almeida DL, Ribeiro RLD (2004). Adubação verde como fonte de nitrogênio para a cultura da berinjela em sistema orgânico. Pesquisa Agropecuária Brasileira 39(8):779-785.

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 Biology and Biochemistry 42:669-678.

Dey R, Pal KK, Bhatt DM, Chauhan SM (2004). Growth promotion and yield enhancement of peanut (*Arachis hypogaea* L) by application of plant growth promoting rhizobacteria. Microbiological Research 159:371-394.

Dobbelaere S, Vanderleyden J, Okon Y (2003). Plant growth promoting effects of diazotrophs in the rhizosphere. Critical Reviews in Plant Sciences 22:107149.

Dwivedi D, Johri BN (2003). Antifungals from fluorescent pseudomonads: biosynthesis and regulation. Current Science 12:1693-1703.

Flores-Felix JD, Lina EM, Marcos-García M, Martínez-Hidalgo P, Mateos PF, Martínez-Molina E, Velázquez ME, García-Fraile P, Rivas R (2013). Use of *Rhizobium leguminosarum* as a potential biofertilizer for *Lactuca sativa* and *Daucus carota* crops. Journal of Plant Nutrition and Soil Science 176:876-882.

Garcia-Fraile P, Carro L, Robledo M, Ramírez-Bahena MH, Flores-Felix JD, Fernández MT, Mateos PF, Rivas R, Igual JM, Martínez- Molina E, Peix A, Velázquez E (2012). Rhizobium Promotes Non-Legumes Growth and Quality in Several Production Steps: Towards a Biofertilization of Edible Raw Vegetables Healthy for Humans. Plos One 7:1-7.

Gholami A, Shahsavani S, Nezarat S (2009). The effect of plant growth promoting rizobacteria (PGPR) on germination, seedling growth and yield of maize. International Journal of Biological Life Sciences 1:35-40.

Glick BR (2005). Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiology Letters 251:1-7.

Glick BR (2012). Plant growth-promoting bacteria: mechanisms and applications. Hindawi Publishing Corporation pp. 1-15.

González JE, Marketon MM (2003). Quorum sensing in nitrogen-fixing rhizobia. Microbiology and Molecular Biology Reviews 67:574-592.

Gopalakrishnan S, Srinivas V, Alekhya G, Prakash B, Kudapa H, Rathore A, Varshney RK (2015). The extent of grain yield and plant growth enhancement by plant growth-promoting broad-spectrum Streptomyces sp. in chickpea. SpringerPlus 4:31.

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

Gururani MA, Upadhyaya CP, Baskar V, Venkatesh J, Nookaraju A, Park SW(2013). Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in Solanum tuberosum through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance. Journal of Plant Growth Regulation 32:245-258.

Hahn L, Sá ELS, Machado RG, Silva WR, Oldra S, Damasceno RG, Schönhofen A(2014). Growth promotion in maize with diazotrophic bacteria in succession with ryegrass and white clover. American and Eurasian Journal of Agriculture and Environmental Science 14(1):11-16.

Hameed S, Yasmin S, Malik KA, Zafar Y (2004). Rhizobium, Bradyrhizobium and Agrobacterium strain isolated from cultivated legumes. Biology and Fertility of Soils 39:179-185.

Hanzelka BL, Greenberg EP (1995). Evidence that the N-terminal region of the Vibrio fischeri LuxR protein constitutes an autoinducer-binding domain. Journal of Bacteriolog 177:815-817.

Hayat R, Ali S, Amara U, Khalid R, Ahmed (2010). Soil beneficial bacteria and their role in plant growth promotion: a review. Annals Microbiology 60:579-598.

James EK, Gyaneshwar P, Barraquio WL, Mathan N, Ladha JK (2000). Endophytic diazotrophs associated with rice. In: Ladha, J.K, Reddy, P.M. (Eds.), The quest for nitrogen fixation in rice. Los Banõs: International Rice Research Institute pp. 119-140.

Jeong J, Guerinot ML (2009). Homing in on iron homeostasis in plants. Trends of Plant Science 14:280-285.

Kang BG, Kim, WT, Yun HS, Chang SC (2010). Use of plant growth-promoting rhizobacteria to control stress responses of plant roots. Plant Biotechnology Reports 4:179-183.

Kennedy IR, Choudhury ATMA, Kecskés ML (2004). Non-symbiotic bacterial diazotrophs in crop-farming systems: can their potential for plant growth promotion be better exploited. Soil Biology and Biochemistry 3:1229-1244.

Khalid A, Arshad M, Zahir ZA (2004). Screening plant growth promoting rhizobacteria for improving growth and yield of wheat. Journal of Applied Microbiology 96:473-480.

Khan MS, Zaidi A, Wani PA (2006). Role of phosphate solubilizing microorganisms in sustainable agriculture - a review. Agronomy for Sustainable Development 27:29-43.

Khan MS, Zaidi A, Wani PA, Oves M (2009). Role of plant growth promoting rhizobacteria in the remediation of metal contaminated soils. Environmental Chemistry Letters 7:1-19.

Kloepper JW, Schroth MN (1978). Plant growth-promoting rhizobacteria on radishes. In: Proceedings of the 4th International Conference on Plant Pathogenic Bacteria. Angers: INRA, 2:879-882.

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

Kokalis-Burelle N, Vayrina CS, Reddy MS, Kloepper JW (2003). Amendment of muskmelon and watermelon transplant media with plant growth promoting rhizobacteria: effects on disease and nematode resistance. Horticultural Technology 13:476-48.

Lambrecht M, Okon Y, Vande Broek A, Vanderleyden J (2000). Indole-3-acetic acid: a reciprocal signaling molecule in bacteria-plant interations. Trends in Microbiology 8:298-300.

LinDermann C, Glover CR (2003). Nitrogen fixation by legumes. College of Agriculture, Consumer and Environmental Sciences. Guide A-129, 4 p.

Lugtenberg B, Kamilova F (2009). Plant-growth-promoting rhizobacteria. Annual Review of Microbiology 63:541-556.

Machado RG (2011). Promoção de Crescimento em Gramíneas Forrageiras por Rizóbios Isolados de Lotus Corniculatus. Dissertação de Mestrado. Universidade Federal do rio Grande do Sul. Porto Alegre 70 p.

Machado RG (2015).Seleção de Bactérias Promotoras de Crescimento de Plantas Forrageiras. Tese de Doutorado. Universidade Federal do rio Grande do Sul. Porto Alegre 123 p.

Marra LM (2011). Solubilisation of inorganic phosphates by inoculant strains from tropical legumes. Scientia Agricola 68(5):603-609.

Miransari M, Smith DL (2009). Rhizobial lipo-chitooligosaccharides and gibberellins enhance barley (*Hoedum vulgare* L.) seed germination. Biotechnology 8:270-275.

Onofre-Lemus J, Hernández-Lucas I, Girard L, Caballero-Mellado J (2009). ACC (1-aminocyclopropane-1- carboxylate) deaminase activity, a widespread trait in Burkholderia species, and its growth promoting effect on tomato plants. Applied and Environmental Microbiology 75:6581-6590.

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

Osorio Filho BD, Gano KA, Binz A, Lima RF, Aguilar LM, Ramirez A, Caballero-Mellado J, Sá ELS, Giondo A (2014). Rhizobia enhance growth in rice plants under flooding conditions. American and Eurasian Journal of Agriculture and Environmental Science 14(8):707-718.

Persello-Cartieaux F, Nussaume L, Robaglia C (2003). Tales from the underground: molecular plant-rhizobacteria interactions. Plant, Cell and Environment 26:189-199.

Pierson LS, Pierson EA (2007). Roles of diffusible signals in communication among plant-associated bacteria. Phytopathology, 97:227-232.

Rajkumar M, Ae N, Prasad MN, Freitas H (2010). Potential of siderophoreproducing bacteria for improving heavy metal phytoextraction. Trends in Biotechnology 28:142-149.

Rocha DJA, Moura AB (2013). Controle biológico da murcha do tomateiro causada por *Ralstonia solanacearum* e *Fusarium oxysporum* f. sp. *lycopersici* por rizobactérias. Tropical Plant Pathology 38:423-430.

Rubio LM, Ludden PW (2008). Biosynthesis of the iron-molybdenum cofactor of nitrogenase. Annual Review of Microbiology 62:93-111.

Saleem M, Arshad M, Hussain S, Bhatti AS (2007). Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. Journal of Industrial Microbiology and Biotechnology 34:635-648.

Sanchez-Contreras M, Bauer WD, Gao M, Robinson JB, Downiel JA (2007). Quorum-sesing regulation in rhizobia and its role in symbiotic interactions with legumes. Philosophical Transactions – The Royal Society Biological Sciences, 362:1149-1163.

Santner A, Estelle M (2009). Recent advances and emerging trends in plant hormone signalling. Nature 459:1071-78.

Souza Júnior IT, Moura AB, Schafer JT, Corrêa BO, Gomes CB (2010).Biocontrole da queima-das-bainhas e do nematoide-das-galhas e promoção de crescimento de plantas de arroz por rizobactérias. Pesquisa Agropecuária Brasileira 45:1259-1267.

Stearns JC, Glick BR (2003). Transgenic plants with altered ethylene biosynthesis or perception. Biotechnology Advances 21:193-210.

Stefan M, Marius M, Dunca S (2008). Plant growth promoting Rhizobacteria can inhibit the in vitro germination of Glycine Max L. seeds. Scientific Annals of "Alexandru Ioan Cuza" University Iasi, Section Genetics and Molecular Biology 3:105-110.

Taiz L, Zeiger E (2013). Fisiologia Vegetal. 5. ed. Porto Alegre: ArtMed 954 p.

Thakuria D, Talukdar NC, Goswami C, Hazarika S, Boro RC, Khan MR (2004). Characterization and screening of bacteria from rhizosphere of rice grown in acidic soils of Assam. Current Science 86:978-985.

Van Loon LC (2007). Plant responses to plant growth-promoting rhizobacteria. European Journal of Plant Pathology 119:243-254.

Vansuyt G, Robin A, Briat JF, Curie C, Lemanceau P (2007). Iron acquisition from Fe-pyoverdine by *Arabidopsis thaliana*. Molecular Plant Microbe Interactions 20:441-447.

Vikram A, Hamzehzarghani H (2008). Effect of phosphate solubilizing bacteria on nodulation and growth parameters of greengram (*Vigna radiate* L. Wilczec). Research Jounal of Microbiology 3:62-72.

Williams P (2007). Quorum sensing, communication and cross-kingdom signalling in the bacterial world. Microbiology 153:3923-3938.

Zafar-Ul-Hye M, Zahir ZA, Shahzad SM, Naveed M, Arshad M, Khalid M (2007). Preliminary screening of rhizobacteria containing ACC-deaminase for promoting growth of lentil seedlings under axenic conditions. Pakistan Journal of Botany 39:1725-1738.

Zahir ZA, Munir A, Asghar HN, Shaharoona B, Arshad M (2008). Effectiveness of rhizobacteria containing ACC deaminase for growth promotion of peas (*Pisum sativum*) under drought conditions. Journal of Microbiology and Biotechnology 18:958-963.

Zehr JP, Jenkins BD, Short SM, Steward GF (2005). Nitrogenase gene diversity and microbial community structure: a cross-system comparison. Environmental Microbiology 5:539-554.