

HARNESSING PGPB FOR SUSTAINABLE CROP PRODUCTION AND ENVIRONMENTAL PROTECTION - A REVIEW

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SUMMARY

Microorganisms are indispensable for sustainable agriculture, as they perform multiple vital functions within the soil-plant ecosystem. They influence soil fertility, crop productivity, and plant health through diverse ecological and biochemical processes. In agricultural systems, microbes act as natural fertilizers, biocontrol agents, and soil engineers, thereby maintaining the balance and productivity of agroecosystems. By facilitating nutrient cycling, decomposing organic matter, and enhancing plant resilience, microorganisms significantly reduce dependence on chemical fertilizers and pesticides. This not only minimizes environmental pollution but also promotes eco-friendly and sustainable farming practices. Among beneficial microorganisms, Plant Growth-Promoting Bacteria (PGPB) represent a distinct group capable of colonizing plant roots and improving overall plant performance. PGPB exert their beneficial effects through both direct and indirect mechanisms: Direct mechanisms: Biological nitrogen fixation, Phosphate solubilisation, Phytohormone production (auxins, cytokinins, gibberellins), Mobilization of essential nutrients. Indirect mechanisms: Suppression of pathogens through antibiotic production and competition, Siderophore production for iron acquisition, Induction of systemic resistance against various biotic stresses, Mitigation of abiotic stresses such as salinity, drought, and heavy metal toxicity. In this review, we discuss the various direct and indirect mechanisms employed by PGPB that contribute to plant growth, soil health, and sustainable crop production.

Key words: Plant Growth-Promoting Bacteria (PGPB), Biological nitrogen fixation, Phosphate solubilisation, Phytohormone, abiotic stress and Biological Nitrogen Fixation (BNF)

Nitrogen is an essential macronutrient required for plant growth and development, as it forms a key component of amino acids, proteins, nucleic acids, and chlorophyll (Singh *et al* 2010). Atmospheric nitrogen (N₂) exists in a highly stable, inert form that plants cannot directly utilize. Biological Nitrogen Fixation (BNF) is a natural process carried out by certain microorganisms that convert atmospheric nitrogen (N₂) into ammonia (NH₃), a plant-available form of nitrogen. Plant Growth-Promoting Bacteria (PGPB), particularly diazotrophic bacteria, play a vital role in Biological Nitrogen Fixation (Table 1).

Phosphate Solubilization: Phosphorus (P) is a vital macronutrient required for plant growth and development, playing a key role in energy transfer, signal transduction, and nucleic acid synthesis. Most soil phosphorus exists in insoluble, unavailable forms. As a result, crops often suffer from phosphorus deficiency despite its abundance in the soil. Backer *et al.* (2018) reported that phosphate-solubilizing bacteria (PSB) are widely distributed in soil and converting bound phosphorus into soluble forms that can be readily absorbed by plants. Several endophytic bacterial genera have been identified as potent phosphate solubilizers, including *Bacillus*,

Burkholderia, *Enterobacter*, *Pantoea*, *Erwinia*, *Pseudomonas*, *Citrobacter*, and *Azotobacter* (Idriss *et al.*, 2002; Rodriguez *et al.*, 2006; Park *et al.*, 2010, Dheeravathu, *et al.*, 2021, Thulasi *et al.*, 2023) (Table 1). The mechanism of phosphate solubilization largely involves the secretion of organic acids (such as gluconic acid, citric acid, and oxalic acid), which chelate cations bound to phosphate, releasing it into a soluble form. The type of organic acid produced depends on the carbon source available. Maximum solubilization has been reported when glucose, sucrose, or galactose serve as the sole carbon source (Khan *et al.*, 2009; Park *et al.*, 2010). Endophytic bacteria can also solubilize inorganic phosphates such as tricalcium phosphate via extracellular acidification and enzymatic activity (Kuklinsky-Sobral *et al.*, 2004; Long *et al.*, 2008; ThamizhVendan *et al.*, 2010; Patel *et al.*, 2012).

Phytohormone Production

Plant Growth-Promoting Bacteria influence plant development not only by improving nutrient availability but also by producing phytohormones such as auxins, cytokinins, and gibberellins. These bacterial-derived compounds mimic or enhance the plant's own hormonal balance, leading to improved growth, development, and stress tolerance. Auxins (Indole-3-Acetic Acid, IAA) are the most commonly reported phytohormones produced by PGPB. Auxins stimulate root elongation, lateral root initiation, and root hair formation, which increases the root surface area for nutrient and water uptake. *Azospirillum*, *Bacillus*, *Pseudomonas*, and *Enterobacter* are well-known IAA producers (Table 1). Cytokinins regulate cell division, shoot initiation, and leaf expansion. Cytokinin-producing bacteria improve shoot growth and delay leaf senescence, thereby enhancing photosynthetic activity. Endophytic bacteria like *Bacillus subtilis* and *Pseudomonas fluorescens* have been reported to release cytokinins (Table 1). Gibberellins (GA) stimulate stem elongation, seed germination, and flowering. Several rhizobacteria, such as *Azospirillum brasilense* and *Herbaspirillum seropedicae*, have been documented to produce GA, which helps plants overcome growth restrictions under stress (Table 1).

Solubilization of other Essential Nutrients

Apart from nitrogen fixation and phosphate solubilization, Plant Growth-Promoting Bacteria (PGPB) also enhance plant growth by mobilizing other

essential nutrients that are otherwise poorly available in soil. These include potassium (K), zinc (Zn), iron (Fe), and sulfur (S), which are vital for plant metabolism and productivity. Large amounts of potassium in soils exist in insoluble mineral forms such as feldspar and mica. Potassium-solubilizing bacteria (KSB), including *Bacillus mucilaginosus* and *Frateuria aurantia*, release organic acids and enzymes that dissolve these minerals, making K available for plant uptake. Enhanced potassium uptake improves drought tolerance, enzyme activation, and disease resistance in crops (Table 1). Zinc is critical for enzyme function, protein synthesis, and auxin metabolism, yet much of it is insoluble in soil. *Pseudomonas* spp. and *Bacillus* spp. can solubilize zinc compounds (e.g., ZnO, ZnCO₃), thereby improving crop growth and yield (Table-1). Iron is often present in insoluble ferric forms (Fe³⁺). PGPB secrete siderophores (small molecules that chelate Fe³⁺),. PGPB not only enhances plant nutrition but also limits iron availability to pathogens, indirectly contributing to disease suppression (Table-1). Sulphur (Oxidation) is essential for amino acids, proteins, and vitamins. Certain PGPB (e.g., *Thiobacillus* spp.) oxidize elemental sulfur to sulfate (SO₄²⁻), a plant-usable form.

Indirect mechanisms: Plant Growth-Promoting Bacteria (PGPB) synthesize secondary metabolites with antimicrobial activity, such as 2,4-diacetylphloroglucinol (DAPG), phenazines, pyrrolnitrin. which inhibit the growth of fungal and bacterial pathogens.

Siderophore Production for Iron Acquisition: Iron is an essential micronutrient for plants, required for processes such as chlorophyll biosynthesis, respiration, and enzymatic activity. In aerobic soils, iron predominantly exists as insoluble ferric ions (Fe³⁺), making it poorly available to plants. Plant Growth-Promoting Bacteria (PGPB) overcome this limitation by producing siderophores-low-molecular-weight, high-affinity iron-chelating compounds.

Iron Solubilization and Uptake: Siderophores bind Fe³⁺ in the soil and form soluble complexes, these complexes are taken up by bacterial or plant receptors, ensuring adequate iron availability to both the microbes and their plant hosts. The common siderophores include catecholates (enterobactin), hydroxamates (ferrichrome), and carboxylates (rhizobactin). **Dual Role in Plant Growth and Disease Suppression:** Siderophore-producing bacteria such as *Pseudomonas*, *Bacillus*, *Azotobacter*, *Burkholderia* enhance plant vigor, photosynthesis, and yield (Table 1).

TABLE 1
Direct and Indirect Mechanisms of PGPB with Representative Genera and Effects on Crops

Mechanism	Representative Genera	Mode of Action	Reported Effects on Crops
Direct Mechanisms			
Biological Nitrogen Fixation	<i>Azotobacter</i> , <i>Azospirillum</i> , <i>Rhizobium</i> , <i>Bradyrhizobium</i>	Conversion of atmospheric N ₂ into plant-available ammonia	Enhanced N availability, improved yield in legumes, cereals
Phosphate Solubilization	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Burkholderia</i> , <i>Enterobacter</i> , <i>Citrobacter</i>	Production of organic acids and phosphatases to solubilize inorganic and organic P	Increased P uptake, improved growth in maize, sugarcane, oilseed crops
Phytohormone Production (auxins, cytokinins, gibberellins)	<i>Azospirillum</i> , <i>Bacillus</i> , <i>Pseudomonas</i> , <i>Klebsiella</i>	Modulation of root architecture, cell division, elongation	Enhanced root and shoot growth, better nutrient acquisition
Mobilization of Essential Nutrients (Zn, K, Fe)	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Paenibacillus</i>	Solubilization/mobilization of micronutrients through organic acids and enzymes	Improved micronutrient uptake, enhanced crop quality and yield
Indirect Mechanisms			
Pathogen Suppression	<i>Pseudomonas</i> , <i>Bacillus</i> , <i>Streptomyces</i>	Antibiotic production, competition for space and nutrients	Reduced soil borne diseases, healthier plants
Siderophore Production	<i>Pseudomonas</i> , <i>Azotobacter</i> , <i>Burkholderia</i>	Sequestration of Fe ³⁺ , limiting pathogen access	Improved iron uptake, suppression of phytopathogens
Induction of Systemic Resistance (ISR)	<i>Pseudomonas fluorescens</i> , <i>Bacillus subtilis</i>	Activation of plant defense pathways (salicylic acid, jasmonic acid, ethylene)	Enhanced resistance against fungal, bacterial, and viral diseases
Mitigation of Abiotic Stress (salinity, drought, heavy metals)	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Arthrobacter</i> , <i>Azospirillum</i>	Production of ACC deaminase, exopolysaccharides, antioxidant enzymes	Increased plant tolerance to stress, stable yields under adverse conditions

Induction of Systemic Resistance in Plants: In addition to directly promoting plant growth, many Plant Growth-Promoting Bacteria (PGPB) enhance plant immunity through a phenomenon known as Induced Systemic Resistance (ISR). ISR is a plant defense mechanism activated by beneficial microbes that primes the plant to respond more effectively against a wide range of pathogens and pests. Unlike pathogen-triggered resistance, ISR does not rely on hypersensitive responses but instead strengthens the plant's innate immune system.

Mechanism of ISR: ISR is mediated through jasmonic acid (JA) and ethylene (ET) signaling pathways, distinct from the salicylic acid (SA)-dependent systemic acquired resistance (SAR). PGPB such as *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Azospirillum* release microbial elicitors (lipopolysaccharides, flagellin, siderophores, and

antibiotics) that trigger ISR in plants. Primed plants show faster and stronger defense responses when challenged by pathogens or environmental stress.

Identification of climate resilient crops: The climate resilient crops such as grasses: guineagrass, bajra - napier hybrids and tri-specific hybrids, dinanath grass, (Dheeravathu *et al.*, 2018, Singh *et al.*, 2020, Dheeravathu *et al.*, 2021a, Dheeravathu *et al.*, 2021b, Dheeravathu *et al.*, 2021c., Dheeravathu *et al.*, 2022a, Dheeravathu *et al.*, 2022b), forage cereals including millets: pearl millet sorghum, kodo millet, (Malathi *et al.*, 2022, Dheeravathu and Vadithe, 2024a, Dheeravathu and Vadithe, 2024b, Sravanthi *et al.*, 2024, Sravanthi *et al.*, 2025), pulses: cowpea, berseem, clitoria, centrosema, siratro (Dheeravathu *et al.*, 2017a, Dheeravathu *et al.*, 2017b, Dheeravathu *et al.*, 2022c., Dheeravathu *et al.*, 2023), have been proven to be climate smart.

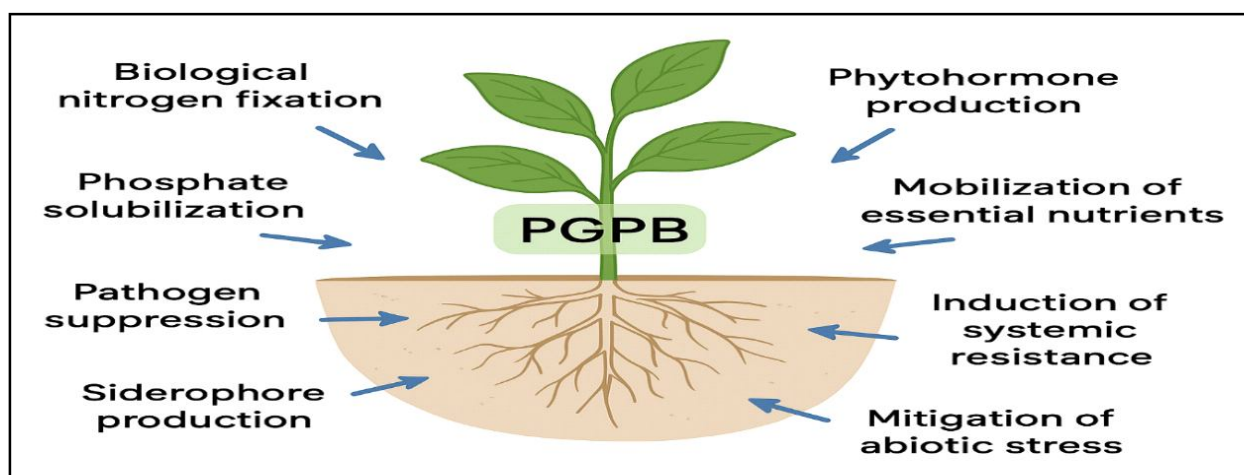


Fig. 1. Schematic diagram of the Plant growth prompting bacteria.

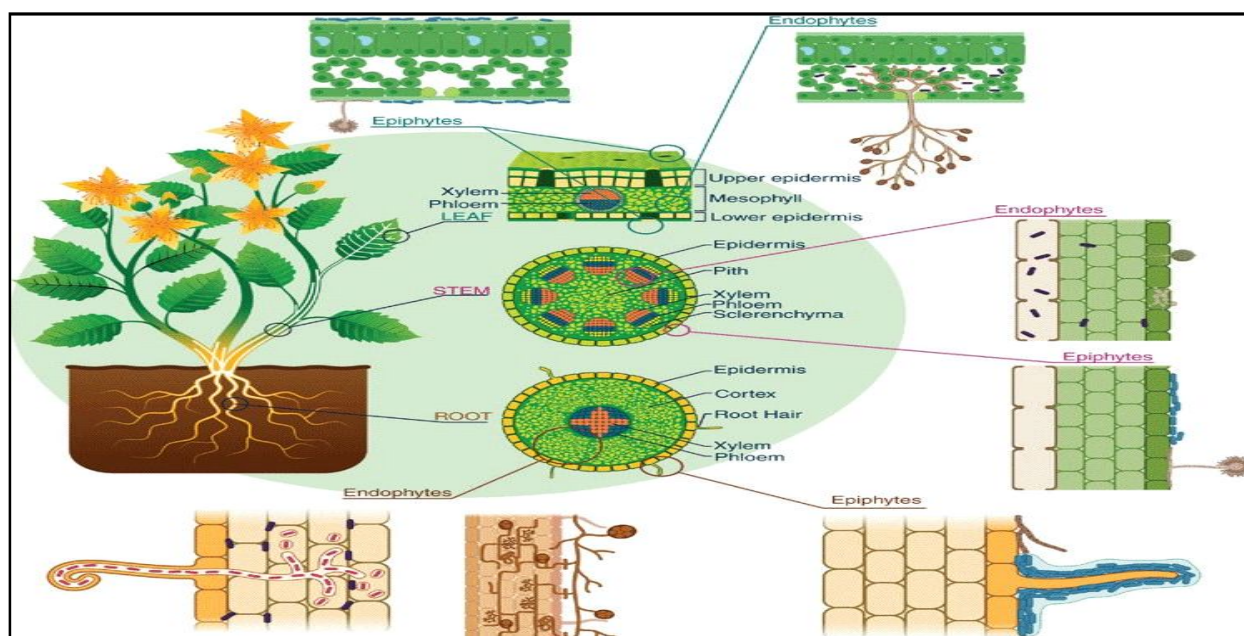


Fig. 2. Schematic diagram of the penetration and colonization of Endophytes into the host.

Mitigation of Abiotic Stresses

Apart from promoting plant nutrition and pathogen resistance, Plant Growth-Promoting Bacteria (PGPB) also play a crucial role in helping plants cope with abiotic stresses such as salinity, drought, and heavy metal toxicity. These stresses severely limit agricultural productivity worldwide, and microbial interventions provide an eco-friendly alternative to chemical amendments.

Salinity Stress and drought stress mitigation: PGPB alleviate salinity stress through, Production of ACC deaminase, which lowers plant ethylene levels and prevents stress-induced growth inhibition. Exopolysaccharide (EPS) production, which

binds excess sodium ions and improves soil aggregation, reducing salt toxicity. Enhanced uptake of K^+ , Ca^{2+} , and Mg^{2+} to maintain ion homeostasis. Example: *Halotolerant Bacillus* and *Pseudomonas* strains improve rice and wheat growth under saline conditions (Table 1). Drought Stress Alleviation: Under water deficit, plants suffer from reduced photosynthesis, stomatal closure, and oxidative stress. PGPB enhancing root growth and architecture for better water uptake (Table 1).

Heavy Metal Stress Management: Heavy metals (Cd, Pb, Hg, As, Cr) disrupt cellular metabolism and accumulate in edible plant parts.

Pseudomonas putida and *Bacillus megaterium* mitigate toxicity through transformation of toxic metals

into less bioavailable forms (e.g., $\text{Cr}^{6+} \rightarrow \text{Cr}^{3+}$): (Table 1).

Volatile Compounds

Endophytic bacteria can produce diverse volatile organic compounds (VOCs) that contribute to signaling, microbial inhibition, and plant growth promotion (Wheatley, 2002; Kai et al., 2009). For instance: *Bacillus* spp. produce 2,3-butanediol and acetoin, which stimulate growth in *Arabidopsis thaliana* (Ryu et al., 2003). *Burkholderia pyrrocinia* releases volatiles such as indole, 1-hexanol, and pentadecane under stress, promoting significant growth enhancement.

Plant Growth Promotion case studies

Jha and Kumar, 2007 inoculated *Klebsiella oxytoca* GR-3 to rice seeds and observed that the root length, shoot height, and chlorophyll content were improved in rice seedlings. Long et al. (2008) reported that increased seed germination and seedling vigor in inoculated endophytes *Solanum nigrum*. Co-inoculation of *Pseudomonas fluorescens* and *Bacillus* spp. increased banana yields by over 50% compared to controls, while also improving chlorophyll content and resistance to banana bunchy top virus (Harish et al., 2009). *Bacillus subtilis* HC8 enhanced tomato growth and protected against root rot disease (Marfanova et al., 2011).

Biological Control Agents

PGPB and other beneficial microbes also act as biological control agents, providing an eco-friendly alternative to chemical pesticides. *Trichoderma*-based formulations have been used in cacao to control black pod disease while also improving flowering and pod development (Tondje et al., 2007; Deberdt et al., 2008). Successful biocontrol formulations must ensure economical production, stability, easy application, and long shelf life. Various carriers such as diatomaceous earth, organic manure, alginate pellets, and starch granules have been explored for delivering these agents effectively (Raj et al., 2003; Schisler et al., 2004).

CONCLUSION

Plant Growth-Promoting Bacteria (PGPB) play a vital role in fostering sustainable agriculture and protecting environmental health. They improve nutrient

uptake, boost plant stress tolerance, produce beneficial bioactive compounds, and minimize reliance on harmful agrochemicals. As a result, PGPB stand out as essential allies in building greener, more resilient, and eco-friendly agricultural systems for the future.

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