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# Role of plant growth promoting rhizobacteria in sustainable agriculture: A review

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**Abstract**
The use of external chemical inputs such as chemical fertilizers and pesticides undoubtedly resulted in huge increase in agricultural products in the past many decades in developing countries like India. Such indiscriminate use of agrochemicals has resulted not only in the deterioration of soil health but also has led to some major environmental disasters and other health related problems, besides increasing the input cost for crop production especially on the marginal farmers. So, the use of plant growth-promoting rhizobacteria (PGPR) as biofertilizers and/or as biocontrol agents to enhance plant growth and yield, suppress diseases in a wide range of agricultural crops and improve the socio-economic status of poor farmers is gaining momentum. The present review highlights the role of plant growth promoting rhizobacteria in the process of crop production and health, development of sustainable agriculture and their commercialization with global applicability.

**Keywords:** Plant growth-promoting rhizobacteria, sustainable agriculture, biofertilizer, biocontrol agent

## Introduction
Agriculture is highly dependent on the use of chemical fertilizers, growth regulators, fungicides and pesticides for obtaining increased yield. This dependence is associated with problems such as environmental pollution, health hazards, interruption of natural ecology, nutrient recycling and destruction of biological communities that otherwise support crop production. The use of bioresources to replace these chemicals is gaining importance. In this context, plant growth promoting rhizobacteria (PGPR) are often considered as novel and potential tool to provide substantial benefits to agriculture. PGPR are a heterogeneous group of bacteria that can be found in the rhizosphere, at root surfaces and in association with roots, which stimulate plant growth through a wide variety of mechanisms like phosphate solubilisation, siderophore production, biological nitrogen fixation, production of 1-Aminocyclopropane-1-carboxylate deaminase (ACC), phytohormone production, exhibiting antifungal activity, production of volatile organic compounds (VOCs), induction of systemic resistance, promoting beneficial plant-microbe symbioses, interference with pathogen toxin production etc. through suppression of deleterious root colonizing microorganisms and by production of plant growth regulators (Kloepper and Schroth, 1981) [59]. PGPR are present in large number on the root surface where the plants exudates provide nutrients (Nelson, 2004) [80]. The beneficial response of crops to inoculation with these PGPR is attributed to better seed germination and seedling emergence, improved nutrition, and reduction in disease incidence an increased crop production. Growth promoting substances are likely to be produced in large quantities by these rhizosphere microorganisms that influence indirectly on the overall morphology of the plants. The concept of PGPR has now been confined to the bacterial strains that can fulfil at least two of the three criteria such as aggressive colonization, plant growth stimulation and biocontrol (Weller *et al.*, 2002; Vessey, 2003) [117, 114].

## Classification of PGPR
In accordance with their degree of association with the plant root cells, PGPRs can be classified into extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) (Martinez-Viveros *et al.*, 2010) [71]. The ePGPRs may exist in the rhizosphere, on the rhizoplane or in the spaces between the cells of root cortex. The bacterial genera such as *Agrobacterium, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcous, Pseudomonas and Serratia* belongs to ePGPR (Gray and Smith, 2005). Whereas, iPGPRs locates generally inside the specialized nodular structures of root cells. They include the endophytes and *Frankia* species both of which can symbiotically fix atmospheric $N_2$ with the higher plants (Verma *et al.*, 2010) [113].

Endophyte includes a wide range of soil bacterial genera such as *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium and Rhizobium* of the family Rhizobiaceae that generally invades the root systems in crop plants to form nodules (Wang and Martinez-Romero, 2000) [116] and stimulates growth either directly or indirectly.

**Mechanism of action**

Plant growth promotion by plant growth promoting rhizobacteria is a well-known phenomenon and there are a number of mechanisms used by PGPR for enhancing plant growth and development in diverse environmental conditions. The effective PGPRs increased plant growth basically by changing the whole microbial community structure in rhizosphere (Kloepper and Schroth, 1981) [59]. PGPR strains can promote plant growth and development either directly due to their ability for enhancing plant nutrition by solubilization of minerals like phosphorus and iron, producing siderophores and enzymes, producing phytohormone (auxin, cytokinins and gibberellins), lowering level of ethylene and inducing systemic resistance (Bhattacharyya and Jha, 2012) [10], or indirectly by biocontrol of deleterious microorganisms or root pathogens that inhibit plant growth, including antibiotic production, parasitism, competition for nutrients and niches within the rhizosphere, synthesis of extracellular enzymes to hydrolyse the fungal cell wall, decreasing pollutant toxicity (Bhattacharyya and Jha, 2012; Podile and Kishore, 2006) [10, 85]. PGPR may use more than one of these mechanisms to enhance plant growth as experimental evidence suggests that the plant growth stimulation is the net result of multiple mechanisms that may be activated simultaneously (Martinez-Viveros *et al*., 2010) [71].

**Table 1:** Forms of PGPRs and their mechanism of action stimulating plant growth

| PGPR forms | Definition | Mechanism of action | References |
|---|---|---|---|
| Biofertilizer | A substance that contains live microorganisms which, when applied on the seed, plant surface or soil, colonizes the rhizosphere and promote plant growth through increased supply of primary nutrients for the host plant | Biological nitrogen fixation Utilization of insoluble phosphorus | Vessey, 2003; Somers *et al.*, 2004; Fuentes-Ramirez and Caballero-Mellado, 2006 [114, 106, 115]. |
| Phyto-stimulator | Microorganism, with the ability to produce phytohormones such as indole acetic acid, gibberellic acid, cytokinins and ethylene | Production of phytohormones | Lugtenberg *et al.*, 2002; Somers *et al.*, 2004 [67, 106]. |
| Biopesticide | Microorganisms that promote plant growth by controlling phytopathogenic agents | Production of antibiotics, siderophores, HCN Production of hydrolytic enzymes Acquired and Induced systemic resistance | Vessey, 2003; Somers *et al.*, 2004; Chandler *et al.*, 2008 [114, 106, 14]. |

**Source:** Martinez-Viveros *et al*., 2010 [71]

**Role of PGPR in agriculture**

**Direct mechanisms**

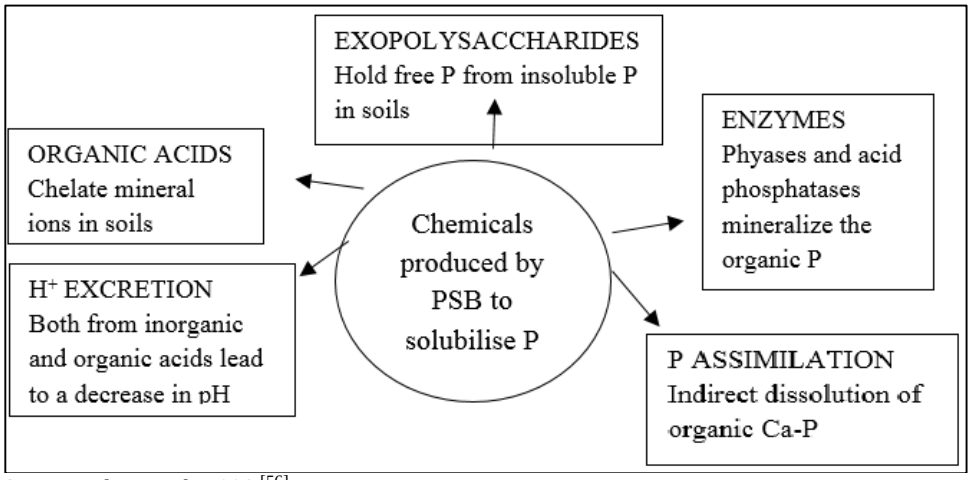
**Nitrogen fixation**

Nitrogen is one of the principal plant nutrients, becoming a limiting factor in agricultural ecosystems due to heavy losses by rainfall or mineral leaching. Plant growth promoting rhizobacteria have the ability to fix atmospheric nitrogen and provide it to plants by two mechanisms: symbiotic and non-symbiotic. Rhizobia are a vast group of rhizobacteria that have the ability to lay symbiotic interactions by the colonization and formation of root nodules with leguminous plants, where nitrogen is fixed to ammonia and make it available for the plant (Ahemad and Kibret (2014) [2]. The plant growth promoting rhizobacteria widely presented as symbionts are *Rhizobium, Bradyrhizobium, Sinorhizobium and Mesorhizobium* with leguminous plants, Frankia with non-leguminous trees and shrubs (Zahran, 2001) [122]. Various rhizobacterial species like *Azotobacter* spp., *Bacillus* spp., *Beijerinckia* spp., etc., have the capacity to fix atmospheric $N_2$ symbiotically. On the other hand, non-symbiotic nitrogen fixation is carried out by free living diazotrophs and this can stimulate non-legume plants growth. Non-symbiotic nitrogen fixing rhizospheric bacteria belonging to genera including *Azoarcus*, *Azotobacter*, *Acetobacter*, *Azospirillum*, *Burkholderia*, *Diazotrophicus*, *Enterobacter*, *Gluconacetobacter*, *Pseudomonas* and *Cyanobacteria (Anabaena, Nostoc*) (Bhattacharyya and Jha, 2012 [10]; Vessey, 2003) [114]. Besides, combined inoculations of rhizobacterial species to improve the quality of soil are also seemed to be a potent area of research in present day agriculture. For instances, combined inoculations of *Bradyrhizobium sp*., with *Pseudomonas striata* have established enhanced nodule occupancy in soyabean resulting in more biological $N_2$ fixation (Dubey, 1996) [25]. Cakmakci *et al.* (2007) [27] studied that on inoculating the barley seeds with five different $N_2$-fixing (*Bacillus licheniformis* RC02, *Rhodobacter capsulatus* RC04, *Paenibacillus polymyxa* RC05, *Pseudomonas putida* RC06, and *Bacillus* OSU-142) and two different phosphate-solubilising (*Bacillus megaterium* RC01 and *Bacillus* M-13) in greenhouse conditions, all bacterial strains fixed $N_2$ and significantly increased the growth of barley and total culturable bacteria count. Maximum $NO_3$-N was found in soil after inoculation with N-fixing *Bacillus* OSU-142, followed by *P. polymyxa* RC05 and *R. capsulatus* RC04.

**Phosphorous solubilization**

Phosphorus is one of the most essential nutrient requirements in plants. Ironically, soils may have large reservoir of total phosphorous (P) but the amounts available to plants are usually a tiny proportion of this total. This low availability of phosphorous to plants is because of the vast majority of soil P is found in insoluble forms, while the plants can only absorb it in two soluble forms, the monobasic ($H_2PO_4^-$) and the dibasic ($HPO_4^{2-}$) ions (Glass 1989) [38]. Several phosphate solubilizing microorganisms (PSMs) are now recorded to convert the insoluble form of phosphorus to soluble form through acidification, secretion of organic acids or protons (Richardson *et al.*, 2009) [91] and chelation and exchange reactions (Hameeda *et al.*, 2008) [48]. Of the various PSMs inhibiting rhizosphere, Phosphate Solubilizing Bacteria (PSB) are considered as promising biofertilizers since they can supply plants with P from sources otherwise poorly available by various mechanisms (Fig. 1) (Khan *et al.*, 2006) [56].

Saprophytic bacteria and fungi are reported for the chelation-mediated mechanisms (Whitelaw, 2000) [118] to solubilise phosphate in soil. Release of plant root exudates such as organic ligands can also alter the concentration of P in soil solution (Hinsinger, 2001) [51].




**Source:** Khan *et al*., 2006 [56]

**Fig 1**: Mechanisms of P solubilization by phosphate solubilizing bacteria

Bacterial genera like *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* are reported as the most significant phosphate solubilizing bacteria (Bhattacharyya and Jha, 2012) [10]. Rhizobacteria can solubilize inorganic P sources and enhance growth and yield of crop plants. The ability of PGPRs to solubilize mineral phosphate, therefore, has been of immense interest to agricultural microbiologists since it can enhance the P uptake of crops. Synthesis of organic acids by rhizosphere microorganisms could be the possible reason for solubilisation of inorganic P sources.

**Potassium solubilization**

Potassium (K) is the third major essential macronutrient for plant growth. The concentrations of soluble potassium in the soil are usually very low and more than 90% of potassium in the soil exists in the form of insoluble rocks and silicate minerals (Parmar and Sindhu, 2013) [82], most of which is unavailable for plant uptake. Potassium deficiency has been reported as one of the major constraints in crop production which might be due to imbalanced fertilizer utilization and depletion of K in the soil system. Since cost of K-fertilizers is increasing every year (Meena *et al.*, 2014) [74] and also use of these fertilizers has harmful effects on the environment, it is necessary to find an alternative indigenous source of K and maintain K level in soils for sustainable crop production (Kumar and Dubey, 2012) [62]. A wide range of bacteria namely *Pseudomonas*, *Burkholderia*, *Acidothiobacillus ferrooxidans*, *Bacillus mucilaginosus*, *Bacillus edaphicus*, *B. circulans* and *Paenibacillus* sp. has been reported to release potassium in accessible form from potassium-bearing minerals in soils (Lian *et al.*, 2002; Sheng, 2005; Liu *et al.*, 2012) [64, 103, 65]. The most important mechanisms involved by these potassium solubilizing bacteria (KSB) in K solubilization from insoluble K-bearing minerals are (i) by lowering the pH, (ii) by enhancing chelation of the cations bound to K and (iii) acidolysis of the surrounding area of microorganism (Meena *et al.*, 2014) [74]. Thus, application of potassium solubilizing plant growth promoting rhizobacteria as biofertilizer for agriculture improvement can reduce the use of agrochemicals and support eco-friendly crop production. Different PGPR species having the ability to solubilize potassium and exerting beneficial effects on growth of various crops are given in Table 2.

**Table 2:** Different PGPR strain as potassium solubilizer in number of crops

| PGPR | Crop | Reference |
|---|---|---|
| *Bacillus edaphicus* | Cotton and rape | Sheng, 2005 [103] |
| *Bacillus mucilaginosus* | Pepper and cucumber | Han *et al*., 2006 [7] |
| *Bacillus cereus* | Sorghum | Badr *et al*., 2006 [49] |
| *Bacillus edaphicus* | Wheat | Sheng and He, 2006 [101] |
| *Bacillus mucilaginous* | Sudan grass | Basak and Biswas, 2008 |
| *Bacillus mucilaginosus, Azotobacter chroococcum and Rhizobium* | Maize and wheat | Singh *et al*., 2010 [9] |
| *Paenibacillus glucanolyticus* | Black pepper | Sangeeth *et al*., 2012 [95] |
| *Enterobacter hormaechei* | Okra | Prajapati *et al*., 2013 [88] |
| *Pseudomonas putida* | Tea | Bagyalakshmi *et al*., 2012 |
| *Enterobacter hormaechei* (KSB-8) | Cucumber | Prajapati and Modi, 2016 [87] |

**Sequestration of Iron by Siderophores**

Iron is one of the bulk minerals present on earth surface, yet it is unavailable in the soil for plants. This is because iron is commonly found in nature in $Fe^{3+}$ form which is meagrely soluble and its concentration is too low to support microbial growth. To survive, the PGPR's synthesize and secrete siderophores that are low molecular iron binding protein compound having a high binding affinity with ferric iron. When Fe is limited, microbial siderophore provide plant with Fe, enhancing their growth. Thus, siderophores act as

solubilizing agents for iron from minerals or organic compounds under conditions of iron limitation (Indiragandhi *et al.*, 2008) [52]. Among PGPRs, fluorescent pseudomonads are widely reported for their broad-spectrum antagonistic activity against number of phytopathogens. Han *et al.* (2005) [50] reported that *Delftia tsuruhatensis* strain, HR4 have suppressed the growth of various plant pathogens like *Pyricularia oryzae*, *Rhizoctonia solani* and *Xanthomonas oryzae*. Different PGPR strains of *Rhizobium meliloti* have been reported to produce siderophores in iron stress conditions (Arora *et al.*, 2001) [5]. Sharma *et al.* (2003) [100] assessed the role of the siderophore-producing *Pseudomonas* strain GRP3 on iron nutrition of *Vigna radiata*. Crowley and Kraemer (2007) [17] also revealed a siderophore mediated iron transport system in oat plants and inferred that siderophores produced by rhizosphere microorganisms deliver iron to oat, which has mechanisms for using Fe-siderophore complexes under iron-limited conditions.

**Production of plant growth regulators**

PGPR can alter root architecture and promote plant development by producing different phytohormones like IAA, gibberellic acid and cytokinins (Kloepper *et al.*, 2007) [58]. Several PGPRs as well as some pathogenic, symbiotic and free living rhizobacterial species are reported to produce IAA and gibberellic acid in the rhizospheric soil and thereby play a significant role in increasing the root surface area and number of root tips in many plants (Han *et al.*, 2005) [50]. Swain *et al.* (2007) [109] reported a positive effect of IAA producing strains of *Bacillus subtilis* on *Dioscorea rotundata* L. They applied a suspension of *B. subtilis* on the surface of the plant, which resulted in an increase in the root: stem ratio as well as number of sprouts as compared with the non-inoculated plants. Similarly, significant shoot growths in maize and rice dwarf mutants were promoted by gibberellins-like substances excreted by *Azospirillum* spp. (Boiero *et al.*, 2007) [12]. Table 3 represents some of the efficient PGPR strains as the producer of different plant growth regulators.

**Table 3**: Efficient PGPR strains as phytohormone producer in numbers of plants

| Hormone produced | PGPR | Host | Reference |
|---|---|---|---|
| IAA | *Agrobacterium* sp. | Lettuce | Bhattacharyya and Jha (2012) [10] |
| | *Azospirillum brasilense* | Wheat | Thakuria *et al.* (2004) [110] |
| | *Bradyrhizobium japonicum* | Maize | Shaharoona *et al.* (2006) [99] |
| | *Rhizobium leguminosarum* | Radish | Bhattacharyya and Jha (2012) [10] |
| | *Rhizobium phaseoli* | Green gram | Zahir *et al.* (2010) [121] |
| | *Bacillus subtilis* | Mustard | Zaidi *et al.* (2006) [123] |
| | *Pseudomonas fluorescens* | Peanut | Dey *et al.* (2004) [22] |
| | *Paenibacillus polymyxa* | Pepper | Phi *et al.* (2010) [83] |
| | *Xanthomonas sp.* RJ3 | Rape | Sheng and Xia (2006) [102] |
| | *Sphingomonas sp., Mycobacterium sp., Bacillus sp., Rhodococcus sp., Cellulomonas sp., Pseudomonas sp.* | Orchid | Tsavkelova *et al.* (2005) [112] |
| Cytokinin | *Paenibacillus polymyxa Pseudomonas* | Wheat | Timmusk *et al.* (1999) [111] |
| | *fluorescens* | Soybean | Bhattacharyya and Jha (2012) [10] |
| | *Rhizobium leguminosarum* | Rape and lettuce | Bhattacharyya and Jha (2012) [10] |
| Gibberellin | *Bacillus* sp. | Alder | Bhattacharyya and Jha (2012) [10] |

IAA-mediated ethylene production could increase root biomass, root hair number and consequently the root surface area of PGPR inoculated tomato plants (Ribaudo *et al.*, 2006) [90]. the fresh weights of shoot and root tissue from inoculated plants were about 40% and 30% higher, respectively, than comparable weights of control plants. A small but statistically significant (about 20%) increase in shoot height was also observed. the amount of IAA in shoots and roots increased upon *Azospirillum* inoculation (7-and 19-fold increase, respectively).

**Lowering Plant Ethylene Levels**

Generally, ethylene is an essential metabolite for the normal growth and development of plants (Khalid *et al.*, 2006) [55], produced endogenously by approximately all plants and also by different biotic and abiotic processes in soils. 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 leading to inhibition of root elongation, as well as symbiotic $N_2$ fixation in leguminous plants and can even result in plant death under extreme conditions. Plant growth promoting rhizobacteria which possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, facilitate plant growth and development by decreasing ethylene levels, inducing salt tolerance and reducing drought stress in plants (Nadeem *et al.*, 2007; Zahir *et al.*, 2008) [78, 120]. Ahmad *et al.* (2013) [3] proved that *Rhizobium* and *Pseudomonas* strains can produce ACC-deaminase and helps in improving the growth, physiology and quality of mung beans under salt-affected environments.

**Production of ACC deaminase and regulation of ethylene level in plants**

Although ethylene is essential for normal growth and development in plants, at high concentration it can be harmful as it induces defoliation and other cellular processes that may lead to reduced crop performance. Using their 1-amino cyclopropane-1-carboxylic acid (ACC) deaminase activity, PGPR can divert ACC from the ethylene biosynthesis pathway in the root system of *Arabidopsis thaliana* plant (Desbrosses *et al.*, 2009) [21]. Thus, rhizobacteria assist in diminishing the accumulation of ethylene levels and re-establish a healthy root system needed to cope with environmental stress. The primary mechanism includes the destruction of ethylene via enzyme ACC deaminase. There are number of publications (Ghosh *et al.*, 2003; Govindasamy *et al.*, 2008; Duan *et al.*, 2009) [36, 44, 24] mentioning rhizosphere bacteria such as *Achromobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas* and *Rhizobium* with ACC deaminase activity. Most of the studies have demonstrated the production of ACC deaminase gene in the

plants treated with PGPR under environmental stress. Grichko and Glick (2001) [46] inoculated tomato seeds with *Enterobacter cloacae* and *Pseudomonas putida* expressing ACC deaminase activity and registered an increase in plant resistance. Ghosh *et al.* (2003) [36] recorded ACC deaminase activity in three Bacillus species namely, *Bacillus circulans* DUC1, *Bacillus firmus* DUC2 and *Bacillus globisporus* DUC3 that stimulated root elongation in *Brassica campestris*. Mayak *et al.* (2004) [73] observed tomato plants inoculated with the bacterium *Achromobacter piechaudii* under water and saline stress conditions and reported a significant increase in fresh and dry weight of inoculated plants.

**Production of volatile organic compounds**

The discovery of rhizobacterial-produced volatile organic compounds (VOCs) constitutes an important mechanism for the elicitation of plant growth by rhizobacteria. Ryu *et al.* (2003) [92] recorded some PGPR strains namely *Bacillus subtilis* GB03, *B. amyloliquefaciens* IN937a and *Enterobacter cloacae* JM22 that released a blend of volatile components, particularly, 2,3-butanediol and acetoin, which promoted growth of *Arabidopsis thaliana*, suggesting that synthesis of bioactive VOCs is a strain-specific phenomenon. Acetoin-forming enzymes have been identified earlier (Forlani *et al*., 1999) [32] in certain crops like tobacco, carrot, maize and rice although their possible functions in plants were not properly established in that period. The VOCs produced by the rhizobacterial strains can act as signalling molecule to mediate plant–microbe interactions as volatiles produced by PGPR colonizing roots are generated at sufficient concentrations to trigger the plant responses (Ryu *et al.*, 2003) [92]. Farmer (2001) [30] identified low-molecular weight plant volatiles such as terpenes, jasmonates and green leaf components as potent signal molecules for living organisms in different trophic levels.

**Growth enhancement**

Application of PGPR strains in agriculture is a potential issue in increasing international demand for food and improving environmental quality. PGPRs have been continuously used to enhance the plant growth, seed emergence and overall yield of crops in different agroecosystems (Minorsky, 2008) [75]. Dobbelaere *et al.* (2001) [23] assessed the inoculation effect of *Azospirillum* sp., on the growth of some agriculturally important plants and observed a significant increase in the dry weight of both the root system and aerial parts of the PGPR inoculated plants, resulting in better development and flowering. Esitken *et al.* (2003) [28] investigated the foliar applications of rhizobacterial microbes in mulberry and apricot and observed better development in total leaf area and chlorophyll production of the inoculated plants. Several PGPR strains such as *Achromobacter xylosoxidans*, *Bacillus subtilis*, *B. licheniformis*, *B. pumilus*, *Brevibacterium halotolerans* and *Pseudomonas putida* are identified as having crucial roles in cell elongation, increasing ACC deaminase activity and plant growth promotion (Sgroy *et al.*, 2009) [98]. Total root length, surface area and volume in tomato and cucumber roots increased after inoculation with *Pseudomonas fluorescens* 92rk and P190r (Saravanakumar and Samiyappan, 2007) [96]. Ahanthem and Jha (2007) [1] observed the response of rice crops, inoculated with arbuscular mycorrhizal (AM) fungi and PGPR in soils differing in nitrogen concentrations and recorded maximum shoot biomass, shoot phosphorus and nitrogen content in the rice plants inoculated with *Azotobacter chroococcum* in combination with *Glomus* sp. There are also reports concerning the root inoculation of apple trees with *Bacillus* M3 and *Microbacterium* FS01, resulting in significant tree growth and yield (Karlidag *et al.*, 2007) [54]. The treatment of seeds or cuttings in some plants with non-pathogenic bacteria, such as *Agrobacterium, Alcaligenes, Bacillus, Pseudomonas, Streptomyces*, etc., induces root formation (Esitken *et al.*, 2003) [28]. This phenomenon might be attributed to the production of auxin, inhibition of ethylene synthesis or mineralization of nutrients by efficient PGPRs (Steenhoudt and Vanderleyden, 2000) [107]. Erturk *et al.* (2010) [27] examined the growth promoting effects of PGPRs on rooting and root growth of *Actinidia deliciosa* stem cuttings and recorded *Bacillus* RC23, *Bacillus* RC03, *B. megaterium* RC01, *B. subtilis* OSU142, *B. simplex* RC19, *Comamonas acidovorans* RC41 and *Paenibacillus polymyxa* RC05 as the successful PGPRs. Datta *et al.* (2011) [18] also observed the effect of three rhizobacteria (*Bacillus* C2, *Bacillus* C25, and *Streptomyces* C32) on the growth and yield of chilli under field conditions and found remarkable increase in growth characteristics such as total number of fruits, fruit weight, and yield.

**Maintenance of soil fertility and nutrient uptake**

PGPR can change the plant physiology and certain nutritional and physical properties of rhizospheric soil and indirectly influence on the colonization patterns of soil microorganisms in that particular region. Inoculation of rhizobacteria increased uptake of nutrient elements like Ca, K, Fe, Cu, Mn and Zn by plants through stimulation of proton pump ATPase (Mantelin and Touraine, 2004) [70]. Reports are available on the combinations of *Bacillus* and *Microbacterium* inoculants to improve the uptake of the mineral elements by crop plants (Karlidag *et al.*, 2007) [54].

This increase in nutrient uptake by plants might be explained through organic acid production by the plants and PGPRs, decreasing the soil pH in rhizosphere. Ample evidences (Forde, 2000; Glass *et al.*, 2002) [31, 37] are there on the maintenance of soil fertility by the rhizobacterial isolates to increase the availability of nutrients for plants. Solubilization of unavailable forms of nutrients is one of the essential criteria in facilitating the transport of most of these nutrients (Glick, 1995) [41].

**Indirect mechanisms**

**PGPR as biocontrol agent**

Competition for nutrients, niche exclusion, parasitism, induced systemic resistance and production of anti-fungal metabolites (AFMs) (contributing to antibiosis) are the probable means responsible for biocontrol activity of PGPRs (Bloemberg and Lugtenberg, 2001; Podile and Kishore, 2006) [11, 85]. A variety of antibiotics have been identified, including compounds such as amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by *pseudomonads* (Loper and Gross, 2007) [66] and oligomycin A, kanosamine, zwittermicin, and xanthobaccin produced by *Bacillus*, *Streptomyces* and *Stenotrophomonas* sp. to prevent the proliferation of plant pathogens (generally fungi) (Compant *et al.*, 2005) [16]. Some rhizobacteria interacts with the plant roots resulting to the phenomenon called induced systemic resistance (ISR) in plant i.e., resistance against some pathogenic bacteria, fungi and viruses (Lugtenberg and Kamilova, 2009) [67]. Among PGPRs, *Pseudomonas* is the best-characterized biocontrol agent at molecular level. Fluorescent pseudomonads are also known to suppress soil

born fungal pathogens by producing antifungal metabolites and by sequestering iron in rhizosphere through the release of iron-chelating siderophores, rendering it unavailable to other organisms (Dwivedi and Johri, 2003) [26]. In soils, antibiotic 2,4-diacetylphloroglucinol (2,4- DAPG) producing *Pseudomonas* sp. was reported for biocontrol of disease in wheat caused by the fungus *Gaeumanomyces graminis* var. tritici (de Souza *et al.*, 2003) [19]. Kidarsa *et al.* (2011) [57] generated information on the biosynthesis of pyoluteorin in *Pseudomonas fluorescens* Pf-5 and 2,4-diacetylphloroglucinol in *P. fluorescens* Q2-87. Ponmurugan *et al.* (2011) [86] screened some efficient *Pseudomonas fluorescens* strain for their plant growth promoting traits and antagonistic activities against tea pathogens such as *Cercospora theae*, *Phomopsis theae* and *Poria hypolateritia*. They also confirmed the presence of various antifungal metabolites in the bacteria which are involved in the growth inhibition of fungal tea pathogen. Application of *Pseudomonas aeroginosa* in combination with common medicinal plant *Launaea nudicaulis* also holds good promises for effective control of root infecting fungi of mungbean (Mansoor *et al.*, 2007) [69].

The strains of *Bacillus subtilis* are the most widely used PGPR due to their disease reducing and antibiotic producing capabilities (Kokalis-Burelle *et al.*, 2006) [60]. Mishra *et al.* (2011) [76] studied that the application of culture filtrate of PGPR *i.e. Bacillus subtilis* MA-2 inhibited the growth of phtytopathogens infecting selected medicinal and aromatic plants, indicating that suppression was due to antifungal compounds in the filtrate. *Bacillus amyloliquefaciens* is known for lipopeptide and polyketide production for biological control activity and plant growth promotion activity against soil borne pathogens (Ongena and Jacques, 2008) [81]. *Azospirillum, Azotobacter, Bacillus, Enterobacter, Paenibacillus, Pseudomonas* and *Streptomyces* are recorded as the potent genera of rhizobacteria acting against the pathogens like tomato mottle virus, tobacco necrosis virus, *Rhizoctonia bataticola*, *Myzus persicae*, *Acyrthosiphon kondoi*, *Fusarium avenaceum* etc. Besides, experiments on the dual effect of PGPR and AM fungi on *Fusarium oxysporum* f. sp., *melongenae* causing brinjal wilt has been done by Kalita *et al.* (2009) [53].

*Rhizobium meliloti* have been reported to exclude the pathogen, *Macrophomina phaseolina*, causing charcoal rot of groundnut. *Micromonospora* sp., *Streptomyces* spp., *Streptosporangium* sp. and *Thermobifida* sp., have shown an enormous potential as biocontrol agents against different root fungal pathogens, indicating the tremendous potentiality of PGPRs as an alternative in controlling plant diseases in agriculture than that of conventional fungicides (Kumar *et al.*, 2009; Franco-Correa *et al.*, 2010; Bhattacharyya and Jha, 2012) [61, 33, 10].

Apart from the production of antibiotic, some rhizobacteria are also capable of producing volatile compound known as hydrogen cyanide (HCN) for biocontrol of black root rot of tobacco, caused by *Thielaviopsis basicola* (Sacherer *et al.*, 1994) [93]. Lanteigne *et al.* (2012) [63] also reported the production of DAPG and HCN by *Pseudomonas* contributing to the biological control of bacterial canker of tomato.

**Resistance to abiotic stress**

Abiotic stresses such as extremely high or low temperature, salinity, drought, acidic soils, and metal toxicity are considered to be the main sources of agricultural yield reduction (Nadeem *et al.*, 2010) [77]. The use of PGPR as elicitors of mechanisms facilitating plant tolerance to abiotic stresses has emerged as a promising strategy to improve plant adaptation and resource use efficiency in hostile environments (Yang *et al.*, 2009) [119]. ACC deaminase is produced by plant growth-promoting bacteria to effectively protect plants against a wide range of abiotic stresses such as drought, salinity, heat, flooding or water logging, and heavy metal stress (Glick, 2014) [40]. Rhizobacteria belonging to the genera *Pseudomonas*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter and Kluyvera* have been documented to have ACC deaminase activity (Saleem *et al.*, 2007) [94].

Some plant growth promoting rhizobacteria produces exo-polysaccharides which can bind cations, including $Na^+$ suggesting a role in mitigation of salinity stress by reducing the content of $Na^+$ available for plant uptake (Arora *et al.*, 2013) [6]. Gururani *et al.* (2013) [47] reported that some free-living PGPR strains produce osmolytes which help plants to increase their osmotic potential within the cell thereby relieving the salinity stress. Marulanda *et al.* (2010) [72] reported that *Bacillus megatertum* strain inoculated into maize roots increased the ability of the root to absorb water under the salinity conditions. Similar behaviour was also found by Gond *et al.* (2015) [42] when *Pantoea agglomerans* was inoculated into the maize roots. Inoculation of jojoba and lettuce plant with *Azospirillum brasilense* was found to improve the salt tolerance (Gonzalez *et al.*, 2015; Gabriela *et al.*, 2015) [43, 35].

Sarma and Saikia (2014) [97] reported that *Pseudomonas aeruginosa* strain has improved the growth of *Vigna radiata* (mung beans) plants under drought conditions. PGPR are also reported as beneficial to the plants like tomatoes and peppers growing on water deficit soils for conferring resistance to water stress conditions (Aroca and Ruiz-Lozano, 2009) [4]. Seed treatment with salinity or drought tolerant isolates of *Trichoderma harzianum* reduced the severity of stress in wheat plants (Rawat *et al.*, 2011; Shukla *et al.*, 2015) [89, 104] under laboratory and greenhouse conditions, respectively.

ACC deaminase activity by the plant growth-promoting rhizobacteria *Burkholderia phytofirmans* helped potato plants to maintain normal growth under heat stress (Saleem *et al.*, 2007) [94]. Pishchik *et al.* (2002) [84] reported that PGPR could attenuate the toxic effect of cadmium pollution on the barley yield, mostly because these bacteria could remove cadmium ions from the soil by binding mechanisms, thereby decreasing cadmium availability in the soil.

***Rhizoremediation***

The application of PGPRs in rhizoremediation technologies is now being considered as effective, since inoculation of PGPR strains could aid remarkable enhancement in plant growth and development on contaminated agroclimatic conditions. Rhizobacteria can directly assist rhizoremediation by producing IAA, biological nitrogen fixation, solubilizing P and secreting siderophores (Denton, 2007) [20]. PGPR strains, pseudomonads and *Acinetobacter* enhance uptake of Fe, Zn, Mg, Ca, K and P by crop plants (Esitken *et al.*, 2006) [29]. Subrahmanyam and Archana (2011) [108] found *Enterobacter* sp. C1D as multi-metal resistant in nature and it had clear positive measurable effects on root length, shoot length, fresh shoot weight, fresh root weight and chlorophyll content of the *Vigna radiata* GM4 in $Cr^{6+}$ amended soils (up to 350 mg $kg^{-1}$). Elevated IAA production probably enables *Enterobacter* sp. C1D to enhance plant growth in $Cr^{6+}$ contaminated soils.

PGPR along with AM fungi are now being utilized in the nutrient poor agricultural soils to increase the solubility of heavy metals and thereby increasing the chances of success in

rhizoremediation. Besides, investigations on the application of PGPR strains in decreasing the bioavailability of toxicity resulting in better growth and development in heavy metal contaminated soils through recycling of nutrients, maintaining soil structure, detoxifying chemicals and controlling pests are also well studied (Denton, 2007) [20].

**Commercial products developed using different PGPR strains**

Numerous work done showed different stages in the process of commercialization include isolation of antagonist strains, screening, fermentation methods, mass production, formulation viability, toxicology, industrial linkages, quality control and field efficacy (Nandakumar *et al*., 2001) [79]. Moreover, commercial success of PGPR strains requires economical and viable market demand, consistent and broad-spectrum action, safety and stability, longer shelf life, low capital costs and easy availability of career materials. Chet and Chernin (2002) [15] and Glick *et al*. (1999) [39] had formulated some of the important PGPR strains along with their commercial products, which are listed in Table 4.

**Table 4:** Commercial products developed using different PGPR strains

| PGPR | Products | Intended crop |
|---|---|---|
| *Agrobacterium radiobacter*<br>*Azospirillum brasilense* | Diegall, Galltrol-A, Nogall, Norbac 84 C<br>Azo-Green | Fruit, nut, ornamental nursery stock and trees |
| Bacillus subtilis GB03 | Kodiak, Kodiak HB, Epic, System 3, Concentrate and Quantum 4000 | Turf and forage crops Cotton and legumes |
| *Bacillus subtilis* GB03 | Campanion | |
| *B. subtilis and* | Bio Yield | Horticultural crops and turf<br>Tomato, cucumber, pepper and tobacco |
| *B.amyloliquefaciens* | Intercept | Maize, vegetables, cotton |
| *Psuedomonas* cepacia | Pix plus | Cotton |
| Bacillus cereus | Blue Circle, Deny, Intercept | Alfalfa, barley, beans, clover, cotton, maize, |
| *Burlkholderia cepacia* | Blight Ban A506, Conquer, Victus | peas, sorghum and wheat |
| *Psuedomonas fluorescens* | | Almond, apple, cherry, mushroom, potato |
| P. chlororaphis | AtEze | Ornamental and vegetable crops |
| *P. syringae* | Bio-save 10, 11, 100, 110, 1000 | Strawberry and tomato, citrus and pome fruit |

**Source:** Glick *et al*. (1999) [39]; Chet and Chernin (2002) [15]

**Conclusion**

Plant growth promoting rhizobacteria, having multiple activities in terms of biofertilization, biocontrol, and bioremediation, all of which exert a positive influence on crop productivity and ecosystem functioning, encouragement should be given to its implementation in agriculture. The of stable formulations of PGPRs should be implemented in agriculture by replacing the use of chemical fertilizers, pesticides and artificial growth regulators which have numerous side-effects to sustainable agriculture. PGPR promote plant growth not only by supplying nutrients to the plant, but also by producing phytohormones, inducing stress resistance, or preventing pathogen-induced plant diseases. Thus, the development of the biofertilizer market and the promotion of bacterial inoculations in the field is an environmentally friendly way to meet the worldwide need to raise crops yields.

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