Scientific Research and Essays Vol. 7(47), pp. 4003-4013, 3 December, 2012
Available online at http://www.academicjournals.org/SRE
DOI: 10.5897/SRE12.646
ISSN 1992-2248 ©2012 Academic Journals

Review

Ecophysiology of plant growth promoting bacteria

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Accepted 12 October, 2012

Plant growth-promoting rhizobacteria (PGPR), are beneficial bacteria that colonize plant roots and enhance plant growth through a variety of mechanisms that include improvement of plant nutrition, production and regulation of phytohormones, and suppression of disease causing organisms. Whereas members of the bacterial genera *Azospirillum* and *Rhizobium* are well-studied examples for plant growth promotion, *Bacillus*, *Pseudomonas*, *Serratia* and *Stenotrophomonas* are model organisms to demonstrate influence on plant health. Based on their ability to stimulate plant growth, it is possible to develop microbial inoculants for use in agricultural biotechnology. Depending on their mode of action and effects, these products can be used as biofertilizers and biocontrol agents. This application can help to minimize dependence on chemical fertilizers which have adverse effects on the environment. Despite their different mechanisms of action, their use has not been developed to its full potential due to inconsistencies in their performance, and their commercialization has been limited to a few developed countries. The purpose of this review is to give an overview on different mechanisms of action involved in plant-growth promotion.

Key words: Rhizobacteria, mechanisms of actions, plant growth-promoting rhizobacteria (PGPR).

INTRODUCTION

Both aboveground and underground parts of the plants constitute an excellent ecosystem for microbial activity and development (Bonaterra et al., 2003). In the numerous interactions between plants and soil, microorganisms play an integral and unique role in ecosystem functions such as decomposing, mineralizing organic matters and releasing as well as transforming inorganic nutrients. These microorganisms are among the most complex, diverse, and important assemblages in the rhizosphere. The rhizosphere is the soil–plant root interphase and, in practice, consists of the soil adhering to the root besides the loose soil surrounding it (Babalola, 2010a). The concept rhizosphere is also defined as the volume of soil surrounding a plant root in which very important and intensive interactions are taking place between soil, microorganisms, and plant roots. Roots provides an important habitat for bacteria, fungi, and very small soil animals. The rhizoplane is the plant root Surface's strongly adhering soil particles. Often, studies of the microbial ecology of the rhizosphere also include the rhizoplane (Figure 1). In this review, the term rhizosphere will be used to refer to both zones.

In fact, plants secrete both high and low-molecular weight compounds from their roots, termed as root exudates. These compounds may act as signal molecules for microbial attraction or be used as carbon sources for microbial nutrition (Antoun and Prevost, 2006). The role of root exudates as signaling molecules has been recently addressed by Rudrappa and associates, who showed that root-secreted malic acid recruits the beneficial soil bacteria *Bacillus subtilis* to the root and this interaction plays a role in plant protection against the foliar pathogen *Pseudomonas syringae*. The release of carbon compounds from plants into the rhizosphere increases microbial biomass and activity (Bashan and de-Bashan, 2005). In the first step, the bacteria multiply near the root and then adhere to it. This allows the bacteria to colonise and enter the root. The bacteria may enter directly through points on the root surface (Bashan and de-Bashan, 2005; Gnanamanickam, 2006). This method depends on the type of plant. Once

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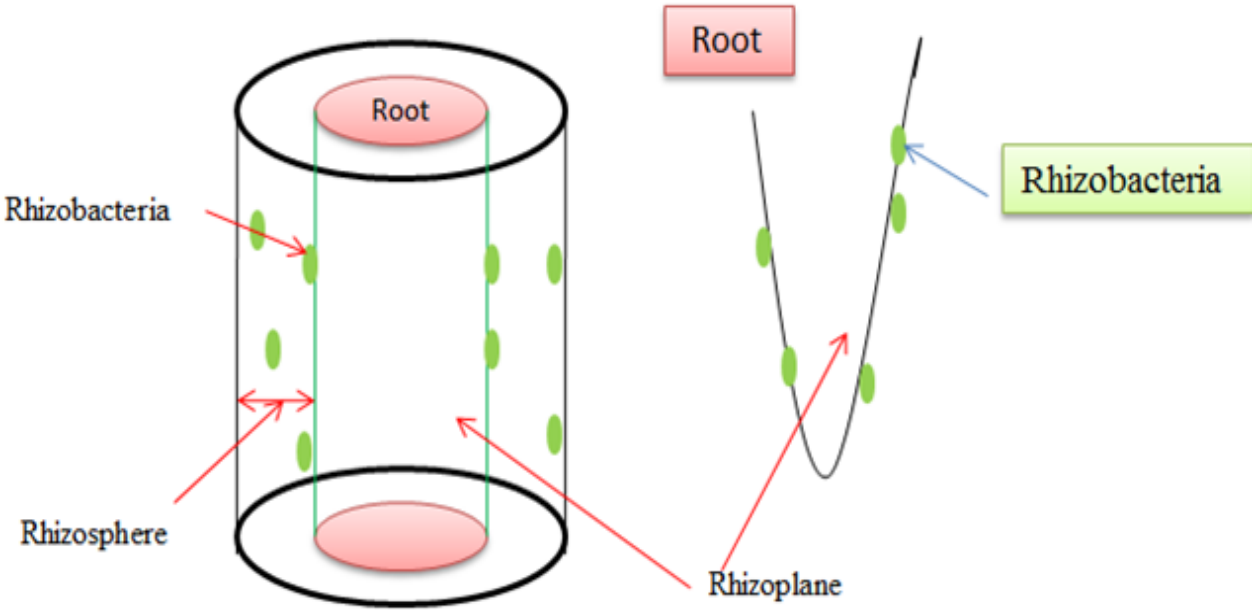

Figure 1. Schematic representation of rhizosphere and rhizoplane modified from Vega (2007).

inside, the bacteria multiply within thin threads. Signals stimulate cell multiplication of both the plant's cells and the bacteria, and this repeated division results in a mass of root cells containing many bacterial cells. This mechanism is most used by fluorescent Pseudomonads due to their nutritional versatility and their rapid growth in the rhizosphere, thereby preventing other bacteria, from reaching the target. Some of these bacteria can change into a form that is able to convert gaseous nitrogen into ammonium nitrogen with the plant host (Lavelle and Spain, 2001). Most of these microorganisms which include bacteria, fungi, protozoa and algae colonise the rhizosphere. Since bacteria are the most abundant among them, they have been classified according to their effects on promoting plant growth and yield and the way they interact with roots, some being pathogenic whereas others trigger beneficial effects (Trivedi and Pandey, 2008; Babalola, 2010a). Among them, *Alcaligenes, Burkholderia*, *Aeromonas*, *Azotobacter*, *Arthrobacter*, *Gluconacetobacter*, *Pseudomonas, Serratia*, *Azoarcus*, *Azospirillum*, *Acinetobacter*, *Klebsiella*, *Bacillus*, *Enterobacter* and *Clostridium* are considered as most important plant growth promoting rhizobacteria (PGPR) because they have beneficial effects on plants directly and indirectly (Figure 2) by enhancing soil fertility (for example, increasing the amount of available nitrogen, and phosphorus and other plant nutrients); synthesizing several different phytohormones such as indole-3-acetic acid (IAA) that can enhance various stages of plant growth; suppressing soil-borne pathogens by the production of hydrogen cyanide, siderophores, antibiotics, and/or competition for nutrients; and improving plant stress tolerance to drought, salinity, and metal toxicity (Table 1). Moreover, some PGPR have the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyses ACC, the immediate precursor of ethylene in plants. In recent years, the concept of PGPR-mediated plant growth promotion is gaining worldwide importance and acceptance (Babalola, 2002; Albino et al., 2006; Gnanamanickam, 2006; Wang et al., 2006; Babalola and Akindolire, 2011; Kucerova et al., 2011). Recently studies have shown that PGPR can be classified into two major groups according to their relationship with the host plants: (1) extracellular PGPR, which exists in the rhizosphere, on the rhizoplane, or in the spaces between cells of the root cortex, and (2) intracellular PGPR, which exist inside root cells, generally in specialized nodular structures (for example, *Bacillus*, *Pseudomonas*, *Azotobacter* etc.) (Babalola, 2002; Thakuria et al., 2004). Beneficial effects of PGPRs have been reported by various workers on a wide range of crops including cereals, pulses, vegetables, oilseeds and plantation crops (Muthuraju and Jaysheela, 2005). Currently, these bacteria are used to sustain agriculture as biofertilizers and biocontrol (Table 2) (Babalola, 2010a). However, an understanding of the basic principles of the function and diversity of microorganisms is necessary before soil microbial technology can be applied in the rhizosphere. The purpose of this review is to give an overview on different mechanisms of action commonly used by PGPR to influence plant growth and health in the natural environment.

DIRECT MECHANISMS OF ACTION

Plant growth-promoting rhizobacteria are associated with many, if not all, plant species and are commonly present

Table 1. Some PGPR and their beneficial effects on plants.

PGPR	Plant species	Effect compared with control	References
Bacillus amyloliquefaciens IN937a and *Bacillus pumilus* T4	*Solanum lycopersicum* L	Bacterium together with reduced amounts of fertilizer promoted tomato growth and increased the uptake of N in tomato	Adesemoye et al. (2010)
Bacillus subtilis	*Arabidopsis thaliana* L	Increased foliar fresh weight	Ryu et al. (2005)
Burkholderia gladioli	*Raphanus sativus* L	Improved the percentage of seed germination under saline conditions	Kaymak et al. (2009)
Pseudomonas aeruginosa	*Abelmoschus esculentus* L; *Lycopersicon esculentum* L; *Amaranthus* sp	Increased growth, early fruiting and increased dry biomass	Adesemoye and Ugoji (2009)
Pseudomonas fluorescens and *Bradyrhizobium* sp	*Origanum majorana* L	Bacteria increased shoot length, shoot weight, number of leaves, number of nodes, and root dry weight, in comparison to control plants or plants treated with other PGPR	Banchio et al. (2008)
Enterobacter sakazakii	*Zea mays* L	Inoculation increased agronomic parameters of maize	Babalola et al. (2003)
Pseudomanas fluorescens biotype G (ACC-5),*Pseudomanas fluorescens* (ACC-14) and *Pseudomonas putida* biotype A (Q-7)	*Pisum sativum* L	Pea improved fresh and dry weight, root length, shoot length, number of leaves per plant and water use efficiency under drought stress	Zahir et al. (2008)
Bacillus M3, *Bacillus* OSU-142 and *Microbacterium* FS01	*Malus domestica* L	Bacterium has the potential to increase yield, growth and nutrition of apple trees	Karlidag et al. (2007)
Pseudomonas sp	*Zea mays* L.	Bacterium caused root elongation in maize	Shaharoona et al. (2006)
Aeromonas hydrophila, *Bacillus insolitus*, *Bacillus* sp.	*Triticum aestivum* L	Increased the dry matter yield of roots, shoots and the mass of rhizosphere soil also increased the rhizosphere soil mass/root mass ratio	Ashraf et al. (2004)
Pseudomonas sp	*Sorghum bicolour* L	Bacterium stimulated *Striga hermonthica* seed germination *in vitro* and in pot	Babalola et al. (2007b)
Citrobacter freundii	*Oryza sativa* L	biofertilizers, comprising strains *Citrobacter freundii* produced a significant increase in rice yield	Nguyen et al. (2003)
Methylobacterium fujisawaense	*Brassica campestris* L	Bacterium promoted root elongation in canola	Madhaiyan et al. (2006)
Pseudomonas aeruginosa and *Serratia liquefaciens*	*Vicia faba* L	Bacteria increased the phytoremediation potential of broad bean plants grown in oily sand	Radwan et al. (2005)
Pseudomonas brassicacearum, P. marginalis, P. oryzihabitan, P. putida, Alcaligenes, xylosoxidans, Bacillus pumilus	*Brassica juncea* L and *Brassica napus* L	Bacteria increased root elongation in cadmium supplemented soil in pot	Belimov et al. (2005)
Enterobacter cloacae	*Brassica napus* L	A significant increase in the root and shoot lengths was observed	Saleh and Glick (2001)
Rhizobium leguminosarum bv. *viciae* 128C53K	*Pisum sativum* L	Bacterium enhanced nodulation in plants	Ma et al. (2003)

Table 2. Plant associated bacteria with biocontrol potential.

Bacteria	Plants species	Effect compared with control	References
Burkholderia cepacia	*Solanum tuberosum* L	Biocontrol agent of *Fusarium* dry rot	Recep et al. (2009)
Burkholderia mallei	*Olea europaea* L	Reduced significantly *in vitro* the fungal growth (Peacock Spot Disease caused by *Cycloconium oleaginum*	Khatib et al. (2010)
Klebsiella oxytoca	*Nicotiana tabacum* L	Induced systemic resistance soft-rot disease pathogen in tobacco	Park et al. (2009)
Klebsiella oxytoca	*Zea mays* L	Stimulation of *Striga* suicidal germination	Babalola and Odhiambo (2008)

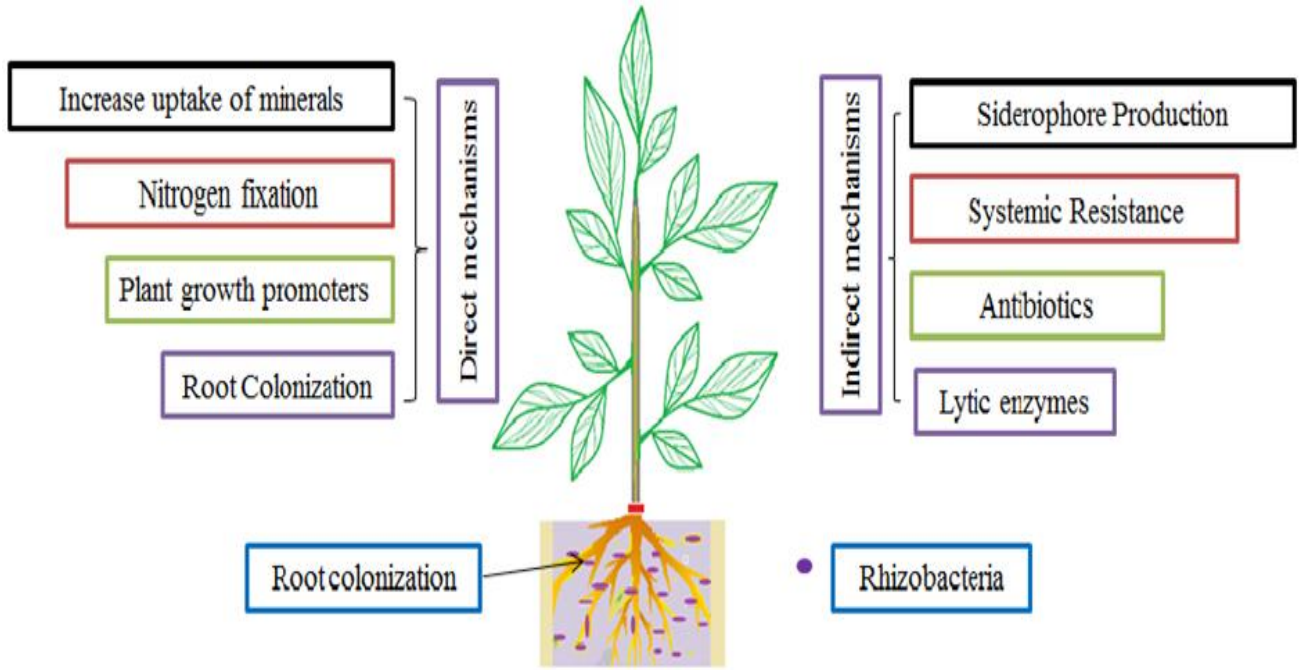

Figure 2. Schematic representation showing direct and indirect mechanisms of plant growth promotion by PGPR.

in many environments. Bacteria that colonize plant roots can function as deleterious or beneficial rhizobacteria. Deleterious bacteria inhibit plant growth while beneficial bacteria PGPR promote the growth of plants. PGPR is the most widely studied group of plant growth promoting bacteria. Beneficial mechanisms by which PGPR enhance plant growth and health are classified into direct and indirect. Direct beneficial mechanisms can be demonstrated by root colonization, production of plant regulators, nitrogen fixation and increasing uptake of minerals (Figure 2).

Root colonization

The dynamics of root colonization by PGPR components of the rhizosphere is basic to the development of the biological control, soil-borne pathogens. Before the expression of their beneficial effects (Table 1), bacteria must be able to colonize and survive in the root surface efficiently. Colonization of the rhizosphere is dependent on various factors such as nature of colonizing organism, composition of root exudates and the PGPR environment (Saleem et al., 2007; Gnanamanickam, 2006).

Distribution of rhizobacteria from the point of inoculation towards the growing roots depends on active motility of bacteria and water flow. The nature of bacteria flagella (through motility), pili, lipopolysaccharides and exopolysaccharides are the most important factors which determine the colonization of the roots by PGPR. Findings by researchers who investigated rhizospheric bacteria such as *Rhizobium*, *Azospirillum* and *Pseudomonas* associated with root mucigel using electron microscopy noticed the presence of fibrillar material surrounding rhizobia attached to the root surface (Fujishige et al., 2006). When plant root colonization of a

strain of *Azospirillum brasilense* was compared with its non-motile mutant the results showed that only the parental strain was able to colonize the roots of the plants near the inoculation point (Benizri et al., 2001). Studies with a fluorescent *Pseudomonas* spp. revealed a positive chemotaxis of the bacteria towards soybean seed or root exudates *in vitro* and in soil (Benizri et al., 2001). The authors observed that the bacterial chemotaxis contributed to adherence of the PGPR to the plant root surface. However, research on spinach roots suggested that water flow plays a capital role in the transport of a PGPR *Pseudomonas* strain to the plant root (Urashima et al., 2004; Babalola, 2010a). The introduced bacteria must be able to grow in a competitive environment with indigenous microorganisms and establish a stable population (Babalola and Glick, 2012). It is important to know that there is a bacterial specificity of colonization according to plant species (Babalola et al., 2007a). For example, different strains of PGPR may colonize one species of plant (For example, maize) at different population densities. Hence, individual PGPR strains may be plant-specific, cultivar-specific or nonspecific for root colonization (Babalola et al., 2007a). After colonization, PGPR strains may interact with the host plant to induce defence mechanisms against pathogens.

Plants secrete substances into the soil referred to as root exudates, which contain carbohydrates, proteins, amino acids, organic acids, vitamins and other nutrients (Babalola, 2010a). Root exudation, thought to be involved in the regulation of PGPR population in the soil and their immediate vicinity and encouraging beneficial symbioses, changes the chemical and physical properties of the soil and inhibits the growth of competing plant species (Gnanamanickam, 2006). The primary colonizers of the microbial population are strongly influenced by the substances secreted as the root exudates and bacteria benefit from these drivers as nutrients (Walker et al., 2003). For instance, *Pseudomonas* spp has been demonstrated to have the ability to catabolize different nutrients and compete for limited carbon source. These bacteria are considered as potent root colonizers (Gnanamanickam, 2006). Rhizosphere microorganisms may also depend on other members of the community to provide nutrient sources as one bacterium may convert a plant exudate into a form that can be used by other soil organisms. Microorganisms are able to survive under a wide range of environmental conditions such as soil temperature, moisture, texture, inorganic and organic constituents and nutrient availability, by rapid adaptation of their structure and physiology (Soutourina et al., 2001). However, temperature and moisture content are fundamental parameters affecting PGPR growth and activity in soils. The effects of temperature fluctuation on PGPR activity have been extensively demonstrated. A study on the leaching of inoculated rhizobacteria in soil microcosms without plants showed that the process was favoured at low temperature (5°C) than at high temperature (25°C) (Benizri et al., 2001). In contrast, experiments on the colonization of the potato rhizosphere by bioluminescent *Pseudomonas* strains showed that the percentage of colonized roots was greater at low temperature (12°C) than at higher temperature (28°C) Benizri et al., 2001).

Plant growth regulators

The production of phytohormones by PGPR is considered to be an important mechanism by which the bacteria promote plant growth, from germination to senescence (Vessey, 2003). The determination of endogenous concentrations of hormones is essential to elucidate the role of a particular hormone in any physiological process. The mechanisms by which PGPR enhance plant growth is through the production of phytohormones such as indole-3-acetic acid (IAA), auxins, ethylene, cytoxin and gibberellin within the root zone (Gnanamanickam, 2006). These are known to function as coordinators of plant growth and development (for example, regulating the density and length of root hairs, thereby increasing the root surface zone which improves absorption of water and nutrients from the soil) (Gray and Smith, 2005). Among them, the most and well-studied are auxins and IAA (Gnanamanickam, 2006).

The plant growth regulator, IAA, is a natural auxin with vast physiological effects which play an important role in plant growth and development, including cell division, cell elongation, cell differentiation, tropism, flower development, and vascular system patterning (Gravel et al., 2007). IAA is synthesized through L-tryptophan metabolism by plants and many soil microorganisms such as PGPR, fungus and algae. Root tissues are more sensitive to fluctuating concentrations of IAA than other plant tissues (Tanimoto, 2005). Several groups (Patten and Glick , 2002; Gravel et al., 2007) have supported this statement and demonstrated that the production of IAA by microorganisms commonly found in the rhizosphere of plants such as *Pseudomonas* spp. and *Rhizobium* spp. is often associated with their potential to stimulate plant growth. In a study on strains of the genus *Vibrio* isolated from an estuarine environment, the authors suggested that the IAA producing *Vibrio* strains have the capacity to interact with their host plants through molecular signaling pathways, possibly contributing to cycles of growth and senescence, and may play a role in shaping the estuarine environment by influencing the aggregation of plant biomass (Gutierrez et al., 2009). In this context, PGPR capable of degrading IAA might have a positive effect on plant growth. However, in a report on the utilization of IAA for growth by *P. putida* strain 1290, it was concluded that the strain has the potential to manipulate IAA concentrations in its interaction with plants and to stimulate plant growth as seed inoculant. Furthermore, a study on the effect of *P. putida* through the production or

degradation of IAA on tomato growth demonstrated that the bacteria had the potential to promote the reproductive growth of tomato plants. However, the synthesis of high quantities of IAA by PGPR has been shown to inhibit the growth of roots rather than promote it (Gravel et al., 2007).

Ethylene is a unique plant growth hormone found only in gaseous form and produced endogenously by almost all plants and also PGPR (Babalola, 2010b). Ethylene is involved in the regulation of numerous physiological processes in plants including seed dormancy, shoot and root growth differentiation, adventitious root formation, leaf and fruit abscission, induction of flowering and increased femaleness in dioeciouse plants, flower and leaf senescence, and fruit ripening (Babalola, 2010b). However, stress conditions such as wounding, drought, chilling temperature, exposure to chemicals and pathogen attack may induce the production of ethylene substantially with a net result of increasing root development (Gnanamanickam, 2006; Babalola, 2010b). On the other hand, overproduction of this hormone has inhibitory effects on root development and may lead to abnormal growth of the plants. It is important to monitor the ethylene concentration in plant roots for normal growth and development of the plants (Saleem et al., 2007). To synthesize this hormone, plants need a precursor. Methionine has been identified as a biochemical and immediate precursor which is converted into ethylene via 1-aminocyclopropane-1-carboxylate (ACC) (Nazli et al., 2008). It has been discovered that some PGPR possess the enzyme ACC deaminase which can cleave ACC, the immediate precursor of ethylene in plants, to α-ketobutyrate and ammonia. The products of this hydrolysis are used by the ACC-degrading bacteria as nitrogen and carbon sources, and thereby, lower the level of ethylene in a developing seedling or stressed plant. Bacteria such as *Alcaligenes* sp., *Bacillus pumilus*, *Pseudomonas* sp., *Variovorax paradoxus*, *Azoarcus*, *Azorhizobium caulinodans*, *Azospirillum* spp., *Gluconacetobacter diazotrophicus*, *Herbaspirillum* spp. and *Burkholderia vietnamiensis* were identified by their ability to grow on minimal media containing ACC as the sole nitrogen source (Dobbelaere et al., 2003). Recently, expression of ACC deaminase activity was found in many strains of *B. unamae* and *B. vietnamiensis*, and the ACC deaminase gene (acdS) was also detected in these species as well as in *B. phymatum*, *B. xenovorans* and *B. caribiensis*. In general, a decreased level of ACC results in a lower level of endogenous ethylene, which eliminates the inhibitory effect of high ethylene concentrations (Shaharoona et al., 2006).

The gibberellins (GA) are a group of phytohormones which acts throughout the life cycle of plants by influencing many physiological effects such as stimulation of seed germination, stem elongation, flower induction, and seed pericarp growth (Boemke and Tudzynski, 2009). Regulation of GA biosynthesis is therefore of fundamental importance to plant growth and the adaptation to the environment. Gibberellin A (GA3) was the first to be discovered. This hormone was originally isolated as the bioactive component of the fungus *Gibberella fujikuroi* that causes foolish rice seedling disease. Currently, there are 136 GAs identified from higher plants, fungi, and bacteria, which are named with a number according to the order of discovery (MacMillan, 2002; Boemke and Tudzynski, 2009). Only a few GAs (GA1 and GA4) were able to act as a hormone in plants (MacMillan, 2002). According to researcher's findings, PGPR species can also synthesize GA1 and GA3 (Gutierrez-Manero et al., 2001). Rhizospheric and/or endophytic *Azospirillum* is among the bacteria producing this hormone. The bacteria produce GA1 and GA3 *in vitro* in chemically defined media. According to Cassán et al., (2001), *Azospirillum* spp. GA1 and GA3 could be produced from different metabolic precursors such as hydroxylation of GA20 for GA1, while GA3 could come from GA9 in the early non-hydroxylative pathway. It has been found also that *Azospirillum* sp. metabolizes d2GA20 to d2GA1 *in vivo* in dy rice mutant seedlings (Cassán et al., 2001).

Cytokinin regulates a wide variety of physiological and developmental processes of plants (Ortiz-Castro et al., 2009). This substance affects many areas of the plant including regulation of root and shoot growth, as well as branching, control of apical dominance in the shoot, chloroplast development and leaf senescence (Oldroyd, 2007). Several reports have shown an involvement of cytokinin signaling in mediating the growth and developmental responses of plants to *B. megaterium*. Stimulation of plant growth by the bacteria requires an intact cytokinin-signaling pathway in *Arabidopsis thaliana* to exert a pronounced growth stimulatory effect in different crop plants (Arkhipova et al., 2005; Ortiz-Castro et al., 2009). This effect can be mediated by different cytokinin receptor homologs (Ortiz-Castro et al., 2009). The presence of different cytokinins in the biomass and the culture medium has been reported (Serdyuk et al., 2003). In the biomass, they are in a free state or bound to certain tRNAs, while in the culture medium, they are found as either adenine derivatives, isoprenylated at the N6 position or as ribosides, such as 6-benzyladenine, N6-isopentenyladenosine, and zeatinriboside. Cytokinins of bacterial origin can improve growth in plant. But a minor overproduction of this compound leads to inhibition of root development, and severely deficient cytokinin mutant plants do not survive. Cytokinins are believed to be the signals involved in mediation of environmental stress from roots to shoots. This balance is influenced by the levels of other growth regulators such as auxins, as well as by environmental cues. Inhibition of root growth by cytokinins is probably mediated by increasing auxin pools. Thus, PGPR can facilitate growth by altering the hormonal balance in the affected plant. Nevertheless, more studies need to be conducted before cytokinin

signalling can be fully understood (Oldroyd, 2007).

Nitrogen-fixation

Nitrogen is one of the most important and common nutrients required for plant growth and development as it forms an integral part of proteins, nucleic acids and other essential biomolecules. The earth's atmosphere is composed with 78% of nitrogen which exists as dinitrogen (N_2) (Babalola, 2010a). This form cannot be directly assimilated by plants but becomes available through the biological nitrogen fixation process that only prokaryotic cells have developed, including some eubacteria, cyanobacteria, and actinomycetes (Gnanamanickam, 2006; Babalola, 2010a). In this process, N_2 is reduced to ammonia by a specialized group of bacteria termed diazotrophs (Franche et al., 2009). The nitrogen fixation reaction is catalyzed by the nitrogenase enzyme. Diastrophic bacteria are an essential part of all ecosystems. Mostly, they are free-living soil organisms (*Azotobacter*), but some plants have developed an association with bacteria, for example, *Azospirillum*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Gluconacetobacter, Herbaspirillum,* and *Burkholderia,* which infect their roots and, in return for sugars from the plant, fix nitrogen which can be used by the plant for growth. These bacteria are valued for their importance in agricultural fertility. *Rhizobium* is the most well-known bacterial species that acts as the primary symbiotic fixer of nitrogen. The bacteria can infect the roots of leguminous plants, leading to the formation of lumps or nodules where the nitrogen fixation takes place. The bacterium system supplies an enzyme called nitrogenase used in catalysing the conversion of nitrogen gas to ammonia for the host plant, and the plant furnishes nutrients and energy for the activities of the bacterium. The reaction requires hydrogen as well as energy from ATP. The nitrogenase complex is sensitive to oxygen and becomes inactivated when exposed to it. This is not a problem with free-living, anaerobic nitrogen-fixing bacteria. Free-living aerobic bacteria have a variety of different mechanisms for protecting the nitrogenase complex, including high rates of metabolism and physical barriers (Gnanamanickam, 2006). For instance, *Azotobacter* overcomes this problem by having the highest rate of respiration of any organism, thus maintaining a low level of oxygen in its cells. *Rhizobium* controls oxygen levels in the nodule with leghaemoglobin. This red, iron-containing protein has a similar function to that of haemoglobin; binding to oxygen. This provides sufficient oxygen for the metabolic functions of the bacteroids but prevents the accumulation of free oxygen that would destroy the activity of nitrogenase. It is believed that leghaemoglobin is formed through the interaction of the plant and the rhizobia; neither can produce it alone (Babalola, 2010a).

Increased uptake of minerals

In addition to nitrogen, phosphorus is considered to be playing an important role in the nutrition and development of plants including, metabolic processes of energy transfer, signal transduction, macromolecular biosynthesis, photosynthesis, and respiration chain reactions (Chang and Yang, 2009). Most agricultural soils contain large reserves of phosphorus, a considerable part of which accumulates as consequence of regular applications. To become available for plant nutrition, the phosphorus must be transformed to inorganic phosphorus. This can happen only with the presence of phosphatase enzymes. However, the major source of phosphatase activity in soil is considered to be of microbial origin (Egamberdiyeva, 2007). In fact, PGPR such as *Pseudomonas, Bacillus, Rhizobium, Burkholderia, Achromobacter, Agrobacterium, Micrococcus, Aerobacter, Flavobacterium* and *Erwinia*, play fundamental roles in biogeochemical phosphorus cycling in natural and agricultural ecosystems. Phosphate-solubilizing microbes can transform the insoluble phosphorus compounds to soluble forms HPO_4^{2-} and $H_2PO^-_4$ by acidification, chelation and exchange reactions (Chang and Yang, 2009). The application of PGPR around the roots of plants, in soils, and in fertilizers has been shown to release soluble phosphorus, promote plant growth, and protect plants from pathogen infection (Chang and Yang, 2009).

INDIRECT MECHANISMS OF ACTION

Indirect mechanisms of action involve the ability of PGPR to: (a) produce antibiotics; (b) successfully compete with pathogens for nutrients on the root; (c) induce systemic resistance by activating the plant defences (Lugtenberg and Kamilova, 2009); and (d) produce siderophores, lytic enzymes, cyanide and ammonia.

Antibiotic production

Antibiotic production is considered as one of the most important tools that PGPR can use to combat proliferation of phytopathogens. In the past years, many different types of antibiotics produced by PGPR including butyrolactones, zwittermycin A, kanosamine, oligomycin A, oomycin A, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, viscosinamide, xanthobaccin, and 2,4-diacetyl phloroglucinol (2,4-DAPG) have been shown to be effective against phytopathogenic agents (Whipps, 2001). Among them, 2, 4-DAPG is one of the most efficient antibiotics in the control of plant pathogens and can be produced by various strains of *Pseudomonas* (Fernando et al., 2006). Previous studies have shown that bacterial biocontrol strains not only show a wide

range of diversity in the type, but also in the number, of antibiotics produced. It has been demonstrated that *B. cereus* strain UW85, *P. fluorescens* strains CHA0 and Pf5 produce numerous antibiotics with different degrees of action against specific pathogenic fungi (Raaijmakers et al., 2002). Many of these antibiotics have a broad-spectrum activity. For illustration, pyrrolnitrin, produced by *Pseudomonas* and *Burkholderia* species, was tested for therapeutic purposes against human pathogenic bacteria and fungi. This antibiotic has also shown activity against a wide range of *Basidiomycetes*, *Deuteromycetes* and *Ascomycetes,* including *Rhizoctonia solani, Botrytis cinerea, Verticillium dahliae* and *Sclerotinia sclerotiorum* (Raaijmakers et al., 2002). This group of antibiotics may offer an unexploited resource for compounds to deal with the alarming ascent of multidrug-resistant human pathogenic bacteria (Compant et al., 2005).

Induced systemic resistance

Induced systemic resistance is defined as the ability of the plant defence system to exclude or overcome completely or in some degree. The effect of a pathogen and pests acquired after appropriate stimulation. When plants are growing, their roots enter quickly into a symbiosis with diverse microorganisms. This symbiosis may play the role of beneficial (aid in the uptake of water and minerals, such as phosphate, and protection of biotic and abiotic stress) or pathogenic agents in the development of plants (Gnanamanickam, 2006). In the case of pathogenic bacteria, the immune response of the plant is characterized by the production of salicylic acid, which in revenge, induces a set of genes encoding pathogenesis-related proteins in the plant (Gnanamanickam, 2006). Some strains of PGPR were shown to act as inducing agents in different plants by producing salicylic acid which is responsible for the induction of induced systemic resistance in plants. Induced systemic resistance was observed first with *Pseudomonas* sp. strain WCS417r against *Fusarium* wilt of carnations and by selected rhizobacteria against the fungus *Colletotrichum orbiculare* in cucumber (Compant et al., 2005). It has been also found that *Bacillus* spp elicits induced systemic resistance and promotes plant growth (Kloepper et al., 2004). Available reports showed that in rice, seed-treatment followed by root-dipping and a foliar spray with *P. fluorescens* strains Pf1 and FP7 induce systemic resistance against the sheath blight pathogen, *R. solani*. PGPR can also induce systemic protection against bacterial diseases. Seed treated with *P. fluorescens* strain 97 protected beans against halo blight disease caused by *P. syringae* pv. *phaseolicola* (Gnanamanickam, 2006). Induction of systemic resistance by PGPR against viral diseases has been reported in cucumber and tobacco plants. Reports on PGPR-mediated induced systemic resistance against insects are restricted to very few crops (Ramamoorthy et al., 2001). These bacteria are protecting plants against damages from several pathogens.

Lytic enzymes

Selected PGPR strains have been found to excrete lytic enzymes that can attack pathogen growth and/or activities (Compant et al., 2005). Lytic enzymes can reduce different polymeric substances such as chitin, proteins, cellulose, hemicellulose and DNA (Vivekananthan et al., 2004). The expression and secretion of these enzymes by different bacteria can sometimes result in the suppression of plant pathogen activities directly (Pal and Gardener, 2006). Chitinase produced by *S. plymuthica* C48 inhibited spore germination and germ-tube elongation in *B. cinerea*; but *Serratia marcescens* was considered to produce extracellular chitinases which act as antagonists against *Sclerotium rolfsii* (Frankowski et al., 2001). It was demonstrated that extracellular chitinase and laminarinase synthesized by *P. stutzeri* lyse mycelia of *F. solani* (Compant et al., 2005). Bacterial species like *Bacillus* have been proved to control the fungal diseases. Recent reports showed that they are capable of lysing chitin, which is a major constituent of the fungal cell wall. In addition these bacteria have the ability to disintegrate proteolytic activity which plays a key role in the nitrogen cycle (Praveen et al., 2012).

Siderophore production

Iron is an essential element to virtually all forms of life and plays an important role in different physiological processes such as respiration, photosynthesis, DNA synthesis and defence against reactive oxygen species (Dellagi et al., 2009). However, its availability is extremely limited by very low solubility of ferric hydroxide complexes at neutral pH (Wensing et al., 2010). To survive in such an environment, plant- associated PGPR have different strategies of obtaining iron from the soil, which include the synthesis of siderophores which are selective ferric ion chelators. These low molecular weight compounds are secreted in response to iron deficiency (Dellagi et al., 2009; Wensing et al., 2010). Siderophores synthesized by fluorescent Pseudomonads have received much attention over the past years, because of their role in the biological control of soil-borne plant pathogens and in disease suppressive soil. *B. megaterium* from tea rhizosphere is able to produce siderophores and thus it helps in plant growth promotion and reduction of disease intensity (Chakraborty et al., 2006). Specific strains of the *P. putida* group have been used as seed inoculants on crop plants to promote growth and increase yields of various crops. Recently, the production of siderophores

by *Ochrobactrum anthropi*, an isolate from the rhizosphere of tea, was reported (Chakraborty et al., 2009).

CONCLUSIONS

The literature clearly demonstrates that PGPR induces plant growth and development through their numerous direct or indirect mechanisms of action. As a consequence, current production methods in agriculture, for example, the improper use of chemical pesticides and fertilizers in agricultural, horticultural and agro-forestry systems, creating a long list of environmental and health problems, will decrease. For this reason, there is an urgent need for research to give a clear definition of which bacterial traits are useful and necessary for different environmental conditions and plants, so that optimal bacterial strains can either be selected and/or improved. The identification of genes and traits involved in the process of root colonization will result in detailed knowledge of bacterial rhizosphere ecology, physiology and its interaction with plant roots, which will facilitate more efficient information and strategies for risk assessment and infection control. In this context, the optimization of PGPR inoculums must be rigorously tested in the presence of diverse biotic and/or abiotic factors. In addition, to maintain the maximum viability and activities of PGPR, appropriate strategies should be developed.

ACKNOWLEDGEMENTS

We thank all the persons who contributed to the improvement of this review, for their valuable comments, suggestions and discussions. OOB would like to thank the National Research Foundation for financial support.

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