International Journal of Plant & Soil Science

Volume 38, Issue 7, Page 116-134, 2026; Article no.IJPSS.160971
ISSN: 2320-7035

Harnessing Plant Growth-promoting Rhizobacteria for Sustainable Maize Production and Protection

Anuradha Ojha [a*], Aakash Ojha [b], Priyanka Sharda [a], Manasa Dasthari [c] and Satyam [d]

[a] Department of Microbiology, Punjab Agricultural University, Ludhiana-141004, Punjab, India.
[b] Department of Agronomy, CSKHPKV, Palampur, Himachal Pradesh- 176062, India.
[c] Department of Agronomy, Sam Higginbottom University of Agriculture, Technology and Sciences, Prayagraj, Uttar Pradesh-211007, India.
[d] Department of Microbiology, Post Graduate Institute, Mahatma Phule Krishi Vidyapeeth, Rahuri, Maharashtra, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/ijpss/2026/v38i76147

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://pr.sdiarticle5.com/review-history/160971

Review Article

Received: 11/04/2026
Published: 20/06/2026

Abstract

Maize (*Zea mays L.*) is a globally important cereal crop, but its productivity is constrained by nutrient deficiencies, soil-borne pathogens and abiotic stresses. Among the major biotic constraints, *Fusarium verticillioides* causes seed rot, seedling blight, stalk rot and ear rot, resulting in substantial yield and quality losses. Plant growth-promoting rhizobacteria (PGPR) have attracted increasing attention as sustainable biological inputs for improving maize growth and plant health. This review examines the role of PGPR in maize production, with emphasis on nutrient acquisition, disease suppression and stress tolerance. In maize

---

**Corresponding author: E-mail: anuradhaojha111@gmail.com;*

Cite as: *Ojha, A., Ojha, A., Sharda, P., Dasthari, M., & Satyam. (2026). Harnessing Plant Growth-promoting Rhizobacteria for Sustainable Maize Production and Protection. International Journal of Plant & Soil Science, 38(7), 116–134. https://doi.org/10.9734/ijpss/2026/v38i76147*

rhizosphere systems, PGPR, including *Bacillus*, *Pseudomonas*, *Azospirillum*, *Azotobacter* and *Enterobacter* spp., enhance plant growth through biological nitrogen fixation, phosphate solubilisation, siderophore production and phytohormone synthesis. These activities can improve root architecture, nutrient uptake and biomass accumulation. PGPR also suppress important maize pathogens, particularly *F. verticillioides*, through competition for nutrients and ecological niches, production of antibiotics and hydrolytic enzymes, secretion of inhibitory volatile compounds and induction of systemic resistance. In addition, PGPR-mediated regulation of 1-aminocyclopropane-1-carboxylate deaminase activity, antioxidant enzymes and biofilm formation can enhance maize tolerance to drought, salinity and other abiotic stresses. Evidence from greenhouse and field studies indicates that PGPR have potential to support maize growth, reduce disease incidence and lessen dependence on chemical fertilisers and pesticides. However, PGPR performance in maize is influenced by bacterial strain, maize genotype, soil properties, environmental conditions and inoculation method. Further maize-specific field validation, stable microbial formulations and integration into locally adapted crop management systems are required for reliable future application in sustainable maize production.

Keywords: Maize; Zea mays; plant growth-promoting rhizobacteria; PGPR; biological control; Fusarium verticillioides; induced systemic resistance; phosphate solubilisation; biological nitrogen fixation; abiotic stress; biofilm formation; sustainable agriculture.

1. Introduction

Maize (*Zea mays L.*), commonly known as corn, is one of the most important and widely cultivated cereal crops in the world due to its versatility and multiple uses. It serves as a staple food for millions of people, a major feed source for livestock, and an important raw material for various industrial applications (Swati et al., 2024). It is rich in carbohydrates and provides essential energy, along with moderate protein content (7–12%) and important micronutrients such as vitamin A, B-complex vitamins, magnesium, and phosphorus (Djalovic et al., 2024). Its wide adaptability to diverse agro-climatic conditions and high photosynthetic efficiency as a C4 plant enable it to perform well under varied environmental conditions, including high temperature and limited water availability (Gheith et al., 2022). In India, maize is the third most important cereal crop after rice and wheat, contributing significantly to food, feed, and industrial sectors, with cultivation carried out in Kharif, Rabi, and spring seasons, where Kharif accounts for the major production share (Shiferaw et al., 2011). In addition, maize is also an important crop in regions like Punjab, where it is cultivated during the Kharif season under favourable agro-climatic conditions and supports livestock feed and agro-industrial uses (Revilla et al., 2022; Bello et al., 2014). Maize-based systems also contribute to sustainable agriculture through intercropping and crop rotation practices that improve soil fertility and farm income diversification (Kheroar & Patra, 2014), while conservation agriculture practices such as zero tillage are being increasingly adopted for long-term productivity improvement (Harish et al., 2022). Furthermore, maize plays a significant role in livestock feed production and industrial applications such as starch and ethanol production (Sahu et al., 2023).

Despite its importance, maize productivity is substantially affected by various biotic and abiotic stresses, leading to yield instability and production losses worldwide (Kimotho & Maina, 2024). Abiotic stresses include drought, temperature extremes, and salinity, whereas biotic stresses involve fungal, bacterial, viral pathogens, nematodes, and insect pests. Among these, soil- and seed-borne fungal pathogens are particularly destructive due to their persistence in soil and ability to survive under unfavourable conditions (Winders & Pechan, 2021). *Fusarium verticillioides* is one of the most important pathogens of maize, causing seed rot, seedling blight, stalk rot, and ear rot, resulting in severe economic losses globally (Goko et al., 2021). Yield losses can reach up to 50% under favourable conditions, particularly during water stress and temperature fluctuations, with severe infections potentially causing complete crop failure (Liu et al., 2022). The pathogen infects maize at multiple growth stages, spreads systemically through vascular tissues, and can be transmitted through infected seeds, ensuring long-term persistence in agroecosystems (Cao et al., 2022). Although resistant cultivars are considered an economical management strategy, their effectiveness is often reduced due to pathogen variability and emergence of new races that overcome host resistance (Song et al., 2024).

Chemical control methods have also been widely used for managing *F. verticillioides*; however, their effectiveness is limited due to high costs, environmental contamination, residue accumulation, and development of fungicide-resistant pathogen strains (Dobrzyński et al., 2023). In this context, plant growth-promoting bacteria (PGPB), particularly genera such as *Pseudomonas* and *Bacillus*, have emerged as sustainable alternatives for disease management and plant growth enhancement (Figueiredo et al., 2008). These bacteria suppress pathogens through mechanisms such as competition, antibiosis, and induction of systemic resistance, while also improving nutrient uptake, root development, and plant vigour (de Souza et al., 2015). Although PGPR have shown significant potential in maize systems, the relationship between in vitro plant growth-promoting traits and their actual biocontrol efficiency against *Fusarium verticillioides* under plant conditions remains insufficiently understood. Therefore, this review focuses on PGPR-mediated mechanisms in maize, highlighting their role in disease suppression, plant growth promotion, and their potential application in sustainable maize production systems.

2. Biological Control

The management of plant diseases holds significant economic importance and plays a vital role in ensuring food safety. In this context, biological control using microbial agents is increasingly becoming an essential component of plant disease management, especially in mitigating root diseases (Meki et al., 2011). Currently, the biological control of soil- and seed-borne fungal pathogens, such as *Fusarium verticillioides* in maize, is primarily addressed through the use of bacterial and fungal antagonists. Strains of *Trichoderma* spp. and certain rhizobacteria, particularly *Pseudomonas* spp. and *Bacillus* spp., have demonstrated effectiveness in controlling *F. verticillioides* infections. These microbes, often isolated from the rhizospheres of maize and other crop plants, not only suppress plant pathogens but also enhance plant growth by aiding in the mobilization and acquisition of essential nutrients from the soil. Biological agents thus serve a dual purpose, functioning both as biopesticides to manage diseases caused by *F. verticillioides* and as biofertilisers by improving nutrient availability to maize plants. Furthermore, the use of these biocontrol agents is environmentally friendly, safer for ecosystems, and poses a significantly lower risk of pollution compared to chemical pesticides. This sustainable approach is a critical step toward achieving healthier crop production and reducing the environmental footprint of disease management practices (Pirttilä et al., 2021). Although numerous studies have demonstrated the ability of PGPR to enhance nutrient acquisition in maize, the magnitude of these effects varies considerably among bacterial strains, maize genotypes, and soil environments. Many reported benefits have been obtained under controlled greenhouse conditions, whereas field performance is often less consistent. Therefore, further field-based investigations are required to identify robust PGPR strains capable of delivering reliable benefits across diverse maize-growing environments.

Several studies have reported the potential of biological agents, particularly plant growth-promoting rhizobacteria, in suppressing *Fusarium verticillioides* and related maize pathogens. However, the level of disease suppression reported varies considerably among studies, ranging from strong inhibition under controlled laboratory conditions to only moderate or inconsistent performance under greenhouse and field conditions. This variation suggests that biocontrol efficiency is highly strain-dependent and influenced by environmental factors, soil microbiome composition, and pathogen variability. Moreover, many earlier studies have focused primarily on in vitro antagonistic activity, with limited validation under plant growth conditions, which restricts the practical applicability of these findings in maize production systems.

2.1 Plant Growth-promoting Rhizobacteria as Efficient Biocontrol Agents and their Mechanisms

Plant growth-promoting rhizobacteria (PGPR), residing in the rhizosphere, rhizoplane, and soil particles associated with plant roots, enhance plant health through various mechanisms (Ahemad & Kibret, 2014). These bacteria form a diverse group, including symbiotic species (*Bradyrhizobium*, *Mesorhizobium*, and *Rhizobium* spp.) and non-symbiotic species such as *Agrobacterium*, *Arthrobacter*, *Azoarcus*, *Azotobacter*, *Azomonas*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Klebsiella*, *Micrococcus*, *Pantoea*, *Pseudomonas*, and *Serratia* spp. These rhizobacteria are utilised as bioinoculants to promote plant growth and act as biocontrol agents against various fungal pathogens. PGPR possess the unique ability to enhance plant growth by colonising the root system and suppressing plant pathogens by outcompeting them in the same habitat (Ahmad et al., 2008). Seed priming with these biocontrol agents is an effective strategy for managing plant pathogens in the spermosphere and rhizosphere. Furthermore, the integration of rhizobacteria with mineral fertilisers has been a long-standing practice to boost crop yields while minimising economic and environmental impacts (Adesemoye et al., 2009).

Fluorescent pseudomonads and *Bacillus* spp. are among the most significant and effective plant growth-promoting rhizobacteria (PGPR) used as biocontrol agents due to their ability to inhibit the mycelial growth of numerous fungal pathogens (Singh et al., 2013). Their strong rhizosphere competence plays a crucial role in suppressing the proliferation of various pathogens. Additional mechanisms for controlling phytopathogenic damage include the physical displacement of pathogens, secretion of siderophores to limit pathogen growth near plant roots, and the production of antibiotics, enzymes, and small volatile or diffusible molecules with anti-phytopathogenic properties. These bacteria also secrete salicylic acid and other elicitors to stimulate the plant's defence mechanisms, indirectly promoting plant growth. Among the recognised biocontrol strategies mediated by PGPR, the induction of systemic resistance (ISR) in plants against a wide range of pathogens has emerged as a significant area of research (Yadav et al., 2023). Studies suggest that PGPR-induced ISR partially overlaps with pathogen-induced systemic acquired resistance (SAR), leading to an overall enhancement of the host plant's resistance. This overlapping mechanism enables PGPR to stimulate the production and activity of pathogenesis-related (PR) proteins in plants, such as peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), chitinases, lipoxygenases, and glucanases. These PR proteins strengthen the plant's defence system, helping to suppress the pathogenic effects (Wang et al., 2016).

In addition to indirectly promoting plant growth by mitigating the harmful effects of phytopathogenic organisms, biocontrol agents also directly enhance plant growth through various mechanisms. These include the production and regulation of plant growth hormones, atmospheric nitrogen fixation, production of siderophores to improve iron uptake from the soil, and the solubilisation of mineral phosphates and other nutrients through the release of organic acids. Currently, agricultural research is increasingly focused on utilising these plant-beneficial biological agents to suppress plant pathogens in combination with cultural practices and chemical control measures as part of integrated management strategies. Furthermore, the application of inoculant-based PGPR on agricultural crops not only boosts plant growth but also reduces the reliance on chemical inputs such as fertilisers and pesticides, thereby minimising environmental degradation (Shah et al., 2021).

2.2 Mode of Action of PGPR as Bioinoculants

Plant growth-promoting rhizobacteria (PGPR) can be broadly categorised into two main groups based on their mode of action: those that contribute to nutrient cycling or biogeochemical processes and phytostimulation, and those that play a role in the biological control of plant pathogens (Riaz et al., 2021). However, this classification often becomes imprecise since many PGPR exhibit characteristics of both groups, promoting plant growth through both direct and indirect mechanisms. Collectively, they function as biofertilisers, rhizoremediators, phytostimulators, and stress controllers (Backer et al., 2018). Understanding the diverse mechanisms by which PGPR promote plant growth is crucial not only for assessing their impact within the rhizosphere and plant systems but also for optimising their application in sustainable agriculture.

3. Mechanisms of PGPR-mediated Growth Promotion in Maize

3.1 Biological Nitrogen Fixation

Plant growth-promoting rhizobacteria (PGPR) play a crucial role in enhancing nutrient uptake or increasing nutrient availability by facilitating nitrogen fixation and solubilising various essential mineral nutrients in the soil (Bhardwaj et al., 2014). Nitrogen, a vital element for all living organisms, is particularly critical for plant growth and productivity. Although nitrogen makes up 78% of the atmosphere, it remains inaccessible to plants since they lack the ability to convert atmospheric dinitrogen into ammonia. Nitrogen fixation is a key process in cycling nitrogen from the atmosphere to the biosphere, serving as a primary input for plant productivity. Certain bacteria and archaea, with few exceptions, possess the ability to fix atmospheric nitrogen through biological nitrogen fixation (BNF), providing approximately 180×10^6 metric tons of fixed nitrogen annually on a global scale, a contribution of immense importance (Ndlazi et al., 2026).

Biological nitrogen fixation (BNF) is a well-established process carried out by bacteria through a complex enzyme system known as nitrogenase, which reduces atmospheric N_2 to ammonia. Symbiotic nitrogen fixation involves a mutualistic relationship between microbes and plants, contributing about 80% of the total nitrogen fixed, while the remaining 20% comes from free-living diazotrophs in associative systems (Mus et al., 2016). Plant growth-promoting rhizobacteria commonly found as symbionts include *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Sinorhizobium* in association with leguminous plants, and *Frankia* with non-leguminous trees and actinorrhizal plant species, all of which are responsible for nitrogen fixation in these crops. Non-symbiotic nitrogen fixation is carried out by free-living diazotrophs that promote the growth of non-leguminous crops such as radish and rice. Examples of non-symbiotic nitrogen-fixing bacteria include *Azotobacter*, *Acetobacter*, *Azoarcus*, *Azospirillum*, *Burkholderia*, *Gluconacetobacter*, *Diazotrophicus*, *Pseudomonas*, and cyanobacteria like *Anabaena* and *Nostoc*. Both symbiotic and non-symbiotic rhizobacteria contain nitrogenase (nif) genes, which are essential for nitrogen fixation. These genes are involved in activating the Fe protein, biosynthesising the iron-molybdenum cofactor, transferring electrons, and regulating the synthesis and function of nitrogenase (Gupta et al., 2019). Non-symbiotic BNF has significant agronomic potential but is limited by the low availability of carbon as an energy source for the energy-intensive nitrogen fixation process. To overcome this, many free-living diazotrophs have developed mechanisms to colonise plant roots as endophytic bacteria (Kuan et al., 2016). Although the nitrogen-fixing ability of certain bacteria has been demonstrated under in vitro conditions, validating these findings in controlled greenhouse and field studies has been more complex and variable. Nevertheless, numerous studies highlight the role of rhizobacteria in fixing substantial quantities of nitrogen in various crops (Singh et al., 2020).

For example, *Azotobacter*, a free-living aerobic nitrogen fixer, has been shown to enhance seed germination, seedling growth, and nitrogen content in plants. Khati et al. (2025) reported that inoculation with plant growth-promoting rhizobacteria (PGPR) increased total nitrogen levels in *Musa* plantlets under hydroponic conditions. Similarly, endophytic diazotrophs in sugarcane have been reported to meet 20–60% of the crop's nitrogen requirements under field conditions. Co-inoculation of PGPR with rhizobia has also been shown to improve nodulation and nitrogen fixation in various crops. Nitrogen balance studies revealed that endophytic bacteria such as *Gluconacetobacter diazotrophicus* could fix up to 150 kg N ha^{-1} yr^{-1} in sugarcane (Figueiredo et al., 2008). Other studies have demonstrated increased yields in cereal crops like wheat, maize, and rice through BNF mechanisms after seed inoculation with *Azospirillum*. Inoculation with *Bacillus pumilus* significantly increased nitrogen uptake in maize plants, with increments of 55.1% and 50.1% observed by the 50th and 60th day, respectively, compared to uninoculated controls (Jha & Saraf, 2015). Similarly, *Klebsiella pneumoniae* produced increases of 61.4% and 48.4%. Biological nitrogen fixation is crucial for sustainable agriculture and offers an eco-friendly alternative to chemical fertilisers. Increasing the use of nitrogen-fixing rhizobacteria in crop cultivation not only enhances plant growth and nitrogen levels in soils but also integrates disease management strategies, promoting both economic and environmental benefits (Kuan et al., 2016).

3.2 Phosphate Solubilisation and Mineralization

Phosphorus (P) is the second most critical nutrient for plants after nitrogen, essential for optimal growth. It plays a vital role in numerous metabolic processes, including photosynthesis, macromolecular biosynthesis, energy transport, signal transduction, and respiration (Khan et al., 2010). Despite being abundant in soils in both organic and inorganic forms, the availability of plant-accessible phosphorus is generally low due to its insoluble, immobile, and precipitated nature. Plants can only efficiently absorb phosphorus in its soluble forms, the monobasic ($H_2PO_4^-$) and diabasic (HPO_4^{2-}) ions (Ul Nisa et al., 2026). While the accessible phosphorus in soils is typically around 1 μmol L^{-1}, whereas plants require approximately 30 μmol L^{-1} to achieve maximum productivity. Although phosphatic fertilisers are available, their effectiveness is limited due to precipitation into insoluble mineral complexes, making them inaccessible to plants. As 95–99% of soil phosphorus exists in unavailable forms, efficient mechanisms are needed to transform it into plant-usable forms (Matse et al., 2020). The fixation and precipitation of phosphorus in soils are highly pH-dependent. In acidic soils, precipitation occurs as aluminum and iron phosphates, while in calcareous soils, high concentrations of calcium phosphates are the primary limiting factor. Microbial activity significantly enhances phosphorus availability by lowering soil pH and releasing orthophosphate from organic and inorganic complexes. Plant growth-promoting bacteria (PGPB) and fungi, such as mycorrhizae, are well-known for their role in solubilising inorganic phosphates and making them accessible to plants. Among the most efficient phosphate-solubilising microorganisms (PSM) are species from the genera *Bacillus*, *Rhizobium*, *Pseudomonas*, and some *Mesorhizobium* spp. These microbes not only solubilise inorganic phosphates, such as tricalcium phosphate, rock phosphate, and aluminum phosphate, but also mineralise organic phosphorus, thereby converting it into plant-available forms (Bouizgarne, 2022). This ability to transform insoluble phosphorus into soluble forms is a key trait of PGPR, contributing significantly to enhanced plant yield. A critical mechanism of phosphate solubilisation involves the secretion of organic acids such as acetic, citric, formic, fumaric, glycolic, lactic, malic, succinic, tartaric, propionic, gluconic, 2-ketogluconic, and oxalic acids. These acids aid in solubilising inorganic phosphorus. Organic phosphorus, which constitutes about 50% of the available phosphorus in soils rich in organic matter, predominantly exists as phytate (Etesami et al., 2015). The mineralisation of organic phosphorus is facilitated by extracellular enzymes such as phosphatases, phytases, phosphonoacetate hydrolases, D-α-glycerophosphatases, and C-P lyases, which catalyse the hydrolysis of phosphoric esters. Studies have demonstrated significant phosphatase activity in the rhizosphere of crops like wheat, maize, and barley, particularly at acidic and neutral pH levels. Most phosphate-solubilising bacteria (PSB) exhibit both solubilisation and mineralisation mechanisms within the same strain, making them highly effective in improving phosphorus availability for agricultural crops (Chungopast et al., 2021).

Among plant growth-promoting rhizobacteria (PGPR) in the soil, 20–40% of the population consists of phosphate-solubilising microorganisms (PSM), making up a significant portion of the rhizospheric bacterial community. Within these bacterial communities, ectorhizospheric strains such as *Pseudomonas* and *Bacillus*, along with endosymbiotic rhizobia, have been identified as highly effective phosphate solubilisers (Sasmita et al., 2022). Species from genera such as *Bacillus*, *Pseudomonas*, and *Burkholderia* are regarded as the most efficient producers of gluconic acid, a key agent in mineral phosphate solubilisation. Symbiotic bacteria, including *Rhizobium leguminosarum* and *Rhizobium meliloti*, as well as the non-symbiotic *Bacillus firmus*, have also been reported to produce 2-ketogluconic acid and phytases, which play a critical role in phosphate solubilisation and mineralisation. Many strains of *Bacillus* produce mixtures of organic acids such as acetic, gluconic, lactic, isovaleric, and isobutyric acids (Chungopast et al., 2021). Additionally, other organic acids, including glycolic, oxalic, malonic, succinic, citric, and propionic acids, along with various phosphate-mineralising enzymes, have been identified in phosphate-solubilising microorganisms. These metabolites and enzymes collectively contribute to the efficient solubilisation and mineralisation of phosphorus in the soil (Sasmita et al., 2022).

3.3 Production of Plant Growth Regulators

The ways in which plant growth-promoting rhizobacteria (PGPR) directly influence plant growth vary across species and strains. Free-living rhizobacteria typically employ multiple mechanisms to stimulate plant growth rather than relying on a single approach. Along with nitrogen fixation and the solubilisation of mineral nutrients in the soil, PGPR produce a wide range of secondary metabolites that play a direct role in promoting plant growth (Alori et al., 2017). Among these secondary metabolites are phytohormones, which are synthesised in minute quantities and function as signalling molecules or chemical messengers in various processes of plant growth and development. The phytohormones produced by higher plants and several soil microorganisms include auxins, gibberellins, cytokinins, ethylene, zeatin, and abscisic acid (Sasmita et al., 2022).

Indole acetic acid (IAA), one of the most physiologically active auxins, is a common product of L-tryptophan metabolism by several plant growth-promoting rhizobacteria (PGPR). IAA plays a crucial role in regulating various processes, including cell elongation, cell division, tissue differentiation, and apical dominance. While auxins influence the entire plant, the production of IAA by PGPR in the rhizosphere primarily promotes the development of longer roots with increased root hairs and lateral roots (Jahn et al., 2021). This enhances the root surface area, improving the plant's nutrient uptake and growth potential. IAA also influences other plant processes, such as responses to light and gravity, photosynthesis, pigment formation, metabolite biosynthesis, and resistance to various stress conditions. It primarily stimulates cell elongation by increasing osmotic content, enhancing water permeability, and reducing cell wall pressure. Approximately 80% of rhizospheric bacteria involved in IAA synthesis belong to genera such as *Agrobacterium*, *Alcaligenes*, *Acetobacter*, *Azospirillum*, *Rhizobium*, *Bradyrhizobium*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, and *Xanthomonas*. PGPR produce IAA through both L-tryptophan-dependent and independent pathways (Amara et al., 2015). Among the L-tryptophan-dependent pathways, three are currently known. L-tryptophan, a key precursor found in root exudates, is widely utilised by these microorganisms for IAA production. However, only a few PGPR are known to produce IAA via the tryptophan-independent pathway. An exception is *Azospirillum brasilense*, where over 90% of IAA is synthesised through the tryptophan-independent pathway, while the remaining 10% is produced using L-tryptophan through tryptophan transaminase activity (Joshi & Napier, 2023).

Gibberellins (GAs) represent a diverse group of molecules that regulate various developmental processes in higher plants, including seed germination, stem elongation, sex expression, breaking dormancy, flowering, and leaf and fruit senescence (Evlat et al., 2023). While the production of gibberellins by microorganisms is relatively rare, certain symbiotic rhizobia and plant-associated bacteria, such as *Bacillus pumilus* and *Bacillus licheniformis*, have been identified as gibberellin producers. Advances in detection techniques have also revealed gibberellin production in other bacterial genera, including *Azospirillum*, *Rhizobium*, *Acetobacter*, Herbaspirillum, Rhodospirillum, *Pseudomonas*, Paenibacillus, and additional *Bacillus* species (Amara et al., 2015). Similarly, cytokinins form another class of phytohormones that play a crucial role in promoting cell division, enlargement, and tissue expansion in plant roots and shoots. Their primary functions include stimulating cell growth and differentiation, enhancing seed germination, supporting embryo vascularization, boosting chlorophyll production, facilitating leaf expansion, maintaining apical dominance, and delaying tissue senescencee or aging. Soil microorganisms, including those from the genera *Bacillus*, *Azospirillum*, Proteus, *Klebsiella*, *Pseudomonas*, and *Xanthomonas*, have been reported to promote seedling growth through cytokinin production (Maheshwari et al., 2015).

4. Mechanisms Involved in Biological Control

Plant growth-promoting rhizobacteria (PGPR) play a crucial role in suppressing plant pathogens, which are aggressive colonisers of the rhizosphere in various crops. PGPR exhibit broad-spectrum antagonistic activity against numerous pathogens. The mechanisms underlying biological control include competition for nutrients, niche exclusion, antibiosis, production of various antimetabolites, and the induction of systemic resistance in crop plants. Several plant-associated microorganisms have been reported to produce antifungal metabolites such as hydrocyanic acid, ammonia, and antibiotics like phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol, pyoluteorin, viscosinamide, and tensin (Bhattacharyya et al., 2020).

4.1 Sequestering Iron

Iron is a critical growth-limiting factor for most living organisms, as it is essential for the activity of heme-enzymes involved in vital processes such as DNA synthesis, respiration, photosynthesis, and nitrogen fixation. Despite being one of the most abundant elements in the Earth's crust, iron is not readily available to plants due to its presence in highly insoluble forms, such as ferric (Fe^{3+}) ions, which are often precipitated as hydroxides, oxyhydroxides and oxides, the predominant forms of iron in nature (Lurthy et al., 2020). In aerobic environments, microorganisms face significant challenges in acquiring iron, as the solubility constant for Fe^{3+} ions is approximately 10^{-38} M. At neutral pH, the concentration of free available iron is as low as 10^{-17} M, far below the 10^{-7} M required for microbial and plant growth. To overcome this limitation, microorganisms have evolved high-affinity iron uptake systems involving the production of siderophores, also known as ionophores. These are low molecular weight (≤ 1000 Da), high-affinity ferric ion chelators synthesised and secreted by microorganisms and plants under iron-deficient conditions (Zhang et al., 2023).

Siderophores are secreted to scavenge iron from mineral phases by forming soluble Fe^{3+} complexes, which are then taken up by active transport systems that are activated only under low iron availability. The scarcity of bioavailable iron in the soil induces competition among rhizosphere microorganisms for siderophore production. The ability to produce siderophores not only enhances the rhizosphere colonization ability of the producing strain but also improves iron nutrition in plants and antagonism against phytopathogens with less efficient iron uptake systems (Mushtaq et al., 2022). Siderophores produced by PGPR effectively bind the majority of Fe^{3+} in the rhizosphere, inhibiting the growth of fungal pathogens by interfering with nucleic acid synthesis, sporulation, and altering cell morphology. These iron chelators bind Fe^{3+}, reduce it to Fe^{2+} and form a hexadentate octahedral complex. The reduced Fe^{2+} is then transported by carrier molecules to the cytoplasm for metabolic activities before being oxidised again. During this process, the siderophores are recycled. In addition to iron, siderophores can form stable complexes with other heavy metals, such as Al, Cd, Cu, Ga, In, Pb, and Zn, as well as radionuclides like U and Np, helping to mitigate the stress caused by high levels of heavy metals in the soil (Misra et al., 2024).

Iron-siderophore complexes play a crucial role in alleviating iron deficiency in plants, thereby directly promoting plant growth. The presence of siderophore-producing PGPR (plant growth-promoting rhizobacteria) in the rhizosphere further accelerates the supply of Fe^{3+} to plants, enhancing their growth and crop productivity (Soares, 2022). Besides restricting competitive microbes by limiting Fe^{3+} availability, siderophores are also recognised for their role in boosting systemic resistance in plants. Moreover, the ability of soil bacteria to improve plant iron nutrition becomes particularly significant under environmental stresses, such as heavy metal pollution. Siderophores, also known as ionophores, are classified based on the type of ligands they use to chelate ferric iron (Sun et al., 2022). The main categories of siderophores include catecholates, hydroxamates, and carboxylates. Catecholate siderophores include enterobactin, produced by *Escherichia coli*; bacillibactin, produced by *Bacillus subtilis* and *Bacillus* anthracis; and vibriobactin, produced by *Vibrio cholerae*. Hydroxamate siderophores include ferrichromes, produced by *Ustilago sphaerogena*; desferrioxamine B (Deferoxamine), produced by *Streptomyces pilosus* and *Streptomyces coelicolor*; and desferrioxamine E, produced by *Streptomyces coelicolor* (Sarwar et al., 2022).

4.2 Antibiosis

Antibiosis plays a pivotal role in the biocontrol of plant diseases, often working synergistically with competition and parasitism. It has been identified as a key mechanism through which rhizobacteria suppress plant pathogens. Antibiotics are a diverse group of low-molecular-weight organic compounds produced by various microorganisms. Plant growth-promoting rhizobacteria (PGPR) produce a wide range of antibiotics, providing them with a competitive advantage and enhancing their microbial fitness in diverse environments (Wang et al., 2021). Among the most extensively studied rhizospheric bacteria for antibiotic production are *Pseudomonas* and *Bacillus* species. *Pseudomonas* strains produce antibiotics such as 2, 4-diacetylphloroglucinol (DAPG), butyrolactones, kanosamine, phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide (PCN), pyoluteorin (Plt), pyrrolnitrin (Prn), aerugine, azomycin, oomycin A, viscosinamide, ecomycins, zwittermycin-A, rhamnolipids, cepaciamide A, pseudomonic acid, cepafungins, hydrocyanic acid, and ammonia (Maurya et al., 2024). Similarly, *Bacillus* species produce a wide range of antibacterial and antifungal antibiotics, including bacilysin, bacillaene, chlorotetain, difficidin, mycobacillin, subtilin, subtilosin A, sublancin, and rhizocticins. Notably, antibiotics like 2, 4-DAPG, PCA, and PCN have been shown to effectively control plant pathogens. Additionally, *Serratia marcescens* has been reported to produce antibiotics (Lee et al., 2022). These antibiotic-producing rhizobacteria have demonstrated efficacy as biocontrol agents against several fungal phytopathogens, including *Sclerotium rolfsii*, *Fusarium oxysporum*, *Fusarium solani*, *Rhizoctonia solani*, *Rhizoctonia bataticola*, and *Macrophomina phaseolina* (Léger et al., 2021).

4.3 Hydrolytic Enzymes (Cell Wall Degrading Enzymes)

Several plant-associated microorganisms exhibit hyperparasitic activity, targeting plant pathogens by secreting cell wall hydrolases. Hyperparasitism involves the physical destruction of the pathogen's cell wall, facilitated by hydrolytic enzymes produced by biocontrol agents. These antagonistic microorganisms attack fungal pathogens by releasing extracellular enzymes capable of lysing pathogen cell walls or degrading their chlamydospores, conidia, sporangia, and zoospores. Cell wall-degrading enzymes, such as β-1, 3-glucanase, chitinase, cellulase, dehydrogenase, lipase, phosphatase, and protease, secreted by biocontrol agents, directly inhibit the mycelial growth of pathogens by breaking down their cell wall (Lazarević et al., 2024). Among these, chitinase and β-1, 3-glucanase are considered the primary lytic enzymes responsible for degrading the chitin and glucan components of fungal cell walls. Chitinases play a crucial role by hydrolysing chitin, a linear β-(1,4)-linked N-acetyl glucosamine polysaccharide that constitutes 22–44% of fungal cell walls. In the genus *Bacillus*, chitin-degrading activity is common, with chitobiosidase enzymes reported to break down the hyphal cell walls of various root-rotting fungal pathogens. Similarly, β-1, 3-glucanase is another vital enzyme produced by antagonistic microorganisms, contributing to the biological control of phytopathogenic fungi by degrading glucan in fungal cell walls (Valys et al., 2023).

Proteases and lipases are other important lytic enzymes involved in breaking down proteins and lipids that are either attached to the cell walls or present inside the cells of pathogens (Sujitha & Shanthi, 2021). Additionally, extracellular enzymes include a wide range of solubilising enzymes that improve nutrient availability for both plants and the microorganisms producing them (Kaur et al., 2016). These enzymes indirectly disrupt the integrity of pathogen cell walls and interfere with metabolic activities within the phytopathogen cells. The production and release of extracellular enzymes by microorganisms are often inducible in the presence of specific substrates, which enhances their hydrolytic activity, particularly in soils heavily infected with fungal pathogens (Baloch, 2025). Thus, plant growth-promoting rhizobacteria (PGPR) play a vital role in promoting plant growth by protecting plants from both biotic and abiotic stresses through the suppression of various fungal pathogens.

4.4 Volatile Antimetabolites

Plant growth-promoting rhizobacteria (PGPR) can inhibit the growth of plant pathogens through various mechanisms, including the secretion of antifungal metabolites (Giorgio et al., 2015). Recently, an additional strategy against phytopathogens has emerged—the production of volatile organic compounds (VOCs) by PGPR, which exhibit inhibitory effects on several phytopathogens. Volatile organic compounds (VOCs) are typically low-molecular-weight (≤300 Da), lipophilic substances with relatively low boiling points. Due to their high vapor pressure, VOCs can easily pass through biological membranes and disperse into the atmosphere or soil at varying concentrations. This enables them to influence the development of neighboring organisms across long distances within ecosystems. VOCs play key roles in various biological processes, such as helping pollinators locate flowers, inhibiting the growth of pathogens, directly combating pathogens, and attracting predators of herbivores, thereby providing indirect defence mechanisms (Tran et al., 2024). These compounds function as signalling molecules, facilitating communication both within and between organisms, as well as among cells within the same population. For instance, Sehrawat et al. (2022) demonstrated the inhibitory effects of antifungal VOCs produced by soybean endophytic bacteria on sclerotia, ascospore germination, and mycelial growth of *Sclerotinia sclerotium* in both in vitro and soil-based experiments. Similarly, strains of rhizobacteria such as *Pseudomonas fluorescens*, *Pseudomonas trivialis*, *Serratia plymuthica*, and *Serratia odorifera* have been reported to produce complex blends of organovolatiles that effectively inhibit the growth of various phytopathogenic fungi.

4.5 Determinants of Volatile Antimetabolites

4.5.1 Hydrogen Cyanide (HCN)

Hydrogen cyanide (HCN) is a broad-spectrum antimicrobial compound produced by plant-associated antagonistic rhizobacteria, playing a significant role in the biological control of soil- and seed-borne pathogens. Certain bacteria, including species of ectorhizospheric *Alcaligenes*, *Aeromonas*, *Azotobacter*, *Bacillus*, *Pseudomonas*, and *Rhizobium* are known to synthesise HCN. As a secondary metabolite, HCN suppresses the growth and development of competing microorganisms within the same habitat (Sagar et al., 2018). It is produced during the early stationary phase of microbial growth and acts as a volatile antimetabolite, effectively inhibiting several metal-containing enzymes, particularly copper-dependent cytochrome c oxidases in the electron transport chain. This disruption of energy production ultimately leads to the death of pathogenic organisms (Sagar et al., 2018). However, the producing the bacteria themselves are protected from the toxic effects of HCN due to conformational changes in their enzymes during the stationary phase. Low oxygen concentrations are known to be essential for the activation of the transcription factor ANR, which positively regulates HCN synthase (Neerincx et al., 2015). This enzyme is encoded by three biosynthetic genes, hcnA, hcnB, and hcnC. The antifungal activity of *Pseudomonas*, *Bacillus*, and *Azotobacter* species is often linked to their production of HCN, siderophores, or a synergistic interaction between these compounds and other metabolites (Rayavarapu & Padmavathi, 2016). Additionally, some cyanogenic rhizobacteria exhibit host-specificity and are closely associated with the roots of their host plants. As a result, hydrogen cyanide-producing rhizobacteria have potential as an environmentally friendly alternative for weed control.

4.5.2 Ammonia Production by Rhizobacteria

Ammonia is another class of volatile compounds, often associated with nitrogen fixation and commonly observed in many legume-associated rhizobacteria (Jha & Saraf, 2015). Biological nitrogen fixation primarily occurs through the symbiotic and non-symbiotic interactions of nitrogen-fixing microorganisms with legumes. These processes involve biochemical reactions that convert atmospheric dinitrogen (N_2) into ammonia (NH_3) (Abdelwahed et al., 2022). Various species, including *Bacillus*, *Pseudomonas*, *Azotobacter*, *Alcaligenes*, *Aeromonas*, *Azospirillum*, *Klebsiella*, certain cyanobacteria, and nearly all rhizobial species, have demonstrated the ability to produce ammonia.

In addition to leguminous crops, plant growth-promoting rhizobacteria (PGPR) also interact with non-leguminous plants such as wheat, maize, rice, sugarcane, *Jatropha*, and cotton, significantly enhancing their vegetative growth and grain yield (Kurt, 2025). For example, *Bacillus subtilis* and *Pseudomonas fluorescens* have been identified as efficient ammonia producers, leading to notable biomass enhancement in the medicinal plant *Geranium* (Gupta et al., 2019). Breedt et al. (2017) reported ammonia production in 95% of *Bacillus* and 94.2% of *Pseudomonas* isolates, which demonstrated inhibitory effects on various phytopathogens under in vitro conditions. Collectively, these findings demonstrate the critical role of ammonia-producing microorganisms in nitrogen fixation, plant growth enhancement, and the biological control of various phytopathogens.

4.6 Plant Growth-promoting Rhizobacteria as Abiotic Stress Mediators

Plants are frequently exposed to harsh environmental conditions such as cold, drought, salinity, radiation, waterlogging, heavy metals, and various pathogens (Etesami et al., 2015). These stressors trigger a shift in plants toward secondary metabolic pathways, leading to increased levels of secondary metabolites like ethylene, proline, and certain phenolic compounds. Elevated levels of these metabolites negatively impact essential processes such as respiration, photosynthesis, and protein synthesis. Among these, excessive ethylene production, often referred to as "stress ethylene, " can result in defoliation, chlorosis, flower wilting, and other cellular disruptions that reduce crop performance and productivity (Bhattacharyya & Jha, 2012).

Many plant growth-promoting rhizobacteria (PGPR) produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which regulates ethylene levels in plants. ACC deaminase mitigates ethylene production by breaking down 1-aminocyclopropane-1-carboxylate, the precursor of ethylene biosynthesis, into α-ketobutyrate (2-oxobutanoate) and ammonia (Moon & Ali, 2022). A variety of rhizobacterial genera, including *Agrobacterium*, *Achromobacter*, *Acinetobacter*, *Alcaligenes*, *Azospirillum*, *Burkholderia*, *Enterobacter*, *Bacillus*, *Pseudomonas*, *Ralstonia*, *Serratia*, and *Rhizobium*, have been identified for their ability to reduce stress-induced ethylene levels (Ahemad & Kibret, 2014). Research has shown that ACC deaminase-producing rhizobacteria not only alleviate stress-related damage in plants but also enhance growth and yield (Singh et al., 2022). For instance, co-inoculating plant growth-promoting strains of *Pseudomonas* with *Rhizobium leguminosarum* containing ACC deaminase activity significantly improved symbiotic parameters, grain yield, and nitrogen content in lentil grains by reducing ethylene production and supplying ammonia for plant assimilation (Iqbal et al., 2012). Furthermore, ACC deaminase activity has been shown to play a crucial role in host nodulation responses. By suppressing elevated ethylene synthesis, it promotes root elongation and nodulation, thereby improving the growth and yield of leguminous crops. Drought and saline conditions in certain soils can significantly disrupt plant nutrition due to high Na^+ levels. These conditions induce hyperionic and hyperosmotic stress, often leading to the generation of reactive oxygen species (ROS), such as superoxide ions (O_2^-), singlet oxygen ($^1O_2$), hydroxyl radicals (OH^-), and hydrogen peroxide (H_2O_2). These ROS oxidise essential biomolecules like lipids, proteins, and nucleic acids into toxic compounds, thereby interfering with critical metabolic processes in plants (Naing et al., 2021).

While plants develop their own antioxidant systems to combat oxidative damage (Nascimento et al., 2018), plant growth-promoting rhizobacteria (PGPR) possess a unique ability to further enhance these systems. PGPR boost the plant's natural defence mechanisms under abiotic stress by inducing the production of ROS-scavenging enzymes such as catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) (Nascimento et al., 2018). Evidence suggests that PGPR can enhance maize tolerance to drought and salinity through multiple physiological and biochemical mechanisms. However, the responses are often strain-specific and influenced by stress severity, soil characteristics, and maize genotype. A deeper understanding of plant–microbe interactions under field conditions is necessary to translate these findings into practical agricultural applications.

4.7 Biofilms

Biofilm are self-produced extracellular polymeric substance (EPS) matrices of microorganisms from one or more species that adhere to biotic or abiotic surfaces (Gebreyohannes et al., 2019). This matrix provides bacteria with structure and protection, enabling them to attach and function collectively through quorum sensing (QS). Biofilms can play a crucial role in biocontrol and plant growth promotion by providing a protective, nutrient-rich environment in which beneficial microorganisms can survive, colonise and interact with the plant host. Biofilms can also enhance microbial attachment and persistence on plant surfaces, allowing for efficient colonization and potential competition against plant pathogens. The biofilm-forming ability of *Bacillus tequilensis* was investigated as it was found to have the highest floc yield at 100 mM NaCl concentration (Haroon et al., 2023). Biofilms can also modulate the plant immune system and induce resistance against various biotic and abiotic stresses. Biofilms can activate the plant defence mechanisms by triggering different signalling pathways, such as salicylic acid, jasmonic acid and reactive oxygen species. Biofilms can also enhance the expression of genes or proteins involved in plant immunity, such as pathogenesis-related proteins, chitinases, glucanases and peroxidases. Some biofilm- producing microorganisms, such as *Pseudomonas* sp., *Bacillus* sp., and *Burkholderia* sp., have been reported to induce systemic resistance in plant against fungal pathogens, insects pests and heavy metals (Bhatia et al., 2021). Biofilm formation can enhance the survival of bacteria under various environmental stresses, including salinity and protect them from desiccation and nutrient uptake. The biofilm formed by *B. tequilensis* was found to contain carbohydrates and protein that bind with sodium ions and provide tolerance against salinity. When *B. tequilensis* was inoculated in the saline soil, it improved the physiology, biochemistry and antioxidant enzyme activities of the maize plant. Overall, the results suggest that the use of *B. tequilensis* as a biocontrol agent can be a sustainable approach to mitigate the stress (Xu et al., 2022).

4.8 Indirect Plant Growth Promotion through Induced Systemic Resistance

Harnessing a plant's natural defence mechanisms has become a focal point in pest and disease management strategies. The process of stimulating plant defence genes through the application of inducing agents is referred to as induced or acquired resistance (Meena et al., 2022). This represents a heightened defensive state in the host plant, triggered by specific environmental stimuli. Induced resistance is broadly categorised into two forms: systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR is typically initiated by necrotising pathogens or specific chemicals, whereas ISR is activated through root colonization by plant growth-promoting microorganisms. These two forms of resistance differ in their elicitors and regulatory pathways (Hossain et al., 2017). SAR generally relies on the accumulation of salicylic acid, while ISR is mediated by ethylene and jasmonic acid signalling pathways.

4.9 PGPR as Biotic Elicitors for Induction of Systemic Resistance

Elicitors, also known as aggressors, are chemical or biological factors from diverse sources that can stimulate physiological and morphological responses in plants. These elicitors can be abiotic, such as metal ions or inorganic compounds, or biotic, typically derived from microorganisms, plant cell wall components, or chemicals released during plant defence responses against insect pests and phytopathogens. When plants are treated with biotic elicitors, they initiate a cascade of natural defence mechanisms, leading to the accumulation of bioactive defensive molecules like phytoalexins and various pathogenesis-related (PR) proteins (Meena et al., 2022). Plant growth-promoting rhizobacteria (PGPR) are particularly recognised as effective biotic elicitors, capable of inducing the production of antimicrobial secondary metabolites in host plants.

4.9.1 Siderophores

Siderophores are small biomolecules produced by microorganisms, such as bacteria and fungi, to scavenge iron from the environment and enhance its availability for plant growth (Verma et al., 2021). Iron is an essential micronutrient required for various plant metabolic processes and its limited availability in soils can impact plant growth and development. Siderophores function by chelating iron, forming soluble complexes that can be taken up by plants. Once the siderophore-iron complex is transported back into the microorganisms, it dissociates in the vicinity of the plant root, allowing the plant to absorb the iron through specific transporters. This process supports physiological processes, such as chlorophyll synthesis, respiration and photosynthesis, which are vital for plant growth (Verma et al., 2021). Studies have shown that the production of siderophores by certain microorganisms promotes plant growth by improving iron availability. Siderophores can also modulate the plant immune system and induce resistance against various biotic stresses. Siderophores can activate the plant defence mechanisms by triggering different signalling pathways, such as salicylic acid, jasmonic acid, ethylene, nitric oxide and reactive oxygen species. Siderophores can also enhance the expression of genes or proteins involved in plant immunity, such as pathogenesis-related proteins, chitinase, peroxidase. Some siderophore-producing microorganisms such as *Pseudomonas* sp., *Bacillus* sp., and *Burkholderia* sp., have been reported to induce systemic resistance in plants against fungal pathogens, insect pests, drought, salinity and heavy metals (Srivastava et al., 2022). Furthermore, Abo-Zaid et al. (2020) examined fluorescent *Pseudomonas* isolates and found that two promising isolates, P. aeruginosa F2 and P. fluorescens JY3, produced significant levels of siderophores. These isolates inhibited the growth of plant pathogenic fungi, *Fusarium oxysporum* and *Rhizoctonia solani* and reduced damping off disease in wheat plants caused by pathogens.

4.9.2 Antibiotics

Antibiotics produced by certain rhizobacteria have also been shown to induce resistance against various fungal pathogens. Fluorescent pseudomonads, for instance, produce a diverse array of antibiotics, including phloroglucinols, phenazines and their derivatives, pyoluteorin and pyrrolnitrin, each with distinct structural configurations. While these antibiotics primarily target the electron transport chain of phytopathogens, studies have highlighted their role in enhancing plant defence mechanisms. For example, 2, 4-diacetylphloroglucinol (2, 4-DAPG), an effective antibiotic produced by *Pseudomonas fluorescens* CHA0, has been reported to induce resistance against the oomycete *Hyaloperonospora arabidopsidis* and the root rot nematode *Meloidogyne javanica* (Suresh et al., 2022). Similarly, DAPG produced by a strain of *Pseudomonas chlororaphis* was found to induce systemic resistance against the bacterial pathogen *Pseudomonas syringae pv. tomato* in *Arabidopsis* plants.

4.9.3 Biocidal Volatiles

Certain volatile organic compounds (VOCs) produced by plant growth-promoting rhizobacteria (PGPR) have been shown to play a significant role in enhancing plant defences against various pathogens. These VOCs include compounds such as undecanone, tridecanone, dodecanone, pyrazines, butanediol, hydroxybutanone, ammonia, allyl alcohol, acrylic acid, benzaldehyde, ethylene, and hydrogen cyanide (HCN). Among them, butanediol and hydroxybutanone, produced by specific strains of *Bacillus subtilis* and *Bacillus amyloliquefaciens*, are considered key elicitors of resistance in *Arabidopsis thaliana* plants against *Erwinia carotovora* (Tilocca et al., 2020). Additionally, research has highlighted the potential of VOCs released by fluorescent pseudomonads to effectively induce resistance against various root and seedling diseases in a wide variety of plant species.

4.9.4 Lipopolysaccharides (LPS)

Lipopolysaccharides (LPS), also known as lipoglycans, are a major component of the outer membrane of Gram-negative plant growth-promoting rhizobacteria (PGPR) and are key determinants in eliciting strong immune responses in plants. The lipid-A moiety of LPS plays a crucial role in enhancing plant defence mechanisms, as it has been shown to induce the production of nitric oxide (NO) in certain plants. The primary mechanism by which LPS induces systemic resistance involves the generation of reactive oxygen species (ROS) in plants (Simpson & Trent, 2019).

However, studies have indicated that the presence of LPS does not always lead to ROS production. For instance, LPS from *Salmonella enterica serovar Typhimurium* failed to induce ROS production in tobacco cell cultures, whereas *Xanthomonas campestris pv. campestris* effectively triggered an oxidative burst under similar conditions (Jain et al., 2019). These findings suggest that LPS produced by certain Gram-negative PGPR not only act as endotoxins to inhibit the growth of plant pathogens in soil but also enhance plant immunity by stimulating defence responses even after infection. This dual role helps reduce disease severity while promoting plant growth and productivity.

4.10 Determinants of ISR

The application of plant growth-promoting rhizobacteria (PGPR) induces significant physiological and metabolic changes in plants. Typically, induced systemic resistance (ISR) mediated by PGPR is associated with the accumulation of pathogenesis- or defence-related proteins in plant tissues, which represent a crucial non-specific defence mechanism against pathogens. The ability of certain rhizobacterial strains to induce pathogenesis-related enzymes is a key factor contributing to their antagonistic potential (Suresh et al., 2022). These defence-related enzymes include chitinase, glucanase, peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), superoxide dismutase (SOD), catalase (CAT), lipoxygenase (LOX), ascorbate peroxidase (APX), and proteinase inhibitors (Arun et al., 2023).

The defence gene products, peroxidase (PO) and polyphenol oxidase (PPO), are known to play a crucial role in reinforcing plant cell walls. These enzymes are also involved in the activation of phenylalanine ammonia-lyase (PAL), which contributes to the biosynthesis of phytoalexins and phenolic compounds. Additionally, lipoxygenases (LOX) play an indirect role in defence responses by facilitating the induction of phytoalexins, further enhancing the plant's defence mechanisms (Arun et al., 2023). These secondary metabolites are highly toxic to pathogens, as they disrupt cell walls and interfere with the metabolism and reproduction of the invading organisms, thereby mitigating disease severity in plants. Additionally, pathogenesis-related (PR) proteins, particularly hydrolytic enzymes such as β-1, 3-glucanases (PR-2 family) and chitinases (PR-3, PR-4, PR-8, and PR-11 families), play a significant role in breaking down fungal cell walls. The chitin and glucan oligomers released during this degradation act as elicitors, triggering various plant defence mechanisms (Islam, 2023).

Polyphenol oxidases (PPOs) represent another class of defensive enzymes that catalyse the oxygen-dependent oxidation of o-dihydroxyphenols into o-quinones, which are more toxic to pathogens than their precursors. Furthermore, PPOs are known to be activated in response to mechanical wounding, bacterial or fungal infections, and treatment with specific elicitors such as jasmonic acid, methyl jasmonate (MeJA), salicylic acid, and systemin. This activation provides an additional layer of defence, helping to protect plants against further attacks by pests and pathogens (Riseh et al., 2024).

5. Conclusion

Plant growth-promoting rhizobacteria represent an important biological resource for improving maize growth, health and resilience. The mechanisms reviewed in this manuscript indicate that PGPR can support plant development by increasing nutrient availability, producing growth-regulating substances, improving root growth and assisting physiological responses under stress. Their role in biological control is also relevant, as several rhizobacterial genera can suppress fungal pathogens through siderophore production, antibiosis, hydrolytic enzymes, volatile compounds, biofilm formation and induced systemic resistance. These activities may reduce disease pressure and contribute to more sustainable crop management when they are used as part of integrated strategies. The evidence also shows that PGPR-mediated responses are not uniform across all conditions. Their effectiveness depends on bacterial strain, host genotype, soil properties, environmental conditions and inoculation method. Therefore, PGPR should be considered a complementary component of maize nutrient and disease management rather than a complete substitute for existing agronomic practices. Future work should prioritise field validation, strain compatibility, formulation stability and consistent performance across diverse maize-growing environments. Particular attention should also be given to native isolates adapted to local soils and management systems. Such efforts will help translate the documented biological potential of PGPR into practical and reliable applications for sustainable maize production.

6. Limitations and Future Perspectives

This review is limited by its reliance on previously published studies, and its conclusions therefore depend on the scope, quality and availability of existing evidence. Reported PGPR effects vary among bacterial strains, maize genotypes, soil types, environmental conditions and experimental methods, which restricts direct comparison among studies. Many investigations have been conducted under laboratory or greenhouse conditions, whereas long-term, multi-location field evaluations remain limited. Consequently, the consistency of PGPR performance against *Fusarium verticillioides* and other stresses under natural maize-growing conditions is still not fully established. Another limitation is that many studies assess individual plant growth-promoting or antagonistic traits separately, although field performance depends on the combined expression of nutrient mobilisation, root colonisation, antibiosis, biofilm formation and induced systemic resistance. Further research should therefore integrate physiological, molecular and field-based approaches to clarify strain stability, persistence and practical effectiveness in diverse agro-ecological systems across contrasting seasons, conditions and locally relevant management practices.

Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abdelwahed, S., Trabelsi, E., Saadouli, I., Kouidhi, S., Masmoudi, A. S., Cherif, A., Mnif, W., & Mosbah, A. (2022). A new pioneer colorimetric micro-plate method for the estimation of ammonia production by plant growth promoting rhizobacteria (PGPR). *Main Group Chemistry, 21*(1), 55–68. https://doi.org/10.3233/MGC-210077

Abo-Zaid, G. A., Soliman, N. A.-M., Abdullah, A. S., El-Sharouny, E. E., Matar, S. M., & Sabry, S. A.-F. (2020). Maximization of siderophores production from biocontrol agents, *Pseudomonas aeruginosa* F2 and *Pseudomonas fluorescens* JY3 using batch and exponential fed-batch fermentation. *Processes, 8*(4), Article 455. https://doi.org/10.3390/pr8040455

Adesemoye, A. O., Torbert, H. A., & Kloepper, J. W. (2009). Plant growth-promoting rhizobacteria allow reduced application rates of chemical fertilizers. *Microbial Ecology, 58*(4), 921–929. https://doi.org/10.1007/s00248-009-9531-y

Ahemad, M., & Kibret, M. (2014). Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *Journal of King Saud University - Science, 26*(1), 1–20. https://doi.org/10.1016/j.jksus.2013.05.001

Ahmad, F., Ahmad, I., & Khan, M. S. (2008). Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiological Research, 163*(2), 173–181. https://doi.org/10.1016/j.micres.2006.04.001

Alori, E. T., Glick, B. R., & Babalola, O. O. (2017). Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Frontiers in Microbiology, 8*, Article 971. https://doi.org/10.3389/fmicb.2017.00971

Amara, U., Khalid, R., & Hayat, R. (2015). Soil bacteria and phytohormones for sustainable crop production. In D. K. Maheshwari (Ed.), *Bacterial metabolites in sustainable agroecosystem* (pp. 87–103). Springer. https://doi.org/10.1007/978-3-319-24654-3_5

Arun, Y. P., Krishnaraj, P. U., Prashanthi, S. K., Kambrekar, D. N., & Bagewadi, B. (2023). Shift in SAR to ISR during the rice–*R. solani* interaction mediated by *Streptomyces hyderabadensis* confers sheath blight resistance in susceptible genotype. *Research Square*. https://doi.org/10.21203/rs.3.rs-2421512/v1

Kaur, H., Kaur, J., & Gera, R. (2016). Plant growth promoting rhizobacteria: A boon to agriculture. International Journal of Cell Science and Biotechnology, 5, 17–22.

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., & Smith, D. L. (2018). Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science, 9*, Article 1473. https://doi.org/10.3389/fpls.2018.01473

Baloch, N. (2025). Microbial contributions to maize crop production: A comprehensive review of challenges and future perspectives. *Discover Agriculture, 3*(1), Article 10. https://doi.org/10.1007/s44279-025-00164-0

Bello, O. B., Olawuyi, O. J., Ige, S. A., Mahamood, J., Afolabi, M. S., Azeez, M. A., & Abdulmaliq, S. Y. (2014). Agro-nutritional variations of quality protein maize (*Zea mays* L.) in Nigeria. *Journal of Agricultural Sciences, Belgrade, 59*(2), 101–116. https://doi.org/10.2298/JAS1402101B

Bhardwaj, D., Ansari, M. W., Sahoo, R. K., & Tuteja, N. (2014). Biofertilizers function as key player in sustainable agriculture by improving soil fertility, plant tolerance and crop productivity. *Microbial Cell Factories, 13*, Article 66. https://doi.org/10.1186/1475-2859-13-66

Bhatia, R., Gulati, D., & Sethi, G. (2021). Biofilms and nanoparticles: Applications in agriculture. *Folia Microbiologica, 66*(2), 159–170. https://doi.org/10.1007/s12223-021-00851-7

Bhattacharyya, P. N., & Jha, D. K. (2012). Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World Journal of Microbiology and Biotechnology, 28*(4), 1327–1350. https://doi.org/10.1007/s11274-011-0979-9

Bhattacharyya, C., Banerjee, S., Acharya, U., Mitra, A., Mallick, I., Haldar, A., Haldar, S., Ghosh, A., & Ghosh, A. (2020). Evaluation of plant growth promotion properties and induction of antioxidative defense mechanism by tea rhizobacteria of Darjeeling, India. *Scientific Reports, 10*, Article 15536. https://doi.org/10.1038/s41598-020-72439-z

Bouizgarne, B. (2022). Phosphate-solubilizing actinomycetes as biofertilizers and biopesticides: Bioformulations for sustainable agriculture. In N. K. Arora & B. Bouizgarne (Eds.), *Microbial BioTechnology for Sustainable Agriculture Volume 1* (pp. 407–428). Springer. https://doi.org/10.1007/978-981-16-4843-4_13

Breedt, G., Labuschagne, N., & Coutinho, T. A. (2017). Seed treatment with selected plant growth-promoting rhizobacteria increases maize yield in the field. *Annals of Applied Biology, 171*(2), 229–236. https://doi.org/10.1111/aab.12366

Cao, A., de la Fuente, M., Gesteiro, N., Santiago, R., Malvar, R. A., & Butrón, A. (2022). Genomics and pathways involved in maize resistance to *Fusarium* ear rot and kernel contamination with fumonisins. *Frontiers in Plant Science, 13*, Article 866478. https://doi.org/10.3389/fpls.2022.866478

Chungopast, S., Thongjoo, C., Islam, A. K. M. M., & Yeasmin, S. (2021). Efficiency of phosphate-solubilizing bacteria to address phosphorus fixation in Takhli soil series: A case of sugarcane cultivation, Thailand. *Plant and Soil, 460*, 347–357. https://doi.org/10.1007/s11104-020-04812-w

Djalovic, I., Grahovac, N., Stojanović, Z., Đurović, A., Živančev, D., Jakšić, S., Jaćimović, S., Tian, C., & Prasad, P. V. (2024). Nutritional and chemical quality of maize hybrids from different FAO maturity groups developed and grown in Serbia. *Plants, 13*(1), Article 143. https://doi.org/10.3390/plants13010143

Dobrzyński, J., Jakubowska, Z., Kulkova, I., Kowalczyk, P., & Kramkowski, K. (2023). Biocontrol of fungal phytopathogens by *Bacillus pumilus*. *Frontiers in Microbiology, 14*, Article 1194606. https://doi.org/10.3389/fmicb.2023.1194606

Etesami, H., Alikhani, H. A., & Hosseini, H. M. (2015). Indole-3-acetic acid and 1-aminocyclopropane-1-carboxylate deaminase: Bacterial traits required in rhizosphere, rhizoplane and/or endophytic competence by beneficial bacteria. In D. K. Maheshwari (Ed.), *Bacterial metabolites in sustainable agroecosystem* (pp. 183–258). Springer. https://doi.org/10.1007/978-3-319-24654-3_8

Evlat, H., Toker, S. K., & Koçyiğit, A. (2023). Screening for agroactive and bioactive metabolites production by actinobacteria isolated from rhizospheric soils. *Biologia, 78*(1), 187–200. https://doi.org/10.1007/s11756-022-01226-0

Figueiredo, M. V. B., Martinez, C. R., Burity, H. A., & Chanway, C. P. (2008). Plant growth-promoting rhizobacteria for improving nodulation and nitrogen fixation in the common bean (*Phaseolus vulgaris* L.). *World Journal of Microbiology and Biotechnology, 24*(7), 1187–1193. https://doi.org/10.1007/s11274-007-9591-4

Gebreyohannes, G., Nyerere, A., Bii, C., & Sbhatu, D. B. (2019). Challenges of intervention, treatment, and antibiotic resistance of biofilm-forming microorganisms. *Heliyon, 5*(8), e02192. https://doi.org/10.1016/j.heliyon.2019.e02192

Gheith, E. M. S., El-Badry, O. Z., Lamlom, S. F., Ali, H. M., Siddiqui, M. H., Ghareeb, R. Y., El-Sheikh, M. H., Jebril, J., Abdelsalam, N. R., & Kandil, E. E. (2022). Maize (*Zea mays* L.) productivity and nitrogen use efficiency in response to nitrogen application levels and time. *Frontiers in Plant Science, 13*, 941343. https://doi.org/10.3389/fpls.2022.941343

Giorgio, A., De Stradis, A., Lo Cantore, P., & Iacobellis, N. S. (2015). Biocide effects of volatile organic compounds produced by potential biocontrol rhizobacteria on *Sclerotinia sclerotiorum*. *Frontiers in Microbiology, 6*, 1056. https://doi.org/10.3389/fmicb.2015.01056

Goko, M. L., Murimwa, J. C., Gasura, E., Rugare, J. T., & Ngadze, E. (2021). Identification and characterisation of seed-borne fungal pathogens associated with maize (*Zea mays* L.). *International Journal of Microbiology, 2021*, 6702856. https://doi.org/10.1155/2021/6702856

Gupta, V. V. S. R., Zhang, B., Penton, C. R., Yu, J., & Tiedje, J. M. (2019). Diazotroph diversity and nitrogen fixation in summer active perennial grasses in a Mediterranean region agricultural soil. *Frontiers in Molecular Biosciences, 6*, 115. https://doi.org/10.3389/fmolb.2019.00115

Harish, M. N., Choudhary, A. K., Kumar, S., Dass, A., Singh, V. K., Sharma, V. K., Varatharajan, T., Dhillon, M. K., Sangwan, S., Dua, V. K., Nitesh, S. D., Bhavya, M., Sangwan, S., Prasad, S., Kumar, A., Rajpoot, S. K., Gupta, G., Verma, P., Kumar, A., & George, S. (2022). Double zero tillage and foliar phosphorus fertilization coupled with microbial inoculants enhance maize productivity and quality in a maize–wheat rotation. *Scientific Reports, 12*, 3161. https://doi.org/10.1038/s41598-022-07148-w

Haroon, U., Munis, M. F. H., Liaquat, F., Khizar, M., Elahi, M., & Chaudhary, H. J. (2023). Biofilm formation and flocculation potential analysis of halotolerant *Bacillus tequilensis* and its inoculation in soil to mitigate salinity stress of chickpea. *Physiology and Molecular Biology of Plants, 29*(2), 277–288. https://doi.org/10.1007/s12298-023-01280-1

Hossain, M. M., Sultana, F., & Islam, S. (2017). Plant growth-promoting fungi (PGPF): Phytostimulation and induced systemic resistance. In D. Singh, H. Singh, & R. Prabha (Eds.), *Plant-microbe interactions in agro-ecological perspectives* (pp. 135–191). Springer. https://doi.org/10.1007/978-981-10-6593-4_6

Iqbal, M. A., Khalid, M., Shahzad, S. M., Ahmad, M., Soleman, N., & Akhtar, N. (2012). Integrated use of *Rhizobium leguminosarum*, plant growth promoting rhizobacteria and enriched compost for improving growth, nodulation and yield of lentil (*Lens culinaris* Medik.). *Chilean Journal of Agricultural Research, 72*(1), 104–110. https://doi.org/10.4067/S0718-58392012000100017

Islam, M. T. (2023). *Understanding and development of environmentally friendly strategies to ameliorate plant stress* [Doctoral dissertation, The Pennsylvania State University]. Penn State Electronic Theses and Dissertations. https://etda.libraries.psu.edu/catalog/19100mki5039

Jahn, L., Hofmann, U., & Ludwig-Müller, J. (2021). Indole-3-acetic acid is synthesized by the endophyte *Cyanodermella asteris* via a tryptophan-dependent and -independent way and mediates the interaction with a non-host plant. *International Journal of Molecular Sciences, 22*(5), 2651. https://doi.org/10.3390/ijms22052651

Jain, S., Dash, P., Minz, A. P., Satpathi, S., Samal, A. G., Behera, P. K., Senapati, S., & others. (2019). Lipopolysaccharide (LPS) enhances prostate cancer metastasis potentially through NF-κB activation and recurrent dexamethasone administration fails to suppress it in vivo. *The Prostate, 79*(2), 168–182. https://doi.org/10.1002/pros.23722

Jha, C. K., & Saraf, M. (2015). Plant growth promoting rhizobacteria (PGPR): A review. *Journal of Agricultural Research and Development, 5*(2), 108–119.

Joshi, C., & Napier, R. (2023). PIN structures shed light on their mechanism of auxin efflux. *Journal of Experimental Botany, 74*(15), 4377–4383. https://doi.org/10.1093/jxb/erad185

Khan, M. S., Zaidi, A., Ahemad, M., Oves, M., & Wani, P. A. (2010). Plant growth promotion by phosphate solubilizing fungi—Current perspective. *Archives of Agronomy and Soil Science, 56*(1), 73–98. https://doi.org/10.1080/03650340902806469

Khati, P., Mishra, P. K., Pal, R. S., & Kant, L. (2025). Enhancing maize growth and drought resilience by synergistic application of plant growth promoting rhizobacteria. *Scientific Reports, 15*, 45440. https://doi.org/10.1038/s41598-025-29110-2

Kheroar, S., & Patra, B. C. (2014). Productivity of maize-legume intercropping systems under rainfed situation. *African Journal of Agricultural Research, 9*(20), 1610–1617. https://doi.org/10.5897/AJAR2013.7997

Kimotho, R. N., & Maina, S. (2024). Unraveling plant–microbe interactions: Can integrated omics approaches offer concrete answers? *Journal of Experimental Botany, 75*(5), 1289–1313. https://doi.org/10.1093/jxb/erad448

Kuan, K. B., Othman, R., Abdul Rahim, K., & Shamsuddin, Z. H. (2016). Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PLOS ONE, 11*(3), e0152478. https://doi.org/10.1371/journal.pone.0152478

Kurt, P. Ö. (2025). Field-based evaluation of multi-strain PGPR to improve *Zea mays* yield and soil nutrient dynamics in semi-arid of Türkiye. *Scientific Reports, 15*, 22553. https://doi.org/10.1038/s41598-025-07643-w

Lazarević, J., Aćimović, M., Pezo, L., Lončar, B., Konstantinović, B., Popov, M., Šovljanski, O., Travičić, V., Sikora, V., & Vujisić, L. (2024). Chemical composition and in vitro biological activity of angelica root and hop strobile essential oils and hydrolates. *Waste and Biomass Valorization, 15*(2), 867–883. https://doi.org/10.1007/s12649-023-02209-1

Lee, J. H., Anderson, A. J., & Kim, Y. C. (2022). Root-associated bacteria are biocontrol agents for multiple plant pests. *Microorganisms, 10*(5), 1053. https://doi.org/10.3390/microorganisms10051053

Liu, N., Chen, Y., Liu, J., Su, Q., Zhao, B., Sun, M., Jia, H., Cao, Z., & Dong, J. (2022). Transcriptional differences between major *Fusarium* pathogens of maize, *Fusarium verticillioides* and *Fusarium graminearum* with different optimum growth temperatures. *Frontiers in Microbiology, 13*, 1030523. https://doi.org/10.3389/fmicb.2022.1030523

Lurthy, T., Cantat, C., Jeudy, C., Declerck, P., Gallardo, K., Barraud, C., Leroy, F., Ourry, A., Lemanceau, P., Salon, C., & Mazurier, S. (2020). Impact of bacterial siderophores on iron status and ionome in pea. *Frontiers in Plant Science, 11*, 730. https://doi.org/10.3389/fpls.2020.00730

Léger, G., Novinscak, A., Biessy, A., Lamarre, S., & Filion, M. (2021). In tuber biocontrol of potato late blight by a collection of phenazine-1-carboxylic acid-producing *Pseudomonas* spp. *Microorganisms, 9*(12), 2525. https://doi.org/10.3390/microorganisms9122525

Maheshwari, D. K., Dheeman, S., & Agarwal, M. (2015). Phytohormone-producing PGPR for sustainable agriculture. In D. K. Maheshwari (Ed.), *Bacterial metabolites in sustainable agroecosystem* (pp. 159–182). Springer. https://doi.org/10.1007/978-3-319-24654-3_7

Matse, D. T., Huang, C.-H., Huang, Y.-M., & Yen, M.-Y. (2020). Effects of coinoculation of *Rhizobium* with plant growth promoting rhizobacteria on the nitrogen fixation and nutrient uptake of *Trifolium repens* in low phosphorus soil. *Journal of Plant Nutrition, 43*(5), 739–752. https://doi.org/10.1080/01904167.2019.1702205

Maurya, S., Thakur, R., Vighnesh, R., Suresh, S., Dang, A., Raj, D., & Srivastava, S. (2024). Eco-friendly management of plant pathogens through secondary metabolites released by fluorescent pseudomonads. *Journal of Pure and Applied Microbiology, 18*(3), 1471–1488. https://doi.org/10.22207/JPAM.18.3.40

Meena, M., Yadav, G., Sonigra, P., Nagda, A., Mehta, T., Swapnil, P., Harish, & Marwal, A. (2022). Role of elicitors to initiate the induction of systemic resistance in plants to biotic stress. *Plant Stress, 5*, 100103. https://doi.org/10.1016/j.stress.2022.100103

Meki, S., Ahmed, S., & Sakhuja, P. K. (2011). Control of chickpea wilt (*Fusarium oxysporum* f. sp. *ciceris*) using *Trichoderma* spp. in Ethiopia. *Archives of Phytopathology and Plant Protection, 44*(5), 432–440. https://doi.org/10.1080/03235400903093071

Misra, S., Semwal, P., Pandey, D. D., Mishra, S. K., & Chauhan, P. S. (2024). Siderophore-producing *Spinacia oleracea* bacterial endophytes enhance nutrient status and vegetative growth under iron-deficit conditions. *Journal of Plant Growth Regulation, 43*(5), 1317–1330. https://doi.org/10.1007/s00344-023-11185-8

Moon, Y. S., & Ali, S. (2022). Possible mechanisms for the equilibrium of ACC and role of ACC deaminase-producing bacteria. *Applied Microbiology and Biotechnology, 106*(3), 877–887. https://doi.org/10.1007/s00253-022-11772-x

Mus, F., Crook, M. B., Garcia, K., Garcia Costas, A., Geddes, B. A., Kouri, E. D., Paramasivan, P., Ryu, M.-H., Oldroyd, G. E. D., Poole, P. S., Udvardi, M. K., Voigt, C. A., Ané, J.-M., & Peters, J. W. (2016). Symbiotic nitrogen fixation and the challenges to its extension to nonlegumes. *Applied and Environmental Microbiology, 82*(13), 3698–3710. https://doi.org/10.1128/AEM.01055-16

Mushtaq, Z., Nazir, A., Asghar, H. N., & Zahir, Z. A. (2022). Interactive effect of siderophore-producing bacteria and L-tryptophan on physiology, tuber characteristics, yield, and iron concentration of potato. *Potato Research, 65*(4), 1015–1027. https://doi.org/10.1007/s11540-022-09565-w

Naing, A. H., Maung, T. T., & Kim, C. K. (2021). The ACC deaminase-producing plant growth-promoting bacteria: Influences of bacterial strains and ACC deaminase activities in plant tolerance to abiotic stress. *Physiologia Plantarum, 173*(4), 1992–2012. https://doi.org/10.1111/ppl.13545

Nascimento, F. X., Rossi, M. J., & Glick, B. R. (2018). Ethylene and 1-aminocyclopropane-1-carboxylate (ACC) in plant–bacterial interactions. *Frontiers in Plant Science, 9*, 114. https://doi.org/10.3389/fpls.2018.00114

Ndlazi, K., Ntshalintshali, S., Buthelezi, L., Klein, A., Keyster, M., Nkomo, M., & Gokul, A. (2026). The potential of *Pseudomonas* spp. as sustainable bioinoculants for enhancing maize growth and integrated management of drought and *Fusarium verticillioides* stress. *Planta, 263*, 58. https://doi.org/10.1007/s00425-025-04906-8

Neerincx, A. H., Mandon, J., van Ingen, J., Arslanov, D. D., Mouton, J. W., Harren, F. J. M., & Cristescu, S. M. (2015). Real-time monitoring of hydrogen cyanide (HCN) and ammonia (NH_3) emitted by *Pseudomonas aeruginosa*. *Journal of Breath Research, 9*(2), 027102. https://doi.org/10.1088/1752-7155/9/2/027102

Ul Nisa, M., Rizvi, Z. F., Hyder, S., Gondal, A. S., Ahmed, I., Riaz, N., Iqra, Martinez, A. C. M., de los Santos-Villalobos, S., & Iqbal, M. (2026). Integrated application of plant growth–promoting rhizobacteria and organic amendments enhances growth and nutrient uptake in maize. *Journal of Agriculture and Food Research, 26*, 102742. https://doi.org/10.1016/j.jafr.2026.102742

Pirttilä, A. M., Mohammad Parast Tabas, H., Baruah, N., & Koskimäki, J. J. (2021). Biofertilizers and biocontrol agents for agriculture: How to identify and develop new potent microbial strains and traits. *Microorganisms, 9*(4), 817. https://doi.org/10.3390/microorganisms9040817

Rayavarapu, V. B., & Padmavathi, T. (2016). *Bacillus* sp. as potential plant growth promoting rhizobacteria. *International Journal of Advanced Life Sciences, 9*(1), 29–36.

Revilla, P., Alves, M. L., Andelković, V., Balconi, C., Dinis, I., Mendes-Moreira, P., Redaelli, R., Ruiz de Galarreta, J. I., Vaz Patto, M. C., Žilić, S., & Malvar, R. A. (2022). Traditional foods from maize (*Zea mays* L.) in Europe. *Frontiers in Nutrition, 8*, 683399. https://doi.org/10.3389/fnut.2021.683399

Riaz, U., Murtaza, G., Anum, W., Samreen, T., Sarfraz, M., & Nazir, M. Z. (2021). Plant growth-promoting rhizobacteria (PGPR) as biofertilizers and biopesticides. In K. R. Hakeem, G. H. Dar, M. A. Mehmood, & R. A. Bhat (Eds.), *Microbiota and biofertilizers* (pp. 181–196). Springer. https://doi.org/10.1007/978-3-030-48771-3_11

Riseh, R. S., Vazvani, M. G., Vatankhah, M., & Kennedy, J. F. (2024). Chitin-induced disease resistance in plants: A review. *International Journal of Biological Macromolecules, 266*, 131105. https://doi.org/10.1016/j.ijbiomac.2024.131105

Sagar, A., Dhusiya, K., Shukla, P. K., Singh, A., Lawrence, R., & Ramteke, P. W. (2018). Comparative analysis of production of hydrogen cyanide (HCN) with production of siderophore (SD) and phosphate solubilization (PS) activity in plant growth promoting bacteria (PGPB). *Vegetos, 31*(2), 130–135. https://doi.org/10.5958/2229-4473.2018.00064.2

Sahu, B., Dash, B., Pradhan, S. N., Nalia, A., & Singh, P. (2023). Fertilizer management in dryland cultivation for stable crop yields. In A. Naorem & D. Machiwal (Eds.), *Enhancing resilience of dryland agriculture under changing climate* (pp. 305–322). Springer. https://doi.org/10.1007/978-981-19-9159-2_16

Sarwar, S., Khaliq, A., Yousra, M., & Sultan, T. (2022). Iron biofortification potential of siderophore producing rhizobacterial strains for improving growth, yield and iron contents of groundnut. *Journal of Plant Nutrition, 45*(15), 2332–2347. https://doi.org/10.1080/01904167.2022.2063733

Sasmita, K. D., Anas, I., Anwar, S., Yahya, S., & Djajakirana, G. (2022). Application of phosphate solubilizing microbes to promote the effectiveness of rock phosphate on cacao seedling growth in acid soil. *AIP Conference Proceedings, 2462*(1), 060011. https://doi.org/10.1063/5.0075843

Sehrawat, A., Sindhu, S. S., & Glick, B. R. (2022). Hydrogen cyanide production by soil bacteria: Biological control of pests and promotion of plant growth in sustainable agriculture. *Pedosphere, 32*(1), 15–38. https://doi.org/10.1016/S1002-0160(21)60058-9

Shah, A., Nazari, M., Antar, M., Msimbira, L. A., Naamala, J., Lyu, D., Rabileh, M., Zajonc, J., & Smith, D. L. (2021). PGPR in agriculture: A sustainable approach to increasing climate change resilience. *Frontiers in Sustainable Food Systems, 5*, 667546. https://doi.org/10.3389/fsufs.2021.667546

Shiferaw, B., Prasanna, B. M., Hellin, J., & Bänziger, M. (2011). Crops that feed the world 6: Past successes and future challenges to the role played by maize in global food security. *Food Security, 3*(3), 307–327. https://doi.org/10.1007/s12571-011-0140-5

Simpson, B. W., & Trent, M. S. (2019). Pushing the envelope: LPS modifications and their consequences. *Nature Reviews Microbiology, 17*(7), 403–416. https://doi.org/10.1038/s41579-019-0201-x

Singh, S. P., Singh, H. B., & Singh, D. K. (2013). Trichoderma harzianum and Pseudomonas sp. mediated management of Sclerotium rolfsii rot in tomato (Lycopersicon esculentum Mill.). *The Bioscan, 8*(3), 801–804. https://thebioscan.com/index.php/pub/article/view/205

Singh, R. K., Singh, P., Li, H.-B., Song, Q.-Q., Guo, D.-J., Solanki, M. K., Verma, K. K., Malviya, M. K., Song, X.-P., Lakshmanan, P., Yang, L.-T., & Li, Y.-R. (2020). Diversity of nitrogen-fixing rhizobacteria associated with sugarcane: A comprehensive study of plant–microbe interactions for growth enhancement in Saccharum spp. *BMC Plant Biology, 20*, Article 220. https://doi.org/10.1186/s12870-020-02400-9

Singh, P., Chauhan, P. K., Upadhyay, S. K., Singh, R. K., Dwivedi, P., Wang, J., Jain, D., & Jiang, M. (2022). Mechanistic insights and potential use of siderophores producing microbes in rhizosphere for mitigation of stress in plants grown in degraded land. *Frontiers in Microbiology, 13*, Article 898979. https://doi.org/10.3389/fmicb.2022.898979

Soares, E. V. (2022). Perspective on the biotechnological production of bacterial siderophores and their use. *Applied Microbiology and Biotechnology, 106*(11), 3985–4004. https://doi.org/10.1007/s00253-022-11995-y

Song, Y., Ma, P., Gao, J., Dong, C., Wang, Z., Luan, Y., Chen, J., Sun, D., Jing, P., Zhang, X., Song, W., Zhou, Z., & Wu, J. (2024). Natural variation in maize gene ZmSBR1 confers seedling resistance to Fusarium verticillioides. *The Crop Journal, 12*(3), 836–844. https://doi.org/10.1016/j.cj.2024.05.003

de Souza, R., Ambrosini, A., & Passaglia, L. M. P. (2015). Plant growth-promoting bacteria as inoculants in agricultural soils. *Genetics and Molecular Biology, 38*(4), 401–419. https://doi.org/10.1590/S1415-475738420150053

Srivastava, P., Sahgal, M., Sharma, K., El Enshasy, H. A., Gafur, A., Alfarraj, S., Ansari, M. J., & Sayyed, R. Z. (2022). Optimization and identification of siderophores produced by Pseudomonas monteilii strain MN759447 and its antagonism toward fungi associated with mortality in Dalbergia sissoo plantation forests. *Frontiers in Plant Science, 13*, Article 984522. https://doi.org/10.3389/fpls.2022.984522

Sujitha, P., & Shanthi, C. (2021). Insights into substrate specificity of proteases for screening efficient dehairing enzymes. *International Journal of Biological Macromolecules, 172*, 360–370. https://doi.org/10.1016/j.ijbiomac.2021.01.065

Sun, Y., Wu, J., Shang, X., Xue, L., Ji, G., Chang, S., Niu, J., & Emaneghemi, B. (2022). Screening of siderophore-producing bacteria and their effects on promoting the growth of plants. *Current Microbiology, 79*(5), Article 150. https://doi.org/10.1007/s00284-022-02777-w

Suresh, P., Rekha, M., Gomathinayagam, S., Ramamoorthy, V., Sharma, M. P., Sakthivel, P., Sekar, K., Arasu, M. V., & Shanmugaiah, V. (2022). Characterization and assessment of 2,4-diacetylphloroglucinol (DAPG)-producing Pseudomonas fluorescens VSMKU3054 for the management of tomato bacterial wilt caused by Ralstonia solanacearum. *Microorganisms, 10*(8), Article 1508. https://doi.org/10.3390/microorganisms10081508

Swati, P., Rasane, P., Kaur, J., Kaur, S., Ercisli, S., Assouguem, A., Ullah, R., Alqahtani, A. S., & Singh, J. (2024). The nutritional, phytochemical composition, and utilisation of different parts of maize: A comparative analysis. *Open Agriculture, 9*(1), Article 20220358. https://doi.org/10.1515/opag-2022-0358

Tilocca, B., Cao, A., & Migheli, Q. (2020). Scent of a killer: Microbial volatilome and its role in the biological control of plant pathogens. *Frontiers in Microbiology, 11*, Article 41. https://doi.org/10.3389/fmicb.2020.00041

Tran, C. V., Vo, T. L., Nguyen, N. T., Truong, M.-N., Tran, Q. T. T., Vo, T. M., & Nguyen, H. T. T. (2024). Volatile components of ethyl acetate extracts from the leaves and rhizomes of Curcuma sahuynhensis and their cytotoxic activity: In vitro and in silico studies. *Egyptian Journal of Chemistry, 67*(9), 253–267. https://doi.org/10.21608/ejchem.2024.253142.8948

Valys, A., Strazdaitė-Žielienė, Ž., Serva, S., & Servienė, E. (2023). Antimicrobial efficacy of plant hydrolates. In *The COINS 2023: International Conference of Life Sciences: Book of abstracts* (p. 12). https://www.thecoins.eu/static/resources/booksofabstracts/COINS2023.pdf

Verma, S., Chakdar, H., Kumar, M., Varma, A., & Saxena, A. K. (2021). Microorganisms as a sustainable alternative to traditional biofortification of iron and zinc: Status and prospect to combat hidden hunger. *Journal of Soil Science and Plant Nutrition, 21*(2), 1700–1717. https://doi.org/10.1007/s42729-021-00473-5

Wang, N., Liu, M., Guo, L., Yang, X., & Qiu, D. (2016). A novel protein elicitor (PeBA1) from Bacillus amyloliquefaciens NC6 induces systemic resistance in tobacco. *International Journal of Biological Sciences, 12*(6), 757–767. https://doi.org/10.7150/ijbs.14333

Wang, L., Liu, W., Tang, J.-W., Wang, J.-J., Liu, Q.-H., Wen, P.-B., Wang, M.-M., Pan, Y.-C., Gu, B., & Zhang, X. (2021). Applications of Raman spectroscopy in bacterial infections: Principles, advantages, and shortcomings. *Frontiers in Microbiology, 12*, Article 683580. https://doi.org/10.3389/fmicb.2021.683580

Winders, J. R., & Pechan, T. (2021). Comparison of homogenization methods for extraction of maize cob metabolites. *African Journal of Biotechnology, 20*(3), 108–114. https://doi.org/10.5897/AJB2020.17246

Xu, S., Cao, Q., Liu, Z., Chen, J., Yan, P., Li, B., & Xu, Y. (2022). Transcriptomic analysis reveals the role of tmRNA on biofilm formation in Bacillus subtilis. *Microorganisms, 10*(7), Article 1338. https://doi.org/10.3390/microorganisms10071338

Yadav, S. S., Arya, A., Tondon, G., & Singh, Y. (2023). Antagonistic microbes mediated modulation of systemic resistance and defense related responses against Dickeya dadantii causing bacterial stalk rot in Sorghum bicolor. *European Journal of Plant Pathology, 167*(4), 833–851. https://doi.org/10.1007/s10658-023-02769-x

Zhang, S., Deng, Z., Borham, A., Ma, Y., Wang, Y., Hu, J., Wang, J., & Bohu, T. (2023). Significance of soil siderophore-producing bacteria in evaluation and elevation of crop yield. *Horticulturae, 9*(3), Article 370. https://doi.org/10.3390/horticulturae9030370

Peer-review history:
The peer review history for this paper can be accessed here:
https://pr.sdiarticle5.com/review-history/160971