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Review

Plant growth promoting rhizobacteria: Beneficial effects for healthy and sustainable agriculture

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It is unanimously admitted that the chemical fertilizers and pesticides used in modern agriculture create a real environmental and public health problems. One of the promising solutions to substitute these agrochemicals products is the use of bio-resources, including plant growth promoting rhizobacteria (PGPR). The PGPR focused more and more scientific attention in recent decades. These rhizospheric bacteria colonize actively the root system of plants and improve their growth and yield. The PGPR use different mechanisms of action to promote plant growth. These mechanisms were grouped into three clusters according to the PGPR effects on plant physiology. These groups are as follow: (i) biofertilization including biological fixation of atmospheric nitrogen, phosphate solubilization, siderophores production and exopolysaccharides production; (ii) phytostimulation including production of indole acetic acid, gibberellins, cytokinins and ethylene; and (ii) biocontrol including induction of systemic resistance, competition for iron, nutrient and space, production of antibiotics, lytic enzymes, hydrogen cyanide and volatile compounds. In view of the latest advances in PGPR biotechnology, this paper proposes to do the review on PGPR in rhizosphere and describes the different mechanisms used by PGPR to promote the plants growth and health. In prospect to a healthy and sustainable agriculture, respectful of environment, the PGPR approach revealed as one of the best alternatives.

Key words: Rhizosphere, plant growth promoting rhizobacteria (PGPR), root colonization, biofertilization, biocontrol, biostimulation, interaction plant-microorganisms, sustainable agriculture.

INTRODUCTION

The galloping growth of world population estimated around 7 billion people and may reach 8 billion by 2020 (Glick, 2012), generates several problems including food insecurity and famine. So it is urgent to double the agricultural production in order to reduce the risk of malnutrition and increased poverty (Soulé et al., 2008). In response to this, new seeds varieties of high-yield were introduced into agricultural production systems in several countries. The use of these new varieties is accompanied by a growing and excessive use of chemical fertilizers and pesticides. Although the use of these chemical products has many advantages such as the ease to

handle and convincing results, they generate the environmental and public health problems. Among these problems, (i) groundwater and crop products contamination by heavy metals from the use of these agricultural inputs, (ii) interruption of the natural ecological cycle of nutrients, (iii) destruction of the soil biological communities, and (iv) physical and chemical deterioration of agricultural soils, can be mentioned. Indeed, the prolonged use of mineral fertilizers without addition of organic matter leads to the poor soils in organic matter, more sensitive to wind and rain erosion (Alalaoui, 2007). Koo et al. (2009) asserted that heavy metals contamination of groundwater and crop products is one of the major causes of the cancer occurrence.

The growing necessity to protect our natural resources, invites to a more restrictive use of fertilizers, pesticides and herbicides from chemical origin. Thus, in order to reduce or change the agrochemical used products and institute sustainable agriculture, respectful of the environment, the use of bio-resources such as plant growth promoting rhizobacteria (PGPR) focuses more and more on the scientific attention.

Indeed, Hiltner (1904), a German researcher has firstly defined the rhizosphere as soil area surrounding the root, directly or indirectly influenced by root and which has a strong microbial activity. The rhizosphere contains different groups of microorganisms such as the fungi, algae, nematodes, actinomycetes, protozoa and bacteria. The group of bacteria is subdivided into three subgroups (neutral, negative or positive) according to their effects on the plant physiology. Thus, PGPR is a group of bacteria capable to actively colonize the plant root system and improve their growth and yield (Wu et al., 2005). The term PGPR was proposed for the first time by Kloepper et al. (1980) and was used specifically for the fluorescent *Pseudomonas* involved in the biological control of pathogens and enhancing plant growth. Later Kapulnik (1981) extended this term to the rhizobacteria capable to promote directly plant growth. Today, the term PGPR is used to refer to all rhizospheric bacteria capable to improve the plant growth by one or more mechanisms (Haghighi et al., 2011). This reviewed article presents the PGPR in rhizosphere and describes the different mechanisms used by PGPR to promote the plants growth and health.

RHIZOSPHERE

According to the foremost definition given by the German scientist, Hiltner L., rhizosphere refers to the soil area surrounding a plant's root, directly or indirectly influenced by the root and which has a strong microbial activity (Hiltner, 1904). The term of rhizosphere comes etymologically from *rhiza* (root) and *sphera* (surroundings). The rhizosphere is subdivided into three separate parts (Figure 1). The first part (Exorhizosphere) corresponds to soil adherent to the root and remains attached to it after vigorous shaking. The second part (Rhizoplane) corresponds to interface soil/root and finally the third part (Endorhizosphere) is the intercellular space between the root tissues inhabited by endophyte bacteria, which does not form symbiotic structures (Bowen and Rovira, 1999).

This particular environment is the seat of important and intense interactions between plant, soil and various associated microorganisms (Nihorimbere et al., 2011; Lemanceau et al., 2006). Several biochemical interactions between plants and soil microorganisms have been reported by Pinton et al. (2007). The biological and physico-chemical characteristics of the rhizosphere depend largely on the nature of the various compounds released by the plant root (exudates) in rhizosphere. The process to excrete the exudates is called rhizodeposition. The roots secrete at the apex a mucilage constituted of carbohydrate polymers that the primary function is to protect root against desiccation (Bais et al., 2006). The root exudates are transported through the cell membrane and excreted in the rhizosphere. The composition and concentration of exudates are strongly influenced by the following factors: plant species, stage of development and plant nutrition, soil type and environmental conditions (temperature, soil water potential and light intensity) (Kochian et al., 2005). The root exudates effects depend on their ability to disseminate as far as possible from rhizoplane (Gupta and Mukerji, 2002).

The rhizosphere is very rich in nutrients such as sugars, amino acids, organic acids, hormones (Badri et al., 2009), nucleotides, fatty acids, sterols, growth factors, enzymes, flavonoids and other small molecules from the plant root exudates. These compounds serve many functions and they pose a significant carbon cost for the plant. The microorganisms found in this medium, require energy for their metabolism. The root exudates will also condition the diversity and density of microorganisms in the rhizosphere. The root exudates can attract beneficial and pathogenic microorganisms as well.

RHIZOSPHERIC MICROFLORA

Rhizosphere is the zone of a few millimeters around the plants root system (Compant et al., 2010), contains a sizeable microbial population (about 10^8-10^9 CFU/g of soil) (Schoenborn et al., 2004). The rhizospheric microflora is naturally made of a complex assembly of prokaryotic and eukaryotic microorganisms (Cardon and

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Gage, 2006). It constitutes of bacteria, fungi, algae, nematodes, actinomycetes and protozoa. The microbial structure of rhizosphere varies according to the plant species, stages of development and soil type (Broeckling et al., 2008). Proteobacteria and Actinobacteria are the microorganisms most frequently found in the rhizosphere of several plant species (Singh et al., 2007). The density and structure of rhizospheric microbial communities (Kowalchuk et al., 2010; Latour et al., 2009) and their metabolic activity (Nannipieri et al., 2008) are significantly different from those of bare soil. Through the root exudates, the plant can limit and/or guide the rhizosphere colonization and create its microbial community. Thus, the microbial population (diversity and load) of rhizosphere depends partly to the quantity and quality of exudates (microorganisms-exudates affinity), but also to microbial interactions (Somers et al., 2004).

RHIZOBACTERIA

Among the microbial community of rhizosphere, bacteria (rhizobacteria) are the most known (95%) and the most abundant because of their high growth rate and ability to use different carbon and nitrogen sources (Glick, 2012). The rhizobacteria concentration in the rhizosphere can reach 10^{12} CFU/g of soil (Foster, 1988). However, in the soils of stressed ecosystem, the load of rhizobacteria may be less than 10^{4} CFU/g of soil (Timmusk et al., 2011).

These rhizobacteria can affect the plants physiology through different ways. Thus, the interactions between rhizobacteria and plant can be beneficial, harmful or neutral (Ordookhani and Zare, 2011). The presence of neutral rhizobacteria in the rhizosphere has probably no effect on plant health. In opposite, phytopathogenic rhizobacteria (*Desulfovibrio*, *Erwinia*, *Agrobacterium*, *Enterobacter* and *Chromobacter*, etc.) affect negatively the plant growth, whereas the beneficial rhizobacteria (*Azospirillum*, *Pseudomonas*, *Bacillus,* etc.) affect positively plant growth and yield through various mechanisms of action. The beneficial rhizobacteria are known under the name 'PGPR'.

PLANT GROWTH PROMOTING RHIZOBACTERIA (PGPR)

PGPR are a group of bacteria capable to actively colonize the plants root system and improve their growth and yield (Wu et al., 2005). They colonize all ecological niches of root to all stages of plant development, even in the presence of a competing microflora. PGPR represent about 2 to 5% of total rhizospheric bacteria (Antoun and Kloepper, 2001). The term PGPR was proposed by Kloepper et al. (1980) and has been used for a long time, especially for fluorescent *Pseudomonas* involved in the pathogens biological control and enhancing plant growth. Later, Kapulnik et al. (1981) extended this term to the rhizobacteria capable to directly promote plant growth. Today, the term of PGPR is used to refer to all bacteria living in the rhizosphere and improve plant growth through one or more mechanisms (Haghighi et al., 2011). A wide range of species belonging to the genus *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus* and *Serratia* was reported as PGPR (Saharan and Nehra, 2011).

The PGPR effects depend on ecological and soil factors, plant species, plant age, development phase and soil type (Werner, 2001). For example, a bacterium which promotes plant growth through nitrogen fixation or phosphorus solubilization (compounds often present at low dose in many soils), certainly not produce beneficial effects to the plant when the soil receives chemical fertilizers. Also, the mutant bacterium *Pseudomonas fluorescens* BSP53a, hyper producing indole acetic acid (IAA) and stimulating root development of blackcurrant (*Ribes nigrum* L.) inhibits root development of Cherry (*Prunus avium* L.) (Dubeikovsky et al., 1993).

MECHANISMS OF ACTION USED BY PGPR TO PROMOTE PLANT GROWTH AND HEALTH

Current knowledge of mechanisms used by PGPR although this is not yet completely elucidated, it is possible to classify them into three groups (Biofertilization, Phytostimulation and Biocontrol) according to the PGPR effects on plant physiology (Table 1).

Root colonization

Root colonization is an essential step in the biological control of pathogens and in the improvement of plants growth by PGPR. The fundamental elements for efficient colonization include the ability of microorganisms to survive after inoculation, to grow in spermosphere (region surrounding the seed) in response to exudates production by seed, to fix on surface of the first roots, and to colonize the entire root system (Nelson, 2004). Especially for endophilic microorganisms, the root colonization includes four steps: (i) attraction, (ii) root recognition, (iii) root adhesion and (iv) root invasion (Nihorimbere et al., 2011). These steps are influenced by biotic and abiotic factors.

Indeed, the seeds colonization is the first step in the root colonization process. The microorganisms that are established on the seeds during the germination can grow and colonize the roots along their length from where they emerge and grow in the soil. Seed colonization during soaking phase has a significant effect on plant growth. Through the markers utilization, Trivedi et al.

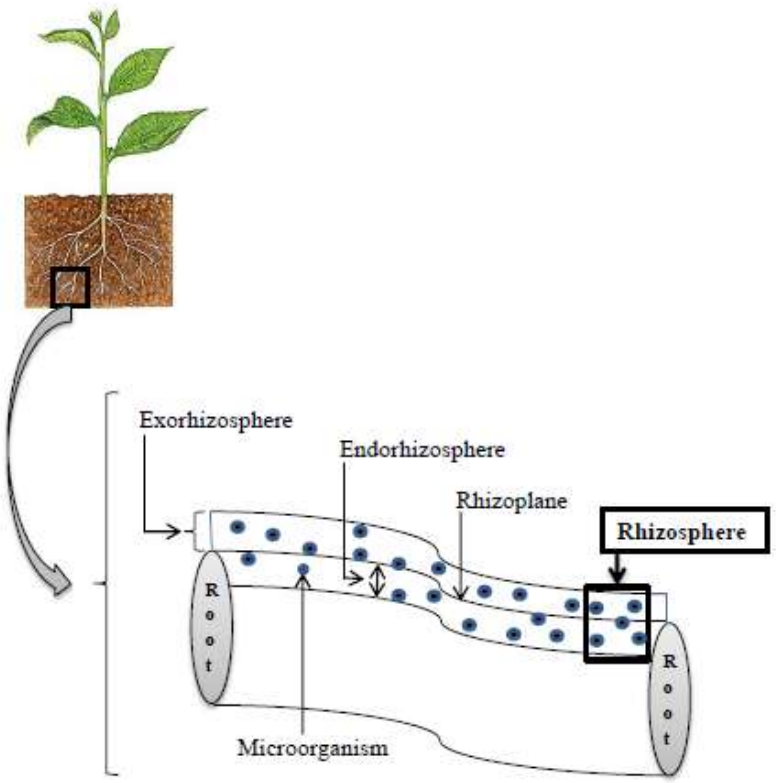

Figure 1. Schematic representation of rhizosphere.

Table 1. Mechanisms used by PGPR to promote plant health and growth;

Functions	Mechanisms	References
Biofertilization	Phosphate solubilization	Yazdani et al. (2009)
	Siderophores production	Vansuyt et al. (2007)
	Exopolysaccharides production	Sandhya et al. (2009)
	Biofixation of atmospheric nitrogen	Weyens et al. (2010)
Phytostimulation	Ethylene production	Glick et al. (2007)
	Cytokinins production	Kang et al. (2009)
	Gibberellins production	Kang et al. (2009)
	Indole Acetic Acid production	Ashrafuzzaman et al. (2009)
Control of pathogens	Antibiotics production	Ongena et al. (2005)
	Lytic enzymes production	Joshi et al. (2012)
	Hydrogen cyanide production	Lanteigne et al. (2012)
	Volatile compounds production	Trivedi et al. (2008)
	Induction of systemic resistance	Doornbos et al. (2012)
	Competition for Iron, nutrient and space	Innerebner et al. (2011)

(2005) showed that rhizobacteria that have promoted the tea growth (*Bacillus subtilis, Bacillus megaterium, and Pseudomonas corrugata*) are those that effectively colonized their root system. These bacteria have greatly colonized the maize rhizosphere (Trivedi and Pandey, 2008).

Biofertilization

The improvement of soil fertility is one of the strategies commonly used to increase agricultural production. PGPR participates in soil fertilization through the biofixation and biosolubilization process.

Biofixation of atmospheric nitrogen

Nitrogen is the main limiting nutrient for plant growth (Munees and Mulugeta, 2014; Chapin and Aerts, 2000). It is the fourth important element of plant dry mass. Nitrogen is an essential constituent of nucleotides, membrane lipids and amino acids (enzymatic and structural proteins) (Marschner, 1995). The most part of this element is in gaseous form (N_2) inaccessible to animals and plants (Pujic and Normand, 2009). The biological fixation of atmospheric nitrogen is an important microbial activity for the maintenance of life on the earth through photosynthesis performed by photosynthetic organisms. About 175 million tons of atmospheric nitrogen are reintroduced annually in life cycle through the biological fixation.

The biological nitrogen fixation is limited to prokaryotes that possess (unlike plant) an enzymatic complex (the dinitrogenase) which catalyses the reduction of atmospheric nitrogen into ammonia ($N_2 + 4H_2 \quad 2NH_3 + H_2$) (Weyens et al., 2010). Nitrogen-fixing bacteria include both free rhizospheric prokaryotic (e.g. *Achromobacter*, *Acetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, *Rhodospirillum*, *Rhodopseudomonas* and *Xanthobacter*) (Tilak et al., 2005) and symbiotic rhizospheric prokaryotes that fix nitrogen only in association with certain plants. This latter group comprises rhizobia (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium* and *Allorhizobium*) associated with leguminous plants and *Frankia* strains, filamentous sporulating bacteria associated with Actinorhizal plants (Gray and Smith, 2005).

Several studies showed that the co-inoculation of *Bradyrhizobium* and PGPR can positively influence the symbiotic nitrogen fixation through the increase of nodules number, nodule dry weight, seed yield, nutrients availability and improvement of nitrogenase activity (Son et al., 2006).

As previously announced, certain non-symbiotic bacteria are also capable to fix atmospheric nitrogen that will be transferred to plants (Bashan and Levanony, 1990). The discovery of nitrogen fixation by non-symbiotic bacteria was made by Beijerinck (1901). However, it is unanimously accepted that non-symbiotic bacteria fix less nitrogen than symbiotic bacteria (James and Olivares, 1997). Despite their low nitrogen fixation power, some PGPR are very effective. The inoculation of several cultures with diazotroph PGPR especially *Azotobacter* and *Azospirillum* has improved the yield of annual and perennial grasses (Tilak et al, 2001). The wheat inoculation with *Azotobacter* has increased their yield of 30% (Gholami et al., 2009; Kloepper and Beauchamp, 1992).

Under normal conditions, the fixing microorganisms benefit from the nitrogen without excretion of nitrogen compounds. But at their death and after decomposition, nitrogen is available to plants providing an average of 25 kg $Nha^{-1}year^{-1}$ at the continents. In most ecosystems and through this process, the fixing microorganisms participate to accumulation of nitrogen compounds over time (Vitousek et al., 2002). This process is then sufficient to maintain the stock of nitrogen compounds in the ecosystem and to restore the losses.

Phosphate solubilization

Phosphorus is a second mineral element after nitrogen that the deficiency crucially limits plant growth (Nisha et al., 2014). Phosphorus represents about 0.2% of plant dry weight and is an essential constituent of nucleic acids, phytin and phospholipids. Phosphorus plays a major role in photosynthesis, respiration, storage and transfer of energy and cell division and elongation (Sagervanshi et al., 2012). It is essential for seed formation which contains the highest phosphorus content of the plant.

The plant absorbs the phosphorus in mono and dibasic ($H_2PO_4^-$, HPO_4^{2-}) soluble forms (Keneni et al., 2010; Ramos Solano et al., 2008). Unfortunately, the great proportion of soil phosphorus (about 95-99%) is in the form of insoluble inorganic phosphates (apatite) or insoluble organic phosphates (inositol phosphate, phosphomonesters and phosphotriesters) unassimilated by the plant (Pérez-Montano et al., 2014; Khan et al., 2007). Phosphorus (highly reactive) is immobilized by precipitation with cations Ca^{2+} and Mg^{2+} in alkaline soils and with Fe^{3+} and Al^{3+} in acid soils (Hesham and El-Komy, 2005). Thus, when applied to an agricultural soil, the soluble inorganic phosphate, the great proportion of this phosphate is rapidly immobilized after application and becomes unavailable to the plant (Vikram and Hamzehzarghani, 2008).

Fortunately, some PGPR possess the ability to solubilize the soil insoluble phosphate in order to make available to the plant. These PGPR are referred by the acronym "Phosphate Solubilizing Bacteria, PSB". The PSB group contains the genus *Pseudomonas*, *Azospirillum*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Arthrobacter*, *Alcaligenes*, *Serratia*, *Enterobacter*, *Acinetobacter*, *Azotobacter*, *Flavobacterium* and *Erwinia* (Zaidi et al., 2009). *Pseudomonas* and *Azospirillum* species isolated from the pepper (*Piper nigrum L*.) rhizosphere have a strong ability to dissolve phosphate under *in vitro* condition (Ramachandran et al., 2007).

PSB make the solubilizing effect through the production of organic acids such as formic acid, propionic acid, lactic acid, glycolic acid, fumaric acid, succinic acid (Vazquez et al., 2000), gluconic acid, 2-ketogluconic, oxalic acid, citric acid, acetic acid and malic acid (Zaidi et al., 2009). These acids reduce the soil pH and cause the dissolution of insoluble phosphate. During the solubilization of rock phosphate by microorganisms, Venkateswarlu et al. (1984) observed a reduction of pH from 7 to 3. The study conducted by Wahyudi et al. (2011), revealed that all *Bacillus* isolates which have significantly improved the soybean (*Glycine max*) growth were able to solubilize the phosphate excepted CR67 isolate.

PSB are also able to mineralize the insoluble organic phosphate through the excretion of extracellular enzymes such as phosphatases (catalysts of the hydrolysis of phosphoric esters), phytases and C-P lyases (Weyens et al., 2010). It should be noted that this two mechanisms (solubilization and mineralization) can coexist within the same PBS (Tao et al., 2008). Several authors have reported the yield increase of Tea (*Camellia sinensis* L.) (Chakraborty et al., 2006), soybean (Abd-Alla, 2001), alfalfa (Medicago *sativa* L.) (Rodríguez, 1999), wheat (*Triticum aestivum* L.) (Whitelaw et al., 1997) and onion (*Allium Cepa*) (Vassilev et al., 1997) by PSB inoculation. The application of phosphate solubilizing microorganisms can reduce phosphorus application to 50% without affecting the maize seeds yield (Yazdani et al., 2009). Thus, the plants inoculation with PSB increases the availability of phosphorus in the rhizosphere and its absorption by the plant.

Iron chelation (siderophores production)

Iron is essential to the functioning of living organisms. It is essential for all life form because it is involved in diverse and essential biological functions. It is the cofactor of many enzymes involved in the electron transfer (mitochondrial respiration) or oxygen transfer (hemoglobin), and in the deactivation of radical oxygen (catalases, peroxidases) (Ganz, 2003). Iron is the fourth most abundant element in ground rock. Unfortunately, this huge quantity of iron is in the ferric ions form (Fe^{3+}) very little assimilated by living organisms (bacteria, plants, etc.) (Ammari and Mengel, 2006). To overcome this difficulty and provide iron to the plant, rhizobacteria have developed various iron uptake strategies to survive and to adapt to their environment. One of these strategies is the production of siderophores.

Siderophores are the molecules of low molecular weight (400 to 1500 Da), having an exceptional affinity for Fe^{3+} (Ka ranging from 10^{23} to 10^{52}) and membrane receptors capable of binding the complex Fe-siderophores in order to facilitate the iron absorption by micro-organisms and plant (Hider and Kong, 2010). They are used in fertilizer formulations for regulation of iron intake in plants, and thus facilitate its growth (Miller and Malouin,1994). Siderophores are produced by a wide variety of microorganisms (bacteria and fungi) and some plants (phyto-siderophores of grasses) (Van der Helm and Winkelmann, 1994). *Agrobacterium*, *Bacillus*, *Escherichia coli*, *Pseudomonas*, *Rhizobium* and many fungi are capable to produce these iron chelating compounds (Zahir et al., 2004).

According to the chemical function involved in the iron chelation, the siderophores are classified into three classes: phenol/catechol, hydroxamate and hydroxycarboxylique acid. Today, more than 500 siderophores are known and the chemical structures of 270 of them were determined (Hider and Kong, 2010).

Several studies have shown the beneficial effects of bacterial siderophores on improving of plant growth. Robin et al. (2008), using the iron-siderophore complex radioactive as the only source of iron, showed that plants are able to absorb the radioactive iron. The iron-pyoverdin synthesized by *P. fluorescens* C7 tested on *Arabidopsis thaliana* plants, has increased the iron level inside the plants and improved their growth (Vansuyt et al.,2007).The siderophores are also involved in chelation of other rhizosphere metals having a low availability to plants such as zinc and lead (Dimkpa et al., 2009).

Extracellular polysaccharides production

The ability to produce polysaccharides is one of the many benefits of rhizobacteria in promoting plant growth. These polysaccharides include structural polysaccharides, intracellular polysaccharides and extracellular polysaccharides (exopolysaccharides, EPS). The main contribution of rhizospheric microorganisms to soil stability is associated to the EPS production. These are in the form of hydrated gels around the cells. They constitute the interface between the microorganisms and their immediate environment. In the rhizosphere, EPS produced by rhizobacteria, enter aggregate soil and alter its porosity (Alami et al., 2000). Thus, the porosity of the soil, which is directly related to soil water transferred to the roots, is partly controlled by bacterial activity. EPS bacterial products on the surface of roots also help maintain the film of water required for the photosynthetic activity and growth of plants. Sandhya et al. (2009) argue that EPS participate in the formation of bacterial aggregates and consequently improve soil aeration, water infiltration and root growth. EPS cover and protect the roots against attacks by pathogenic microorganisms. They are used as delete molecules in plant defense mechanisms against pathogens.

In salt stress condition, the EPS chelate cations available in the root zone, thus contributing to reduce the salinity of the rhizosphere. The bacterial EPS in conditions of water stress in the soil can limit or delay the middle of desiccation. Conversely, in case of excess water (rain, floods), EPS contribute to avoid dispersion of

soils clayey (Henao and Mazeau, 2009).

Phytostimulation

Phytohormones are chemical messengers that influence the ability of plants to respond to their environment. They are organic compounds which are generally effective at very low concentrations. Botanists recognize five main groups of plant hormones: (i) Auxins (ii) Gibberellins, (iii) Ethylene, (iv) Cytokinins, and (v) abscisic acid. Only the first four are involved in the phytostimulation by rhizobacteria.

Indole acetic acid production

Auxin (from the Greek "auxien", which means "increase") is the first plant hormone discovered by Darwin (1880) in canary seed (*Phalaris canariensis*). Therefore, auxin was isolated from several other plants. Indole Acetic Acid (IAA) includes the plant hormones belonging to auxin group. IAA is a molecule signal, involving in the regulation of plant development, specifically in organogenesis, cell division, cell differentiation and genes regulation (Ryu and Patten, 2008).

Although the plant is able to synthesize the IAA, it responds positively to an IAA exogenous supply, at certain stages of its development cycle (Khalid et al., 2006). The stimulation of plants growth by rhizobacteria is often associated with their ability to produce IAA (Patten and Glick, 2002). Shobha and Kumudini (2012) reported that several species of *Bacillus* spp., *Pseudomonas* species, *Azotobacter* species, *Azospirillium* species, *Phosphobacteria* species, *Glucanoacetobacter* species, *Aspergillus* species and *Penicillium niger* can produce IAA. The production of IAA by PGPR depends on species and strains and is also influenced by the culture conditions, stage of development and availability of substrates in the rhizosphere (Ashrafuzzaman et al., 2009). It has been reported that the wheat inoculation with *Azotobacter* and *Bacillus* has increased its seeds yield of 30 and 43% respectively. This increase due to the production of certain growth hormones such as IAA (Kloepper et al., 1991).

The microbial production of IAA makes several metabolic pathways (Persello-Cartieaux et al., 2003). Although some pathways independent of tryptophan have been identified in some microorganisms, tryptophan remains the most common and major precursor of IAA biosynthesis by microorganisms. The four main metabolic pathways dependent of tryptophan are: tryptophol, tryptamine, indole-3-pyruvic acid and indole-3-acetamide pathway (Bartel, 1997). Gravel et al. (2007) have shown that the rhizobacteria *Pseudomonas putida* and *Trichoderma atroviride* synthesized *in vitro* IAA in the presence of L-tryptophan. When these researchers inoculated tomato plants with previous rhizobacteria in addition with several concentrations of L-tryptophan, they found that the higher concentration of L-tryptophan increased more than tomato plants developed. Let note that the tryptophan is naturally excreted by the tomato plant through the root exudates. Thus, the majority of auxins found in the tomato rhizosphere come from the microbial biosynthesis (Kamilova et al., 2006). Several studies have shown that some microorganisms produce low quantity of auxins in the absence of L-Tryptophan become strong producing of auxins in the presence of L-tryptophan (Zahir et al., 2004). Zahir et al. (2010) observed an increase up to 8 times auxin production by *Rhizobium* strains after addition of L-tryptophan to the culture medium.

The plant response to IAA addition varies according to plant species, IAA concentration, complexity of tissue and stage of plant development (Glick, 2012). IAA is strongly involved in the tomatoes fruition especially during fruit setting and its final development phase (Srivastava and Handa, 2005). It has been shown by Xie et al. (1996) that the synthesis of great quantity of IAA by rhizobacteria inhibits the development of the plant root system. Indeed, the root level of endogenous IAA can be suboptimal or optimal for plant growth (Pilet and Saugy, l987). Through the additional effect, the exogenous IAA (produced by rhizobacteria) brings the IAA levels of plant to optimum or supra optimal (Glick, 2012). In the first case, there has been an improvement of the plant growth due to the induction of a better development of the root system (initialization of root elongation and cell division), which improves the plant nutrition through a more absorption of water and nutrient. In the second case, a root inhibition will be observed. Thus, the bacterial IAA can have an inhibitory effect on root growth from a certain concentrations. Tanimoto (2005) says that the development of the root system can be greatly affected by external sources of growth regulators.

Spaepen et al. (2007) affirmed that the IAA plays a very important role in root elongation and root hairs proliferation. San Francisco et al. (2005) showed that the application of exogenous IAA increases the phosphorus level in roots of Pepper plants under hydroponic conditions. Moreover, Patten and Glick (2002) also reported that low levels of IAA can stimulate root elongation, while optimal levels of biosynthesized IAA stimulate the lateral and adventitious roots formation.

Gibberellins and cytokinins production

Rhizobacteria have the capacity to produce phyto-hormones cytokinins and gibberellins (Van Loon, 2007). The evaluation of ability to produce plant hormones of 24 *Streptomyces* strains in broth medium, revealed that all strains synthesized cytokinins and gibberellins (Mansour et al., 1994). The improvement of plant growth by some PGPR producing cytokinins or gibberellins was reported (Kang et al., 2009). The mechanisms used by cytokinins and gibberellins synthesized by rhizobacteria to promote plant growth are still not well understood. The assumptions

so far are based on the conventional knowledge on the role of cytokinins and gibberellins in the plant physiology and those relating to the plant response to the addition of purified hormones. Among other effects, cytokinins and gibberellins are involved in plant morphology modifying and in the stimulation of development of the plant aerial part (Van Loon, 2007).

Ethylene regulation

Ethylene is one of the small bioactive molecules known as a plants growth inhibitor. At low concentrations, ethylene can promote the growth of several plant species, including *Arabidopsis* (Pierik et al., 2006) by the stimulation of seed germination, initiation of root growth, fruit ripening and activation of other phytohormones synthesis. However, the moderate or high levels of ethylene induced the inhibition of root elongation, *Rhizobium* species nodulation and plant-mycorrhiza interactions, the wilting flowers, the falling leaves, and disruption of plant response to biotic and abiotic stress (Abeles et al., 1992). Thus, the elevation of ethylene concentration (> 25 µg/L) under stress conditions caused by heavy metals (Belimov et al., 2005), pathogens (Wang et al., 2000), drought (Mayak et al., 2004a), salinity (Mayak et al., 2004b) and organic contaminants (Reed and Glick, 2005) induces the inhibition of hair formation and root elongation and therefore a reduced vegetable growth.

The decrease of the high levels of ethylene in the plant can be performed through the degradation of its direct precursor 1-aminocyclopropane-1-carboxylic acid (ACC) using the ACC-deaminase enzyme. This enzyme is expressed in several rhizobacteria (e.g. *Alcaligenes* species, *Bacillus pumilus*, *Burkholderia cepacia*, *Enterobacter cloacae*, *Methylobacterium fujisawaense*, *Ralstonia solanacearum*, *Pseudomonas* spp. and *Variovorax paradoxus*). These rhizobacteria through the ACC-deaminase can degrade plant ACC to α-ketobutyrate and ammonium (Glick et al., 2007). The consequence of this degradation is the reduction of ethylene produced by the plant. Through this mechanism, the PGPR producing ACC-deaminase regulates the ethylene level in the plant and prevents the growth inhibition caused by high levels of ethylene.

BIOCONTROL OF SOIL-BORNE PHYTOPATHOGENIC MICROORGANISMS

PGPR involved in the biological control of soil-born phytopathogenic organisms through certain mechanisms such as: production of antagonistic metabolites (antibiotics, lytic enzymes, hydrogen cyanide, volatile compounds and siderophores), induction of systemic resistance and nutrients and space competition. In study conducted by Noumavo et al. (2015), *Streptomyces hygroscopicus*, *Ectocarpus fasciculatus*, *Pseudomonas aeruginosa*, *P. putida*, *P. fluorescens* and *Azospirillum lipoferum* inhibited mycelial growth of *Fusarium verticillioides* and *Aspergillus ochraceus* pathogens of maize plants. *P. fluorescens* and *P. aeruginosa* were highly antagonistic against *F. verticillioides* (52.24% of mycelial growth inhibition) and *A. ochraceus* (58.33% of mycelial growth inhibition).

Antibiotic production

The antibiosis is probably the best known and perhaps the most important mechanism used by PGPR to limit the pathogens invasion in the plant tissue. It consists to inhibit the development of plant pathogenic microorganisms through the production of secondary metabolites of low molecular weight, possessing antifungal and/or antibiotics properties. *Bacillus*, *Streptomyces*, and *Stenotrophomonas* strains produce a wide range of potent antifungal metabolites such as oligomycin-A, xanthobaccin (Compant et al., 2005), zwittermicin-A, kanosamine and lipopeptides of the surfactins, iturins and fengycin family (Ongena and Thonart, 2006). *Pseudomonas* strains are known for the production of amphisin, 2,4-diacetylphloroglucinol (DAPG) oomycin-A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and the cyclic lipopeptides (Loper and Gross, 2007). It was recently demonstrated the role of these lipopeptides in protective effect of a particular *B. subtilis* strain against *Pythium ultimum* pathogen of bean plants (Ongena et al., 2005) and against mould gray of apple after harvesting (Touré et al., 2004).

This metabolites production is influenced by abiotic factors (oxygen, moisture, temperature, pH and soil nitrogen, micronutrients and organic matter content), biotic factors (vegetable specie, pathogen organisms, native microflora, and density of strains producing metabolites) and some other.

Lytic enzymes production

Some PGPR strains have the ability to degrade fungal cell walls through the production of hydrolytic enzymes such as chitinases, dehydrogenases, β-glucanases, lipases, phosphatases, proteases, hydrolases, exo and endo-polygalacturonases, pectinolyases and cellulases (Joshi et al., 2012; Whipps, 2001). Various *Pseudomonas* strains showed *in vitro* antifungal activity against three zoospores fungi (Sharma et al., 2009). These authors proved that the antifungal activity is due to the production of rhamnolipid causing the lysis of plasma membrane of zoospores fungi. This PGPR lytic activity allows to protect the plant against biotic stress through the pathogens elimination.

Hydrogen cyanide and volatile compounds production

The antagonistic activity of PGPR also results in the

production of volatile compounds. The best known compound is hydrogen cyanide (HCN). Devi et al. (2007) reported the excretion of HCN by rhizospheric strains. *Pseudomonas* strains producing HCN are used in biological control against bacterial canker of tomato (Lanteigne et al., 2012). *P. corrugata* showed antagonistic activity against *Alternaria alternata* and *Fusarium oxysporum* pathogen microorganisms of several cultures such as maize (Trivedi et al., 2008). This antagonism has been associated with the production of volatile compounds, although *P. corrugata* also produced some hydrolytic enzymes. *Bacillus subtilis* strains isolated from tea, producing volatile antifungal compounds induced structural defects on six pathogenic fungi under *in vitro* culture conditions (Chaurasia et al., 2005). *B. megaterium* inhibits the growth of two plant pathogens *A. alternata* and *F. oxysporum* through the production of volatile compounds (Trivedi and Pandey, 2008).

Induction of systemic resistance

PGPR can trigger the plants inducible defense mechanisms, phenotypically similar to normal defense reaction of plants, when attacked by a pathogen (Pieterse et al., 2009). This phenome non called Induced Systemic Resistance (ISR) can make the plant much stronger hardy against future aggression of pathogens (Van Loon, 2007). This phenomenon of systemic resistance induction by rhizobacteria is considered as a promising strategy for biological control of plant disease (Ramos Solano et al., 2008). The ISR can be induced by a wide range of microorganisms included Gram-positive bacteria such as *B. pumilus*, or Gram-negative bacteria belonging to the genus *Pseudomonas* (*P. fluorescens, P. putida*, *P. aeruginosa*), and enterobacteria such as *Serratia* (*Serratia marcesens*, *Serratia plymuthica*) or *Pantoea agglomerans* (Jourdan et al., 2009). The IRS protects the plants against a large spectrum of pathogens not only fungal, bacterial and viral, but also against certain diseases caused by insects and nematodes (Durrant and Dong, 2004). Several bacterial metabolites can induce an IRS. These metabolites include lipopolysaccharides (LPS), siderophores, cyclic lipopeptides, 2,4-diacetylphloroglucinol, homoserine lactones, and volatile compounds such as acetoin and 2,3-butanediol (Doornbos et al., 2012).

Competition for space, nutrients and iron

Although it is difficult to directly demonstrate, the indirect evidences showed that the competition between pathogens and PGPR may limit the incidence and severity of plant pathology. The rapid and abundant root colonization by PGPR, which occupies the infection sites of plant pathogens and uses most of the available nutrients, makes difficult the development of pathogens. Lemanceau and Heulin (1998) affirmed that high and active microbial biomass reduces the probability of pathogen to infect the plant. This makes the nutrient competition an important mean of biological control (Benitez et al., 2004). Beside the intrinsic growth capacity of PGPR, the other properties enhancing the root colonization are mobility (presence of flagellum), chemotaxis, lipopolysaccharide (LPS), the ability to synthesize vitamins and macromolecules and the capacity to use the compounds excreted by the roots (Lugtenberg and Kamilova, 2009). In a series of experiments, researchers have shown that the treatment of tomato leaves with *Pseudomonas syringae* pv. prevented *Sphingomonas* species to cause the disease symptoms (Innerebner et al., 2011).

Another form of competition is established between the pathogens and PGPR. This is the struggle for iron. Indeed, iron is an essential element for the growth and survival of most phytopathogenic fungi. Then, some PGPR synthesize siderophores that chelate iron in the rhizosphere and thus inhibiting the pathogens growth.

CONCLUSION

This paper showed the beneficial effects of PGPR. PGPR improve soil fertility through increase plant nutrients (nitrogen, phosphorus and iron) available in soil. The phytohormones produced by PGPR are assimilated by plant for best growth. Also, PGPR inhibit plant pathogens growth through the production of antagonistic metabolites, induction of systemic resistance and nutrients and space competition. Additionally, PGPR polysaccharides alter soil porosity and consequently improve soil aeration. It is therefore clear that the objectives of chemical fertilizers and pesticides use can be reached with PGPR use. These rhizobacteria are the best alternatives to use of chemical fertilizers and pesticides that generate many problems such as groundwater and crop products contamination by heavy metals from there, interruption of the natural ecological cycle of nutrients, destruction of the soil biological communities and physical and chemical deterioration of agricultural soils. Thus, this technology based on the PGPR use, should be integrated into agricultural production strategies of all countries to a healthy and sustainable agriculture.

Conflict of Interests

The authors have not declared any conflict of interests.

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