# Plant Growth Promoting Rhizobacteria: A Critical Review

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#### Abstract

Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria that aggressively colonize plant roots and benefit plants by providing growth promotion. Inoculation of crop plants with certain strains of PGPR at an early stage of development improves biomass production through direct effects on root and shoots growth. Inoculation of ornamentals, forest trees, vegetables, and agricultural crops with PGPR may result in multiple effects on early-season plant growth, as seen in the enhancement of seedling germination, stand health, plant vigor, plant height, shoot weight, nutrient content of shoot tissues, early bloom, chlorophyll content, and increased nodulation in legumes. PGPR are reported to influence the growth, yield, and nutrient uptake by an array of mechanisms. They help in increasing nitrogen fixation in legumes, help in promoting free-living nitrogen-fixing bacteria, increase supply of other nutrients, such as phosphorus, sulphur, iron and copper, produce plant hormones, enhance other beneficial bacteria or fungi, control fungal and bacterial diseases and help in controlling insect pests. There has been much research interest in PGPR and there is now an increasing number of PGPR being commercialized for various crops. Several reviews have discussed specific aspects of growth promotion by PGPR. In this review, we have discussed various bacteria which act as PGPR, mechanisms and the desirable properties exhibited by them.

Keywords: PGPR; Siderophore; Phosphate solubilisation; Antifungal; Biocontrol; Systemic resistance; Plant growth promotors.

#### 1. Introduction

Plant growth in agricultural soils is influenced by many abiotic and biotic factors. There is a thin layer of soil immediately surrounding plant roots that is an extremely important and active area for root activity and metabolism which is known as rhizosphere. The rhizosphere concept was first introduced by Hiltner to describe the narrow zone of soil surrounding the roots where microbe populations are stimulated by root activities [1]. The original concept has now been extended to include the soil surrounding a root in which physical, chemical and biological properties have been changed by root growth and activity [2]. A large number of microorganisms such as bacteria, fungi, protozoa and algae coexist in the rhizosphere. Bacteria are the most abundant among them. Plants select those bacteria contributing most to their fitness by releasing organic compounds through exudates [3] creating a very selective environment where diversity is low [4, 5]. Since bacteria are the most abundant microorganisms in the rhizosphere, it is highly probable that they influence the plants physiology to a greater extent, especially considering their competitiveness in root colonization [6, 7].

Microorganisms that colonize the rhizosphere can be classified according to their effects on plants and the way they interact with roots, some being pathogens whereas other trigger beneficial effects. Rhizobacteria inhabit plant roots and exert a positive effect ranging from direct influence mechanisms to an indirect effect. So, the bacteria inhabiting the rhizosphere and beneficial to plants are termed PGPR [8]. In the last few years, the number of PGPR that have been identified has seen a great increase, mainly because the role of the rhizosphere as an ecosystem has gained importance in the functioning of the biosphere. Various species of bacteria like Pseudomonas, Azospirillum, Azotobacter, Klebsiella, Enterobacter, Alcaligenes, Arthrobacter, Burkholderia, Bacillus and Serratia have been reported to enhance the plant growth [9-12]. There are several PGPR inoculants currently commercialized that seem to promote growth through at least one mechanism; suppression of plant disease (termed Bioprotectants), improved nutrient acquisition (Biofertilizers), or phytohormone production (Biostimulants). Inoculant development has been most successful to deliver biological control agents of plant disease i.e. organisms capable of killing other organisms pathogenic or disease causing to crops. Various bacteria which are predominantly studied and increasingly marketed as the biological control agents includes the genera Bacillus, Streptomyces, Pseudomonas, Burkholderia and Agrobacterium. They suppress plant disease through at least one mechanism; induction of systemic resistance, and production of siderophores or antibiotics. Exposure to the PGPR triggers a defence response by the crop as if attacked by pathogenic organisms. Siderophores produced by some PGPR scavenge heavy metal micronutrients in the rhizosphere (e.g. iron) starving pathogenic organisms of proper nutrition to mount an attack of the crop. Antibiotic producing PGPR releases compounds that prevent the growth of the pathogens. Bioprotectants are currently being studied by the laboratories of Fernando and Daayf in the Department of Plant Science, University of Manitoba. Biofertilizers-nitrogen fixing bacteria are also available for increasing crop nutrient uptake of nitrogen from nitrogen fixing bacteria associated with roots (Azospirillum). Nitrogen fixing biofertilizers provide only a modest increase in crop nitrogen uptake (at best an increase of 20 Kg N acre<sup>-1</sup>). The elemental sulphur present in

the soil must be transformed or oxidised into sulphate by the bacteria before it is available for plants. The inoculation of sulphur-oxidizing bacteria (*Thiobacillus*) onto the seeds of high S-demanding crops has proved to be quite successful in making sulphur more available for the plants. The rock phosphate is an approved source of phosphorus but its availability to plants is limited under most growing conditions. Phosphorus oxidizing bacteria help in making this phosphorus available to the plants. The phytohormones they produce include indole-acetic acid, cytokinins, gibberellins and inhibitors of ethylene production. Rhizoremediers PGPR also help in degrading organic pollutants. *Azospirillum* sp. shows osmoadaptation and can survive under salinity/osmolarity due to the accumulation of compatible solutes. The bacteria like *P. fluorescens* can survive under dry conditions and hyperosmolarity.

The use of PGPR offers an attractive way to replace chemical fertilizer, pesticides, and supplements; most of the isolates result in a significant increase in plant height, root length, and dry matter production of shoot and root of plants. PGPR help in the disease control in plants. Some PGPR especially if they are inoculated on the seed before planting, are able to establish themselves on the crop roots. PGPR as a component in integrated management systems in which reduced rates of agrochemicals and cultural control practices are used as biocontrol agents. Such an integrated system could be used for transplanted vegetables to produce more vigorous transplants that would be tolerant to nematodes and other diseases for at least a few weeks after transplanting to the field [13]. Selected strains of beneficial PGPR trigger a plant mediated induced systemic resistance (ISR) response that is effective against a broad spectrum of plant pathogens. ISR is a plant-mediated mechanism it resembles classic pathogen-induced resistance, in which non-infected parts of previously pathogen-infected plants become more resistant to further infection [14]. In forestry, the potential of inoculating tree roots with PGPR has been recognised. There has been a new focus on investigating the application of PGPR and fungi to commercial forestry operation especially in the areas of enhancing tree growth and survival of tree seedlings though microbially mediated phytohormone production [15].

#### 2. Plant growth promoting rhizobacteria (PGPR)

The recognition of plant growth-promoting rhizobacteria (PGPR), a group of beneficial plant bacteria, as potentially useful for stimulating plant growth and increasing crop yields has evolved over the past several years to where today researchers are able to repeatedly use them successfully in field experiments. Increased growth and yields of potato, sugar beet, radish and sweet potato [16] have been reported. Commercial applications of PGPR are being tested and are frequently successful; however, a better understanding of the microbial interactions that result in plant growth increases will greatly increase the success rate of field applications [17]. PGPR, root-colonizing bacteria are known to influence plant growth by various direct or indirect mechanisms. Several chemical changes in soil are associated with PGPR. Plant growth-promoting bacteria (PGPB) are reported to influence the growth, yield, and nutrient uptake by an array of mechanisms. Some bacterial strains directly regulate plant physiology by mimicking synthesis of plant hormones, whereas others increase mineral and nitrogen availability in the soil as a way to augment growth. The isolates could exhibit more than two or three PGP traits, which may promote plant growth directly or indirectly or synergistically [12, 18]. The plant growth stimulating efficiency of bacterial inoculants is affected by soil nutritional condition. The bacterial inoculation has a much better stimulatory effect on plant growth in nutrient deficient soil than in nutrient rich soil [19]. The simultaneous screening of rhizobacteria for growth promotion under gnotobiotic conditions and in vitro production of auxins is a useful approach for selecting effective PGPR [20]. Some PGPR releases a blend of volatile components like 2, 3-butanediol and acetoin that promote growth of Arabidopsis thaliana [21]. The diazotroph bacterial inoculation significantly increases the seed cotton yield, plant height and microbial population in soil [22]. Double and triple combination of IBA, bacteria and carbohydrates are more effective in increasing rooting capacity and more quality rooting in case of apple [23]. The bacteria isolated from composts which included farm waste compost (FWC), rice straw compost (RSC), Gliricidia vermin compost (GVC), and macrofauna associated with FWC when applied with composts show the synergistic effect on the growth of pearl millet [24]. The use of PGPR with P-enriched compost in an integrated manner improves the growth, yield and nodulation in chickpea [25].

# 3. Applications of PGPR

# 3.1 Biological nitrogen fixation

A number of bacterial species belonging to genera *Azospirillum*, *Alcaligenes*, *Arthrobacter*, *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* are associated with the plant rhizosphere and are able to exert a beneficial effect on plant growth [26, 27]. The important role is played by plants in selecting and enriching the types of bacteria by the constituents of their root exudates. Thus, the bacterial community in the rhizosphere develops depending on the nature and concentrations of organic constituents of exudates, and the corresponding ability of the bacteria to utilize these as sources of energy [28]. There is a continuum of bacterial presence in soil rhizosphere, rhizoplane and internal of the plant tissues [29]. Rhizospheric bacterial communities however have efficient systems for uptake and catabolism of

organic compounds present in root exudates [30]. Several bacteria help to derive maximum benefit from root exudates by their ability to attach to the root surfaces (rhizoplane). Since associative interactions of plants and microorganisms must have come into existence as a result of co evolution, the use of latter group as bio inoculants must be pre-adapted, so that it fits into a longterm sustainable agricultural system. PGPR are commonly used as inoculants for improving the growth and yield of agricultural crops and offers an attractive way to replace chemical fertilizers, pesticides, and supplements [31]. The use of bio-fertilizer and bioenhancer such as N<sub>2</sub> (nitrogen) fixing bacteria and beneficial micro-organism can reduce chemical fertilizer applications and consequently lower production cost. Utilization of PGPR in order to increase the productivity may be a viable alternative to organic fertilizers which also helps in reducing the pollution and preserving the environment in the spirit of an ecological agriculture [32]. Thus rhizospheric bacteria can be a promising source for plant growth promoting agent in agriculture [33] and are commonly used as inoculants for improving the growth and yield of agricultural crops. PGPR or combinations of PGPR and AMF can improve the nutrient use efficiency of fertilizers and allow reduced application rates of chemical fertilizers [34]. The use of PGPR isolates as inoculants biofertilizers is beneficial for rice cultivation as they enhance growth of rice and by inducing other plant growth promoting traits [31]. Applying the combined inoculation of PGPR as biofertilizer affects beneficially the yield and growth of chickpea in field conditions [35]. Biological nitrogen fixation contributes 180 X 10<sup>6</sup> metric tons/year globally, out of which symbiotic associations' produces 80% and the rest comes from free-living or associative systems [36]. The ability to reduce and derive such appreciable amounts of nitrogen from the atmospheric reservoir and enrich the soil is confined to bacteria and Archaea [37]. These include symbiotic nitrogen fixing (N<sub>2</sub>-fixing) forms, viz. *Rhizobium*, the obligate symbionts in leguminous plants and Frankia in non-leguminous trees, and non-symbiotic (free-living, associative or endophytic) N<sub>2</sub>-fixing forms such as cyanobacteria, Azospirillum, Azotobacter, Acetobacter diazotrophicus, Azoarcus etc.

#### 3.1.1 Symbiotic nitrogen fixers

Two groups of nitrogen fixing bacteria have been studied extensively, which includes *Rhizobia* and *Frankia*. *Frankia* forms root nodules on more than 280 species of woody plants from 8 different families [38] however, its symbiotic relationship is not as well understood. *Frankia* is known to form effective symbiosis with the species of *Alnus* and *Casuarina* [39-42]. A number of individual species may improve plant nutrition by releasing plant growth regulators, siderophores and hydrogen cyanide or may increase phosphate availability [43]. An increase in rhizosphere populations has been reported after crop rotation with non-legumes [44] with abundance benefiting subsequent crops [45]. A considerable change in taxonomic status has come about during the last years. Sahgal and Johri [46] outlined the status of rhizobial taxonomy and enlisted 36 species distributed among seven genera (*Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium, Methylobacterium, Rhizobium* and *Sinorhizobium*) derived, based on the polyphasic taxonomic approach. Under different agro-climatic conditions, legumes of economic importance are grown in India and presence of native rhizobia has therefore been anticipated.

#### 3.1.1.1 Rhizobium

When rhizobia colonize the roots from non-legume plant in a non specific relationship the strains from this genus may behave as PGPR. Under the All India Coordinated Pulse Improvement Programme, an extensive survey of nodulation status of legumes, viz. chickpea, pigeonpea, moongbean, soybean and groundnut with native rhizobia during 1967–72 [47, 48] and in 1977–80 [49] has belied this assumption since except for groundnut, at more than 50% of the places surveyed most legumes nodulated poorly. Another survey determined the serological types of the native rhizobial population, frequency of effective types and the fate of the introduced antigenic type in competition with the native types in chickpea [47, 50, 51] moongbean [52], groundnut [53, 54] and clover [55] and revealed that only 20-30% of indigenous rhizobia are effective. Field trials conducted in India showed that depending on the leaume, soil and agroclimatic conditions nearly 50% of nitrogenous fertilizer could be saved through rhizobial inoculations with considerable increase in yield [56, 57]. Inoculation of *Rhizobium* sp. causes a greater increase in growth and yield and the number of nodules per root system is significantly higher in plants inoculated with *Rhizobium* sp. compared to plants without *Rhizobium* sp. under field condition [58]. In addition to their beneficial  $N_2$ -fixing activity with legumes, rhizobia can improve plant P nutrition by mobilizing inorganic and organic P. Many rhizobia isolates from different cross-inoculation groups of rhizobia, isolated from soils in Iran are able to mobilize P from organic and inorganic sources [59]. Conjunctive use of Rhizobium with Phosphate Solubilising Bacteria (PSB) revealed synergistic effect on symbiotic parameters and grain yield of mungbean. Phosphate solubilizing bacteria improves the competitive ability and symbiotic effectiveness of inoculated Rhizobium sp. in lentil under field conditions [60]. Data recorded from tillage versus no-tillage experiment revealed more nodulation and leghaemoglobin content in no-tillage treatment [61]. The single and dual inoculation Rhizobium and phosphorus (P) solubilising bacteria with fertilizer (P<sub>2</sub>O<sub>5</sub>) significantly increases root and shoot weight, plant height, spike length, grain yield, seed P content, leaf protein and leaf sugar content of the wheat crop in a P deficient natural non-sterilized sandy loam soil and is 30-40% better than only P fertilizer for improving grain yield [62]. The P-solubilising strains and the N<sub>2</sub>-fixing bacterial strains have great potential in being formulated and used as biofertilizers [63].

# 3.1.1.2 Bradyrhizobium

*Bradyrhizobium* species are Gram-negative bacilli (rod shaped) with a single subpolar or polar flagellum. They are a common soil dwelling microorganism that can form symbiotic relationships with leguminous plant species where they fix nitrogen in exchange for carbohydrates from the plant. Like other rhizobia, they have the ability to fix atmospheric nitrogen into forms readily available for other organisms to use. They are slow growing in contrast to *Rhizobium* species, which are considered fast growing rhizobia. In a liquid media broth, it takes *Bradyrhizobium* species 3-5 days to create a moderate turbidity and 6-8 hours to double in population size. They tend to grow best with pentoses as a carbon source [64]. Some studies indicate that co-inoculation of *Bradyrhizobium* and certain PGPRs can positively affect symbiotic nitrogen fixation by enhancing both root nodule number or mass, dry weight of nodules, yield components, grain yield, soil nutrient availability and increasing the nitrogenase activity [65-67] and increases the nodulation and nitrogen fixation in *Glycine max*. at a low root zone temperature [68, 69]. The competition between PGPR and *B. japonicum* for the niches in the rhizoplane, production of auxins, and induction of systemic resistance (ISR) by the production of siderophores or by lipopolysaccharides present in the outer membrane (LPS) are the probable reasons for the enhancement of the biological nitrogen fixation, nodulation and growth of *Lupinus al.bus* 1. cv *Multolupa* by plant growth promoting rhizobacteria [70].

# 3.1.2 Non-symbiotic nitrogen fixers

Non-symbiotic nitrogen fixation has a great agronomic significance. One main limitation that it faces is the availability of carbon and energy source for the energy intensive nitrogen fixation process. However, this limitation can be compensated by moving closer to or inside the plants, viz. in diazotrophs present in rhizosphere, rhizoplane or those growing endophytically. Some important non-symbiotic nitrogen-fixing bacteria include *Azoarcus* sp., *Gluconacetobacter diazotrophicus, Herbaspirillium* sp., *Azotobacter* sp. [71, 72], *Achromobacter, Acetobacter, Al.cal.igenes, Arthrobacter, Azospirillum, Azomonas, Bacillus, Beijerinckia, Clostridium, Corynebacterium, Derxia, Enterobacter, Klebsiella, Pseudomonas, Rhodospirillum, RhodoPseudomonas* and *Xanthobacter* [73].

# 3.1.2.1 Azotobacter

The family Azotobacteriaceae comprises of two genera [74] namely, *Azomonas* (non-cyst forming) with three species (*A. agilis*, *A. insignis* and *A. macrocytogenes*) and *Azotobacter* (cyst forming) comprising of 6 species [75], namely, *A. chroococcum*, *A. vinelandii*, *A. beijerinckii*, *A. nigricans*, *A. armeniacus* and *A. Paspali*. *Azotobacter* is generally regarded as a free-living aerobic nitrogen-fixer. Azotobacter paspali, which was first described, by Dobereiner and Pedrosa [76] has been isolated from the rhizosphere of *Paspalum notatum*, a tetraploid subtropical grass, and is highly host specific. Various crops in India have been inoculated with diazotrophs particularly *Azotobacter* and *Azospirillum* [77, 78]. Reports prove that application of *Azotobacter* and *Azospirillum* improves the yield of both annual and perennial grasses [79]. Saikia and Bezbaruah [80] reported increased seed germination of *Cicer arietinum*, *Phaseolus mungo*, *Vigna catjung* and *Zea mays*. *Azotobacter* strains could affect seed germination and seedling growth [81] in a plant. It has been shown that wheat yield increased up to 30% with *Azotobacter* inoculation [82, 83].

# 3.1.2.2 Azospirillum

Since 1970's, Azospirillum strains have been isolated and used [84]. This group of free-living rhizobacteria encompasses ten species, each one classified according to its particular biochemical and molecular characteristics; A. lipoferum and A. brasilense [85]; A. amazonense [86]; A. halopraeferens [87]; A. irakense [88]; A. largimobile [89]; A. doebereinerae [90]; A. Oryzae [91]; A. melinis [92] and recently A. canadensis [93]. Although Azospirillum was first isolated from cereals and most of its initial inoculation has been done on the main cereal crops and, there are more non-cereal species successfully inoculated with Azospirillum than cereals. Azospirillum strains have no preferences for crop plants or weeds or for annual or perennial plants and can be successfully applied to plants that have no previous history of Azospirillum in their roots. It appears that Azospirillum is not a plant specific bacterium and is a general root colonizer [for details on plant species see 94, 95]. Members of the genus Azospirillum fix nitrogen under microaerophilic conditions and are frequently associated with root and rhizosphere of a large number of agriculturally important crops and cereals. Sen [96] made one of the earliest suggestions that the activity of associated nitrogen fixing bacteria such as Azospirillum could meet the nitrogen nutrition of cereal crops. After establishing in the rhizosphere, Azospirilla usually, but not always, promote the growth of plants [97, 98, 94]. Although they posses N<sub>2</sub>-fixing capability (~1-10 kg N/ha), the increase in yield is mainly attributed to improved root development due to the production of growth promoting substances and consequently increased rates of water and mineral uptake [99-101]. Isolation and characterization of bacterial diversity from endorhizosphere of sugarcane (Saccharum sp.) and rye grass (Lolium perenne) sugested that Azospirillum isolates from sugarcane and rye grass exhibited maximum nitrogenase activity among Azospirillum, Bacillus, E. coli and Pseudomonas [102].

#### 3.1.2.3 Acetobacter

Acetobacter has gained importance as an inoculant for sugarcane [103, 104]. This bacterium successfully colonizes sugarcane varieties in India where the chemical N fertilization is completely avoided for at least two successive years and replaced by organic manures [105]. The family Acetobacteriaceae includes genera, Acetobacter, Gluconobacter, Gluconoacetobacter and Acidomonas. Based on 16S rRNA sequence analysis, the name Acetobacter diazotrophicus has been changed to Gluconoacetobacter diazotrophicus [106]. G. diazotrophicus isolated from various sources does not exhibit much variation in the genetic diversity [107, 108]. However, Suman et al. [109] found that the diversity of the isolates of G. diazotrophicus by RAPD analysis was more conspicuous than that reported on the basis of morphological and biochemical characters. Certain genetically related groups of G. diazotrophicus or its ancestors have acquired the capability of colonizing plants by themselves or with the aid of the vectors such as insects or fungi [110]. G. diazotrophicus has been found to harbour plasmids of 2–170 kb [111].

#### 3.1.2.4 Azoarcus

Azoarcus, which is an aerobic/microaerophilic nitrogen-fixing bacterium, was isolated from surface-sterilized tissues of kaller grass (*Leptochloa fusca* L Kunth) [112] and can infect roots of rice plants as well. Kallar grass used as a pioneer plant in Pakistan on salt-affected low fertility soils as it is a salt-tolerant grass. The genus *Azoarcus* has been identified, with two species, *A. indigens* and *A. communis*, and three additional unnamed groups, which were distinct at species level. Nitrogen fixation by *Azoarcus* is extremely efficient.

#### 3.1.3 Bacillus

Bacillus is the most abundant genus in the rhizosphere, and the PGPR activity of some of these strains has been known for many years, resulting in a broad knowledge of the mechanisms involved [113, 114]. There are a number of metabolites that are released by these strains [115], which strongly affect the environment by increasing nutrient availability of the plants [45]. Naturally present in the immediate vicinity of plant roots, B. subtilis is able to maintain stable contact with higher plants and promote their growth. In a micropropagated plant system, bacterial inoculation at the beginning of the acclimatisation phase can be observed from the perspective of the establishment of the soil microbiota rhizosphere. Bacillus licheniformis when inoculated on tomato and pepper shows considerable colonisation and can be used as a biofertiliser without altering normal management in greenhouses [116]. Jaizme-Vega et al. [117] evaluated the effect of a rhizobacteria consortium of Bacillus spp. on the first developmental stages of two micropropagated bananas and concluded that this bacterial consortium can be described as a prospective way to increase plant health and survival rates in commercial nurseries. Bacillus is also found to have potential to increase the yield, growth and nutrition of raspberry plant under organic growing conditions [118]. Bacillus megatorium is very consistent in improving different root parameters (rooting performance, root length and dry matter content of root) in mint [119]. The PSB Bacillus megaterium var. phosphaticum and Potassium Solubilising Bacteria (KSB) Bacillus mucilaginosus when inoculated in nutrient limited soil showed that rock materials (P and K rocks) and both bacterial strains consistently increased mineral availability, uptake and plant growth of pepper and cucumber, suggesting its potential use as fertilizer [120, 121]. The Bacillus pumilus 8N-4 can be used as a bio-inoculant for biofertilizer production to increase the crop yield of wheat variety Orkhon in Mongolia [122].

#### 3.1.4 Pseudomonas

*Pseudomonas* sp. is ubiquitous bacteria in agricultural soils and and has many traits that make them well suited as PGPR. The most effective strains of *Pseudomonas* have been *Fluorescent Pseudomonas* spp. Considerable research is underway globally to exploit the potential of one group of bacteria that belong to *Fluorescent pseudomonads* (FLPs). FLPs help in the maintenance of soil health and are metabolically and functionally most diverse [123, 124]. The presence of *Pseudomonas fluorescence* inoculant in the combination of microbial fertilizer plays an effective role in stimulating yield and growth traits of chickpea [35]. Isolates of FLPs from roots, shoots, and rhizosphere soil of sugarcane provides significant increases in fresh and dry masses [125]. Field trials of a pseudomonad strain (GRP3) lead to a great increase in yield of legumes [126]. Specific strains of the *Pseudomonas fluorescens-putida* group have recently been used as seed inoculants on crop plants to promote growth and increase yields. These pseudomonads, termed PGPR, rapidly colonize plant roots of potato, sugar beet and radish, and cause statistically significant yield increases up to 144% in field tests [127-132]. The occurrence and activity of soil microorganisms are affected by a variety of environmental factors (e.g. soil type, nutrient abundance, pH, moisture content) as well as plant-related factors (species, age). So, while working on two winter wheat cultivars it was found that the genus *Pseudomonas* show higher counts, thus the population size of bacteria of the genus *Pseudomonas* depends on the development phase of wheat plants [133].

# 3.2 PGPR in HCN production

One group of microorganisms which acts as biocontrol agents of weeds include the Deleterious Rhizobacteria (DRB) that can colonize plant root surfaces and able to suppress plant growth [134]. Many DRB are plant specific [135]. Cyanide is a dreaded chemical produced by them as it has toxic properties. Although cyanide acts as a general metabolic inhibitor, it is synthesized, excreted and metabolized by hundreds of organisms, including bacteria, algae, fungi, plants, and insects, as a mean to avoid predation or competition. The host plants are generally not negatively affected by inoculation with cyanide-producing bacterial strains and host-specific rhizobacteria can act as biological weed-control agents [136]. A secondary metabolite produced commonly by rhizosphere pseudomonads is Hydrogen Cyanide (HCN), a gas known to negatively affect root metabolism and root growth [137] and is a potential and environmentally compatible mechanism for biological control of weeds [138]. The HCN production is found to be a common trait of Pseudomonas (88.89%) and Bacillus (50%) in the rhizospheric soil and plant root nodules [139, 115] and is a serious environmental pollutant and a biocontrol metabolite in Pseudomonas species. It was previously not known if glycine was a carbon precursor for HCN in Pseudomonas aeruginosa. Castric [140] presented evidence that glycine is an HCN precursor for P. aeruginosa, but that this process differs significantly from cyanogenesis in other bacteria because: (i) other amino acids besides glycine stimulate HCN production; and (ii) both carbons of glycine are used as sources of cyanide carbon. The level of HCN produced in root-free soil by P. putida and A. delafieldii generally increased with higher amounts of supplemental glycine, with P. putida typically generating more HCN (8-38 µM) at a given glycine level [141]. The sorghum seedlings [Sorghum bicolor (L) Moench] of different genotypes differ in associations with soil microorganisms and differentially affect the number of FLPs in cropping systems [142]. Some of the recent studies have indicated that and some of the Pseudomonas spp. metabolites such as HCN may enhance plant establishment. Wani et al. [143] tested the rhizosphere isolates for HCN producing ability in vitro to find that most of the isolates produced HCN and helped in the plant growth. The isolates from the rhizospheric soil of chickpea also exhibits more than two or three PGPR traits including HCN production, which promotes plant growth directly or indirectly or synergistically [12]. The rhizosphere competent Mesorhizobiumloti MP6 produces hydrocyanic acid (HCN) under normal growth conditions and enhances the growth of Indian mustard (Brassica campestris) [144]. Bacterial isolates belonging to genera Bacillus and Pseudomonas isolated from rhizospheric soils of mustard produces HCN and application of herbicides (quizalafop-p-ethyl & clodinafop) do not have any significant change in HCN production by these isolates [145]. The entomopathogenic bacterium Pseudomonas entomophila produces HCN which is a secondary metabolite and is implicated in biocontrol properties and pathogenicity exerted by other bacteria [146]. The Pseudomonas fragi CS11RH1 (MTCC 8984), a psychrotolerant bacterium produces hydrogen cyanide (HCN) and the seed bacterization with the isolate significantly increases the percent germination, rate of germination, plant biomass and nutrient uptake of wheat seedlings [147].

# 3.3 Plant growth producers

Plant hormones are chemical messengers that affect a plant's ability to respond to its environment. Hormones are organic compounds that are effective at very low concentration; they are usually synthesized in one part of the plant and are transported to another location. They interact with specific target tissues to cause physiological responses, such as growth or fruit ripening. Each response is often the result of two or more hormones acting together. Because hormones stimulate or inhibit plant growth, many botanists also refer to them as plant growth regulators. Botanists recognize five major groups of hormones: auxins, gibberellins, ethylene, cytokinins, and abscisic acid.

IAA (indole-3-acetic acid) is the member of the group of phytohormones and is generally considered the most important native Auxin [31]. It functions as an important signal molecule in the regulation of plant development including organogenesis, tropic responses, cellular responses such as cell expansion, division, and differentiation, and gene regulation [148]. Diverse bacterial species possess the ability to produce the auxin phytohormone IAA. Different biosynthesis pathways have been identified and redundancy for IAA biosynthesis is widespread among plant-associated bacteria. Interactions between IAA-producing bacteria and plants lead to diverse outcomes on the plant side, varying from pathogenesis to phytostimulation. Reviewing the role of bacterial IAA in different microorganism-plant interactions highlights the fact that bacteria use this phytohormone to interact with plants as part of their colonization strategy, including phytostimulation and circumvention of basal plant defense mechanisms. Moreover, several recent reports indicate that IAA can also be a signaling molecule in bacteria and therefore, can have a direct effect on bacterial physiology [149]. There are numerous soil microflora involved in the synthesis of auxins in pure culture and soil [150]. The potential for auxin biosynthesis by rhizobacteria can be used as a tool for the screening of effective PGPR strains [151]. Accumulating evidence indicates that PGPR influence plant growth and development by the production of phytohormones such as auxins, gibberellins, and cytokinins. The effects of auxins on plant seedlings are concentration dependent, i.e. low concentration may stimulate growth while high concentrations may be inhibitory [152]. Different plant seedlings respond differently to variable auxin concentrations [153] and type of microorganisms [154]. The strains which produce the highest amount of auxins i.e. indole acetic acid (IAA) and indole acetamide (IAM) in non-sterilized soil, causes maximum increase in growth and yield of the wheat crop [151]. Even the strains, which produce low amounts of IAA, release it continuously, thus improving plant growth [155]. The isolates producing a large amount of IAA support the plant like L al. bescens H. et Arn. in adverse ecological conditions [156]. The survival of bacteria in the rhizosphere as well as the root and shoot weight

of wheat plants are positively affected by the addition of IAA [157]. Originally isolated from the roots of the epiphytic orchid Dendrobium moschatum, the strains of Rhizobium, Microbacterium, Sphingomonas, and Mycobacterium genera are among the most active IAA producers [155]. Biostimulant species of Pseudomonas and Bacillus can produce yet not well characterized phytohormones or growth regulators that cause crops to have greater amounts of fine roots which have the effect of increasing the absorptive surface of plant roots for uptake of water and nutrients. Rhizobia are the first group of bacteria, which are attributed to the ability of PGPR to release IAA that can help to promote the growth and pathogenesis in plants [158]. The IAA production is studied in *Rhizobium* strains associated only with a few legume hosts [159-161]. Nevertheless, Sridevi and Mallaiah [162] showed that all the strains of Rhizobium isolated from root nodules of Sesbania sesban (L) Merr. produces IAA. The Rhizobium sp. isolated from the root nodules of common pulse plant Vigna mungo (L) Hepper is found to provide high levels of IAA to young and healthy root nodules [158]. All the Rhizobium spp. isolated from Crotalaria sp. are found positive for IAA production, but the isolates differ significantly in auxin production depending upon the cultural conditions. The experiment indicates that Rhizobia can be used as bioenhancer and biofertilizer for wheat production as it can uptake more nutrients (N, P and K) by producing IAA and subsequently increases the plant root system [163]. Among all the isolates maximum amount of IAA is produced by isolate from C. retusa [164]. Independent of the origin (rhizosphere vs. phyllosphere), bacterial strains produced IAA, which accounts for the overall synergistic effect on growth of peas and wheat. The highest concentration of IAA is produced by bacterial strain P. fluorescens and Kocuria varians [165, 154]. While working on chickpea it is found that all the isolates of Bacillus, Pseudomonas and Azotobacter produced IAA, whereas only 85.7% of Rhizobium was able to produce IAA [12]. Pseudomonas fluorescens B16 is a plant growth-promoting rhizobacterium and produces Pyrrologuinoline Quinone which is a plant growth promotion factor [166]. However, the ability of Azotobacter to produce plant growth promoting substances such as phytohormone and IAA is attributed more to yield improvement rather than to diazotrophic activity. Pseudomonas bacteria, especially P. fluorescens and P. putida are the most important kinds of PGPR which produce auxin and promote the yield. Khakipour et al. [167] evaluated the auxin productivity potential in studied Pseudomonas strains through chromatography, using HPLC devise; comparing the methods used and appointing IAA synthesize method by the studied strains in the applied cultivars. In fact, a variety of auxins like indole-3-acetic acid (IAA), indole-3-pyruvic acid, indole-3-butyric acid and indole lactic acid [168, 169]; cytokinins [170, 171] and gibberellins [172] are detected, with auxin production being quantitatively most important [173]. Azospirillum brasilense strain SM has the potential to be a competent rhizospheric bacterium as it triggers the IAA accumulation under nutrient stresses, likely environmental fluctuations and long-term batch cultures and beneficially influences the growth of sorghum. Further, it also has the ability to promote the growth of a number of other plants like Mung bean, Maize, and Wheat [174]. Some of the P-solubilizing bacteria and fungi act as plant growth promoters due to their ability to produce IAA but there is a different IAA production potential among PSB and PSF isolates [175]. Bacillus megaterium from tea rhizosphere is able to produce IAA and thus it helps in the plant growth promotion [176]. The cytokinin receptors play a complimentary role in plant growth promotion by *B. megaterium* [177].

Some microorganisms produce auxins in the presence of a suitable precursor such as L-tryptophan. The tryptophan increases the production of IAA in *Bacillus amyloliquefaciens* FZB42 [178]. Tien *et al.* [179] showed that *Azospirillum* is able to produce auxins when exposed to tryptophan. Plants inoculated with the rhizobia together with Ag<sup>+</sup> ion and L-tryptophan (Trp), give the highest root dry weight, and significantly increase the uptake of N, P and K compared to non-inoculated control plants [163]. Karnwal [180] tested *Fluorescent Pseudomonas* isolates for their ability to produce indole acetic acid in pure culture in the absence and presence of L-tryptophan and found that for both strains, indole production increased with increases in tryptophan concentration.

Isolates producing IAA have stimulatory effect on the plant growth. When the crop is inoculated with the isolates capable of IAA production significantly increases the plant growth by the N, P, K, Ca and Mg uptake of sweetpotato cultivar [181]. There is a significant increase in rooting and root dry matter of cuttings of eucalypts when grown on IAA producing rhizobacteria-inoculated substrate. Some rhizobacterial isolates stimulates the rhizogenesis and plant growth, maximizing yield of rooted cuttings in clonal nurseries [182]. When cucumber, tomato and pepper are inoculated with different strains of PGPR which produce IAA, there is a significant increase in the growth of the vegetables [183]. IAA of microbial origin plays a major role in promotion of orchid germination, at least when the bacterial strains are in tight association with the seeds. *Azospirillum brasilense* strain Az39 and *Brayrhizobium japonicum* strain E109 both are able to excrete IAA into the culture medium, at a concentration sufficient to produce morphological and physiological changes in young seed tissues of Corn (*Zea mays* L) and Soybean (*Glycine max* L) and are responsible for their early growth promotion [184]. The use of PGPR isolates is beneficial for rice cultivation as they enhance the growth of rice by inducing IAA production [31]. A plant growth promoting consortium comprising two species, *Burkholderia* sp. MSSP and *Sinorhizobium meliloti* PP3 with abilities to produce IAA when tested on *Cajanus cajan* show exceptional increase in seedling growth [185].

#### 3.4 Siderophore production

Iron is an essential growth element for all living organisms. The scarcity of bioavailable iron in soil habitats and on plant surfaces foments a furious competition [186]. Under iron-limiting conditions PGPB produce low-molecular-weight compounds called siderophores to competitively acquire ferric ion [187]. Siderophores (Greek: "iron carrier") are small, high-affinity iron chelating compounds secreted by microorganisms such as bacteria, fungi and grasses [188-190]. Microbes release siderophores to scavenge iron from these mineral phases by formation of soluble Fe<sup>3+</sup> complexes that can be taken up by active transport mechanisms. Many siderophores are non-ribosomal peptides [191], although several are biosynthesised independently [192]. Siderophores are also important for some pathogenic bacteria for their acquisition of iron [191]. Siderophores are amongst the strongest binders to Fe<sup>3+</sup> known, with enterobactin being one of the strongest of these [193]. Distribution of siderophoreproducing isolates according to amplified ribosomal DNA restriction analysis (ARDRA) groups, reveals that most of the isolates belong to Gramnegative bacteria corresponding to the Pseudomonas and Enterobacter genera, and Bacillus and Rhodococcus genera are the Gram-positive bacteria found to produce siderophores [194].

Examples of siderophores produced by various bacteria and fungi:





Enterobactin, a catecholate siderophore.

A myriad of environmental factors modulate siderophores synthesis, including pH, the level of iron and the form of iron ions, the presence of other trace elements, and an adequate supply of carbon, nitrogen, and phosphorus [195]. The bacterial growth as well as siderophore production is stimulated by (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and amino acids however, the optimum siderophore yield is obtained with urea [196]. The rhizobacteria able to produce siderophores *in vitro* increases early soybean growth in non-sterile soil [197]. Production of siderophores by plant growth promoting rhizobacteria is detected via the chrome azurol S assay, a general test for siderophores, which is independent of siderophore structure. The siderophores are produced by various bacteria and fungi. Siderophores are usually classified by the ligands used to chelate the ferric iron. The major groups of siderophores include the catecholates (phenolates), hydroxamates and carboxylates (e.g. derivatives of citric acid). The high-resolution analysis of catechol-type siderophores using polyamide thin layer chromatography has been performed by Xie *et al.* [198]. TLC methods are found very effective for separating simple catechol compounds such as 2, 3-dihydroxybenzoic acid (2, 3-DHBA) and catechol after carrying out the sidero-analysis of *Pseudomonas putida* it is revealed that this siderophore molecule contains hydroxamate as well as catecholate iron chelating groups and confirmed that this siderophores belongs to pyoverdine

type [199]. Rhizobium strains isolated from the root nodules of the Sesbania sesban (L) Merr. show the ability to produce hydroxamate-type of siderophores [200]. Rhizobial isolates belonging to genera Rhizobium sp. and Mesorhizobium sp. produces only catecholate type of siderophores [201]. Jurkevitch et al. [202] studied the differential availabilities of the hydroxamate siderophores ferrioxamine B (FOB) and ferrichrome (FC) and the pseudobactin siderophores as sources of Fe for soil and rhizosphere bacteria and found that the ability of bacteria to utilize a large variety of siderophores confers an ecological advantage. Some of the examples of Hydroxamate siderophores are: the siderophore ferrichrome is produced by Ustilago sphaerogena, Desferrioxamine B (Deferoxamine) is produced by Streptomyces pilosus and Streptomyces coelicolor, Desferrioxamine E is produced by Streptomyces coelicolor, Fusarinine C is produced by Fusarium roseum and Ornibactin is produced by Burkholderia cepacia. Acinetobacter calcoaceticus obtained from wheat rhizosphere in black cotton soils of North Maharashtra region produces catechol type of siderophores during exponential phase which is influenced by iron content of medium [203]. There are some examples of Catecholate siderophores like the siderophores Enterobactin is produced by Escherichia coli, bacillibactin is produced by Bacillus subtilis and Bacillus anthracis and vibriobactin is produced by Vibrio cholerae. The examples of siderophores with mixed ligands are the siderophores azotobactin is produced by Azotobacter vinelandii, pyoverdine is produced by Pseudomonas aeruginosa and versiniabactin is produced by Yersinia pestis. Some poaceae (grasses) including wheat and barley produce a class of sideorphores called phytosiderophores or mugineic acids. The majority of the strains of endophytic actinomycetes produce antibiotic siderophores [204]. Although various bacterial siderophores differ in their abilities to sequester iron, in general, they deprive pathogenic fungi of this essential element since the fungal siderophores have lower affinity [205]. Some PGPB strains go one-step further and draw iron from heterologous siderophores produced by cohabiting microorganisms [205-209, 187]. Pseudomonas sp. have the capacity to utilize siderophores produced by diverse species of bacteria and fungi, and Pseudomonas putida can utilize the heterologous siderophores produced by rhizosphere microorganisms to enhance the level of iron available to it in the natural habitat [205]. The two strains Fluorescent Pseudomonas and Pseudomonas fluorescens NCIM 5096 along with P. putida NCIM 2847 produce maximum yield of hydroxamate type of siderophore in the modified succinic acid medium (SM).

Soil bacteria isolates incluing *Azotobacter vinelandii* MAC 259 and *Bacillus cereus* UW 85 produces siderophores and they can be used as efficient PGPR to increase the yield of the crop [210]. *Bacillus megaterium* from tea rhizosphere is able produce siderophore and thus it helps in the plant growth promotion and reduction of disease intensity [176]. *E. coli* isolated and characterized from endorhizosphere of sugarcane (*Saccharum* sp.) and rye grass (*Lolium perenne*) is found to produce maximum siderophores and thus is found to help in the growth of the plants [211]. Specific strains of the *Pseudomonas fluorescens-putida* group have recently been used as seed inoculants on crop plants to promote growth and increase yields of various crops. These results prompted Kloepper *et al.* [212] to investigate the mechanism by which plant growth was enhanced. A previous study indicated that PGPR increase plant growth by antagonism to potentially deleterious rhizoplane fungi and bacteria, but the nature of this antagonism was not determined [213]. They presented evidence that PGPR exert their plant growth-promoting activity by depriving native microflora of iron. PGPR produces extracellular siderophores (microbial iron transport agents) [189] which efficiently complex environmental iron, making it less available to certain native microflora [212]. The siderophores production by *Bacillus* and *Pseudomonas* when assessed both in the presence and in absence of technical grade of herbicides (quizalafop-p-ethyl & clodinafop) show that the metabolic activities of plant growth promoting rhizobacteria (PGPR) decline following herbicides application [214].

# 3.5 Phosphate Solubilizing Bacteria (PSB)

The improvement of soil fertility is one of the most common strategies to increase agricultural production. The biological nitrogen fixation is very important in enhancing the the soil fertility. In addition to biological nitrogen fixation, Phosphate solubilization is equally important. Phosphorus (P) is major essential macronutrients for biological growth and development. Microorganisms offer a biological rescue system capable of solubilising the insoluble inorganic P of soil and make it available to the plants. The ability of some microorganisms to convert insoluble phosphorus (P) to an accessible form, like orthophosphate, is an important trait in a PGPB for increasing plant yields [215, 216]. The rhizospheric phosphate utilizing bacteria could be a promising source for plant growth promoting agent in agriculture [33]. The use of phosphate solubilising bacteria as inoculants increases the P uptake by plants [216, 217]. Among the heterogeneous and naturally abundant microbes inhabiting the rhizosphere, the Phosphate Solubilising Microorganisms (PSM) including bacteria have provided an alternative biotechnological solution in sustainable agriculture to meet the P demands of plants. These organisms in addition to providing P to plants also facilitate plant growth by other mechanisms. Current developments in our understanding of the functional diversity, rhizosphere colonizing ability, mode of actions and judicious application are likely to facilitate their use as reliable components in the management of sustainable agricultural systems [218]. PSM include largely bacteria and fungi. The most efficient PSM belong to genera Bacillus, Rhizobium and Pseudomonas amongst bacteria, and Aspergillus and Penicillium amongst fungi. Within rhizobia, two species nodulating chickpea, Mesorhizobium ciceri and Mesorhizobium mediterraneum, are known as good phosphate solubilizers [219]. However, it is known that every aspect of the process of nodule formation is limited by the availability of P.

Legumes like alfalfa and clover show a high positive response to P supplementation [220], but most of the supplemented P become unavailable when its reacts with soil components. Many soil microorganisms are able to solubilise this unavailable P through their metabolic activities exudating organic acids, which directly dissolve the rock phosphate, or chelating calcium ions that release P to the solution. About 95% of Gram-positive soil bacilli belong to the genus *Bacillus* [221]. Members of *Bacillus* species are able to form endospores and hence survive under adverse conditions; some species are diazotrophs such as *Bacillus subtilis* [222], whereas others have different PGPR capacities [116, 223, 113, 45]. While working with two *Bacillus* strains, Orhan *et al.* [118] found that *Bacillus* M<sub>3</sub> alone or in combination with *Bacillus* OSU-142 have the potential to increase the yield, growth and nutrition of raspberry plant under organic growing conditions. Bacterial strains *Azotobacter vinelandii* and *Bacillus cereus* when tested *in vitro* are found to solubilise Phosphate and thus help in the growth of plant [210]. *Bacillus megaterium* from tea rhizosphere is able to solubilize phosphate and thus it helps in the plant growth promotion [176]. The group of *Rhizobium leguminosarum* bv. *viciae* mobilized in liquid TCP Sperber medium significantly releases more P than other rhizobia tested. The efficient mineral phosphate solubilising phenotype in Gram-negative bacteria has resulted from extracellular oxidation of glucose to gluconic acid *via* the quinoprotein glucose dehydrogenase [224].

In a screening of 4800 bacterial isolates from the root-free soil, rhizosphere and rhizoplane of *P. Juliflora* growing in alkaline soils, the incidence of PSB was highest in the rhizoplane, followed by rhizosphere and root-free soil [225]. Isolates from the rhizosphere of Soyabean are found to solubilise P *in vitro* along with other plant growth promoting traits and increases the soyabean growth [197]. Bacterial isolates *Pseudomonas* sp. and *Azospirillum* sp. from the rhizosphere soil and root cuttings of *Piper nigrum* L exhibits high phosphate solubilising ability *in vitro* [226]. The organism *Pseudomonas putida* exhibits a battery of PGPR traits including enhanced production of plant growth hormone indoleacetic acid. AM fungi are known to enhance plant uptake of phosphorus (P) and other mineral nutrients [227]. *E. coli* isolated and characterized from endorhizosphere of sugarcane (*Saccharum* sp.) and rye grass (*Lolium perenne*) is found to solubilise phosphate and thus is found to help in the growth of the plants [211]. The majority of the strains of endophytic actinomycetes can solubilize [204].

Identification and characterization of soil PSB for the effective plant growth-promotion broadens the spectrum of phosphate solubilizers available for field application. The application of PSM and PGPR together can reduce P application by 50% without any significant reduction of grain yield in corn *Zea mays* [228]. The PSB inoculation with mineral phosphorus raises the efficiency of P fertilizer and decreases the required P rate to plants. It also enhances vegetative growth and fruit quality, in addition to reduce the pollution of environment [229]. The use of PGPR isolates as inoculants is beneficial for rice cultivation as they enhance the growth of rice and phosphorus solubilisation [31].

#### 3.6 Biocontrol agents

PGPR are indigenous to soil and the plant rhizosphere and play a major role in the biocontrol of plant pathogens. They can suppress a broad spectrum of bacterial, fungal and nematode diseases. PGPR can also provide protection against viral diseases. The use of PGPR has become a common practice in many regions of the world. Although significant control of plant pathogens has been demonstrated by PGPR in laboratory and greenhouse studies, results in the field have been inconsistent. Recent progress in our understanding of their diversity, colonizing ability, and mechanism of action, formulation and application should facilitate their development as reliable biocontrol agents against plant pathogens. Some of these rhizobacteria may also be used in integrated pest management programmes. Greater application of PGPR is possible in agriculture for biocontrol of plant pathogens and biofertilization [230]. The bacterial strains isolated from Lolium perenne rhizosphere are capable of acting as plant growth promoting bacteria and as biocontrol agents as they show various plant growth promoting activities [231]. A major group of rhizobacteria with potential for biological control is the Pseudomonades [232]. Pseudomonas sp. is ubiquitous bacteria in agricultural soils. Tremendous progress has been made in characterizing the process of root colonization by pseudomonads, the biotic and abiotic factors affecting colonization, bacterial traits and genes contributing to rhizosphere competence, and the mechanisms of pathogen suppression [233]. Pseudomonads possess many traits that make them well suited as biocontrol and growth-promoting agents [234]. These include the ability to (i) grow rapidly in vitro and to be mass produced; (ii) rapidly utilize seed and root exudates; (iii) colonize and multiply in the rhizosphere and spermosphere environments and in the interior of the plant; (iv) produce a wide spectrum of bioactive metabolites (i.e., antibiotics, siderophores, volatiles, and growth-promoting substances); (v) compete aggressively with other microorganisms; and (vi) adapt to environmental stresses. In addition, pseudomonads are responsible for the natural suppressiveness of some soils to soil borne pathogens [235]. The major weakness of pseudomonads as biocontrol agents is their inability to produce resting spores (as do many Bacillus spp.), which complicates formulation of the bacteria for commercial use. Fluorescent Pseudomonas spp. has been studied for decades for their plant growth-promoting effects through effective suppression of soil borne plant diseases. Among various biocontrol agents, Fluorescent pseudomonads, equipped with multiple mechanisms for biocontrol of phytopathogens and plant growth promotion, are being used widely [236-239] as they produce a wide variety of antibiotics, chitinolytic enzymes, growth promoting hormones, siderophores, HCN and catalase, and can solubilize phosphorous [236, 240-242]. Pseudomonas fluorescens MSP-393, a plant growth-promoting rhizobacterium is an efficient biocontrol agent in rice grown in saline soils of coastal ecosystems [243]. Cold-tolerant fluorescent *Pseudomonas* isolated from Garhwal Himalayas act as potential plant growth promoting and biocontrol agents in pea [244].

Cyanide production is one of the possible ways by which rhizonbacteria may suppress plant growth in soil. Rudrappa *et al.* [245] elucidated the role of cyanide production in pseudomonad virulence affecting plant root growth and other rhizospheric processes. Growth inhibition of lettuce and barnyard grass by volatile metabolites of the cyanogenic rhizobacteria confirmed that HCN is the major inhibitory compound produced [246]. Leafy spurge is a serious invasive weed of grasslands of the northern Great Plains of the U.S. and Prairie Provinces of Canada. Leafy spurge is very difficult to control with herbicides, insect biological control agents, and other cultural practices. A synergism between plant-associated microorganisms and root-damaging insects is the most effective condition for inducing disease and subsequent mortality of leafy spurge [247]. The plant-parasitic nematodes are among the most destructive plant pests, causing substantial economic losses to agronomic crops worldwide. HCN is potentially an important compound with activity against RKN as well as *C. elegans*, and *C. elegans* can act as a useful model system for studying plant-parasitic nematode control using *Pseudomonas* [248]. Multitrophic interactions mediate the ability of fungal pathogens to cause plant disease and the ability of bacterial antagonists to suppress disease. A pathogen metabolite functions as a negative signal for bacterial antibiotic (HCN) biosynthesis, which can determine the relative importance of biological control mechanisms available to antagonists and which may also influence fungus-bacterium ecological interactions [249]. Positive correlations are found between HCN production *in vitro* and plant protection in the cucumber/*Pythium ultimum* and tomato/*Fusarium oxysporum* f. sp. *radicis-lycopersici* pathosystems [250].

*Bacillus subtilis* is also used as a biocontrol agent. This prevalent inhabitant of soil is widely recognized as a powerful biocontrol agent. In addition, due to its broad host range, its ability to form endospores and produce different biologically active compounds with a broad spectrum of activity, *B. subtilis* as well as other *Bacilli* are potentially useful as biocontrol agents [251]. *Bacillus megaterium* from tea rhizosphere is able to solubilize phosphate, produce IAA, siderophore and antifungal metabolite and thus it helps in the plant growth promotion and reduction of disease intensity [176]. Two strains [*Bacillus thuringiensis* (*kurstaki*) and *Bacillus sphaericus*] have the ability to solubilise inorganic phosphates and help in the control of the lepidopteron pests [252].

Arbuscular Mycorrhizal (AM) fungi are ubiquitous in nature and constitute an integral component of terrestrial ecosystems, forming symbiotic associations with plant root systems of over 80% of all terrestrial plant species, including many agronomically important species. AM fungi are particularly important in organic and/or sustainable farming systems that rely on biological processes rather than agrochemicals to control plant pathogens. Of particular importance is the bioprotection conferred to plants against many soil born pathogens such as species of *Aphanomyces, Cylindrocladium, Fusarium, Macrophomina, Phytophthora, Pythium, Rhizoctonia, Sclerotinium, Verticillium* and *Thielaviopsis* and various nematodes by AM fungal colonisation of the plant root [253]. AM fungi are known to enhance plant uptake of other mineral nutrients [227] and this enhanced plant development leads to disease escape or to heigher tolerance against soil-born pathogens [254].

Azospirillum spp. is not considered a classic biocontrol agent of soil-borne plant pathogens. However, A. Brasilense have moderate capabilities of biocontrolling crown gall-producing Agrobacterium [255]; bacterial leaf blight of mulberry [256]; and bacterial leaf and/or vascular tomato diseases [257, 258]. In addition, the proliferation of other non-pathogenic rhizosphere bacteria can be restricted by A. brasilense [259]. These Azospirillum antibacterial activities could be related to its already known ability to produce bacteriocins [260] and siderophores [261, 262]. In addition, A. brasilense was recently reported to synthesize phenylacetic acid (PAA), an auxin-like molecule with antimicrobial activity [263]. Recently, actinobacteria residing in plants called endophytic actinomycetes, have been reported as new sources for bioactive compounds [264-266] and had beneficial effects to the host plant by protecting plant from pathogens [267].

# 3.7 Antifungal activity

PGPR improve plant growth by preventing the proliferation of phytopathogens and thereby support plant growth. Some PGPR synthesize antifungal antibiotics, e.g. *P. fluorescens* produces 2,4-diacetyl phloroglucinol which inhibits growth of phytopathogenic fungi [268]. Certain PGPR degrade fusaric acid produced by *Fusarium* sp. causative agent of wilt and thus prevents the pathogenesis [269]. Some PGPR can also produce enzymes that can lyse fungal cells. For example, *Pseudomonas stutzeri* produces extracellular chitinase and laminarinase which lyses the mycelia of *Fusarium solani* [270]. In recent years, *fluorescent Pseudomonas* has been suggested as potential biological control agent due to its ability to colonize rhizosphere and protect plants against a wide range of important agronomic fungal diseases such as black root-rot of tobacco [271], root-rot of pea [272], root-rot of wheat [273], damping-off of sugar beet [274-276] and as the prospects of genetically manipulating the producer organisms to improve the efficacy of these biocontrol agents [277]. A concern is shown on the use of FLPs in crop

plants as the antifungal substances released by the bacterium, particularly 2, 4-diacetylphloroglucinol (DAPG) could affect the arbuscular mycorrhizal fungi [278]. Gaur et al. [279] confirmed that DAPG producing pseudomonads recovered from wheat rhizosphere did not adversely affect AM colonization. However, given the toxicity of DAPG, such an inhibition may probably be dependent on the amounts released by the bacterium. Fluorescent pseudomonads exhibit strong antifungal activity against P. oryzae and R. solani mainly through the production of antifungal metabolites [280]. One of the isolate of a fluorescent Pseudomonas spp. EM85 is found to be strongly antagonistic to Rhizoctonia solani, a causal agent of damping-off of cotton [281]. The P. oryzihabitans and X. nematophila strains produce secondary metabolites and suppress Pythium and Rhizoctonia species which also causes damping-off of cotton [282]. Fluorescent pseudomonads also exhibits strong antifungal activity against Rhizoctonia bataticola and Fusarium oxysporum found in rice and sugarcane rhizosphere, mainly through the production of antifungal metabolites [276]. Xanthomonas oryzae pv. oryzae and Rhizoctonia solani – the bacterial leaf blight (BB) and sheath blight (ShB) pathogens of rice (Oryza sativa) are suppressed by indigenous Pseudomonas strains isolated from rhizosphere of rice cultivated in the coastal agri-ecosystem under both natural and saline soil conditions [283]. Isolates of Pseudomonas fluorescens from rice rhizosphere are also shown to exhibit strong antifungal activity against P. oryzae and R. solani mainly through the production of antifungal metabolites [284]. 50-60% of fluorescent pseudomonads recovered from the rhizosphere and endorhizosphere of wheat grown in Indo-Gangetic plains are antagonistic towards Helminthosporium sativum [279]. Zadeh et al. [285] worked to show the antagonistic potential of non-pathogenic rhizosphere isolates of fluorescent Pseudomonas in the biocontrol of Pseudomonas Savastanoi which is the causative agent of Olive knot disease. P. corrugata, a form that grows at 4°C under laboratory conditions [286], produces antifungals such as diacetylphloroglucinol and/or phenazine compounds. Pseudomonas fluorescens CHA0 suppresses black root rot of tobacco, a disease caused by the fungus Thielaviopsis basicola [271] and contributes in the biocontrol of Meloidogyne javanica, the root-knot nematode, in situ [287]. In addition, certain soils from Morens, Switzerland, are naturally suppressive to Thielaviopsis basicola-mediated black root rot of tobacco, and fluorescent pseudomonads populations producing the biocontrol compounds [288]. Pseudomonas shows biocontrol potential against Phytopathogenic fungi in vivo and in vitro conditions from chickpea rhizosphere [289]. P. putida has potential for the biocontrol of root-rot disease complex of chickpea by showing antifungal activity against *Macrophomina phaseolina*. It has also been shown that anaerobic regulator ANR-mediated cyanogenesis contributes to the suppression of black root rot [290]. Pseudomonas strains acts as the effective candidates in suppressing P. capsici in all seasons of plant growth as Fluorescent pseudomonad antagonizes all the reproductive phases of the Phytophthora capsici, the causal organism of foot rot disease [291]. Some metabolites produced by Pseudomons aeruginosa Sha8 produces toxic volatile compound which reduces the growth of both F. oxysporium and Helmithosporium sp. while, A. niger is not affected [292]. B. luciferensis strain KJ2C12 reduces Phytophthora blight of pepper by protecting infection courts through enhanced effective root colonization with protease production and an increase of soil microbial activity [293]. Lima bean (Phaseolus lunatus L) plants release hydrogen cyanide (HCN) in response to damage caused by natural enemies, thereby directly defending plant tissue [294]. The bacteria Pseudomonas fluorescens CHAO shows biocontrol against the ciliated protozoa Tetrahymena pyriformis which feeds on it [295].

The nutritional superiority of more vigorous AM plants has been proposed to be a mehanism in reduction of root diseases [227]. Wild rhizobial cultural filterates and/or AM plants are found to have a significant antagonistic effect against soil born pathogenic fungi and therefore enhances the plant resistance to diseases [296]. Siderophore mediated antagonism by *Acinetobacter calcoaceticus* is observed against common phytopathogens viz., *Aspergillus flavus*, *A. niger, Colletotrichum capsicum* and *Fusarium oxysporum* [203].

Soil application of bacterial PSMs manages the wilt of tomato caused by *Fusarium oxysporum* f. sp. *lycopersici* [297]. Inoculation of pepper with the phosphate solubilising bacteria significantly reduces the Phytophthora blight or crown blight of peppers and increases the yield compared to untreated controls [298]. *Azotobacter* isolates, *Pseudomonas* and *Bacillus* showed broad-spectrum antifungal activity on Muller-Hinton medium against *Aspergillus*, one or more species of *Fusarium* and *Rhizoctonia bataticola* [139].

# 3.8 PGPR action under stressed conditions

Agricultural crops are exposed to many stresses that are induced by both biotic and abiotic factors. These stresses decrease yields of crops and represent barriers to the introduction of crop plants into areas that are not suitable for crop cultivation. The occurrence and activity of soil microorganisms are affected by a variety of environmental factors as well as plant-related factors (species, age). Abiotic stress factors include high and low temperature, salinity, drought, flooding, ultraviolet light, air pollution (ozone) and heavy metals. The yield losses associated with abiotic stresses can reach 50% to 82%, depending on the crop. In many semi-arid and arid regions of the world, crop yield is limited due to increasing salinity of irrigation water as well as soil salinity. Under high salinity, plants exhibit a reduced leaf growth rate due to decreased water uptake, which restricts photosynthetic capacity. Plant involves a number of metabolic and physiological changes in response to salt stress and water deficiency (drought) [299]. The inoculation of salt-stressed plants with PGPR strains alleviates the salinity stress in plants. Soil

salinity is one of the most severe factors limiting nodulation, yield and physiological response in soybean. An increase in salinity in the soil causes a physiological response or disorder in lettuce plants [300]. The long-term goal of improving plant–microbe interactions for salinity affected fields and crop productivity can be met with an understanding of the mechanism of osmoadaptation in *Azospirillum* sp. The synthesis and activity of nitrogenases in *A. brasilense* is inhibited by salinity stress [301]. Tripathi *et al.* [302] reported that in *Azospirillum* sp. there is an accumulation of compatible solutes such as glutamate, proline, glycine betaine and trehalose in response to salinity/osmolarity; proline plays a major role in osmoadaptation through increase in osmotic stress that shifts the dominant osmolyte from glutamate to proline in *A. brasilense*. Azospirillum-inoculated sorghum plants had more water content, higher water potential, and lower canopy temperature in their foliage. Hence, they were less drought-stressed than noninoculated plants. Saleena *et al.* [303] have studied the diversity of indigenous *Azospirillum* sp. associated with rice cultivated along the coastline of Tamil Nadu.

The PGPR containing ACC deaminase are present in various soils and offer promise as a bacterial inoculum for improvement of plant growth, particularly under unfavourable environmental conditions such as flooding, heavy metals, phytopathogens, drought and high salt. Ethylene is an important phytohormone, but over-produced ethylene under stressful conditions can result in the inhibition of plant growth or death, especially for seedlings. PGPR containing ACC deaminase can hydrolyze ACC, the immediate precursor of ethylene, to F-ketobutarate and ammonia, and in this way promote plant growth. Inoculation of crops with ACC deaminase-containing PGPR may assist plant growth by alleviating deleterious effects of salt stress ethylene [304].

The establishment and performance of PSM is however affected severely under stressed conditions such as high salt, pH and temperature prevalent in degraded ecosystems represented by alkaline soils with tendency to fix phosphorus [305]. Production of microbial metabolites results in a decrease in soil pH, which probably plays an important role in the solubilization [306] thus, there is a close relationship found between the phosphate solubilising activity and low pH levels in the growth medium which suggests that phosphate solubilization is the result of organic acids released from bacterial metabolism [307, 59, 252]. An inverse relationship between pH and P solubilization is found while working on *Arthrobacter ureafaciens*, *Phyllobacterium myrsinacearum*, *Rhodococcus erythropolis* and *Delftia* sp. They are being reported for the first time as PSB after confirming their capacity to solubilise considerable amount of tricalcium phosphate in the medium by secreting organic acids and thus decreasing the pH of the soil [216]. The inoculation of some microorganisms that solubilises the insoluble phosphates, into a microcosm containing soil from a barren lakeside area enhances the plant growth significantly and this plant growth promoting capability can be used for the rapid revegetation of barren or disturbed land [308]. Savannas are natural ecosystems that predominate in the tropics. These systems usually have acid soils with low fertility in which nutrients, especially phosphorus, are scarce.

The metal resistant PGPB can serve as an effective metal sequestering and growth-promoting bioinoculant for plants in metalstressed soil [309]. The deleterious effects of heavy metals taken up from the environment on plants can be lessening with the use of PGP bacteria or mycorrhizal fungi [310-312]. The soil microbes, plant growth promoting rhizobacteria (PGPR), Psolubilizing bacteria, mycorrhizal-helping bacteria (MHB) and arbuscular mycorrhizal fungi (AMF) in the rhizosphere of plants growing on trace metal contaminated soils plays an important role in phytoremediation [313]. Phytoremediation provides a cheap, energy efficient detoxification method that manipulates intrinsic plant characteristics to concentrate the metal contamination in shoot biomass and reduce the bioavailability of the heavy metals. Soil microbes mitigate toxic effects of heavy metals on the plants through secretion of acids, proteins, phytoantibiotics, and other chemicals [312]. Jing et al. [314] reviewed recent advances in effect and significance of Rhizobacteria in phytoremediation of heavey metal contaminated soils. Cd in soil induces plant-stress ethylene biosynthesis [315] and probably contributes to the accumulation of ACC in roots, the PGPR protect the plants against the inhibitory effects of cadmium [316]. ACC deaminase lowers the ethylene production under cadmium stress condition when measured in vitro ethylene evolution by wheat seedlings treated with ACC deaminase positive isolates [317]. A plant growth-promoting bacterium, Kluyvera ascorbata SUCD165 contains high level of heavy metals is resistant to the toxic effects of  $Ni^{2+}$ ,  $Pb^{2+}$ ,  $Zn^{2+}$ , and  $CrO_4$  –. This bacterium decreases nickel toxicity in the seedlings [318]. Wu *et al.* [319] carried a greenhouse study with Brassica juncea to critically evaluate effects of bacterial inoculation on the uptake of heavy metals from Pb-Zn mine tailings by plants. The presence of these beneficial bacteria stimulated plant growth and protected the plant from metal toxicity; it had little influence on the metal concentrations in plant tissues, but produced a much larger aboveground biomass and altered metal bioavailability in the soil. As a consequence, higher efficiency of phytoextraction was obtained compared with control treatments. The organism *Pseudomonas putida* is also tolerant to number of heavy metals at higher levels. These characteristics make P. putida an excellent candidate for field application in contaminated soil [320]. P. fluorescens can survive under dry conditions and hyperosmolarity [321]. The hydroxamate siderophores contained in culture filtrates of S. acidiscables E13 promotes Cowpea growth under nickel contamination by binding iron and nickel, thus playing a dual role of sourcing iron for plant use and protecting against nickel toxicity [322].

PGPR can have positive effects on vigour and productivity, especially under stress conditions. Seed inoculations with PGPR in asparagus (*Asparagus officinalis* L) results in a positive response and enhances plant growth under drought [323]. The phosphate-solubilising microorganisms can interact positively in promoting plant growth as well as P uptake of maize plants, leading to plant tolerance improving under water deficit stress conditions [324]. On the basis of mutational studies of *Azospirillum*, Kadouri *et al.* [325] proved the role of PHB synthesis and accumulation in enduring various stresses, viz. UV irradiation, heat, osmotic pressure, osmotic shock and desiccation. *Azospirillum*-inoculated wheat (*T. aestivum*) seedlings subjected to osmotic stress developed significant higher coleoptiles, with higher fresh weight and better water status than non-inoculated seedlings [326, 327]. A multi-process phytoremediation system (MPPS) utilizes plant/PGPR (plant growth promoting rhizobacteria) interactions to mitigate stress ethylene effects, thereby greatly increasing plant biomass, particularly in the rhizosphere and it also causes the decontamination of persistent petroleum and organic contaminants in soil [328].

#### 4. Mechanism shown by PGPR

Induced Systemic Resistance (ISR) of plants against pathogens is widespread phenomenon that а has been intensively investigated with respect to the underlying signalling pathways as well as to its potential use in plant protection. Elicited by a local infection, plants respond with a salicylic-dependent signalling cascade that leads to the systemic expression of a broad spectrum and long-lasting disease resistance that is efficient against fungi, bacteria and viruses. Salicylic acid (SA) has an important role in the signalling pathway leading to ISR. After infection, endogenous levels of SA increase locally and systemically, and SA levels increase in the phloem before ISR occurs. SA is synthesized in response to infection both locally and systemically; de novo production of SA in non-infected plant parts might therefore contribute to systemic expression of ISR [329]. Compared to pathogens inducing SAR, non-pathogenic rhizobacteria inducing ISR trigger a different signaltransduction pathway not dependent on the accumulation of the SA and activation of Pathogensis-related (PR)-genes but dependent on precipitation of ethylene and jasmonic acid [330]. Evaluation of growth promotion and induced systemic disease resistance (ISR) in cucumber mediated by plant growth-promoting rhizobacteria (PGPR), with and without methyl bromide soil fumigation proves that in cucumber production systems, withdrawal of methyl bromide does not negatively impact PGPR mediated ISR, and also that PGPR have potential as an alternative to methyl bromide fumigation [331]. The plant growthpromoting Pseudomonas strains, which induced resistance systematically in watermelon to gummy stem rot, are investigated on their induced systemic resistance (ISR) - related characteristics by Lee et al. [332]. Their work supports the concept that PGPR can protect plants against the pathogens by inducing defense mechanisms by iron-binding siderophore, HCN and other associates. The plant growth promoting rhizobacteria induced systemic protection against Tomato late blight [333]. Under in vitro conditions P. fluorescens (ENPF1) and P. chlororaphis isolate (BCA) promotes plant growth and induce systemic resistance against stem blight pathogen Corynespora cassiicola in P. amarus [334]. The involvement of ISR is typically studied in systems in which the Pseudomonas bacteria and the pathogen are inoculated and remain spatially separated on the plant, e.g., the bacteria on the root and the pathogen on the leaf, or by use of split root systems. Since no direct interactions are possible between the two populations, suppression of disease development has to be plant-mediated [335]. The combination of two bacilli strains with chitosan results in significant growth promotion that is correlated with induced resistance in tomato (Lycopersicon esculentum), bell pepper (Capsicum annuum), cucumber (Cucumis sativus) and tobacco (Nicotiana tabacum) [13]. P. fluorescens can survive under dry conditions and hyperosmolarity, the gene AlgU is a crucial determinant of this adaptation [321]. Some PGPR strains release a blend of volatile organic compounds (VOCs) that promote growth in Arabidopsis seedlings and induce resistance against *Erwinia carotovora* subsp. carotovora [336]. Plant growth promotion induced by the antagonistic fungus, Pythium oligandrum, is the result of a complex interaction which includes an indirect effect through control of pathogens in the rhizosphere and/or a direct one mediated by plant-induced resistance [337].

Enzymatic pathways involving hydrolytic, oxidative, reductive, and substitution/transfer reactions are implicated in detoxification of cyanide by bacteria and fungi. The enzyme rhodanese from cyanogenic bacterium *Pseudomonas aeruginosa* involved in transfer reactions causes cyanide detoxification [338]. The enzymes like chitinase, β-1, 3 Glucanase and Cellulase are involved in antagonistic action of *Pseudomonas* against fungal pathogens [289]. The enzyme formamide hydro-lyase is involved in HCN detoxification in sorghum infected by *Gloeocercospora sorghi* [339]. The HCN synthase which produces HCN is encoded by three biosynthetic genes (*hcnA*, *hcnB*, and *hcnC*), but little is known about the diversity of these genes in *fluorescent Pseudomonas* spp and in other bacteria [250]. The PCR amplification of hydrogen cyanide biosynthetic locus hcnAB in *Pseudomonas* spp. has been done. The PCR-based assay targeting hcnAB which are essential genes for hydrogen cyanide (HCN) biosynthesis, allows sensitive detection of HCN+ pseudomonads between logs 2.9 and 3.5 cells per PCR reaction tube [340]. RhdA, a thiosulfate: cyanide sulphur transferase (rhodanese) is a cytoplasmic enzyme acting as the principal rhodanese in *P. aeruginosa*. It is regarded as an effector of *P. aeruginosa* intrinsic resistance to cyanide, insofar as it provides the bacterium with a defense mechanism against endogenous cyanide toxicity, in addition to cyanide-resistant respiration [338]. Infact in *P. fluorescens*, the anaerobic regulator ANR and the global activator GacA are both required for the maximal expression of the HCN biosynthetic genes *hcnABC*. So, we can conclude that cyanogenesis is sequentially activated by ANR at the level of transcription

and by components of the GacA network at the level of translation. In the biocontrol strain CHA0 of *Pseudomonas fluorescens*, the response regulator GacA is essential for the synthesis of extracellular protease (AprA) and secondary metabolites including hydrogen cyanide [341, 342]. In the plant-beneficial rhizosphere bacterium *Pseudomonas fluorescens* CHA0, the GacS/GacA system is essential for the production of antibiotic compounds and hence for biological control of root-pathogenic fungi. The differential expression of three small RNAs facilitated the fine tuning of GacS/A-controlled cell population density-dependent regulation in *P. fluorescens* [343].

The aromatic amino acid-dependent expression of Indole-3-Pyruvate decarboxylase which is a key enzyme in the production of indole-3-acetic acid (IAA) in rhizobacterium *Enterobacter cloacae*UW5 is regulated by TyrR protein [344]. Siderophore biosynthesis is generally tightly regulated by iron-sensitive Fur proteins, the global regulators GacS and GacA, the sigma factors RpoS, PvdS, and FpvI, quorum-sensing autoinducers such as *N*-acyl homoserine lactone, and site-specific recombinases [345, 346]. However, some data demonstrate that none of these global regulators is involved in siderophore production. Neither GacS nor RpoS significantly affects the level of siderophores synthesized by *Enterobacter cloacae* CAL2 and UW4 [347]. RpoS is not involved in the regulation of siderophore production by *Pseudomonas putida* strain WCS358 [348]. In addition, GrrA/GrrS, but not GacS/GacA, are involved in siderophore synthesis regulation in *Serratia plymuthica* strain IC1270, suggesting that gene evolution occurred in the siderophore-producing bacteria [349].

Kumar *et al.* [276] carried out the genotyping of the antifungal compounds while working on rice and sugarcane. A large group of bacteria originating from the roots of pea, lentil, and chickpea grown in Saskatchewan shows several plant growth-promoting traits, suppresses legume fungal pathogens and promotes plant growth. Several of these isolates have the potential for development as biofertilizers or biopesticides for western Canadian legume crops [350].

#### 5. Conclusion

Plant growth promoting rhizobacteria (PGPR) are a heterogeneous group of bacteria that can be found in the rhizosphere, at root surfaces and in association with roots, which can improve the extent or quality of plant growth directly and/or indirectly. In last few decades a large array of bacteria including species of Pseudomonas, Azospirillum, Azotobacter, Klebsiella, Enterobacter, Alcaligenes, Arthrobacter, Burkholderia, Bacillus, Rhizobium and Serratia have reported to enhance plant growth. The direct promotion by PGPR entails either providing the plant with plant growth promoting substances that are synthesized by the bacterium or facilitating the uptake of certain plant nutrients from the environment. The indirect promotion of plant growth occurs when PGPR prevent deleterious effects of one or more phytopathogenic microorganisms. The exact mechanisms by which PGPR promote plant growth are not fully understood, but are thought to include (i) the ability to produce or change the concentration of plant growth regulators like indoleacetic acid, gibberellic acid, cytokinins and ethylene [351, 352], (ii) asymbiotic N<sub>2</sub> fixation [353], (iii) antagonism against phytopathogenic microorganisms by production of siderophores [354], antibiotics [275] and cyanide [355] (iv) solubilization of mineral phosphates and other nutrients [356, 357]. Some PGPR may promote plant growth indirectly by affecting symbiotic N<sub>2</sub> fixation, nodulation or nodule occupancy [358]. However, role of cyanide production is contradictory as it may be associated with deleterious as well as beneficial rhizobacteria [359, 360]. In addition to these traits, plant growth promoting bacterial strains must be rhizospheric competent, able to survive and colonize in the rhizospheric soil [197]. Unfortunately, the interaction between associative PGPR and plants can be unstable. The good results obtained in vitro cannot always be dependably reproduced under field conditions [361, 362]. The variability in the performance of PGPR may be due to various environmental factors that may affect their growth and exert their effects on plant. The environmental factors include climate, weather conditions, soil characteristics or the composition or activity of the indigenous microbial flora of the soil. To achieve the maximum growth promoting interaction between PGPR and nursery seedlings it is important to discover how the rhizobacteria exerting their effects on plant and whether the effects are altered by various environmental factors, including the presence of other microorganisms [363]. Therefore, it is necessary to develop efficient strains in field conditions. One possible approach is to explore soil microbial diversity for PGPR having combination of PGP activities and well adapted to particular soil environment.

As our understanding of the complex environment of the rhizosphere, of the mechanisms of action of PGPR, and of the practical aspects of inoculant formulation and delivery increases, we can expect to see new PGPR products becoming available. The success of these products will depend on our ability to manage the rhizosphere to enhance survival and competitiveness of these beneficial microorganisms [364]. Rhizosphere management will require consideration of soil and crop cultural practices as well as inoculant formulation and delivery [364, 365]. Genetic enhancement of PGPR strains to enhance colonization and effectiveness may involve addition of one or more traits associated with plant growth promotion [366, 352, 367]. Genetic manipulation of host crops for root-associated traits to enhance establishment and proliferation of beneficial microorganisms [368, 369] is being pursued. The use of multi-strain inocula of PGPR with known functions is of interest as these formulations may increase consistency in the field [370, 371]. They offer the potential to address multiple modes of action, multiple pathogens, and temporal or spatial variability. PGPR offer an environmentally sustainable approach to increase crop production

and health. The application of molecular tools is enhancing our ability to understand and manage the rhizosphere and will lead to new products with improved effectiveness [372].

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