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Plant Growth-Promoting Rhizobacteria (PGPR): Potential as Effective Biofertilizer and Biocontrol Agent for Sustainable Agriculture

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Abstract:

Plant growth-promoting rhizobacteria (PGPR), which are free-living soil microorganisms, live in the rhizosphere and the plant's roots. They can directly promote plant development by fixing nitrogen, solubilizing, and acquiring minerals (phosphorus, potassium, and other vital elements), regulating phytohormones, or indirectly by regulating plant pathogens through the synthesis of numerous secondary products, including antibiotics, siderophores, hydrolytic enzymes, and even promoting systemic resistance in plants. Numerous PGPR strains from various taxonomic families have favorable impacts on plants. Both the biofertilizer and the biocontrol activities of PGPRs substantially impact the wellness and yield of plants. These activities can be thought of as two aspects of the same coin. Using PGPR as a robust biofertilizer and/or biocontrol agent is a viable replacement for chemical fertilizers and pesticides that can help grow ecologically friendly and sustainable agriculture. The various strategies that rhizobacterial strains employ to encourage plant growth are described in this review.

Keywords: Biofertilizers, Biocontrol, Plant growth promoting rhizobacteria (PGPR), Photostimulation, Phytopathogens, Sustainable agriculture, Systemic resistance.

Abbreviations: PGPR- Plant growth-promoting rhizobacteria, BNF- Biological nitrogen fixation, PGP- Plant growth promotion, ISR- Induced systemic resistance

Introduction

The regrettable consequence of the rise in human population worldwide is that the current rate of food supply may soon no longer be adequate to satisfy the dietary requirements of everyone living today. Raising agricultural output is therefore crucial while minimizing harm to the ecosystem and environment.

Farmers are relying more and more on chemical pesticides and fertilizers to solve this issue and increase plant yields. To meet the rising need for food, efficient and biological agricultural practices are required because the indiscriminate usage of chemical pesticides and fertilizers harms the ecosystem and environment. In the context of an ecological agriculture system, the application of PGPR may be a good replacement for chemical fertilizers and pesticides to increase productivity while at the same time lowering pollution and safeguarding the environment. According to past studies, PGPR affects development, nutrient uptake, and production rate through various processes (1–3).

Soil is a home to diverse microorganisms including bacteria, fungi, and protozoa, among them bacteria are more frequently found the Rhizosphere, associated with plant growth. The rhizosphere, a microscopic soil layer surrounding plant roots, is vital for root activity and metabolism (2). This zone is nutrient-rich as compared to the bulk soil due to the release of various root exudates (Root exudates are substances that roots exude into the soil like amino acids, organic acids, sugars, polysaccharides, and vitamins), which support the growth of the rhizobacteria (4). Root exudates allow interaction between microorganisms and plants, helping plant growth promotion and inducing defenses against plant pathogens (5). Bacteria can efficiently colonize the rhizosphere and root region, thus influencing plant growth directly and indirectly, and are hence referred to as rhizobacteria that promote plant growth (PGPR) (6).

Numerous bacterial strains from various taxonomic families that live in plant roots and their rhizosphere are included in PGPR. Several bacterial species have been reported to promote plant growth, including *Rhizobium*, *Pseudomonas*, *Bacillus*, *Klebsiella*, *Azotobacter*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Rhodococcus*, *Agrobacterium*, *Erwinia*, *Chromobacterium*, *Sinorhizobium*, *Flavobacterium*, *Burkholderia*, *Micrococcus* (Table 2). They accelerate plant development through a variety of processes, such as BNF, the solubilization of nutrients and minerals in the soil, the production of numerous plant growth regulators, and the defence of plants against phytopathogens through the inhibition or control of these organisms (2,3). Along with these, PGPR helps alleviate biotic and abiotic stress, indirectly enhancing plant growth (5,7). Such multidimensional utility of PGPR makes them a promising tool as a biofertilizer and biocontrol to be exploited in agriculture to create agricultural systems that are sustainable and eco-friendly.

Forms of PGPR

PGPR are categorized into two types based on their location: symbiotic intracellular plant growth-promoting rhizobacteria (iPGPR) and free-living extracellular plant growth-promoting rhizobacteria (ePGPR). iPGPR live inside

root cells, often in specialized structures like nodules, enhancing nutrient mobilization. In contrast, ePGPR live in the rhizosphere, on the root surface, or in the intercellular spaces of the root cortex, colonizing plant tissue intercellularly (8). The different bacterial genera for both types are listed in Table 1.

Mechanism of action

PGPR enhances plant growth through various activities. They are be classified into two major types based on their mode of action:(a) biofertilizers ,which improve the plant nutrition and (b) biopesticides, which primarily combat diseases by the producing metabolites as shown in fig.1. PGPR enhances plant growth by beneficially altering the entire microbial in the rhizosphere by producing a variety of chemicals/metabolites (5). They promote plant growth by a direct mechanism involving nitrogen fixation, solubilization of plant essential minerals and nutrients, phytohormone production, or by an indirect mechanism showing biocontrol activity by producing various metabolites, including volatile organic compounds (VOC), enzymes, antibiotics, and exopolysaccharides (3,9).

A. Biofertilizer activity

Nitrogen (N₂) fixation

Nitrogen (N) is the most crucial nutrient for plant growth and productivity. About 78% of the N₂ is freely available in the environment, but plant can utilize it. They absorb nitrogen in the forms of nitrate (NO₃⁻) and ammonia (NH₄⁺), with nitrate being the primary form in soil (10). Microorganisms, known as diazotrophs or nitrogen fixers, convert atmospheric N₂ into a plants usable form through biological nitrogen fixation (BNF). Plants absorb nitrate via the nitrification process (11). When the plant uses nitrate (NO₃⁻), bicarbonate (HCO₃⁻) is released, which raises the pH of the rhizosphere and enhances the availability of other vital micronutrients for plants, including Zn, Ca, and Mg (12).

Rhizobia are the most studied PGPR due to their N₂ fixing capacity. Root-associated rhizobia can penetrate root tissue utilizing the structure called an infection thread, leading to root nodule formation. It includes symbiotic bacteria like *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Mesorhizobium*, While the free-living diazotrophic bacteria of the genera *Azoarcus*, *Azotobacter*, *Klebsiella*, *Beijerinckia*, *Pantoea*, *Gluconacetobacter*, *Azospirillum*, *Enterobacter*, *Flavobacterium*, *Bacillus*, and *Azospirillum* stimulate the growth of non-leguminous plants through non-symbiotic interaction (13). Furthermore, Sibponkrung et al. reported the combined inoculation of *Bacillus velezensis* S141 with *Bradyrhizobium diazoefficiens* USDA110 significantly induced nodule formation in soybean (14). One of the most significant plant growth-promoting scenario is nitrogen fixation by symbiotic or free-living bacteria, which offers a low-cost, environmentally benign, and sustainable solution.

Phosphate solubilization

Phosphorus (P), is the second-most significant nutrient for plant growth, essential for key metabolic functions, like photosynthesis, respiration, energy transmission, signal transduction, and macromolecular biosynthesis (15). Phosphorus (P), widely distributed in soils in both inorganic and organic forms, plants can only absorb P as negatively charged monobasic (H_2PO_4^-) and dibasic (HPO_4^{2-}) ions (16). In agricultural, phosphate fertilizers are typically administered in huge quantities to boost phosphorus availability for plants, but 75% to 90% of this fertilizer often become in soil immobilized and precipitated by metal ions present in soil like Fe, Al, and Ca, thus making it unavailable to plant. The long-term effects of this insoluble P, leads to serious environmental issues such as eutrophication, soil fertility loss, and carbon footprint (17). To address this, phosphate-solubilizing microorganisms (PSMs) play crucial role in converting insoluble phosphates into the forms that plant can easily utilize it. PSM employ various mechanisms for P solubilization, including the release of organic and inorganic acids, H^+ ion secretion, H_2S generation, excretion of the enzyme (phytases and phosphatase), chelation, solubilization and phosphate mineralization fig (2). (17–19). Phosphate solubilization involves the production of organic acids by rhizobacteria to chelate metal ions or lower soil pH, enhancing P availability (20).

Fig. 2- Rhizobacteria's solubilization of phosphorus is depicted schematically (adapted from Khan et al., 2009)

Bacteria belong to genus *Arthrobacter ureafaciens*, *Arthrobacter*, *Bacillus*, *Chryseobacterium*, *Delftia*, *Delftia* sp., *Gordonia*, *Phyllobacterium*, *Rhodococcus*, *Phyllobacterium myrsinacearum*, *Serratia*, and *Rhodococcus erythropolis* has been reported for phosphate solubilization (21). Also, some legume nodulating bacterial strains like *Rhizobium tropici* (CIAT 899T) and *Rhizobium etli* (UFLA 02-100) can solubilize P (22). One study reported that bacterial strain of *Enterobacter* (EnHy 401) produces exopolysaccharides along with organic acids responsible for P solubilization (23). Some phosphate solubilizing genes were isolated and characterized from various rhizobacterial species (24) by thus also suggest need for genome based study and further incorporation of it for sustainable agriculture.

Potassium solubilization

Potassium (K) is the third essential macronutrient for plant growth, crucial for processes like turgor pressure regulation, photosynthesis, stomatal activity, nutrient transport, and the synthesis of carbohydrates, proteins, and starch well as activating more than 60 enzymes (25). Despite its importance, the soil has small fraction of soluble potassium, with more than 90% of K is found in insoluble rocks and silicate minerals (26). There are four different forms of k present in soil – water soluble, exchangeable, non-exchangeable (solid), and mineral K; thus,

the available concentration of K for the plant is about 1-2% (27,28). Potassium-solubilizing bacteria (KSB) in the rhizosphere can convert insoluble potassium into a form that plants can absorb as potassium ions (K^+) from soil. Potassium-solubilizing bacteria (KSB) can solubilize potassium, and the rhizosphere is the home to large populations of these bacteria (29). The bacteria that solubilize or mobilize potassium do so by synthesizing organic and inorganic acids, acidolysis, chelation, exchange reactions, and polysaccharide formation (30). *Bacillus* spp. can mobilize potassium from minerals compounds (silicate, feldspar, and illite) and set it aside for the plant utilization (31). Plant Growth Promoting Rhizobacteria such as *Acidithiobacillus ferrooxidans*, *Arthrobacter* sp., *Bacillus mucilaginosus*, *Bacillus circulans*, *Burkholderia*, *Bacillus edaphicus*, *Enterobacter hormaechei*, *Paenibacillus mucilaginosus*, *Paenibacillus glucanolyticus*, *Cladosporium*, *Pseudomonas*, *Aminobacter*, and *Sphingomonas*, have been reported to solubilize potassium (32). By using potassium-solubilizing PGPR strain as biofertilizer, and agriculture can be improved by using fewer agrochemicals and promoting the growth of environmentally friendly crops. Despite the crucial role of potassium in plant growth, limited studies have been conducted on potassium solubilization by microorganisms. This area requires further investigation to better understand and harness the potential of KSB in enhancing potassium availability to plants.

Siderophore-mediated iron acquisition

Iron (Fe) is a vital micronutrient in plants, playing key roles in photosynthesis, mitochondrial respiration, the synthesis of nucleotides, chlorophyll, and thylakoid, chloroplast development, metal homeostasis, and a component of prosthetic groups of several proteins, (33,34). Iron ion (Fe) can exist in two forms the ferric (Fe^{3+}) and the ferrous (Fe^{2+}). Insoluble Fe^{3+} is the most prevalent element in soil, while Fe^{2+} is more soluble, they are readily oxidized into Fe^{3+} (35) and, therefore, not available to plants. Excess concentration of iron is also toxic; thus plants have evolved mechanisms to tightly regulate iron uptake, transport, and storage (36). Two distinct mechanisms for acquiring iron from the soil have evolved in plants i.e reduction and chelation based. Non-graminaceous plants typically employ the reduction-based method, where plant roots release protons and phenolic molecules, leading to rhizosphere acidification and promoting Fe^{3+} solubility. Only graminaceous plants adopt the chelation-based method these plants release iron-chelating phytosiderophores into the rhizosphere. These phytosiderophore has high affinity and specificity towards ferric ions (Fe^{3+}) and thus form a complexes with Fe^{3+} ions.

Siderophores are low molecular weight (10 kDa) iron-chelating substances secreted by rhizobacteria to aid plant growth in iron-deficient environments. They are responsible for the dissolution, chelation, and transport of ferric ions (Fe^{3+}) (37). Because iron exists in various forms with varying solubilities in natural

systems, the availability of iron depends on siderophores' ability to chelate the metal from its complexes (38). Based on their structural features and functional groups, siderophores are classified into four types viz. carboxylate, hydroxamates, catecholate, and mixed siderophore. The structure and functions of each type of siderophore are excellently reviewed (39). Numerous studies have been reported for plant growth promotion via siderophore-mediated Fe-uptake. For example - Cytochrome b5 reductase 1 (CBR1) plays an important role in rhizosphere acidification and thus enhances Fe uptake in *Arabidopsis thaliana* (40). Crowley et al. identified the siderophore-mediated iron acquisition/transport system in oat plants (41). PGPR drives a vital role in iron absorption in rhizospheric soil and facilitates plant growth thanks to its ability to create a siderophore.

Phyto-stimulation

Plant hormones or Phytohormones are naturally occurring group of organic compounds that promote plant growth and development (79). A plant's life cycle, including germination, rooting, growth, blooming, fruit ripening, foliage, and death, are regulated by physiological intercellular mediators (80). Even at low concentration, they can promote, inhibit or modify the plant's development and growth. Abiotic stressors like salt, drought and heavy metal stress are all known to be reduced by these phytohormones, which are also recognized for encouraging plant development (56,72). Auxin, gibberellins (GA), cytokinins (CK), abscisic acid (ABA), ethylene, etc., are the known classical phytohormones (81). Researchers have investigated additional plant growth regulators, including salicylic acid, brassinosteroid, jasmonic acid, and strigolactone (79,82). These plant growth regulators are produced by plants and by some soil microbes. It is believed that, this is one of the effective methods by which many rhizobacteria enhance plant growth is the production of phytohormones.

Auxin

Auxin is a critical phytohormone that is essential for the growth and development of plants. It is intricately involved in the following functions: cell division, cell elongation, branching, phototropism gravitropism, meristem formation, fruit development, controlling of senescence (senescence is the degradation of plant organs), inhibits or delays abscission of leaves and flowers, and fruits, apical dominance (the inhibition of lateral buds formation), and augment the production of adventitious roots (80,83,84). Auxins may be natural or synthetic. Naturally occurring auxins are indole-3-acetic acid (IAA) and its derivatives, while Synthetic auxins are 2, 4-dichlorophenoxyacetic acid (2, 4- D) and naphthalene acetic acid (NAA) (85). Indole-3- acetic acid (IAA) is the most prevalent and natural auxin, and microorganisms only differ in their synthesis process based on the plant and microbes. Sapenean et al. (86) and George et al. (85) reported the different pathways involved in IAA synthesis by bacteria (see fig.3). Many rhizobacteria, as

well as some pathogenic, symbiotic, and free-living bacterial species, possess the capacity to synthesize IAA (86,87). Bacteria belonging to *Pseudomonas*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Agrobacterium*, *Pantoea*, *Rhizobium*, *Bradyrhizobium*, *Klebsiella*, *Alcaligenes*, *Achromobacter*, *Flavobacterium*, *Arthrobacter*, *Rhodococcus*, *Sphingomonas*, *Stenotrophomonas*, *Microbacterium*, *rcinetobacter*, *Corynebacterium*, *Micrococcus*, and *Streptomyces* genera have been reported for IAA production (83,87). Auxin is often interchanged with IAA throughout the literature. The synergetic effect of auxin with jasmonic acid (JA) and salicylic acid (SA) on the growth and defence system of the plant is well explained by Naseem et al. (2015) (88), where exogenous auxin activates jasmonic acid-dependent-plant resistance and suppresses salicylic acid-dependent resistance and promote plant growth. Concentration of auxin produced by the strain determines the auxin's stimulatory effect on the host plant (89). Understanding and harnessing the effects of auxin, particularly its interactions with other phytohormones, could offer valuable insights for optimizing plant growth and defense mechanisms. Future research should focus on fine-tuning auxin levels in agricultural practices to enhance crop yield and resilience against environmental stressors.

Fig.3-Different pathways involved in the bacterial synthesis of IAA. [IAAId - indole-3-acetaldehyde; IAM -indole-3-acetamide; IPDC - indole-3-pyruvate decarboxylase; Trp – tryptophan] (Adopted from Spaepen et al., 2007).

Gibberellin

Gibberellin is a vital phytohormone that stimulates plant growth and development. Chemically gibberellins are gibberellic acids (GA) (90). More than 136 gibberellin molecules have been discovered until now and are represented as GA1-GA136. But only a few are bioactive and found in bacteria. Gibberellic acids such as GA3, GA7, GA1, and GA4 are this group's biologically active and best-studied phytohormones (61). Tetracyclic diterpenes, which make up GA, significantly impact various plant developmental processes, including stem lengthening, seed germination, bolting, leaf expansion, sex differentiation, fruit development, blooming, and senescence postponement (71). GA regulates the amount of root hair, which contributes to its role in promoting root growth, it also have been reported to synthesize amylase hydrolytic enzyme during seed germination; thereby, it is involved in breaking seed dormancy (80,82,90). In addition to this GA is also implicated in the regulation of responses of plant to various environmental conditions like salinity, drought, temperature, flooding and heavy metal stress (91–93). Thus, it is an important plant growth regulator that alleviates many plants' biotic and abiotic stress. At low salinity, tomato plants treated with GA reduced stomatal resistance and increased water usage effectiveness (94). When plants are subjected to biotic and abiotic stress, GA accumulates quickly (92). Plant growth enhancement benefits greatly by bacterial

derived GA. Phytohormones like auxin, GA, and CK play a major role in fruit set (first step of fruit development), and their increased level during fruit development lead to the production of parthenocarpic or seedless fruit formation in tomato (95). These suggest that GA also has some role in fruit setting and flowering. GA synthesis has been observed in the following genera *Achromobacter*, *Gluconobacter*, *Acinetobacter*, *Rhizobia*, *Azotobacter*, *Bacillus*, *Herbaspirillum*, *Azospirillum*, *Pseudomonas*, *Flavobacterium*, *Micrococcus*, *Agrobacterium*, *Leifsonia*, *Clostridium*, *Rhizobium*, and *Xanthomonas* (70,87).

Cytokinin (CKs)

CK is yet another key plant growth regulator. CKs are purine derivatives and plant hormones which play crucial roles in cell division, seed germination, root development, bud release, fruit development, chlorophyll buildup, leaf expansion, and the delay of senescence (80). CK is produced by a variety of rhizobacteria, including those of the genera *Rhizobium*, *Azotobacter*, *Azospirillum*, *Arthrobacter*, *Bacillus*, *Rhodococcus*, *Agrobacterium*, *Pseudomonas*, and *Paenibacillus* (87). *Rhizobium japonicum* (96) and *Bradyrhizobium japonicum* (97) generated CK, which nodulated soybean roots and stimulated cell proliferation in the soybean. In addition, cytokinins help plants to deal with various biotic and abiotic stresses, including salinity and drought (98). CKs produce by PGPR is a useful biocontrol tool for combating a wide range of phytopathogens. The biostimulation and biocontrol activity of CK-producing rhizobacteria is comprehensively reviewed by Akhtar et al. (2020) (99). Inoculation of lettuce plants with *Bacillus subtilis* raised the CK content of both shoots and roots. Also, it changed the concentration of abscisic acid (ABA) and indolyl-3-acetic acid (IAA) in the lettuce plants (60). Soybean and corn seed germination and early seedling growth can be stimulated by the inoculation of either *Azospirillum brasilense* strain Az39 or *Bradyrhizobium japonicum* strain E109. These microorganisms can produce the plant growth regulators IAA, zeatin (Z), and gibberellic acid (GA3) (65) Therefore, PGPR strains that produce CK and other plant hormones may represent a more sustainable and environmentally friendly alternative to chemical fertilizers.

ABA

ABA, a naturally occurring plant growth regulator similar to other phytohormones, is crucial for abscission processes (the separation of plant components, mainly dead leaves and mature fruit) and dormancy. Because of its role in stomatal closure, the transpiration rate (100) gets reduced, and the pathogen entrance gets blocked (101). The importance of ABA in the development of nodules was established by Suzuki et al. (2004) (102). ABA can be synthesized by a number of PGPR strains, including *Azospirillum brasilense*, *Bacillus licheniformis*, *Bacillus pumilus*, *Brevibacterium halotolerans*, *Lysinibacillus fusiformis*, *Bacillus licheniformis*, *Bacillus pumilus*, and

Rhodococcus sp (103). Increased endogenous ABA content makes plants more resistant to drought stress after inoculation with *Azospirillum brasilense* sp 245 or *Azospirillum lipoferum* USA 59b in the case of *Arabidopsis thaliana* or maize, respectively (46,104). Thus, ABA is also referred as a stress hormone because it shields plants from the damaging effects of environmental stresses such as drought, salinity, cold, and flooding (105). ABA-producing bacteria, such as *Azospirillum brasilense* and *Bacillus subtilis*, were found to lessen cadmium (Cd) contamination in *Brassica chinensis* in an investigation by Pan et al. (2019) (47). Under a range of situations, ABA has a beneficial effect on stomatal activity, seed dormancy, and other aspects of plant growth. The PGPR varieties favor either an ABA-dependent or -independent strategy to promote plant development.

Ethylene

A unique class of plant hormone called ethylene is essential for several physiological processes in plants, such as development, fruit ripening, senescence, and abscission (106,107), and protect against biotic and abiotic stress. Ethylene, a gaseous plant hormone, can stimulate or inhibit plant development, depending on its concentration. As ethylene is useful at low concentrations but hazardous at high concentrations for plant health, thus it is necessary to maintain moderate conc. of ethylene levels in plants (108). This can be attained by inference of PGPRs with 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity. The ACC deaminase enzyme regulates the high levels of ethylene in plants, and PGPR plays a role in this process. Plants use this enzyme to convert ACC (an immediate precursor of ethylene production in plants) into α -ketobutyrate and ammonia, neutralizing the harmful effects of ethylene accumulation on the growth and development of the plant (109). PGPRs with ACC deaminase activity promote plant growth by reducing the negative effects of environmental stresses such as salt, drought, temperature, and flooding (109). *Aneurinibacillus aneurinilyticus* and *Paenibacillus* strains expressing ACC deaminase ameliorated the harmful effects of salt stress on French bean seedlings. Compared to control plants, groundnuts infected with *Pseudomonas fluorescens* strain TDK1 exhibiting ACC deaminase activity had greater salinity resistance and higher yield (76).

Understanding the mechanisms of PGPR-dependent plant growth stimulation and enhanced resilience to biotic and abiotic challenges relies heavily on PGPR strains' ability to produce various phytohormones or to affect plant homeostasis.

B. Biocontrol activity

There are a number of issues in the agricultural system that can restrict plant growth. The pathogenic microorganisms are major reason for decreased agricultural production. The application of microorganisms instead chemical pesticides, insecticides, and herbicides to treat plant diseases is a more eco-friendly approach and a safe and viable alternative. Rhizobacterial ability to

suppress diseases depends on how susceptible the phyto-pathogen is to the rhizobacterium antimicrobial compounds. Antibiotics, siderophores, hydrogen cyanide, volatile organic compounds (VOC), extracellular enzymes, polysaccharides, and competition for nutrients with pathogenic bacteria in the rhizosphere are all ways in which this biocontrol activity manifests itself (2,110).

Furthermore, it stimulates plant responses that induce systemic resistance (ISR) and systemic acquired resistance (SAR). Table 3 shows several important PGPR strains used in disease control. Following is a quick explanation of how the various metabolites produced by PGPR contribute to the biocontrol activity by inhibiting the growth of harmful bacteria.

Antibiotic

Beneficial rhizobacteria can secrete antibiotics and other chemicals that suppress plant pathogen and diseases. One common biocontrol strategy PGPR uses is antibiosis, which is the production of antibiotics. Antibiotics are a class of chemical compounds has a broad spectrum activity against various microorganism (111). A large number of studies have sought to prove that antibiotics, by either increasing their synthesis or interrupting the genes involved in the synthesis, may be used to inhibit the growth of pathogenic fungi and bacteria. An example is the inability of an antibiotic of fluorescent pseudomonad spp. without the antibiotic production gene suppress phytopathogens growth, in comparison to the wild-type strain, demonstrates that the antibiotics play crucial role in biocontrol. Some of the antibiotics that PGPRs generate include pyoluteorin, phenazine-1-carboxamide (PCN), pyrrolnitrin, 2,4-diacetylphloroglucinol (DAPG), rhamnolipids, phenazine-1-carboxylic acid (PCA), fengycin, surfactin, polymyxins, fusaricidin, iturin, circulin, colistin, viscosinamide, kanosamine, and zwittermycin (110,112). These antibiotics fight against diverse bacteria, fungi, and viruses thus indirectly stimulate plant growth and development. Numerous species of *Pseudomonas* and *Bacillus* produce antimicrobial compounds with broad-spectrum activity against many phytopathogens, making them promising candidates for use as biocontrol agents in agriculture. Since PGPRs can produce more than one antibiotic, they could be a powerful biocontrol agent.

Siderophore-mediated biocontrol activity

Iron is a micronutrient that nearly every living thing requires. In soil, iron can be found in both ferric (Fe^{3+}) and ferrous (Fe^{2+}) ions, but neither is available to bacteria or plants (2). Siderophore, a low-molecular-weight iron chelator molecule secreted by bacteria, has a high affinity for ferric ion (Fe^{3+}), binding strongly with iron and rendering it unavailable to pathogens, hence inhibiting their proliferation in the rhizosphere (113). These siderophores' probable mode of action involves competition for iron between the PGPR and phytopathogens

(114). Providing iron to plants or displaying antagonism against harmful microbes are two ways in which siderophores mediate plant growth. Biocontrol activity of *Pseudomonas fluorescens* strains A1, BK1, and TL3B1 against the pathogen *Erwinia carotovora* was initially described by Kloepper et al. (1980) (114). Siderophores produced by various rhizobacterium exhibit broad-spectrum antagonistic activity against various phytopathogens, including *Pseudomonas tolaasii* (77), *Fusarium oxysporum* f. sp. *dianthi* (Fod) (76), *Phytophthora* sp., *Aspergillus niger*, *A. flavus*, *A. tubingensis*, *Alternaria alternata* (115), *Colletotrichum gloeosporioides* (116), *Fusarium oxysporum* f. sp. *lycopersici* (78), *Alternaria* sp., *Aspergillus brasiliensis*, *Rhizoctonia* sp., *Colletotrichum* sp., and *Curvularia* sp. (80). Thus, PGPR promoting plant growth through siderophore production could be a sustainable approach to crop health management.

Volatile organic compounds (VOCs)

The ability to produce volatile organic molecules is crucial to plant development. Aldehydes, ketones, aromatics, sulfides, and alcohol are all volatile chemicals that are produced by various bacteria (111). Rhizobacterial VOCs have been known to have antibacterial, antifungal, and nematicidal activity and to promote plant growth. However, a VOC's high concentration may have the opposite effect. VOC also aids in plant growth stimulation by regulating the synthesis or metabolism of plant hormones (117) (118). Root architecture, lateral and primary root length, and lateral root number on *A. thaliana* were all altered due to the presence of VOCs generated by *Bacillus* sp. (110). *Paenibacillus polymyxa* KM2501-1 produced volatile chemicals with nematicidal activity against *Meloidogyne incognita*. A special "honey-trap" mechanism of action is observed as synthesized compounds such as furfural acetone and 2-decanol that can lure *M. incognita* and subsequently kill it by touch or fumigation (120)(120). Two volatile chemicals, 3-hydroxy-2-butanone (acetoin) and 2, 3-butanediol, are released by *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937, and they stimulate plant development and elicit ISR in *Arabidopsis* (121). The tomato wilt pathogen *Ralstonia solanacearum* is effectively suppressed by volatiles produced by *Bacillus amyloliquefaciens* SQR-9. These volatiles include heptadecane, 2-tridecanone, 2-nonanone, nonanal, n-hexanoic acid, 2-decanone, 2-undecanone, among others (122). Rhizobacterial strains of *Bacillus* sp., *Paenibacillus* sp., and *Xanthomonas* sp. were shown to be effective in preventing rice root-knot nematode *Meloidogyne graminicola* infestation through the formation of VOCs in a recent study (123). Fungi, including *Botrytis cinerea*, *Phytophthora cactorum*, *Rosellinia necatrix*, and *Fusarium equiseti*, were successfully inhibited by *Pseudomonas* spp. and *Bacillus* spp., which produce VOCs (124). VOCs generating PGPR strains are increasingly being recognized as efficient biocontrol agents against a wide range of fungal diseases and nematodes because of their low environmental impact and ability to provide lasting crop protection.

Production of extracellular enzymes

The release of cell wall-disintegrating enzymes is a crucial mechanism used by biocontrol agents. Hydrolytic enzymes are so named because of their ability to break down polymeric molecules found in a cell wall (125). Hydrolytic enzymes such as protease, chitinase, cellulase, glucanase, etc., produced by PGPR strains, thus allowing them to destroy the cell wall of various phytopathogenic fungi (64). The following are some of the many instances used to investigate these consequences better: the cellulolytic and chitinolytic enzymes produced by *Paenibacillus* sp. compromise the structural integrity of the cell walls of *P. parasitica* and *F. oxysporum*, respectively (126). The enzyme chitinase suppresses many fungal diseases, which hydrolyzes the glycosidic connections between chitin, a significant component of the fungal cell wall. *Bacillus* spp. BPR6 and BPR7, which produce the chitinase, suppress the growth of a number of different phytopathogens, including *Macrophomina phaseolina*, *Fusarium oxysporum*, *F. solani*, *Sclerotinia sclerotiorum*, *Rhizoctonia solani*, and *Colletotricum* sp. (127). In addition, *Bacillus subtilis* (strain 330-2) produces a complex of hydrolytic enzymes, including β -1,3-glucanases, β -1,4-glucanase, and proteases, that are involved in the degradation of the fungal cell wall, resulting in the strain's strongest antagonistic activity against many *Rhizoctonia solani*, *Botrytis cinerea*, *Fusarium oxysporum*, *Alternaria alternata*, *Cochliobolus heterostrophus*, and *Nigrospora oryzae* (128). The strains of PGPR that produce hydrolytic enzymes are the safest, most sustainable, and environmentally benign method of pest control since they demonstrate antagonistic activity against a wide range of phytopathogens without harming plant tissues.

Induced systemic resistance (ISR)

Rhizobacteria are capable of inducing an important defense mechanism known as Induced systemic resistance (ISR). The term ISR describes the way in which a plant's defense mechanism is bolstered against infections by a combination of bacterial metabolites. Plants can develop resistance to some harmful microbes like fungi, bacteria, and viruses, when such microbes interact with the plant's root, as described by Lugtenberg and Kamilova (2009) (1). PGPR controlling pathogens and thus indirectly promoting plant growth, also stimulates plant responses, including ISR and SAR (4).

Both ISR and SAR share similar phenotypes, where pathogens and insects trigger SAR, and beneficial rhizobacteria trigger ISR (5,129). The elicitor and regulatory pathways involved in the induction of systemic resistance in plants are the primary determinants of whether a plant exhibits SAR or ISR. A plant's SAR depends on salicylic acid pathways, while ISR relies on jasmonic acid and ethylene (130). Salicylic acid has been shown to have a key role in the generation of systemic resistance against blue mold disease of tobacco triggered by PGPR, as shown by Zhang et al., 2002 (131). Systemic resistance against late blight, produced by *Phytophthora infestans* on tomatoes, has been elicited using PGPRs,

Bacillus pumilus SE34, and *Pseudomonas fluorescens* 89B61, and the severity of the disease has been reduced (132). Efficient elicitors of ISR include volatile chemicals, siderophores, antibiotics, and enzymes. ISR has been linked to the production of antioxidant enzymes such as phenylalanine ammonia-lyase (PAL), peroxidase (PO), and polyphenol oxidase (PPO) in plants (133,134). Enhanced activity of PO, PPO, and PAL enzymes was seen in cucumbers where ISR against *Pythium aphanidermatum* was mediated by PGPR (135).

Conclusion

Recently, there has been a rise in the application of beneficial bacteria in agriculture. It is crucial to generate multifunctional inoculants for agriculture to isolate and identify these bacteria and assess their plant growth-promoting (PGP) activities. While most PGPR research has focused on a single mechanism, understanding the many factors contributing to PGPR's success could one day aid in its commercial manufacturing. There are currently many investigations into the solubilization of nitrogen and phosphate. Still, there is a need to investigate the solubilization of potassium, as it is the third key required macro-nutrient for plant growth. In conclusion, PGPRs are capable of reducing the use of chemical fertilizers, pesticides, and artificial plant growth regulators that have a harmful effect on the ecosystem, and they are also responsible for increasing productivity and soil fertility, the two most crucial factors in preserving an eco-friendly and sustainable agricultural system.

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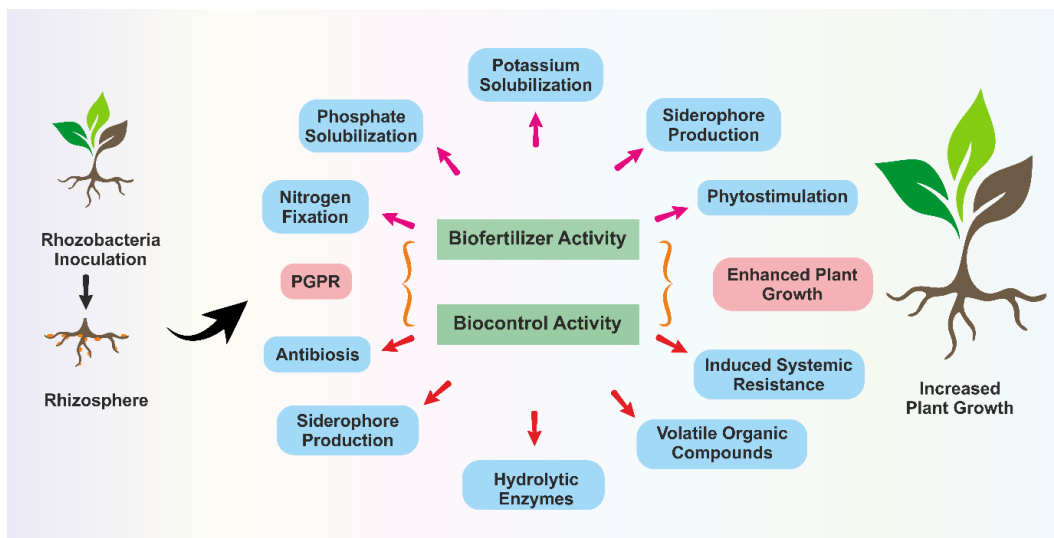


Fig. 1

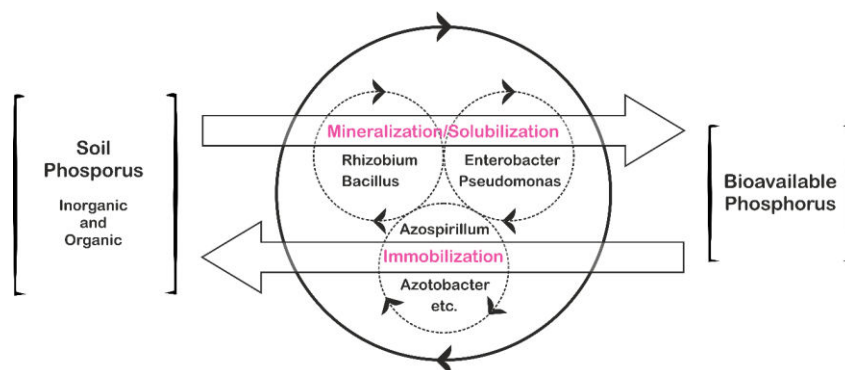


Fig. 2

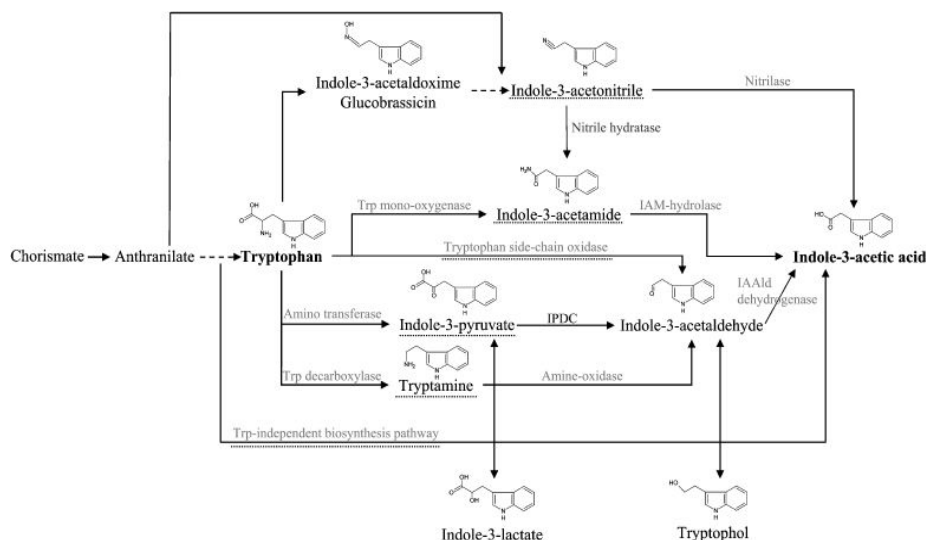


Fig. 3

Table 1:

PGPR	Bacterial genera	Refernces
ePGPR	Bacillus, Azotobacter, Arthrobacter, Burkholderia, Caulobacter, Erwinia, Chromobacterium, Enterobacter, Flavobacterium, Micrococcous, klebsiella, Azospirillum, Pseudomonas and Serratia	(8)
iPGPR	Rhizobium, Bradyrhizobium, Sinorhizobium, Mesorhizobium and frankia	

Table 1: Classification of different bacterial genera on the basis of their location

Table 2:

PGPR STRAIN	PLANT	MODE OF ACTION	EFFECT ON PLANT	REFEREE NCES
Achromobacter xylooxidans	Potato	P solubilization, IAA production	A considerable elevation in chlorophyll a and b is also indicated by a rise in shoot and root length, shoot fresh and dry weight, root fresh and dry weight, and N and K concentration.	(42)
Acinetobacter calcoaceticus SE370	Cucumber, Chinese cabbag	GA, Phosphate solubilization	Improved the plant's height, dry weight, and shoot length considerably.	(43)

	e, and crown daisy			
Aneurinibacillus aneurinilyticus	French bean	ACC deaminase activity	Alleviated salt stress and increased root length (110%), fresh root weight (45%), shoot length (60%), shoot fresh weight (255%), root biomass (220%), shoot biomass (425%), and total chlorophyll content (57%)	(44)
Azospirillum spp.(Az 19)	Maize	Nitrogen fixation, siderophore ,	Reduced effects of drought and salt tolerance.	(45)
Azospirillum brasilense Sp 245	Arabidopsis thaliana	Abscisic acid (ABA) , IAA production	Modifications to the root architecture, reductions in stomatal conductance, enhancements to proline, and increases in relative leaf water level. Elevation in auxin level, increasing the amount of lateral roots and root hairs	(46) 125
Azospirillum brasilense, Bacillus subtilis	Pakchoi (Brassic a chinensis)	Abscisic acid (ABA)	Lowered cadmium Cd stress and gives higher biomass and chlorophyll content, Improves the level of antioxidant compounds,	(47)
Azotobacter chroococcum	a. Maize b. Coriander, c. Olive tree	Biocontrol Nitrogen fixation, Potassium solubilization,	a. Highest biomass, seedling height, and nutrient uptake b. antagonistic activity against P. macrosporus and greatly lowered the degree of stem galling. c. Increases fruit weight and yield and alleviates stress under calcareous soil	128)(48) (49)
Azotobacter sp. (SR-4)	Bottle gourd (Lauki),	Nitrogen fixation	Plant height, leaf length/width, fruit size, and number of fruits per plant when	(50)
Bacillus	mung	P	Stimulate the growth of lateral	(51)

thuringiensis	bean	solubilization, IAA production	roots and root hairs to increase the lengthening of the shoot and the root.	
Bacillus amyloliquefaciens	Arabidopsis,	VOCs	Increase Fe and Se uptake in plants, regulate the nutrient acquisition	(52)
Bacillus amyloliquefaciens	Banana	ND	Plant height, leaf number, leaf area, pseudostem thickness, root and shoot fresh weight, root and shoot dry weight	(53)
Bacillus amyloliquefaciens SQR9	Cucumber	IAA production, voc, and phytase	Increases cucumber yield (90.0%), shoot height (71.6%), root length (56.3%) and root surface area(65.6 %)	(54)
Bacillus licheniformis Am2, Bacillus subtilis BC1, Pseudomonas aeruginosa E2	Cucumber	cytokinin production	Increased cell division as well as increases in the fresh weight and size of cucumber cotyledons	(55)
a. Bacillus licheniformis strain A2 b. Bacillus mucilaginosus MCRCp1	Groundnut	Phosphate solubilization, IAA production N ₂ fixation,	a. Elevation in fresh biomass (28%), total length (24%), and root length (17%). b. Increased groundnut plant dry matter (125%), root length, and oil content (35.41%)	(56), (57)
Bacillus megaterium var. phosphaticum	Pepper, Cucumber	P solubilization	Raised shoot and dry root weight	(58)
Bacillus megaterium, Azospirillum brasilense and Pseudomonas fluorescens	Cauliflower	Nitrogen fixation, P solubilization	Observed higher leaf length, leaf width, stem height, and plant weight, thereby increasing production	(59)
Bacillus megaterium	Olive tree	Nitrogen-fixing, P and K solubilization, phytohormones	Improves yield, fruit weight, and flesh oil content of the olive tree	(49)

		production		
Bacillus mucilaginosus, Azotobacter chroococcum,	Maize, Wheat	Potassium solubilization	A greater amount of biomass and potassium possessed by plants, in addition to an increased amount of chlorophyll and crude protein included in plant tissue.	(32)
Bacillus spp.	Maize	phosphate solubilization, phytohormone production, HCN, hydrolytic enzymes	Increases plant biomass, relative water content, leaf water potential, root adhering soil/root tissue ratio, aggregate stability, and alleviates salt stress	
Bacillus subtilis	Lettuce	Phytohormones production- IAA, GA, ABA, CKs	Increases shoot and root weight of the plant	(60)
Bacillus subtilis	Soybean	Antibiotic, IAA, ABA	Elevated the outgrowth of lateral roots and root hairs effective against soybean seed fungi	(61)
Bacillus subtilis IB-22	Wheat	Cytokinin production	Increased leaf length, width, and chlorophyll content.	(62)
Bacillus velezensis LDO2	Peanut	Antibiotic	Substantial increases in peanut seedling height, root length, and root dry weight, as well as the dry seedling weight of peanut seedlings.	(63)
Bacillus. subtilis RMB5, Pseudomonas aeruginosa FB2	Arugula	Antibiotic production, Hydrolytic enzymes, IAA production, nitrogen fixation, P solubilization	Increases plant height and biomass	(64)

		n		
Bradyrhizobium diazoefficiens USDA110 +Bacillus velezensis S141	Soybean	Nitrogen fixation	Significantly increases nitrogen use efficacy, nodule number, dry nodule weight, size of nodules, and total plant dry weight	(14)
Bradyrhizobium japonicum E109, Azospirillum brasilense strain Az39	Corn, Soybean	IAA, GA3, Cytokinin	Enhance the germination of seeds, the establishment of nodules, and the early growth of maize and soybean seedlings.	(65)
Burkholderia sp. GZ18	M. micrantha	Potassium solubilization,	Boosts the potassium level and plant mass of M. micrantha	(66)
Bacillus aryabhatai RS341 Brevibacterium epidermidis RS15, Micrococcus yunnanensis RS222	red pepper seedlings	ACC deaminase	When red pepper exposed to NaCl, PGPR strains shows increases in both their fresh and dry weights (150 mmol)	(67)
Chryseobacterium spp. C138	Tomato	Siderophore production	Enhances Fe uptake in Fe-starved tomato plant condition	(68)
Klebsiella sp.IG 3	Oat	Phosphate solubilization, Potassium solubilization, ACC deaminase	Increases the chlorophyll, proline, total sugar, and total protein content of oat seedlings under saline stress.	(69)
KSB1 (KJ410663)	Maize	Potassium solubilization	Enhanced plant height, number of leaves, stem girth and chlorophyll content, and K supply to crop	(29)
Leifsonia soli sp. SE134	Cucumber, tomato, and radish	GA production	Increased the biomass, hypocotyl, and root lengths of all plant	(70)
Leifsonia xyli SE134	Tomato	IAA and GA production	Improved phosphorus and iron levels in plants raised under significant copper stress help lessen copper's negative effects on plants.	(71)

Mesorhizobium ciceri IC53	Chickpea (Cicer arietinum L.)	Phytohormones	Enhanced nodule formation and stimulation of root and shoot biomass	(72)
Paenibacillus polymyxa strain E681,	Pepper, Cucumber, Sesame	Antibiotic production	Protect the plant from various biotic and abiotic stress	(73)
Pseudomonas aeruginosa	Elaeis guineensis (oil palm)	Hydrolytic enzymes, phosphate solubilization, IAA production	Exhibits antagonistic activity against fungal pathogens	(74)
Pseudomonas aeruginosa strains RSP5 and RSP8	Maize	siderophore mediated Fe uptake	Increase in shoot length, root length, cob length, grain number, and iron content of stem, leaf, and seed.	(75)
Pseudomonas fluorescens	Groundnut	ACC deaminase activity	Improves groundnut seedling and protect the plant from saline stress	(76)
Pseudomonas fluorescens 2-79	Turmeric	Antibiotic	Significantly increases the vigor index of turmeric plants, root length (10.70 cm), and shoot length (14.36 cm) and reduces the incidence of rhizome rot disease	(77)
Pseudomonas strain GRP3	Mung bean	Siderophore production	Reduction in chlorotic symptoms of plants and also enhanced chlorophyll level	(33)
Rhizobium meliloti	Cotton	Nitrogen fixation, Phosphate solubilization	Phosphorus content was significantly increased in plants	(72)
Rhizobium strain Rr2	Chickpea	IAA, GA production	Increases plant biomass and nodulation	(78)
Sphingomonas sp. LK11 Serratia marcescens TP1	Soybean	Abscisic acid (ABA) and gibberline	Stimulate shoot and root growths	(72).

		production	
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Table 2: Effect of different PGPR (Plant Growth Promoting Rhizobacterial) Strains on Plants

Table 3:

Plant	pathogen/ disease	PGPR strain	References
Arugula	Fusarium oxysporum, Fusarium moniliforme, Rhizoctonia solani, Aspergillus niger, Colletotrichum gloeosporioides, Colletotrichum falcatum, and Aspergillus flavus.	Bacillus. subtilis RMB5	(64)
Coriander	stem gall disease	Azotobacter chroococcum, Pseudomonas putida)	(48)
Cucumber	Fusarium wilt Pythium aphanidermatum- Root and crown rot Pythium damping-off disease	Paenibacillus sp. 300 P. corrugata strain 13. Enterobacter cloacae	(136), (135) , (137)
Cucurbits	Xanthomonas campestris, Pectobacterium carotovorum	Bacillus subtilis	(138),
Maize	Colletotrichum dematium, Rhizoctonia solani and Sclerotium rolfsii	Pseudomonas strains GRP3A	(115)
Mung Bean	Web Blight Disease	Pseudomonas fluorescens (Psf 173)	(139)
Oil Palm	Basal stem rot (BSR)	P. aeruginosa (UPM P3)	(74)
Peanut	Rhizoctonia solani and Sclerotium rolfsii. Aspergillus flavus	Bacillus subtilis isolate B4 Bacillus velezensis LDO2	(140) (63)
Pepper	Damping off of pepper, Botrytis cinerea, Fusarium solani	P. fluorescence Bacillus sp.	(141), (142)
Rice	Fusarium oxysporum, F. moniliforme, F. solani, Trichoderma atroviride and T. reesei, rice root-knot nematode (Meloidogynegraminicola)	Bacillus NH-100, Bacillus sp. and Xanthomonas sp.	(143), (123)

Sisal	Sisal bole rot	Burkholderia sp.	(144)
Soursop	Colletotrichum gloeosporioides	Bacillus atrophaeus	(145)
Soyabean	Phytophthora sojae	Paenibacillus sp.,-S1	(146)
Strawberry	Anthracoise disease	Azospirillum brasiliense	(147)
Sugarcane	Colletotrichum falcatum	Ochrobactrumintermedium (TRD14),Bacillus sp. (RSC29 and KR91), Acinetobacter sp. (PK9)	(148)
Tobacco	Thielaviopsis basicola- black root rot Peronospora tabacina- blue mold of tobacco -	Serratia marcescens, Bacillus pumilus	(149), (131)
Tomato	Ralstonia solanacearum (RS) Fusarium Wilt Botrytis cinerea	Bacillus amyloliquefaciens SQR-9 P. fluorescens. Paenibacillus terrae AY-38	(122) (150) (151)
Turmeric	Pythium aphanidermatum- rhizome rot disease	Pseudomonas fluorescens	(77)
Wheat	Root rot disease- Gaeumannomyces graminis var. tritici.	Pseudomonas fluorescens 2-79	(152)
	Fusarium graminearum	Paenibacillus sp.,Pantoea sp.	(153)

Table 3: Biological control by PGPR against certain diseases, and pathogens in different plants