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Role of plant growth promoting rhizobacteria (PGPR) in sustainable agriculture

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Abstract

Sustainable agriculture involves the successful management of agricultural resources to satisfy human needs while maintaining or enhancing environmental quality without exploiting the natural resources of future generations. The chemical fertilizers used in the agriculture to increase yields, kill pathogens, pests, and weeds, have a big harmful impact on the ecosystem. Plant Growth Promoting Rhizobacteria (PGPR) are a group of bacteria that enhances plant growth and development with no negative side effects. The productive efficiency of a specific PGPR may be further enhanced with the optimization and acclimatization according to the prevailing soil conditions. In future, they are expected to replace the chemical fertilizers, pesticides and artificial growth regulators which have numerous side-effects to sustainable agriculture. The important advances on plant-PGPR cooperation will be brought in the future by combining both ecology and functional biology approaches.

Keywords: Plant growth promoting rhizobacteria (PGPR), plant growth, sustainable agriculture

Introduction

In modern cultivation process indiscriminate use of fertilizers, particularly the nitrogenous and phosphorus, has led to substantial pollution of soil, air and water. Excessive use of these chemicals exerts deleterious effects on soil microorganism, affects the fertility status of soil and also pollutes environment [1]. The application of these fertilizers on a long term basis often leads to reduction in pH and exchangeable bases thus making them unavailable to crops and the productivity of crop declines. To obviate this problem and obtain higher plant yields, farmers have become increasingly dependent on chemical sources of nitrogen and phosphorus. Besides being costly, the production of chemical fertilizers depletes nonrenewable resources, the oil and natural gas used to produce these fertilizers, and poses human and environmental hazards [2].

In recent years considerable attention has been paid to PGPR to replace agrochemicals (fertilizers and pesticides) for the plant growth promotion by a variety of mechanisms that involve soil structure formation, decomposition of organic matter, recycling of essential elements, solubilization of mineral nutrients, producing numerous plant growth regulators, degrading organic pollutants, stimulation of root growth, crucial for soil fertility, biocontrol of soil and seed borne plant pathogens and in promoting changes in vegetation [3]. An understanding of plant growth promoting rhizobacteria and their interactions with biotic and abiotic factors is indispensable in bioremediation techniques [4] energy generation processes and in biotechnological industries such as pharmaceuticals, food, chemical, and mining. Furthermore plant growth promoting rhizobacteria can reduce chemical fertilizers application and economically, environmentally beneficial for lower production cost as well as recognize the best soil and crop management practices to achieve more sustainable agriculture as well as fertility of soil [5].

PGPR promote plant growth by exploiting either of direct or indirect mechanism. The direct mechanism of plant growth promotion by PGPR include production of metabolites, that is, phytohormones or enhanced availability of nutrients. In contrast, induced systemic resistance, antibiotic protection against pathogens, reduction of iron availability by sequestration with siderphores, synthesis of antifungal enzymes or lytic enzymes are included in indirect mechanisms of growth promotion by PGPR [6-8].

Mechanism of PGPR

PGPR are capable of enhancing plant growth either directly or indirectly through multifarious ways (Fig. 1) [9]. Direct mechanisms involve various processes such as phosphate solubilization, nitrogen fixation, production of siderophore, HCN, ammonia, vitamins, and phytohormones (such as auxin, cytokinin, and gibberellins), whereas indirect mechanisms involve that mechanism, which does not directly involve in growth promotion but plays role in the path of synthesis. Indirect mechanisms include ACC deaminase activity, production of antibiotics, hydrolytic enzymes, ISR of phytopathogens [10, 11].

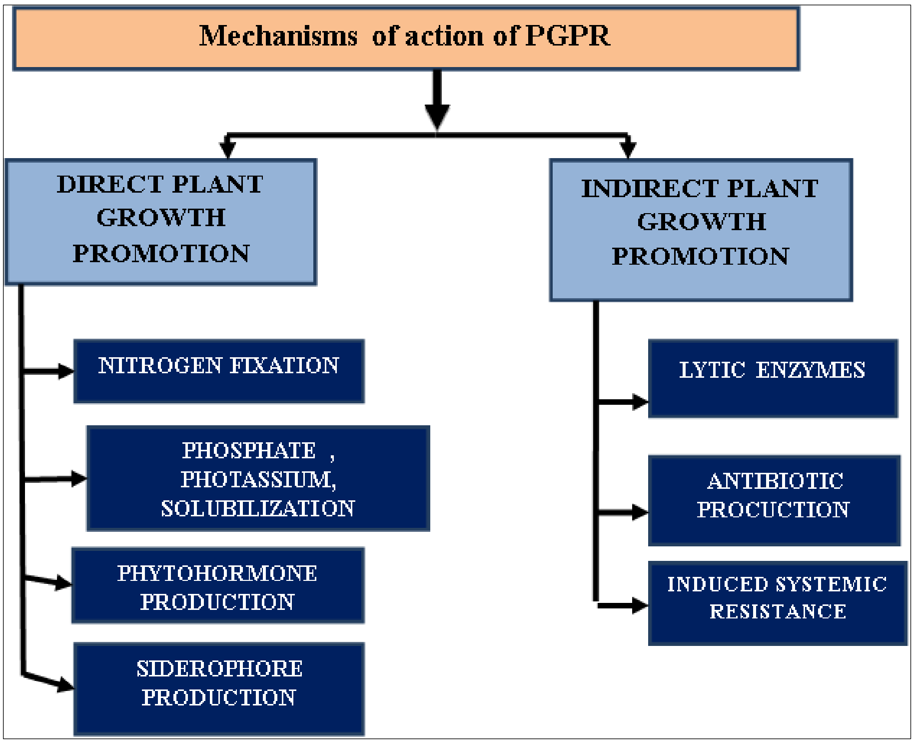

Fig 1: Mechanisms of action of PGPR

Nitrogen fixation

More than 78% of nitrogen is present in the atmospheres inert gas which is insoluble to the plants [15]. Nitrogen fertilizer is applied to supply nitrogen for the growth and productivity of the plants. However, less than half of applied nitrogen is effectively absorbed by plants with the rest being lost through volatilization or leaching subsequent polluting the environment [13]. Nitrogen is converted into ammonia (plant utilizable forms) by nitrogen-fixing organisms using a complex enzyme system called nitrogenous [16]. Biological nitrogen fixation is a process that accounts for almost two-thirds of nitrogen fixed worldwide which is carried out either symbiotic or free-living between microbes and plants [14]. Symbiotic nitrogen fixation carried out between legume and symbiotic microorganisms such as *Rhizobium*, *Mesorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium*, and *Sinorhizobium* which has been described as nitrogen-fixing PGPR with significant ability to promote plant growth and yield [17, 18]. Whereas, free-living nitrogen-fixing PGPR include *Azotobacter*, *Azospirillum*, *Herbaspirillum*, *Bacillus*, *Burkholderia*, and *Paenibacillus*, which havebeen shown to attach to the root and efficiently colonizeroot surfaces [12].

Phosphate solubilization

After nitrogen, the essentiality of phosphorus surpasses every other element. Phosphorus is generally high in the soil (typically between 400 and 1200 mg kg^{-1} of soil) but very insoluble and unavailable to support plant growth. Unavailable phosphorus can either be seen as inorganic minerals such as apatite or in organics as in inositol phosphate, phosphomon- esters and phosphotriesters [19]. An inadequate or short supply form of P usually restrains plant growth. Hence, phosphate solubilizing ability in PGPR is very crucial. PGPR directly solubilize and mineralize inorganic phosphorus or aids the flow of organic phosphorus via microbial turnover and/or enhancing the root system [20]. Organic acids are released by bacteria which in turn reduces the pH in the root region, as a result, the trapped forms of phosphate like $Ca_3(PO_4)_2$ in calcareous soils are released. Other than supplying the available cumulated phosphate (through solubilization), phosphorus biofertilizers further aid in improving the ability of organism N_2 -fixation and make Zn, Fe etc. available, via the synthesis of some plant growth-promoting compounds. It could be inferred that phosphate solubilizing bacteria provide a biotechnological key in sustainable agriculture, most especially in phosphorus-deficient soils.

Potassium solubilization

Potassium (K) is the third significant fundamental macronutrient for plant development. The convergences of solvent potassium in the soil are generally low and over 90% of potassium in the soil exists as insoluble rocks and silicate minerals. Additionally, because of imbalanced fertilizer application, potassium insufficiency is getting to be one of the significant limitations in production stage. Without sufficient potassium, the plants will have ineffectively created roots, develop gradually, produce little seeds and have bring down yields. This underscored the pursuit to locate an option indigenous wellspring of potassium for plant take-up and to keep up potassium status in soils for managing crop production [21]. Plant development elevating rhizobacteria can solubilize potassium rock through generation and emission of natural acids. Potassium solubilizing plant development advancing rhizobacteria, for example, *Acidothiobacillus ferrooxidans, Bacillus edaphicus, Bacillus mucilaginosus, Burkholderia, Paenibacillus* sp. what's more, *Pseudomonas* has been accounted for to discharge (Fig 2) potassium in open shape from potassium bearing minerals in soils [22].

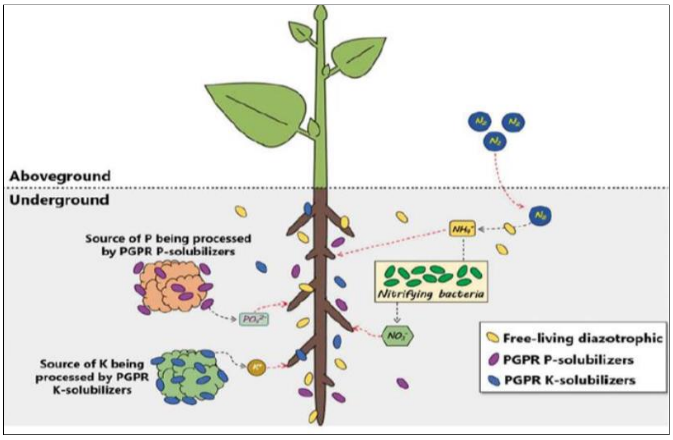

Fig 2: Modes of N, P and K improvement for soil and plants mediated by PGPR. Free living diazotrophic bacteria are able to capture N from the atmosphere and release it to plants as ammonium or nitrate)

Phytohormone production

A wide range of microorganisms found in the rhizosphere are able to produce substances that regulate plant growth and development. Plant growth promoting rhizobacteria produce phytohormones such as auxins, cytokinins, gibberellins and Ethylene can affect cell proliferation in the root architecture by overproduction of lateral roots and root hairs with a subsequent increase of nutrient and water uptake [24].

Indole acetic acid (IAA)

Among plant growth regulators, indole acetic acid (IAA) is the most common natural auxin found in plants and its positive effect on root growth [26]. Up to 80% of rhizobacteria can synthesize indole acetic acid (IAA) colonized the seed or root surfaces is proposed to act in conjunction with endogenous IAA in plant to stimulate cell proliferation and enhance the host's uptake of minerals and nutrients from the soil [25]. Indole acetic acid affects plant cell division, extension, and differentiation; stimulates seed and tuber germination; increases the rate of xylem and root development; controls processes of vegetative growth; initiates lateral and adventitious root formation; mediates responses to light, gravity and florescence; affects photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful conditions [27]. Tryptophan is an amino acid commonly found in root exudates, has been identified as main precursor molecule for biosynthesis of IAA in bacteria [28]. The biosynthesis of indole acetic acid by plant growth promoting rhizobacteria involves formation via indole-3- pyruvic acid and indole-3-acetic aldehyde, which is the most common mechanism in bacteria like *Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Enterobacter* and *Klebsiella* [29]. Root growth promotion by the free living PGPR e.g., *Alkaligenes faecalis*, *Enterobacter cloacae,Acetobacter dizotrophicous*, species of *Azospirillum*, *Pseudomonas*and *Xanthomonas* sp. has been related to low level of IAA secretion.

Cytokinins and Gibberellins

Cytokinins are a class of phytohormones that are known to promote cell divisions, cell enlargement and tissue expansion in certain plant parts [33]. Plant responses to exogenous applications of cytokinins promote seed germination, the release of buds from apical dominance, stimulation of leaf expansion and reproductive development, retardation of senescence, enhanced cell division, enhanced root development, inhibition of root elongation, shoot initiation, or certain other physiological responses [30]. The role of cytokinins producing bacterial genera including *Pseudomonas*, *Klebsiella*, *Enterobacter*, *Achromobacter*, *Bacillus*, *Paenibacillus*, *Azotobacter*, *Agrobacterium*, *Azospirillum*, *Flavobacterium*, and *Arthrobacter* in plant growth regulation [31, 34, 35].

Gibberellin has a vital role in seed germination and emergence, floral induction, flower and fruit development, and steam and leaf growth whereas the most dominant physiological effect of GA is shoot elongation [32]. Gibberellin is naturally produced by higher plants, fungi and bacteria [34]. A variety of PGPR producing GA include *Acetobacter diazotrophicus*, *Azospirillumlipoferum*, *Bacillus pumilus*, *Bacillus cereus*, *Bacillus macrolides* and *Herbaspirillum seropedicae*, *Acinetobactercalcoaceticus* [31].

Ethylene

Ethylene is another plant hormone known to regulate many processes such as the ripening of fruits, the abscission of leaves, or the ripening of fruits (Fig 3) [37]. Moreover, at high concentrations, ethylene induces the defoliation and cellular processes that lead to the inhibition of root and stem growth together with premature senescence, all of which lead to poorer crop performance [38]. The plants synthesized 1-aminocyclopropane-1-carboxylate (ACC), which is the precursor for ethylene, in response to exposure to various types of environmental stress, such as cold, drought, flooding, infections with pathogens, and the presence of heavy metals [39]. High levels of ethylene, produced under stress conditions, can halt certain processes such as root elongation or nitrogen fixation in legumes [40], and cause premature senescence [36].

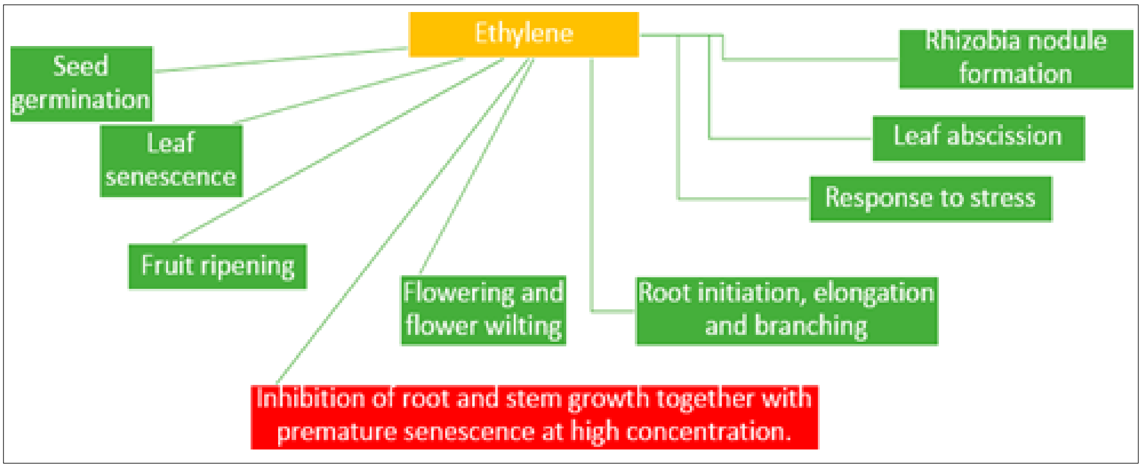

Fig 3: The phytohormone ethylene affects a large number of different processes in the growth and development of a plant

Siderophores production

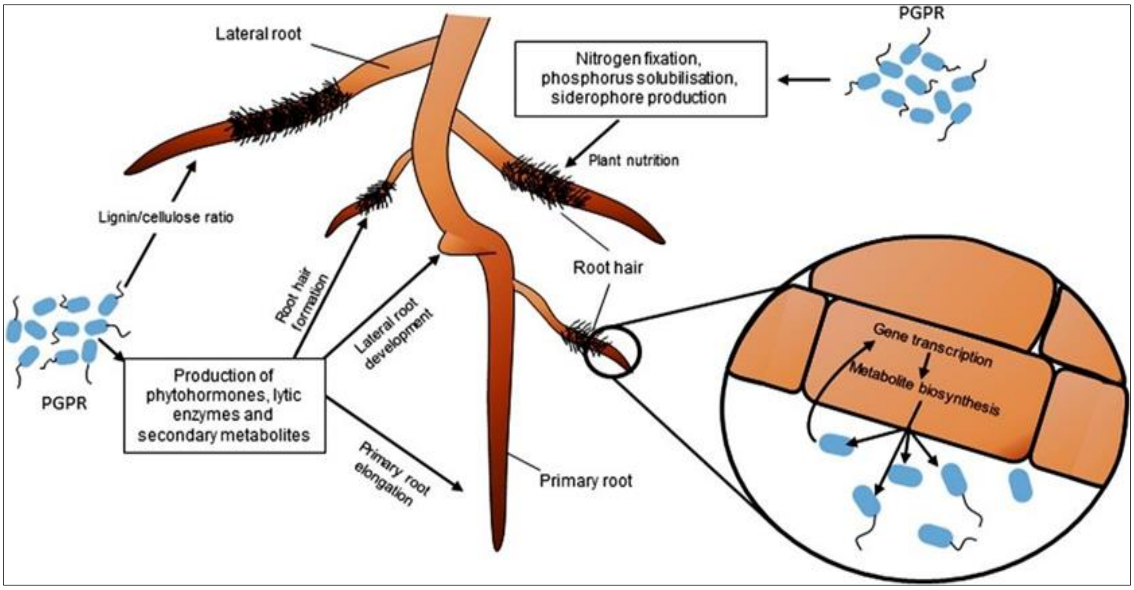

Fig 4: The possible mode of action used by plant growth promoting rhizobacteria (PGPR) towards growth promotion in plants. The flow and location of nitrogen fixation, phosphorus solubilization, and siderophore production are shown

Siderophores are the molecules of low molecular weight (400 to 1500 Da), having an exceptional affinity forFe3+ (Ka ranging from 1023 to 1052) and membrane receptors capable of binding the complex Fe-siderophores in order to facilitate the iron absorption by microorganisms and plant [41]. They are used in fertilizer formulations for regulation of iron intake in plants, and thus facilitate its growth [42]. Siderophores are produced by a wide variety of microorganisms (bacteria and fungi) and some plants (phyto-siderophores of grasses) [43]. *Agrobacterium*, *Bacillus*, *Escherichia coli*, *Pseudomonas*, *Rhizobium* and many fungi are capable to produce these iron chelating compounds [45].

Several studies have shown the beneficial effects of bacterial siderophores on improving of plant growth. Robin *et al*. (2008), using the iron-siderophore complex radio active as the only source of iron, showed that plants are able to absorb the radioactive iron. The iron pyoverd in synthesized by *P. fluorescens* C7 tested on *Arabidopsis thaliana* plants, has increased the iron level inside the plants and improved their growth [46]. The siderophores are also involved in chelation of other rhizosphere metals having a low availability to plants such as zinc and lead [47].

Some microorganisms produce siderophore that chelates the available iron and competitively prevents the iron nutrition of phytopathogen [49]. Siderophore is produced by *Alcaligenes*, *Pseudomonas*, *Bradyrhizobium*, *Bacillus*, *Enterobacter* and *Rhizobium* [48]. Siderophore production confers competitive advantages to PGPR that can colonize roots and exclude other microorganisms from this ecological niche. Under highly competitive conditions, the ability to acquire iron via siderophores may determine the outcome of competition for different carbon sources that are available as a result of root exudation or rhizo-deposition [50]. The flow and location of nitrogen fixation, phosphorus solubilization, and siderophore production are shown in figure 4.

Indirect mechanisms

Lytic enzyme production

Some PGPR strains have the ability to degrade fungal cell walls through the production of hydrolytic enzymes such as chitinases, dehydrogenases, β-glucanases, lipases, phosphatases, proteases, hydrolases, exo and endopolygalacturonases, pectinolyases and cellulases [51]. Various *Pseudomonas* strains showed *in vitro* antifungal activity against three zoospores fungi [52]. These authors proved that the antifungal activity is due to the production of rhamno lipid causing the lysis of plasma membrane of zoospores fungi. This PGPR lytic activity allows to protect the plant against biotic stress through the pathogens elimination.

Antibiotics

Many of the PGPR strains produce antibiotics that are inhibitory to plant pathogens and suppress their growth [53]. Various interactions shown between multiple groups of soil organisms are common, such as predation and competition for resources [54]. Numerous PGPR, such as *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Bacillus velezensi*, *P. putida*, *P. fluorescens*,*Pseudomonas brassicacearum*, and *Paenibacillus polymyxa* producedifferent antibiotics, such as surfactin, bacillomycin, fengycin, iturin, 2,4-diacetylphloroglucinol, polymyxin and fusaricid in, which strongly inhibit the growth of *Ralstoniasolanacearum* [55].

Induced systemic resistance

Induced systemic resistance PGPR systemically activate the plant’s latent defense mechanism and hence, improve plant resistance against pathogens called induced systemic resistance (ISR) [55-56]. There are many reports where PGPR have been found to induce plant defense by inhibiting the pathogens. For instance, *Bacillus amyloliquefaciens*, *Lactobacillusparacasei*, *P. fluorescens*, and *P. putida* induce IRS against phytopathogens of tomato [57, 58–60].

Characterisitcs of an ideal PGPR

A rhizobacterial strain is considered to be a putative PGPR if it possesses specific plant growth promoting traits and can enhance plant growth upon inoculation. An ideal PGPR strain should fulfill the following criteria [61]:

1. It should be highly rhizosphere-competent and eco-friendly.
2. It should colonize the plant roots in significant numbers upon inoculation.
3. It should be able to promote plant growth.
4. It should exhibit a broad spectrum of action.
5. It should be compatible with other bacteria in the rhizosphere.
6. It should be tolerant of physicochemical factors like heat, desiccation, radiations, andoxidants.
7. It should demonstrate better competitive skills over the existing rhizobacterial communities.

Conclusion

Keeping in view the above-given discussion on the Plant Growth Promoting Rhizobacteria (PGPR) are a group of bacteria that enhances plant growth and development with no negative side effects. The productive efficiency of a specific PGPR may be further enhanced with the optimization and acclimatization according to the prevailing soil conditions. In future, they are expected to replace the chemical fertilizers, pesticides and artificial growth regulators which have numerous side-effects to sustainable agriculture. The important advances on plant-PGPR cooperation will be brought in the future by combining both ecology and functional biology approaches. The use of PGPR is environmental friendly approach. Agriculturists from all over the world should focus on the research centered on unrevealing the hidden potential of these microorganisms.

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