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Plant Growth Promoting Rhizobacteria (PGPR) - Prospective and Mechanisms: A Review

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Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria that colonize plant roots, which is an important environment for plant microbe interactions. PGPR have attracted special attention for their ability to enhance productivity, sustainability and profitability when food security and rural livelihood are a key priority. Chemical fertilizers used in agriculture and pathogenic microorganisms attacking plants show harmful impact on the ecosystem. The potentiality of PGPR offers an attractive way to replace the use of chemical fertilizers, pesticides and other supplements. PGPR affect plant growth and development directly or indirectly, either by releasing plant growth regulators or other biologically active substances, and uptake of nutrients through fixation and mobilization, reducing harmful effects of pathogenic microorganisms on plants and by employing multiple mechanisms of action. Besides they play an important role in soil fertility. This review intends to elucidate the diverse mechanism of plant growth promoting rhizobacteria in promoting crop production and developing sustainable agriculture.

Keywords: PGPR, Siderophore, Phytohormone, Antibiosis, ISR.

Agriculture, the science or the practice of cultivating plants, animals and other life forms, is certainly one of the factors that boost human civilization and development. Development of agriculture is an evolutionary process that ultimately transformed plants from being independent, wild progenitors into fully dependent, domesticated cultivars with the concomitant evolution of agricultural economics (Zeder, 2009[1]). This relationship between humans, the earth and food sources further confirm soil as the foundation of agriculture, and microbes play a vital role in sustaining our natural ecosystems. Soil, the dynamic and valuable natural resource harbouring a vast collection of microorganisms, is vital for the production of food and fibre, in addition involved in the maintenance of global nutrient balance and ecosystem function (Bishnoi, 2015[2]). Agricultural sustainability, food security and energy renewability depends on a healthy and fertile soil. Imbalance in nitrogen cycling, nutritional status, physical and biological properties of soil, incidence of pests and diseases, fluctuating climatic factors and abiotic stresses are the interlinked contributing factors for reduced agricultural productivity ((Gopalakrishnan *et al*., 2015[3]).). The existing approaches to agriculture include the use of chemical fertilizers, herbicides, fungicides and insecticides. These fertilizers have become essential components of modern agriculture because they provide essential plant nutrients such as nitrogen, phosphorus and potassium. However, the overuse of fertilizers can cause unanticipated environmental impacts (Shenoy *et al*., 2001[4]; Adesemoye *et al*., 2009[5])

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and encounter problems such as, development of resistance by pathogen to fungicides and rapid degradation of the chemicals.

Towards a sustainable agricultural vision, crops produced need to be equipped with disease resistance, salt tolerance, drought tolerance, heavy metal stress tolerance and better nutritional value. To accomplish the above desired crop properties, one possibility is to use soil microorganisms. The main functions of these bacteria are (1) to supply nutrients to crops, (2) to stimulate plant growth, (3) to control or inhibit the activity of plant pathogens, (4) to improve soil structure, and (5) bioaccumulation or microbial leaching of inorganics (Hayat *et al*., 2010[6]). More recently, bacteria have also been used in soil for the mineralization of organic pollutants, i.e. bioremediation of polluted soils (Burd *et al*., 2000[7]; Zhuang *et al*., 2007[8]; Zaidi *et al*., 2008[9]). Multiple types of biological interactions between microorganisms and plants take place in the soil (Gouda *et al*., 2018[10]). This review provides an environment friendly approach to increase crop production and health, development of sustainable agriculture as well as fertility of soil exploiting plant growth promoting rhizobacteria

Rhizosphere

Rhizosphere is a 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[11]). Diverse communities of beneficial soil microorganisms are associated with the root systems of all higher plants (Khalid *et al*., 2006[12]). It is quiet common that the bacterial population in the rhizosphere are 100–1,000 times higher than the surrounding soil, also known as the bulk soil which are not penetrated by plant roots and have lower microbial communities within it. In contrast the rhizosphere is heavily influenced by microbes that 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 (Jha *et al*., 2010[13]; Govindasamy *et al*., 2011[14]). Plant roots synthesize, accumulate and secrete a diverse array of compounds. The exudation of a wide range of chemical compounds modifies the chemical and physical properties of the soil and thus, regulates the structure of soil microbial community in the immediate vicinity of root surface (Dakora and Phillips, 2002[15]). Root exudates include the releasing of ions, oxygen, water, and organic compounds, such as sugars, organic acids, amino acids, enzymes, growth factors and others. The composition of these exudates is dependent upon the physiological status and species of plants and microorganisms (Kang *et al*., 2010[16]). Moreover, these exudates also promote the plant-beneficial symbiotic interactions and inhibit the growth of the competing plant species (Nardi *et al*., 2000[17]; Haas and Defago, 2005[18]). The sugars, amino acids, flavanoids, proteins, and fatty acids secreted by plant roots help to structure the associated soil microbiome (Badri *et al*., 2009[19]; Dennis *et al*., 2010[20]; Doornbos *et al*., 2012[21]). The quantity and composition of root exudates vary with plant developmental stage and the proximity to neighbouring species (Chaparro *et al*., 2012[22]). From these plant-derived small organic molecules, a fraction is further metabolized by microorganisms in the surrounding area as carbon and nitrogen sources, and some microbe-oriented molecules are subsequently re-taken up by plants for growth and development (Kang *et al*., 2010[16]).

Apart from the rhizosphere, the rhizoplane is the root surface including the strongly adhering soil particles while the root itself is a component of the system, because many micro-organisms (like endophytes) also colonize the root tissues (Barea *et al*., 2005[23]). Plant rhizospheric region is a dynamic and versatile environment of acute plant microbe interactions for tackling essential macro and micro nutrients from a confined nutrient pool. They play a significant role both under stressed and normal conditions for improving plant growth and developmental processes (Zahir *et al*., 2004[24]; Glick *et al*., 2007[25]). Currently, it is recognized that the rhizosphere microbiome harbours thousands of different bacterial, archaeal, viruses, fungal and other eukaryotic taxa (Lagos *et al*., 2015[26]). Though numerous microorganisms coexist in the rhizospheric region, bacteria are the abundant among them. The bacteria colonizing the rhizosphere habitat are called rhizobacteria (Kloepper *et al.,* 1991[27]) which influence the plant growth in a most significant manner (Uren, 2007[28]). Rhizospheric bacteria participate in the geochemical cycling of nutrients especially carbon, nitrogen, phosphorus and micronutrients as iron,

manganese, zinc and copper, and determine their availability for plants and soil microbial community. Plant carbon photosynthates allocated to the root and rhizosphere are key microbial activities important for plant nutrition such as organic matter decomposition, phosphate solubilisation, nitrogen fixation, mycorrhizal nutrient transport and bio control of root pests (Larsen *et al*., 2015[29]).

Plants only prefer those bacteria contributing close to their relevance by releasing sugars, amino acids, organic acids, vitamins, enzymes and organic or inorganic ions through root exudates (Gray and Smith, 2005[30]; Gopalakrishnan *et al*.,2015[3]) producing a environment where diversity is low (Das *et al*., 2013[31]). In spite of the numerous bacteria in soil, three types of interaction takes place between rhizosphere bacteria and plants which are the positive, negative and neutral interactions. Mostly, commensalism is exhibited where a harmless interaction with the host plants is exhibited without affecting the plant physiology, whereas in negative interaction phototoxic substances are produced by rhizosphere bacteria. Positive interaction exerts a positive growth. Multiple microbial interactions enhance bio control in the rhizosphere region (Whipps, 2001[32]). In this regard, the use of naturally occurring and environmentally safe products such as plant growth-promoting rhizobacteria (PGPR) has found a potential role in developing sustainable systems in crop production.

Plant growth promoting rhizobacteria (PGPR)

Plant growth promoting rhizobacteria (PGPR), a diverse group of soil bacteria, are key components of soil plant systems, where they are engaged in an intense network of interactions in the rhizosphere, thus affecting the plant growth and yield. It was Kloepper and Schroth (1981[33]), who coined the term plant growth promoting rhizobacteria for these beneficial microbes. Numerous species of soil bacteria which flourish in the rhizosphere of plants, but which may grow in, on, or around plant tissues, and stimulate plant growth by a plethora of mechanisms (Vessey, 2003[34]). PGPR's are the potential tools for sustainable agriculture and trend for the future; they not only ensure the availability of essential nutrients to plants but also enhance the nutrient use efficiency (Khalid *et al*., 2009[35]). The beneficial effects of PGPR involve boosting key physiological processes, including water and nutrient uptake, photosynthesis, and source-sink relationships that promote growth and development (Illangumaran and Smith, 2017[36]). 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 (Goswami *et al*., 2016[37]). Gray and Smith (2005[30]) have shown that the PGPR associations range in the degree of bacterial proximity to the root and intimacy of association. The three distinct characteristics of PGPR are they must be able to colonize the root, they must survive and multiply in microhabitats associated with the root surface, in competition with other microbiota, at least for the time needed to express their plant promotion/ protection activities and they must promote plant growth (Kloepper, 1994[38]; Lucy *et al*., 2004[39]).

Based on their relationship with the plants PGPR are classified into two groups, symbiotic bacteria and freeliving rhizobacteria (Khan, 2005[40]). On the basis of their residing sites: iPGPR (Verma *et al*., 2010[41]) (i.e., symbiotic bacteria), example *Rhizobia* sp. and *Frankia* sp., which live inside the plant cells, produce nodules, and are localized inside the specialized structures; and ePGPR (i.e., free-living rhizobacteria), which live outside the plant cells and do not produce nodules, but still prompt plant growth (Gray and Smith, 2005[30]). Depending on their functional activities PGPR are categorized as (i) biofertilizers (increasing the availability of nutrients to plant); (ii) phytostimulators (plant growth promotion, generally through phytohormones); (iii) rhizoremediators (degrading organic pollutants); and (iv) biopesticides (controlling diseases, mainly by the production of antibiotics and antifungal metabolites) (Antoun and Prevost, 2005[42]). Many literature studies also show that a single PGPR will often reveal multiple modes of action including biological control (Kloepper, 2003[43]; Vessey, 2003[34]; Ahmad *et al*., 2008[44]). Genera of PGPR include *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Pseudomonas*, *Acetobacter*, *Micrococcus*, *Burkholderia*, *Bacillus*, *Paenibacillus*, *Agrobacterium*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Azospirillum*, *Flavobacterium*, *Serratia*, *Rhizobium* and some

are members of the Enterobacteriaceae (Niranjan Raj *et al*., 2005[45]; Bhattacharyya and Jha, 2012[46]).

Commercialization

A number of PGPR bacterial strains are commercially available in the form of formulated products which is used as biofertilizers and biocontrol agents. For the more extensive commercialization of plant growth promoting bacterial (PGPB) strains, a number of aspects need to be determined which include (i) determination of the traits with appropriate biological activities; (ii) consistency among regulatory agencies in different countries regarding what strains can be released to the environment, and under what conditions genetically engineered strains are suitable for environmental use; (iii) a better understanding of the advantages and disadvantages of using rhizospheric versus endophytic bacteria; (iv) selection of PGPB strains that function optimally under specific environmental conditions (Fravel, 2007[47]; Arora *et al*., 2010[48]; Glick, 2012[49]; Gupta *et al*., 2015[50]). Moreover, commercial success of PGPR strains requires cost-effective and viable market demand, constant and broad spectrum action, safety and stability, longer shelf life, low investment and easy availability of career materials. Inorder to retain the confidence of farmers on the efficacy of the antagonistic strain quality control is vital (Bhattacharyya and Jha, 2012[46]). According to Nandakumar *et al.* (2001[51]) different stages in the process of commercialization include isolation of antagonist strains, screening, pot tests and field efficacy, mass production and formulation development, fermentation methods, formulation viability, toxicology, industrial linkages and quality control. The selection of best antagonistic strain is carried out by screening the biocontrol ability of rhizosphere bacteria for antagonism against *Sclerotium rolfsii,* the causal organism of root or collar rot in sunflower. The antagonists were tested for suppression of *S. rolfsii* rot of sunflower in greenhouse as seed and soil treatment (Rangeshwaran and Prasad, 2000[52]). Potential antagonists *Trichoderma harzianum* and *Pseudomonas* spp. are tested for their efficacy in field trials against *Sclerotium rolfsii rot* in tomato. Consortium of these bio-agents resulted in plant growth promotion, yield and simultaneously reduce the disease severity (Singh *et al.,* 2013[53]). Due to variations in environmental factors a good biocontrol agent under *in vitro* conditions not succeeds in *in vivo* conditions. Similarly, the method of application also influences the success of field trials. Repeated laboratory works followed by field experiments are needed to establish excellent biocontrol agents into commercial products particularly against plant fungal pathogens (Suprapta, 2012[54]). Thus, isolation of an effective strain is a prime criterion for better agricultural development. The first commercial product of *Bacillus subtilis* was developed during 1985 in United States (U.S.). 60–75% of cotton, peanut, soya bean, corn, vegetables and small grain crops raised in U.S. are now treated with commercial product of *B. subtilis*, which become effective against soil borne pathogens such as *Fusarium* and *Rhizoctonia* (Nakkeeran *et al*., 2005[55]).

Other commercialized plant growth promoting bacterial strains include *Agrobacterium radiobacter, Azospirillum brasilense, Azospirillum lipoferum, Azotobacter chroococcum, Bacillus fimus, Bacillus licheniformis, Bacillus megaterium, Bacillus mucilaginous, Bacillus pumilus, Bacillus* spp., *Bacillus subtilis, Bacillus subtilis* var. *amyloliquefaciens, Burkholderia cepacia, Delfitia acidovorans, Paenobacillus macerans, Pantoea agglomerans, Pseudomonas aureofaciens, Pseudomonas chlororaphis, Pseudomonas fluorescens, Pseudomonas solanacearum, Pseudomonas* spp., *Pseudomonas syringae, Serratia entomophilia, Streptomyces griseoviridis, Streptomyces* spp., *Streptomyces lydicus* and various *Rhizobia* spp. (Figueiredo *et al*., 2010[56]; Glick, 2012[49]). PGPR-based commercialization is at a boom and several industries are commercializing bacterial and fungal strains as PGPR-based biofertilizers, of which some of the important PGPR strains along with their commercial products are portrayed here. The U.S. market based on the information of the committee of biological products from the American Phytopatology Society (APS) in 2005 has registered the following products: ten products based on the *Bacillus sp.* (BioYield, Companion, EcoGuard, HiStick N/T, Kodiak , Mepplus, Serenade, Sonata, Subtilex, Yield- Shield), two products with *Burkholderia cepacia* (Deny and Intercept), and five products based on *Pseudomonas sp.* (AtEze, Bio-save, BlightBan, Frostban, Spot-Less) (Figueiredo *et al*., 2010[56]). Bio-formulation of *Fusarium*

oxysporum is commercialized by Biofox which is effective against *Fusarium moniliforme*. Bacterial bioformulation of *Pseudomonas aureofaciens* commercialized by Ecosoil is effective against Dollar spot, Anthracnose, *Pythium aphanidermatum*, and *Michrochium patch* (pink snow mold). *Streptomyces griseoviridis* strain K61 has been commercially formulated by AgBio 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. 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 (Goswami *et al*., 2016[37]). In India, more than 40 stakeholders from different provinces have registered themselves for the mass production of PGPRs with Central Insecticide Board (CSI), Faridabad, Haryana through collaboration with Tamil Nadu Agricultural University, Coimbatore, India (Bhattacharya and Jha, 2012[46]). Since crops are grown under a diversity of climatic and environmental conditions causes disparity in the potentiality of PGPR based Biofertilizers (Kamilova *et al*., 2015[57]). However, with better shelf life and possessing efficient strains it is possible to develop better biofertilizers exploiting PGPR in sustainable agriculture, for enhancing productivity (Glick, 2014[58]).

Mechanisms of PGPR

The mechanisms by which bacteria can influence plant growth differ among species and strains, PGPR affect plant growth in two different ways, indirectly or directly (Castro *et al*., 2009[59]). There are two mechanisms for promoting plant growth. The direct promotions of plant growth by PGPR involve either providing the plant with resources they lack. This facilitates higher plant yield. Biological means of providing the nutrients such as nitrogen and phosphorus are ideal than chemical sources which are expensive and cause environmental hazards or through compound's that are synthesized by the bacterium, for example phytohormones (Lucy *et al*., 2004[40]; Khalid *et al*., 2004[60]; Glick, 2012[49]). Indirectly, the bacteria may exert a positive influence on plant growth by lessening certain deleterious effects of a pathogenic organism by producing antagonistic substances.

Direct Mechanisms

The direct mechanisms observed in PGPR include N_2-fixation, mobilization of nutrients *via* production of phosphatases, siderophores, or organic acids, and production of phytohormones and enzymes.

Nitrogen Fixation

Nitrogen being a primary limiting factor in agriculture found deficient due to various environmental factors. 65% of the nitrogen currently utilized in agriculture is obtained through biological nitrogen fixation, also important to sustain crop production systems in future (Dakora, 2003[61]). PGPR strains play a major role in nitrogen fixation and make it assimilable form for plants. Nitrogenase (nif) genes required for nitrogen fixation in nitrogen fixing bacteria are more complex. So for improving this process genetic strategies have been utilized to modify the genes (Glick, 2012[49]; Souza *et al*., 2015[62]). PGPR follow two mechanism of nitrogen fixation. In symbiotic nitrogen fixation, legume crops undergo biological nitrogen fixation through symbiotic association with bacteria and meet their own needs without depending external sources (Bhattacharyya and Jha, 2012[46]; Gopalakrishnan *et al*., 2015[3]). Symbiotic bacteria which act as PGPR are *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Mesorhizobium* with leguminous plants, *Frankia* with non-leguminous trees and shrubs (Zahran, 20016[3]). Free living nitrogen fixers, which are non symbiotic types survive close to root without penetration, fixed nitrogen that are acquired through uptake contribute to the nitrogen account of the plants (Goswami *et al*., 2016[37]). Non-symbiotic nitrogen fixing rhizospheric bacteria belongs to genera including *Azoarcus*, *Azotobacter*,

Acetobacter, *Azospirillum*, *Burkholderia*, *Diazotrophicus*, *Enterobacter*, *Gluconacetobacter*, *Pseudomonas* and Cyanobacteria, *Anabaena, Nostoc* (Vessey, 2003[34]).

Many species of microorganisms are used in the cultivation of plants of economic interest, facilitating the host plant growth without the use of nitrogenous fertilizers. For instance, the production of soybean (*Glycine max* L.) is an excellent example of the efficiency of biological nitrogen fixation through the use of different strains of *Bradyrhizobium* sp., such as *B. japonicum* and *B. elkanii* (Alves *et al.*, 2004[64]; Torres *et al.*, 2012[65]). The importance of endophytic nitrogen fixing bacteria has also been the object of studies in non leguminous plants such as sugarcane (*Saccharum officinarum* L.) (Thaweenut *et al.*, 2011[66]). Other studies have suggested that *Bradyrhizobia* colonize and express *nif* H not only in the root nodules of leguminous plants but also in the roots of sweet potatoes (*Ipomoea batatas* L.), acting as diazotrophic endophytes (Terakado-Tonooka *et al.*, 2008[67]). The plant growth promoting bacteria related to genus *Azospirillum* have been largely studied because of their efficiency in promoting the growth of different plants of agronomical interest. The genus *Burkholderia* includes species that fix nitrogen *B. vietnamiensis*, a human pathogenic species, was efficient in colonizing rice roots and fixing nitrogen (Govindarajan *et al.*, 2008[68]). In addition to *Burkholderia*, the potential of biological nitrogen fixation and endophytic colonization of bacteria belonging to the genera *Pantoea*, *Bacillus* and *Klebsiella* were also confirmed in different maize genotypes (Ikeda *et al.*, 2013[69]).

Phosphate solubilisation

Next to nitrogen, phosphorus is the important key element in the nutrition of plants. It exists in both inorganic (bound, fixed, or labile) and organic (bound) forms. The availability of phosphorus to plants is influenced by pH, compaction, aeration, moisture, temperature, texture and organic matter of soils, crop residues, extent of plant root systems and root exudate secretions and available soil microbes (Gopalakrishnan *et al*., 2015[3]). Phosphorus is involved in metabolic processes of plant, as photosynthesis, energy transfer, signal transduction, macromolecular biosynthesis and respiration (Khan *et al*., 2010[70]). Soil phosphorus cycle mediate phosphorus availability to plants. PGPR's directly solubilise and mineralise inorganic phosphorus or facilitate the mobility of organic phosphorus through microbial turnover and/or increase the root system (Richardson and Simpson, 2011[71]). These bacteria secrete different types of organic acids which lower the pH in the rhizosphere and thus release the phosphorus available to plants (Kaur *et al*., 2016[72]). Bacteria from genera such as *Achromobacter, Agrobacterium, Bacillus, Enterobacter, Erwinia, Escherichia, Flavobacterium, Mycobacterium, Pseudomonas* and *Serratia* are highly efficient in solubilising unavailable complexed phosphate into available inorganic phosphate ion (Goldstein, 2001[73]). *Rhizobia*, including *R. leguminosarum*, *R. meliloti, Mesorhizobium mediterraneum, Bradyrhizobium* sp. and *B. japonicum* are the potential phosphate solubilizers (Vessey, 2003[34]; Egamberdiyeva *et al*., 2004[74]; Rodrigues *et al*., 2006[75]).

Siderophore

The transition metal iron is an essential micronutrient and bioactive metal crucial for the growth and metabolism of bacteria. Iron plays a key role in electron transport, oxidation–reduction reactions, detoxification of oxygen radicals, synthesis of DNA precursors and in many other biochemical processes (Hider and Kong, 2010[76]). Based on their iron-coordinating functional groups, structural features and types of ligands, bacterial siderophores have been classified into four main classes such as carboxylates, hydroxamates, phenol catecholates and pyoverdines (Mohandas, 2004[77;] Fernandez *et al*., 2005[78]). Generally, rhizobacteria differs regarding the siderophore cross-utilizing ability. Some are capable of using siderophores of the same genus (homologous siderophores) while others could utilize those produced by other rhizobacteria of different genera (heterologous siderophores) (Khan *et al*., 2009[79]).

In aerobic environments, iron occurs in the form of insoluble hydroxides and oxyhydroxides are not accessible to both plants and microbes (Rajkumar *et al*., 2010[80]). Being a transition element, iron gets rapidly oxidized from soluble ferrous (Fe^2) to insoluble ferric (Fe^3) state (Murugappan *et al*., 2012[81]). Siderophores enhances the iron bioavailability by influencing the low solubility of iron (Wittenwiler, 2007[82]). Siderophores attach on the mineral surface and

facilitate dissolution by coordinating the iron atom in a soluble complex (Kraemer *et al*., 2006[83]). Under iron limiting conditions microorganisms and plants rely on chelating agents to solubilise and transport inorganic iron. The membrane receptor and the ferric siderophore transporter are the common transporter for high affinity microbial acquisition of iron (Neilands, 1981[84]; Crowley *et al*., 1991[85]). Microbes release siderophores to scavenge iron from these mineral phases by formation of soluble Fe^{3+} complexes that can be taken up by active transport mechanisms (Saharan and Nehra, 2011[86]). Bacteria secrete the siderophore to overcome the iron limitation and provide plants with Fe, enhancing their growth directly by increasing the availability of iron in the soil surrounding the roots (Krewulak and Vogel, 2008[87]; Vejan *et al*., 2016[88]). Plants uptake iron when they are able to recognize the bacterial ferric-siderophore complex (Masalha *et al.,* 2000[89]). Not only iron, siderophores also form stable complexes with other heavy metals that are of environmental concern, such as cadmium, copper, lead and zinc, as well as with radionuclide's including uranium (Neubauer *et al*., 2000[90]). Binding of the siderophore to a metal increases the soluble metal concentration (Rajkumar *et al*., 2010[80]). Hence, bacterial siderophores help to alleviate the stresses imposed on plants by high soil levels of heavy metals.

Microorganisms have evolved highly specific pathways that employ low molecular weight, high affinity iron chelators to solubilise iron prior to transport. Gram-negative bacteria take up ferri-siderophore complexes *via* specific outer membrane receptors in a process that is driven by the cytosolic membrane potential and mediated by the energy-transducing TonB-ExbB-ExbD system. Bacteria, such as Gram-positive, that lack an outer membrane, use binding-protein-dependent ABC permeases to allow ferri-siderophores to traverse their cytosolic membrane (Crowely *et al*., 1991[85]; Andrews *et al.,* 2003[91]).

Phytohormones

Chemicals occurring naturally within plant tissues have a regulatory, rather than a nutritional role in growth and development. These compounds, which are generally active at very low concentrations, are known as phytohormones or plant growth substances (George *et al*., 2008[92]). Classes of well-known phytohormones include auxins, gibberellins, cytokinins, ethylene, and abscisic acid. Soil microrganisms, particularly the rhizosphere bacteria, possess the potential to produce these hormones (Zakir *et al*., 2004[24]).

Indole-3-acetic acid

Indole-3-acetic acid (IAA) is the member of the group of phytohormones and is generally considered the most important native auxin which is low-molecular weight, organic substances. This substance termed auxin was identified as indole-3-acetic acid (Kögl and Kostermans, 1934[93]; Went and Thimann, 1937[94]). This phytohormone auxin is a key regulator of many aspects of plant growth and development, including cell division and elongation, differentiation, tropisms, apical dominance, senescence, abscission, and flowering (Woodward and Bartel, 2005[95] ; Teale *et al.*, 2006[96] ; Ahemad and Kibret, 2014[97]). The auxin level is usually higher in the rhizosphere, where high percentage of rhizosphere bacteria is likely to synthesize auxin as secondary metabolites because of the rich supplies of root exudates. The production of auxin (IAA), has been recognized as an important factor in direct plant-growth-promoting abilities of rhizosphere bacteria (Dilfuza, 2011[98]). For various PGPR, it has been demonstrated that enhanced root proliferation is related to bacterial IAA biosynthesis. Upon inoculation of plants with PGPR, a change in root architecture is observed, mainly as an increase in root hairs and lateral roots and shortening of the root length. Also, rhizobacterial IAA loosens plant cell walls and as a result facilitates an increasing amount of root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (Glick, 2012[49]). Moreover, down-regulation of IAA as signalling is associated with the plant defense mechanisms against a number of phyto-pathogenic bacteria as evidenced in enhanced susceptibility of plants to the bacterial pathogen by exogenous application of IAA or IAA produced by the pathogen (Spaepen and Vanderleyden, 2011[99]).

IAA biosynthesis is widespread among plant-associated bacteria (Patten and Glick, 1996[100]; Giickmann *et al*., 1998[101]). Bacteria can use this phytohormone to interact with plants as part of their colonization strategy, including phytostimulation and basal plant defense mechanisms. IAA can also be a signaling molecule in bacteria and therefore

can have a direct effect on bacterial physiology (Spaepen *et al*., 2007[102]). More than 80% of the bacteria isolated from the rhizosphere are capable to synthesize IAA (Khalid *et al*., 2004[60]). IAA production under *in vitro* condition has been reported by many researches, in *Azospirillum* sp. (Lambrecht *et al*., 2000[103]; Dobbelaere *et al*., 2001[104]), *Azotobacter* sp. (Zahir *et al*., 2000[105]), *Azotobacter chrococcum, Bacillus megaterium* BHUPSB14, *Pseudomonas fluorescens, P.putida* (Patten and Glick, 2002[106]; Verma *et al*., 2010[41]; Peyvandi *et al*., 2010[107]), *Rhizobium* sp. (Ghosh *et al*., 2008[108]), *Pseudomonas aeruginosa* (Khare and Arora, 2010[109]), *Acetobacter diazotrophicus* L1(Patil *et al*., 2011[110]) and in *Rhizobium leguminosarum* (Dazzo *et al*., 2000[111]). Tsavkelova *et al*. (2006[112]) observed IAA production in fungi in genera *Aspergillus* sp., *Fusarium* sp. and *Paecilomyces* sp. Ruanpanun *et al*. (2010[113]) found high IAA producing nematophagous actinomycete and fungal isolates such as *Streptomyces* sp. and in *Aspergillus* sp.

Bacterial production of IAA suggests that the pathways involved in IAA production may play an important role in defining the effect of the bacterium on the plant. Though bacterial biosynthesis of IAA can occur by a variety of pathways, tryptophan has been identified as a main precursor for IAA biosynthesis pathways in bacteria (Sarwar and Kremer, 1995[114]; Patten and Glick, 1996[100]; Kravchenko *et al*., 2004[115]; Kamilova *et al*., 2006[116]). According to Ghosh and Basu (2006[117]) among the three different isomers of tryptophan, the bacteria produced higher amount of IAA with the supplementation of L-tryptophan (138 µg/ml) than in D-tryptophan (15 µg/ml) or DL-tryptophan (84 µg/ml). In earlier work Dullaart (1970[118]) explained this process due to the utilisation of this essential amino acid partly in protein synthesis and partly for the formation of other indole compounds in addition to IAA. The indole-3-acetamide (IAM) pathway is the best characterized pathway in bacteria. In this two-step pathway tryptophan is first converted to IAM by the enzyme tryptophan-2-monooxygenase (IaaM), encoded by the iaaM gene. In the second step IAM is converted to IAA by an IAM hydrolase (IaaH), encoded by iaaH. In plant-associated bacteria, both the IAM and the indole-3- pyruvic acid (IPyA) pathway are distributed among the sequenced genomes. Phytopathogenic organisms tend to use the IAM pathway to produce IAA, whereas beneficial bacteria tend to use the IPyA pathway (Spaepen *et al*., 2007[102]; Mano and Nemoto, 2012[119]). This helps the bacteria to evade the plant regulatory signals and so the IAA induces uncontrolled growth in plant tissues. In contrast the useful bacteria such as PGPR synthesize IAA *via* the indole pyruvic acid pathway and the IAA secreted is thought to be strictly regulated by the plant regulatory signals (Patten and Glick, 1996[100]).

Cytokinins

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[120]). Cytokinins play a major or minor role throughout development, from seed germination to leaf and plant senescence and modulate physiological processes important throughout the life of the plant, including photosynthesis and respiration (Salisbury and Ross, 1992[121]; Arshad and Frankenberger, 1993[122]). Plants and plant associated microorganisms have been found to contain over 30 growth promoting compounds of the cytokinin group. It has been found that as many as 90% of microorganisms found in the rhizosphere are capable of releasing cytokinins (Nieto and Frankenberger, 1990[123]). Several plant growth promoting rhizobacteria *Azotobacter* sp., *Rhizobium* sp., *Pantoea agglomerans, Rhodospirillum rubrum, Pseudomonas fluorescens, Bacillus subtilis* and *Paenibacillus polymyxa* can produce cytokinins along with other growth-promoting substances (Gutiérrez-Mañero *et al*., 2001[124]). Cytokinin production has been reported in various PGPR, like *Arthrobacter giacomelloi, Azospirillum brasilense, Bradyrhizobium japonicum, Bacillus licheniformis, P.fluorescens and Paenibacillus polymyxa* (Timmusk *et al*., 1999[125]; Per-rig *et al*., 2007[126]). 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 (Frankenberger and Arshad, 1995[127]).

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[128]). These are synthesized by higher plants, fungi, and bacteria. They are involved in several plant 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[129]). They can also regulate root hair abundance and hence promotes the root growth (Bottini *et al*., 2004[130]). The ability of bacteria to synthesize gibberellins-like substances was first described in *Azospirillum brasilense* (Tien *et al*., 1979[131]) and *Rhizobium* (Williams and Mallorca, 1982[132]). 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* (Joo *et al*., 2005[133]; Tsakelova *et al*., 2006[112]; Hayat *et al*., 2010[6]). Plant growth promotion by gibberellin-producing plant growth promoting bacteria and this positive effect on plant biomass is frequently associated with an increased content of gibberellins in plant tissues was reported by several workers (Joo *et al*., 2005[133]; Kang *et al*., 2010[16]).

Abscisic acid

Abscisic 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 by and transport in plant and its presence in the rhizosphere could be extremely important for plant growth under water stress conditions (Frankenberger and Arshad, 1995[127]). *Rhizobium* sp., *B. japonicum* and *Azospirillium* sp. had been reported to produce abscisic acid (Dangar and Basu, 1987[134]; Dobbelaere *et al*., 2003[135]; Boiero *et al*., 2007[136]).

Ethylene

Apart from being a plant growth regulator, ethylene has also been recognized as a stress hormone (Saleem *et al*., 2007[137]). Ethylene is essential for the growth and development of plants, but it has different effects on plant growth depending on its concentration in root tissues. At high concentrations, it can be harmful, as it induces defoliation and cellular processes that lead to inhibition of stem and root growth as well as premature senescence, all of which lead to reduced crop performance (Li *et al*., 2005[138]; Bhattacharyya and Jha, 2012[46]). Under stress conditions like those generated by salinity, drought, water logging, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. Plant growth promoting rhizobacteria which possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which is the precursor for ethylene (Chen *et al*., 2013[139]) is secreted into the rhizosphere and is readsorbed by the roots, where it is converted into ethylene. This accumulation of ethylene leads to a downward spiral effect, as poor root growth leads to a diminished ability to acquire water and nutrients, which, in turn, leads to further stress (Martinez-Viveros *et al.,* 2010[140]). The destruction of ethylene is done by PGPR *via* the enzyme ACC deaminase. This enzyme can diminish or prevent some of the harmful effects of the high ethylene levels (Glick *et al*., 1998[141]). The ACC deaminase acts on ACC, an immediate ethylene precursor in higher plants, degrading this chemical to alphaketobutyrate and ammonium, (Glick *et al*., 1998[141]; Mayak *et al*., 2004[142]). Rhizosphere bacteria with ACC deaminase activity belonging to the genera, *Achromobacter* (Govindasamy *et al*., 2008[143]), *Azospirillum* (Li *et al*., 2005[138]), *Bacillus* (Ghosh *et al*., 2003[144]), *Enterobacter* (Li and Glick, 2001[145]), *Pseudomonas* (Govindasamy *et al*., 2008[143]) and *Rhizobium* (Duan *et al*., 2009[146]) have been isolated from different soils.

Indirect Mechanisms

There are many indirect ways through which PGPR act as plant growth promoters with their biocontrol properties and induction of systemic resistance against phytopathogens. Plant growth promoting organisms have certain properties for biocontrol of various phytopathogens. This includes (1) production of antibiotics; (2) secretion of siderophores enabling iron uptake depriving the fungal pathogens in the vicinity; (3) production of lytic enzymes such as chitinase, â-1, 3 glucanase, protease and lipase which lyse the pathogenic fungal and bacterial cell walls; (4) induces systemic resistance in plants by metabolites (Zahir *et al.,* 2004[24]; Hafeez *et al.*, 2006[147]; Narayanasamy, 2008[148]; Reddy, 2013[149]).

Antibiotics

One of the most effective mechanism by which PGPR employ to prevent proliferation of phytopathogens is the synthesis of antibiotics. Antibiotics include a heterogeneous group of organic, low-molecular-weight compounds that are deleterious to the growth or metabolic activities of other microorganisms (Duffy, 2003[150]). There are six classes of antibiotic compounds linked to the biocontrol of root diseases are, phenazines, phloroglucinols, pyoluteorin, pyrrolnitrin, cyclic lipopeptides (all of which are diffusible) and hydrogen cyanide (HCN which is volatile) (Haas and Défago, 2005[18]). The mechanism of action is to inhibit synthesis of pathogen cell walls, influence membrane structures of cells and inhibit the formation of initiation complexes on the small subunit of the ribosome (Maksimov *et al.*, 2011[151]). An efficient antibiotic, 2, 4-diacetylphloroglucinol (DAPG) produced by pseudomonads, causes membrane damage to *Pythium* spp. and is particularly inhibitory to zoospores of this oomycete (de Souza *et al.*, 2003[152]).

Lytic enzymes

The growth and activities of pathogens can be suppressed by the secretion of lytic enzymes. These are cell wall degrading enzymes such as glucanases, proteases, chitinases, and lipases etc, secreted by biocontrol strains of PGPR involved in the lysis of fungal cell wall (Neeraja *et al*., 2010[153]).These enzymes either digest the enzymes or deform components of cell wall of fungal pathogens. Hydrolytic enzymes directly contribute in the parasitisation of phytopathogens and rescue plant from biotic stresses. The role of three types of chitinolytic enzymes are as follows (a) 4-β-ILT-acetylglucosaminidases splits the chitin polymer into GlcNAc monomers in an exo-type fashion; (b) endochitinases cleave randomly at internal sites over the entire length of the chitin microfibril; and (c) exochitinases catalyse the progressive release of diacetylchitobiose in a stepwise fashion such that no monosaccharides or oligosaccharides are formed (Haran *et al*., 1996[154]). β -Glucanases can act *via* two possible mechanisms, Exo-β-glucanases hydrolyse the β-glucan chain by sequentially cleaving glucose residues from the non-reducing end. Endo- β -glucanases cleave β-linkages at random sites along the polysaccharide chain, releasing smaller oligosaccharides (Pitson *et al*., 1993[155]).

Induced systemic resistance

The uses of plant growth promoting strains are reported to trigger the resistance of plants against pathogens (Ramamoorthy *et al*., 2001[156]). Induced resistance (ISR) is a state of enhanced defensive capacity developed by a plant when appropriately stimulated. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistance which can be differentiated on the basis of the nature of the elicitor and the regulatory pathways involved (Choudhary *et al*., 2007[157]). SAR can be triggered by exposing the plant to virulent, avirulent, and non pathogenic microbes and involves accumulation of pathogenesis-related proteins (chitinase and glucanase), and salicylic acid. ISR does not involve the accumulation of pathogenesis-related proteins or salicylic acid, but instead, relies on pathways regulated by jasmonate and ethylene and these hormones stimulate the host plant's defense responses against a variety of plant pathogens (Yan *et al*., 2002[158]; Glick, 2012[49]). Bacterial components too induce induced systemic resistance such as lipopolysaccharides, flagella, siderophores, etc., (Doombos *et al*., 2012[159]). PGPR-mediated induced systemic resistance has been shown to effectively suppress Phytophthora blight caused by *Phytophthora capsici* on squash (Zhang *et al*., 2010[160]).

CONCLUSION

Plant growth promoting rhizobacteria in rhizosphere soil is highly dynamic, more versatile in transforming, mobilizing and solubilising the nutrients. Therefore, the rhizobacteria are the dominant deriving forces in recycling the soil nutrients and consequently, they are crucial for soil fertility. They may be extensively used in plant growth promotion as it acts as a plant nourishment and enrichment source which would replenish the nutrient cycle between the soil and plant roots , exhibits detoxifying potential, controls phytopathogen thereby exerts a positive influence on crop productivity and ecosystem functioning, hence can be implemented in agriculture. With better research and development,

these microbial populations use would become a reality and instrumental and build stability and productivity of agro-ecosystems, thus leading us towards an ideal agricultural system with sustainability, improvement in human health, benefits environment and ecosystem and leads to the production of adequate food for the increasing world population.

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