International Journal of Current Trends in
Pharmacobiology and Medical Sciences
Volume 2 • Number 1 (January-2017) • ISSN: 2456-2432
Journal homepage: www.ijctpms.com

Review Article

Properties and Application of Plant Growth Promoting Rhizobacteria

Zerihun Tsegaye*, Fassil Assefa and Dereje Beyene

Addis Ababa university, College of Natural Science, Department of Microbial, Cellular and Molecular Biology and Ethiopian Biodiversity Institute, Microbial Biodiversity Directorate, Addis Ababa, Ethiopia

Corresponding author.

Abstract

Plant growth promoting rhizobacteria are the soil bacteria inhabiting around or on the root surface that directly involved in promoting plant growth and development through production and secretion of various regulatory chemicals in the vicinity of rhizosphere. Properties of plant growth promoting rhizobacteria facilitate the plant growth directly by either assisting in nutrients acquisition or modulating plant hormone levels, or indirectly by decreasing the inhibitory effects of various pathogens on plant growth and development in the forms of the bio-control agents. Various studies have documented the increased health and productivity of different plant species by the application of plant growth promoting rhizobacteria as biofertilizers under both normal and stressed conditions. PGP rhizobacteria improve seed germination, root development, increase crop yield, restore natural soil fertility, decrease pollutant toxicity, provide protection against plant pathogens and environmental stress and also decrease the global dependence on hazardous agricultural inorganic chemicals which destabilize the agro-ecosystems. In future Bio-fertilizers or bio-protectants might replace inorganic chemical fertilizers and pesticides which is very expensive and environmental unfriendly synthetic substances.

Article Info

Accepted: 19 January 2017
Available Online: 25 January 2017

Keywords

Biocontrol
Biofertilizer
Bioprotectant
Chemical fertilizers
Rhizobacteria

Introduction

The rhizosphere is the zone of soil surrounding a plant root where the biology and chemistry of the soil are influenced by the root. In the rhizosphere, very important and intensive interactions take place between the plant, soil, microorganisms and soil microfauna, influenced by compounds exuded by the root and by microorganisms feeding on these compounds (Antoun and Prévost, 2006). The microbial population present in the rhizosphere is relatively different from its surroundings due to the presence of root exudates that function as a source of nutrients for microbial growth (Burdman et al., 2000). It is rich in nutrients for microbes compared to the bulk soil; this is shown by the quantity of bacteria that are present surrounding the roots of the plants, generally 10 to 100 times higher than in the bulk soil (Weller and Thomashow, 1994).

Rhizosphere has been broadly subdivided into the following three zones (Pratibha et al., 2013). (1). Endorhizosphere (interior of the root): that consists of the root tissue including the endodermis and cortical layers; (2). Rhizoplane (interior of the root): is the root surface where soil particles and microbes adhere. It consists of epidermis, cortex and mucilaginous

polysaccharide layer; (3). Ectorhizosphere: that consists of soil immediately adjacent to the root. Stimulation of microbial proliferation around the root due to the release of various organic compounds by the roots is known as the rhizospheric effect. The ability to secrete a vast array of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots, with nearly 49% of all photosynthetically fixed carbon being transferred to the rhizosphere through root exudates (Prakash and Karthikeyan, 2013).

The rhizosphere is the front-line between plant roots and soil-borne pests. Therefore it seems logical that microorganisms that colonize the same niche could be ideal candidates for sustainable agriculture (Weller and Thomashow, 1994). In the rhizosphere, bacteria are the most abundant microorganisms (Antoun and Prévost, 2006). Rhizobacteria are rhizosphere-competent bacteria that aggressively colonize plant roots; they are able to multiply and colonize all the ecological niches found on the roots at all stages of plant growth, in the presence of a competing microflora (Muleta et al., 2007). Rhizobacteria can have a neutral, detrimental or beneficial effect on plant growth. Deleterious rhizobacteria are presumed to adversely affect plant growth and development through the production of undesirable metabolites (phytotoxins).

The structure of the rhizobacterial community is affected by several factors including plant genotype and is determined by the amount and composition of root exudates (Marschner et al., 2004). In addition, the soil type and fertility are contributing factors that also shape the community (Innes et al., 2004). The interaction or communication between plants and rhizobacteria occurs through chemical signals released by both partners. The rhizobacterial community may influence this interaction by exuding compounds as a means of communication that is recognizable by neighboring bacteria and root cells of host plants (Gray and Smith, 2005). Thus forms of communication can affect plant growth, nutrient status and also susceptibility to stress and pathogens in the host plant (Morgan et al., 2005).

Beneficial rhizobacteria are termed either plant growth promoting rhizobacteria (PGPRB) or plant health promoting rhizobacteria (PHPRB) according to their mode of action. The term PGPR was first used by Kloepper (1994) and investigations on PGPRB have been escalating at an ever increasing rate since then. PGPRB grow in, on, or around root plant tissue that enhance plant growth or reduce disease damage from soil-borne plant pathogens and/or reduce abiotic or biotic stress (Vessey, 2003). Kloepper (1994) stated that the PGPRB are characterized by the following features (i) they must be able to colonize the root surface (ii) They must survive and multiply in microhabitats associated with the root surface, in competition with other micro biota and (iii) they must promote plant growth (Munees and Mulugeta, 2014).

The enhancement of plant growth can vary depending on colonization site of PGPRB on the host plant. PGPRB may colonize the rhizosphere, the surface of the root, or even superficial intercellular spaces (McCully, 2001). The process of root colonization is under the influence of various parameters such as bacterial traits, root exudates and several other biotic and a biotic factor (Benizri et al., 2001). Some authors reported that bacterial cells first colonize the rhizosphere following inoculation into soil (Gamalero et al., 2009). Then, bacterial cells may occurred as single cells attached to the root surfaces, and subsequently converted into doublets on the rhizodermis, forming a string of bacteria (Compant et al., 2010).

Colonization may then occur on the whole surface and bacteria can even establish as micro-colonies or bio-films (Benizri et al., 2005). It is important to note that the root system is not colonized in a uniform manner, different population densities being reported for the diverse root zones. For example, *Kluyvera ascorbata* colonized the upper two-thirds of the surface of canola roots, but no bacteria were detected around root tips (Vessey, 2003). Non-uniform bacterial colonization along the root can be explained by different factors such as varying root exudation patterns, bacterial quorum sensing effects as well as many others (Compant et al., 2010). The benefits of PGPRB for plant growth, which include increases in: seed germination rate, root growth, leaf area, shoot and root weights , yield, chlorophyll content, biocontrol, hydraulic activity, tolerance to drought, (Muleta et al, 2007). According to the Woyessa and Assefa (2011) report, inoculation of teff crops with *Pseudomonas fluorescent* increases mean root dry weight (39%), root shoot ratio (42%), and grain yield (28%) and also inoculation of *Bacillus subtilis* increase mean root dry weight (28%), root shoot ratio (19 %) and grain yield (44%).

Organisms identified as PGP rhizobacteria have diverse taxonomy (Glick, 1995), and include Fermicutes or Gram

positive bacteria (e.g., members of the Actinomycetales, including *Frankia* and *Streptomyces* and including *Bacillus* and *Paenibacillus*). Gram negative organisms include various subdivisions of the Proteobacteria: Rhizobiaceae (*Rhizobium*, *Bradyrhizobium*), Rhodospirillaceae (*Azospirillum*), and Acetobacteraceae (*Acetobacter*) in the α-Proteobacteria; members of the Burkholderia group (*Burkholderia*) in the β-Proteobacteria, and members of the Enterobacteriaceae (*Enterobacter*, *Pantoea*, *Serratia*) and Pseudomonaceae (*Pseudomonas*, *Flavimonas*) in the γ-Proteobacteria exhibiting successful rhizosphere colonization.

Properties of plant growth promoting rhizobacteria

PGP rhizobacteria directly contribute to the plant growth through the biologically nitrogen fixation, enhancing plant nutrition by solubilization of minerals like phosphorus, zinc and potassium. phytohormone production like auxins, cytokinins, gibberellins, ethylene and abscissic acid. PGP rhizobacteria indirectly benefit the plant growth by the bio-control of deleterious microorganisms or root pathogens that inhibit plant growth, including antibiotic production, synthesis of extracellular enzymes to hydrolyze the fungal cell wall, induction of systemic resistance, siderophore production (Bhattacharyya and Jha, 2012), decreasing pollutant toxicity (Zahir et al., 2003) and competition for nutrients and niches within the rhizosphere,

Direct plant growth promoting properties of PGP rhizobacteria

Biological nitrogen fixation (BNF)

Nitrogen (N) is the most vital nutrient for plant growth and productivity. It is required for cellular synthesis of enzymes, proteins, chlorophyll, DNA and RNA, and is therefore important in plant growth and production of food and feed. Although, there is about 78% N_2 in the atmosphere, it is unavailable to the growing plants. BNF is a process in which the atmospheric N_2 is converted into plant-utilizable forms by nitrogen fixing microorganisms using a complex enzyme system known as nitrogenase (Kim and Rees, 1994). Globally, BNF accounts for approximately two-thirds of the nitrogen fixed. BNF occurs, generally at mild temperatures, by nitrogen fixing microorganisms, which are widely distributed in nature (Raymond et al., 2004). Furthermore, BNF represents an economically beneficial and environmentally sound alternative to chemical fertilizers (Ladha et al., 1997).

Nitrogen fixing organisms are generally categorized as (a) symbiotic N_2 fixing bacteria including members of the family rhizobiaceae which forms symbiosis with leguminous plants (e.g. rhizobia) (Ahemad and Khan, 2012) and non-leguminous trees (e.g. *Frankia*) and (b) non-symbiotic (free living, associative and endophytes) nitrogen fixing forms such as cyanobacteria (*Anabaena*, *Nostoc*), *Azospirillum*, *Azotobacter*, *Gluconoacetobacter diazotrophicus* and *Azocarus*, etc. (Riggs et al., 2001). However, non-symbiotic nitrogen fixing bacteria provide only a small amount of the fixed nitrogen that the bacterially-associated host plant requires (Glick, 2012).

PGP rhizobacteria that fix N_2 in non-leguminous plants are also called as diazotrophs capable of forming a non obligate interaction with the host plants (Glick et al., 1999).According Zewdie et al. (2000) report inoculation of tef crops with *Azospirillum* isolates significantly increase grain yield up to 12% and total nitrogen up to 5% over un inoculated teff variety under greenhouse experimentation.

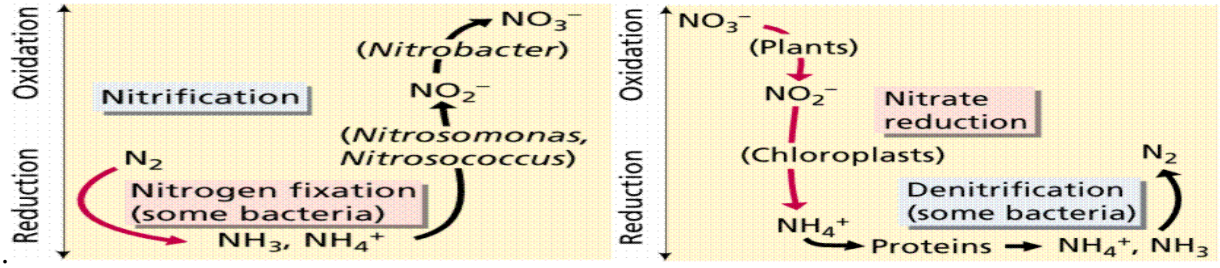

Fig. 1: Biological nitrogen fixation (Source: http://www.sinauer.com/).

Solubilization of minerals - Phosphate solubilization

Phosphorus (P), the second important plant growth-limiting nutrient after nitrogen, is abundantly available in soils in both organic and inorganic forms (Khan et al., 2009). However, although (P) is abundant in soils in both inorganic form (originating mainly from applied P fertilizer) and organic form (derived from

microorganisms, animals and plants) (Paul and Clark, 1989), it is still one of the major plant growth limiting nutrients. Despite of large reservoir of P, the amount of available forms to plants is generally low. This low availability of phosphorous to plants is due to the fact that the majority of P present in the soil is found in insoluble forms, while the plants are able to absorb it only in the soluble forms such as the monobasic ($H_2PO^-_4$) and the diabasic $(HPO_2)^{-4}$ ions.

Plants absorb fewer amounts of applied phosphatic fertilizers and the rest is rapidly converted into insoluble complexes in the soil (McKenzie and Roberts, 1990). But regular application of phosphate fertilizers is not only costly but is also environmentally undesirable. This has led to search for an ecologically safe and economically reasonable option for improving crop production in low P soils. In this context, microorganisms such as PGPRB possessing phosphate solubilizing activity, often termed as phosphate solubilizing microorganisms (PSM), may provide the available forms of P to the plants and hence a viable substitute to chemical phosphatic fertilizers (Richardson et al., 2009). Typically, the solubilization of inorganic phosphorus occurs as a consequence of the action of low molecular weight organic acids which are synthesized by various soil bacteria (Zaidi et al., 2009).

The mineralization of organic phosphorus occurs through the synthesis of a variety of different enzymes such as phosphatases, catalyzing the hydrolysis of phosphoric esters (Glick, 2012). Importantly, phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao et al., 2008). Though, PSB are commonly found in most soils; their establishment and performances are severely affected by environmental factors especially under stress conditions (Ahemad and Khan, 2010a, b; Ahemad and Khan, 2012). Bacterial strains belonging to genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Aerobacter*, *Flavobacterium* and *Erwinia* have the ability to solubilize insoluble inorganic phosphate compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyl apatite and rock phosphate (Rodríguez and Fraga, 1999).

Strains from genera *Pseudomonas*, *Bacillus* and *Rhizobium* are among the most powerful phosphate solubilizers. The production of organic acids especially gluconic acid seems to be the most frequent agent of mineral phosphate solubilization by bacteria such as *Erwinia herbicola*, *Pseudomonas cepacia* and *Burkholderia cepacia* (Rodríguez and Fraga, 1999). Another organic acid identified in strains with phosphate-solubilizing ability is 2- ketogluconic acid, which is present in *Rhizobium leguminosarum*. Strains of *Bacillus* sp. were found to produce mixtures of lactic, isovaleric, isobutyric, and acetic acids (Suman et al., 2001). Other organic acids, such as glycolic acid, oxalic acid, malonic acid, succinic acid, citric acid and propionic acid, have also been identified among phosphate solubilizers.

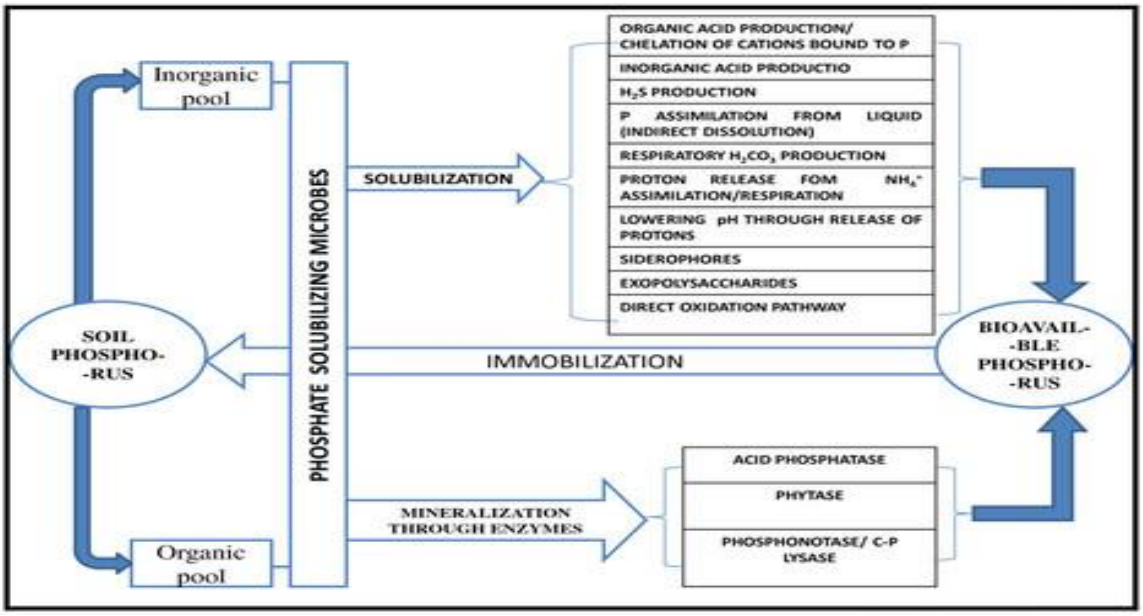

Fig. 2: Mechanism of phosphate solubilization by rhizobacteria (Khan et al., 2009).

Potassium solubilization

Potassium is available in four forms in the soil which are K ions (K^+) in the soil solution, as an exchangeable cation, tightly held on the surfaces of clay minerals and organic matter, tightly held or fixed by weathered micaceous minerals, and present in the lattice of certain K containing primary minerals. There are several processes that contribute to the availability of potassium in the soil. Potassium is already available in the soil for plant uptake; however the concentration of potassium is affected by soil weathering, cropping history and use of fertilizers. Thus, the amount present is insufficient to meet crop requirement. More than 90% of potassium in the soil exists in the form of insoluble rocks and silicate minerals. Potassium solubilizing bacteria (KSB) such as *Acidothiobacillus, Burkholderia* and *Pseudomonas* has been reported to release potassium in accessible form from potassium bearing minerals in soils. KSB are able to solubilize potassium rock through production and secretion of organic acids.

Zinc Solubilization

Zn is an important component of different enzymes catalyzing many metabolic reactions in plants. The essential processes of life in plants are influenced by Zn, such as (a) nitrogen metabolism i.e. nitrogen and protein uptake quality; (b) photosynthesis i.e. synthesis of chlorophyll and carbon anhydrase activity (c) resistance against biotic and abiotic stresses i.e. resistant against oxidative damage. Zinc also plays a significant role in plant resistance against diseases, photosynthesis, cell membrane integrity, protein synthesis, pollen formation and enhances the level of antioxidant enzymes and chlorophyll within plant tissues (Sbartai et al., 2011). Moreover, Zn is critical as a co-factor for the activity of more than 300 enzymes (Mccall et al., 2000). In addition, Zn is required for the production of phytohormones such as absicic acid, auxin, gibberellins and cytokinins and its deficiency results in an impairment of growth of plant cells. Therefore, Zn deficiency in plants seriously affects various vital processes occurring within plants (Younas et al., 2014). Zn deficiency also significantly affects the root system including poor development of roots.

Inorganic fertilizers (zinc sulfate (ZnSO4) are recommended as good source of Zn but they are quickly fixed on soil medium, causing poor availability to plants. Zn SB produced different organic acids such as 2- ketogluconic acid (Fasim et al., 2002), 5-ketogluconic acid (Saravanan et al., 2007) for the mobilization of Zn (Tariq et al., 2007). These bacteria can be used to solubilize insoluble sources of Zn such as ZnO and ZnCO3 because most of the soils are rich in Zn contents but less in soluble Zn. *Bacillus* and *Pseudomonas spp.* have much potential to solubilize these sources in soil system for taking economically efficient Zn (Saravanan, 2003).

Phytohormone production

Phytohormones are the chemical messengers that play crucial role in the natural growth and occur in low concentration. These phytohormones shape the plant, also affecting seed growth, time of flowering, sex of flowers, senescence of leaves, and fruits. They also affect gene expression and transcription levels, cellular division and growth. In targeted cells phytohormones also regulate cellular processes, pattern formation, vegetative and reproductive development and stress responses. Thus, all the major activities like formation of leaf, flowers and development and ripening of fruit are regulated and determined by hormones. In order to decrease the negative effects of the environmental stressors caused due to growth limiting environmental conditions, plants mostly attempt to adjust the levels of their endogenous phytohormones (Salamone et al., 2005). While this strategy is sometimes successful, rhizosphere microorganisms may also produce or modulate phytohormones under *in vitro* conditions. So that many PGPB can alter phytohormone levels and thereby affects the plant's hormonal balance and its response to stress (Glick et al., 2007).

Auxin

Indole-3-acetic acid (indole acetic acid, IAA) is one of the most common as well as the most studied auxins, and much of the scientific literature considers auxin and IAA to be interchangeable terms (Spaepen et al., 2007). Its main function is cell division, cell elongation, differentiation, and extension. But it has been known that plant responses to IAA vary from plant to plant in terms of sensitivity. Generally, IAA released by rhizobacteria interferes with many plant developmental processes because the endogenous pool of plant IAA may be altered by the acquisition of IAA that has been secreted by soil bacteria (Glick, 2012). Advancement in understanding the IAA signaling pathway in plants showed that the role of auxins in plant–microorganism

interactions appears diverse, varying from pathogenesis to phytostimulation. A number of studies have clearly shown that IAA can be a signaling molecule in microorganisms, in both IAA producing and IAA-nonproducing species.

Bacteria isolated from the rhizosphere and rhizoplane of various crops are more active in producing auxins than those from root free soil because of rich supplies of substrates exuded from roots compared with non-rhizosphere soil (Strzelczyk and Pokojska, 1984). A 3-fold higher IAA content was found in the rhizosphere compared with non rhizosphere environments (Narayanaswami and Veerraju, 1969). It has been estimated that 80% of bacteria isolated from the rhizosphere can produce IAA (Patten and Glick, 1996; Ahmad et al., 2008). Similarly, over 66% of wild Arabica coffee-associated rhizobacteria secreted IAA (Muleta et al., 2007).

The variation of IAA production among the PGPRB was reported by (Prakash and Karthikeyan, 2013) in which bacterial strains isolated from rhizospheric soil of Melaiyar and Nagapattinam districts in Tamil Nadu and were identified as *Azospirillum sp*, *Bacillus sp*, *Pseudomonas sp*, and *Azotobacter sp* (Prakash and Karthikeyan, 2013). The IAA production varied among those species, which are *Pseudomonas sp* were produced (94%), *Azospirillum sp* (80%), *Azotobacter sp* (65%) and *Bacillus sp* (40%).

Its variation may be based on environmental stress factors which modulate the IAA biosynthesis in different bacteria include acidic pH, osmotic and matrix stress, carbon limitation and genetic factors (Sudha et al., 2012). Among genetic factors, both the location of auxin biosynthesis genes in the bacterial genome (either plasmid or chromosomal) and the mode of expression (constitutive vs. induced) have been shown to affect the level of IAA production (Somers, et al., 2004). The location of auxin biosynthesis genes can affect the IAA level, as plasmids are mostly present in multiple copies while in the chromosomal DNA resulting in a lower IAA production (Spaepen and Vanderleyden, 2007). Lucy et al. (2004) have shown that IAA-producing PGPRB increase root growth and root length, resulting in greater root surface area, which enables the plant to access more nutrients from soil. Tryptophan is an amino acid, serves as a physiological precursor for biosynthesis of auxins in higher plants and in microbes. Root exudates are natural sources of TRP for the rhizosphere microflora, which may enhance auxin biosynthesis in the rhizosphere (Martens and Frankenberger, 1994). TRP stimulates the IAA production and thus regulates the IAA biosynthesis by inhibiting anthranilate that is a major precursor for tryptophan because it seems to reduce IAA synthesis (Figure 3).

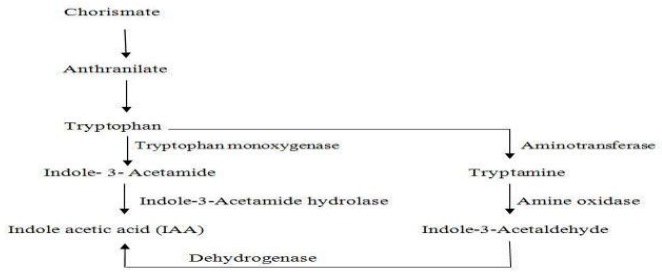

Fig. 3: IAA synthesis by tryptophan dependent pathway.

Cytokinin

Cytokinins are a class of phytohormones which are known to promote cell divisions, cell enlargement and tissue expansion in certain plant parts (Werner et al., 2003). A few PGPRB strains were reported to produce cytokinins and gibberellins. Bacteria like *Azospirillum* and *Pseudomonas* sp. produce cytokinins and gibberellins, in addition to IAA. Plant responses to exogenous applications of cytokinin result in either one of the following effects a) enhanced cell division b) enhanced root development c) enhanced root hair formation d) inhibition of root elongation e) shoot initiation and certain other physiological responses.

Cytokinins are usually present in small amounts in biological samples and their identification and quantification is difficult. Timmusk et al. (1999) reported the production of cytokinins by a free living soil bacterium *Pseudomonas. polymyxa* using immunoaffinity chromatography (IAC). Salamone et al. (2005) have shown higher production of the cytokinins isopentenyl adenosine (IPA), zeatin riboside (ZR) and dihydroxyzeatin riboside (DHZR) by the wild type strain *Pseudomonas fluorescens* G20-18.

Gibberellins

Gibberellins are a class of phytohormones most commonly associated with modifying plant morphology by the extension of plant tissue, particularly stem tissue (Salisbury, 1994). These are synthesized by higher plants, fungi, and bacteria. They are involved in several plants developmental processes, including cell division

and elongation, seed germination, stem elongation, flowering, fruit setting, and delay of senescence in many organs of a range of plant species (MacMillan, 2002). They can also regulate root hair abundance and hence promotes the root growth. Production of gibberellins had been detected in different bacterial genera that inhabit the plant root system including *Azotobacter*, *Arthrobacter*, *Azospirillum*, *Pseudomonas*, *Bacillus*, *Acinetobacter*, *Flavobacterium*, *Micrococcus*, *Agrobacterium*, *Clostridium*, *Rhizobium*, *Burkholderia*, and *Xanthomonas*. Plant growth promotion by gibberellin-producing PGPB and this positive effect on plant biomass is frequently associated with an increased content of gibberellins in plant tissues was reported by several workers (Kang et al., 2010).

Lowering of ethylene production

Ethylene is an essential metabolite for the normal growth and development of plants (Shaharoona e*t al.*, 2006). Ethylene stimulates senescence and leaf and fruit abscission, inhibits plant growth (*i.e*. roots) and triggers cell death near infection sites. In agriculture it is important to control ethylene levels, often by lowering them in order to prevent economic losses. This plant growth hormone is produced endogenously by approximately all plants and is also produced by different biotic and a biotic processes in soils and is important in inducing multifarious physiological changes in plants. Apart from being a plant growth regulator, ethylene has also been established as a stress hormone (Saleem et al., 2007). Under stress conditions such as salinity, drought, water logging, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. For instance, the high concentration of ethylene induces defoliation and other cellular processes that may lead to reduced crop performance (Bhattacharyya and Jha, 2012).

1-aminocyclopropane-1-carboxylate (ACC) is the immediate direct physiological precursor of ethylene. Several soil microorganisms, mainly *Pseudomonas* sp. synthesize the enzyme ACC deaminase (reviewed by Glick et al., 1999) which degrades ACC, thus preventing plant production losses by inhibitory levels of ethylene. Currently, bacterial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter, Achromobacter, Agrobacterium, Alcaligenes, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Ralstonia, Serratia* and *Rhizobium* etc. (Ahemad and Kibret, 2014). PGPB bind to the surface of either the seed or root of a developing plant in response to tryptophan and other small molecules in the seed or root exudates rhizobacteria synthesize and secrete the auxin (IAA), some of which is taken up by the plant (Figure.4). This IAA together with endogenous plant IAA can stimulate plant cell proliferation and elongation, or it can induce the activity. The ACC deaminase in PGP rhizobacteria degrades the ethylene precursor ACC. According to the Muleta et al., (2007) report over 27% of rhizobacteria (all *Pseudomonas* sp.) isolated from wild *Coffea Arabica* rhizospheres were able to degrade ACC. The ACC deaminase in PGPRB lowers ethylene level in plants by degrading ACC to ammonia and a-Ketobutyrate.

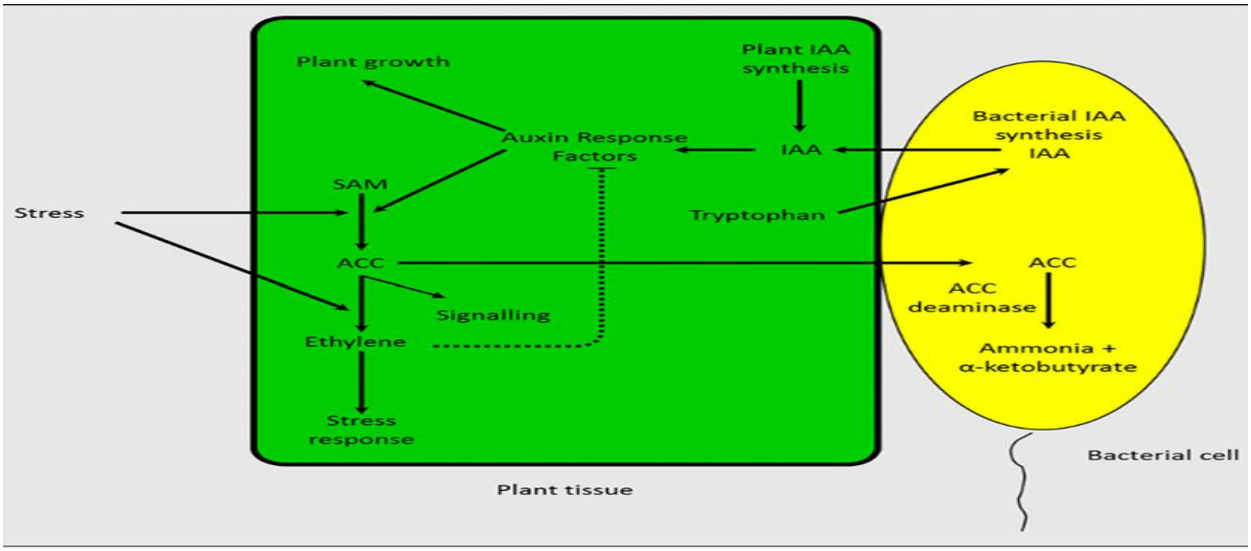

Fig. 4: Mechanism of ACC deaminase source reference Glick and Pasternak (2003).

Lowering ethylene in plants can alleviate stress and thereby improve plant growth. Inoculation with PGPRB combined with ACC deaminase activity could be quite helpful in promoting plant growth and development under stress conditions by reducing stress-induced ethylene production. Glick et al. (1999) put forward the theory that the mode of action of some PGPRB was the production of ACC deaminase. Those authors suggested that ACC deaminase activity would decrease ethylene production in the roots of host plants and result in root lengthening. In some cases, the growth promotion effects of ACC deaminase-producing PGPR appear to be best expressed in stressful situations.

Abscissic acid

Abscissic acid (ABA) plays a primary role in water-stressed environment, such as found in arid and semiarid climates where it helps in combating the stress through stomatal closure of leaves. Therefore, its uptake, transportation in plant and its presence in the rhizosphere could be extremely important for plant growth under water stress conditions. In addition, ABA has also been detected by radioimmunoassay or TLC in supernatants of *Azospirillium* and *Rhizobium* sp. cultures.

Production of siderophores

Iron is one of the major elements in the earth's crust but soil organisms such as plants and microbes have difficulty in obtaining sufficient iron to support their growth because of ferric oxides formation under aerobic conditions, which cannot be readily transported into cells. Under iron starvation, bacteria and plants secrete small, specialized efficient iron (III) chelator molecules commonly known as siderophores. After the iron-siderophore complexes have formed, these now soluble complexes are internalized via active transport into the cells by specific membrane receptors (Glick et al., 1999). Following either cleavage or reduction to the ferrous state, the iron is released from the siderophore and used by a cell (Glick et al., 1999). Lankford (1973) coined the term siderophore to describe low molecular weight (approximately 600 to 1500 daltons) molecules that bind ferric iron with an extremely high affinity. Siderophore was derived from a Greek term meaning iron carrier. The dominant iron-binding ligands of siderophores are hydroxamates and phenolates, but carboxylate, oxazoline, α-hydroxy carboxylate and keto hydroxyl bidentate siderophores have also been found.

Many bacteria are capable of producing more than one type of siderophore or have more than one iron-uptake system to take up multiple siderophores (Neilands, 1981). Wide arrays of beneficial plant-associated bacterial genera: *Pseudomonas, Azotobacter, Bacillus*, *Serratia*, *Azospirillum* and *Rhizobium* secrete various types of siderophores (Glick et al., 1999; Loper and Henkels 1999). Bacterial siderophores in which the hydroxamate ligands are based on D- or L-ornithine include the ornibactins from *Burkholderia cepacia*, which contain one carboxylate and two hydroxamate ligands (Stephan et al., 1993) and the pyoverdines from *Pseudomonas* sp. which may have one or two hydroxamate groups. According to the Muleta et al., (2007) report 67 % of wild Arabica coffee-associated rhizobacteria produces siderophores.

Siderophore production confers competitive advantages to PGPRB that can colonize roots and exclude other microorganisms from this ecological niche. Under highly competitive conditions, the ability to acquire iron via siderophores may determine the outcome of competition for different carbon sources that are available as a result of root exudation or rhizo-deposition. Among most of the bacterial siderophores studied, those produced by *Pseudomonades* are known for their high affinity to the ferric ion. The potent siderophore is pyoverdin, for example, can inhibit the growth of bacteria and fungi that present less potent siderophores in iron-depleted media *in vitro* (Kloepper et al., 1980).

Indirect plant growth promoting properties of PGP rhizobacteria

Pathogenic microorganisms affecting plant health are a major and chronic threat to food production and ecosystem stability worldwide (Compant et al., 2010). Diverse PGP rhizobacteria antagonize the root pathogens through one or more different mechanisms, for example by production of bacterial allelochemicals such as volatile or non-volatile antibiotics, detoxification enzymes, lytic enzymes and other secondary metabolites like HCN (Podile and Kishore, 2006). Production of these compounds is highly influenced by the qualitative and quantitative nutrient availability and is also subjected to quorum sensing.

Production of antibiotics

Many PGP rhizobacteria have the ability to produce peptide antibiotics. These are oligopeptides that inhibit

synthesis of pathogens cell walls, influence membrane structures of cells and inhibit the formation of initiation complex on small subunit of ribosomes (Maksimov, et al., 2011). A variety of antibiotics have been identified, including compounds such as amphisin, 2,4- di-acetyl phloroglucinol, hydrogen cyanide, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by *Pseudomonades* and oligomycin A, kanosamine, zwittermicin A, and xanthobaccin produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas sp* (Compant et al., 2010). More than 12 antibiotics are synthesized by *Bacillus subtilis* strains: bacillomicin, mycobacillin, fungi statin, iturin, phengicin, plipastatin, surfactin, bacilizin, etc. Antibiotics are active with both Gram positive and Gram negative bacteria (eg., polymyxin, circulin, and colistin) and pathogenic fungi *Alternaria solani, Aspergillus flavus, Botryosphaeria ribis, Colletotrichum gloeosporioides, Fusarium oxysporum, Helminthosporium maydis, Phomopsis gossypii* (Maksimov, et al., 2011). *Fluorescent pseudomonads* have been shown to produce a range of antibiotics (Muleta et al., 2007), *e.g.* 2,4- diacetylphloroglucinol, which suppress the growth of various soil-borne fungal phytopathogens (Mazzola, 2002).

Hydrogen cyanide (HCN) production

Considerable numbers of free-living rhizospheric bacterial communities, mainly *Pseudomonas sp*. (Ahmad et al., 2008; Muleta et al., 2007), are capable of generating HCN by oxidative decarboxylation from direct precursors such as glycine, glutamate, or methionine. Other rhizobacterial genera reported to produce HCN include *Bacillus* (Ahmad et al., 2008) and *Chromobacterium* (Muleta et al., 2007).

HCN secreted by *Pseudomonas fluorescent* strain CHAO has been demonstrated to stimulate root hair formation and suppress back root rot caused by *Thielaviopsis basicola* in tobacco plant (Voisard et al., 1989). Cyanogenesis in bacteria accounts in part for the biocontrol capacity of the strains that suppress fungal diseases of some economically important plants (Voisard et al., 1989).

Production of lytic enzymes

Some bacteria, especially *Bacillus* and *Pseudomonas* species are suppress growth and development of fungi both by secreting lytic enzymes such as chitinases and glucanases. Use of the bacteria producing chitinases to biological protection of crops from pathogens, especially those that contain chitin and glucans within their cell wall structure, is the most prominent approach in the agriculture (Maksimov, et al., 2011). Several studies have demonstrated the production of lytic enzymes by rhizospheric bacteria involved in the control mechanisms against plant root pathogens including *Fusarium oxysporium* and *Rhizoctonia solani*. Hydrolytic enzymes act as agents for prevention of plant diseases (van Loon, 2007) by causing lysis of deleterious microbes in the close vicinity of the plant as they secretes increased level of cell wall lytic enzymes (chitinases, glucanases and proteases) (Raval and Desai, 2012).

Many *Pseudomonas* and *Bacillus* species are capable of producing some of these hydrolytic enzymes (Muleta et al., 2007). For example, *Pseudomonas stutzeri* produces extracellular chitinase and ß-1,3-glucanase, which lyse the pathogen *Fusarium* sp.. *Cladosporium werneckii* and *B. cepacia* can hydrolyze fusaric acid (produced by *Fusarium*), which causes severe damage to plants. Antagonistic or biocontrol activity of *Pseudomonas fluorescent* may also be due to the production of different types of cell wall degrading enzymes like chitinase, protease and β-1, 3 glucanase. These enzymes are supposed to degrade the cell wall of various bacterial and fungal plant pathogens. Interestingly, some allelochemicals produced by PGPB are finding new uses as experimental pharmaceuticals, and this group of bacteria may offer a resource for compounds to deal with the alarming ascent of multidrug-resistant human pathogenic bacteria (Compant et al., 2010).

Induction of systemic disease resistance (ISR)

ISR is a bio-control agents that induce a sustained change in plant, increasing its tolerance to infection by pathogen. Some PGPB can trigger the phenomenon of ISR which is phenotypically similar to systemic acquired resistance (SAR) which occurs when plants activate their defense mechanism in response to primary infection by a pathogen. ISR involves jasmonate and ethylene signaling molecules within the plant that stimulates the host plant's response to a range of pathogens without requiring direct interaction between the resistance-inducing microorganisms and the pathogen.

Pseudomonas siderophores have also been implicated in inducing systemic resistance (ISR) in plants (Leeman

et al., 1996), *i.e*. enhancement of the defence capacity of the plant against a broad spectrum of pathogens. Exposure to pathogens, PGPRB and microbial metabolites stimulates the plant's natural self-defence mechanisms before a pathogenic infection can be established, effectively `immunizing' the plant against fungal, viral and bacterial infections. Protection occurs by accumulation of compounds such as salicylic acid, which plays a central protective role in acquired systemic resistance, or by enhancement of the oxidative enzymes of the plant. While acquired systemic resistance is induced upon pathogen infection, induced systemic resistance can be stimulated by other agents, such as PGPRB inoculants (Figure.5). ISR does not accumulate SA and, instead, is dependent on accumulation of ethylene and jasmonic acid (JA) (Pieterse et al., 1998).

This suggests that combining bacterial traits that trigger either the SA, or the ethylene- or JA-dependent response can improve biological control. Disease resistance induction is an active plant defense process that is activated by biotic and abiotic inducers which depends on physical or chemical barriers of the host (Uknes et al., 1993). Besides ethylene and jasmonate, other bacterial molecules such as the O-antigenic side chain of the bacterial outer membrane protein lipopolysaccharide, flagellar fractions, pyoverdine, (Siddiqui and Shoukat, 2003), cyclic lipopeptide surfactants (Tran et al., 2007) have been implicated as signals for the ISR. It can induce alterations in host physiology leading to an over expression of plant defensive chemicals including pathogenesis-related proteins (PR) such as chitinases, peroxidases, super oxide dismutase, phenylalanine ammonia-lyase, phytoalexins, and polyphenol oxidase enzymes.

ISR is not specific against particular pathogen but helps the plant to control diseases. Various PGPRB strains have the ability to induce systemic disease resistance in plants against broad spectrum phytopathogens. Induction of systemic disease resistance in faba bean (*Vicia faba* L.) against bean yellow mosaic potyvirus (BYMV) *via* seed bacterization with *Pseudomonas fluorescent* and *Rhizobium leguminosarum* has been investigated by Elbadry et al. (2006). Induction of systemic resistance by *Pseudomonas putida* strain 89B - 27 and *Serratia marcescens* strain 90–166 against *Fusarium* wilt of cucumber incited by *Fusarium oxysporum* has been investigated by Liu et al. (1995). Kloepper (1994) treated cucumber seeds with rhizobacterial strains like *Pseudomonas putida* 89B-27 and *Serratia marcescens* 90–166 and recorded a significant decrease in incidence of bacterial wilt. Similar investigations on the treatment of cucumber seeds against angular leaf spot disease caused by *Pseudomonas syringae* pv. *lachrymans*.

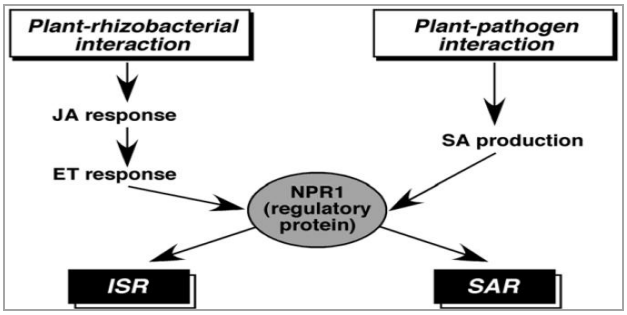

Fig. 5: Mechanism of IRS by PGPR bacteria.

Table 1. Summary of direct and indirect plant growth promoting properties of the PGPR bacteria.

PGPB properties	Beneficial effect for plant	PGPR involved	References
Biological nitrogen fixation: symbiotic, associative or free living nitrogen fixers	Enhancement in the nitrogen content of soil and hence improvement in plant growth and yield	*Enterobacter, Frankia, Pseudomonas, Rhizobium, Azospirillum, Alcaligenes, Azotobacter, Acetobacter, Bacillus, Burkholderia,*	Zewdie et al. (2000)
Phytohormone production	Influence plant physiology leading to growth promotion	*Rhizobium, Pseudomonas, Azotobacter, Bacillus, Enterobacter, Alcaligenes Xanthomonas*	Muleta et al. (2007)
Siderophore production	Enhance ferric ions solubilization and improve iron availability for plants.	*Pseudomonas, Bacillus, Serratia, Rhodococcus, Acinetobacter*	Muleta et al. (2007) Zamin et al. (2011) Sahu and Sindhu (2011)
Phosphate solubilization	Convert insoluble forms of phosphorus to plant accessible form and making it available to the plants	*Bacillus, Pseudomonas, Rhizobium, Serratia, Kushneria, Rhodococcus, Arthrobacter*	Muleta et al. (2007) Woyessa and Assefa (2011)

PGPB properties	Beneficial effect for plant	PGPR involved	References
Antagonistic behavior: extracellular lytic enzymes and HCN production	Cell lysis of soil borne fungal pathogens of plants.	*Pseudomonas, Bacillus, Serratia*	Muleta et al. (2007)
ACC deaminase	Degradation of ACC and reduce ethylene production	*Pseudomonas, Bacillus*	Muleta et al. (2007)
Metal resistance	Sequestering metal	*Pseudomonas*	Rajkumar and Freitas (2008)

Competition

Competition for nutrients and suitable niches is another key mechanism among pathogens and PGP rhizobacteria in bio-control of some plant. Rhizobactria sometimes compete with the deleterious microbes for the nutrient which is present in trace amount and that can limit the disease causing agent. Members of the *Pseudomonades* are highly efficient in competition for root resources among PGP rhizobacterial communities (Barea et al., 2002).This can be explained when there are abundant non-pathogenic rhizobacteria in soil which would rapidly colonize the surfaces of plants and also utilize nutrient available and therefore inhibit the growth of pathogenic microbes. These mechanisms are considered critical because they are difficult to study in the system but competition for the nutrient between PGPRB and pathogens is considered the most important interaction that indirectly supports the growth stimulation of the plants by inhibiting the growth of pathogens.

Importance of plant growth promoting rhizobacteria

Enhancement of root growth and nutrient uptake

The treatment of seeds with non pathogenic bacteria, such as *Agrobacterium, Alcaligenes, Bacillus, Pseudomonas, Streptomyces*, etc., induces root formation. This phenomenon might be attributed to the production of auxin, inhibition of ethylene synthesis or mineralizaton of nutrients by efficient PGPRB (Steenhoudt and Vanderleyden, 2000). More likely, PGPRBs have been reported for their immense potential to alter several hormonal pathways that could account for different morphological changes in plants like an increased elongation rate of lateral roots, resulting in more architecture in branched root system of growing plants. Inoculation of rhizobacteria increased uptake of nutrient elements like Ca, K, Fe, Cu, Mn and Zn by plants through stimulation of proton pump ATPase (Mantelin and Touraine, 2004) Reports are available on the combinations of *Bacillus* and *Microbacterium* inoculants showing improved uptake of the mineral elements by crop plants. This increase in nutrient uptake by plants might be explained through organic acid production by the plants and PGPRBs, decreasing the soil pH in rhizosphere. Ample evidences are there on the maintenance of soil fertility by the rhizobacterial isolates increasing the availability of nutrients for plants.

Develop resistance to drought stress

Drought stress causes limitation to the plant growth and productivity of agricultural crops particularly in arid and semi-arid areas. Inoculation of plants with PGPRB can enhance the drought tolerance that might be due to the production of IAA, cytokinins, antioxidants and ACC deaminase. PGPRB are also reported as beneficial to plants like tomatoes and peppers growing on water deficit soils for conferring resistance to water stress conditions. More investigations into the mechanisms by which PGPRB elicit tolerance to specific stress factors would improve our knowledge on use of these rhizobacteria in agriculture to provide induced systemic tolerance to water stress.

Application of plant growth promoting rhizobacteria

In accordance with the mechanisms presented by PGPRB, they have been classified as biofertilizers, phytostimulators and biopesticides (biocontrol agents) to describe their activities and mechanisms by which these functions are achieved.

PGPR acts as bio-fertilizers

Vessey (2003) defines bio-fertilizer as a substance which contains living microorganisms which, when applied to seed, plant surfaces, or soil colonizes the rhizosphere or the interior of the plant and promotes growth by increasing the supply or availability of primary nutrients to the host plant. Bio-fertilizers have a natural mechanism to supply nutrients to plants by solubilizing phosphorus, nitrogen fixation and by synthesis of plant growth promoting substances. There are microbes present in bio-fertilizers that increase the soil natural nutrient cycle and help in building soil organic matter and maintain the soil fertility. One of the

preferred microorganisms that has gained worldwide acceptance as beneficial bacteria is PGPRB. Phytostimulator describes the microorganism with the ability to produce or change the concentration of growth regulators such as IAA, GBA, cytokinin and ethylene (Lugtenberg and Kamilova, 2009; Somers et al., 2004). Biopesticide or biocontrol agent includes microorganisms that promote plant growth through the control of phytopathogenic agents, mainly through the production of antibiotics and antifungal metabolites such antibiotics, siderophores, HCN and antifungal metabolites, production of enzymes that degrade the cellular wall of the fungi (Vessey, 2003; Somers et al., 2004). The main advantage of using bio-fertilizer is being cheaper and safer than chemical pesticides.

PGPR as biocontrol agents

Competition for nutrients, niche exclusion, ISR and production of anti-fungal metabolites (AFMs) is the probable means responsible for biocontrol activity of PGPRBs (Bloomberg and Lugtenberg, 2001). Most of the PGPRBs are recorded to produce AFMs of which phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol (DAPG), pyoluteorin, viscosinamide and tensin are the frequently detected classes. A list of PGPRB strains used as biocontrol agents against a large number of phytopathogens and insects affecting crop plants (Table 2).

Table 2. PGPR used as biocontrol agents against different diseases, pathogens and insects affecting different crops.

PGPRBs	Crops	Disease/pathogen/insect	References
Bacillus amyloliquefaciens	Tomato	Tomato mottle virus	Murply et al. (2000)
Pseudomonas fluorescens	Tobacco	Tobacco necrosis virus	Park and Kloepper (2000)
Enterobacter sp.	Chickpea	*Fusarium avenaceum*	Hynes et al. (2008)
Azospirillum brasilense	*Prunus cerasifera* L.	Rhizosphere fungi	Russo et al. (2008)
Paenibacillus polymyxa	Sesame	Fungal disease	Ryu et al. (2006)
Bacillus licheniformis	Pepper	*Myzus persicae*	Lucas et al. (2004)

PGPR acts as rhizoremediation

PGP Rhizobacteria colonizes in rhizosphere remove environmental pollutants or prevents pollution through degradation of the toxic substance present in their vicinity. PGPRB has also been used to remediate contaminated soils and mineralize toxic organic compounds in association with plants. The combined use of PGPR and specific contaminant-degrading bacteria can successfully remove complex contaminants. The application of certain PGP rhizobacteria can increase the uptake of Ni from soils by changing its phase. Important genera of PGPR bacteria used in natural and man-created rhizoremediation includes *Bacillus, Pseudomonads, Methanobacteria, Ralstonia* and *Deinococcus, etc*. (Saier, 2007). *Rhodobacter* can fix carbon and nitrogen from air to make biodegradable plastics (Sasikala and Ramana, 1995). Bacteria *Ralstonia metallidurans* and *Deinococcoccus radiodurans* can tolerate high levels of toxic metals and radioactivity, respectively. These bacteria can also be used to clean up pollutants in iron, copper, silver and uranium mines. Specific bacteria facilitate the removal of carbon, nitrogen and phosphorus compounds while others remove toxic metals, aromatic compounds, herbicides, pesticides and xenobiotics in multi-step processes involving both aerobic and anaerobic metabolism.

Commercialization of PGPR

In the mid 1990s in the USA, *Bacillus subtilis* started to be used as seed dressing, with registrations in more than seven crops (Moar et al., 1994). This was the first major commercial success in the use of an antagonist (Bio-control). Commercial development has already been accomplished with two products marketed as Kodiak and Epic (Gustafson inc.), in which two different *Bacillus subtilis* biocontrol strains were combined with a fungicide (Carboxin PCNB-metalaxyl) for use against soil borne diseases.

The application of five commercial chitosan-based formulations of carefully chosen PGPRB developed at Auburn University, USA has previously shown demonstrable increase in the growth of nursery-raised plants such as cucumber, pepper and tomato among others. Seedlings of three IP50 and Jyothi raised in rice field soil amended with each of the formulations in a 1:40 (formulation: soil) ratio have shown significant two-fold increase in root and shoot length, and grain yield. These observations suggest that application of

such commercial bacterial formulations can serve as microbial inoculants for the improvement of rice growth (Vasudevan et al., 2002).

Conclusion

- PGPR bacteria have a multiple activities directed towards plant growth promotion and controlling pollutants and pesticides.
- It plays an important role in increase the yield of plants and has beneficial effect on the ecological system.
- It decrease the global dependence on hazardous agrochemicals which destabilize the agro-ecosystems
- In future they might replace chemical fertilizers and pesticides which have many bad effects on agriculture

Conflict of interest statement

Authors declare that they have no conflict of interest.

References

Ahemad, M., Kibret, M., 2014. Mechanisms and application s of plant growth promoting rhizobacteria: Current perspective. J King Saud Univ. Sci. 26, 1-20.

Ahemad, M., Khan, M.S., 2010a. Influence of selective herbicides on plant growth promoting traits of phosphate solubilizing of tomato plants (*Lycopersicon esculentum*) for their use as potential plant *Enterobacter asburiae* strain PS2. Res. J. Microbiol. 5, 849-857.

Ahemad, M., Khan, M.S., 2010b. Plant growth promoting activities of phosphate-solubilizing *Enterobacter asburiae* as influenced by fungicides. Eurasia. J. Biosci. 4, 88-95.

Ahmad, F., Ahmad, I., Khan, M.S., 2008. Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. Microbiol. Res. 163, 173-181.

Antoun, H., Beauchamp, C.J., Goussard, N., Chabot, R., Lalande, R., 1998. Potential of *Rhizobium* and *Bradyrhizobium* species as plant growth promoting rhizobacteria on non-legumes: Effect on radishes (*Raphanus sativus* L.). Plant Soil. 204, 57-67.

Barea, J.M., Azcón, R., Azcón-Aguilar, C., 2002. Mycorrhizosphere interactions to improve plant fitness and soil quality Antonie Van Leeuwenhoek. 81, 343-351.

Benizri, E., Baudoin, E., Guckert, A., 2001. Root colonization by inoculated plant growth rhizobacteria. Biocont. Sci. Technol. 11, 557-574.

Bhattacharyya, P.N., Jha, D.K., 2012. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. World J. Microbiol. Biotechnol. 28, 1327-1350.

Bloomberg, G.V., Lugtenberg, B.J.J., 2001. Molecular mechanism of plant growth promotion and biocontrol by rhizobacteria. Curr. Opin. Plant Biol. 4, 343-350.

Burdman, S., Jurkevitch, E., Okon, Y., 2000. Recent advances in the use of plant growth promoting rhizobacteria (PGPR) in agriculture. In: Microbial Interactions in Agriculture and Forestry (Eds.: Subba Rao, N.S., Dommergues, Y.R.). Science Publishers, Enfield, NH, USA. pp.229-250.

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

Elbadry, M., Taha, R.M., Eldougdoug, K.A., Gamal-Eldin, H., 2006. Induction of systemic resistance in faba bean (*Vicia faba* L.) to bean yellow mosaic potyvirus (BYMV) via seed bacterization with plant growth promoting rhizobacteria. J. Plant Dis. Prot. 113, 247-251.

Gamalero, E., Lingua, G., Berta, G., Glick, B. R., 2009. Beneficial role of plant growth promoting bacteria and arbuscular mycorrhizal fungi on plant responses to heavy metal stress. Can. J. Microbiol. 55, 512-514.

Glick, B.R., Cheng, Z., Czarny, J., Duan, J., 2007. Promotion of plant growth by ACC deaminase-producing soil bacteria. Eur. J. Plant Pathol. 119, 329-339.

Glick, B.R., 2005. Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol. Lett. 251, 1-7.

Glick, B.R., 2012. Plant Growth-Promoting Bacteria: Mechanisms and Applications. Hindawi Publishing Corporation, Scientifica.

Glick, B.R., Patten, C.L., Holguin, G., Penrose, G.M., 1999. Biochemical and Genetic Mechanisms Used by Plant Growth Promoting Bacteria. Imperial College Press, London.

Gray, E. J., Smith, D. L., 2005. Intracellular and extracellular PGPR: Commonalities and distinctions in the plant-bacterium signaling processes. Soil Biol. Biochem. 37, 395-412.

Hynes, R.K., Leung, G.C.Y., Hirkala, D.L.M., Nelson, L.M., 2008. Isolation, selection and characterization of beneficial rhizobacteria from pea, lentil and chickpea grown in Western Canada. Can. J. Microbiol. 54, 248-258.

Innes, L., Hobbs, P.J., Bardgett, R.D., 2004. The impacts of individual plant species on rhizosphere microbial communities in soils of different fertility. Biol. Fertil. Soils. 40, 7-13.

Kang, S.M., Joo, G. J., Hamayun, M. et al., 2009. Gibberellin production and phosphate solubilization by newly isolated strain of *Acinetobacter calcoaceticus* and its effect on plant growth. Biotechnol. Lett. 31(2), 277-281.

Khan, M. S., Zaidi, A., Wani, P. A., 2007. Role of phosphate-

solubilizing microorganisms in sustainable agriculture-a review. Agron. Sustain. Develop. 27(1), 29-43.

Kim, J., Rees, D.C., 1994. Nitrogenase and biological nitrogen fixation. Biochemistry. 33, 389-397.

Kloepper, J.W., Leong, J., Teintze, M., Schroth, M.N., 1980. Enhanced plant growth by siderophores produced by plant growth promoting rhizobacteria. Nature. 286, 885-886.

Kloepper, J.W., 1994. Plant growth-promoting rhizobacteria (other systems). In: *Azospirillum*/Plant Associations (Ed.: Okon, Y.). CRC Press, Boca Raton, FL, USA. pp.111-118.

Ladha, J.K., de Bruijn, F.J., Malik, K.A., 1997. Introduction: assessing opportunities for nitrogen fixation in rice-a frontier project. Plant Soil. 124, 1-10.

Lugtenberg B., Kamilova, F., 2009. Plant-growth-promoting rhizobacteria. Annu. Rev. Microbiol. 63, 541-556.

Marschner, P., Crowley, D., Yang, C. H., 2004. Development of specific rhizosphere bacterial communities in relation to plant species, nutrition and soil type. Plant Soil. 261, 199-208.

McKenzie, R.H., Roberts, T.L., 1990. Soil and fertilizers phosphorus update. In: Proceedings of Alberta Soil Science Workshop, Feb. 20–22, Edmonton, Alberta. pp.84-104.

Morgan, J. A. W., Bending, G. D., White, P. J., 2005. Biological costs and benefits to plant–microbe interactions in the rhizosphere. J. Exp. Bot. 56, 1729-1739.

Muleta, D., Assefa, F., Granhall, U., 2007. *In vitro* antagonism of rhizobacteria isolated from *Coffea arabica* L. against emerging fungal coffee pathogens. Eng. Life Sci. 7, 1-11.

Prakash, P, Karthikeyan, B., 2013. Isolation and purification of plant growth promoting rhizobacteria (PGPR) from the rhizosphere of *Acorus calamus* grown soil. Ind. Streams Res. J. 3, 1-13.

Rodriguez, H., Fraga, R., 1999. Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol. Adv. 17, 319-339.

Salamone, I.E.G., Hynes, R.K., Nelson, L.M., 2005. Role of cytokinins in plant growth promotion by rhizosphere bacteria in PGPR: Biocontrol and biofertilization (Ed.: Siddiqui, Z.A.). Springer, Amsterdam, The Netherlands. pp.173-195.

Spaepen, S, Vanderleyden, J., Remans, R., 2007. Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiol. Rev.31, 425-448.

Tao, G.C., Tian, S.J., Cai, M.Y., Xie, G.H., 2008. Phosphate solubilizing and -mineralizing abilities of bacteria isolated from soils. Pedosphere. 18, 515-523.

Vessey, J. K., 2003. Plant growth promoting rhizobacteria as biofertilizers. Plant Soil. 255, 571-586.

Weller, D.M., Thomashow, L.S., 1994. Current challenges in introducing beneficial microorganisms into the rhizosphere. In: Molecular Ecology of Rhizosphere Microorganisms: Biotechnology and Release of GMOs (Eds.: O'Gara, F., Dowling, D.N., Boesten, B.). VCH: New York, NY, USA. pp.1-18.

Woyessa, D., Assefa, F., 2011. Diversity and plant growth promoting properties of rhizobacteria isolated from tef under greenhouse condition. Res. J. Microbiol. 6, 343-355.

Zahir, Z. A., Arshad, M., Frankenberger, W. T. J., 2003. Plant growth promoting rhizobacteria: Applications and perspectives in agriculture. Adv. Agron. 81, 97-168.

Zaidi, A., Khan, M.S., Ahemad, M., Oves, M., 2009. Plant growth promotion by phosphate solubilizing bacteria. Acta Microbiol. Immunol. Hungarica. 56, 263-284.

Zewdie, S., Assefa, F., Fetene, M., 2000. Effects of *Azospirillum* isolates on the growth and nitrogen content of tef. J. Sci. 23(2), 247-262.

Zhang, H., Sekiguchi, Y., Hanada, S., Hugenholtz, P., Kim, H., 2003. *Gemmatimonas aurantiaca* gen. nov, sp. nov, a Gram-negative, aerobic, polyphosphate accumulating microorganism, the first cultured representative of the new bacterial phylum Gemmatimonadetesphyl. nov. Int. J. Syst. Evol. Microbiol. 53, 1155-1163.

How to cite this article:
Tsegaye, Z., Assefa, F., Beyene, D., 2017. Properties and application of plant growth promoting rhizobacteria. Int. J. Curr. Trend. Pharmacobiol. Med. Sci. 2(1), 30-43.