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Does a Plant Growth Promoting Rhizobacteria Enhance Agricultural Sustainability?

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Rhizosphere soil has large diversity of microbial community, including microorganisms which caused plant growth promoting activity. The plant growth promoting rhizobacteria (PGPR) colonize roots, increased root branching, root number and enhanced growth through direct and indirect mechanisms. PGPR modified root architecture by production of phytohormones, siderophores, HCN, Nitrogen fixation and Phosphate solubilization mechanisms. PGPR also modify root functioning, improve plant nutrition and influence the physiology of the whole plant. N-fixers and P-solubilizers play key role in plant growth and yield of various crops. However the PGPR also play very crucial role to maintain the soil fertility and health. In this paper, we address the effect of PGPR on growth, yield and fertility status in rhizosphere soil. Synergetic interactions of combined inoculation of PGPR strains might be more effective for various crops growth and yield. PGPR along with integrated nutrient management may be more effective for growth, yield and fertility status under sustainable agriculture.

Key words: N-fixers, PGPR, phytohormone, P-solubilizers, rhizosphere, Siderophores, Yield.

Nitrogen, phosphorus and potassium are major crops nutrients which improved growth and yield of crops[1]. Indigenous eco-friendly microorganisms enhanced soil-plant-environmental sustainability. Plant growth promoting microorganisms activates enzymes, maintains cell turgor, enhances photosynthesis, reduces respiration, helps in transport of sugars and starches, increases disease resistance and helps the plant better to withstand stress, helps in nitrogen uptake and is essential for protein synthesis. It is imperative to utilize renewable input which can maximize the ecological benefits, minimize the environmental hazards and enhance the agricultural sustainability[2]. The crops rhizosphere is an important soil ecological environment for soil–plant–microbe interactions. It involves colonization by a variety of indigenous micro-organisms in and around the roots which may result in symbiotic, associative, neutralistic or parasitic relations within the soil–plant system, depending on the type of microorganism, soil nutrient status, and plant defence system and soil environment. Intensive farming practices that maximize yields through mineral fertilizers, which are not only costly but may also create environmental problems.

N-fixers, P, K, Zn-solubilizing microorganism enhanced the plant available form

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of nutrients in soil-plant system which significant influences growth, yield and nutrients uptake by crops, either directly or indirectly as well as maintained soil fertility and their health[3]. The global nitrogen cycle pollutes groundwater and increases the risk of chemical spills and its low availability due to the high losses by emission or leaching which enhance the soil as well as environmental pollution and disturbed indigenous microorganisms and their plant growth promoting activities. However, eco-friendly microorganisms or indigenous micro flora have capacity to fix the atmospheric nitrogen to plant available nitrogen. Its play a key role for plant growth and development, biological nitrogen fixation accounts for about 60% of the earth's available nitrogen which represents an economically beneficial and environmentally sound alternative to chemical fertilizers[4]. A number of biological nitrogen fixing bacterial species acting as biofertilizers associated with the plant rhizosphere and are able to exert a beneficial effect on plant growth[5]. On the other hand soils generally contain a large amount of total unavailable P, only a small quantity is available for plant uptake. Plants obtain P as orthophosphate anions (predominantly as HPO_4^{2-} and $H_2PO_4^{1-}$) from the soil solution. Orthophosphate is rapidly depleted in the vicinity of plant roots, and as such a large concentration gradient occurs across the rhizosphere between bulk soil and the root surface[6]. phosphorous and potassium solubilizing bacteria solubilized unavailable P K to plant available form of nutrients by secreting various organic acids which supply of available P to the root surface, and its availability as influenced by root to exploit new regions of soil are of greater importance for P acquisition than the kinetics associated with its uptake[7].

The importance of root growth for the efficient capture of P is well documented and in many cases is a specific response of plants to P deficiency[2]. In soil-plant ecosystem characteristics of roots that facilitate soil exploration and P uptake include; rapid rate of root elongation and high root to shoot biomass ratio, increased root branching in surface soils and nutrient rich regions[8].

Nitrogen fixers and P- solubilizer bacteria act as plant growth promoting rhizobacteria (PGPR) for secretion of various hormones, siderophore production, HCN production which enhanced the growth and yield of plants[5]. Biofertilizers have emerged as a new concept of PGPR means the product containing carrier based (solid or liquid) living microorganisms which are agriculturally useful in terms of nitrogen fixation, phosphorus solubilization or nutrient mobilization, to increase the productivity of the soil and/or crop[9]. Several microorganisms and their association with crop plants are being exploited in the production of biofertilizers. Crop plants needs specific nutrients essential for their growth and development. Proper availability of these nutrients is required to obtain the optimum crop yield[10].

PGPR can affect plant growth either indirectly or directly; (a) indirect plant growth promotion occurs when bacteria lessen or prevent the deleterious effects of one or more phytopathogenic organisms. However, (b) direct promotion of plant growth by PGPRs involves either providing plants with a compound synthesized by the bacterium or facilitating the uptake of certain essential nutrients from the environment[11]. Mechanisms of plant growth promotion, PGPR must colonize the rhizosphere around the roots, the root surface or within root tissues[12]. In general, these can be separated into extracellular PGPR (ePGPR), existing in the rhizosphere, on the rhizoplane or in the spaces between cells of the root cortex, and intracellular PGPR (iPGPR), which exist inside root cells, generally in specialized nodular structures. Seeds inoculation with PGPRs was well documented to increase nodulation, growth, uptake and yield response of crop plants[2].

Mechanism of plant growth promoting rhizobacteria (PGPRs)

Direct Mechanism

Biological nitrogen fixation

Nitrogen is one of the most essential nutrients that required for plant growth and productivity as well as it forms an integral part of proteins, nucleic acids and other essential biomolecules[13]. More than 80 % of nitrogen is present in the atmosphere which is unavailable to plants. It needs to be converted into ammonia, an available form to plants and other eukaryotes. Biological nitrogen fixation involves the conversion of nitrogen to ammonia by microorganisms using a complex enzyme system identified as nitrogenase[14]. PGPMs belonging to the genera

Acinetobacter, Alcaligenes, Arthrobacter, Azospirillium, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Rhizobium, *Mycobacterium* and *Serratia* which are known to fix atmospheric molecular nitrogen through symbiotic and asymbiotic or associative nitrogen fixing processes[5] (fig.1). The amount of N_2 -fixation by *Bacillus* sp. was 24 and 40 mg N fixed g-^{1} C consumed under shaking and as well as static conditions[15]. *Bacillus, Klebsiella, Pseudomonas*, *Enterobacter* having N_2-fixation efficiencies of these isolates ranged from 14.9 to 2.1 mg N fixed per g C oxidized, being highest for *Bacillus* and lowest with *Enterobacter*[16]. *B. megaterium, A. chlorophenolicus* and *Enterobacter* sp. produced 11.8, 15.0 and 9.9 N_2^- fixed mg N g^{-1} C oxidized[5].

Many researchers reported that *Rhizobium* sp., a group of soil bacteria that fix atmospheric N_2 in root nodules of leguminous plants, were the first biofertilizers identified and have been commercially used as inoculants for legumes for over 100 years[17]. Increasing and extending the role of PGPRs as biofertilizers would reduce the need for chemical fertilizers, decrease adverse environmental effects and improved soil fertility status. Therefore, in the development and implementations of sustainable agriculture techniques, biofertilization is of great importance in alleviating environmental pollution and the deterioration of nature[18]. These PGRRs have been increase plant growth through production of phytohormones, increased nutrient uptake, enhanced stress resistance, biocontrol of both major and minor plant pathogens[19] and improved water status[20]. However, these plant-microbial interactions are dependent on plant genotype[21] and site-specific soil conditions[22].

Solubilization of phosphorus

Phosphorus is second mineral nutrients after nitrogen is most commonly limiting the growth of terrestrial plants. Soils may have large reserves of total P, but the amount available to plants is usually a low proportion of this total. Indian soils are normally deficient in available phosphorus even though the bound component may be sufficient or in abundant[23]. The low availability of P to plants is because the vast majority of soil P is found in insoluble forms, and plants can only absorb P in two soluble forms, the monobasic ($H_2PO_4^{''}$) and the diabasic ($HPO_4^{2''}$) ions[24]. P-solubilization in the rhizosphere is the most common mode of action implicated in PGPRs that enhance nutrient availability to host plants[25]. Phosphorus biofertilizers could help increase the availability of phosphates accumulated in the soil and could enhance plant growth by increasing the efficiency of biological nitrogen fixation and the availability of Fe and zinc (Zn) through production of plant growth promoting substances[26]. The rhizosphere of cereal crops was found to be a harbor of a large

Table 1. Effect of different plant growth promoting rhizobacteria on crops growth and yield

Crop	PGPRs	Positive impact on crops	References
Solanum tuberosum	*B. polymyxa, P. striata*	Yield and P uptake	63
Musa paradisiacal	*Azospirillum, Azotobacter*	Number of leaves and girth	64
Brassica nigra	*Azotobacter, Azospirillum*	Seed yield	65
Brassica oleracea	*Azospirillum* sp.	Growth and yield	66
Triticum aestivum	*B. polymyxa cloacae*	Yields	67
Piper nigrum	*P. fluorescens*	Nutrient uptake	50
Vigna radiate	*A. chroococcum, G. fasciculatum*	Root infection, NP uptake	68
Arachis hypogaea	*P. fluorescent*	Yield, inhibited pathogens	69
Piper nigrum	*P. fluorescens*	Nutrient uptake	70
Rubus ideus	*Bacillus* sp.	Yield	71
Helianthus annuus	*Bacillus* M-13	yield, oil and protein content	72
Malus domestica	*Agrobacterium rubi, B. subtilis,*	Leaf area, annual shoots	73
Fragaria ananassa	Bacillus and Pseudomonas	Yield, NPK uptake	74
Cucurbita pepo	*P. putida, B. lentus,*	Higher oil, seed, fruit yield	75
Brassica oleracea	PGPR MK5, MK7, MK9	Curd diameter	76
Triticum aestivum	*B.megaterium megaterium, A.chlorophenolicus* and *Enterobacter*	Yield	5

number of phosphate solubilizing bacteria[27] that have been showed to play an effective role in P uptake and growth promotion[28] (Fig.1).

Solubilization of potassium

Soil-plant-microbe interaction has got much importance in recent decades. Many types of microorganisms are known to inhabit soil, especially rhizosphere and play important role in plant growth and development. It is well known that a considerable number of microorganisms (bacterial and fungal) species possess a functional relationship and constitute a holistic system with plants. They are able to easily multiply in a rhizosphere to promote plant growth and yield[29]. Farmers where not applied chemical fertilizers in manage and balance way for crop production, because they are not aware about how much fertilizer is necessary for plant and it varies from crop to crop. There is a very big gap between researchers and farmers. Most of the farmers only use urea as nitrogen some di-ammonium phosphate as phosphorous but only few of them use K-fertilizer as murate of potash for crop production. Therefore, available forms of potassium decrease in soil due to removal by the crop in higher amount. However crop residue has more potassium content than other elements. Nowadays farmers are not added crop residue in the soil that is one considerable reason for the depilation of potassium in soil system, which ultimately shows the poor crop performance. To mitigate this and to maintain fertility status of soil, the balanced used of chemical fertilizers is needed, though it is found to be a costly affair and also environmentally undesirable[30]. K-solubilizing bacteria are able to release potassium from insoluble minerals[31]. In addition, researchers have discovered that K-solubilizing bacteria can provide beneficial effects on plant growth through suppressing pathogens and improving soil nutrients and structure. For example, certain bacteria can weather silicate minerals to release potassium, silicon and aluminum, and secrete bio-active materials to enhance plant growth. These bacteria are widely used in biological K-fertilizers and biological leaching[32].

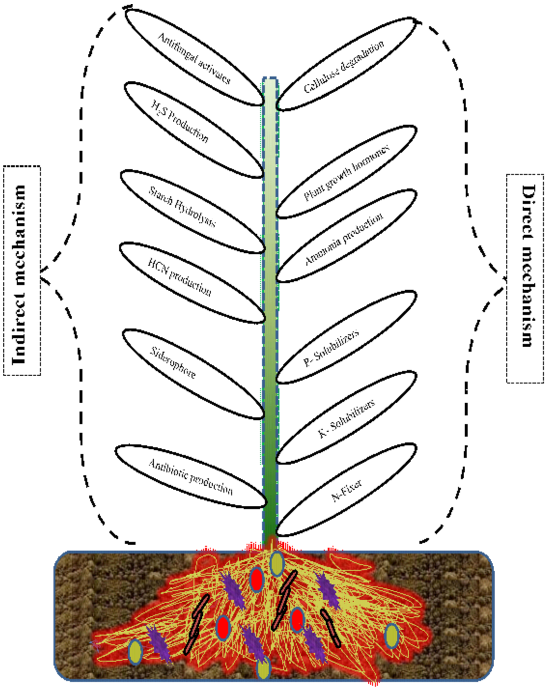

Fig. 1. Mechanism of plant growth promoting rhizospheric microorganisms (a). Direct mechanism (e.g., N_2-fixer, phosphorous, potassium and zinc solubilization etc.). (b). indirect mechanism (e.g. IAA, GAs, cytokinins and certain VOCs etc.), both mechanism enhance plant mineral uptake and productivity of crop

Production of Hydrogen cyanide (HCN)

HCN is a volatile, secondary metabolite that inhibited the development of microorganisms and negatively affects the growth and development of plants[33]. HCN is a powerful suppresses of many metal enzymes mainly copper containing cytochrome C oxidases. HCN is formed from glycine through the action of HCN synthetase enzyme, which is associated with the plasma membrane of certain rhizobacteria[34]. To date various bacterial genera have shown to be capable of producing HCN, including *Alcaligenes*, *Aeromonas*, *Bacillus*, *Pseudomonas*, *Enterobacter* and *Rhizobium* species[5] (fig.1). Group of *Pseudomonas* present within the rhizosphere has common trait for HCN production, with some studies showing that about 50% of Pseudomonas isolated from potato and wheat rhizosphere is able to produce HCN *in vitro*[35]. Various studies attribute a disease protective effect to HCN, e.g. in the suppression of "root-knot" and black rot in tomato and tobacco root caused by the nematodes *Meloidogyne javanica* and *Thielaviopsis basicota*, respectively[33]. HCN also control subterranean termite *Odontotermes obesus*, an important pest in agricultural and forestry crops in India[36]. However, there are investigations reporting harmful effects on plants, inhibition of energy metabolism of potato root cells[37] and reduced root growth in lettuce[38]. Likewise, HCN inhibits the primary growth of roots in Arabidopsis due to the suppression of an auxin responsive gene[39].

Siderophores production

Siderophores are small high-affinity iron chelating compounds secreted by plant and microorganisms and act as strong soluble Fe^{3+} binding chelating agent. These compounds are produced by many bacteria in response to iron deficiency which normally occurs in neutral to alkaline pH soils, due to low iron solubility at elevated pH[40]. Iron is essential for cellular growth and metabolism, such that Fe acquisition through siderophore production plays an essential role in determining the competitive fitness of bacteria to colonize plant roots and to compete for iron with other microorganisms in the rhizosphere[41]. Siderophore producing PGPR can prevent the proliferation of pathogenic microorganisms by sequestering Fe^{3+} in the area around the root[33] (fig.1). Many plants can use various bacterial siderophores as iron sources, although the total concentrations are probably too low to contribute substantially to plant iron uptake. Plants also utilize their own mechanisms to acquire iron; dicots via a root membrane reductase protein that converts insoluble Fe^{3+} into the more soluble Fe^{2+} ion, or in the case of monocots by production of phytosiderophores[41]. Various studies have isolated siderophore producing bacteria belonging to the *Bradyrhizobium*, *Bacillus*, *Enterobacter Pseudomonas*, *Rhizobium*, *Serratia* and *Streptomyces*[2, 5].

Production of phytohormones

One of the direct mechanisms by which PGPR promote plant growth through production of plant growth regulators or phytohormones[11]. The role of auxins, cytokinins, gibberellins, ethylene and absicisic acids (ABA) which, when applied to plants, help in increasing plant yield and growth[42] (fig.1). Microbial production of individual phytohormones such as auxins and cytokinins has been reviewed by various authors over the years[2].

Auxins

Microorganisms produce indole-3-acetic acid (IAA) in the presence of the precursor tryptophan or peptone. Auxin helps in cell enlargement, cell division, root initiation, root growth inhibition, increased growth rate, phototropism, geotropism and apical dominance in some of the plant[42]. Eighty percent of microorganisms isolated from the rhizosphere of various crops have the ability to produce auxins as secondary metabolites[43]. Bacteria belonging to the genera *Azospirillum*, *Pseudomonas*, *Xanthomonas*, and *Rhizobium* as well as *Alcaligenes faecalis*, *Enterobacter cloacae*, *Serratia marcescens*, *Mycobacterium* sp., *Burkholderia*, *Azotobacter Bacillus cereus* and *Bradyrhizobium japonicum* have been shown to produce auxins which help in stimulating plant growth[44] (fig.1). Various metabolic pathways such as (a) indole-3-acetamide pathway, (b) indole-3-pyruvic acid pathway, (c) tryptophan side chain pathway, (d) tryptamine pathway and (e) indole-3-acetonitrile pathway are involved in the production of IAA. PGPR strains produced 24.6 $\mu g ml^{-1}$ of auxins in the presence of the precursor L-tryptophan in the medium, which was 184-fold more than that without L-tryptophan[45] and good production of indole acetic acid (IAA) by bacterial strains in a medium with 100 $\mu g ml^{-1}$ of tryptophan[5].

Other phytohormones

Production of other phytohormone by PGPR has been identified, but not nearly to the same extent as bacteria which produce IAA. Cytokinins are a class of phytohormones which are known to promote cell divisions, cell enlargement, and tissue expansion in certain plant parts[46] (Table 1). Researchers have recently begun to identify cytokinin production by bacteria. Gibberellins (gibberellic acid; GA) are a class of phytohormones mostly associated with modifying plant morphology by the extension of plant tissue, particularly stem tissue[47]. The four different forms of GA are produced by *Bacillus pumilus* and *Bacillus licheniformis*[48]. Ethylene is the only gaseous phytohormone. It is also known as the 'wounding hormone' because its production in the plant can be induced by physical or chemical perturbation of plant tissues[47]. Among its myriad of effects on plant growth and development, ethylene production can cause an inhibition of root growth. Mode of action of some PGPR was the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme which could cleave ACC, the immediate precursor to ethylene in the biosynthetic pathway of ethylene in plants[49]. They submitted that ACC deaminase activity would decrease ethylene production in the roots of host plants and result in root lengthening.

Indirect mechanism of growth promotion

The indirect mechanism of plant growth occurs when bacteria lessen or prevent the detrimental effects of pathogens on plants by production of inhibitory substances or by increasing the natural resistance of the host. Phytopathogenic microorganism can control by releasing siderophores, B-1, 3-glucanase, chitinases, antibiotics, fluorescent pigment or by cyanide production[50].

Antifungal activity

Many rhizobacteria including fluorescent *Pseudomonas* secrete a variety of antifungal molecule under in vitro condition[2]. There are several reports on in vitro antagonism of pathogenic fungi and field performance by bacteria recovered from the rhizosphere[51]. The rhizoshere and root zone of tea (*Camellia sinensis*) is a good habitat for PGPR strains represented by *Bacillus, Proteus* and *Pseudomonas* and was found inhibitory to phytopathogenic fungi viz., *Fusarium oxysorum* under *in vitro* condition[2]. Suppression of soil borne plant pathogens by siderophore producing pseudomonads was observed[52] and the wild type strain was more effective in suppressing disease compared to non-siderophore-producing mutants. *Pseudomonas* sp. strains MRS23 and CRP55b showed varying diameters of inhibition zones for the four pathogenic fungi, *Aspergillus* sp. *F. oxysporum, P. aphanidermatum* and *R. solani*[53].

Siderophore activity

Siderophore production is a crucial feature for the suppression of plant pathogens and promotion of plant growth. Siderophore production was observed as a mechanism of biocontrol of bacterial wilt disease in the fluorescent pseudomonads RBL 101 and RSI 125[54]. The catechol siderophore biosynthesis gene in *Serratia marcescens* associated with induced resistance in cucumber against anthracnose[55]. Pseudomonads also produce two siderophores one is pyochelin and other salicylic acid, the pyochelin is contribute to the protection of tomato plants from *Pythium* by *Pseudomonas aeruginosa* 7NSK2[56]. Different environmental factors can also influence the quantity of siderophores produced[57].

Increasing the availability of nutrients in the rhizosphere

There is ample evidence that the mode of action of many PGPRs which increasing the availability of nutrients for the plant in the rhizosphere[29]. Fixation of nitrogen, solubilization of unavailable forms of nutrients, siderophore production, IAA and ammonia production are methods for increasing nutrients in rhizosphere[58]. With regard to the increase in K uptake due to the application of biofertilizer[59] that organic acids, e.g. citric, oxalic, tartaric, succinic etc., produced by isolated K-solubilizing rhizobateria are able to chelate metals and mobilize K from K-containing minerals[60].

Effect of PGPR on crop growth and yield

Phosphate solubilizing and Nitrogen fixing bacteria are also known to increase N and P uptake resulting in better growth and higher yield of crop plants[3] (Table 1). Most soil bacteria can solubilize insoluble phosphates; particularly *Pseudomonas, Enterobacter* and *Bacillus*[61]. Furthermore, combined inoculations of N_2-fixing and P-solubilizing bacteria were more effective than single inoculation possibly by providing a more balanced nutrition for plants[5]. Dual inoculations increased yields in many crops compared to single inoculations with N_2-fixing or P-solubilizing bacteria[62].

CONCLUSION

Plant growth promoting rhizobacteria play important role in agriculture for the growth and yield of plants and also maintained the soil fertility status. The efficient PGPR strains might be performed better in agriculture system which reduced the chemical and fertilizers input in soil. It is cost effective technology in sustainable agriculture. Plant growth promoting rhizobacteria have ability to interact with plants in various ways in soil microbial populations, ranging from commensalism to mutualism. With this plant microbes interaction of PGPR, plays a major role by enhancing growth and health of widely diverse plants and soils. Bacterial modulation of plant auxin distribution and independently of IAA production by PGPR has also been revealed for growth promotion. Combined inoculation of PGPR strains might be more suitable than alone, for growth and yield of plants and consequently maintained soil fertility and health. However, they also play vital role in eco-friendly environment through decreased the level of pesticides used in agricultures. Distinct PGPR populations present in a same soil can express plant-beneficial properties in concert. The relationships between plants and their rhizo-microbes are complex and vary both according to plant genotypes and soil inhabiting populations.

Future Prospectus and challenges

Now a days recent progress in rhizospheric modification understanding of PGPR diversity, colonization ability, mechanisms of action, formulation, and application should facilitate their development as reliable components in the management of eco-friendly and sustainable agricultural systems. PGPR-mediated agriculture is now gaining worldwide importance and acceptance for an increasing number of crops and managed ecosystems as the safe method of nutrient solubilization and plant growth promoting activities. The new tools of genetic modification in PGPR such as importation and release of nutrients from fixed form to plant available form and natural enemies and improved germplasm, breeding and field testing should quickly move genetic modification research and technology into a new era. Some challenges in our knowledge often hinder attempts to optimize the nutrient solubilization and plant growth promoting activities by employing tailored application strategies. More detailed research are needed on the composition of the rhizosphere modification, the soil-plant-environmental system effect on rhizospheric bacterial population dynamics. An attempt to overcome problems of varying efficacy may be attained by strain mixing, significant control of plant pathogens or direct enhancement of plant development has been demonstrated by PGPR in the laboratory, greenhouse, results in the field have been less consistent. Because of these and other challenges in screening, formulation, and application, PGPR have yet to fulfill their promise and potential as commercial inoculants sustainable agricultural ecosystems.

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