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Mechanistic insights into plant growth promoting rhizobacteria with focus on root soil interactions, functional attributes and agricultural sustainability

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Abstract

Plant growth promoting rhizobacteria (PGPR) are beneficial microorganisms that play a crucial role in enhancing crop growth, productivity and resilience to environmental stresses. They colonize the root zone of plants, forming a symbiotic relationship that benefits both the plants and the microorganisms. In recent years, understanding the mechanisms by which PGPR influence plant growth and exploring their potential in sustainable agricultural practices has been the center of attention for the scientific community. Acting as bioinoculants, PGPR improve plant health through various mechanisms, including nutrient solubilization, hormone production and induction of systemic resistance against pathogens. PGPR are receiving a considerable attention because of the beneficial effects they offer, which can replace the utilization of chemical fertilizers, harmful pesticides and other supplements that are not appropriate for crop plants. Soil microbial communities are said to be a boon for agriculture because they play a pivotal role in the colonization of root-soil environments and carry out a wide variety of interactive activities. Furthermore, PGPR can alleviate biotic and abiotic stresses and help plants to survive, grow and develop under adverse conditions. This comprehensive review explores the multifaceted applications of PGPR in promoting crop development, increasing yield and improving stress tolerance, with a focus on drought, salinity and nutrient deficiency. In addition, the role of PGPR in advancing sustainable agriculture is discussed, highlighting its potential as an eco-friendly alternative to chemical fertilizers and pesticides. This review also examines the current challenges in PGPR application and suggests future research directions to optimize their use in modern farming systems. By integrating PGPR into sustainable agricultural practices, we can address global food security challenges while minimizing their environmental impacts.

Keywords PGPR, Rhizosphere, Abiotic stress, Biofertilizer, Sustainability

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1 Introduction

Agricultural sustainability is one of the most pressing global challenges today, with increasing demand for food production driven by a growing population and shrinking arable land. To meet rising agricultural demands, intensive farming is traditionally dependent on synthetic fertilizers and chemical inputs. While these practices have proven effective in increasing crop yields, they have also resulted in considerable environmental degradation, soil nutrient depletion, and a marked decline in biodiversity [1–3]. Consequently, the search for eco-friendly and sustainable alternatives has become a focal point for modern agriculture. In this context, plant growth promoting rhizobacteria (PGPR) have emerged as a promising solution, offering natural bioinoculants that enhance plant growth, productivity and resilience to environmental stresses.

PGPR are a diverse group of beneficial bacteria that colonize plant roots and establish symbiotic relationship with plants. These bacteria promote plant growth through several direct and indirect mechanisms including nutrient solubilization, production of plant hormones (auxins, gibberellins and cytokinins), nitrogen fixation and induction of systemic resistance against pathogens [4]. These microorganisms inhabit either the rhizosphere, the narrow soil zone influenced by root exudates or the root interior (endosphere), depending on their colonization strategy [5, 6]. Rhizospheric PGPR remain externally associated with roots forming close interactions through chemotaxis-driven movement towards root exudates. Whereas endophytic PGPR penetrate root tissues, colonize intercellular spaces and sometimes vascular tissues without causing harm [7, 8]. The ability of PGPR to establish successful colonization is influenced by multiple factors such as plant species, root exudate composition, soil type, and environmental conditions [9]. Once established, PGPR facilitate plant growth by promoting nutrient acquisition (e.g., nitrogen fixation, phosphate solubilization), producing phytohormones, mitigating biotic and abiotic stresses, and enhancing soil health [4, 10]. Understanding the colonization patterns of PGPR is therefore critical for optimizing their application as bioinoculants in sustainable agriculture.

The colonization of plant roots by PGPR is a multi-step process involving recognition, attachment, establishment, and proliferation, ultimately determining the extent and nature of plant-microbe interactions [7, 8]. Broadly, PGPR colonize either the rhizospheric zone or the endosphere and the localization of these bacteria influences both their mode of action and their efficacy. PGPR reside externally in the narrow region of soil influenced by root exudates. Root exudates contain amino acids, organic acids, sugars, and secondary metabolites that act as chemoattractants, guiding bacteria towards the root surface via chemotaxis [11, 12]. Once in proximity, bacteria adhere to the root epidermis through the production of extracellular polymeric substances (EPS), adhesins, and fimbriae. Rhizospheric colonizers often form biofilms which enhance persistence and stress tolerance, and facilitate continuous exchange of signaling molecules and metabolites with the plants [13]. Endophytic PGPR enter plant roots through natural openings (e.g., root hairs, cracks at lateral root emergence sites) or via enzymatic degradation of cell walls [6]. After entry, they colonize intercellular spaces and sometimes vascular tissues without eliciting pathogenic responses. Endophytes can spread systemically to aerial plant parts, providing benefits such as improved nutrient assimilation, enhanced stress resistance, and systemic induced resistance against pathogens [8, 14]. Successful colonization depends on host genotype, root architecture, and the

biochemical composition of root exudates, which vary with plant developmental stages and environmental conditions [9, 15]. Soil characteristics such as pH, moisture, and organic matter content also shape microbial community assembly. Additionally, the compatibility between bacterial traits (e.g., motility, EPS production, stress tolerance) and host physiology plays a critical role. The localization pattern determines the functional outcomes of PGPR. Rhizospheric colonizers primarily influence nutrient solubilization, pathogen suppression in the rhizosphere, and improvement of soil structure. Whereas endophytes can modulate plant metabolism more directly by producing phytohormones, fixing nitrogen within plant tissues, and priming systemic plant defense responses [4, 10]. Understanding these patterns enables targeted bioinoculant development and improving their consistency in field performance.

PGPR are highly effective in enhancing plant resilience to both biotic and abiotic stresses, such as drought, salinity and nutrient deficiencies [10]. By improving nutrient availability and stimulating root growth, PGPR not only enhance crop yield but also contribute to long-term soil health and fertility [16]. Microorganisms found in rhizospheric soil can be used as bioinoculants to overcome the problems associated with environmental stresses such as drought, salinity, flooding and anoxia [17]. The application of PGPR as bioinoculants has gained increasing attention because of their potential to reduce dependency on chemical inputs, promoting sustainable agricultural practices and mitigating the adverse effects of climate change on crop production [18]. These bioinoculants offer a viable alternative for achieving higher yields without compromising the soil integrity or environmental health. Studies have shown that inoculating crops with PGPR can improve water and nutrient uptake, enhance photosynthesis and increase plant biomass particularly under stressful conditions [19]. Despite their proven benefits, the widespread adoption of PGPR in agriculture is limited by several factors including variability in field performance, inconsistent results across different crops and challenges in formulation and application [20]. Therefore, further research is needed to optimize the use of PGPR in diverse agro-ecosystems, understand their interactions with plants and soil microbiomes, and develop cost-effective formulations that ensure their efficacy in field conditions. Climate change alters soil nutrient availability, modifies physicochemical properties, and disrupts microbial biodiversity ultimately impacting soil health. In combination with imbalanced nutrient management and the decline in soil organic matter, these changes significantly hamper crop productivity [21, 22]. Rhizobacteria play a crucial role in biogeochemical cycling and crop production enhancement. Rhizomicrobiomes are essential for agricultural crops because of the rich diversity of root exudates and plant cell debris that attracts a variety of microbes for colonization [23].

Plant growth promoting bacteria are associated with various plant species and are commonly found in diverse habitats. About 2–5% of the bacteria present in the rhizosphere have been found to promote plant growth and contribute to sustainable agriculture [24]. The interaction of PGPR with host plants is a complex and mutually dependent association which involves two partners along with environmental factors of the rhizosphere region [25]. A study has shown that there are a variety of noticeable PGPR that are capable of promoting the growth and development of several vegetable crops (like potato, onion and pepper). These PGPR generally belong to the genera *Bacillus*, *Azotobacter*, *Enterobacter*, *Pseudomonas*, and *Azospirillum* [26]. Consequently, various plant growth promoting rhizobacteria are being explored and literature suggests that PGPR

can serve as a boon for sustainable agriculture in the near future [27]. These microorganisms operate in an interlocked network and the different keystone species are also significant for plant-microbial interactions [28, 29]. This comprehensive review aims to provide insights into the role of PGPR as bioinoculants in enhancing crop growth, productivity and their functional attributes. It explores the underlying mechanisms through which PGPR promote plant health, evaluates their applications in sustainable agriculture, and highlights current challenges and future perspectives. By integrating PGPR into modern farming practices, we can contribute to global food security while minimizing the environmental impact of agriculture.

2 Rhizosphere and microbial diversity

The plant rhizosphere is composed of many microorganisms that influence plant physiology and morphology, thereby improving plant development through hormonal secretion and acting as plant pathogen protectants [30]. It is an important zone of soil that surrounds the plant roots, making it a hotspot for the richness and diversity of microorganisms. The plant rhizosphere also attracts bacteria from the soil environment [31]. Garcia et al. [32], defined rhizosphere as an immediate zone in the soil that surrounds the roots of a plant where intense chemical and biological parameters occur in a narrow sleeve around the root hair axes. The rhizosphere is the region where plant roots get influenced by strong microbial activity in the soil. It is the place where microorganisms can communicate with each other by exchanging different signalling molecules mainly through Quoram sensing [33]. This diversity is influenced by multiple factors including plant species, soil type, root exudates, and environmental conditions [34]. The rhizosphere plays an important role in fostering beneficial microbial communities that enhance nutrient uptake, suppress pathogen growth and improve plant stress tolerance. These interactions are driven largely by root exudates that are compounds released by plant roots into the surrounding soil, which provide nutrients for microorganisms and in turn help plants to access nutrients and defend themselves against environmental stresses [11]. Bacteria are the most abundant and functionally diverse microorganisms found in the rhizosphere. Many rhizobacteria, classified as PGPR stimulate plant growth via various mechanisms. They affect germination rate, drought tolerance and crop yield under adverse conditions. Because of the metabolites they produce, the use of microbes in agriculture for crop protection against plant pathogens and pests, as well as for biological disease control, could offer a viable option for plant disease control [35, 36]. Microorganisms present in the rhizosphere are vital for plant health and biogeochemical processes and redesigning the rhizosphere may eventually eliminate the usage of agrochemicals by replacing beneficial microbes for their roles. Understanding the community structure and variety of active microbes in the rhizosphere is therefore critical for improving plant development and agricultural output [37].

Because of the negative impacts of chemical fertilizers on the environment, PGPR bioinoculants, which are an important part of organic farming play a critical role in ensuring long-term soil fertility and sustainability. They are one of the most significant components and remarkable tools for sustainable agriculture. Likewise, the long-term use of biofertilizers containing PGPR is ecofriendly, economical, efficient, and productive [38–40]. The use of microbial inoculants has been studied to enhance sustainable agricultural production which is widely accepted practice in intensive cropping in

different parts of the world [40]. Studies have shown that different bacterial genera (such as *Acetobacter, Acinetobacter, Alcaligenes, Arthrobacter, Azoarcus, Azospirillum, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Derxia, Enterobacter, Gluconacetobacter, Herbaspirillum, Klebsiella, Ochrobactrum, Pantoae, Pseudomonas, Rhodococcus, Serratia, Stenotrophomonas, and Zoogloea*) are some of the prominent soil microorganisms that release inorganic nutrients from the organic reserves at a high rate that can sustain rapid plant growth [41].

The rhizosphere is one of the most important regions of soil bacteria that express beneficial plant activities (Fig. 1) [42]. Soil acts as a storehouse of microorganisms and approximately less than 5% of the total soil space is occupied by these bacteria. Some microorganisms have a huge potential for growth promotion in plants and also act as bio-control agents for pathogens [43]. In the soil, the most abundant and one of the major groups of microorganisms are bacteria that are present in rhizospheric soil ranging between 10^{-6} and 10^{-8} colony forming units (CFU) per gram. PGPR have been studied on a larger scale that colonize the root surface area and closely adhere to the soil interface in the rhizosphere [44].

Plant growth promotion through PGPR is mediated by the secretion and production of various substances due to the alteration of the microbial community present in the rhizospheric niche [45]. The use of these rhizobacteria is also helpful in augmenting the growth and stress tolerance of certain crops; therefore, it is a step towards attaining sustainable agriculture [46–50]. The microbial diversity in the rhizosphere plays a critical role in plant health and productivity. Moreover, the presence of diverse microbial

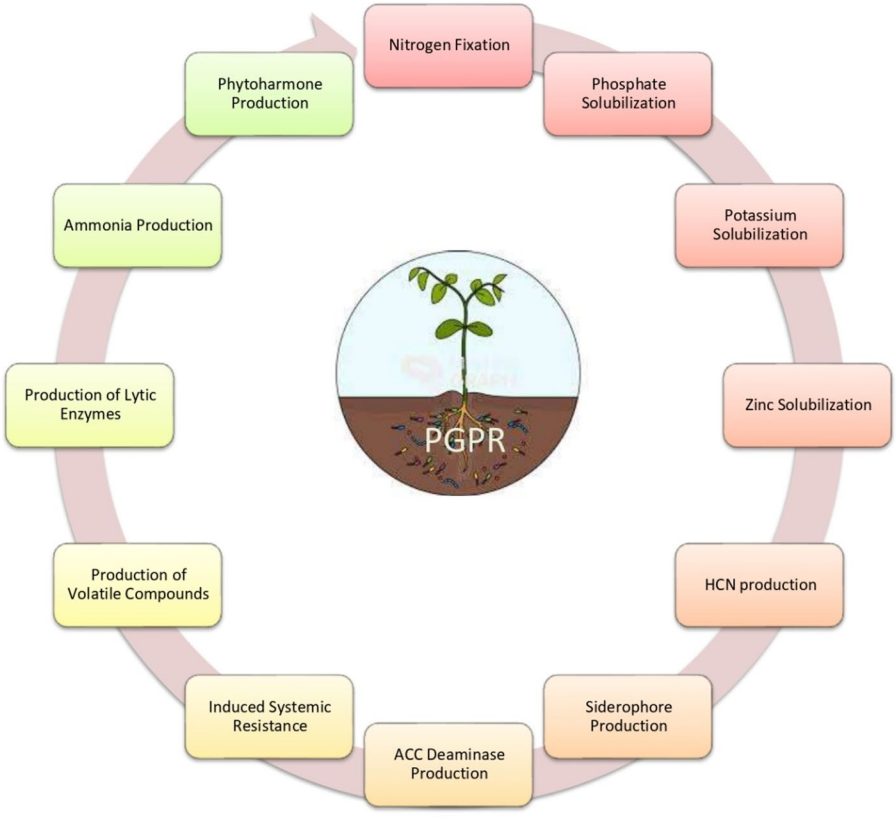


Fig. 1 Schematic representation of plant growth promoting traits exhibited by rhizobacteria

communities introduces functional redundancy, wherein multiple species are capable of performing similar ecological roles. This redundancy ensures that vital processes like nutrient cycling persists even when certain species are lost or disrupted by environmental changes [51]. Different microbial species possess specialized abilities to solubilize or fix a range of nutrients, thereby enhancing their availability for plant uptake and growth. For instance, phosphate-solubilizing bacteria convert insoluble phosphorus into forms that plants can absorb, whereas nitrogen-fixing bacteria provide nitrogen [52]. Microbial diversity also contributes to disease suppression by outcompeting pathogens for nutrients and space, thereby reducing the likelihood of pathogen colonization. Moreover, certain beneficial microorganisms produce antimicrobial compounds that inhibit pathogen growth and protect plants from diseases [53]. Under stressful conditions such as drought or nutrient deficiency, microbial diversity can enhance plant resilience. Certain PGPR help plants to tolerate abiotic stress by modulating hormonal levels, producing stress-relief enzymes and improving root architecture which allows for better water and nutrient uptake [54].

The microbial diversity in the rhizosphere is shaped by a complex interplay of plant, soil, and environmental factors. Plant root exudates, consisting of sugars, amino acids, organic acids, phenolic compounds, and various secondary metabolites act as a rich nutrient source that supports and stimulates microbial communities in the rhizosphere. The composition of root exudates can shape the microbial community by selectively promoting the growth of beneficial microbes while suppressing pathogens [11]. Different plant species produce distinct exudates which lead to unique microbial communities associated with each species. For example, legumes are known to associate with nitrogen-fixing bacteria such as *Rhizobium*, whereas grasses may host a higher diversity of mycorrhizal fungi [55]. Soil type and properties including soil texture, pH, moisture, and organic matter content also strongly influence the structure and diversity of microbial communities in the rhizosphere. Soils rich in organic matter tend to support higher microbial diversity, because organic matter provides a continuous supply of nutrients for microbes [34]. Similarly, soil pH affects the availability of nutrients and can determine the microbial species that thrive in the rhizosphere [56]. Environmental conditions such as temperature, moisture, and nutrient availability all affect microbial diversity. Microbial activity generally increases with temperature and moisture, leading to dynamic microbial communities in warm and moist environments. However, under stressful conditions such as drought or salinity, microbial diversity may decrease but specific stress-tolerant microbial populations may become dominant [57].

3 Underlying mechanisms of plant growth promoting rhizobacteria

Plant growth promoting rhizobacteria stimulate plant growth through both direct and indirect mechanisms (Fig. 2) [58]. They are pivotal for enhancing nutrient uptake, promoting root architecture, increasing stress tolerance and acting as biocontrol agents against plant pathogens. The use of PGPR in agriculture is a sustainable approach to increase crop yield while reducing the need for chemical inputs such as fertilizers and pesticides. Consequently, in the direct mechanism, rhizobacteria stimulate crop production by enhancing the soil nutrients for e.g., nitrogen fixation [59], solubilization of minerals such as phosphorous, potassium, and iron [60], and production of enzymes, siderophores [61], and different phytohormones [62]. Indirect mechanisms involve plant

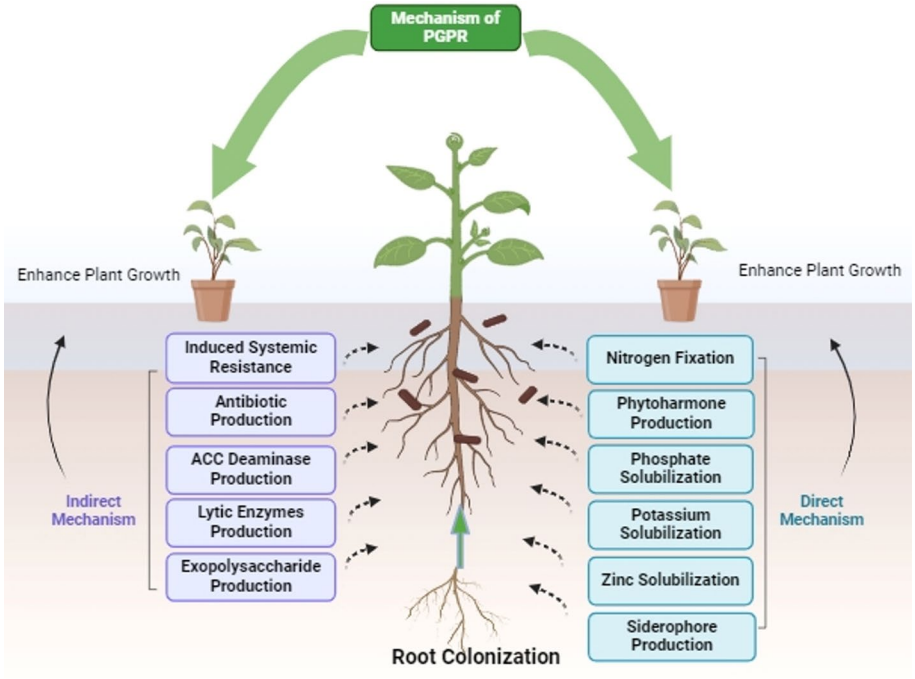


Fig. 2 Illustration of underlying mechanisms of growth promotion employed by PGPR

growth promotion by producing antagonistic substances such as diacetylphloroglucinol, hydrogen cyanide (HCN), phenazine, prevention of the deleterious effects of phytopathogens, heavy metal detoxification and biofilm formation [19, 63–65]. Understanding the mechanisms and types of PGPR actions is essential for their utilization in agriculture to promote sustainable and eco-friendly practices. They play crucial roles in enhancing plant health, nutrient uptake and overall crop productivity.

In addition to the aforementioned mechanisms, plant growth promoting rhizobacteria produce various lytic enzymes such as glucanase and chitinase which degrade the cell wall of fungal pathogens and induce systemic resistance throughout the plant system. Moreover, PGPR can influence plant growth both directly and indirectly with these effects often being strain-specific or varying among species [66]. Studies have suggested that PGPR mediated plant growth promotion takes place through the modification of the whole microbial group found in the rhizospheric niche by the production of different substances [67]. Usually, PGPR enhance plant growth through a direct mechanism by facilitating various resource acquisitions such as phosphorous, nitrogen, and vital minerals via biological nitrogen fixation; iron sequestration through siderophore production; phosphate mineral solubilization; and modulation of phytohormones as auxins, cytokinins (CKs), gibberellins (GAs) and nitric oxide (NO). They also contribute significantly through indirect mechanisms in the rhizosphere such as induced systemic resistance (ISR) and the biosynthesis of stress alleviating phytohormones like ethylene regulation via the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase and the production of jasmonic acid (JA) which collectively enhance plant resilience under stress conditions. The mechanisms by which PGPR promote plant growth are multifaceted and involve direct benefits such as nutrient mobilization and phytohormone production as well as indirect benefits through soil improvement and stress mitigation. Understanding

these mechanisms can aid in the development of sustainable agricultural practices that harness the potential of PGPR to enhance crop productivity.

3.1 Direct effects of PGPR

Plant growth promoting rhizobacteria directly affect plant growth through several mechanisms. These interactions enhance nutrient uptake, promote root development, and enhance overall plant health. In addition, the direct mechanism of PGPR provides mechanical support and facilitates water and mineral uptake [10]. This direct mechanism includes microbial activities like nutrient solubilization, production of phytohormones, root development, induction of systemic resistance and production of bioactive compounds and phytostimulants. Understanding these mechanisms is essential for leveraging PGPR in sustainable agriculture and improving crop yields. PGPR also enhances the crop yield by the production of plant growth regulators. At a very low concentration these regulators enhance the plant development by influencing various physiological and morphological processes [68]. Numerous microbes can produce several plant growth regulators such as auxins, gibberellins, abscisic acid (ABA), cytokinins, and ethylene (ET). Various rhizobacteria have been reported to produce auxins (for example, *Agrobacterium*, *Pseudomonas*, *Azospirillum*, and *Erwinia*) [69]. Nutrient mobilization is one of the primary mechanisms through which PGPR enhance plant growth. These beneficial microorganisms play a crucial role in increasing the availability of essential nutrients in the rhizosphere, thereby promoting healthy plant growth.

Plant growth promoting rhizobacteria are major components of biofertilizers because of their ability to improve plant health and productivity through various biological mechanisms. The use of PGPR as biofertilizers is becoming an increasingly sustainable alternative to chemical fertilizers which maintain soil fertility, reduce environmental pollution, and promote sustainable agriculture. The application of PGPR as biofertilizers is not only environmentally friendly but also economically beneficial to farmers contributing to both improved crop yields and reduced costs. Khoso et al. [70]. , reported that PGPR improves the uptake of mineral nutrients in crop plants which is required for optimum growth and development. PGPR can function as biofertilizers through several direct and indirect mechanisms. These include enhancing nutrient availability (such as nitrogen, phosphorus, and other micronutrients), producing plant hormones, and protecting plants from stress and diseases. Furthermore, the use of PGPR based biofertilizers reduces reliance on synthetic fertilizers leading to lower input costs for farmers and minimizing environmental pollution caused by fertilizer runoff. PGPR assist plants in tolerating abiotic stresses such as drought, salinity, and heavy metal toxicity, thereby enhancing plant health and productivity under suboptimal growth conditions. PGPR contribute to the reduction of greenhouse gas emissions (such as nitrous oxide) from synthetic nitrogen fertilizers, and reduce soil degradation and promote long-term agricultural sustainability. PGPR based biofertilizers can be categorized into several types based on the microbial species and their specific functions. Nitrogen biofertilizers contain nitrogen-fixing bacteria such as *Rhizobium*, *Azospirillum*, *Azotobacter* which convert nitrogen into forms available to plants [4, 71]. Phosphate-solubilizing biofertilizers enhance the availability of phosphorus by solubilizing insoluble phosphate compounds in the soil with notable examples including *Pseudomonas fluorescens* and *Bacillus subtilis* [4, 10]. Potassium-solubilizing biofertilizers harbor bacteria that solubilize potassium,

improving potassium availability in the soil such as *Bacillus mucilaginosus*, *Frateuria aurantia* [72]. Multifunctional biofertilizers combine diverse plant growth promoting rhizobacteria, capable of performing multiple beneficial functions such as nitrogen fixation, phosphate solubilization, and phytohormone production. For example, biofertilizers formulated with a synergistic blend of *Azospirillum*, *Pseudomonas*, and *Bacillus* sp. have been found to enhance nutrient availability, promote root development and support overall plant growth more effectively [52, 73]. The key aspects of nutrient mobilization by PGPR are described in Sect. 3.1.1–3.1.7.

3.1.1 Nitrogen fixation

Nitrogen (N) is an essential macronutrient for plant growth and plays a crucial role in the synthesis of proteins, nucleic acids, and chlorophyll. Despite its abundance in the atmosphere (approximately 78%), nitrogen exists predominantly as inert nitrogen gas (N_2) which plants cannot directly utilize [74, 75]. To overcome this, certain bacteria known as diazotrophs possess the ability to fix atmospheric nitrogen into ammonia (NH_3) a form that plants can assimilate. This process known as biological nitrogen fixation (BNF) is a key mechanism in sustainable agriculture that reduces the need for synthetic nitrogen fertilizers. Certain PGPR convert atmospheric nitrogen into a usable form that plants can utilize. This enhances nitrogen availability for plants. These bacteria form mutualistic relationships with plants particularly legumes, where they colonize plant roots and form specialized structures called nodules [76]. Inside these nodules, the bacteria fix nitrogen, supplying the host plant with ammonia in exchange for carbon compounds and a protective environment. Additionally, nitrogen fixing bacteria known as "Diazotrophs" are classified as symbiotic (e.g., *Frankia* and *Rhizobium)*, free living endophytes or root endophyte microbes (e.g., *Azotobacter* and *Azospirillum*) [77]. Nitrogen-fixing PGPR can significantly enhance soil nitrogen levels, particularly in agricultural settings where synthetic fertilizers may be limited or undesirable. This can improve plant growth and yield considerably.

3.1.2 Phosphate solubilization

Phosphorus (P) is an essential macronutrient for plant growth and plays a critical role in energy transfer, photosynthesis and nutrient transport. However, a significant portion of phosphorus in soils exists in insoluble forms making it unavailable to plants. Plant growth promoting rhizobacteria contribute to the solubilization of insoluble phosphates by producing organic acids, thereby enhancing phosphorus availability in the rhizosphere and promoting plant growth. This improves the nutrient status of the soil and enhance plant nutrient uptake [60, 78]. Certain PGPR such as *Bacillus*, *Pseudomonas*, *Rhizobium* sp. and *Mycobacterium* are particularly effective in this process and can solubilize insoluble phosphate through the secretion of organic acids such as citric acid, gluconic acid, oxalic acid, acetic acid, and lactic acid [52, 79]. These organic acids can chelate metal cations and lower the pH of the soil or rhizosphere converting insoluble phosphate compounds like tricalcium phosphate, dicalcium phosphate, and hydroxyapatite into soluble forms (e.g., $H_2PO_4^-$), which can be absorbed by plant roots [60, 80]. Some PGPR can release protons (H^+ ions) into the rhizosphere leading to soil acidification. This decrease in pH enhances the solubility of phosphate minerals converting insoluble forms into soluble forms. PGPR improves phosphorus availability in the soil, facilitating better root uptake

and overall plant growth. Phosphatase enzymes produced by PGPR play a crucial role in hydrolyzing the organic phosphates present in the soil. PGPR may also participate in ion exchange processes. The combined action of these mechanisms contributes to the solubilization of insoluble phosphates in the soil ultimately availability of P to plants [78]. This process is beneficial for plant growth, especially in phosphorus-deficient soils and can be harnessed in agriculture to improve the nutrient uptake efficiency and crop productivity. Phosphate-solubilizing PGPR play a vital role in sustainable agriculture by reducing the need for chemical fertilizers. By enhancing phosphorus bioavailability in soils with low phosphorus levels or high phosphate fixation, these bacteria contribute to improved plant growth and yield. Phosphate-solubilizing PGPR also improve soil health by promoting beneficial microbial communities, enhancing nutrient cycling, and contributing to overall plant resilience against abiotic stresses [81].

Plants only absorb P in its soluble form (monobasic (H_2PO_4) and dibasic (HPO_4) ions) [82]. However, the use of phosphate fertilizers is both costly and environmentally unsustainable. In this context, phosphate-solubilizing microorganisms present in the rhizosphere commonly referred to as phosphate-solubilizing rhizobacteria (PSRB) or phosphate-solubilizing bacteria (PSB) play a vital role in converting insoluble phosphates into plant available forms, thereby meeting the phosphorus requirements of plants in an eco-friendly and efficient manner [83] (Fig. 3).

3.1.3 Potassium mobilization

Potassium (K) is a key macronutrient critical for maintaining water balance, enzyme activation, and the regulation of various physiological processes in plants. Although

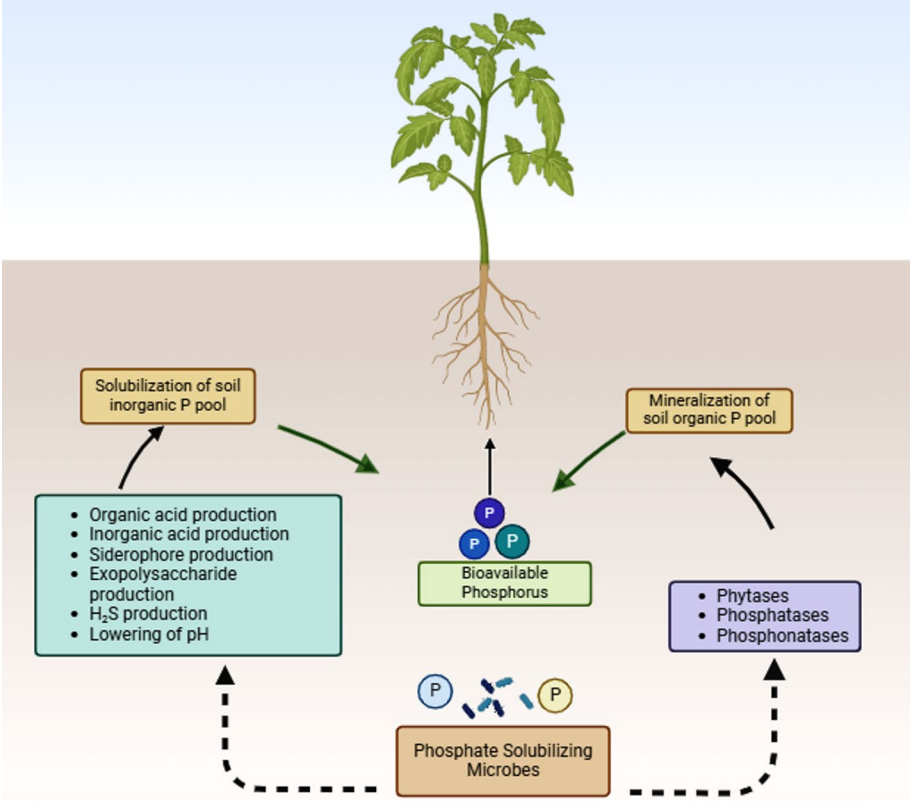


Fig. 3 Mechanism of phosphate solubilization by PSB

potassium is abundant in many soils, it is often found in insoluble mineral forms such as mica, feldspar, and illite which are not directly available for plant uptake. Plant growth promoting rhizobacteria are well known for their ability to enhance plant nutrient uptake by mobilizing essential nutrients including potassium, which is often present in insoluble forms in the soil [84]. Potassium is crucial for enzyme activation, osmoregulation, and photosynthesis [85]. PGPR solubilizes potassium from insoluble mineral sources primarily through the production of organic acids and enzymes [86, 87]. These acids such as gluconic acid, citric acid, and oxalic acid, lower the pH of the rhizosphere which enhances the dissolution of potassium-containing minerals and releases K^+ ions into the soil solution making them available for plant uptake. These organic acids chelate cations such as calcium, magnesium, and iron from potassium bearing minerals, weakening the mineral structure and releasing potassium ions. *Bacillus mucilaginosus* is a well-known potassium-solubilizing bacterium that releases organic acids to mobilize potassium from insoluble minerals [87]. The ability of PGPR to solubilize these nutrients plays a significant role in sustainable agriculture by reducing the need for chemical fertilizers and enhancing plant growth. Certain PGPR also secrete enzymes that degrade potassium containing minerals. These enzymes act synergistically with organic acids to increase the dissolution of potassium from its mineral form. Several genera of PGPR are known for their ability to solubilize potassium. *Bacillus* species, particularly *B. mucilaginosus* and *Bacillus edaphicus* have been extensively studied for their potassium-solubilizing abilities. These bacteria are capable of producing a wide range of organic acids that release potassium from insoluble mineral forms, thereby improving potassium availability to plants [88]. *Pseudomonas* strains have also been found to release potassium from soil minerals through acid production. They enhance plant root surface area and nutrient uptake by promoting root growth which further improves potassium uptake from the rhizosphere [89]. Potassium plays a vital role in several physiological processes including osmoregulation and water balance (potassium helps to regulate stomatal opening and closing, thus controlling water loss through transpiration and maintaining turgor pressure in plant cells), photosynthesis, enzyme activation (potassium is an activator of enzymes involved in photosynthesis and is essential for ATP synthesis, protein synthesis, and carbohydrate metabolism), and stress resistance (adequate potassium nutrition improves plant tolerance to various biotic and abiotic stresses, including drought, salinity, and pathogen attacks) [84, 85]. Inoculation with K-solubilizing bacteria has been found to increase biomass, root vigor, and K content in leaves and stems of tobacco, wheat and tomatoes [86, 90].

In an experiment with wheat, the application of *B. mucilaginosus* significantly enhanced K uptake leading to increased plant height, root length, and biomass production under K deficient conditions [87]. By using PGPR to mobilize potassium from insoluble soil reserves, farmers can reduce their dependency on chemical fertilizers leading to more eco-friendly and cost-effective agricultural practices. Additionally, these PGPR enhance soil health by promoting microbial diversity and improving soil structure. In a field study with wheat and maize, the use of potassium-solubilizing bacteria (*Bacillus* sp. and *Pseudomonas* sp.) reduced the need for chemical potassium fertilizers and resulted in a substantial increase in crop yield and potassium use efficiency [90].

3.1.4 Zinc solubilization

Zinc (Zn) is an essential micronutrient that plays a critical role in the synthesis of proteins, nucleic acids, and in the regulation of plant hormone activities. Zn deficiency in soils can lead to chlorosis, reduced photosynthetic activity, impaired plant growth, reduced yields, and lower nutritional quality. However, zinc is often present in insoluble forms such as zinc oxide (ZnO), zinc carbonate ($ZnCO_3$), and zinc sulfide (ZnS) which are not readily available to plants. Zinc-solubilizing PGPR can convert insoluble zinc compounds into bioavailable forms through secretion of organic acids, siderophores, and other chelating agents. These organic acids such as gluconic acid and citric acid assist in dissolving zinc from mineral complexes by lowering the soil pH and forming soluble zinc-organic acid complexes. *P. fluorescens* releases organic acids and siderophores which solubilize zinc from zinc oxide making it available for plant uptake [91]. Zinc-solubilizing PGPR not only improve zinc uptake in plants but also enhance overall plant health by promoting root elongation, increasing chlorophyll synthesis, and enhancing resistance to environmental stresses. Zinc is also a cofactor for numerous enzymes and is involved in the synthesis of auxins that regulate plant growth. Application of zinc-solubilizing bacteria such as *Bacillus aryabhattai* and *Pseudomonas aeruginosa* has been shown to enhance zinc uptake in crops such as wheat and maize leading to better growth and higher grain yield [92]. Siderophores are high affinity iron chelating compounds secreted by many PGPR. While their primary function is to sequester iron from the environment, they can also enhance zinc availability by forming soluble zinc-siderophore complexes. These zinc-siderophore complexes are more easily absorbed by plants than insoluble zinc minerals. *P. putida* secretes siderophores that chelate zinc and increase its bioavailability, thereby enhancing zinc uptake by cucumber plants [92]. PGPR can also solubilize zinc by producing chelating agents and other metabolites that bind to it and enhance its solubility. These compounds destabilize the zinc complexes in the soil allowing the release of zinc ions into the soil solution for plant uptake. *Bacillus aryabhattai* strains have been shown to solubilize zinc via the secretion of various chelating agents and organic acids [93]. Furthermore, zinc is required for the activity of numerous enzymes involved in nitrogen metabolism, protein synthesis, and carbonic anhydrase function all of which are crucial for optimal plant growth and development. Solubilizing zinc from insoluble forms ensures a consistent supply of this essential nutrient supporting robust plant growth. In maize and wheat, application of zinc-solubilizing bacteria like *P. aeruginosa* resulted in improved enzyme activity and enhanced protein content in grains [93]. The application of zinc-solubilizing bacteria such as *B. aryabhattai* increases auxin levels in wheat plants, promoting better root development and higher zinc uptake [93]. PGPR that solubilize zinc maintain the optimal zinc levels, enhances chlorophyll production, and improves photosynthetic efficiency. For instance, in cucumber plants, *P. fluorescens* improves chlorophyll content and overall plant health by enhancing zinc solubilization and uptake [94].

Several genera of PGPR are capable of solubilizing zinc including *Pseudomonas* sp., which are effective zinc-solubilizers. Their use has been widely studied in various crops such as wheat, maize, and cucumber [92]. *Bacillus* strains are known for their ability to solubilize zinc via the production of chelating agents and organic acids. They are highly effective in zinc-deficient soils and have shown significant results in promoting zinc uptake and plant growth in crops such as wheat and maize [93]. The

use of zinc-solubilizing PGPR in agriculture offers a sustainable approach to improve zinc nutrition in crops, reducing the need for chemical zinc fertilizers. This biological method not only enhances plant growth but also contributes to soil health by promoting microbial diversity and improving nutrient cycling. By utilizing PGPR for zinc solubilization, farmers can reduce the application of zinc-based fertilizers which are often costly and contribute to environmental pollution. The natural solubilization of Zn by PGPR ensures a continuous supply of nutrients to plants without the need for synthetic inputs making this approach more environmentally sustainable. In an experiment with wheat, the application of potassium and zinc-solubilizing bacteria improved nutrient uptake and resulted in a significant increase in yield compared with untreated controls [95].

3.1.5 Stimulation and production of phytohormones

Plant growth promoting rhizobacteria enhance plant development not only through nutrient mobilization but also by producing and modulating phytohormones which are key regulators of plant growth and stress responses. The interaction between PGPR and phytohormones such as auxins, gibberellins, cytokinins, and ethylene significantly impacts root architecture, shoot development and the overall ability of plants to withstand environmental stressors [96, 97]. These hormones play crucial role in plant development including cell division, elongation and, differentiation. At very low concentrations, these phytohormones affect the plants both physiologically and morphologically [68]. Phytohormones can alter plant growth patterns and results in better branched roots with a wider surface area. Because of this, plants receive a greater area and are able to access extra minerals and nutrients from the soil. In addition, phytohormones can play a pivotal role in the symbiotic development of legume-rhizobia through Nod factor signalling [98].

3.1.5.1 Auxin Auxin is one of the most essential hormone that influences plant growth and development through various processes such as tropic responses and organogenesis. Auxins also participate in cellular responses such as cell expansion, cell division, and cell differentiation along with gene regulation [99]. Auxins, particularly Indole-3-Acetic Acid (IAA) are among the most widely studied phytohormones produced by PGPR. PGPR produce a variety of auxins (such as, IAA, IBA (indole-3-butyric acid), IPA (indole-3-pyruvic acid), tryptophol (TOL) and ILA (indole lactic acid). Of these, IAA is the most important auxin produced in presence of L-tryptophan as a precursor by *Azospirillum*, *Pantoea*, *Pseudomonas*, *Bacillus*, *Rhizobium*, *Alcaligenes*, and *Enterobacter*. IAA production by PGPR typically occurs through a tryptophan-dependent pathway. The presence of tryptophan in root exudates stimulates PGPR to produce IAA which then influences the plant-root system leading to enhanced lateral root formation and root hair development [100]. In leguminous crops, the nodules have a higher concentration of IAA than the roots. The accumulation of auxin in the nodules of legumes can be attributed to rhizobia [98]. In plant-microbe interactions, the role of IAA varies from phytostimulation to pathogenesis and it also takes part in the degradation of aromatic amino acids [101]. Species such as *Azospirillum*, *Pseudomonas*, *Erwinia* and *Agrobacterium* have been found to produce IAA and enhance growth parameters and development in crops (such as seedling, root length, root hairs, branching, and root surface area [101]. Earlier, studies had demonstrated that *Rhizobium* strains associated with legumes produce IAA and

show their potential for lateral growth development along with enhanced nodulation and delayed senescence in nodules [102].

3.1.5.2 Gibberellin Gibberellins (GAs) are a group of plant hormones that regulate various developmental processes including seed germination, stem elongation, flowering, and fruit development. The production of gibberellins by rhizobacteria enhances hormonal balance in plants often resulting in better growth, increased stress tolerance, and improved nutrient uptake. PGPR-induced gibberellin production has been documented in various bacterial genera including *Acinetobacter*, *Azospirillum*, *Bacillus*, *Pseudomonas*, and *Rhizobium* [103–105]. PGPR synthesize gibberellins through biochemical pathways similar to those in plants. For example, the mevalonate and methylerythritol phosphate pathways are involved in isoprenoid biosynthesis leading to gibberellin formation. These microbial gibberellins are excreted into the rhizosphere where they influence the hormonal signaling. The interaction between PGPR and plant roots enables the bacteria to modulate the GA levels in the plants. The synthesis of gibberellins by PGPR enhances stem elongation and leaf expansion allowing plants to achieve greater photosynthetic efficiency. This increased efficiency results in enhanced biomass accumulation and improved overall plant growth. Several species of *Azospirillum* have been found to produce gibberellins, contributing to improved root and shoot growth in plants such as wheat and maize. *Azospirillum lipoferum* and *A. brasilense* are well-documented producers of gibberellins which play a role in the enhanced development of lateral roots and overall biomass accumulation [106, 107]. *Bacillus pumilus* and *Bacillus licheniformis* have been documented to produce high amount of gibberellins which promote seed germination and shoot elongation in plants [108]. The genus *Bacillus* is another important group of gibberellin-producing PGPR. Studies have shown that *Bacillus megaterium* and *B. pumilus* can increase the length and biomass of various plants through the secretion of gibberellins [105, 107]. Several other strains of *Pseudomonas* have demonstrated the ability to synthesize gibberellins [107].

3.1.5.3 Abscisic acid (ABA) Abscisic acid (ABA) is a plant hormone that plays a critical role in regulating abiotic stress responses, seed dormancy, stomatal closure, and other physiological processes in plants. Although traditionally considered an endogenous plant hormone, recent research indicates that certain PGPR can produce ABA contributing to plant stress tolerance and growth promotion. While ABA is commonly associated with stress responses including drought and salinity, some PGPR are capable of producing or inducing ABA synthesis in plants. ABA synthesis in plants typically involves the carotenoid pathway and similar pathways are present in some PGPR. These bacteria can either produce ABA or modulate ABA production within plants through various signaling mechanisms. Studies have demonstrated that ABA produced by PGPR contributes to the regulation of key plant processes such as stomatal behavior, root growth, and stress tolerance under drought and salinity stress [109]. ABA produced by PGPR operates by interacting with endogenous hormone signaling pathways in plants. When plants are exposed to stress conditions, microbial ABA can enhance or synergize with the own ABA level of plants leading to quicker and more effective physiological responses such as stomatal closure and osmotic balance regulation [110]. The increase in ABA production help plants to conserve water by closing their stomata, thereby reducing water loss during drought

conditions. PGPR such as *Bacillus* sp. have been reported to modulate ABA levels in plants that help to improve drought tolerance in wheat by inducing higher ABA levels and reducing stomatal conductance [111].

Several strains of *Azospirillum* produce ABA which help plants to cope with water stress [112]. For instance, *A. brasilense* has been shown to increase ABA levels in plants such as maize which subsequently enhances stomatal closure, reduces transpiration, and improves water-use efficiency [113]. Certain species of *Bacillus* have been found to produce ABA or enhance the ABA content in plants under stressful conditions. *Bacillus amyloliquefaciens* has been reported to increase ABA content in wheat plants under drought conditions which is associated with improved stress tolerance and growth performance. *P. fluorescens* is another rhizobacterium capable of ABA production [113]. This bacterium has been linked to improved drought tolerance in various crops through its ability to modulate ABA signaling in plants. Under drought stress, plants colonized by *Pseudomonas* showed increased ABA levels contributing to improved water retention and growth stability [114]. Symbiotic bacteria such as *Rhizobium* are not only involved in nitrogen fixation but can also influence ABA production in leguminous plants. These bacteria enhance plant ABA levels particularly under stress conditions such as drought and salinity, thereby contributing to better plant-water relations and stress adaptation [115, 116].

The production of ABA by PGPR is particularly valuable in agriculture where crops frequently encounter environmental stresses such as drought and salinity. PGPR that produce or modulate ABA provide an eco-friendly approach to enhance plant resilience without the need for chemical interventions. This hormonal interaction help plants to maintain osmotic balance, reduce water loss, and sustain growth even under suboptimal conditions. Moreover, the use of ABA-producing PGPR aligns well with sustainable agricultural practices by reducing the dependency on synthetic agrochemicals and enhancing plant-soil-microbe interactions that promote natural stress tolerance mechanisms [117].

3.1.5.4 Cytokinin Cytokinins are phytohormones that help plants in root and shoot cell division. It promotes cell growth and differentiation in crop plants [118]. They also affect apical dominance in plants; therefore, they are used by farmers to increase the overall production of crops. Cytokinins produced by PGPR promote shoot proliferation, enhance leaf formation, and influence nutrient mobilization by stimulating the translocation of nutrients from the roots to shoots. In many PGPR, cytokonins are apparently expressed; therefore, their application and potential to growing crops helps in the modification of crop plant phytohormone composition. Several PGPR strains have been found to be capable of producing cytokinins including *Azotobacter* sp., *Rhizobium* sp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *B.subtilis* and, *P.fluorescens* [119, 120]. Cytokinins are derivatives of purines and are classified based on their potential to enhance cell division (i.e., cytokinesis), cell enlargement and tissue development in plants. PGPR produced cytokonins affect the auxin to cytokinin ratio and hence regulates the crop root architecture. Cytokinins promote plant growth in many crops such as rapeseed and soybean. These may play a pivotal role in rhizobial infection and nodule differentiation in legumes [120].

3.1.6 Modulation of ethylene via ACC deaminase activity

Ethylene is a pivotal phytohormone that aids plants in their physiological responses at low concentrations. Ethylene is a stress-related phytohormone that is involved in the regulation of plant responses to biotic and abiotic stresses [4]. Under stressful conditions, plants often produce excessive amounts of ethylene which can inhibit root and shoot growth. Many PGPR contain the enzyme ACC deaminase which breaks down ACC, the precursor of ethylene into α-ketobutyrate and ammonia, thereby lowering ethylene levels in plants (Fig. 4). PGPR mitigates stress responses in plants leading to enhanced root growth and improved tolerance to stresses such as drought, salinity, and pathogen attacks [121, 122]. Morgan and Drew found that increased and accumulated ethylene concentrations in plants cause stress responses; therefore, to eliminate this, plants increase their tolerance. It also intensifies senescence and stress response symptoms [117]. When ethylene level is elevated, it has been seen that it gradually suppresses the growth of plant roots and shoots with the formation of infection thread [123]. Several PGPR are known to secrete ACC deaminase which reduces elevated ethylene production in crop plants [122, 123]. Different studies have shown that inoculating PGPR strains that produce ACC deaminase directly mitigates environmental stress. The significant areas of cultivated soil are under biotic and abiotic environmental stresses such as phytopathogenic infection and high salt availability [123]. ACC decreases the level of "stress ethylene," which inhibits plant growth and development. Repeated inoculation of highly effective rhizobia [116] and co-inoculation with other efficient PGPR have improved the growth and yield of plants [124, 125].

A variety of PGPR contain the vital enzyme ACC deaminase which regulates ethylene production by metabolizing ACC (an intermediate precursor of ethylene biosynthesis in higher plants) into α-ketobutyrate and ammonia. According to Hontzeas et al., 2004b, ACC deaminase-producing bacteria also alleviate the need for plants to actively defend themselves against different environmental stressors [125]. High temperatures can induce ethylene production which leads to stress responses. ACC deaminase helps to maintain optimal ethylene levels and prevent the detrimental effects of heat stress on plant growth and development. ACC deaminase-producing PGPR help to regulate ethylene levels preventing excessive activation of defense responses and minimizing damage during pathogen attacks, and can also induce ethylene production in plants. The use of ACC deaminase-producing PGPR in agriculture can enhance the resilience of plants to

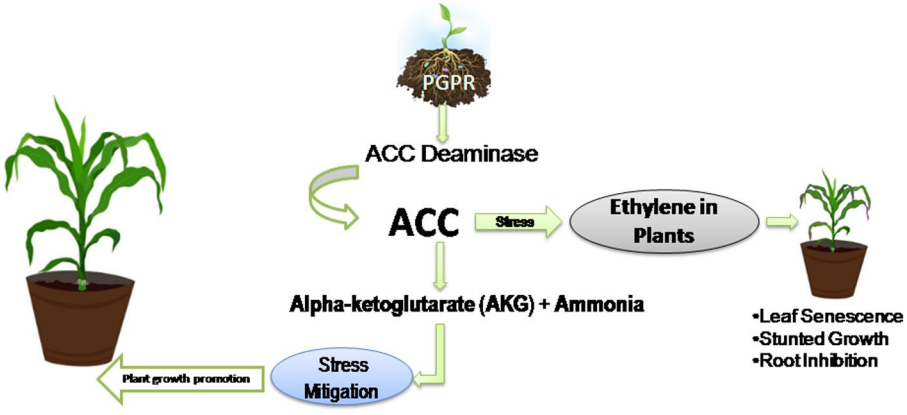


Fig. 4 Plant growth promotion through modulation of ethylene by ACC deaminase activity of PGPR

a wide range of stresses, contributing to sustainable and improved crop production in challenging environments.

3.1.7 Siderophore production

Siderophores are low molecular weight iron bound compounds that chelate ferric iron (Fe^{3+}) in the environment. Iron (Fe) is the fourth essential micronutrient element in the earth's crust. However, it is not available for crop plants as it is present in the insoluble form (Fe^{3+}). To overcome with this problem, PGPR strains secrete iron scavengers (siderophores). These siderophores chelate iron and hence are further transported to the cells of microorganisms [126, 127]. Siderophores producing PGPR enhance plant growth production very efficiently and also control the several plant diseases relieving the pathogen of iron nutrition. These siderophore characteristics were found to be more effective and hence useful for the proper growth and development of crop plants. In addition, siderophores form stable complexes with several other metals that are of environmental concern (such as Cd, Al, Cu, Ga, Pb, Zn, and In) [128].

3.2 Indirect effects of PGPR

The indirect mechanism of PGPR includes inhibitory effects against various phytopathogens by secreting different antagonistic compounds that have a defensive nature (i.e., hydrogen cyanide, bacteriocins, and hydrolytic enzymes). Several bacterial genera (such as *Bacillus*, *Burkholderia*, *Staphylococcus*, *Serratia*, *Pseudomonas*, *Enterobacter*, *Herbaspirillum* etc. are known to have potential against phytopathogens [125–127]. Van loon et al., revealed that PGPR can inhibit the growth of other microorganisms by efficiently mineralizing nutrients, thereby gaining a competitive advantage in the rhizosphere. In addition, PGPR induced systemic resistance (ISR) decreases the activity of pathogens [129]. Many studies have revealed the applications of several PGPR that help to control pathogenic diseases through biological control. The use of biocontrol agents for plant growth promotion by rhizobacteria is a major indirect mechanism [9]. PGPR include different modes of activities such as niche exclusion and induced systemic resistance and play a vital role in the production of several antifungal metabolites. Many studies have found that numerous PGPRs have the potential to produce antifungal metabolic compounds (such as phenazines, HCN, pyrrolnitrin, 2,4-diacetylphloroglucinol, pyoluteorin, tensin, and viscosinamide [130, 131].

3.2.1 Induced systemic resistance (ISR)

PGPR can trigger a plant immune response through ISR. By stimulating the production of defense-related compounds such as phenolics, flavonoids, and pathogenesis-related (PR) proteins, PGPR make plants more resistant to a wide range of pathogens. This reduction in disease pressure leads to healthier plants that can devote more energy to growth and production. Certain PGPR including *Pseudomonas* and *Bacillus* species can trigger systemic resistance in plants. ISR is a defense mechanism that primes plants to respond more effectively to pathogen attacks. PGPR stimulate the production of signaling molecules such as jasmonic acid and ethylene which activate defense-related genes in plants. ISR enhances the ability of plants to resist infections from a wide range of pathogens, reduces disease outbreaks and improves growth and productivity [130, 132].

3.2.2 Antibiotic production and pathogen suppression

Many PGPR produce natural antibiotics, enzymes, and secondary metabolites that directly inhibit the growth of pathogenic microorganisms, such as fungi, bacteria, and nematodes. PGPR indirectly enhance plant health and productivity by suppressing diseases in the rhizosphere thereby reducing the need for chemical pesticides. Some PGPR produce antibiotics or antimicrobial substances that inhibit the growth of plant pathogens. For example, *P. fluorescens* and *B. subtilis* produce antibiotics such as phenazines, pyoluteorin, and bacillomycin. These substances suppress soil-borne pathogens such as *Fusarium*, *Pythium*, and *Rhizoctonia* which cause root diseases. By controlling pathogenic microbes in the rhizosphere, PGPR reduce the incidence of diseases leading to healthier plants and higher crop yields [133, 134].

PGPR can outcompete harmful pathogens for essential nutrients and colonize spaces in the rhizosphere. This mechanism known as "competitive exclusion," limits the resources available for pathogen growth, thereby suppressing the growth of harmful microbes. *Bacillus* and *Pseudomonas* species effectively colonize the root surface and form a protective barrier [135, 136]. PGPR indirectly reduce disease pressure and enhance plant health by preventing colonization by pathogenic organisms [64, 135]. Some PGPR produce enzymes such as chitinases, cellulases, and glucanases which break down the cell walls of pathogenic fungi and bacteria. *Bacillus* and *Serratia* species are known to produce these lytic enzymes which degrade the structural components of pathogens and render them inactive. By lysing pathogenic cells, PGPR provides biocontrol against a range of fungal and bacterial diseases [138, 139]. Some PGPR also produce volatile organic compounds (VOCs) that can directly inhibit pathogen growth or trigger plant defense mechanisms. VOCs such as HCN, acetoin, and 2,3-butanediol are known to suppress soil-borne pathogens and enhance plant growth by modulating plant hormonal pathways contributing to both pathogen suppression and enhanced plant vigor, improving overall plant health and productivity [104, 140].

4 Enhanced root architecture and soil health

The root system is crucial for plant growth and development and acts as the primary interface between the plant and its environment. Root architecture, the spatial configuration of the root system directly affects abilty of plants to acquire water and nutrients. Additionally, soil health defined as the continued capacity of the soil to function as a living ecosystem is essential for sustaining agricultural productivity. The use of PGPR has been shown to enhance root architecture and improve soil health, thereby contributing to sustainable agriculture. Their role in enhancing root architecture and improving soil health is pivotal to sustainable agriculture and crop productivity. By directly influencing root growth, architecture, and soil structure, PGPR enhance nutrient and water uptake, improve plant resilience to environmental stresses, and promote long-term soil fertility. Since plant growth and productivity largely depend on the efficiency of the root system which is the critical interface between plants and soil, PGPR play a key role in optimizing these interactions. A well-developed root system is essential for optimal nutrient uptake, water absorption, and overall plant health. The application of PGPR can lead to significant improvements in root architecture which is directly linked to increased nutrient and water absorption, and plant productivity. Plant roots are fundamental for the uptake of water and nutrients, anchoring plants in the soil, and interacting with soil

microorganisms. The ability of plants to thrive is largely dependent on the structure and efficiency of their root systems which is known as root architecture. In addition to architecture, soil health also plays a vital role in sustaining plant growth. The concept of soil health encompasses the biological, chemical, and physical properties of soil that support plant and microbial life [139, 141]. Plant growth promoting rhizobacteria enhance both root architecture and soil health and offer a sustainable solution for improving crop productivity. This review explores the mechanisms by which PGPR contributes to root development and soil health and how these interactions benefit plant growth and resilience.

4.1 Root growth stimulation

PGPR influence root architecture by producing plant hormones such as IAA, gibberellins, and cytokinins. These hormones regulate root cell elongation, lateral root formation, and root hair development leading to more efficient nutrient and water uptake. Many PGPR, such as *Azospirillum* and *Pseudomonas* produce IAA, which stimulates root elongation, lateral root development, and root hair formation. Studies have demonstrated that crops inoculated with IAA-producing PGPR exhibit significant improvements in root length, surface area, and branching, resulting in enhanced nutrient acquisition [4, 100].

By producing phytohormones such as IAA and gibberellins, PGPR stimulates root elongation, increases root hair density, and promotes lateral root formation. An improved root system allows the plant to access water and nutrients from a greater soil volume making it more resilient to suboptimal growing conditions such as drought or nutrient deficiency. One of the most well-known mechanisms by which PGPR influences root architecture is the production of plant hormones such as IAA. Studies have shown that PGPR strains including *A. brasilense* produce significant amounts of IAA which promotes root elongation, increases the number of lateral roots, and enhances root hair development. According to Dobbelaere et al. (2003), plants inoculated with IAA-producing PGPR exhibit improved root systems which increase their ability to uptake water and nutrients from the soil [104].

4.2 Root hair development

Root hairs increase the surface area for nutrient and water absorption particularly for immobile nutrients such as phosphorus. PGPR promote root hair formation, enhancing the ability of plants to access nutrients in the soil [10]. Root hairs, which are extensions of root epidermal cells, play a crucial role in nutrient uptake particularly in phosphorus-deficient soils. PGPR such as *Pseudomonas* and *Bacillus* species have been shown to enhance root-hair formation. This increased root surface area improves nutrient acquisition particularly phosphorus as noted in the earlier studies [10]. In addition, improved root hair density also facilitates the uptake of less mobile nutrients such as iron and zinc, contributing to better plant growth.

4.3 Stress resilient root systems

Under stress conditions such as drought or salinity, plants often suffer from reduced root growth. However, PGPR can mitigate these effects by modulating hormone levels and enhancing root development. For example, a research study has shown that wheat

plants treated with drought-tolerant PGPR strains developed deeper and more robust root systems, improving water absorption in deeper soil layers [54]. PGPR enhance root system architecture in a way that improves plant tolerance to abiotic stresses such as drought and salinity. Previous studies demonstrated that plants inoculated with PGPR showed more extensive root systems and better survival under drought conditions owing to improved water absorption [141]. This is further supported by the findings of other researchers (2011), who reported that PGPR-inoculated plants exhibited enhanced root growth and increased root biomass under salinity stress [142].

4.4 Soil aggregation and structure

Soil structure is critical for root growth and plant health because it affects water infiltration, aeration, and root penetration. PGPR contribute to improved soil structure by producing EPS which promote the aggregation of soil particles. These aggregates enhance soil porosity, water retention, and root penetration. EPS produced by bacteria like *Bacillus* and *Pseudomonas* act as "glue" that binds soil particles, improving soil aggregation and stability [143, 144]. The soil aggregates improve soil aeration, water retention, and microbial activity all of which create a more favorable environment for plant growth. Furthermore, EPS-producing bacteria also maintain the soil structure which supports healthy root growth and improves water retention [145]. Improvements in soil structure also reduce erosion ensuring long-term soil health and fertility.

5 Impact of PGPR on root-soil interactions

5.1 Induced systemic resistance (ISR)

PGPR can also induce systemic resistance in plants enhancing their ability to resist soilborne pathogens. This mechanism referred to as ISR involves the activation of plant defense pathways enabling plants to defend themselves against diseases. This is particularly important for root health because healthy roots are essential for nutrient and water absorption. An earlier study found that PGPR-induced systemic resistance not only improves plant disease resistance but also promotes more robust root systems [129].

5.2 Improvement of water retention

Soil treated with PGPR showed enhanced water retention owing to better soil structure and root development. Improved water retention is especially beneficial in arid and semi-arid regions where water is a limiting factor for plant growth. PGPR such as *Azospirillum* and *Pseudomonas* help plants to maintain higher water-use efficiency by improving the root architecture and soil moisture availability [146, 147].

5.3 PGPR and soil health

5.3.1 Improvement of soil structure

The soil structure plays a pivotal role in soil health by influencing water retention, root penetration, and microbial diversity. PGPR contribute to better soil structure by producing EPS. These polysaccharides promote the formation of soil aggregates which improve soil porosity and water retention. EPS-producing PGPR such as *Bacillus* species help to stabilize soil aggregates and enhance soil aeration and moisture retention [145]. This also improves the capacity of the soil to support plant roots leading to enhanced root proliferation.

5.3.2 Promotion of soil microbial activity and soil health

PGPR not only improve root architecture but also enhance soil health by fostering a more diverse and active soil microbiome. The presence of beneficial microorganisms in the soil aids in nutrient cycling, organic matter decomposition, and pathogen suppression. As noted in earlier studies, PGPR enhance microbial activity in the rhizosphere by increasing the availability of nutrients such as nitrogen and phosphorus promoting the growth of other beneficial soil microbes [4]. This contributes to a healthier and more resilient soil ecosystem which benefits plant growth in the long term. PGPR enhance soil health by fostering microbial diversity in the rhizosphere. Diverse microbial communities support nutrient cycling, organic matter decomposition, and pathogen suppression. The presence of beneficial microorganisms in soil promotes long-term soil fertility and resilience to environmental stressors. Meanwhile, inoculation with PGPR increases microbial activity in the rhizosphere leading to improved nutrient cycling and higher organic matter content [146]. This enhances the overall health and fertility of the soil, thereby promoting sustainable crop production.

5.3.3 Nutrient cycling and availability

PGPR improve the availability of key nutrients in the soil particularly nitrogen, phosphorus, and iron. Many PGPR such as *Rhizobium* and *Azospirillum* fix atmospheric nitrogen making it available for plant uptake. Additionally, phosphorus-solubilizing PGPR such as *Pseudomonas* secrete organic acids that convert insoluble phosphorus into forms that plants can absorb [147]. Improved nutrient availability supports healthy root development and enhances the overall fertility of the soil.

PGPR play a critical role in nutrient cycling by facilitating the solubilization and availability of essential nutrients such as nitrogen, phosphorus, and iron. These nutrients are often present in insoluble forms which make them inaccessible to plants. PGPR such as *Rhizobium* and *Pseudomonas* enhance nutrient uptake through biological nitrogen fixation and phosphorus solubilization. Phosphorus is a limiting nutrient in many soils. PGPR can solubilize phosphate compounds by producing organic acids that convert insoluble phosphorus into forms that plants can use [52]. This increases phosphorus availability in the rhizosphere, thereby promoting root growth and overall plant health. Moreover, symbiotic PGPR such as *Rhizobium* fix atmospheric nitrogen and convert it into ammonia which plants can use for growth. This process is critical for leguminous crops and enhances soil fertility [148].

6 Attributes and applications of PGPR

In commercial agricultural practices, bacteria with plentiful beneficial characteristics are found advantageous from an economical perspective. In world today, the high production of crops along with eco-friendly biofertilizers is an indispensable need for economic growth. PGPR have been flourishing due to their impressive results as well as they are attaining great attention by different agricultural scientists [149, 150]. Various crop plants are known for their economic significance and are grown in monocultures and adaptations are required for their optimal development, growth, and production as well as their protection against pests and pathogenic organisms [151, 152]. Numerous studies have been conducted in the field of stress physiology to determine the attributes and importance of PGPR. A lot of PGPR are known which showed their remarkable results

in the plant growth promotion and their development (depicted in Table 1). At present, there is foremost need for the commercialization of important strains of PGPR and for this, it is necessary that the association between industries and research scientists is imperative. Nelson suggested that the identification and assortment of efficient PGPR strains for commercialization is a major challenge faced by research scientists [153]. Although various PGPR have been explored in laboratory settings, their commercialization in fields by farmers has also been maximized on a large scale. Therefore, PGPR products generally face various obstacles to their availability in the market. Many PGPR products are already available in the market [154]. In different countries, PGPR are already being used such as Sweden, Denmark, Belgium, Italy, Spain, Portugal, United Kindom, Austria and many others which are generally utilized as biofertilizers, rhizoremediators, phytostimulators, and bio-pesticides that may result in plant growth and development [155]. Economically available PGPR comprise *Azospirillium*, *Bacillus*, *Burkholderia*, and *Serretia* [156, 157]. Bacteria with numerous benefits have been found very advantageous in the field of commercial agriculture and are also significant for bioeconomy. It has been reported by different scientists that the mixing of a bacterium (*B. amyloliquefaciens*) with a fungus named as (*Trichoderma virens*) showed significant results in the improvement and production yield of two different crops namely corn and tomato which are commercially available in the market [155, 156]. Several commercially available bacterial biofertilizers demonstrate crop-specific advantages. For instance, companies such as Excalibur SA (ABM) integrate *Trichoderma*, a naturally occurring soil fungus with *Bradyrhizobium*, a nitrogen-fixing bacterium to enhance soybean crop growth. Moreover, inoculation with the Nitrogen fixing bacteria as PGPR (such as, *Azospirrillum* and *Azobacter*) showed half-rate of Nitrogen fertilizer application with increased seed and oil quality of sesame [157, 158].

7 Future perspectives

The significance of PGPR has been widely seen all over the world for their capability in improvement and sustainability of crops and soil fertility. This review showed the effectiveness of various PGPR for enhancing the growth, yield and development of crops. These rhizobacterial strains exert numerous beneficial effects via both direct and indirect mechanisms. Therefore, PGPR have several potential applications for the enhancement and sustainability of crops including phytohormone production, phosphate solubilization, iron sequestration by siderophores (iron chelators), and production of various vitamins and antibiotics. In addition, production of cell wall degrading enzymes, systemic resistance and mitigation of stress-induced ethylene by ACC-deaminase activity are some other activities. Different types of cropping such as mixed cropping, intercropping, and rotation of leguminous crops with non-leguminous crops have been engaged in biological nitrogen fixation. Besides these PGPRs are known for their multiple activities under normal as well as in stress conditions, their proficient role in sustainable agriculture have been noticed on a large scale. Moreover, an in-depth study is required to envisage colonization potential, establishment, and plant response under different field conditions. Therefore, it is essential to identify potent and novel unculturable rhizobacterial strains by using high throughput sequencing processes as well as systematic strategies for better efficiency should be carried out. Continued research in biotechnology may lead to the development of genetically modified PGPR strains with

Table 1 Properties, mechanisms and the associated PGPR advantageous for crop growth and development

PGPR Activity	Bacterial Species	Effect on Plant Growth	Mechanism of Action	Citations & References
Nitrogen Fixation	*Rhizobium*, *Bradyrhizobium*	Enhances nitrogen availability, improving plant growth and yields.	Symbiotic nitrogen fixation: Forms root nodules in legumes, converting atmospheric nitrogen (N_2) into ammonia (NH_3) for plant use.	[4, 30, 158]
Phosphate Solubilization	*Pseudomonas*, *Bacillus*	Increases phosphorus uptake, improving root development and energy transfer.	Solubilizes insoluble phosphorus compounds, making phosphorus available to plants.	[4, 10, 52]
Potassium Solubilization	*Bacillus mucilaginosus*, *Frateuriaaurantia*	Enhances photosynthesis and drought resistance.	Solubilizes potassium from minerals, making it accessible for plant uptake.	[72, 89]
Siderophore Production	*Pseudomonas*, *Azotobacter*	Prevents iron deficiency (chlorosis), improving growth and health.	Produces siderophores that bind iron, making it available to plants.	[10, 159, 160]
Phytohormone Production	*Azospirillum*, *Pseudomonas*	Promotes root elongation, increases biomass, and improves stress resistance.	Produces plant hormones like indole-3-acetic acid (IAA), gibberellins, and cytokinins, enhancing plant growth and stress resilience.	[161,162
ACC Deaminase Production	*Pseudomonas*, *Bacillus*	Reduces ethylene levels, promoting root and shoot growth under stress.	Produces ACC deaminase, an enzyme that breaks down ACC (ethylene precursor), reducing stress-related ethylene accumulation in plants.	[136, 163,164]
Induced Systemic Resistance (ISR)	*Bacillus*, *Pseudomonas*	Enhances pathogen resistance, reducing disease incidence.	Activates plant defense mechanisms (ISR), priming plants for faster immune responses against pathogens.	[7, 128, 132]
Antibiotic Production (Biocontrol)	*Bacillus subtilis*, *Pseudomonas fluorescens*	Protects plants from soil-borne pathogens, promoting healthier growth.	Produce antibiotics and antifungal compounds that suppress pathogen growth.	[51,133, 165]
Organic Matter Decomposition	*Pseudomonas*, *Bacillus*	Increases nutrient availability, enhancing plant health and vigor.	Breaks down organic matter, releasing essential nutrients like nitrogen, phosphorus, and potassium for plant uptake.	[4, 7, 16]
Mycorrhizal Association	*Azospirillum*, *Pseudomonas*	Enhances nutrient absorption, particularly phosphorus, improving plant health.	Promotes colonization by mycorrhizal fungi, facilitating nutrient uptake and improving plant resistance to environmental stresses.	[16, 166,167]
Hydrogen Cyanide (HCN) Production	*Pseudomonas fluorescens*, *Serratiamarcescens*	Suppresses root pathogens, promoting root health.	Produces hydrogen cyanide (HCN), which inhibits the growth of plant pathogens.	[4, 7, 137]
Biofilm Formation	*Bacillus subtilis*, *Pseudomonas*	Enhances colonization and nutrient acquisition, improving plant-microbe interactions.	Forms biofilms on root surfaces, which improve root colonization and protect against pathogens.	[137, 158, 168]
Heavy Metal Detoxification	*Pseudomonas*, *Bacillus*	Increases tolerance to heavy metal stress, improving plant growth.	Produces enzymes and siderophores that chelate heavy metals, reducing their toxicity to plants.	[4]

enhanced plant growth promoting traits. This can result in custom-designed bacteria tailored to specific crops and environmental conditions. Advances in omics technologies such as genomics, transcriptomics, proteomics, and metabolomics can provide a deeper understanding of the molecular interactions between PGPR and plants. This knowledge can be leveraged to optimize the selection and application of PGPR to improve plant growth. The manipulation and engineering of plant-associated microbial communities including PGPR could become a focus of research. Understanding the intricacies of the plant microbiome and harnessing the synergistic interactions among various microorganisms may lead to more effective and sustainable agricultural practices. The future of PGPR holds promise for addressing the challenges in agriculture and promoting more sustainable and resilient food production systems. Continued research, innovation, and collaboration will be essential in unlocking the full potential of PGPR for the benefit of global agriculture. Future perspectives will involve educating farmers, agronomists, and stakeholders about the benefits of PGPR and how to integrate them into existing agricultural practices. Meanwhile, increased awareness can drive the adoption and contribute to sustainable agricultural development.

8 Conclusion

Plant growth promoting rhizobacteria have numerous abilities that promote plant growth. They represent a powerful tool for advancing sustainable agriculture by enhancing nutrient uptake, producing phytohormones, suppressing pathogens, and improving plant resilience to abiotic stresses such as drought, salinity, and temperature extremes. Their dual role through direct mechanisms (e.g., nitrogen fixation, phosphate solubilization) and indirect mechanisms (e.g., induced systemic resistance, siderophore production) makes them multifunctional bioinoculants capable of boosting crop productivity while minimizing reliance on chemical inputs. As agriculture faces mounting challenges from climate change, food security demands, and environmental degradation, PGPR offer an eco-friendly, cost-effective, and scalable alternative. However, it is also clear that we are aware of only a small amount of their efficacy and a lot more remains unexplored. Future research should focus on exploring unculturable microbial diversity, optimizing inoculant formulations, and tailoring applications to specific crops and soil conditions. With continued innovation and commercialization, PGPR have the potential to revolutionize crop management practices making them central to the development of sustainable and climate-resilient farming systems.

Author contributions

Mir Sajad Rabani and Mahendra K. Gupta contributed equally to the conception and design of the study. Mir Sajad Rabani and Anjali Pathak were responsible for writing the manuscript and performing data analysis. Meenakshi Shrivastav prepared the diagrams and contributed to proofreading and editing. All authors including Gupta and Rabani reviewed and approved the final version of the manuscript.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Ethical approval is not applicable.

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The authors declare no competing interests.

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