SOIL & CROP SCIENCES | REVIEW ARTICLE

Portraying mechanics of plant growth promoting rhizobacteria (PGPR): A review

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Abstract: Population growth and increase in food requirement is the global problem. It is inevitable to introduce new practices that help to increase agricultural productivity. Use of plant growth promoting rhizobacteria (PGPR) has shown potentials to be a promising technique in the practice of sustainable agriculture. A group of natural soil microbial flora acquire dwelling in the rhizosphere and on the surface of the plant roots which impose beneficial effect on the overall well-being of the plant are categorized as PGPR. Researchers are actively involved in understanding plant growth promoting mechanics employed by PGPR. Broadly, these are divided into direct and indirect mechanics. Any mechanism that directly enhances plant growth either by providing nutrients or by producing growth regulators are portrayed as direct mechanics. Whereas, any mechanisms that protects plant from acquiring infections (biotic stress) or helps plant to grow healthily under environmental stresses (abiotic stress) are considered indirect mechanics. This review is focused to describe cogent mechanics employed by PGPR that assists plant to sustain healthy growth. Also, we emphasized on the PGPR-based products which have been commercially developed exploiting these mechanics of PGPR.

Subjects: Agronomy; Environment & Agriculture; Food Science & Technology; Plant & Animal Ecology; Soil Sciences

Keywords: plant growth-promoting rhizobacteria (PGPR); indole acetic acid (IAA); phosphate solubilization; siderophore production; antibiotic production; induced systematic resistance (ISR); ACC deaminase

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PUBLIC INTEREST STATEMENT

New and improved eco friendly techniques has to be introduced in the agriculture practices owing to the constant increase in the food demand due to growing global population. Use of chemical fertilizers do give good agricultural productivity but it slowly deteriorates agriculture land. Use of biofertilizers is an eco friendly substitution to the use of chemical fertilizers. Biofertilizers are composed of bacterial species which are beneficial to the plant growth and such microbes are termed as plant growth-promoting rhizobacteria (PGPR). Researchers are studying these microbes for the past 30 years to understand the mechanics employed by PGPR to support plant growth. Over the period of time, some of the mechanics of PGPR are well understood which we like to portray in this review.
1. Introduction
Worldwide growth in population, increase in the demand of global food production, and environmental damage causing problems in agriculture yield are major concerns to the world. These problems may soon cause insufficiency to feed all of the world’s population (Ladeiro, 2012). Current population of world is 7 billion and expected to reach 10 billion by next 50 years. Agricultural strategies to feed all of these individuals are an important challenge in twenty-first century (Glick, 2014). For the same it is essential that agricultural productivity should be significantly increased within the next few decades.

Adding up in to the above mentioned constrains, there is loss in the productivity of agricultural production due to environmental abiotic and biotic stresses posed on the crops growing in the field. Abiotic stresses such as soil salinization, soil sodification, drought, soil pH, and environmental temperature are major limiting factors in crop production. Soil salinization and soil sodification are one of the most widespread soil degradation processes on the earth endangering the potential use of soils (Ladeiro, 2012; Rengasamy, 2006). Soil salinization affects an estimated 1–3 million hectares in Europe, mainly in the Mediterranean countries. Drought is another influencing factor aiding soil degradation and soil desertification. The Global Assessment of Soil Degradation (GLASOD) estimated that about 13% (or 850 million ha) of the land in Asia and the Pacific is degraded due to soil salinization, soil sodification, and drought (Ladeiro, 2012). Outside Asia, 104 million ha were estimated to be degraded in the Pacific subregion where large-scale clearance of forest land has caused a decline in soil structure and fertility. Another abiotic factor, water erosion is a severe threat to soil degradation that occurs in the Himalayas, Central Asia, China, the South Pacific, and Australia, while the GLASOD study indicated that in the South Asian subregion Afghanistan, India, Iran, and Pakistan are the worst affected by wind erosion (Ladeiro, 2012).

On the other hand, biotic stress that causes reduction in agricultural yield is due to the diseases caused in field crops by other living organisms, such as bacteria, viruses, fungi, and parasites. Out of all these, two-third of total diseased plants are infected by fungi. These diseases decrease the annual agriculture yield by at least 30% globally (Fisher et al., 2012). Thus, abiotic factors and stress have always played major role in reducing agriculture yield. Any technology that is hypothesized overcome such constrains in food production is inevitable. The only visible solutions that can produce more agricultural yield are: (1) Better Agricultural land management; (2) Greater use of chemicals including fertilizers; (3) Safe and efficient Pesticides and herbicides; (4) More farm mechanization; (5) Greater use of transgenic crops; and (6) Expanded use of plant growth-promoting rhizobacteria (PGPR) (Glick, 2014).

Several of the above-mentioned solutions to enhance agricultural yield will only be effective in the short term as the world we live is finite with limited resources, so any effective and longer term solutions to provide food for the world must include sustainable and eco friendly biological solutions. To this end, the persistent use of PGPR in agriculture is a striking technology hypothesized to overcome this constrain. In context to this problem, Glick (2014) quoted “Scientists have dramatically increased our knowledge of the mechanisms employed by PGPR in the past 15–20 years, additional understanding of the fundamental mechanisms employed by these bacteria will likely hasten the acceptance of these organisms as suitable and effective adjuncts to agricultural practice.” Thus, to isolate and characterize PGPR aiming to understand fundamental mechanics for enhancing any sort of plant growth under stress condition should be the primary agenda of the research.

2. Plant growth-promoting rhizobacteria
Microbial populations are found to be present in diverse ecological niches, including extreme environments present in both lithosphere and hydrosphere, where their metabolic abilities play a critical role in geochemical nutrient cycling (Aeron, Kumar, Pandey, & Maheshwari, 2011; Daniel, 2005; Jha, Aeron, Patel, Maheshwari, & Saraf, 2011). Soil bacterial population, in particular, have the ability to grow rapidly and utilize a very wide range of different substances as nutrient sources. Bacterial flora are dispersed within the soil, often attached to soil particles, many interact with the roots of plants.
Rhizosphere is one such well-characterized ecological niche comprising volume of soil surrounding plant roots with highest bacterial population that are influenced by root exudates as defined by Hiltner (1904). It is quiet common that the bacterial population in the rhizosphere are 100–1,000 times higher than in bulk soil. This is because such bacteria possess metabolic versatility to adapt and utilize root exudates efficiently. Also, 15% of the root surface is covered by microbial populations belonging to several bacterial species (Govindasamy et al., 2011; Jha, Patel, Rajendran, & Saraf, 2010). Plant photosynthetic product (about 5 to 30%) is secreted by roots in form of different sugars which in turn is utilized by microbial populations (Glick, 2014). Subsequent metabolic activities of these bacteria in the rhizosphere kindle mineral nutrient transport and uptake by plant roots (Glick, 1995). Plant growth-promoting rhizobacteria (PGPR) include bacteria that reside in the rhizosphere and improve plant health ultimately aiding to augment plant growth. Majority of credible group of PGPR belongs to genera *Acinetobacter*, *Agrobacterium*, *Arthobacter*, *Azotobacter*, *Azospirillum*, *Burkholderia*, *Bradyrhizobium*, *Rhizobium*, *Frankia*, *Serratia*, *Thiobacillus*, *Pseudomonads*, and *Bacillus* (Glick, 1995; Vessey, 2003). In the last 10 years, the role of the rhizosphere as an ecological niche in the functioning of the biosphere has allowed PGPR to gain importance which eventually aided research to understand the mechanics of PGPR in the rhizosphere. A putative rhizobacteria qualifies as PGPR when it is able to produce a positive effect on the plant upon inoculation, hence demonstrating good competitive skills over the existing rhizosphere communities. Generally, about 2–5% of rhizosphere bacteria are PGPR (Antoun & Prévost, 2006; Jha et al., 2010; Sgroy et al., 2009; Siddikee, Chauhan, Anandham, Han, & Sa, 2010). PGPRs are the potential tools for sustainable agriculture and trend for the future. One of the mechanisms by which bacteria are adsorbed onto soil particles is by ion exchange. A soil is said to be naturally fertile when the soil organisms are releasing inorganic nutrients from the organic reserves at a rate sufficient to sustain rapid plant growth.

Looking backwards in detail, the importance of rhizobacteria for the plant health was showed by Kloepper and Schroth (1978) during Fourth International Congress of Bacterial Plant Pathogens, conducted in France. However, the term PGPR was coined by the same author in 1980 (Good et al., 1994). Currently, the number of works per year on this topic has increased, creating a new discipline that has changed the basic traditional concepts of plant physiology and microbial ecology. Later, Bashan and Holguin (1998) proposed a revision of the original definition of the term PGPR, since there are a number of bacteria that have a beneficial effect on the plant even though they are outside the rhizosphere environment. The augmentative effect of PGPR occurs through various mechanisms. The role of PGPR is not solely implemented by the direct effect of a single bacterial strain but by the molecular dialogue established among soil micro-organisms and plant. With this knowledge, let us see in detail the mechanics employed by PGPR for plant growth promotion.

3. Direct and indirect mechanics of PGPR

A thorough understanding of the plant growth-promoting (PGP) mechanics is inevitable to manipulate the rhizosphic flora in order to maximize the processes that strongly enrich plant productivity. PGP mechanisms have been grouped traditionally into direct and indirect mechanisms. The difference between the two is not always evident, indirect mechanisms, as a general rule, are those that happen outside the plant, while direct mechanisms are those that occur inside the plant and directly affect the plant’s metabolism (Antoun & Prévost, 2006; Glick, 1995; Siddikee et al., 2010; Vessey, 2003). Accordingly, direct mechanisms include those that affect the balance of plant growth regulators, either because the micro-organisms themselves release growth regulators that are integrated into the plant or because the micro-organisms act as a sink of plant-released hormones, and those that induce the plant’s metabolism leading to an improvement in its adaptive capacity (Glick, 2014; Govindasamy et al., 2011). Whereas, indirect mechanism require the participation of the plants defensive metabolic processes, which respond to the signal sent from the bacteria influencing the plant. Two important mechanisms are included in this group: induction of systemic resistance to plant pathogens (biotic stress) and protection against unhealthy environment conditions (abiotic stress) (Aeron et al., 2011; Glick, 2014; Jha et al., 2011; Ramos-Solano, Barriuso, & Gutiérrez-Mañero, 2008).
3.1. Direct mechanics of PGPR

3.1.1. Biological nitrogen fixation

Bacterial strains possessing the trait of nitrogen fixation are classified into two categories. First category includes root/legume-associated symbiotic bacteria which possess the specificity and infect the roots to produce nodule e.g. strains of *Rhizobium*. Other group of bacteria are the so-called free-living nitrogen fixers which do not possess specificity to plant (Oberson et al., 2013). Examples of such free-living nitrogen fixers include *Azospirillum*, *Azotobacter*, *Burkholderia*, *Herbaspirillum*, *Bacillus*, and *Paenibacillus* (Goswami, Parmar, Vaghela, Dhandhukia, & Thakker, 2015; Heulin, Achouak, Berge, Normand, & Guinebretière, 2002; Seldin, Van Elsas, & Penido, 1984; von der Weid, Duarte, von Elsas, & Seldin, 2002). Although free-living nitrogen fixers do not penetrate the plant’s tissues, yet a very close relationship is established where these bacteria live sufficiently close to the root such that the atmospheric nitrogen fixed by the bacteria that is not used for their own benefit, but is taken up by the plant allowing better availability of nitrogen absorption. This relationship is described as a non-specific and loose symbiosis. Stacey, Burris, and Evans (1992) report that the amount of nitrogen fixed ranges between 20 and 30 kg per hectare per year. Species belonging to *Azotobacter* and *Azospirillum* are the most widely used in agricultural trials. The first report appeared in 1902 and it was widely used across the globe till date (Bhattacharyya & Jha, 2012). Several strains of these genera have gained importance as along with nitrogen fixation they also enhance plant growth by producing phytohormones including indole-3-acetic acid, gibberellic acid, and cytokinins. Application of *Azotobacter chroococcum* and *Azospirillum brasilense* inoculants in agriculture, especially in cereals has resulted in notable increases in crop yields (Oberson et al., 2013).

Over the period of time, strains other than *Azotobacter* and *Azospirillum* that have gained importance due to nitrogen fixation ability are strains of *Bacillus* and *Paenibacillus* as they have been reported to possess *nif* gene cluster which is responsible to code nitrogenase enzyme, a key enzyme required for fixing nitrogen. *Bacillus azotoфиксans*, *Bacillus macerans*, and *Bacillus polymyxa*, were identified as nitrogen fixers, based on nitrogenase activity (Seldin et al., 1984) however, after reclassification, these organisms are now classified in *Paenibacillus* genus. *Paenibacillus odorifer*, *Paenibacillus graminis*, *Paenibacillus peoriae*, and *Paenibacillus brasiliensis* have been described as nitrogen fixers (Heulin et al., 2002; von der Weid et al., 2002). Other *Paenibacillus* species viz. *P. azotoфиксans*, *P. macerans*, *P. polymyxa*, *P. graminis*, and *P. odorifer* were identified to possess the presence of *nif* gene cluster (Heulin et al., 2002). Ding, Wang, Liu, and Chen (2005) isolated and identified nitrogen-fixing strains from plant rhizospheres in Beijing region, reporting the presence of *nif* genes in both genera *Bacillus* and *Paenibacillus*. Several reports suggesting the presence of nitrogen-fixing ability by *P. polymyxa* are available (Govindasamy, Senthilkumar, & Upendra-Kumar, 2008). Guemouri-Athmani et al. (2000) measured the nitrogenase activity of several strains of *P. polymyxa* recovered from Algerian soil using acetylene reduction assay which showed only 14 of the 23 strains tested were able to reduce acetylene. *P. azotoфиксans* (ATCC 35681T) is most efficient nitrogen-fixing bacterium studied so far among the genus *Paenibacillus* and *Bacillus* (Govindasamy et al., 2008; Seldin et al., 1984). Hence, nitrogen fixation is considered as an important trait of PGPRs as it directly provides nitrogen to the plant. Nitrogen-fixing strains are marketed as biofertilizers for 20 years and they are considered important for agriculture (Goswami et al., 2015; Heulin et al., 2002).

3.1.2. Phosphate solubilization

After nitrogen, phosphorous is the most limiting nutrient for plants. Despite profound abundant reserves of phosphorous, it is not available in form suitable for plant uptake. Plants are only able to absorb mono- and dibasic phosphate which are the soluble forms of phosphate (Jha, Patel, & Saraf, 2012; Jha & Saraf, 2015). Micro-organisms mineralize organic phosphorus in soil by solubilizing complex-structured phosphates viz. tricalcium phosphate, rock phosphate, aluminum phosphate, etc. which turns organic phosphorous to inorganic form ultimately aiding the phosphate availability to plants. These phosphate-solubilizing bacteria use different mechanism(s) to solubilize the insoluble forms of the phosphate. The primary mechanism of phosphate solubilization is based on organic acid secretion by microbes because of sugar metabolism. Organisms residing in the rhizosphere...
utilize sugars from root exudates; metabolize it to produce organic acids (Goswami, Dhandhukia, Patel, & Thakker, 2014; Goswami, Pithwa, Dhandhukia, & Thakker, 2014). These acids released by the micro-organisms act as good chelators of divalent Ca²⁺ cations accompanying the release of phosphates from insoluble phosphatic compounds. Many of the phosphate-solubilizing microbes lower the pH of the medium by secretion of organic acids such as acetic, lactic, malic, succinic, tartaric, gluconic, 2-ketogluconic, oxalic and citric acids (Patel, Goswami, Dhandhukia, & Thakker, 2015; Rodríguez & Fraga, 1999) and their detection using high-performance liquid chromatography (HPLC) is also reported (Buch, Archana, & Naresh-Kumar, 2008). The involvement of micro-organisms in the solubilization of inorganic phosphates was known since 1903 (Kucey, Janzen, & Leggett, 1989).

It is estimated that phosphate-solubilizing micro-organisms constitute 20–40% of the culturable population of soil micro-organisms of which significant proportion of these bacteria can be isolated from rhizosphere soil (Chabot, Antoun, & Cescas, 1993). Most phosphate solubilizers isolated from the rhizosphere of various plants are known to be metabolically more active than those isolated from sources other than rhizosphere. Phosphate tends to react with calcium (Ca), iron (Fe), or aluminum (Al) leading to its precipitation making it unavailable for plant uptake. Inorganic phosphate in acidic soils is associated with Al and Fe compounds, whereas calcium phosphates are found in calcareous soils in the form of inorganic phosphates. Organic phosphate makes up a large fraction of soluble phosphate which is about 50% in soils with high organic matter (Barber, 1995). Hexaphosphate salt of inositol, so-called phytate, is the major form of phosphate in organic form which constitute up to 80% of the total organic phosphate (Alexander, 1977). Although micro-organisms are known to produce phytases that can hydrolyze phytate, however phytate tends to form insoluble complexes with Fe, Al, and Ca and accumulates in soils (Alexander, 1977; Jha et al., 2012).

Among the soil bacterial communities, ectorrhizospheric (residing on roots and in rhizospheric soil) strains from *Pseudomonas* and *Bacilli*, and endosymbiotic (residing within the roots/nodules) rhizobia have been described as effective phosphate solubilizers (Goswami, Patel, et al., 2014). *Bacillus megaterium*, *B. circulans*, *B. coagulans*, *B. subtilis*, *P. polymyxa*, *B. sircalmous*, and *Pseudomonas striata* could be referred as the most important strains (Govindasamy et al., 2013; Goswami, Vaghela, Parmar, Dhandhukia, & Thakker, 2013; Kucey et al., 1989). *Pseudomonas fluorescens*, *Erwinia herbicola*, *Pseudomonas cepacia*, and *Burkholderia cepacia* are reported as efficient producers of gluconic acid which is the most frequent agent in mineral phosphate solubilization (Rodríguez & Fraga, 1999). *Rhizobium leguminosarum* is reported to produce 2-ketogluconic acid which aids in the solubilization of phosphate. *Rhizobium meliloti* and *Bacillus firmus* produce 2-ketogluconic acid (Banik & Dey, 1982; Halder & Chakrabartty, 1993; Halder, Mishra, Bhattacharyya, & Chakrabartty, 1990). Mixtures of lactic, isovaleric, isobutyric, and acetic acids are frequently produced by the strains of *Bacillus licheniformis* and *B. amyloliquefaciens*. 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 (Banik & Dey, 1982; Chen et al., 2006; Illmer & Schinner, 1992; Jha & Saraf, 2015). Figure 1 shows the schematic summary of phosphate solubilization mechanism employed by PGPR.

### 3.1.3. Phytohormone production

Classes of well-known phytohormones include auxins, gibberellins, cytokinins, ethylene, and abscisic acid and soil micro-organisms, particularly the rhizosphere bacteria, do possess the potential to produce these hormones (Arshad & Frankenberger, 1998; Patten & Glick, 1996). Plant responds to any phytohormone in the rhizosphere that are supplemented externally or been produced by microbial flora residing in the rhizosphere. These phytohormones can mediate processes including plant cell enlargement, division, and extension in symbiotic as well as non-symbiotic roots (Glick, 2014; Patten & Glick, 1996).

#### 3.1.3.1. Indole-3-acetic acid (IAA)—an auxin produced by several PGPR

Phytohormones, especially auxins control several stages of plant growth and development such as cell elongation, cell division, tissue differentiation, and aid apical dominance. The microbial biosynthesis and the fundamental
mechanism of auxins action on plant have undergone intense investigation. Auxin, indole-3-acetic acid (IAA), is an important phytohormone produced by several strains of PGPR and it is well-known that treatment of IAA-producing rhizobacteria increases the plant growth (Amara, Khalid, & Hayat, 2015; Kaymak, 2011; Vessey, 2003). Primarily, IAA is known to stimulate both rapid (e.g. increase in cell elongation) and long-term (e.g. cell division and differentiation) responses in plants. Plant under the long-term treatment of IAA has highly developed roots, which in turn allows the plant to uptake better nutrients ultimately aiding overall growth of the plant (Aeron et al., 2011). About 80% of the bacterial flora in the rhizosphere produce IAA; so applying such micro-organisms in the field enhance the endogenous IAA levels of plant and therefore, it has remarkable effect on plant growth. Auxins are known to effect whole plant but as PGPRs produce IAA in the rhizosphere, plant roots are relatively more affected by these IAA produced by PGPR and so plant roots are principally affected (Salisbury, 1994). IAA released by rhizobacteria mainly affect the root system by increasing its size and weight, branching number, and the surface area in contact with soil. All these changes lead to an increase in its ability to probe the soil for nutrient exchange, therefore improving plant’s nutrition pool and growth capacity (Gutierrez-Manero et al., 2001; Ramos-Solano et al., 2008). IAA also drives the differentiation of adventitious roots from stem as auxins induce stem tissues to redifferentiate as root tissue. Etesami, Alikhani, and Hosseini (2015) reported that the PGPRs residing in rhizosphere, rhizoplane, and endophytic niches can produce IAA and support plant growth.

Different PGPRs possess different routes for the synthesis of IAA. IAA is synthesized by plant-associated microbes via L-tryptophan-dependent and independent pathways, and three L-tryptophan-dependent pathways are known. Most of these PGPRs utilize L-tryptophan which is secreted in root exudates as a precursor for IAA production. Very few examples of IAA produced by L-tyrptophan independent pathway are known, one of the most studied organism which produces IAA by this route is Azospirillum brasilense, where more than 90% of IAA produced is by L-tryptophan independent pathway and remaining 10% IAA is produced by utilizing L-tryptophan. However, the exact pathway and enzymes used for IAA synthesis by this route is still not known (Jha & Saraf, 2015; Spaepen, Vanderleyden, & Remans, 2007).

Three L-tryptophan-dependent routes for the production from L-tryptophan is described in Figure 2. Briefly, bacteria such as Rhizobium, Bradyrhizobium, and Azospirillum synthesize IAA via the Indole-3-pyruvic acid (IPyA) pathway (Burdman, Jurkevitch, Okon, Subba-Rao, & Dommergues,
On the other hand, some pathogenic bacteria such as *Agrobacterium tumefaciens*, *Pseudomonas syringae*, *Pantoea agglomerans*, *Rhizobium*, *Bradyrhizobium*, and *Erwinia herbicola* synthesize IAA predominantly via the indole-3-acetamide (IAM) pathway (Dobbelaere, Vanderleyden, & Okon, 2003), whereas, *Bacillus subtilis*, *B. licheniformis*, *B. megaterium*, etc. produce IAA via tryptamine pathway.

3.1.3.2. Cytokinins: Cytokinins represent another class of phytohormones produced by microorganisms (Persello-Cartieaux, Nussaume, & Robaglia, 2003). Frankenberger and Arshad (1995) elaborate the role of auxins, cytokinins, gibberellins, ethylene and abscisic acids which, when applied to plants, help in increasing plant yield and growth. Similar to IAA, plant responses to exogenous applications of cytokinin result in enhanced cell division, enhanced root development, enhanced root hair formation, inhibition of root elongation, shoot initiation, or certain other physiological responses (Amara et al., 2015; Frankenberger & Arshad, 1995; Jha & Saraf, 2015). Cytokinins are N6-substituted amino-purines which, when applied to plants, influence their physiological and developmental processes (Maheshwari, Dheeman, & Agarwal, 2015; Salisbury & Ross, 1992). Other processes such as developmental processes such as the formation of embryo vasculature, nutritional signaling, leaf expansion, branching, chlorophyll production, root growth, promotion of seed germination, and delay of senescence are also heavily influenced by cytokinins (Wong, Tan, Ge, Chen, & Yong, 2015).

Cytokinin production in several plant-associated microbes has been well characterized (Kado, 1984; Kaiss-Chapman & Morris, 1977). These microorganisms, which belong to diverse genera such as *Pseudomonas*, *Azospirillum*, and *Bacillus* have been isolated from a wide range of plant species, such as barley, canola, bean, and *Arabidopsis* (Alexandre, Jocaud, Faure, & Bally, 1996; Persello-Cartieaux et al., 2001). Ortiz-Castro, Valencia-Cantero, and López-Bucio (2008) reported the identification of a *Bacillus megaterium* strain that promoted the growth of *A. thaliana* and *P. vulgaris* seedlings through cytokinins production. Other different bacterial genera *Proteus*, *Klebsiella*, and *Escherichia coli* have been found to be able to synthesize cytokinins.
Escherichia, Pseudomonas, and Xanthomonas have also been reported to possess the ability to produce cytokinins (Maheshwari et al., 2015).

Most abundant cytokinins are adenine-type, where the N6 position of adenine is substituted with an isoprenoid, such as in zeatin, or an aromatic side chain, such as in kinetin. Zeatin can be synthesized in two different pathways: the tRNA pathway and the adenosine monophosphate (AMP) pathway (Figure 3). In the tRNA pathway zeatin is a recycled product of isopentenylated tRNAs. In the AMP pathway, zeatin is synthesized from an isopentenyl donor, dimethylallyldiphosphate (DMAPP), and AMP, adenosine diphosphate (ADP), or adenosine triphosphate (ATP) by isopentenyl transferases. After synthesis cytokinins can be glucosylated. In brief, for biosynthesis of cytokinins, two pathways have been proposed: direct pathway, involving development of DMAPP and N6-isopentenyladenosine monophosphate (i6 AMP) from AMP, followed by formation zeatin-type compounds from hydroxylation of the side chain; and indirect pathway, in which cytokinins are released by turnover of tRNA containing cis-zeatin (Amara et al., 2015). Zeatin, a type of cytokinin, is widely produced by PGPR and their pathways of biosynthesis are vividly shown in Figure 3.

Researchers back in early 1970s have proved the production of cytokinins by microbes. Phillips and Torrey (1972) reported cytokinin-like substances in the culture filtrates of Rhizobium leguminosarum.
and *Bradyrhizobium japonicum* 61A68, which was later identified as zeatin. Upadhyaya, Letham, Parker, Hocart, and Dart (1991) recorded the production of isopentenyladenine (IPA) and zeatin (Z) in substantial amounts by two Rhizobium strains ANU 240 and IC 3342. Garcia de Salamone, Hynes, and Nelson (2001) reported the growth-promoting effect of *Pseudomonas* G20-18 on wheat and radish plants by production of cytokinin. Later, Karnwal and Kaushik (2011) reported the production of IPA, dihydroxyzeatin riboside (DHZR), and zeatin riboside (ZR) by *Pseudomonas fluorescens* AK1 and *Pseudomonas aeruginosa* AK2 and showed growth promotion in rice seedling. Over the course of time, more than 30 different growth-promoting cytokinins compounds have been found in plants, plant-associated micro-organisms, and in *in vitro* conditions most of the micro-organisms are capable of releasing cytokinins with different proportions (Amara et al., 2015; Maheshwari et al., 2015).

3.1.3. Gibberellins: Gibberellins (GAs) are a large group of phytohormones which constitute as many as 136 different structured molecules. It is a group of phytohormones that influence many developmental processes in higher plants, including seed germination, stem elongation, flowering, and fruit setting (Hedden & Phillips, 2000). To date, 136 GAs from 128 plant species are known, 28 GAs from 7 fungal species, and only 4 GAs (GA1, GA3, GA4, and GA20) from 7 bacterial species have been identified (MacMillan, 2001). Plant growth promotion by PGPR species that produce GAs has been reported (Atzorn, Crozier, Wheeler, & Sandberg, 1988; Bastián et al., 1998; Gutierrez-Manero et al., 2001). The production of gibberellins by bacillus strains is rare, with only two strains being documented that are capable to produce gibberellins are *B. pumilus* and *B. licheniformis* (Gutierrez-Manero et al., 2001). The common structure of these class of growth regulators, is a skeleton of 19–20 carbon atoms. The reason for the pronounced effect of gibberellins is that these hormones can be translocated from the roots to the aerial parts of the plant. The effects in the aerial part are notable and more so when the bacteria also produce auxins that stimulate the root system by enhancing the nutrient supply to facilitate growth in the aerial part (Wong et al., 2015).

The first report of gibberellin characterization in bacteria using physicochemical methods was by Atzorn et al. (1988), who demonstrated the presence of GA1, GA4, GA7, and GA20 in gnotobiotic cultures of *Rhizobium meliloti*. Apart from *Azospirillum* sp. and *Rhizobium* sp. production of gibberellin-like substances has also been claimed in numerous bacterial genera, although the techniques used (TLC, bioassays, and HPLC-UV) are of poor resolution and lack reliability. Using explicit physicochemical methods, such as Gas Chromatography-Mass Spectroscopy (GC-MS), production of gibberellins was confirmed in *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae* (Bastión et al., 1998), and *Bacillus* sp. (Gutierrez-Manero et al., 2001) in addition to *Azospirillum* sp. Over the course of time, detection and quantification of gibberellins is possible using spectroscopy, high-performance thin layer chromatography, HPLC, etc. The extraction and detection procedures for quantifying gibberellins from microbes are described by Patel et al. (2015).

In fungi, the general pathway is similar to that of higher plants, although the genes and enzymes involved differ. Effect of PGPR producing GAs on plant is not exactly known but such bacteria are used in the seed germination. Whereas, several reports suggests that GAs producing fungi are considered as phytopatogens (Malonek et al., 2005). Discovery of this group of plant hormones is linked to the study of pathogen fungus *Giberella fujikuroi*, and several published report suggest that pathogenic fungi produce GAs (Kudoyarova, Arkhipova, & Melent’ev, 2015).

3.2. Indirect mechanics of PGPR

3.2.1. Siderophore production

Iron is an essential nutrient for plants. It acts as a cofactor in a number of enzymes essential to important physiological processes such as respiration, photosynthesis, and nitrogen fixation so its deficiency is exhibited in severe metabolic modifications. Iron is quite abundant in soils but is frequently unavailable for plants or soil micro-organisms. Predominant chemical specie, Fe$^{3+}$ is the oxidized form that reacts to form insoluble oxides and hydroxides inaccessible to plants and micro-organisms. Plants have developed two strategies for efficient iron absorption. The first
consists of releasing organic compounds capable of chelating iron, thus rendering it soluble where it
diffuses toward the plant, gets reduced, and absorbed by means of an enzymatic system present in
the cell membrane of the plant. The second strategy consists of absorbing the complex formed by
the organic compound and Fe$^{3+}$, where the iron is reduced inside the plant and readily absorbed.
Some rhizosphere bacteria are able to release iron-chelating molecules to the rhizosphere and
hence serve to attract iron towards the rhizosphere where it can be absorbed by the plant (Payne,
1994).

Siderophores are low-molecular weight compounds, usually below 1 kDa, which contain func-
tional groups capable of binding iron in a reversible way. The most frequent functional groups are
hydroximates and catechols, in which the distances among the groups involved are optimal to bind
iron. Siderophore concentration in soil is approximately around 10$^{-30}$ M. Siderophore-producing bac-
teria usually belong to the genus Pseudomonas, where the most studied organisms are Pseudomonas
fluorescens and Pseudomonas aeruginosa which release pyochelin and pyoverdine type of sidero-
phores (Haas & Défago, 2005). Rhizosphere bacteria release these compounds to increase their com-
petitive potential, since these substances have an antibiotic activity and improve iron nutrition for
the plant (Glick, 1995). Siderophore-producing rhizobacteria improve plant health at various levels:
they improve iron nutrition, inhibit the growth of other micro-organisms with the release of their
antibiotic molecule, and hinder the growth of pathogens by limiting the iron available for the patho-
gen, generally fungi, which are unable to absorb the iron–siderophore complex (Shen, Hu, Peng,
Wang, & Zhang, 2013).

3.2.2. Chitinase and glucanase production by PGPR
One of the major mechanisms used by biocontrol agents to control soil borne pathogens involves
the production of cell wall-degrading enzymes (Chet, Ordentlich, Shapira, & Oppenheim, 1990;
Kobayashi, Reedy, Bick, & Oudemans, 2002). Cell wall-degrading enzymes such as β-1,3-glucanase,
chitinase, cellulase, and protease secreted by biocontrol strains of PGPR exert a direct inhibitory ef-
fect on the hyphal growth of fungal pathogens by degrading their cell wall. Chitinase degrades chi-
tin, an insoluble linear polymer of β-1, 4-N-acetyl-glucoseamine, which is the major component of
the fungal cell wall. The β-1,3-glucanase synthesized by strains of Paenibacillus and Streptomyces
spp. can easily degrade fungal cell walls of pathogenic F. oxysporum, is reported (Compant, Duffy,
Nowak, Clement, & Barka, 2005). In a similar manner, Bacillus cepacia synthesizes β-1,3-glucanase,
which destroys the cell walls of the soil borne pathogens R. solani, P. ultimum, and Sclerotium rolfsii
(Compant et al., 2005). Potential biocontrol agents with chitinolytic activities include B. licheniformis,
B. subtilis, and B. thuringiensis (Sadfi, Cherif, Fliss, Boudabbous, & Antoun, 2001). Among the Gram-negative bacteria, Serratia marcescens, Enterobacter agglomerans,
Pseudomonas aeruginosa, and P. fluorescens have been found to possess chitinolytic activities
(Neiendam-Nielsen & Sørensen, 1999).

Cell wall-degrading enzymes of rhizobacteria affect the structural integrity of the walls of the
target pathogen (Budi et al., 2000). Someya et al. (2000) studied the chitinolytic and antifungal ac-
tivities of a potent biocontrol strain of Serratia marcescens B2 against the soil borne pathogens
Rhizoctonia solani and Fusarium oxysporum. The mycelia of the fungal pathogens co-inoculated with
this strain showed various abnormalities such as partial swelling in the hyphae and at the tip, hyphal
curling, or bursting of the hyphal tip. Examples of protection from phytopathogenic infection as a
result of the activity of cell wall-degrading enzymes include control of Sclerotium rolfsii and F. ox-
ysporum on beans (Felse & Panda, 2000). Thus, the production of these enzymes by PGPR can cate-
gorize them as biocontrol agent against fungal pathogens.

3.2.3. Antibiotic production by PGPR
Utilization of microbial antagonists against plant pathogens in agricultural crops has been proposed
as an alternate to chemical pesticides. PGPRs belonging to Bacillus and Pseudomonas species play an
active role in the suppression of pathogenic micro-organisms producing antibiotics. These bacterial
antagonists enforce suppression of plant pathogens by the secretion of extracellular metabolites that are inhibitory even at low concentration.

Bacteria belonging to Bacillus genus produce a wide variety of antibacterial and antifungal antibiotics. Some of these compounds including subtilin, subtilosin A, TasA, and sublancin are well known and are derived from ribosomal origin, but others, such as bacilysin, chlorotetain, mycobacillin, rhizoctinics, bacillaene, difficidin, and lipopeptides belonging to the surfactin, iturin, and fungycin families, are formed by non-ribosomal peptide synthetases (NRPS) and/or polyketide synthases (PKS) (Leclere et al., 2005). The model organism B. subtilis 168 and the plant root-colonizing B. amyloliquefaciens FZB42 produce a wide variety of antibacterial and antifungal antibiotics, and their gene clusters involved in antibiotics biosynthesis have been identified. In B. amyloliquefaciens FZB42 (Chang, Chen, & Jao, 2007), the nine gene clusters (srf, bmy, fen, nrs, dhb, bac, mln, boe, dfn) direct the synthesis of bioactive peptides and polyketides by the enzymes NRPSs and PKSs.

Antibiotics are also produced by strains of Pseudomonas where Pseudomonas fluorescens and Pseudomonas aeruginosa are thoroughly studied. Antibiotics produced by these strains include 2,4 Diacetyl Phloroglucinol (DAPG), Phenazine-1-carboxylic acid (PCA), Phenazine-1-carboxamide (PCN), Pyoluteorin (Plt), Pyrrolnitrin (Pn), Oomycin A, Viscosinamide, Butyrolactones, Kanasamine, Zwittermycin-A, Aerugin, Rhamnolipids, Cepaciamide A, Ecomycins, Pseudomonic acid, Azomycin, antitumor antibiotics FR901463, Cepafungins and antibiotic Karalicin. These antibiotics are known to possess antiviral, antimicrobial, insect and mammalian antifeedant, antihelminthic, phytotoxic, antioxidant, cytotoxic, antitumor, and PGP activities (Hammer, Hill, Lam, Van Pée, & Ligon, 1997).

Other than the mentioned PGPR traits, functions carried out by these organisms in the rhizosphere are shown in Figure 4. Briefly, PGPR elude soil acidification by increasing the pH and producing capsular envelope to protect itself. PGPR alters root exudates either directly or indirectly through other beneficial microbes like arbuscular mycorrhizal (AM) fungi, thereby facilitating root colonization. PGPR improve root colonization by undergoing phase variation. Toxins produced by roots and soil-inhabiting pathogens can also be degraded by PGPR (Dutta & Podile, 2010).

### 3.2.4. Induced systematic resistance

PGPR provides alternate strategy to protect plant from diseases via induced systematic resistance (ISR). The process where treatment of plant by PGPR elicits host defense as indicated by reduction in severity or incidence of disease caused by pathogens that are spatially separated from the inducing agent is termed as ISR by van Loon, Bakker, and Pieterse (1998). Mostly, non-specific character of induced resistance constitutes an increase in the level of basal resistance to several pathogens simultaneously, which is of benefit under natural conditions where multiple pathogens remain

**Figure 4. Interaction of plant root exudates, pathogens, PGPR, and other beneficial microbes in the rhizosphere as described by Dutta and Podile (2010).**
present (Van Loon & Bakker, 2006; Thakker, Patel, & Dhandhukia, 2011; Thakker, Patel, & Kothari, 2007). PGPR such as Pseudomonas strains are known to induce systemic resistance in carnation, radish, and Arabidopsis, where the the “O antigenic side chain” of the bacterial outer membrane lipopolysaccharides acts as an inducing determinant, while pseudobactin siderophores produced by strains Pseudomonas induce systemic resistance in tobacco and Arabidopsis. Another type of siderophore, pseudomanine produced by strains of Pseudomonas induces salicylic acid production in radish ultimately enhancing plant’s defense (Van Loon & Bakker, 2006). Thus, inducing rhizobacteria in the plant roots produce signal, which spreads systemically within the plant and increases the defensive capacity of the distant tissues from the subsequent infection by the pathogens (Thakker, Patel, & Dhandhukia, 2012).

3.2.5. PGPR modulates plant stress markers under abiotic stress

Plants are exposed to wide range of environmental stresses like high temperature, cold, drought, salinity, alkalinity UV, and pathogen infection. Abiotic stress is the primary cause of crop loss worldwide by more than 30%. Among these stresses, salinity is considered one of the major abiotic stresses that limits crop yield due to reduction in photosynthesis, respiration, and protein synthesis (Ahmad & Prasad, 2011). Salinity causes nutritional disorders in plants which lead to deficiencies of several nutrients and drastically increasing Na⁺ levels (Zahedi, Fazeli, Zavareh, Dorry, & Gerayeli, 2012). The primary effect of salinity stress is hyperionic and hyperosmotic stress and in severe cases causes oxidative stress in plants (Parvaiz, Khalid, Ashwani, Muhammad, & Nudrat, 2012). Oxidative stress is responsible for the generation of reactive oxygen species (ROS) which are deleterious to plants (Azooz, Youssef, & Ahmad, 2011). ROS such as hydrogen peroxide (H₂O₂), superoxide ions (O₂⁻), singlet oxygen (¹O₂), and hydroxyl radical (OH⁻) etc. are toxic molecules for plant metabolism (Parvaiz et al., 2012).

ROS are highly reactive and cause damage to biomolecules such as lipids, proteins, and nucleic acids (Apel & Hirt, 2004). To minimize the effect of oxidative stress, plants have developed efficient antioxidant system that can protect them from this disaster (Azooz et al., 2011; Parvaiz et al., 2012). The ROS scavenging enzymes include peroxidase (POX), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR) (Apel & Hirt, 2004; Koyro, Ahmad, & Geissler, 2012) and are present in different cellular compartments as isoenzymes especially in chloroplast and mitochondria (Apel & Hirt, 2004). ROS generation and increased activity of many antioxidant enzymes during salt stress have been reported widely (Rasool, Ahmad, Siddiqi, & Ahmad, 2013). According to several researchers across the globe, there is a belief that the application of PGPR in such plants affected by salinity modulates the levels of POX, SOD, CAT, APX, GR, etc. For an instance, ChunJuan et al. (2012) reported that the application of a PGPR strain B. cereus AR156 on tomato (Lycopersicon esculentum) under such abiotic stress showed enhanced activities of SOD, POX, and CAT in the plant probably indicating enhance defense activation when treated with PGPR. Also, PGPR elicit induced systemic resistance (ISR) (ISR is defensive capacity developed by the plant when stimulated by diverse agents including rhizobacteria) in plants by increasing the physical and mechanical strength of the cell wall along with changing the physiological and biochemical reactions of the host. This results in the synthesis of defense chemicals such as chitinase, peroxidase, and pathogenesis-related proteins (Silva et al., 2004).

In addition to above-mentioned stress marker enzymes, L-proline (an amino-acid) is an important stress marker molecule which gets accumulated in the plant tissues under several abiotic stress including salinity stress. Its accumulation increases under salinity stress and it protects folded protein structures against denaturation, stabilizes cell membranes by interacting with phospholipids, functions as a hydroxyl radical scavenger, or serves as an energy and nitrogen source. On the whole, L-proline plays a major role in osmotic adjustment in plant. A report by Razi and Sen (1996) suggested foliar application of a diazotrophic Klebsiella sp. could ameliorate drought stress effects on wetland rice, as grain yield increased, together with increased nutrient uptake and L-proline content. Thus, it is evident that PGPR modulates the level of plant stress markers under abiotic stresses.
3.2.6. Production of 1-aminocyclopropane-1-carboxylic acid deaminase

1-aminocyclopropane-1-carboxylic acid (ACC) is the precursor of phytohormone ethylene. Ethylene is produced naturally in plants, however its levels increases dramatically under abiotic stresses such as drought, salinity, or flooding of water (Etesami et al., 2015; Jha & Saraf, 2015). Ethylene is also known as stress hormone of plant and it has detrimental effect on plant, where it causes leaf abscission, leaf senescence, chlorosis, flower wilting, etc. Several PGPR possess ability to produce an enzyme, ACC deaminase (EC 4.1.99.4) that degrades ACC inhibiting its conversion to ethylene. Plant surviving under abiotic stress produces larger volumes of ACC which is cleaved in to ammonia and α-ketobutyrate by bacterial ACC deaminase, which forbids production of ethylene. In this way, ACC deaminase producing PGPR protects plants surviving under abiotic stress from detrimental effects of ethylene (Glick, 2014). Mayak, Tirosh, and Glick (2004) showed that the ACC deaminase-containing bacterium Achromobacter piechaudii ARV8 could mask drought and salinity stress in tomato plants. Ali, Charles, and Glick (2012) showed that ACC deaminase-producing Pseudomonas fluorescens YsS6 and Pseudomonas migulae 8R6 could effectively delay flower senescence of carnation. In the same way, ACC deaminase-producing PGPR can protect plant from stress induced by temperature, water flooding, ultraviolet radiations, and heavy metals (Ali et al., 2012; Glick, 2014; Mayak et al., 2004).

4. Commercialization of PGPR as biofertilizers and biocontrol agents

Several PGPR bacterial strains are commercially available in the form of formulated products which is used as biofertilizers and biocontrol agents (Gohel, Singh, Vimal, Ashwini, & Chhatpar, 2006; Jha & Saraf, 2015; Sethi, Sahu, & Adhikary, 2014). Fungal biofertilizers are usually prepared as powder formulation, granular powder, and fluid-bed granules using dextrin as binder. Alginate gel are used to prepare bacterial and fungal formulations (Desai, Reddy, & Kloepper, 2002). Bacterial biofertilizers are formulated in variety of ways and available in the market. Formulation of the sporulating, Gram-positive bacteria are resistant to desiccation. Gram-positive micro-organisms possess heat-resistant spores that are exploited to formulate stable and dry powder products (Kamilova, Okon, de Weert, & Hora, 2015). Alternative to solid-powdered formulation is the suspension of organisms in oil, where the purpose is to exclude oxygen which prevents respiration (Honeycutt & Benson, 2001; Kamilova et al., 2015). Addition of silica gel to oil formulation enhances the shelf life as it is reported to mutate conidia (Tariq, John, & Powell, 1999).

PGPR-based commercialization is at a boom and several industries are commercializing bacterial and fungal stains as PGPR-based biofertilizers, of which some examples are portrayed here: bio-formulation of Fusarium oxysporum is commercialized by Biofox (www.biofox.com) which is effective against Fusarium moniliforme. Bacterial bioformulation of Pseudomonas aureofaciens commercialized by Ecosoil (www.ecosoil.com) is effective against Dollar spot, Anthracnose, Pythium aphanidermatum, and Michrochium patch (pink snow mold). Streptomyces griseoviridis strain K61 has been commercially formulated by AgBio (http://www.agbio-inc.com) which is known to inhibit Fusarium spp., Alternaria brassicola, Phomopsis spp., Botrytis spp., Pythium spp., and Phytophthora spp. that cause seed, root, stem rot, and wilt disease of ornamental and vegetable crops. A biofertilizer containing spores of Bacillus licheniformis SB3086 produced by Novozymes can act as phosphate solubilizer strain and is also effective against Dollar spot disease of plants (http://www.bioag.novozymes.com/en/products/unitedstates/biocontrol/Documents/14004_ActinovateSP_LG_18oz_3x5%205bklet_USA_4.pdf). Commercial bioformulation of Coniothyrium minitans produced by BIOVED, Ltd., Hungary, is effective in suppressing Sclerotinia sclerotiorum and Sclerotinia minor which are phytopathogens infecting cucumber, lettuce, capsicum, tomato, and ornamental flowers. Commercial biocontrol “EcoGuard,” marketed as a concentrated suspension of spores of Bacillus licheniformis SB3086 has been found effective as a natural inhibitor of a variety of agronomically important fungal diseases—particularly dollar spot and anthracnose (https://www.harrells.com/uploads/products/labels/ecogua.pdf).

Despite several Gram-negative bacterial strains known to possess efficient biocontrol ability, they are difficult to formulate as they do not produce spores, their formulations have short shelf life, and the bacteria gets easily killed when the formulations are desiccated (Kamilova et al., 2015; Sethi et al., 2014).
The problems faced by biocontrol developers is that crops are grown under a multiplicity of climatic and environmental conditions which include temperature, rainfall, soil type, crop variety which change from farm to farm or even within one field, and such variations causes disparity in the potentiality of PGPR-based Biofertilizers (Kamilova et al., 2015). However, over the period of time, researchers have been able to develop better biofertilizers with improved shelf life and possessing better and efficient strains. From present scenario for the use of PGPR in sustainable agriculture, there is still a huge scope of enhancing agricultural productivity using this technique (Glick, 2014).

5. Conclusion and future prospects
Population of the world is constantly increasing and so is the demand for food. Over the period of last 40 years, PGPR has shown promises to support sustainable agriculture. Researchers have begun to develop a much more in complexity and detailed understanding of the mechanics employed by PGPR to facilitate the growth in plants. Summary of mechanics employed by PGPR is portrayed in Figure 5. Such understanding has allowed the use of PGPR in agriculture. Despite such lengthy research over the period of several decades a lot more work, both basic and applied, remains to be done to unfold some hidden potentials of PGPR which may not be known yet. Focusing commercial market of PGPR as biofertilizers, lot of hard work is still to be done. Despite several potential PGPR been discovered by researchers, they have not been commercialized efficiently. On the whole, it can be said that researchers have understood the basic mechanics of PGPR, still some research is to be carried out to better understand how microbes and plant interact and, on commercial scale, lot of effort is still required to make PGPR an efficient technique in sustainable agriculture.
rhizoplane and/or endophytic competence by beneficial bacteria. In D. K. Maheshwari (Ed.), Bacterial metabolites in sustainable agroecosystem (pp. 183–258). Springer International. doi:10.1007/978-3-319-24654-3_8
Felise, P. A., & Panda, T. (2000). Production of microbial chitinases—A revisit. Bio过程 Engineering, 23, 127–134. doi:10.1016/S0006-0919(00)0009171
Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., & Gurr, S. J. (2012). Emerging fungal threats to animal, plant and ecosystem health. Nature, 484, 186–194. doi:10.1038/nature10947
Frankenberg, Jr., W. T., & Arshad, M. (1995). Phytohormones in soils: Microbial production and function. New York, NY: Marcel Dekker.
Garcia de Salamone, I. E., Hynes, R. K., & Nelson, L. M. (2001). Production of microbial chitinases–A revisit. Bioprocess Engineering, 186–194. doi:10.1038/nature10947
Glick, B. R. (2014). Bacteria with ACC deaminase can promote plant growth by free-living bacteria. Canadian Journal of Microbiology, 47, 404–411. doi:10.1139/w01-029
Glick, B. R. (1995). The enhancement of plant growth by free-living bacteria. Canadian Journal of Microbiology, 41, 109–117. doi:10.1139/m95-015
Glick, B. R. (2014). Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research, 169, 30–39. doi:10.1016/j.micres.2013.09.009
Gohel, V., Singh, A., Viral, M., Ashwini, P., & Chhatpar, H. S. (2006). Bioprospecting and antifungal potential of chitinolytic microorganisms. African Journal of Biotechnology, 5, 54–72. Retrieved from http://hdl.handle.net/1807/66640
Good, X., Kellogg, J. A., Wagoner, W., Longhoff, D., Matsumura, W., & Bestwick, R. K. (1994). Reduced ethylene synthesis by transgenic tomatoes expressing S-adenosylmethionine hydrolase. Plant Molecular Biology, 26, 781–790. doi:10.1007/BF00028848
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2014). Screening of PGPR from saline desert of Kutch: Growth promotion in Arachis hypogea L. var. MS A2. Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2015.1127500
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2011). Describing Paenibacillus mucilaginosus strain N3 as an efficient plant growth promoting rhizobacteria (PGPR). Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2016.1000714
Goswami, D., Dhandhukia, P., Patel, P., & Thakker, J. N. (2014). Elucidating multifaceted urease producing marine Bacillus sp. isolated from polychaete worm, PGPR: A novel IAA-producing bacteria isolated from saline desert of Kutch: Growth promotion in Arabidopsis thaliana (L.) Heynh. Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2016.1000714
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2011). Describing Paenibacillus mucilaginosus strain N3 as an efficient plant growth promoting rhizobacteria (PGPR). Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2016.1000714
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2011). Describing Paenibacillus mucilaginosus strain N3 as an efficient plant growth promoting rhizobacteria (PGPR). Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2016.1000714
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2014). Elucidating multifaceted urease producing marine Pseudomonas aeruginosa B6 as a cogent PGPR and bio-control agent. Plant Growth Regulation. doi:10.1007/s10725-014-9949-1
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2011). Describing Paenibacillus mucilaginosus strain N3 as an efficient plant growth promoting rhizobacteria (PGPR). Cogent Food & Agriculture, 1(1), 1000714. doi:10.1080/23311932.2016.1000714
Goswami, D., Parmar, S., Vaghela, H., Dhandhukia, P., & Thakker, J. N. (2011). Screening of PGPR from saline desert of Kutch: Growth promotion in Arachis hypogea by Bacillus licheniformis sp. nov., isolated from plant roots, soil and food. International Journal of Systematic and Evolutionary Microbiology, 50, 607–616. doi:10.1099/ijs.0.01883-0
Histner, L. (1934). About recent experiences and problems in the field of soil bacteriology with special consideration of green manure and follow. Arbeiten der Deutschen Landwirtschaftlichen Gesellschaft, 98, 59–78.
Honeycutt, E. W., & Benson, D. M. (2001). Formulation of bineculeo Rhizoctonia spp. and biocontrol of Rhizoctonia solani on impatiens. Plant Disease, 85, 1241–1248. doi:10.1094/PDIS.2001.85.12.1241
Hillmer, P., & Schinner, F. (1992). Solubilization of inorganic phosphates by microorganisms isolated from forest soils. Soil Biology and Biochemistry, 24, 389–395. doi:10.1016/S0038-0717(92)80919-9
Hussain, J., Jha, C. K., Patel, D., Rajendran, N., & Saraf, M. (2009). Stimulation of the growth of tomato by Paenibacillus sp. isolated from soil. Biotechnology, 5, 781–790. doi:10.1099/ijbs.0.012075-0
Ishida, T., Fukuoka, M., & Kato, S. (1985). Phytostimulation of plant-growth-promoting rhizobacteria (PGPR): A review. E3 Journal of Agricultural Research and Development, 5, 108–119.
Jha, C. K., Aeron, A., Patel, B. V., Maheshwari, D. K., & Saraf, M. (2011). Enterobacter: Role in plant growth promotion. In D. K. Maheshwari (Ed.), Bacteria in agrobiology: Plant growth responses (pp. 159–182). Berlin: Springer Berlin Heidelberg.
Jha, C. K., & Saraf, M. (2012). Stimulation of the growth of Jatropha curcas by the plant growth promoting bacterium Enterobacter carotovorum MSA2. World Journal of Microbiology and Biotechnology, 28, 891–899. doi:10.1007/s11274-011-0886-0
Jha, C. K., Patel, D., Rojedran, N., & Saraf, M. (2010). Combinatorial assessment on dominance and informative diversity of PGPR from rhizosphere of Jatropha curcas L. Journal of Basic Microbiology, 50, 211–217. doi:10.1002/jobm.200900072
Kado, C. I. (1994). Phytohormone-mediated tumorigenesis by plant pathogenic bacteria. In E. S. Dennis & B. Hohn (Eds.), Genes involved in microbe-plant interactions (pp.
Rodriguez, H., & Frago, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnology Advances, 17, 319–339. doi:10.1016/S0734-9750(99)00014-2

Sadj, N., Cherif, M., Fliss, I., & Antoun, H. (2001). Evaluation of bacterial isolates from salty soils and Bacillus thuringiensis strains for the biocontrol of Fusarium dry rot of potato tubers. Journal of Plant Pathology, 83, 101–117. Retrieved from http://www.jstorer.org/stable/1199806

Salisbury, F. B. (1994). The role of plant hormones. In R. E. Wilkinson (Ed.), Plant–environment interactions (pp. 39–81). New York, NY: Marcel Dekker.

Salisbury, F. B., & Ross, C. W. (1992). Salinity stress and plant growth. In R. E. Wilkinson (Ed.), Plant–environment interactions (pp. 39–81). New York, NY: Marcel Dekker.

Sadfi, N., Cherif, M., Fliss, I., Boudabbous, A., & Antoun, H. (2015). Evaluation of bacterial isolates from salty soils and Bacillus thuringiensis strains for the biocontrol of Fusarium dry rot of potato tubers. Journal of Plant Pathology, 83, 101–117. Retrieved from http://www.jstorer.org/stable/1199806

Someya, N., Kataoka, N., Kornagata, T., Hirayae, K., Hibi, T., & Akatsu, K. (2000). Biological control of cyclamen wilt disease by Serratia marcescens strain B2. Plant Disease, 84, 334–340. doi:10.1094/PDIS.2000.84.4.334

Sgroy, V., Cassán, F., Masciarelli, O., Del Papa, M. F., Logares, A., & Luna, V. (2009). Isolation and characterization of endophytic plant growth-promoting (PGP) or stress homeostasis-regulating (PSHR) bacteria associated to the halophyte Prosopis strombuliferra. Applied Microbiology and Biotechnology, 85, 371–381. doi:10.1007/s00253-009-1216-3

Sethi, S. K., Sahu, J. K., & Adhikary, S. P. (2016). Microbial biofertilizers and their pilot-scale production. Microbial Biotechnology: Progress and Trends, 2. Retrieved from https://books.google.co.in/books?hl=en&lr=&id=wDS5DSRBQBAAJ&oi=fnd&pg=PPA297&dq=Constrains+in+biofertilizer+commercialization&ots=UtiqPjm6uQ&sig=1PaYsw_VnEwrID4PpzEpEyrNOkA#v=onepage&q=Constrains%20in%20biofertilizer%20commercialization&f=false

Shen, X., Hu, H., Peng, H., Wang, W., & Zhang, X. (2013). Comparative genomic analysis of four representative plant growth-promoting rhizobacteria in Pseudomonas. BMC Genomics, 14, 271. doi:10.1186/1471-2164-14-271

Siddique, M. A., Chauban, P. S., Anandham, R., Han, G. H., & Sa, T. (2010). Isolation, characterization, and use for plant growth promotion under salt stress of ACC deaminase-producing halotolerant bacteria derived from coastal and adjacent soils. Journal of Microbiology and Biotechnology, 20, 1577–1584. doi:10.4014/jmb.1007.07011

Silva, H. S. A., Romeiro, R. D. S., Macnaghn, D., Helfeld-Vieira, B. A. D., Pereira, M. C. B., & Mounteer, A. (2004). Rhizobacterial induction of systemic resistance in tomato plants: Non-specific protection and increase in enzyme activities. Biological Control, 29, 288–295. doi:10.1016/S0921-8964(03)00163-4

Someya, N., Kataoka, N., Kornagata, T., Hirayae, K., Hibi, T., & Akatsu, K. (2000). Biological control of cyclamen wilt disease by Serratia marcescens strain B2. Plant Disease, 84, 334–340. doi:10.1094/PDIS.2000.84.4.334

Sopoep, S., Vanderleyden, J., & Remans, R. (2007). Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiology Reviews, 31, 425–448. doi:10.1111/j.1574-6976.2007.00072.x

Stacey, G., Burris, R. H., & Evans, H. J. (Eds.). (1993). Biological nitrogen fixation. Berlin: Springer Science & Business Media.

Tariq, M. B., John, G. H., & Powell, K. A. (1999). Microbial biopesticides: The European scene. In F. R. Hall & J. J. Menn (Eds.), Biopesticides: Use and deliver (pp. 23–24). Totowa, NJ: Human Press.

Thakker, J. N., Patel, N., & Kothari, L. L. (2007). Fusarium oxysporum derived elicitor-induced changes in enzymes of banana leaves against wilt disease. Journal of Mycology and Plant Pathology, 37, 510–513.

Thakker, J. N., Patel, P., & Dhandhukia, P. C. (2011). Induction of defense-related enzymes in susceptible variety of banana: Role of Fusarium-derived elicitors. Archives of Phytopathology and Plant Protection, 44, 1976–1984. doi:10.1080/03235408.2011.559302

Thakker, J. N., Patel, S., & Dhandhukia, P. C. (2012). Induction of defense-related enzymes in banana plants: Effect of live and dead pathogenic strain of Fusarium oxysporum f. sp. cubense. ISRN Biotechnology. doi:10.5402/2013/601301

Upadhyaya, N. M., Letham, D. S., Parker, C. W., Hocart, C. H., & Dart, P. J. (1991). Do rhizobia produce cytokinins? Biochemistry International, 24, 123–130. Retrieved from http://www.sciencedirect.com/science/article/pii/0304407691902002

van Loon, L. C., Bakker, P. A. H. M. (2008). Induced systemic resistance as a mechanism of disease suppression by rhizobacteria. In Z. A. Siddiqui (Ed.), PGRP: Biocontrol and biofertilization (pp. 39–66). Dordrecht: Springer Netherlands.

van Loon, L. C., Bakker, P. A. H. M., & Pieterse, C. M. J. (1998). Systemic resistance induced by rhizosphere bacteria. Annual Review of Phytopathology, 36, 453–483. doi:10.1146/annurev.phyto.36.1.453

Vessey, J. K. (2003). Plant growth promoting rhizobacteria as biofertilizers. Plant and Soil, 255, 571–586. doi:10.1023/A:1026037216893

von der Weid, I., Duarte, G. F., van Elsas, J. D., & Seldin, L. (2002). Pseudobacillus brasiliensis sp. nov., a novel nitrogen-fixing species isolated from the maize rhizosphere in Brazil. International Journal of Systematic and Evolutionary Microbiology, 52, 2147–2153. doi:10.1099/ijs.0.02272-0

Wong, W. S., Tan, S. N., Ge, L., Chen, X., & Yong, J. W. H. (2015). The importance of phytohormones and microbes in biofertilizers. In D. K. Maheshwari (Ed.), Bacterial metabolites in sustainable agroecosystem (pp. 105–158). Springer International. doi:10.1007/978-3-319-24654-3_6

Zahedi, A. M., Fazeli, I., Zavareh, M., Dorry, H., & Gerayeli, N. (2012). Evaluation of the sensitive components in seedling growth of common bean (Phaseolus vulgaris L) affected by salinity. Asian Journal of Crop Science, 4, 159–164. Retrieved from http://agris.fao.org/agris-search/search.do?recordID=DJ2012076165

http://dx.doi.org/10.1080/23311932.2015.1127500

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http://dx.doi.org/10.1080/23311932.2015.1127500
