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Practical significance of plant growthpromoting rhizobacteria in sustainable agriculture: a review

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Abstract

Plant growth-promoting rhizobacteria (PGPR) are naturally occurring bacteria that intensively colonize plant roots and are crucial in promoting the crop growth. These beneficial microorganisms have garnered considerable attention as potential bio-inoculants for sustainable agriculture. PGPR directly interacts with plants by providing essential nutrients through nitrogen fixation and phosphate solubilization and accelerating the accessibility of other trace elements such as Cu, Zn, and Fe. Additionally, they produce plant growthpromoting phytohormones, such as indole acetic acids (IAA), indole butyric acids (IBA), gibberellins, and cytokinins.PGPR interacts with plants indirectly by protecting them from diseases and infections by producing antibiotics, siderophores, hydrogen cyanide, and fungal cell wall-degrading enzymes such as glucanases, chitinases, and proteases. Furthermore, PGPR protects plants against abiotic stresses such as drought and salinity by producing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase and modulating plant stress markers. Bacteria belonging to genera such as Bacillus, Pseudomonas, Burkholderia, Pantoa, and Enterobacter exhibit multiple plant growth-promoting traits, that can enhance plant growth directly, indirectly, or through synergetic effects. This comprehensive review emphasizes how PGPR influences plant growth promotion and presents promising prospects for its application in sustainable agriculture.

Keywords: biofertilizer, phytohormone, rhizobacteria, sustainable agriculture

Introduction

The human population has exponentially grown over the past few years. As estimated by the United Nations, the world population will reach 8.5 and 9.7 billion by 2030 and 2050, respectively (UN, 2019). With the increasing global population, the world faces challenges in sustaining the life on Earth. In this context, the agriculture sector is tasked with fulfilling the future food requirements



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the Creative Commons Attribution Non-Commercial License (http://creativecommons.org/licenses/bync/4.0/) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited. of communities (Walpola and Yoon, 2012); however, the increasing demand needs to be met with great care considering environmental concerns (Sagbara et al., 2020).

The agricultural sector is a key contributor to many developing countries' economic and social development, where national food and nutritional security are top priorities (Singh, 2013). The rapid exploitation of natural resources, reckless development of agricultural land, and extensive use of synthetic compounds due to the increasing demand for agricultural products are frequently reported. These observed practices include managing agricultural land, reducing chemical fertilization, planting cover crops, applying eco-friendly management, and integrating ecosystems and agriculture (FAO, 2023). In this context, adopting environment friendly agricultural techniques, such as using favorable soil microorganisms, has been widely popularized owing to the high costs and negative environmental impacts associated with synthetic chemicals (Singh, 2013; Gupta et al., 2021; Ghani et al., 2022). For example, the excessive application of chemical fertilizers accelerates the degradation of soil organic matter, decreases soil fertility, and weakens the soil structure (Bhatt et al., 2019; Kang et al., 2019).

The purpose of this study was to review the practical significance of plant growth-promoting rhizobacteria (PGPR) in sustainable agriculture and the summarize their characteristics and mechanisms of plant growth promotion. Furthermore, this study revealed an eco-friendly agricultural approach to crop production.

What is the plant growth-promoting rhizobacteria (PGPR)?

Biotic and abiotic factors influence crop growth and yield (Saharan and Nehra, 2011). The actions of different microscopic forms, such as algae, bacteria, fungi, protozoa, and actinomycetes, are considered biotic factors, with 95% contribution from bacteria, which are the most common microorganisms in this context (Glick, 2012). Microorganisms generally have both beneficial and non-beneficial effects on crop growth and yield (Miransari, 2014). The rhizosphere is the area in the root zone of plants where many microorganisms reside. This thin soil layer is an important factor in the active zones of metabolism and root activity (Saharan and Nehra, 2011). Microbial activity in the rhizosphere influences the status of root exudates and, thereby, the availability of nutrients (Backer et al., 2018). Therefore, the absolute effect of microbes on plant performance can vary from positive to negative (Khalid et al., 2004). Plant growth-promoting bacteria (PGPB) are free-living organisms or members of specific symbiotic relationships. PGPBs have been identified as an indispensable component of the rhizosphere which enhances the growth of host plants through various direct or indirect mechanisms. Some are involved in nitrogen fixation (Rawat et al., 2021), solubilization of insoluble phosphate and potassium, and production of siderophores and phytohormones. Their role in heavy metal resistance has also been reported (Chu et al., 2021). Their stress responses include 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase production. PGPR promotes drought tolerance and halotolerance of plants through various mechanisms, as shown in Fig. 1 (Gupta et al., 2021; Mansour et al., 2021).

Bacterial genera such as *Bacillus, Brevibacillus, Burkholderia, Pseudomonas, Agrobacterium, Thiobacillus, Streptomyces Klebsiella, Acetobacter, Rhizobium, Azospirillum, Azotobacter, and Serratia are known PGPR that enhance the growth of host plants (Radhakrishnan et al., 2017; Guo et al., 2020). They inhabit the roots of plants by colonizing the rhizosphere, root surface, or intercellular spaces of root cells (Miransari, 2014).*

The close relationship between PGPR and host plants benefits the host plant primarily by making nutrients available for plant uptake (Verma et al., 2010). The effectiveness of this relationship depends on the population density of microorganisms and the period during which the PGPR remains in the rhizosphere. Therefore, inoculating host plants with PGPR could

increase their population density for a certain period (Bhattacharyya and Jha, 2012). High population densities of bacteria in the rhizosphere, comprising different PGPR types that exhibit a wide range of effects on crop productivity, enhance the circulation and plant uptake of nutrients (Singh, 2013). Due to their rapid growth rate, adaptability to diverse environmental conditions, and ability to metabolize a range of natural, and xenobiotic compounds, PGPR are considered successful rhizobacteria in soil ecosystems (Bhattacharyya and Jha, 2012).

Commercial preparations of several PGPR inoculants have also been shown to promote plant growth through various mechanisms, such as the production of phytohormones, disease suppression, and improvement of nutrient acquisition (Saharan and Nehra, 2011).

As stated by Singh (2013) inoculation with PGPR induces plant growth, thereby enhancing yield through the enhancement of phosphorus or potassium solubilization and nitrogen and other element uptake (Fig. 1). They promote root growth while increasing the effective surface area of the root system. Table 1 shows the some of the PGPR tested for various crop species.

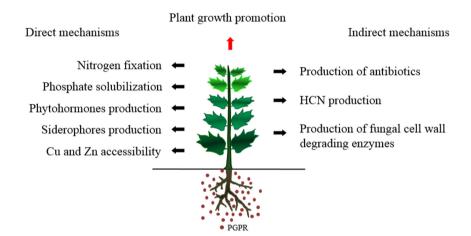


Fig. 1. Growth promotion characteristics by plant growth promoting rhizobacteria (PGPR). HCN, hydrogen cyanide.

Table 1. Plant growth promoting rhizobacteria tested for various crop species.

PGPR	Plant	Consequences of addition of PGPR	References
Bacillus subtilis subsp.,	Oryza sativa	Improve growth and productivity under drought stress	Abd El-Mageed et al. (2022)
Bacillus megaterium			
Bacillus spp.,	Cannabis sativa	Improve rooting speed of cuttings, yield attributes, and	Lyu et al. (2022)
Muci laginibacter spp.,		physiological variables	
Pseudomonas spp.			
Bacillus licheniformis	Solanum tuberosum	Enhanced leaf gas exchange rates, including photosynthesis rate, stomatal conductance and transpiration rate at early seedling stage	Liu et al. (2022)
Azotobacter chroococcum,	Fragaria × ananassa	Enhance anti-herbivore defence system against two-spotted spider	Hosseini et al. (2021)
Azospirillum brasilense,	(strawberry)	mites, improve nutritional status of plants	
Pseudomonas brassicacearum			
Bacillus a myloliquefaciens,	Piper nigrum	Enhance anti-herbivore defence system against two-spotted spider	Pappas et al. (2021)
Pseudomonas spp.	~	mites and green peach aphids	~ ~
Pseudomonas putida KT2440	Glycine max	Improve seed germination and stem length under saline conditions	Costa-Gutierrez et al. (2020)
Pseudomanas PS01	Arabidopsis thaliana	Improve seed germination and plant growth under salt stress	Chen et al. (2021)
Bacillus tequilensis SSB07	Glycine max	Improve shoot length, biomass, leaf area, and photosynthetic pigments under normal growth conditions and heat stress	Kang et al. (2019)
Rhizobium leguminismarum,	Triticum spp.	Increase the yield and phosphorus uptake	Singh (2013)
Pseudomonas spp.			

PGPR, plant growth-promoting rhizobacteria.

Use of PGPR in Agriculture and their Relevant Mechanisms

PGPR can be used as a bio-fertilizer

The increased use of chemical fertilizers in agriculture is a matter of great concern because of their possible environmental and health risks (Verma et al., 2010). Biofertilizers have received wide recognition as viable alternatives to chemical fertilizers (Hayat et al., 2012). When used as a biofertilizer, PGPR can colonize the rhizosphere or interior parts of plants, enhance nutrient availability, and further influence the plants by their involvement in nitrogen fixation and phosphate solubilization (Bhattacharyya and Jha, 2012). In addition to enhancing mineral and nitrogen availability in soil, some bacterial strains can directly regulate plant physiology by simulating plant hormone synthesis (Saharan and Nehra, 2011). A previous study reported that PGPR enhances soil fertility and promotes safflower growth by increasing the activity of soil urease, phosphatase, and invertase enzymes (Nosheen and Bano, 2014). Furthermore, it is recommended that PGPR treatment could potentially replace 50 - 75% of chemical fertilizers.

PGPR is involved in nitrogen fixation

Nitrogen, a key nutrient required for plant growth, is often reported as a limiting factor in many agricultural fields owing to heavy nitrogen losses (Perez-Montano et al., 2014). Nitrogen-fixing bacteria are important in agro-ecosystems because they can influence nitrogen availability and uptake by plants (Gopalakrishnan et al., 2017). Symbiotic nitrogen fixation through Rhizobium and Bradyrhizobum is significant in soils with low amounts of nitrogen because of nodule formation on the roots of species such as soybeans, peas, peanuts, and alfalfa (Hayat et al., 2012). Nitrogen-fixing rhizobacteria that colonize the rhizosphere are good examples of legume-rhizobial symbiosis (Verma et al., 2010). They convert atmospheric nitrogen to ammonia, which could subsequently act as a source of nitrogen for plants. Among the most studied rhizobia, the ability of Rhizobium, Bradyrhizobium, Allorhizobium, Azorhizobium, Mesorhizobium, and Sinorhizobium fix nitrogen in legumes has been proven (Verma et al., 2010). Bradyrhizobium is a common soil-dwelling microorganism that forms symbiotic relationships with legumes and exchanges nitrogen with carbohydrates from the host plant (Saharan and Nehra, 2011). During the signal exchange process of *Rhizobium*-legume symbiosis, flavonoids are released by the legume, providing signals to the bacterium to secrete Nod factors. Cereals grown in inter-cropping systems or crop species that rotate with legumes benefit from Rhizobium-legume symbiosis (Hayat et al., 2012). In these systems, plant root hairs induce root nodules, on which Rhizobium bacteria fix atmospheric nitrogen (Verma et al., 2010). Free-living nitrogen-fixing bacteria that associate with roots, such as Azotobacter, Paenibacillus, Burkholderia, Bacillus, Azospirillum, and Herbaspirillum, can facilitate nitrogen uptake (Goswami et al., 2016). These bacteria maintain close interactions with the plant roots and feed on root exudates containing proteins, amino acids, enzymes, vitamins, sugars, organic acids, and hormones (Tabassum et al., 2017). Furthermore, some rhizobia can enhance phosphorus availability by mobilizing inorganic and organic phosphorus (Saharan and Nehra, 2011).

PGPR affected phosphate solubilization

Phosphorus (P), a key element for plant growth (Rawat et al., 2021), is generally unavailable for plant uptake because of its insoluble form, which often limits the productivity of agricultural ecosystems (Singh, 2013; Lin et al., 2016). When

a phosphate fertilizer is applied to the soil, a substantial portion of the phosphorus is rapidly converted into insoluble forms and forms complexes with Al and Fe in acidic soils and with Ca in calcareous soils (Walpola and Arunakumara, 2015). The accumulation of inorganic insoluble phosphates in the soil and their transfer to water bodies can have undesirable effects on the environment (Gatiboni et al., 2020). Microorganisms capable of converting insoluble phosphates into soluble forms are known as phosphate-solubilizing bacteria (Hayat et al., 2012).

Phosphate-solubilizing bacteria (PSB) produce and release low-molecular-weight organic acids (e.g., citric acid, lactic acid, gluconic acid, 2-ketogluconic acid, oxalic acid, tartaric acid, succinic acid, malonic acid, glutaric acid, malic acid, and acetic acid) that can lower the pH of the soil solution and facilitate solubilization (Patel and Saraf, 2017). In addition, some inorganic acids such as sulfuric acid, nitric acid, carbonic acid, and hydrochloric acid also contribute significantly to phosphate solubilization (Rawat et al., 2021). Mineralization of organic phosphates also occurs through the hydrolysis of phosphate esters by excreted extracellular enzymes such as acid and alkaline phosphatases, phytases, phosphatases, and C-P lysases (Alori et al., 2017). Strains belonging to the genera *Bacillus, Pseudomonas, Enterobacter, Rhizobium, Arthrobacter*, and *Burkholderia* are found the most efficient at promoting plant growth (Jha and Saraf, 2015; Islam et al., 2016; Kang et al., 2019). Their role in phosphate solubilization reduces the dependency on phosphatic fertilizers while minimizing environmental contamination. Plant growth promotion and increased phosphorous availability with the inoculation of phosphate-solubilizing bacteria have been assessed under green-house and field conditions; some are listed in Table 2.

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Phosphate-solubilizing microorganisms	Host plant	Plant growth promotion	References
Pseudomonas spp. JP233	Zea mays	Reduce Pleachate loss, improve Pabsorption and use of soil available P	Yu et al. (2022)
Bacillus aryabhattai B8W22	Zea mays + Glycine max	Improve the plant growth, available P content and plant P uptake	Song et al. (2021)
Pseudomonas sp., Burkholderia sp., Paraburkholderia sp., Novosphingobium sp., Ochrobactrum sp.	Cunninghamia lanceolata (Chinese fr.)	Increased plant height, stem diameter and the biomass of roots, stems and leaves, increased total N, total P, total K, Mg and Fe contents in leaf	Chen et al. (2021)
Pseudomonas putida, Pseudomonas fluorescens, Bacillus subtilis	Sorghum bicolor	Increased plant growth as well as the content of Mn, Zn, Cu, and K	Abbaszadeh-Dahaji et al. (2020)
Bacillus xiamenensis PM14	Saccharum officinarum	Suppress red rot disease symptoms in sugarcane and enhance plant growth	Amna et al. (2020)
Bacillus subtilis 320	Zea mays	Improve yield and P in the plants	Lobo et al. (2019)
Azospirilum brasilense, P. fluorescens	Zea mays	Improved grain yield	Di Salvo et al. (2018)

Table 2. Plant growth promoting phosphate solubilizing bacteria with their host plants.

PGPR, plant growth-promoting rhizobacteria.

PGPR induces siderophore production

Siderophores are high-affinity microbial iron-chelating low molecular weight (< 1.5 kDa) compounds that are metabolites of PGPR released into iron-limited rhizospheric soil (Khan et al., 2018; Wang et al., 2022). Siderophores produced by some PGPR can scavenge micronutrients such as iron, discouraging pathogenic microorganisms from maintaining their nutrition thereby reducing disease incidence (Saharan and Nehra, 2011). These PGPRs in the rhizosphere can increase the rate of Fe^{3+} availability, enabling absorption by plants (Kramer et al., 2020). These siderophilic bacteria are major assets to plants as they maintain and provide iron (Khan et al., 2018). *Bacillus* spp. are highly regarded in this context because they can produce different siderophores that maintain ionic balance and suppress the iron requirements of pathogenic microorganisms

(Radhakrishnan et al., 2017). Wang et al. (2022) that isolated 21 siderophilic bacterial species from the rhizosphere of Paris polyphylla var, yunnanensis found that Bacillus spp, were the dominant species. In addition, Xu et al. (2020) reported that siderophore-producing pathogenic bacteria such as Mycobacterium tuberculosis cause severe tissue damage and bleeding through the continuous chelation of their host's iron.

PGPR regulates certain phytohormones

Certain bacteria stimulate plant growth by producing various substances, such as growth-stimulating phytohormones (Numan et al., 2018). Phytohormones are biochemical molecules that regulate various functions in plants (Miransari, 2014). They can stimulate the physiological activities of plants even at low concentrations (Hayat et al., 2012). Among the known phytohormones, auxins, such as indole-3-butyric acid (IBA), indole-3-acetic acid (IAA), cytokinins, gibberellic acid (GA₃), ethylene, and abscisic acid (ABA) have been extensively studied for their ability to enhance plant growth and development (dos Santos et al., 2020). IAA is the most common and widely studied auxin and is produced by more than 80% of bacteria isolated from the rhizosphere (dos Santos et al., 2020). IAA induces the growth and development of different plant parts, including stems, leaves, flowers, and roots (Phillips et al., 2011). It stimulates the mortification, elongation, and differentiation of plant cells, germination of seeds and tubers, pigment formation, metabolite biosynthesis, formation of lateral roots in dicotyledons, and formation of adventitious roots in monocotyledons. IAA can loosen cell walls and facilitate root exudation, which ultimately enhances the uptake of additional nutrients. This is further facilitated by the increased surface area and length of the roots, although higher concentrations of IAA may negatively affect plant root growth (Glick, 2012; Duca et al., 2014). Azospirillum brasilense, Pantoea rodasii LGM 26273, Enterobacter ludwigii DSM 16688, Enterobacter hormaechei ATCC 49162, Burkholderia phytofirmans, and Bacillus subtilis are efficient plant-growth-promoting bacterial species that synthesize IAA (Walpola and Arunakumara, 2015; Patel et al., 2016; Poupin et al., 2016).

Cytokinins and gibberellins are two others important phytohormones that are produced by rhizobacteria. Zeatin and kinetin are relatively abundant cytokinins (O'Brien and Benkova, 2013). Cytokinins stimulate shoot formation, root development, and cell division while regulating plant growth (Jha and Saraf, 2015; Khan et al., 2018). The combined effects of cytokinins and auxins are important for meristem function, root architecture, reproductive organ development, and lateral organ development in the shoots (Schaller et al., 2015). Gibberalins are involved in seed germination, shoot growth, flowering, and fruit setting (Saleem et al., 2015). They regulate the size of the root and leaf meristems (Martínez et al., 2018). Ethylene is another well-known hormone and the simplest molecule that can enhance plant biological activity (Glick, 2012). Table 3 depicts the different phytohormones produced by PGPR.

PGPR	Phytohormones	References	
Bacillus tequilensis SSB07	Gibberellins GA ₁ , GA ₃ , GA ₅ , GA ₈ , GA ₁₉ , GA ₂₄ , GA ₅₃ , indole-3- acetic acid, abscisic acid	Kang et al. (2019)	
Lysinibacillus sphaericus	Indole-3-acetic acid	Breedt et al. (2017)	
Pseudomonas stutzeri, Stenotrophomonas maltophilia, P. putida	Indole-3-acetic acid, gibberellic acid, Cytokinins	Patel et al. (2016)	
Azospirillum lipoferum	Abscisic acid	Cohen et al. (2009)	

Table 3. Phytohormone produced by plant growth promoting rhizobacteria

GPR, plant growth-promoting rhizobacteria

PGPRs act as biological control agents

Rhizobacteria can act as bio-control agents to alleviate various pathogenic diseases and are widely regarded as environmentally-friendly approaches (Qiao et al., 2017). PGPR facilitates antagonistic interactions between pathogens and bio-control agents (Table 4). The induction of host resistance is another mechanism by which PGPR protects plants (Singh, 2013). As bio-control agents, PGPR is effective in suppressing diseases in living plants, but their role in minimizing postharvest diseases was also reported (Lugtenberg and Kamilova, 2009). Several bacterial genera, including Pseudomonas, Bacillus, Burkholderia, Streptomyces, and Agrobacterium, have been studied for their ability to act as bio-control agents. They could suppress plant diseases by inducing systemic resistance and producing siderophores, bacteriocins, hydrolytic enzymes, antibiotics, or other hydrolytic enzymes (Umer et al., 2021). The most widely recognized mechanism by which PGPR can suppress disease is by producing metabolites that can directly act on pathogens since they compete with pathogens for nutrients and specific niches in the roots (Figueiredo et al., 2010). Some anti-fungal metabolites, such as antibiotics, hydrogen cyanide, and fungal cell wall-lysing enzymes can improve plant growth by suppressing phytopathogens. Siderophores chelate iron, making it unavailable to pathogens. Additionally, they can induce systemic resistance (Singh, 2013). As reported Saharan and Nehra (2011), the growth of pathogens can be suppressed by PGPR through the antibiotic production. The use of PGPRs as bio-control agents is summarized in Table 4. A wide range of fungal diseases can be managed using PGPR and bacterial endophytes; however, an appropriate delivery system has yet to be established Singh (2013). Table 4 also summarizes the fungicidal activities of PGPRs.

PGPR and PGPF	Activity as the bio-control agent	References
Candida lusitaniae Cl-28,	Reduced post-harvest and wilt diseases severity caused by Penicillium expansum in	Fernandez-San Millan et al.
Candida oleophila Co-13,	grape and apple plants	(2021)
Debaryomyces hansenii Dh-67,		
Hypopichia pseudoburtonii Hp-54		
Trichoderma spp.	Suppressed downy mildew disease caused by Sclerospora graminicola in pearl millet	Nandini et al. (2021)
Azotobacter chroococcum,	Exert adverse effects on life history and population dynamics of two-spotted spider mites	Hosseini et al. (2021)
Azospirillum brasilense,	in above ground tissue of strawberry plants	
Pseudomonas brassicacearum		
Bacillus amyloliquefaciens B10W10,	Controlled brown rot disease caused by Monilinia fructigena in apple	Lahlali et al. (2020)
Pseudomonas spp. B11W11,		
Bacillus amyloliquefaciens B10W10,		
Pseudomonas spp. B11W11		
Pantoa agglomerans ACBP2,	Inhibit fire blight caused by Erwinia amylovora in apple plants	Bahadou et al. (2018)
Bacillus amyloliquefaciens LMR2,		
Brevibacterium. halotolerans (SF3, SF4),		
Bacillus mojarvensis SF16		
Pseudomonas fluorescens PF15,	Reduce disease incidence of Fusarium wilt in tomato	Boukerma et al. (2017)
P. putida PP27		
Methylobacterium aminovorans,	Biocontrol of Rhizoctonia Solani in Soybean seedlings	Omara et al. (2017)
Methylobacterium rhodinum,		
Bradyrhizobium japonicum St. 110,		
Bacillus megaterium var. phosphaticum,		
Trichoderma viride		
Bacillus subtilis LHS11 and FX2	Biocontrol agents in rapeseed plants rapeseed plants against Sclerotinia sclerotiorum	Sun et al. (2017)
Pseudomonas stutzeri,	Suppression of the pathogen Phytophthora capsici in cucumber plants	Islam et al. (2016)
Bacillus subtilis,		
Stenotrophomonas maltophilia,		
Bacillus amyloliquefaciens		

Table 4. PGPR as bio-control agents against plant diseases.

PGPR, plant growth-promoting rhizobacteria; PGPF, plant growth-promoting fungi.

PGPRs act as biotic elicitors

Elicitors are chemicals or biofactors of diverse origins (Glick, 2012; Breedt et al., 2017; Chu et al., 2019; Ghani et al., 2022). They induce physiological and morphological alterations in the targeted living creatures (Sekar and Kandavel, 2010). As stated by Bhattacharyya and Jha (2012), the accumulation of phytoalexin in plants could be triggered by elicitors. Furthermore, they augment the physiological and morphological responses of plants. Abiotic elicitors include inorganic compounds and metal ions, while biotic elicitors include chemicals released by plants, fungi, bacteria, and viruses. Biotic elicitors display an array of defense mechanisms, as they can induce the secretion of defensive bioactive molecules, such as phytoalexins (Bhattacharyya and Jha, 2012). A range of metabolites, including picrocrocin, ajmalicine, hyoscyamine, serpentine, crocetin, and scopolamine, have been reported to be produced by PGPR. These metabolites elicit both physiological and morphological responses in plants (Bhattacharyya and Jha, 2012).

PGPR is used for rhizoremediation

Under contaminated soil conditions, inoculation with PGPR strains has been shown to assist plant growth and development; hence, the application of PGPRs for rhizoremediation is very effective in polluted soils (Table 5). Degradation of organic pollutants can be facilitated with the use of PGPR rhizo-remediers (Saharan and Nehra, 2011). PGPR and arbuscular mycorrhizal fungi have been reported to be effective in enhancing the solubility of certain heavy metals in nutrient-deficient agricultural soils (Bhattacharyya and Jha, 2012).

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PGPR	Pollutants	Rhizoremediation activity	References
Enterobacter cloacae MUG75	Agricultural area with repeated application of profenofos	Degraded 90% profenofos	Ghani et al. (2022)
Enterobacter cloacae	Soil samples polluted with crude oil	Hydrocarbon biodegradation	Ejaz et al. (2021)
Pseudomonas baetica B2, Pseudomonas moraviensis B1	Mercury-contaminated soils	In situ phy to-rhizoremediation m ercury- contaminated soils.	Gonzalez et al. (2021)
Bacillus spp. PRB101	Endosulfan	Increase the deconta mination of endosulfan stressed soil and decline endosulfan concentration in the plant tissues.	Rani et al. (2021)
Micrococcus luteus	As (III)	Decrease of NaAsO ₂ toxic effect in <i>in</i> vitro grapevines inoculated with <i>M. luteus</i>	Pinter et al. (2017)
Alcaligenes feacalis RZS2, Pseudomonas a eruginosa RZS3	Heavy metal contaminated soil	Bioremediation of heavy metal ions like MnCl ₂ .4H ₂ O, NiCl ₂ .6H ₂ O, ZnCl ₂ , CuCl ₂ , CoCl ₂	Patel et al. (2016)
Pseudomonas aeruginosa, Bacillus subtilis, Acinetobacter lwoffii	Egyptian crude oil	Bioremediation of oils spills individually	Al-Wasify and Aboelwafa (2009)

Table 5. Plant growth promoting rhizobacteria as bioremediation agents.

PGPR, plant growth-promoting rhizobacteria.

PGPRs act as multifunctional agents

The effectiveness of PGPR has been reported to differ according to the growing conditions of the crops; thus, the intended outcome is sometimes difficult to achieve (Ahemad and Kibret, 2014). *Azospirillum* sp. can withstand a certain degree of salinity or osmolarity, as the species can accumulate compatible salts and exhibit osmoadaptation (Saharan and Nehra, 2011). As reported by Saharan and Nehra (2011), *Pseudomonas. fluorescens* can withstand a certain level of drought and

hyperosmolarity. PGPRs are ideal candidates for organic agriculture, where using synthetic plant growth regulators has been prohibited Singh (2013). Once seeds are inoculated before planting, PGPR is generally established in the rhizosphere of the crop Saharan and Nehra (2011).

Conclusion

Excessive use of inorganic fertilizers and pesticides for improved agricultural production severely contributes to the deterioration of soil fertility and negatively impacts the environment. This has become a matter of great concern, and there is an urgent need for alternative strategies to address these issues. Therefore, the use of plant-growth-promoting rhizobacteria to enhance soil fertility and plant growth via various mechanisms is vital. This review highlights the practical significance of PGPR, which can be effectively used in sustainable agriculture as biofertilizers and biocontrol agents for many crop species. However, it is important to note that specific studies have reported negative effects on soil health and plant growth when using PGPR under saline conditions. Therefore, further research is required to assess their performance under varying field conditions with specific crop species to broaden their application in sustainable agriculture.

Conflict of Interests

No potential conflict of interest relevant to this article was reported.

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References

Abbaszadeh-Dahaji P, Masalehi F, Akhgar A. 2020. Improved growth and nutrition of sorghum (*Sorghum bicolor*) plants in a low-fertility calcareous soil treated with plant growth-promoting rhizobacteria and Fe-EDTA. Journal of Soil Science and Plant Nutrition 20:31-42.

- Abd El-Mageed TA, Abd El-Mageed SA, El-Saadony MT, Abdelaziz S, Abdou NM. 2022. Plant growth-promoting rhizobacteria improve growth, morph-physiological responses, water productivity, and yield of rice plants under full and deficit drip irrigation. Rice 15:16.
- Ahemad M, Kibret M. 2014. Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. Journal of King Saud University-Science 26:1-20.
- Al-Wasify RS, Aboelwafa AM. 2009. Biodegradation of crude oil using local isolates. Australian Journal of Basic and Applied Sciences 3:4742-4751
- Alori ET, Glick BR, Babalola OO. 2017. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. Frontiers in Microbiology 8:971.
- Amna, Xia Y, Farooq MA, Javed MT, Kamran MA, Mukhtar T, Ali J, Tabassum T, Rehman SU, Munis MFH, et al. 2020. Multi-stress tolerant PGPR *Bacillus xiamenensis* PM14 activating sugarcane (*Saccharum officinarum* L.) red rot disease resistance. Plant Physiology and Biochemistry 151:640-649.
- Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, Subramanian S, Smith DL. 2018. Plant growthpromoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Frontiers in Plant Science 9:1473.
- Bahadou SA, Ouijja A, Karfach A, Tahiri A, Lahlali R. 2018. New potential bacterial antagonists for the biocontrol of fire blight disease (*Erwinia amylovora*) in Morocco. Microbial Pathogenesis 117:7-15.
- Bennis M, Perez-Tapia V, Alami S, Bouhnik O, Lamin H, Abdelmoumen H, Bedmar EJ, El Idrissi MM. 2022. Characterization of plant growth-promoting bacteria isolated from the rhizosphere of *Robinia pseudoacacia* growing in metal-contaminated mine tailings in Eastern Morocco. Journal of Environmental Management 304:114321.
- Bhatt MK, Labanya R, Joshi HC. 2019. Influence of long-term chemical fertilizers and organic manures on soil fertility-A review. Universal Journal of Agricultural Research 7:177-188.
- Bhattacharyya PN, Jha DK. 2012. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. World Journal of Microbiology and Biotechnology 28:1327-1350.
- Boukerma L, Benchabane M, Charif A, Khélifi L. 2017. Activity of plant growth promoting rhizobacteria (PGPRs) in the biocontrol of tomato Fusarium wilt. Plant Protection Science 53:78-84.
- Breedt G, Labuschagne N, Coutinho TA. 2017. Seed treatment with selected plant growth-promoting rhizobacteria increases maize yield in the field. Annals of Applied Biology 171:229-236.
- Chen J, Zhao G, Wei Y, Dong Y, Hou L, Jiao R. 2021. Isolation and screening of multifunctional phosphate solubilizing bacteria and its growth-promoting effect on Chinese fir seedlings. Scientific Reports 11:9081.
- Chu TN, Tran BTH, Van Bui L, Hoang MTT. 2019. Plant growth-promoting rhizobacterium *Pseudomonas* PS01 induces salt tolerance in *Arabidopsis thaliana*. BMC Research Notes 12:11.
- Cohen AC, Travaglia CN, Bottini R, Piccoli PN. 2009. Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. Botany 87:455-462.
- Costa-Gutierrez SB, Lami MJ, Santo MCCD, Zenoff AM, Vincent PA, Molina-Henares MA, Espinosa-Urgel M, de Cristóbal RE. 2020. Plant growth promotion by *Pseudomonas putida* KT2440 under saline stress: Role of *eptA*. Applied Microbiology and Biotechnology 104:4577-4592.
- Di Salvo LP, Cellucci GC, Carlino ME, de Salamone IEG. 2018. Plant growth-promoting rhizobacteria inoculation and nitrogen fertilization increase maize (*Zea mays* L.) grain yield and modified rhizosphere microbial communities. Applied Soil Ecology 126:113-120.
- dos Santos RM, Diaz PAE, Lobo LLB, Rigobelo EC. 2020. Use of plant growth-promoting rhizobacteria in maize and sugarcane: Characteristics and applications. Frontiers in Sustainable Food Systems 4:136.
- Duca D, Lorv J, Patten CL, Rose D, Glick BR. 2014. Indole-3-acetic acid in plant-microbe interactions. Antonie Van Leeuwenhoek 106:85-125.
- Ejaz M, Zhao B, Wang X, Bashir S, Haider FU, Aslam Z, Khan MI, Shabaan M, Naveed M, Mustafa A. 2021. Isolation and characterization of oil-degrading *Enterobacter* sp. from naturally hydrocarbon-contaminated soils and their potential use against the bioremediation of crude oil. Applied Sciences 11:3504.

- FAO (Food and Agricultural Organization of the United Nations). 2023. Sustainable agricultural practices. Accessed in https://www.fao.org/agriculture/crops/thematic-sitemap/theme/spi/soil-biodiversity/agriculture-and-soil-biodiversity/sustainable-agricultural-practices/en/ on 30 October 2023.
- Fernandez-San Millan A, Larraya L, Farran I, Ancin M, Veramendi J. 2021. Successful biocontrol of major postharvest and soil-borne plant pathogenic fungi by antagonistic yeasts. Biological Control 160:104683.
- Figueiredo MDVB, Seldin L, Araujo FFD, Mariano RDLR. 2010. Plant growth promoting rhizobacteria: Fundamentals and applications. Plant Growth and Health Promoting Bacteria. pp. 21-43. Springer, Berlin, Heidelberg, Germany.
- Gatiboni L, Brunetto G, Pavinato PS, George TS. 2020. Editorial: Legacy phosphorus in agriculture: Role of past management and perspectives for the future. Frontiers in Earth Science 8:619935.
- Ghani MU, Asghar HN, Niaz A, Zahir ZA, Nawaz MF, Häggblom MM. 2022. Efficacy of rhizobacteria for degradation of profenofos and improvement in tomato growth. International Journal of Phytoremediation 24:463-473.
- Glick BR. 2012. Plant growth-promoting bacteria: Mechanisms and applications. Scientifica 2012:963401.
- González D, Blanco C, Probanza A, Jiménez PA, Robas M. 2021. Evaluation of the PGPR capacity of four bacterial strains and their mixtures, tested on *Lupinus albus* var. Dorado seedlings, for the bioremediation of mercury-polluted soils. Processes 9:1293.
- Gopalakrishnan S, Srinivas V, Samineni S. 2017. Nitrogen fixation, plant growth and yield enhancements by diazotrophic growth-promoting bacteria in two cultivars of chickpea (*Cicer arietinum* L.). Biocatalysis and Agricultural Biotechnology 11:116-123.
- Goswami D, Thakker JN, Dhandhukia PC. 2016. Portraying mechanics of plant growth promoting rhizobacteria (PGPR): A review. Cogent Food and Agriculture 2:1127500.
- Guo Y, Ren C, Yi J, Doughty R, Zhao F. 2020. Contrasting responses of rhizosphere bacteria, fungi and arbuscular mycorrhizal fungi along an elevational gradient in a temperate montane forest of China. Frontiers in Microbiology 11:2042.
- Gupta A, Bano A, Rai S, Kumar M, Ali J, Sharma S, Pathak N. 2021. ACC deaminase producing plant growth promoting rhizobacteria enhance salinity stress tolerance in *Pisum sativum*. 3 Biotech 11:514.
- Hayat R, Ahmed I, Sheirdil RA. 2012. An overview of plant growth promoting rhizobacteria (PGPR) for sustainable agriculture. Crop Production for Agricultural Improvement. pp. 557-579. Springer, Dordrecht, Netherlands.
- Hosseini A, Hosseini M, Schausberger P. 2021. Plant growth promoting rhizobacteria enhance defense of strawberry plants against spider mites. Frontiers in Plant Science 12:783578.
- Islam S, Akanda AM, Prova A, Islam MT, Hossain MM. 2016. Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect on plant growth promotion and disease suppression. Frontiers in Microbiology 6:1360.
- Jha CK, Saraf M. 2015. Plant growth promoting rhizobacteria (PGPR): A review. E3 Journal of Agricultural Research and Development 5:108-119.
- Kang SM, Khan AL, Waqas M, Asaf S, Lee KE, Park YG, Kim AY, Khan MA, You YH, Lee IJ. 2019. Integrated phytohormone production by the plant growth-promoting rhizobacterium *Bacillus tequilensis* SSB07 induced thermotolerance in soybean. Journal of Plant Interactions 14:416-423.
- Khalid A, Arshad M, Zahir ZA. 2004. Screening plant growth-promoting rhizobacteria for improving growth and yield of wheat. Journal of Applied Microbiology 96:473-480.
- Khan A, Singh P, Srivastava A. 2018. Synthesis, nature and utility of universal iron chelator-Siderophore: A review. Microbiological Research 212-213:103-111.
- Kramer J, Özkaya Ö, Kümmerli R. 2020. Bacterial siderophores in community and host interactions. Nature Reviews Microbiology 18:152-163.
- Lahlali R, Mchachti O, Radouane N, Ezrari S, Belabess Z, Khayi S, Mentag R, Tahiri A, Barka EA. 2020. The potential of novel bacterial isolates from natural soil for the control of brown rot disease (*Monilinia fructigena*) on apple fruits. Agronomy 10:1814.
- Lin S, Litaker RW, Sunda WG. 2016. Phosphorus physiological ecology and molecular mechanisms in marine phytoplankton. Journal of Phycology 52:10-36.

- Liu J, Zhang J, Zhu M, Wan H, Chen Z, Yang N, Duan J, Wei Z, Hu T, Liu F. 2022. Effects of plant growth promoting rhizobacteria (PGPR) strain *Bacillus licheniformis* with biochar amendment on potato growth and water use efficiency under reduced irrigation regime. Agronomy 12:1031.
- Lobo LLB, dos Santos RM, Rigobelo EC. 2019. Promotion of maize growth using endophytic bacteria under greenhouse and field conditions. Australian Journal of Crop Science 13:2067-2074.

Lugtenberg B, Kamilova F. 2009. Plant-growth-promoting rhizobacteria. Annual Review of Microbiology 63:541-556.

- Lyu D, Backer R, Smith DL. 2022. Three plant growth-promoting rhizobacteria alter morphological development, physiology, and flower yield of *Cannabis sativa* L. Industrial Crops and Products 178:114583.
- Mansour E, Mahgoub HAM, Mahgoub SA, El-Sobky ESEA, Abdul-Hamid MI, Kamara MM, AbuQamar SF, El-Tarabily KA, Desoky ESM. 2021. Enhancement of drought tolerance in diverse *Vicia faba* cultivars by inoculation with plant growth-promoting rhizobacteria under newly reclaimed soil conditions. Scientific Reports 11:24142.
- Martínez C, Espinosa-Ruiz A, Prat S. 2018. Gibberellins and plant vegetative growth. Annual Plant Reviews, Volume 49. In The gibberellins edited by Hedden P, Thomas SG. pp. 285-322. John Wiley & Sons Ltd., New Jersey, USA.

Miransari M. 2014. Plant growth promoting rhizobacteria. Journal of Plant Nutrition 37:2227-2235.

- Nandini B, Puttaswamy H, Saini RK, Prakash HS, Geetha N. 2021. Trichovariability in rhizosphere soil samples and their biocontrol potential against downy mildew pathogen in pearl millet. Scientific Reports 11:9517.
- Nosheen A, Bano A. 2014. Potential of plant growth promoting rhizobacteria and chemical fertilizers on soil enzymes and plant growth. Pakistan Journal of Botany 46:1521-1530.
- Numan M, Bashir S, Khan Y, Mumtaz R, Shinwari ZK, Khan AL, Khan A, Al-Harrasi A. 2018. Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: A review. Microbiological Research 209:21-32.
- O'Brien JA, Benkova E. 2013. Cytokinin cross-talking during biotic and abiotic stress responses. Frontiers in Plant Science 4:451.
- Omara A, Hauka F, Afify A, Nour El-Din M, Kassem M. 2017. The role of some PGPR strains to biocontrol *Rhizoctonia solani* in soybean and enhancement the growth dynamics and seed yield. Environment. Biodiversity and Soil Security 1:47-59.
- Pappas ML, Samaras K, Koufakis I, Broufas GD. 2021. Beneficial soil microbes negatively affect spider mites and aphids in pepper. Agronomy 11:1831.
- Patel PR, Shaikh SS, Sayyed RZ. 2016. Dynamism of PGPR in bioremediation and plant growth promotion in heavy metal contaminated soil. Indian Journal of Experimental Biology 54:286-290.
- Patel T, Saraf M. 2017. Biosynthesis of phytohormones from novel rhizobacterial isolates and their in vitro plant growth-promoting efficacy. Journal of Plant Interactions 12:480-487.
- Pérez-Montaño F, Alías-Villegas C, Bellogín RA, del Cerro P, Espuny MR, Jiménez-Guerrero I, López-Baena FJ, Ollero FJ, Cubo T. 2014. Plant growth promotion in cereal and leguminous agricultural important plants: From microorganism capacities to crop production. Microbiological Research 169:325-336.
- Phillips KA, Skirpan AL, Liu X, Christensen A, Slewinski TL, Hudson C, Barazesh S, Cohen JD, Malcomber S, McSteen P. 2011. *Vanishing tassel2* encodes a grass-specific tryptophan aminotransferase required for vegetative and reproductive development in maize. The Plant Cell 23:550-566.
- Pinter IF, Salomon MV, Berli F, Bottini R, Piccoli P. 2017. Characterization of the As (III) tolerance conferred by plant growth promoting rhizobacteria to *in vitro*-grown grapevine. Applied Soil Ecology 109:60-68.
- Poupin MJ, Greve M, Carmona V, Pinedo I. 2016. A complex molecular interplay of auxin and ethylene signaling pathways is involved in *Arabidopsis* growth promotion by *Burkholderia phytofirmans* PsJN. Frontiers in Plant Science 7:492.
- Qiao J, Yu X, Liang X, Liu Y, Borriss R, Liu Y. 2017. Addition of plant-growth-promoting *Bacillus subtilis* PTS-394 on tomato rhizosphere has no durable impact on composition of root microbiome. BMC Microbiology 17:131.
- Radhakrishnan R, Hashem A, Abd_Allah EF. 2017. *Bacillus*: A biological tool for crop improvement through biomolecular changes in adverse environments. Frontiers in Physiology 8:667.
- Rani R, Kumar V, Gupta P, Chandra A. 2021. Potential use of *Solanum lycopersicum* and plant growth promoting rhizobacterial (PGPR) strains for the phytoremediation of endosulfan stressed soil. Chemosphere 279:130589.

- Rawat P, Das S, Shankhdhar D, Shankhdhar SC. 2021. Phosphate solubilizing microorganisms: Mechanism and their role in phosphate solubilization and uptake. Journal of Soil Science and Plant Nutrition 21:49-68.
- Sagbara G, Zabbey N, Sam K, Nwipie GN. 2020. Heavy metal concentration in soil and maize (*Zea mays* L.) in partially reclaimed refuse dumpsite 'borrow-pit' in Port Harcourt, Nigeria. Environmental Technology & Innovation 18:100745.
- Saharan BS, Nehra V. 2011. Plant growth promoting rhizobacteria: A critical review. Life Sciences and Medicine Research 21:1-30.
- Saleem M, Asghar HN, Khan MY, Zahir ZA. 2015. Gibberellic acid in combination with pressmud enhances the growth of sunflower and stabilizes chromium (VI)-contaminated soil. Environmental Science and Pollution Research 22:10610-10617.
- Schaller GE, Bishopp A, Kieber JJ. 2015. The yin-yang of hormones: cytokinin and auxin interactions in plant development. The Plant Cell 27:44-63.
- Sekar S, Kandavel D. 2010. Interaction of plant growth promoting rhizobacteria (PGPR) and endophytes with medicinal plants-New avenues for phytochemicals. Journal of Phytology 2:91-100.
- Singh JS. 2013. Plant growth promoting rhizobacteria. Resonance 18:275-281.
- Song C, Wang W, Gan Y, Wang L, Chang X, Wang Y, Yang W. 2021. Growth promotion ability of phosphate-solubilizing bacteria from the soybean rhizosphere under maize-soybean intercropping systems. Journal of the Science of Food and Agriculture 102:1430-1442.
- Sun G, Yao T, Feng C, Chen L, Li J, Wang L. 2017. Identification and biocontrol potential of antagonistic bacteria strains against *Sclerotinia sclerotiorum* and their growth-promoting effects on *Brassica napus*. Biological Control 104:35-43.
- Tabassum B, Khan A, Tariq M, Ramzan M, Khan MSI, Shahid N, Aaliya K. 2017. Bottlenecks in commercialisation and future prospects of PGPR. Applied Soil Ecology 121:102-117.
- Umer M, Mubeen M, Iftikhar Y, Shad MA, Usman HM, Sohail MA, Atiq MN, Abbas A, Ateeq M. 2021. Role of rhizobacteria on plants growth and biological control of plant diseases: A review. Plant Protection 5:59-73.
- UN (United Nations). 2019. World population prospects 2019. Highlights. ST/ESA/SER.A/423. Accessed in https:// www.un.org/en/desa on 17 August 2022.
- Verma JP, Yadav J, Tiwari KN, Lavakush, Singh V. 2010. Impact of plant growth promoting rhizobacteria on crop production. International Journal of Agricultural Research 5:954-983.
- Walpola BC, Arunakumara KKIU. 2015. Assessment of phosphate solubilization and indole acetic acid production in plant growth promoting bacteria isolated from green house soils of Gonju-Gun, South Korea. Tropical Agricultural Research and Extension 18:31-39.
- Walpola BC, Yoon MH. 2012. Prospectus of phosphate solubilizing microorganisms and phosphorus availability in agricultural soils: A review. African Journal of Microbiology Research 6:6600-6605.
- Wang Y, Zhang G, Huang Y, Guo M, Song J, Zhang T, Long Y, Wang B, Liu H. 2022. A potential biofertilizer—Siderophilic bacteria isolated from the rhizosphere of *Paris polyphylla* var. *yunnanensis*. Frontiers in Microbiology 13:870413.
- Xu C, Lin P, Sun L, Chen H, Xing W, Kamalanathan M. 2020. Micolecular nature of marine particulate organic iron-carrying moieties revealed by electrospray ionization fourier transform ion cyclotron resonance mass spectrometry (ESI-FTICRMS). Frontiers in Earth Science 8:266.
- Yu H, Wu X, Zhang G, Zhou F, Harvey PR, Wang L, Fan S, Xie X, Li F, Zhou H, Zhao X. 2022. Identification of the phosphorus solubilizing bacteria strain JP233 and its effects on soil phosphorus leaching loss and crop growth. Frontiers in Microbiology 13:892533-892533.