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An Introduction to Mechanistic Insights into Plant Growth Promoting Bacteria for Sustainable Agriculture

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Abstract

Plant growth promoting bacteria (PGPB) contribute significantly to sustainable agriculture to enhance nutrient availability, regulating plant hormones, and improving tolerance to environmental stresses. This review provides a detailed examination of the mechanistic basis of PGPB-mediated growth promotion, including nitrogen fixation by symbiotic and free-living diazotrophs, solubilization of phosphorus and zinc through microbial metabolism, iron acquisition via siderophore production. The capacity of PGPB to modulate phytohormone levels, particularly auxins, cytokinins, gibberellins, and ethylene, plays a central role in optimizing plant growth and stress adaptation. Despite their multifunctionality, the practical application of PGPB is constrained with inconsistent field performance caused by ecological and environmental factors. Advances in microbial formulation, co-inoculation strategies, and selection of naturally efficient strains are discussed as potential solutions. This is to emphasize the necessity of integrating microbial ecology with agronomic practices with a view to fully realizing the benefits of PGPB in sustainable crop production.

Keywords: Mechanisms of plant–microbe interaction; Biological nitrogen fixation; Phosphate and zinc solubilization; Siderophore production; Phytohormone regulation.

Introduction

The increasing dependence of modern agriculture on synthetic fertilizers, particularly nitrogen- and phosphorus-based inputs derived from nonrenewable petroleum resources, has raised serious concerns regarding economic sustainability, environmental degradation, and human health. Excessive use of chemical fertilizers contributes to soil fertility decline, groundwater contamination, greenhouse gas emissions, and disruption of soil microbial communities. In this context, plant growth-promoting bacteria (PGPB) have emerged as an ecologically sound and economically viable alternative for sustainable crop production. Although atmospheric nitrogen constitutes nearly 78% of the Earth’s atmosphere, it is unavailable to plants in its molecular form and must first be reduced to ammonia before assimilation into proteins, nucleic acids, and other essential biomolecules (Bøckman, 1997). Biological nitrogen fixation (BNF), carried out exclusively by prokaryotic microorganisms, plays a central role in replenishing soil nitrogen and reducing dependence on chemical fertilizers (Giller, 2001; Saikia & Jain, 2007; Chowdhury, 2020; Chowdhury, 2022). Symbiotic nitrogen-fixing bacteria, particularly rhizobia, form highly

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efficient associations with leguminous plants, while free-living and associative diazotrophs such as *Azospirillum*, *Azotobacter*, cyanobacteria, and actinomycetes also contribute to nitrogen inputs, albeit at lower levels (James & Olivares, 1997; Shridhar, 2012). Nitrogen fixation is mediated by the nitrogenase enzyme complex, a highly conserved and energetically demanding metalloenzyme encoded by nif genes, whose expression is tightly regulated by oxygen and nitrogen availability (Dean & Jacobson, 1992, Chowdhury *et al.,* 2025). Advances in molecular genetics have demonstrated that manipulating nif gene regulation, bacterial respiration, hydrogen recycling, and oxygen protection mechanisms can significantly enhance nitrogenase efficiency and plant productivity (Ramírez et al., 1999; Marroquí *et al*., 2001; Peralta *et al*., 2004; Ureta *et al.,* 2005). However, regulatory constraints have limited the field application of genetically modified nitrogen-fixing bacteria, prompting the selection of naturally efficient strains for commercial biofertilizer development. Beyond nitrogen fixation, phosphorus solubilization represents another critical plant growth-promoting trait. Although soils often contain large amounts of total phosphorus, its bioavailability is extremely low due to fixation with calcium, iron, and aluminum or its presence in insoluble mineral and organic forms (Goldstein, 1994; Khan *et al*., 2007). Phosphate-solubilizing bacteria (PSB) mobilize unavailable phosphorus through the production of organic acids, proton extrusion, chelation, and phosphatase and phytase enzymes, thereby enhancing phosphorus uptake and plant growth (Rodriguez & Fraga, 1999; Chen *et al*., 2006; Jeffries *et al*., 2003). Numerous bacterial genera have been identified as effective PSB across diverse soil types and cropping systems. Micronutrient availability, particularly zinc and iron, also significantly influences plant productivity. Zinc deficiency is widespread in agricultural soils due to its low solubility and fixation in mineral forms, resulting in impaired auxin biosynthesis and stunted plant growth (Gandhi *et al*., 2014). Zinc-solubilizing bacteria enhance Zn bioavailability through organic acid production and pH modification, offering a sustainable alternative to chemical zinc fertilizers (Saravanan *et al*., 2007). Similarly, iron scarcity in aerobic soils has driven the evolution of microbial siderophores, high-affinity iron-chelating compounds that facilitate iron acquisition by both microbes and plants, and improve plant nutrition under iron-limiting conditions (Neilands, 1981; Guerinot & Ying, 1994; Uddin & Chowdhury, 2022; Sultana & Chowdhury, 2022). In addition to nutrient mobilization, PGPB influence plant growth by modulating phytohormone levels which regulates root architecture, lateral root formation, and nutrient uptake, although its effects are concentration-dependent and context-specific (Patten & Glick, 1996; Spaepen *et al*., 2007). Cytokinin- and gibberellin-producing bacteria further contribute to cell division, shoot and root development, and stress tolerance, often enhancing plant performance under adverse environmental conditions (Arkhipova *et al*., 2005; Bottini *et al*., 2004). Ethylene, a key stress hormone, can inhibit root elongation and nodulation when produced in excess. Many PGPB mitigate stress-induced ethylene accumulation through the enzyme ACC deaminase, which degrades the ethylene precursor ACC, thereby promoting plant growth under biotic and abiotic stress conditions such as salinity, drought, flooding, heavy metal toxicity, and pathogen attack (Glick *et al*., 2007; Ma *et al*., 2003).

Despite demonstrated benefits of PGPB, their field performance remains inconsistent due to environmental variability, competition with native microbiota, and limited rhizosphere competence. Recent strategies, including co-inoculation with complementary microorganisms, encapsulation technologies, and targeted strain selection, have shown promise in enhancing inoculant survival and efficacy (Bashan & Gonzalez, 1999). Overall, PGPB represent a cornerstone of

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environmentally sustainable agriculture which we expect mostly.

Nitrogen-fixing Bacteria

Symbiotic Nitrogen-Fixing Bacteria

Modern agriculture relies heavily on chemical nitrogen fertilizers derived from petroleum. These fertilizers are not only expensive but also deplete nonrenewable resources and pose environmental and health risks (Chowdhury & Billah, 2020). Using biological nitrogen fixation as an alternative to chemical fertilizers would be both economically and ecologically advantageous. Although nitrogen is abundant in the atmosphere, plants can only use it after it is converted to ammonia, which is incorporated into proteins, nucleic acids, and other biomolecules. Agriculturally, nitrogen-fixing microorganisms such as various *Rhizobia* species—each specific to certain host plants—are commonly used. Nitrogen-fixing (diazotrophic) bacteria use the enzyme nitrogenase, a two-component metalloenzyme, to convert atmospheric nitrogen into ammonia. Introducing leghemoglobin or bacterial hemoglobin genes (e.g., from *Vitreoscilla* sp.) into *Rhizobium* can enhance nitrogenase activity and plant nitrogen content. Ethylene produced in response to rhizobial infection can inhibit nodulation; however, certain *Rhizobia* strains counteract this by producing rhizobitoxine or ACC deaminase, reducing ethylene levels and increasing nodule number and plant biomass. Although only 1–10% of field strains naturally have ACC deaminase (Duan et al., 2009), engineered strains have shown improved nodulation and plant growth (Ma *et al*., 2004). Due to regulatory issues, genetically modified rhizobia are not widely used, but commercial inoculant producers are selecting strains with active ACC deaminase. Biological nitrogen fixation has a vital role in restoring soil nitrogen levels and reducing dependence on synthetic fertilizers. When rhizobia interact with legume roots, they form an efficient nitrogen-fixing symbiosis (Giller, 2001; Young & Haukka, 1996).

Associative Nitrogen-Fixing Bacteria

Other nitrogen-fixing bacteria are also employed, although associative bacteria typically contribute only a small fraction of fixed nitrogen directly to the plant. In free-living and associative diazotrophs, nif genes are generally chromosomal. The regulatory complexity of nif gene expression has limited efforts to genetically enhance nitrogen fixation. Since nitrogen fixation consumes large amounts of ATP, it is advantageous to direct bacterial carbon resources toward oxidative phosphorylation rather than glycogen storage. For example, a glycogen synthase–deficient *R. tropici* strain increased both nodule formation and plant dry weight in beans compared to the wild type. Genetic manipulation of nif genes can enhance nitrogen fixation, plant dry weight, seed yield, and seed nitrogen content. These effects were further amplified in a poly-β-hydroxybutyrate–negative strain, likely due to increased ATP production. A limitation of nitrogen fixation is the wasteful reduction of protons to hydrogen gas (H_2) by nitrogenase. Some diazotrophs possess hydrogenase enzymes that recycle H_2, improving nitrogen fixation and plant growth. In *Rhizobium leguminosarum*, increasing hydrogenase expression doubled activity and reduced H_2 loss, thereby increasing nitrogen availability to plants (Saikia & Jain, 2007; Lanier *et al*., 2005; Kabir *et al*., 2025; Kumar *et al*., 2025).

Free-Living Nitrogen-Fixing Bacteria

The chemical signaling between compatible rhizobial strains and legume plants, known as molecular dialogue, initiates nodule formation. Within the rhizosphere, rhizobia respond to chemotactic signals and plant-derived growth-enhancing compounds. *Azotobacter* species are obligate aerobes but can grow under low oxygen levels, and their ecological distribution depends on environmental conditions that determine soil survival. Cyanobacteria, or blue-green algae, are

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a diverse group of prokaryotes that form complex communities such as cyanobacterial mats and serve as major nitrogen fixers in freshwater, marine, and terrestrial ecosystems. In marine environments, cyanobacteria are a critical nitrogen source, with much understanding derived from studies on *Trichodesmium* spp. in tropical oligotrophic waters Cyanobacteria also fix nitrogen in terrestrial habitats ranging from rainforests to deserts due to adaptations such as desiccation resistance. Because of their nitrogen-fixing ability, cyanobacterial mats have long been used as biofertilizers. *Nostoc* and *Anabaena* are notable examples that fix nitrogen in association with the aquatic fern *Azolla*, making *Azolla* an important natural nitrogen source in wetland rice cultivation, particularly when incorporated into soil as green manure (Matthew *et al*., 2008).

Phosphate Solubilizing Bacteria

Phosphorus (P) plays a fundamental role in plant growth and development, contributing to critical physiological processes such as energy transfer, root development, and photosynthesis. Despite its importance, phosphorus is frequently found in insufficient amounts in many agricultural soils, particularly in highly weathered or intensively cultivated lands. As a result, the application of phosphatic fertilizers is often essential to meet crop nutrient demands and to offset phosphorus deficiencies arising from various soil-related constraints. Significant losses of available phosphorus occur due to strong soil fixation mechanisms and surface runoff from phosphorus-enriched fields, which further reduce its availability to plants. Phosphate ions are chemically reactive and readily interact with soil constituents, leading to their immobilization through the formation of insoluble complexes with cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^{3+}), and aluminum (Al^{3+}), depending on soil pH, mineralogy, and other physicochemical properties. Moreover, a substantial proportion of soil phosphorus is present in stable mineral and inorganic forms that undergo very slow dissolution, thereby releasing phosphorus at a rate insufficient to satisfy immediate crop requirements. Consequently, these factors collectively limit phosphorus bioavailability in soils and necessitate careful phosphorus management strategies in agricultural systems. Microorganisms play an important role in converting these insoluble inorganic phosphates into plant-available forms through mechanisms (Fig. 1) such as acidification, chelation, ion exchange, and the production of organic acids like gluconic acid (Chen *et al*., 2006).

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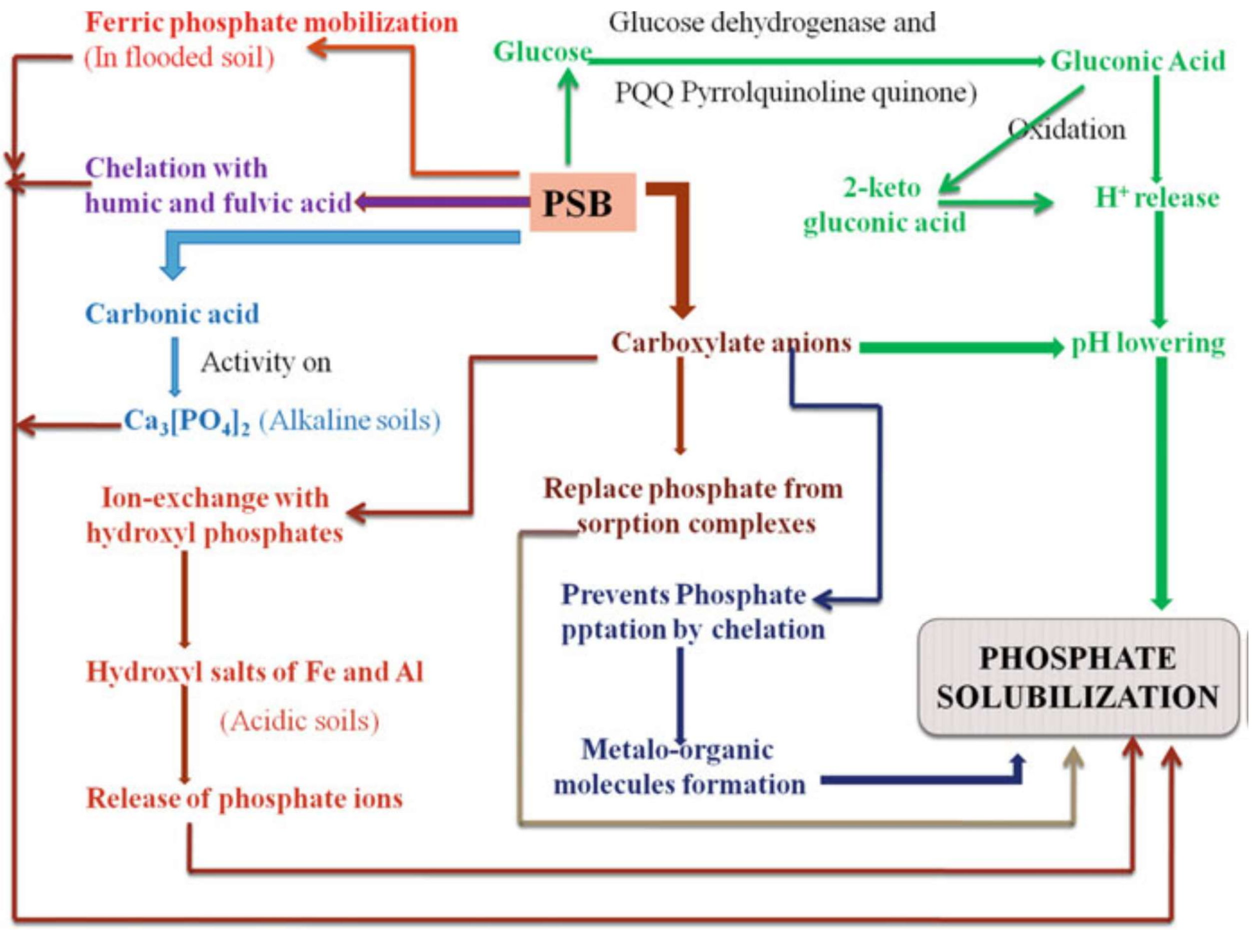

Fig. 1. Substances produced by PSB

Phosphate-solubilizing bacteria (PSB) facilitate the mobilization of phosphorus in soils primarily through several biochemical mechanisms, including the secretion of low-molecular-weight organic acids, the production of acid phosphatase enzymes, and the release of protons into the surrounding soil environment. These processes lower the pH of the rhizosphere and promote the dissolution of insoluble inorganic phosphate compounds, thereby enhancing phosphorus availability to plants. In addition to these well-established mechanisms, phytase-mediated phosphate mobilization represents another important pathway, particularly for organic forms of soil phosphorus. Organic phosphorus can constitute approximately 30–50% of the total phosphorus pool in soils, with a substantial fraction occurring as phytate, a highly stable and poorly available compound for direct plant uptake. Phytase enzymes catalyze the hydrolysis of phytate, releasing inorganic phosphate that can be readily utilized by plants. Phytase-producing rhizobacteria have been reported across a wide range of bacterial genera, including *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Serratia*, and *Staphylococcus*, highlighting their ecological diversity and functional significance in soil phosphorus cycling. Recent experimental findings further suggest that environmental factors such as salinity strongly influence phosphate solubilization efficiency. Optimal phosphorus solubilization has been observed at NaCl concentrations ranging from 0 to 1.25%, whereas higher salt levels substantially reduce bacterial activity and prolong the solubilization process, increasing the time required from approximately 48 hours to as much as 72 hours (Deshwal & Kumar, 2013). Although soils generally contain between 400 and 1,200 mg kg^{-1} of phosphorus (P), the concentration of soluble P

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is often very low, typically around 1 mg kg^{-1} or less (Goldstein, 1994). In soil systems, phosphorus (P) predominantly occurs in forms that are poorly soluble and therefore not readily available for plant uptake. These forms can be broadly classified into two major categories: inorganic mineral phosphorus and organic phosphorus compounds. The mineral phosphorus fraction mainly consists of calcium- and phosphate-bearing minerals such as apatite, hydroxyapatite, and oxyapatite, which are highly stable and dissolve very slowly under natural soil conditions. In contrast, the organic phosphorus pool comprises a diverse range of compounds derived from plant residues, microbial biomass, and soil organic matter. This fraction includes inositol phosphates (commonly referred to as phytate), as well as phosphomonoesters, phosphodiesters, and phosphotriesters, all of which require enzymatic mineralization by soil microorganisms before phosphorus can be released in a plant-available inorganic form (Khan *et al*., 2007; Mahmud *et al*., 2025).

Since phosphorus is an essential macronutrient for plants but has limited bioavailability, it is often a growth-limiting factor (Feng *et al*., 2004). To meet plants' nutritional needs, P is typically applied as chemical fertilizers produced through energy-intensive processes (Goldstein *et al*., 1993). However, only a limited proportion of the phosphorus applied through fertilizers becomes readily available for plant uptake, as approximately 75–90% of added phosphorus is rapidly immobilized in soil through precipitation reactions with various metal cations. These reactions result in the formation of sparingly soluble phosphate compounds with elements such as calcium, iron, and aluminum, depending on soil pH and mineral composition, thereby substantially reducing phosphorus bioavailability. As a result, a large pool of soil phosphorus remains unavailable to crops despite repeated fertilizer applications. In this context, phosphate-solubilizing bacteria (PSB) play a pivotal role in soil biogeochemical cycling and sustainable nutrient management. By employing diverse biochemical mechanisms to solubilize and mineralize insoluble phosphorus compounds, PSB convert fixed and unavailable phosphorus into plant-accessible forms, thereby enhancing phosphorus use efficiency, supporting plant growth, and contributing to improved soil fertility and crop productivity (Rodriguez & Fraga, 1999). The primary mechanism employed by PSB for solubilizing inorganic P is the production of low-molecular-weight organic acids, such as gluconic and citric acids (Bnayahu 1991; Rodriguez *et al*., 2004). These acids chelate cations and acidify the soil, releasing soluble phosphate (Kpomblekou & Tabatabai, 1994; Bnayahu, 1991). Additional mechanisms include proton (H^+) release (Illmer & Schinner, 1992), production of chelating compounds (Sperber 1958; Duff & Webley, 1959), and synthesis of inorganic acids (Hopkins & Whiting, 1916). Exopolysaccharides produced by PSB also indirectly aid solubilization by binding free phosphate, influencing the equilibrium of phosphate availability (Yi *et al*., 2008). Organic P is mineralized through phosphatase enzymes including phosphomonoesterases, phosphodiesterases, and phosphotriesterases which hydrolyze phosphoric esters (Rodriguez & Fraga, 1999). Some bacterial strains can perform both solubilization and mineralization of P (Tao *et al*., 2008). Several bacterial genera are capable of phosphate solubilization, including *Pseudomonas* (Di Simine *et al.,* 1998; Gulati *et al*., 2008; Park *et al*., 2009; Malboobi *et al*., 2009), *Bacillus* (De Freitas *et al*., 1997; Toro *et al*., 1997; Rojas *et al*., 2001; Sahin *et al*., 2004), *Rhizobium* (Halder *et al*., 1991; Abd-Alla, 1994; Chabot *et al*., 1996), *Burkholderia* (Tao *et al*., 2008; Jiang *et al*., 2008), *Enterobacter* (Toro *et al*., 1997; Sharma *et al*., 2005), and *Streptomyces* (Molla *et al*., 1984; Mba 1994; Hamdali *et al.,* 2008; Chang and Yang, 200). Recent research has extended beyond *Streptomyces* to investigate the potential of non-*Streptomyces* actinomycetes, including species such as *Micromonospora endolithica*, which have demonstrated a strong capacity for phosphorus solubilization in soil

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environments. These microorganisms are capable of mobilizing substantial quantities of insoluble phosphorus through the production of both acid and alkaline phosphatases, as well as through the secretion of a diverse range of organic acids that facilitate phosphate dissolution. Notably, some of these actinomycetes enhance plant growth even in the absence of other well-known plant growth–promoting substances, such as auxins, cytokinins, or gibberellins, indicating that phosphorus mobilization alone can significantly influence plant development. Nevertheless, while phosphate solubilization is a key trait associated with plant growth–promoting bacteria, its overall contribution to plant performance may, in certain cases, be less apparent when compared with other microbial activities that also affect plant growth. Despite these interacting and sometimes confounding factors, a substantial body of evidence consistently demonstrates a positive relationship between phosphate-solubilizing bacterial activity and increased phosphorus accumulation in plant tissues, underscoring the agronomic significance of PSB in enhancing nutrient uptake and crop productivity (Rodriguez & Fraga, 1999).

In addition to the fact that certain phosphate-solubilizing bacterial (PSB) strains exhibit limited competence in colonizing the rhizosphere, their overall effectiveness is strongly influenced by the specific host plant species and prevailing soil characteristics. The ability of PSB to mobilize phosphorus varies widely depending on the dominant forms of phosphate present in the soil. For example, many PSB strains are particularly efficient at solubilizing calcium-bound phosphate (Ca–P) complexes, which are commonly found in neutral to alkaline soils. In contrast, the solubilization of iron-bound phosphate (Fe–P) and aluminum-bound phosphate (Al–P), which dominate in acidic soils, occurs far less frequently and often with reduced efficiency. As a result, the release of plant-available soluble phosphorus tends to be substantially higher in calcareous soils rich in Ca–P compounds, whereas phosphorus mobilization is comparatively limited in soil types such as alfisols, where Fe–P and Al–P forms are more prevalent (Gyaneshwar *et al.*, 2002). In many soil systems, even when phosphate-solubilizing bacterial (PSB) populations are present at relatively high densities, the concentration of soluble phosphorus does not always increase in direct proportion to their abundance. This lack of a linear response may be attributed to several factors, including the physiological condition and metabolic activity of the bacterial cells, which strongly influence their phosphate-solubilizing efficiency. Moreover, the quantity of phosphorus released solely through microbial solubilization processes is, in some cases, insufficient to bring about a substantial improvement in plant biomass or overall growth performance. To overcome these limitations, agricultural practices often involve the inoculation of crops with PSB at concentrations significantly higher than those naturally occurring in soils, with the aim of enhancing phosphorus availability in the rhizosphere. However, inconsistent outcomes across different crops, soil types, and environmental conditions have constrained the widespread commercial adoption of PSB-based biofertilizers. To improve their field performance and longevity, various formulation strategies have been developed, among which the encapsulation of PSB cells in non-toxic polymeric materials such as alginate has shown considerable promise. This approach not only prolongs the shelf life of the inoculant but also protects bacterial cells from environmental stresses, facilitates their survival in soil, and enables a gradual and sustained release of viable microorganisms into the soil environment (Bashan & Gonzalez, 1999; Bashan *et al.*, 2002). Encapsulation often proves more effective than applying free-living bacterial suspensions, improving plant growth promotion and phosphate solubilization activity, as seen in lettuce (*Lactuca sativa*) inoculated with encapsulated *Enterobacter* cells (Vassileva *et al.*,

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1999, 2000, 2006a, b; Vassilev and Vassileva, 2004). Maximum plant growth stimulation is often achieved when PSB are co-inoculated with bacteria possessing complementary abilities, such as nitrogen fixation (Valverde *et al*., 2006; Matias *et al*., 2009), or with mycorrhizal (Ray *et al*., 1981; Azcón-Aguilar *et al*., 1986; Babana and Antoun, 2006; Matias *et al*., 2009) or nonmycorrhizal fungi (Babana & Antoun, 2006). The use of mixed microbial inoculants possessing multiple plant-beneficial traits has emerged as a promising strategy to enhance nutrient availability and overall plant performance. For instance, mangrove seedlings co-inoculated with the nitrogen-fixing bacterium *Phyllobacterium* sp. and the phosphate-solubilizing bacterium *Bacillus licheniformis* exhibited significantly higher levels of biological nitrogen fixation and phosphate solubilization than seedlings treated with either microbial culture alone. This synergistic interaction between functionally distinct microorganisms highlights the advantage of using consortium-based inoculants, as combined activities can more effectively improve nutrient cycling, nutrient uptake, and plant growth than single-strain applications (Rojas *et al*., 2001). When these two bacterial strains were co-cultured under in vitro conditions, clear metabolic interactions were observed, whereby each microorganism influenced the physiological activity of the other. Specifically, co-cultivation resulted in enhanced nitrogen fixation by *Phyllobacterium* sp. and increased phosphate-solubilizing activity in *Bacillus licheniformis*, suggesting a degree of functional synergy between the two organisms. Despite these positive microbial interactions, no statistically significant differences in plant growth were detected between plants receiving the combined inoculation and those treated with individual bacterial strains, indicating that enhanced microbial activity does not always translate directly into measurable plant growth responses. As an alternative strategy to improve the effectiveness of plant growth–promoting bacteria (PGPB), genetic engineering approaches have been proposed to enable the expression or overexpression of genes involved in phosphate solubilization and related traits. Such targeted genetic modifications may enhance inoculant performance while minimizing competition among microorganisms, a common challenge associated with mixed inoculant formulations. Nevertheless, despite the scientific potential of genetically modified PGPB, the environmental release of genetically engineered microorganisms remains highly controversial in many regions of the world, largely due to regulatory restrictions and political or societal concerns rather than fundamental scientific or technical limitations (Rodriguez *et al*., 2006).

However, a significant constraint in the practical and large-scale application of these microorganisms lies in their inconsistent performance in mobilizing phosphorus under field conditions. Such variability is often attributed to intense competition with indigenous soil microbial communities, which can limit the establishment, survival, and functional activity of introduced phosphate-solubilizing bacteria (PSB). In addition, fluctuating environmental factors such as soil pH, moisture content, temperature, and nutrient status can further restrict the growth and metabolic efficiency of PSB, thereby reducing their capacity to solubilize phosphorus. Moreover, a portion of the soluble phosphorus released through microbial activity may be rapidly assimilated into microbial biomass, temporarily immobilizing it and consequently decreasing its immediate availability for plant uptake. This microbial immobilization can also influence phosphorus dynamics by slowing its fixation into insoluble forms, adding further complexity to the net availability of phosphorus in soil–plant systems.

Zinc Solubilizing Bacteria

Zinc is a vital micronutrient required for a wide array of metabolic processes in plants, and its deficiency can significantly impair crop growth, development, and productivity. Intensive

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agricultural practices and conventional soil management often deplete large amounts of zinc from the soil's natural reserves, creating a reliance on external zinc supplementation. Although total zinc concentrations in soils may appear adequate, much of this zinc exists in poorly soluble mineral forms, including smithsonite ($ZnCO_3$), sphalerite (ZnS), zincite (ZnO), franklinite ($ZnFe_2O_4$), willemite (Zn_2SiO_4), and hopeite ($Zn_3(PO_4)_2 \cdot 4H_2O$), which are largely unavailable to plants. Consequently, substantial quantities of zinc fertilizers are frequently required to fulfill crop nutrient demands. Even so, applied zinc compounds, such as zinc sulfate, often undergo chemical transformations that render them unavailable; for example, $Zn(OH)_2$ forms at pH 7.7–9.1, $ZnCO_3$ precipitates in calcium-rich alkaline soils, and $Zn(PO_3)_4$ forms in neutral to alkaline soils with high phosphorus content, resulting in accumulation of zinc in non-bioavailable forms. Zinc deficiency in plants is closely linked to reduced levels of auxins, particularly indole-3-acetic acid (IAA), as zinc is an essential cofactor in IAA biosynthesis. A deficiency in IAA leads to stunted plant growth and poor development. Several rhizospheric bacteria are capable of producing IAA in vitro, either in the presence or absence of tryptophan, the main physiological precursor of this phytohormone. This underscores the importance of developing strategies to release sufficient zinc from its unavailable soil forms to support normal plant growth. Soil microorganisms enhance zinc availability primarily through the secretion of organic acids, which chelate metal cations and reduce rhizospheric pH, facilitating solubilization. Interestingly, the addition of ZnO or $ZnCO_3$ does not always lead to a measurable drop in medium pH, likely due to the buffering properties of these compounds; notably, ZnO can consume two protons per mole during solubilization, affecting pH dynamics. The production of gluconic acid is closely linked to the phosphorylative and direct oxidative pathways of glucose metabolism, mediated by pyrroloquinoline quinone (PQQ)-dependent glucose and gluconate dehydrogenases. Therefore, isolating and characterizing zinc-solubilizing bacteria represents an environmentally sustainable and effective approach for alleviating zinc deficiency in crops, reducing the need for excessive chemical fertilizer application while promoting plant growth and productivity (Saravanan *et al*., 2007).

Iron Chelation and Siderophores

Iron is the fourth most abundant element in the Earth's crust, yet in aerobic soils, it predominantly exists in forms such as hydroxides, oxyhydroxides, and oxides, which are poorly soluble and therefore largely unavailable to living organisms. The concentration of bioavailable iron in soil is extremely low, ranging from approximately 10^{-7} M at pH 3.5 to as little as 10^{-23} M at pH 8.5. Both microorganisms and plants have relatively high iron requirements—on the order of 10^{-5} to 10^{-7} M for bacteria and 10^{-4} to 10^{-9} M for plants—making iron limitation a critical challenge, particularly in the rhizosphere where bacteria, fungi, and plant roots compete for this essential micronutrient. To overcome iron scarcity, bacteria produce low-molecular-weight chelators known as siderophores, which exhibit exceptionally high affinity for Fe^{3+} (with association constants, Ka, ranging from 10^{23} to 10^{52}). Bacteria also possess specific membrane receptors that facilitate uptake of the Fe–siderophore complex, ensuring efficient iron acquisition under limiting conditions. Among these siderophores, many *Pseudomonas* species and related genera secrete water-soluble, yellow–green fluorescent pigments known as pyoverdines. Structurally, pyoverdines consist of a quinoline-derived chromophore, a peptide chain, and an acyl side chain, which collectively give bacterial colonies their characteristic fluorescence. To date, approximately 100 distinct pyoverdines have been identified, representing about 20% of all known microbial siderophores. The ability to produce pyoverdines confers a

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competitive advantage to fluorescent pseudomonads by enhancing iron acquisition relative to other microorganisms. Pyoverdine synthesis is tightly regulated not only by iron availability but also through quorum-sensing mechanisms mediated by N-acyl homoserine lactone signaling, which coordinates production based on bacterial population density. Plants have evolved two main strategies to acquire iron from soils. Strategy I, employed by dicotyledons and non-graminaceous monocots, involves acidifying the rhizosphere through proton (H^+) extrusion and reducing Fe^{3+} to the more soluble Fe^{2+} form, which can then be taken up by root cells via specific transporters. In contrast, Strategy II, characteristic of grasses and other graminaceous plants such as wheat, barley, rice, and maize, relies on the secretion of specialized Fe^{3+} chelators called phytosiderophores. These compounds bind ferric iron to form soluble Fe–phytosiderophore complexes, which are subsequently recognized and absorbed by dedicated root transporter proteins, allowing efficient iron uptake under conditions of low soil availability (Curie *et al*., 2001; Von Wirén *et al*., 1994). Iron availability in the rhizosphere is influenced by soil characteristics as well as plant- and microbe-derived compounds (Robin *et al*., 2008; Lemanceau *et al*., 2009). Iron nutrition in plants can also shape rhizosphere microbial communities. For instance, transgenic tobacco plants overexpressing ferritin accumulate more iron, leaving less bioavailable iron in the rhizosphere. This change significantly altered the composition of the bacterial community compared to nontransformed plants (Robin *et al*., 2006). Siderophores play a key role in both promoting plant growth and enhancing plant health (Robin *et al*., 2008). Their benefits have been demonstrated by supplying radiolabeled ferric-siderophores to plants as the sole iron source (Crowley *et al.,* 1988; Duijff *et al*., 1994a, b; Walter *et al*., 1994; Yehuda *et al*., 1996; Siebner-Freibach *et al*., 2003; Jin *et al*., 2006). Evidence for their role in plant nutrition is also seen in the absence of iron-deficiency symptoms, such as chlorosis, and the relatively high iron content in roots of plants grown in nonsterile soil compared to sterile conditions (Masalha *et al*., 2000). For instance, mung bean (*Vigna radiata* L. Wilzeck) plants inoculated with the siderophore-producing *Pseudomonas* strain GRP3 exhibited less chlorosis and higher chlorophyll levels under iron-limiting conditions than uninoculated plants (Sharma *et al*., 2003). Similarly, the Fe–pyoverdine complex produced by *Pseudomonas fluorescens* C7 was efficiently taken up by *Arabidopsis thaliana*, increasing iron content in plant tissues and improving growth (Vansuyt *et al*., 2007). Bacterial siderophores are particularly important under environmental stresses such as heavy metal contamination. Microbial metabolites, especially siderophores, can bind various metals including magnesium, manganese, chromium (III), gallium (III), cadmium, copper, nickel, arsenic, lead, zinc, and radionuclides like plutonium (IV), as well as iron (Malik, 2004; Nair *et al*., 2007). By supplying iron to plants, siderophores can also help mitigate stress caused by elevated soil metal concentrations (Diels *et al*., 2002; Belimov *et al*., 2005; Braud *et al*., 2006). For example, *Kluyvera ascorbata*, a PGPB capable of producing siderophores, protected canola, Indian mustard, and tomato from nickel, lead, and zinc toxicity, with the siderophore-overproducing mutant SUD165/26 providing even greater protection, as evidenced by increased plant biomass and chlorophyll in nickel-contaminated soil (Burd *et al*., 1998, 2000).

Nevertheless, the contribution of siderophores to the mitigation of metal-induced stress is not always consistent and can depend on the specific metal and plant–microbe interaction. For example, in *Arabidopsis thaliana* exposed to nickel toxicity, studies with *Pseudomonas putida* ARB86 revealed that both a siderophore-deficient mutant and a siderophore-overproducing mutant were equally effective in alleviating nickel-induced stress symptoms, performing similarly to the wild-type strain. This observation suggests that nickel detoxification in

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this system may occur through mechanisms independent of siderophore production, highlighting that the protective role of siderophores can be context-specific and that other bacterial processes may contribute to metal stress alleviation in plants (Someya *et al*., 2007). Similarly, studies have shown that two siderophore-producing bacterial strains were able to decrease zinc uptake in willow (*Salix caprea*), indicating that bacterial siderophores can chelate metals in the soil and consequently restrict their availability for plant absorption. In contrast, a *Streptomyces* strain lacking siderophore production was found to enhance the uptake of both zinc and cadmium by plants, demonstrating that mechanisms other than siderophore-mediated chelation can significantly influence metal accumulation. These findings underscore the complexity of plant–microbe–metal interactions and suggest that multiple bacterial traits, beyond siderophore synthesis, contribute to the modulation of metal availability and uptake in plants (Kuffner *et al*., 2008).

Overall, the influence of siderophores in soils contaminated with metals is highly complex and context-dependent. Their effects are shaped by multiple factors, including the chemical and physical composition of the soil, the specific types and concentrations of metals present, the chemical nature and affinity of the siderophore involved, and the plant species under consideration. Consequently, the role of siderophores in modulating metal availability and plant uptake cannot be generalized and must be assessed individually for each soil–plant–microbe system to accurately determine their impact.

Modulation of Phytohormone Levels

Phytohormones, including auxins, cytokinins, gibberellins, ethylene, and abscisic acid (ABA), play a fundamental role in controlling and coordinating various aspects of plant growth and developmental processes (Salisbury & Ross, 1992). When plants are exposed to suboptimal or stressful environmental conditions, the endogenous concentrations of these hormones may be insufficient to sustain optimal growth, development, or productivity. To address this limitation, commercial plant growth stimulants often incorporate specific phytohormones or hormone-like compounds that can enhance critical physiological processes, such as seed and tuber germination, root initiation and elongation, vegetative growth, or fruit maturation and ripening. These exogenous applications help to compensate for hormonal deficiencies, thereby improving plant performance under challenging conditions (Tsakelova *et al*., 2006). Many microorganisms in the rhizosphere are capable of producing or influencing phytohormone levels under laboratory conditions (De Salamone *et al*., 2005; Sharmin *et al*., 2025; Mahmud *et al*., 2025). As a result, plant growth-promoting bacteria (PGPB) that can alter hormone levels may significantly influence the plant's hormonal balance.

Auxin

Auxins are key regulators of plant growth and development, influencing cell division, elongation, and differentiation, as well as promoting processes such as seed and tuber germination, xylem and root development, and overall vegetative growth. They play a central role in inducing lateral and adventitious roots, mediating responses to environmental cues like light and gravity, and contributing to flowering and fruit formation. In addition, auxins affect photosynthetic activity, pigment synthesis, metabolite production, and plant responses to various stresses (Tsakelova *et al*., 2006). Among naturally occurring auxins, indole-3-acetic acid (IAA) is the most extensively studied, and the terms "auxin" and "IAA" are often used interchangeably. In plants, IAA is predominantly found in conjugated forms, which are essential for its transport, storage, and protection from enzymatic degradation (Seidel *et al*., 2006).

The physiological effects of auxins are highly dependent on plant species, tissue type, and developmental stage, with effective

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concentrations varying widely. Suboptimal levels of auxin may have little or no effect, while excessive concentrations can inhibit growth (Peck & Kende, 1995). For instance, primary root elongation in *Arabidopsis thaliana* seedlings was promoted only by exogenous IAA concentrations in the narrow range of 10^{-10} to 10^{-12} M (Evans *et al*., 1994). Soil microorganisms capable of producing auxins can modulate the endogenous auxin pool of plants. The effect of bacterial IAA on plant growth can be either beneficial or detrimental, depending on the plant's intrinsic auxin levels and sensitivity. Bacterial IAA may optimize the plant's hormonal balance to stimulate growth, or, if present in excess, it may surpass physiological thresholds and inhibit development (Pilet & Saugy, 1987).

Auxin production is widespread among soil microorganisms, with estimates suggesting that approximately 80% of soil bacteria, including streptomycetes, methylobacteria, cyanobacteria, and certain archaea, are capable of synthesizing indole-3-acetic acid (IAA). While some of these bacteria are pathogenic, many are free-living or symbiotic plant growth–promoting bacteria (PGPB) that contribute positively to plant development. Bacterial IAA is predominantly produced via tryptophan-dependent pathways, which include indole-3-acetamide, indole-3-pyruvate, tryptamine, tryptophan side-chain oxidase, and indole-3-acetonitrile pathways, as well as tryptophan-independent routes. These pathways may be constitutively expressed or inducible and can be encoded on chromosomal or plasmid DNA. Environmental factors such as stress conditions, pH fluctuations, osmotic changes, carbon starvation, and root exudates can influence IAA biosynthesis, though regulatory mechanisms vary among pathways and bacterial species, making it difficult to define a universal model of IAA regulation. Bacterial IAA plays a pivotal role in plant–microbe interactions, particularly in promoting root development and nodulation. It enhances lateral and adventitious root formation, improving nutrient and water uptake while stimulating microbial colonization on root surfaces. For example, the PGPB *Pseudomonas putida* GR12-2, which produces moderate levels of IAA, increased taproot elongation in canola seedlings by 35–50% compared with an IAA-deficient mutant or uninoculated controls. Conversely, inoculation with an IAA-overproducing mutant of the same strain on mung bean cuttings resulted in a greater number of roots that were shorter, due to a combined effect of auxin and ethylene: bacterial IAA elevated ACC synthase activity, increasing ACC and ethylene levels, which subsequently inhibited root elongation. These observations indicate that IAA production alone does not fully account for the plant growth promoting effects of *P. putida* GR12-2. Most *Rhizobium* species also produce IAA (Badenochjones *et al*., 1983), and modulation of auxin levels within host plants is important for nodule formation. Application of low exogenous IAA concentrations (up to 10^{-8} M) can enhance nodulation in *Medicago* and *Phaseolus vulgaris*, whereas higher concentrations are inhibitory. Furthermore, IAA concentrations are higher in root nodules than in non-nodulated roots. Mutants of *Bradyrhizobium elkanii* deficient in IAA synthesis form fewer nodules on soybean roots compared to the wild type, and nodules induced by low-IAA mutants of *Rhizobium* sp. NGR234 contain less IAA than those formed by the wild-type strain, indicating that a portion of nodule IAA is of bacterial origin. IAA-producing PGPB can also enhance plant tolerance to environmental stresses. For instance, IAA promoted root and shoot elongation in wheat seedlings under high salinity conditions. Similarly, inoculation of *Medicago truncatula* with the IAA-overproducing strain *Sinorhizobium meliloti* DR-64 improved salt tolerance, leading to increased proline accumulation and elevated activities of antioxidant enzymes such as superoxide dismutase, peroxidase, glutathione reductase, and ascorbate peroxidase, compared to plants inoculated with the parental strain. IAA is also rapidly biodegradable, and several bacteria

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capable of degrading IAA have been isolated from soils and plant tissues. In *Pseudomonas putida* 1290, the iac locus, a cluster of ten genes, was identified for IAA catabolism and shows similarity to genes involved in the degradation of indole and related aromatic compounds (Leveau & Gerards, 2008). Through IAA degradation or inactivation, bacteria can modulate the plant's auxin pool, thereby influencing plant growth, development, and physiological responses.

IAA

While plants are capable of synthesizing their own indole-3-acetic acid (IAA), rhizospheric microorganisms also make a substantial contribution to the overall auxin pool available to plants. The auxins produced by plants and microbes differ primarily in their biosynthetic origins, which are influenced by the specific species involved. Numerous bacterial genera are capable of producing significant quantities of IAA, thereby influencing plant development and growth. In the context of *Rhizobium–legume* symbiosis, microbial auxin plays a critical role in modulating the expression of plant genes involved in signal recognition and facilitates bacterial attachment to the root surface, processes that are essential for successful nodule formation and the establishment of a functional symbiotic relationship (De Salamone *et al.*, 2005).

Cytokinins and Gibberellins

Cytokinins, which are N6-substituted aminopurines, serve as central regulators of a wide range of plant physiological processes. They are involved in promoting cell division, breaking bud dormancy, activating seed germination, enhancing branching and root growth, increasing chlorophyll content, expanding leaf area, and delaying senescence. Cytokinins also regulate the expression of expansin proteins, which loosen plant cell walls and facilitate turgor-driven cell expansion, thereby influencing both cell size and shape. The gene responsible for cytokinin synthesis was first identified in *Agrobacterium tumefaciens* and later discovered in methylotrophic and methanotrophic bacteria, highlighting the capacity of many plant growth-promoting bacteria (PGPB) to produce cytokinins. Interestingly, the plant gene encoding isopentenyl-transferase, the key cytokinin biosynthesis enzyme, was not definitively identified until 2000, confirming that plants synthesize cytokinins endogenously. Inoculation of seeds with cytokinin-producing bacteria generally elevates cytokinin levels in plants, resulting in enhanced growth and developmental processes. Environmental stresses, such as drought, can also increase endogenous cytokinin concentrations, occasionally triggering higher ethylene production that may inhibit root elongation. In legumes, higher plant cytokinin levels positively correlate with the ability of *Rhizobia* to form nodules. Cytokinins are also important for rhizobial infection and nodule differentiation; for example, a *Rhizobium* strain engineered to produce the cytokinin trans-zeatin, but unable to synthesize Nod factors, induced nodule-like structures on *Medicago sativa* roots, although these structures were not colonized by the bacteria. This finding suggests that cytokinins can partially mimic the morphogenetic effects of Nod factors. Recent studies emphasize the role of cytokinin receptors in mediating plant growth stimulation by cytokinin-producing PGPB. For instance, *Bacillus megaterium* UMCV1 promoted growth in *Arabidopsis thaliana* by inducing short taproots, highly branched lateral roots, and elongated root hairs, effects attributed solely to cytokinin production and independent of auxin or ethylene signaling. Given that many cytokinin-producing PGPB enhance growth across diverse crops, these effects are likely mediated by multiple cytokinin receptor homologs (Patil & Patil, 2012).

Gibberellins (GAs) are diterpenoid acids found in plants, fungi, and bacteria, composed of isoprene units that typically form four-ring structures. To date, over 130 different gibberellins have been identified. GAs regulate

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cell division and elongation and are involved in crucial developmental processes, including seed germination, stem elongation, flowering, fruit setting, and delaying senescence. They also affect root growth by influencing root hair formation and often interact with other phytohormones to modulate the plant's overall hormonal balance and growth patterns. Bacterial gibberellin production was first reported in *Azospirillum brasilense* and *Rhizobium* species and has since been observed in various root-associated bacteria. Plant growth promotion by gibberellin-producing PGPB is frequently associated with increased GA levels in plant tissues. These changes may result from direct bacterial synthesis, deconjugation of glucosylgibberellins, or chemical activation of previously inactive gibberellin forms, collectively contributing to enhanced plant growth and development (Patil & Patil, 2012; Rahman *et al*., 2025). Cytokinins are adenine-derived compounds, with zeatin being the most prominent and widely studied member of this group. Numerous rhizosphere-associated bacteria are capable of synthesizing cytokinins in pure culture, and these bacterial cytokinins can be incorporated into the plant's endogenous cytokinin pool, thereby influencing various growth and developmental processes. It is generally believed that cytokinins produced by rhizospheric bacteria contribute to maintaining the plant's internal cytokinin balance, which in turn affects physiological processes such as cell division, overall growth, nutrient transport, delay of senescence, and enhancement of plant defense responses. Through these mechanisms, cytokinins play a crucial role in balancing plant growth and stress resistance. For example, Großkinsky *et al.* (2016) demonstrated that *Pseudomonas fluorescens* G20–18 effectively suppresses *Pseudomonas syringae* infection in *Arabidopsis*, helping to preserve tissue integrity and maintain overall biomass. Mutant strains of G20–18 deficient in cytokinin production exhibited reduced biocontrol activity, whereas restoring cytokinin synthesis reinstated the protective effect, highlighting the importance of bacterial cytokinins in plant–microbe interactions. Cytokinin and auxin production can also act as virulence factors in pathogenic bacteria such as *Agrobacterium tumefaciens*, which induces crown gall formation by transferring genes encoding auxin and cytokinin synthesis into the plant genome. Similarly, *Agrobacterium rhizogenes* interferes with plant cytokinin metabolism, causing the formation of excessive roots at infection sites rather than callus tissue, further illustrating how bacterial manipulation of cytokinin pathways can significantly alter plant morphology and development (Lugtenberg *et al*., 2013).

ACC-Deaminase Activity

Under various environmental stresses plants synthesize 1-aminocyclopropane-1-carboxylate (ACC), a direct precursor of the growth hormone ethylene (Glick *et al*., 2007). Elevated ethylene levels under stress can inhibit plant growth and development. Certain plant growth-promoting rhizobacteria (PGPR) possess ACC-deaminase activity, an enzyme that hydrolyzes ACC into α-ketobutyrate and ammonia, thereby lowering ethylene concentrations in plants and mitigating its negative effects. Bacteria exhibiting ACC-deaminase activity have been identified in multiple genera. Soilborne fluorescent pseudomonads, in particular, have garnered considerable attention due to their metabolic versatility, strong root-colonizing ability, and capacity to produce a range of enzymes and metabolites that help plants tolerate both biotic and abiotic stresses. Glick *et al.* (1999) proposed a model explaining how ACC-deaminase-producing PGPR reduce ethylene levels and promote plant growth. In this model, PGPR first colonize the seed surface or root system in response to tryptophan and other amino acids released by seeds. The bacteria then synthesize indole-3-acetic acid (IAA), which, in combination with plant-derived IAA, stimulates ACC synthase activity, converting S-adenosyl-L-methionine into ACC. By metabolizing ACC via

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ACC-deaminase, inoculated PGPR effectively reduce stress-induced ethylene accumulation, enabling plants to maintain growth and resilience under adverse environmental conditions (Saini *et al*., 2015).

Ethylene

Ethylene biosynthesis in higher plants involves three key enzymes. First, S-adenosyl-L-methionine (SAM) synthetase catalyzes the conversion of methionine into SAM. Next, 1-aminocyclopropane-1-carboxylic acid (ACC) synthase hydrolyzes SAM into ACC and 5′-methylthioadenosine. Finally, ACC oxidase converts ACC into ethylene, carbon dioxide, and cyanide. Ethylene plays a crucial role in multiple aspects of plant development, including fruit ripening, flower senescence, and leaf or petal abscission, and it is also essential for plant responses to a wide range of biotic and abiotic stresses. The term “stress ethylene” refers to the elevated ethylene production triggered by environmental challenges such as extreme temperatures, high light intensity, flooding, drought, exposure to toxic metals or pollutants, radiation, wounding, herbivory, salinity, and pathogen infection (Morgan & Drew, 1997).

The effects of stress-induced ethylene can be dual: it may exacerbate stress symptoms or activate protective responses that improve plant survival, depending on factors such as plant species, developmental stage, and the nature of the stress. This is described by a two-phase model: an initial small ethylene peak triggers protective mechanisms, including the transcription of pathogenesis-related genes and the establishment of acquired resistance. If stress persists, a second, larger ethylene peak occurs within 1–3 days, leading to senescence, chlorosis, and organ abscission, which can significantly reduce plant growth and survival. In 1978, an enzyme capable of degrading the ethylene precursor ACC into ammonia and α-ketobutyrate was first isolated from *Pseudomonas* sp. strain ACP. Subsequent research revealed that ACC deaminase activity is widespread among soil microorganisms, including fungi such as *Penicillium citrinum* and numerous bacterial genera (Ma *et a*l., 2003). For instance, approximately 12% of *Rhizobium* isolates from southern and central Saskatchewan were found to possess ACC deaminase. Bacterial IAA, together with endogenous plant IAA, can stimulate plant growth or induce ACC synthase, converting SAM to ACC. Some ACC is exuded from roots or seeds, where it is taken up by bacteria and degraded by ACC deaminase into ammonia and α-ketobutyrate, thereby lowering ethylene levels that could otherwise inhibit plant growth. Under controlled conditions, inoculation with ACC deaminase-producing bacteria predominantly enhances root elongation. These bacteria also improve nodulation and mycorrhizal colonization by locally reducing ethylene concentrations, as observed in crops such as pea and cucumber. Overall, ACC deaminase-producing bacteria help plants cope with a broad spectrum of ethylene-inducing stresses, including flooding, contamination with organic pollutants such as polycyclic aromatic hydrocarbons and petroleum hydrocarbons, heavy metal toxicity (e.g., nickel, lead, zinc, copper, cadmium, cobalt, and arsenic), salinity, drought, and pathogen attack, thus promoting plant growth and resilience under adverse environmental conditions (Wang *et al*., 2000; Hao *et al*., 2007).

Conclusion

The collective findings discussed in this review underscore plant growth-promoting bacteria (PGPB) as essential contributors to sustainable and resilient agricultural systems. PGPB enhance plant growth, nutrition, and stress tolerance through a wide range of complementary mechanisms, including biological nitrogen fixation, solubilization of phosphate and zinc, siderophore-mediated iron acquisition, modulation of phytohormones, and ACC-deaminase-mediated alleviation of stress-induced ethylene accumulation. By performing these multifunctional roles, PGPB enable crops to utilize soil nutrient reserves more efficiently

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and reduce reliance on synthetic fertilizers derived from nonrenewable resources. Nitrogen-fixing bacteria, particularly rhizobia and associative diazotrophs, are central to replenishing soil nitrogen pools and improving plant productivity, while phosphate-solubilizing and micronutrient-mobilizing bacteria address critical limitations in the availability of phosphorus, zinc, and iron. In addition to nutrient acquisition, PGPB influence plant growth by regulating hormonal balances: through the production or degradation of auxins, cytokinins, gibberellins, and ethylene, these bacteria optimize root system architecture, developmental dynamics, and responses to both biotic and abiotic stresses. Collectively, these integrative functions highlight the ecological sophistication of plant–microbe interactions in the rhizosphere and illustrate the potential of PGPB to contribute significantly to environmentally sustainable and productive agricultural systems. Despite their proven potential, the inconsistent performance of PGPB under field conditions remains a major challenge, largely due to environmental variability, competition with native microbiota, and limited rhizosphere competence. Emerging strategies such as strain selection, co-inoculation with complementary microorganisms, and encapsulation technologies offer promising avenues to improve inoculant survival, efficacy, and reproducibility. While genetic engineering presents additional opportunities to enhance specific plant-beneficial traits, its application is constrained by regulatory and societal considerations, emphasizing the importance of exploiting naturally efficient strains. Overall, PGPB represent a scientifically robust and environmentally sound alternative to conventional agrochemical inputs. Their integration into crop management practices has the potential to improve nutrient use efficiency, maintain soil health, mitigate environmental impacts, and ensure long-term agricultural sustainability. Continued interdisciplinary research, coupled with advances in formulation and delivery technologies, will be crucial for translating the biological potential of PGPB into reliable field-level benefits for global food production systems.

References

Abd-Alla, M. H. (1994). Use of organic phosphorus by *Rhizobium leguminosarum* biovar *viciae* phosphatases. *Biology and Fertility of Soils, 18*, 216–218.

Arkhipova, T. N., Veselov, S. U., Melentiev, A. I., Martynenko, E. V., & Kudoyarova, G. R. (2005). Ability of bacterium *Bacillus subtilis* to produce cytokinins and to influence the growth and endogenous hormone content of lettuce plants. *Plant and Soil, 272*, 201–209.

Azcón-Aguilar, C., Gianinazzi-Pearson, V., Fardeau, J. C., & Gianinazzi, S. (1986). Effect of vesicular-arbuscular mycorrhizal fungi and phosphate-solubilizing bacteria on growth and nutrition of soybean in a neutral-calcareous soil amended with ^{32}P-^{45}Ca-tricalcium phosphate. *Plant and Soil, 96*, 3–15.

Babana, A. H., & Antoun, H. (2006). Effect of Tilemsi phosphate rock-solubilizing microorganisms on phosphorus uptake and yield of field-grown wheat (*Triticum aestivum* L.) in Mali. *Plant and Soil, 287*, 51–58.

Bashan, Y., & Gonzalez, L. E. (1999). Long-term survival of the plant growth-promoting bacteria *Azospirillum brasilense* and *Pseudomonas fluorescens* in dry alginate inoculant. *Applied Microbiology and Biotechnology, 51*, 262–266.

Bashan, Y., Hernandez, J. P., Leyva, L. A., & Bacilio, M. (2002). Alginate microbeads as inoculant carriers for plant growth-promoting bacteria. *Biology and Fertility of Soils, 35*, 359–368.

Belimov, A. A., Hontzeas, N., Safronova, V. I., Demchinskaya, S. V., Piluzza, G., Bullitta, S., & Glick, B. R. (2005). Cadmium-tolerant plant growth-promoting bacteria associated with the roots of Indian mustard (*Brassica juncea* L. Czern.). *Soil Biology and Biochemistry, 37*, 241–250.

Bnayahu, B. Y. (1991). Root excretions and their environmental effects: Influence on availability of phosphorus. In Y. Waisel, A. Eshel, & U.

https://doi.org/10.5281/zenodo.18068530

Kafkafi (Eds.), *Plant roots: The hidden half* (pp. 529–557).

Bøckman, O. C. (1997). Fertilizers and biological nitrogen fixation as sources of plant nutrients: Perspectives for future agriculture. *Plant and Soil, 194*, 11–14.

Bottini, R., Cassán, F., & Piccoli, P. (2004). Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. *Applied Microbiology and Biotechnology, 65*, 497–503.

Boukhalfa, H., & Crumbliss, A. L. (2002). Chemical aspects of siderophore mediated iron transport. *Biometals, 15*, 325–339.

Braud, A., Jézéquel, K., Vieille, E., Tritter, A., & Lebeau, T. (2006). Changes in extractability of Cr and Pb in a polycontaminated soil after bioaugmentation with microbial producers of biosurfactants, organic acids and siderophores. *Water, Air, and Soil Pollution, 6*, 261–279.

Budzikiewicz, H. (2004). Siderophores of the Pseudomonadaceae sensu stricto (fluorescent and non fluorescent *Pseudomonas* spp.). In W. Herz, H. Falk, & G. W. Kirby (Eds.), *Progress in the chemistry of organic natural products* (pp. 81–237).

Burd, G. I., Dixon, D. G., & Glick, B. R. (1998). A plant growth-promoting bacterium that decreases nickel toxicity in seedlings. *Applied and Environmental Microbiology, 64*, 3663–3668.

Burd, G. I., Dixon, D. G., & Glick, B. R. (2000). Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. *Canadian Journal of Microbiology, 46*, 237–245.

Chabot, R., Antoun, H., & Cescas, M. P. (1996). Growth promotion of maize and lettuce by phosphate-solubilizing *Rhizobium leguminosarum* biovar *phaseoli*. *Plant and Soil, 184*, 311–321.

Chang, C. H., & Yang, S. S. (2009). Thermo-tolerant phosphate-solubilizing microbes for multi-functional biofertilizer preparation. *Bioresource Technology, 100*, 1648–1658.

Chen, Y. P., Rekha, P. D., Arun, A. B., Shen, F. T., Lai, W. A., & Young, C. C. (2006). Phosphate-solubilizing bacteria from subtropical soil and their tricalcium phosphate-solubilizing abilities. *Applied Soil Ecology, 34*, 33–41.

Cooper, J. E. (2007). Early interactions between legumes and rhizobia: Disclosing complexity in a molecular dialogue. *Journal of Applied Microbiology, 103*, 1355–1365.

Chowdhury, M. H., & Billah, S. M. (2020). Effect of organic and inorganic fertilizers on the yield response of red amaranth (*Amaranthus cruentus*). *International Research Journal of Advanced Science, 1*(2), 38–41.

Chowdhury, M. H. (2020). Effect of heavy metal on bacterial population and diversity of Gopalpur soil series. *International Journal of Applied Chemical and Biological Sciences, 1*(4), 20–24.

Chowdhury, M. H. (2022). Bacterial population and characterization of Sonatala and Bajoa soil series of Bangladesh. *International Journal of Applied Chemical and Biological Sciences, 3*(2), 44–49.

Chowdhury, M. J., Ara, J., Hossain, M. F., Salwa, M., Tina, S. A., Das, J., Awal, A., & Chowdhury, M. H. (2025). Enumeration, isolation and characterization of bacteria of Gangachara and Palashbari soil series of Bangladesh. *International Journal of Progressive Research in Engineering Management and Science, 5*(2), 1094–1098.

Crowley, D. E., Reid, C. P. P., & Szaniszlo, P. J. (1988). Utilization of microbial siderophores in iron acquisition by oat. *Plant Physiology, 87*, 685–688.

Curie, C., & Briat, J. F., & Walker, E. L. (2003). Iron transport and signalling in plants. *Annual Review of Plant Biology, 54*, 183–206.

Curie, C., Panaviene, Z., Loulergue, C., Dellaporta, S. L., & Briat, J. F. (2001). Maize yellow stripe 1 encodes a membrane protein directly involved in Fe(III) uptake. *Nature, 409*, 346–349.

Dean, D. R., & Jacobson, R. (1992). Biochemical genetics of nitrogenase. In G. Stacey, R. H. Burris, & H. J. Evans (Eds.), *Biological nitrogen fixation* (pp. 763–817).

https://doi.org/10.5281/zenodo.18068530

De Freitas, J. R., Banerjee, M. R., & Germida, J. J. (1997). Phosphate-solubilizing rhizobacteria enhance the growth and yield but not phosphorus uptake of canola (*Brassica napus* L.). *Biology and Fertility of Soils, 24*, 358–364.

De Salamone, I. E. G., Hynes, R. K., & Nelson, L. M. (2005). Role of cytokinins in plant growth promotion by rhizosphere bacteria. In Z. A. Siddiqui (Ed.), *PGPR: Biocontrol and biofertilization* (pp. 173–195).

Deshwal, V. K., & Kumar, P. (2013). Effect of salinity on growth and PGPR activity of pseudomonads. *Journal of Academia and Industrial Research, 2*, 353–356.

Diels, L., van der Lelie, N., & Bastiaens, L. (2002). New developments in treatment of heavy metal contaminated soils. *Reviews in Environmental Science and Biotechnology, 1*, 75–82.

Di Simine, C. D., Sayer, J. A., & Gadd, G. M. (1998). Solubilization of zinc phosphate by a strain of *Pseudomonas fluorescens* isolated from a forest soil. *Biology and Fertility of Soils, 28*, 87–94.

Duijff, B. J., Bakker, P. A. H. M., & Schippers, B. (1994a). Ferric pseudobactin 358 as an iron source for carnation. *Journal of Plant Nutrition, 17*, 2069–2078.

Duan, J., Müller, K. M., Charles, T. C., Vesely, S., & Glick, B. R. (2009). 1-Aminocyclopropane-1-carboxylate (ACC) deaminase genes in rhizobia from southern Saskatchewan. *Microbial Ecology, 57*, 423–436.

Duff, R. B., & Webley, D. M. (1959). 2-Ketogluconic acid as a natural chelator produced by soil bacteria. *Chemical Industry*, 1376–1377.

Eide, D., Broderius, M., Fett, J., & Guerinot, M. L. (1996). A novel iron regulated metal transporter from plants identified by functional expression in yeast. *Proceedings of the National Academy of Sciences USA, 93*, 5624–5628.

Evans, M. L., Ishikawa, H., & Estelle, M. A. (1994). Responses of *Arabidopsis* roots to auxin studied with high temporal resolution: Comparison of wild type and auxin-response mutants. *Planta, 194*, 215–222.

Feng, K., Lu, H. M., Sheng, H. J., Wang, X. L., & Mao, J. (2004). Effect of organic ligands on biological availability of inorganic phosphorus in soils. *Pedosphere, 14*, 85–92.

Gandhi, A., Muralidharan, G., Sudhakar, E., & Murugan, A. (2014). Screening for elite zinc-solubilizing bacterial isolate from rice rhizosphere environment. *International Journal of Recent Scientific Research, 5*, 2201–2204.

Glick, B. R., Cheng, Z., Czarny, J., & Duan, J. (2007). Promotion of plant growth by ACC deaminase-producing soil bacteria. *European Journal of Plant Pathology, 119*, 329–339.

Glick, B. R., Todorovic, B., Czarny, J., Cheng, Z., & Duan, J. (2007). Promotion of plant growth by bacterial ACC deaminase. *Critical Reviews in Plant Sciences, 26*, 227–242.

Giller, K. E. (2001). *Nitrogen fixation in tropical cropping systems* (2nd ed.). CAB International.

Goldstein, A. H., Rogers, R. D., & Mead, G. (1993). Mining by microbe. *Biotechnology, 11*, 1250–1254.

Goldstein, A. H. (1994). Involvement of the quinoprotein glucose dehydrogenase in the solubilization of exogenous phosphates by gram-negative bacteria. In A. Torriani-Gorini, E. Yagil, & S. Silver (Eds.), *Phosphate in microorganisms: Cellular and molecular biology* (pp. 197–203).

Großkinsky, D. K., Tafner, R., Moreno, M. V., Stenglein, S. A., García de Salamone, I. E., Nelson, L. M., Novák, O., Strnad, M., van der Graaff, E., & Roitsch, T. (2016). Cytokinin production by *Pseudomonas fluorescens* G20-18 determines biocontrol activity against *Pseudomonas syringae* in *Arabidopsis*. *Scientific Reports, 6*, 23310.

Guerinot, M. L., & Ying, Y. (1994). Iron: Nutritious, noxious, and not readily available. *Plant Physiology, 104*, 815–820.

Gulati, A., Rahi, P., & Vyas, P. (2008). Characterization of phosphate-solubilizing fluorescent pseudomonads from the rhizosphere of seabuckthorn growing in the cold deserts of Himalayas. *Current Microbiology, 56*, 73–79.

https://doi.org/10.5281/zenodo.18068530

Gyaneshwar, P., Naresh Kumar, G., Parekh, L. J., & Poole, P. S. (2002). Role of soil microorganisms in improving P nutrition of plants. *Plant and Soil, 245*, 83–93.

Halder, A. K., Misra, A. K., & Chakrabarty, P. K. (1991). Solubilization of inorganic phosphates by *Bradyrhizobium*. *Indian Journal of Experimental Biology, 29*, 28–31.

Hamdali, H., Hafidi, M., Virolle, M. J., & Ouhdouch, Y. (2008). Rock phosphate-solubilizing actinomycetes: Screening for plant growth-promoting activities. *World Journal of Microbiology and Biotechnology, 24*, 2565–2575.

Hao, Y., Charles, T. C., & Glick, B. R. (2007). ACC deaminase from plant growth promoting bacteria affects crown gall development. *Canadian Journal of Microbiology, 53*, 1291–1299.

Hopkins, C. G., & Whiting, A. L. (1916). Soil bacteria and phosphates. III. *Agricultural Experiment Station Bulletin, 190*, 395–406.

Illmer, P., & Schinner, F. (1992). Solubilization of inorganic phosphates by microorganisms isolated from forest soil. *Soil Biology and Biochemistry, 24*, 389–395.

James, E. K., & Olivares, F. L. (1997). Infection of sugar cane and other graminaceous plants by endophytic diazotrophs. *Critical Reviews in Plant Sciences, 17*, 77–119.

Jeffries, P., Gianinazzi, S., Perotto, S., & Turnau, K. (2003). The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. *Biology and Fertility of Soils, 37*, 1–16.

Jiang, C. Y., Sheng, X. F., Qian, M., & Wang, Q. Y. (2008). Isolation and characterization of a heavy metal-resistant *Burkholderia* sp. from heavy metal-contaminated paddy field soil and its potential in promoting plant growth and heavy metal accumulation in metal-polluted soil. *Chemosphere, 72*, 157–164.

Jin, C. W., He, Y. F., Tang, C. X., Wu, P., & Zheng, S. J. (2006). Mechanisms of microbially enhanced Fe acquisition in red clover (*Trifolium pratense* L.). *Plant, Cell & Environment, 29*, 888–897.

Kabir, M. R., Hasan, S. M. K., Chy, M. A. H., Miah, M. S., Billah, S. M., & Chowdhury, M. H. (2025). Assessment of soil bacterial population and characterization of Akdala and Nachol series of Bangladesh. *GRS J Mul Res Stud, 2*(7), 1–5.

Khan, M. S., Zaidi, A., & Wani, P. A. (2007). Role of phosphate-solubilizing microorganisms in sustainable agriculture: A review. *Agronomy for Sustainable Development, 27*, 29–43.

Kpomblekou, K., & Tabatabai, M. A. (1994). Effect of organic acids on release of phosphorus from phosphate rocks. *Soil Science, 158*, 442–453.

Kumar, A., Akter, S., Rahman, M. A., Ali, S. Y., & Chowdhury, M. H. (2025). The functional architecture of soil biodiversity: Chemical, biological and ecosystem engineers. *International Journal of Modern Science and Research Technology, 3*(11), 321–338.

Lanier, J. E., Jordan, D. L., Spears, J. F., Wells, R., & Johnson, P. D. (2005). Peanut response to inoculation and nitrogen fertilizer. *Agronomy Journal, 97*, 79–84.

Lemanceau, P., Bauer, P., Kraemer, S., & Briat, J. F. (2009). Iron dynamics in the rhizosphere as a case study for analyzing interactions between soils, plants and microbes. *Plant and Soil, 321*, 513–535.

Leveau, J. H. J., & Gerards, S. (2008). Discovery of a bacterial gene cluster for catabolism of the plant hormone indole 3-acetic acid. *FEMS Microbiology Ecology, 65*, 238–250.

Lugtenberg, B., Malfanova, N., Kamilova, F., & Berg, G. (2013). Plant growth promotion by microbes. In F. J. de Bruijn (Ed.), *Molecular microbial ecology of the rhizosphere* (pp. 39–66).

Ma, W., Charles, T. C., & Glick, B. R. (2004). Expression of an exogenous 1-aminocyclopropane-1-carboxylate deaminase gene in *Sinorhizobium meliloti* increases its ability to nodulate alfalfa. *Applied and Environmental Microbiology, 70*, 5891–5897.

https://doi.org/10.5281/zenodo.18068530

Ma, W., Guinel, F. C., & Glick, B. R. (2003). The *Rhizobium leguminosarum* bv. *viciae* ACC deaminase protein promotes the nodulation of pea plants. *Applied and Environmental Microbiology, 69*, 4396–4402.

Mahmud, M. K., Azad, M. A. K., Awal, A., Akhter Tina, S., Das, J., Salwa, M., & Chowdhury, M. H. (2025). Isolation and characterization of bacteria of Amnura and Baliadangi soil series of Bangladesh. *International Journal of Applied Chemical and Biological Sciences, 6*(1), 1–6.

Mahmud, M. K., Rahman, M. M., Chy, M. A. H., Kabir, M. R., Nazmul, K. M., Akhter, M. K., & Chowdhury, M. H. (2025). Isolation and characterization of soil bacteria: A review. *International Journal of Modern Science and Research Technology, 3*(10), 22–33.

Malik, A. (2004). Metal bioremediation through growing cells. *Environmental International, 30*, 261–278.

Malboobi, M. A., Behbahani, M., Madani, H., Owlia, P., Deljou, A., Yakhchali, B., Moradi, M., & Hassanabadi, H. (2009). Performance evaluation of potent phosphate-solubilizing bacteria in potato rhizosphere. *World Journal of Microbiology and Biotechnology, 25*, 1479–1484.

Marroquí, S., Zorreguieta, A., Santamaría, C., Temprano, F., Soberón, M., Megías, M., & Downie, J. A. (2001). Enhanced symbiotic performance by *Rhizobium tropici* glycogen synthase mutants. *Journal of Bacteriology, 183*, 854–864.

Marschner, H. (1995). *Mineral nutrition of higher plants* (2nd ed.). Academic, London.

Matias, S. R., Pagano, M. C., Carvalho-Muzzi, F., Oliveira, C. A., Almeida-Carneiro, A., Horta, S. N., & Scotti, M. R. (2009). Effect of rhizobia, mycorrhizal fungi and phosphate-solubilizing microorganisms in the rhizosphere of native plants used to recover an iron ore area in Brazil. *European Journal of Soil Biology, 45*, 259–266.

Matthew, C. J., Bjorkman, K. M., David, M. K., Saito, M. A., & Zehr, J. P. (2008). Regional distributions of nitrogen-fixing bacteria in the Pacific Ocean. *Limnology and Oceanography, 53*, 63–77.

Masalha, J., Kosegarten, H., Elmaci, O., & Mengel, K. (2000). The central role of microbial activity for iron acquisition in maize and sunflower. *Biology and Fertility of Soils, 30*, 433–439.

Mba, C. C. (1994). Rock phosphate solubilizing and cellulolytic actinomycetes isolates of earthworm casts. *Environmental Management, 18*, 257–261.

Meyer, J. M., & Abdallah, M. A. (1978). The fluorescent pigment of *Pseudomonas fluorescens*: Biosynthesis, purification and physico-chemical properties. *Journal of General Microbiology, 107*, 319–328.

Meyer, J. M., Gruffaz, C., Raharinosy, V., Bezverbnaya, I., Schäfer, M., & Budzikiewicz, H. (2008). Siderotyping of fluorescent *Pseudomonas*: Molecular mass determination by mass spectrometry as a powerful pyoverdine siderotyping method. *Biometals, 21*, 259–271.

Mirleau, P., Delorme, S., Philippot, L., Meyer, J. M., Mazurier, S., & Lemanceau, P. (2000). Fitness in soil and rhizosphere of *Pseudomonas fluorescens* C7R12 compared with a C7R12 mutant affected in pyoverdine synthesis and uptake. *FEMS Microbiology Ecology, 34*, 35–44.

Mirleau, P., Philippot, L., Corberand, T., & Lemanceau, P. (2001). Involvement of nitrate reductase and pyoverdine in competitiveness of *Pseudomonas fluorescens* strain C7R12 in soil. *Applied and Environmental Microbiology, 67*, 2627–2635.

Molla, M. A. Z., Chowdhury, A. A., Islam, A., & Hoque, S. (1984). Microbial mineralization of organic phosphate in soil. *Plant and Soil, 78*, 393–399.

Morgan, P. W., & Drew, C. D. (1997). Ethylene and plant responses to stress. *Physiologia Plantarum, 100*, 620–630.

Nair, A., Juwarkar, A. A., & Singh, S. K. (2007). Production and characterization of siderophores and its application in arsenic removal from contaminated soil. *Water, Air, and Soil Pollution, 180*, 199–212.

https://doi.org/10.5281/zenodo.18068530

Neilands, J. B. (1981). Iron adsorption and transport in microorganisms. *Annual Review of Nutrition, 1*, 27–46.

Park, K. H., Lee, C. Y., & Son, H. J. (2009). Mechanism of insoluble phosphate solubilization by *Pseudomonas fluorescens* RAF15 isolated from ginseng rhizosphere and its plant growth-promoting activities. *Letters in Applied Microbiology, 49*, 222–228.

Patil, N. G., & Patil, V. R. (2012). Isolation and characterization of actinomycetes producing gibberellic acid. *International Journal of Scientific Research, 3*, 1400–1403.

Patten, C. L., & Glick, B. R. (1996). Bacterial biosynthesis of indole-3-acetic acid. *Canadian Journal of Microbiology, 42*, 207–220.

Peck, S. C., & Kende, H. (1995). Sequential induction of the ethylene biosynthetic enzymes by indole-3-acetic acid in etiolated peas. *Plant Molecular Biology, 28*, 293–301.

Peralta, H., Mora, Y., Salazar, E., Encarnación, S., Palacios, R., & Mora, J. (2004). Engineering the *nifH* promoter region and abolishing poly-β-hydroxybutyrate accumulation in *Rhizobium etli* enhance nitrogen fixation in symbiosis with *Phaseolus vulgaris*. *Applied and Environmental Microbiology, 70*, 3272–3281.

Pilet, P. E., & Saugy, M. (1987). Effect on root growth of endogenous and applied IAA and ABA. *Plant Physiology, 83*, 33–38.

Rahman, M. M., Ahmed, M. E., Kumar, A., Rahman, M. A., & Chowdhury, M. H. (2025). Ecological review on heavy metal interactions with bacterial dynamics of soil. *GRS J Mul Res Stud, 2*(11), 50–56.

Ramírez, M., Valderrama, B., Arredondo-Peter, R., Soberón, M., Mora, J., & Hernández, G. (1999). *Rhizobium etli* genetically engineered for the heterologous expression of *Vitreoscilla* sp. hemoglobin: Effects on free-living and symbiotic growth. *Molecular Plant–Microbe Interactions, 12*, 1008–1015.

Ray, J., Bagyaraj, D. J., & Manjunath, A. (1981). Influence of soil inoculation with vesicular arbuscular mycorrhizal (VAM) and a phosphate dissolving bacteria on plant growth and ^{32}P uptake. *Soil Biology and Biochemistry, 13*, 105–108.

Robin, A., Mougel, C., Siblot, S., Vansuyt, G., Mazurier, S., & Lemanceau, P. (2006). Effect of ferritin over-expression in tobacco on the structure of bacterial and pseudomonad communities associated with the roots. *FEMS Microbiology Ecology, 58*, 492–502.

Robin, A., Vansuyt, G., Hinsinger, P., Meyer, J. M., & Briat, J. F., Lemanceau, P. (2008). Iron dynamics in the rhizosphere: Consequences for plant health and nutrition. *Advances in Agronomy, 99*, 183–225.

Robinson, N. J., Procter, C. M., Connolly, E. L., & Guerinot, M. L. (1999). A ferric-chelate reductase for iron uptake from soils. *Nature, 397*, 694–697.

Rodriguez, H., & Fraga, R. (1999). Phosphate-solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances, 17*, 319–339.

Rodriguez, H., Fraga, R., & Gonzalez, T., & Bashan, Y. (2006). Genetics of phosphate solubilization and its potential applications for improving plant growth-promoting bacteria. *Plant and Soil, 287*, 15–21.

Rodriguez, H., Gonzalez, T., Goire, I., & Bashan, Y. (2004). Gluconic acid production and phosphate solubilization by the plant growth-promoting bacterium *Azospirillum* spp. *Naturwissenschaften, 91*, 552–555.

Rojas, A., Holguin, G., Glick, B. R., & Bashan, Y. (2001). Synergism between *Phyllobacterium* sp. (N_2-fixer) and *Bacillus licheniformis* (P-solubilizer), both from a semiarid mangrove rhizosphere. *FEMS Microbiology Ecology, 35*, 181–187.

Sahin, F., Çakmakçı, R., & Kantar, F. (2004). Sugar beet and barley yields in relation to inoculation with N_2-fixing and phosphate-solubilizing bacteria. *Plant and Soil, 265*, 123–129.

Saikia, S. P., & Jain, V. (2007). Biological nitrogen fixation with non-legumes: An achievable target or a dogma? *Current Science, 92*, 317–322.

https://doi.org/10.5281/zenodo.18068530

Saini, P., Khanna, V., & Gangwar, M. (2015). Mechanisms of plant growth promotion by rhizobacteria. *Journal of Pure and Applied Microbiology, 9*, 1163–1177.

Salisbury, F. B., & Ross, C. W. (1992). *Plant physiology*. Wadsworth, Belmont, CA.

Saravanan, V. S., Kalaiarasan, P., Madhaiyan, M., & Thangaraju, M. (2007). Solubilization of insoluble zinc compounds by *Gluconacetobacter diazotrophicus* and the detrimental action of zinc ion (Zn^{2+}) and zinc chelates on root-knot nematode *Meloidogyne incognita*. *Letters in Applied Microbiology, 44*, 235–241.

Sharma, A., Johria, B. N., Sharma, A. K., & Glick, B. R. (2003). Plant growth-promoting bacterium *Pseudomonas* sp. strain GRP3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilzeck). *Soil Biology and Biochemistry, 35*, 887–894.

Sharma, V., Kumar, V., Archana, G., & Kumar, G. N. (2005). Substrate specificity of glucose dehydrogenase (GDH) of *Enterobacter asburiae* PSI3 and rock phosphate solubilization with GDH substrates as C sources. *Canadian Journal of Microbiology, 51*, 477–482.

Akter, S., Kabir, M. R., Nazmul, K. M., Ali, S. Y., & Chowdhury, M. H. (2025). Turning back the carbon clock: Restoring soil organic matter for a sustainable future. *International Journal of Modern Science and Research Technology, 3*(12), 1–10.

Shridhar, B. S. (2012). Review: Nitrogen fixing microorganisms. *International Journal of Microbiological Research, 3*, 46–52.

Siebner-Freibach, H., Hadar, Y., & Chen, Y. (2003). Siderophores sorbed on Ca-montmorillonite as an iron source for plants. *Plant and Soil, 251*, 115–124.

Someya, N., Sato, Y., Yamaguchi, I., Hamamoto, H., Ichiman, Y., Akutsu, K., Sawada, H., & Tsuchiya, K. (2007). Alleviation of nickel toxicity in plants by a rhizobacterium strain is not dependent on its siderophore production. *Communications in Soil Science and Plant Analysis, 38*, 1155–1162.

Spaepen, S., Vanderleyden, J., & Remans, R. (2007). Indole-3-acetic acid in microbial and microorganism–plant signaling. *FEMS Microbiology Reviews, 31*, 425–448.

Sperber, J. I. (1958). The incidence of apatite-solubilizing organisms in the rhizosphere and soil. *Australian Journal of Agricultural Research, 9*, 778–781.

Stintzi, A., Evans, K., Meyer, J. M., & Poole, K. (1998). Quorum-sensing and siderophore biosynthesis in *Pseudomonas aeruginosa*: lasR/lasI mutants exhibit reduced pyoverdine biosynthesis. *FEMS Microbiology Letters, 166*, 341–345.

Sultana, T., & Chowdhury, M. H. (2022). Effect of heavy metal on soil respiration. *African Journal of Advanced Pure and Applied Sciences, 1*(4), 133–138.

Sunithakumari, K., Padma Devi, S. N., & Vasandha, S. (2016). Zinc solubilizing bacterial isolates from the agricultural fields of Coimbatore, Tamil Nadu, India. *Current Science, 110*, 196–205.

Tao, G. C., Tian, S. J., Cai, M. Y., & Xie, G. H. (2008). Phosphate-solubilizing and -mineralizing abilities of bacteria isolated from soils. *Pedosphere, 18*, 515–523.

Toro, M., Azcón, R., & Barea, J. M. (1997). Improvement of arbuscular mycorrhiza development by inoculation of soil with phosphate-solubilizing rhizobacteria to improve rock phosphate bioavailability (^{32}P) and nutrient cycling. *Applied and Environmental Microbiology, 63*, 4408–4412.

Tsakelova, E. A., Klimova, S. Y., Cherdyntseva, T. A., & Netrusov, A. I. (2006). Microbial producers of plant growth stimulators and their practical use: A review. *Applied Biochemistry and Microbiology, 42*, 117–126.

Uddin, M. N., & Chowdhury, M. H. (2022). Enumeration, isolation and characterization of bacteria of Gopalpur soil series of Bangladesh. *Interdisciplinary Journal of Applied and Basic Subjects, 2*(2), 21–26.

Ureta, A. C., Imperial, J., Ruiz-Argüeso, T., & Palacios, J. M. (2005). *Rhizobium*

https://doi.org/10.5281/zenodo.18068530

leguminosarum biovar *viciae* symbiotic hydrogenase activity and processing are limited by the level of nickel in agricultural soils. *Applied and Environmental Microbiology, 71*, 7603–7606.

Valverde, A., Burgos, A., Fiscella, T., Rivas, R., Velazquez, E., Rodríguez-Barrueco, C., Cervantes, E., Chamber, M., & Igual, J. M. (2006). Differential effects of coinoculations with *Pseudomonas jessenii* PS06 (a phosphate-solubilizing bacterium) and *Mesorhizobium ciceri* C-2/2 strains on the growth and seed yield of chickpea under greenhouse and field conditions. *Plant and Soil, 287*, 43–50.

Vansuyt, G., Robin, A., Briat, J. F., Curie, C., & Lemanceau, P. (2007). Iron acquisition from Fe-pyoverdine by *Arabidopsis thaliana*. *Molecular Plant-Microbe Interactions, 4*, 441–447.

Vassileva, M., Azcón, R., Barea, J. M., & Vassilev, N. (1999). Effect of encapsulated cells of *Enterobacter* sp. on plant growth and phosphate uptake. *Bioresource Technology, 67*, 229–232.

Vassileva, M., Azcón, R., Barea, J. M., & Vassilev, N. (2000). Rock phosphate solubilization by free and encapsulated cells of *Yarrowia lipolytica*. *Process Biochemistry, 35*, 693–697.

Vassilev, N., Medina, A., & Vassileva, M. (2006a). Microbial solubilization of rock phosphate on media containing agro-industrial wastes and effect of the resulting products on plant growth and P uptake. *Plant and Soil, 287*, 77–84.

Vassilev, N., & Vassileva, M., & Nikolaeva, I. (2006b). Simultaneous P-solubilizing and biocontrol activity of microorganisms: Potentials and future trends. *Applied Microbiology and Biotechnology, 71*, 137–144.

Vassilev, N., & Vassileva, M. (2004). Multifunctional properties of a plant growth promoting bacterium entrapped in k-carrageenan. In J. L. Pedraz, G. Orive, & D. Poncelet (Eds.), *XII international workshop on bioencapsulation, Vitoria, Univ Pais Vasco, 24–26 September 2004* (pp. 162–166).

Vert, G., Grotz, N., Dedaldechamp, F., Gaymard, F., Guerinot, M. L., & Briat, J. F., Curie, C. (2002). IRT1, an *Arabidopsis* transporter essential for iron uptake from the soil and for plant growth. *Plant Cell, 14*, 1223–1233.

Vikram, A., & Hamzehzarghani, H. (2008). Effect of P-solubilizing bacteria on nodulation and growth parameters of greengram (*Vigna radiata* L. Wilczek). *Research Journal of Microbiology, 3*, 62–72.

Von Wirén, N., Mori, S., Marschner, H., & Römheld, V. (1994). Iron inefficiency in maize mutant ys1 (*Zea mays* L. cv yellow-stripe) is caused by a defect in uptake of iron phytosiderophores. *Plant Physiology, 106*, 71–77.

Walter, A., Römheld, V., Marschner, H., & Crowley, D. E. (1994). Iron nutrition of cucumber and maize: Effect of *Pseudomonas putida* YC3 and its siderophore. *Soil Biology and Biochemistry, 26*, 1023–1031.

Wang, C., Knill, E., Glick, B. R., & Defago, G. (2000). Effect of transferring 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase genes into *Pseudomonas fluorescens* strain CHA0 and its gacA derivative CHA96 on their growth-promoting and disease-suppressive capacities. *Canadian Journal of Microbiology, 46*, 898–907.

Yehuda, Z., Shenker, M., Römheld, V., Marschner, H., Hadar, Y., & Chen, Y. (1996). The role of ligand exchange in the uptake of iron from microbial siderophores by gramineous plants. *Plant Physiology, 112*, 1273–1280.

Yi, Y., Huang, W., & Ge, Y. (2008). Exopolysaccharide: A novel important factor in the microbial dissolution of tricalcium phosphate. *World Journal of Microbiology and Biotechnology, 24*, 1059–1065.

Young, J. P. W., & Haukka, K. E. (1996). Diversity and phylogeny of rhizobia. *New Phytologist, 133*, 87–94.

https://doi.org/10.5281/zenodo.18068530