



The multifunctional role of *Pseudomonas spp.* as plant growth-promoting rhizobacteria (PGPR): A sustainable approach to biofertilization and plant health

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ARTICLE INFO

Keywords:

Biofertilizer
Rhizosphere
Nitrogen-fixers
Phosphorus-solubilizers
Phosphorus-mobilizers

Article history

Submitted: 2024-08-25

Revised: 2025-06-03

Accepted: 2025-08-27

Available online: 2026-05-16

Published regularly:

June 2026

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ABSTRACT

Sustainable agriculture relies on maintaining healthy, ecologically balanced soil. The excessive use of chemical fertilizers has resulted in declining soil fertility, biodiversity loss, and structural degradation. In particular, the use of biofertilizers containing microbial inoculants that enhance plant growth and soil health offers a promising alternative by improving nutrient availability, suppressing pathogens, and restoring soil ecosystems. Studies have shown that rhizosphere microbes can enhance plant growth and control diseases by producing phytohormones and aiding nutrient uptake. Many bacterial genera can be used as biofertilizers, including nitrogen-fixers, phosphorus-solubilizers, potassium-solubilizers (K-solubilizers), and others. Among the diverse plant growth-promoting rhizobacteria (PGPR), species within the *Pseudomonas* genus have emerged as promising candidates due to their exceptional versatility and resilience. *Pseudomonas spp.* exhibits a wide array of plant growth-promoting traits, including atmospheric nitrogen fixation, solubilization of phosphorus and potassium, and the secretion of phytohormones such as indole-3-acetic acid (IAA) and gluconic acid. By systematically linking their metabolic traits to specific soil health and crop productivity outcomes, this review provides new insights into their potential application in sustainable and climate-resilient agriculture. Several *Pseudomonas* species have been extensively utilized as biofertilizers due to their multifunctional traits, adaptability to a wide range of soil environments, and capacity to enhance plant health under both biotic and abiotic stress conditions. The primary objective of this review is to present a comprehensive overview of biofertilizer mechanisms and the functional roles of *Pseudomonas spp.*, including selected strains known to improve plant growth and soil fertility.

How to Cite: Reza, S.A., Han, M., Uddin, M.K., Kasim, S., Zuan, A.T.K., Anwar, F., Raguraj, S. (2026). The multifunctional role of pseudomonas spp. as plant growth-promoting rhizobacteria (PGPR): A sustainable approach to biofertilization and plant health. Sains Tanah Journal of Soil Science and Agroclimatology, 23(1), 12-37. <https://doi.org/10.20961/stjssa.v23i1.93264>

1. INTRODUCTION

1.1. Fundamental concept of biofertilizers

Biofertilizers constitute formulations that contain viable or dormant microbial strains, which improve plant nutrient acquisition through active colonization of the rhizosphere, thus increasing nutrient accessibility to plant root systems. Improving nutrient effectiveness in soil to stimulate plant development and enhance overall productivity represents a fundamental aspect of rhizosphere management, which stands at the core of sustainable agriculture (Singh et al., 2021). Nevertheless, successful rhizosphere management involves complex ecological challenges, especially within

sustainable and climate-resilient farming approaches. Biofertilizers operate by encouraging beneficial relationships between plants and microorganisms within the rhizosphere, commonly when administered through soil or seed treatments (Prasad et al., 2019). The utilization of microbial inoculants via seed coating, root dipping, or soil amendment has been extensively practiced for decades as an approach to improve plant physiological development, enhance nutrient acquisition, and support crop health and resilience (Nosheen et al., 2021). These inoculants enable functions including symbiotic and non-symbiotic nitrogen fixation,

biodegradation of xenobiotic compounds, enhancement of plant growth, and biocontrol of phytopathogens (Sammauria et al., 2020). The main microbial groups utilized in biofertilizer production encompass bacteria, fungi, and cyanobacteria (commonly known as blue-green algae). One of the earliest recorded practices involved large-scale rhizobial inoculation of leguminous crops in the early 20th century to improve biological nitrogen fixation and soil fertility (Backer et al., 2018).

During recent years, commercial formulations containing genera such as *Bacillus*, *Pseudomonas*, and *Glomus* have been developed. Reviews have additionally documented the functions of microbial taxa, including *Bacillus*, *Pseudomonas*, and *Actinobacteria* (Shivlata & Satyanarayana, 2017), and *Lactobacillus* (Lamont et al., 2017). Other beneficial genera, such as *Acetobacter*, *Azospirillum*, *Paenibacillus*, *Serratia*, *Burkholderia*, *Herbaspirillum*, and *Rhodococcus*, also provide significant contributions to crop performance (Babalola, 2010). Within these, *Pseudomonas* spp. have surfaced as highly promising plant-associated microbes owing to their extensive range of plant growth-promoting (PGP) characteristics. These encompass improved nutrient solubilization and availability (particularly N, P, K, Zn, and S), regulation of phytohormones, suppression of plant pathogens through biocontrol activity, and alleviation of both biotic and abiotic stresses (Dorjey et al., 2017). In summary, *Pseudomonas* spp. possesses considerable potential in improving plant growth, crop yield, and resilience under both greenhouse and field conditions.

There exists growing evidence that urbanization, climate change, and the excessive utilization of agrochemicals are disrupting the environment and affecting food security. Agricultural soils are experiencing quality loss, deterioration of physical and chemical properties, and biological health decline due to indiscriminate agrochemical usage (Novo et al., 2018). Generating more food on limited arable land while protecting the environment has emerged as a key challenge of the millennium. The utilization of microorganisms in agriculture can progressively reduce dependence on chemical fertilizers, fostering biological sustainability (Ortiz-Castro et al., 2009). Rhizosphere management involves improving soil nutrient efficiency to enhance plant growth and productivity (Singh et al., 2022). Biofertilizers facilitate plant growth by suppressing soil-borne pathogens and improving nutrient uptake and utilization efficiency (Thomas & Singh, 2019). This process supports multiple interactions within the rhizosphere that establish pathways for improving plant health and nutrient availability. Core mechanisms encompass increased symbiotic and non-symbiotic nitrogen fixation, degradation of xenobiotic chemicals, plant development enhancement, and biological control of pathogenic bacteria (Laslo et al., 2012). The utilization of microbial-based agricultural inputs, including single strains and microbial consortia, has a lengthy history in sustainable farming. Since the early 1900s, rhizobial inoculants have been applied to leguminous crops to improve biological nitrogen fixation and soil fertility (Backer et al., 2018). Contemporary biofertilizers are developed using diverse formulation techniques, including solid and liquid forms, incorporation of cell protectants such as glycerol, lactose, and starch, selection of suitable carrier materials, and

efficient delivery systems (Novo et al., 2018). Recent advances include entrapment or microencapsulation, nano-immobilization of microbial inoculants, and biofilm-based formulations, all designed to enhance microbial viability, stability, and field performance (Arora et al., 2018).

Microorganisms typically isolated from roots are termed plant growth-promoting rhizobacteria (PGPR). In recent decades, bio-based approaches have gained momentum as core strategies for sustainable agriculture. Various bacterial genera, such as *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, and notably *Pseudomonas*, are recognized as effective PGPR. These can be classified according to their location: extracellular PGPR (ePGPR), which inhabit the rhizosphere, rhizoplane, or intercellular spaces of the root cortex; and intracellular PGPR (iPGPR), which colonize root cells, often within specialized structures such as nodules (Figueiredo et al., 2010). PGPR establishes complex, beneficial interactions with plants, promoting health, nutrient acquisition, and stress resilience (Bhattacharyya & Jha, 2012). They produce and release secondary metabolites that suppress phytopathogens and facilitate nutrient uptake from the root environment (Singh et al., 2019). Through direct and indirect mechanisms, these materials contribute to nutrient cycling and yield improvement in agroecosystems (Prasad et al., 2019). Given their capacity to function as both biofertilizers and biopesticides, PGPR are increasingly viewed as viable alternatives to chemical agro-inputs.

PGPR-based biofertilizers have demonstrated the potential to partially substitute chemical fertilizers at a considerably lower cost, with yield increases of approximately 20%-35% compared to untreated controls (Basu et al., 2021). These beneficial microbes function as ecological engineers, contributing to sustainable soil fertility management and reducing dependence on synthetic inputs. Implementing PGPR in agriculture represents an environmentally friendly, resource-efficient approach to improving food production while conserving natural resources (Prasad et al., 2019). They also enhance micronutrient utilization efficiency, plant development, and tolerance to environmental stresses (Gray & Smith, 2005; Yadav et al., 2018). Furthermore, PGPR and bacterial endophytes are acknowledged for their role in the biological control of plant diseases (Beneduzi et al., 2012). In developing biofertilizer formulations, there is an increasing emphasis on selecting strains with multifunctional capabilities. Utilizing a single strain that can solubilize nutrients, produce phytohormones, and suppress pathogens offers strategic advantages for next-generation biofertilizers (Singh et al., 2021). One such example is the genus *Pseudomonas*, particularly *P. fluorescens*, *P. aeruginosa*, *P. putida*, and *P. stutzeri*, which have been extensively recognized for their PGP traits. These include nutrient solubilization, phytohormone production, biocontrol of phytopathogens, and enhanced plant resilience under abiotic stress (Ahemad & Khan, 2010; Dorjey et al., 2017; Molina et al., 2020).

The objective of this review is to evaluate the potential of *Pseudomonas* spp. as PGPR, with emphasis on their functional mechanisms as biofertilizers and biocontrol agents.

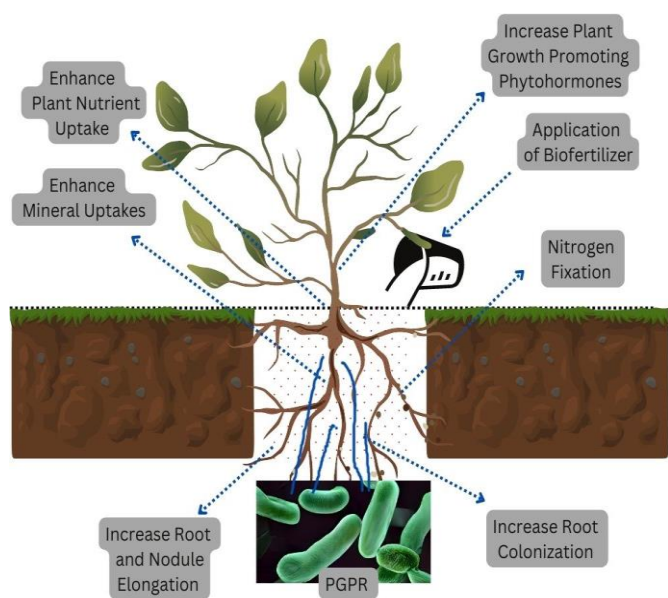


Figure 1. Schematic representation of the direct mechanisms employed by plant growth-promoting rhizobacteria (PGPR)

This paper aims to evaluate the various roles of *Pseudomonas* strains such as *P. fluorescens*, *P. aeruginosa*, *P. putida*, and *P. stutzeri* in nutrient solubilization, phytohormone production, and induced systemic resistance; to assess their performance under abiotic and biotic stress; and to highlight their practical applications in sustainable agriculture. The novelty of this review lies in its integrative focus on the multifunctionality of *Pseudomonas* spp. as both biofertilizers and bioprotectants, providing a consolidated understanding of their direct and indirect PGP mechanisms. It also examines different biofertilizer types targeting specific nutrient management processes that enhance the viability and effectiveness of soil management systems.

1.2. Mechanisms through which microbial inoculants promote plant growth

PGPR facilitates plant growth via two fundamental modes of operation: direct and indirect pathways. Both serve essential functions as biofertilizers by improving nutrient accessibility, promoting plant growth, and enhancing resistance to biotic and abiotic stress factors. Specific strains generate antifungal compounds, such as antibiotics, hydrolytic enzymes that break down fungal cell walls, and hydrogen cyanide, which assist in suppressing pathogenic fungi (Arora et al., 2018).

Direct pathways encompass the enhancement of nutrient acquisition and the regulation of plant hormone concentrations. These comprise biological nitrogen fixation, solubilization of phosphorus and potassium, siderophore-mediated iron absorption, and the synthesis of phytohormones, including auxins, gibberellins, and cytokinins (Singh et al., 2019). Figure 1 and 2 demonstrates the principal direct and indirect pathways by which PGPR improve plant growth.

Microorganisms enhance plant growth not merely through nutrient-associated processes but also by indirectly safeguarding plants against detrimental pathogens. These

indirect pathways mainly operate by inhibiting or neutralizing the activity of phytopathogens within the rhizosphere. One significant characteristic is the microbial synthesis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase. This relates to the enzymatic function of certain beneficial soil microorganisms, especially PGPR, which break down ACC, the direct precursor of ethylene in plants. Additionally, beneficial microbes may release antibiotics and hydrolytic enzymes that break down pathogen cell walls, and they may also activate induced systemic resistance (ISR) within the host plant. Together, these mechanisms improve plant health, strengthen stress resilience, and enhance overall productivity by minimizing the effects of biotic stressors (Fig. 2) (Gupta et al., 2015).

Remarkably, numerous PGPR strains, including *Pseudomonas fluorescens* and *P. putida*, demonstrate both types of mechanisms simultaneously. For instance, siderophore synthesis enhances iron availability (a direct advantage) while simultaneously inhibiting pathogen growth (an indirect advantage) (Dorjey et al., 2017). Species within the *Pseudomonas* genus function as PGPR through different direct mechanisms. The functional convergence of these mechanisms contributes to the adaptability and effectiveness of PGPR, making them essential to sustainable and integrated nutrient management systems. These mechanisms encompass improving plant nutrient absorption by enabling the fixation of atmospheric nitrogen and the solubilization of essential minerals such as potassium, zinc, and iron.

Furthermore, *Pseudomonas* spp. facilitates plant development by regulating endogenous phytohormone concentrations. This control assists in preventing the excessive accumulation of hormones such as auxins, cytokinins, gibberellins, abscisic acid, and ethylene, which, if overproduced, may result in phytotoxic effects (Basu et al., 2021). Figure 3 represents an integrated overview of the direct and indirect biological processes and synergistic interactions of plant growth-promoting rhizobacteria (PGPR).

Apart from nutrient acquisition and hormonal equilibrium, *Pseudomonas* spp. is also recognized for their capacity to strengthen plant defense mechanisms. These bacteria produce bioactive compounds that display antagonistic activity against phytopathogens and pest organisms, thus decreasing disease occurrence and insect damage (Quan et al., 2010). One notable defense strategy encompasses the activation of systemic resistance,

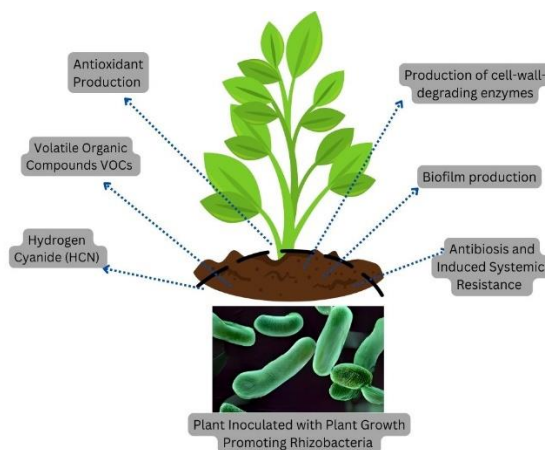


Figure 2. A schematic view of PGPR indirect mechanisms

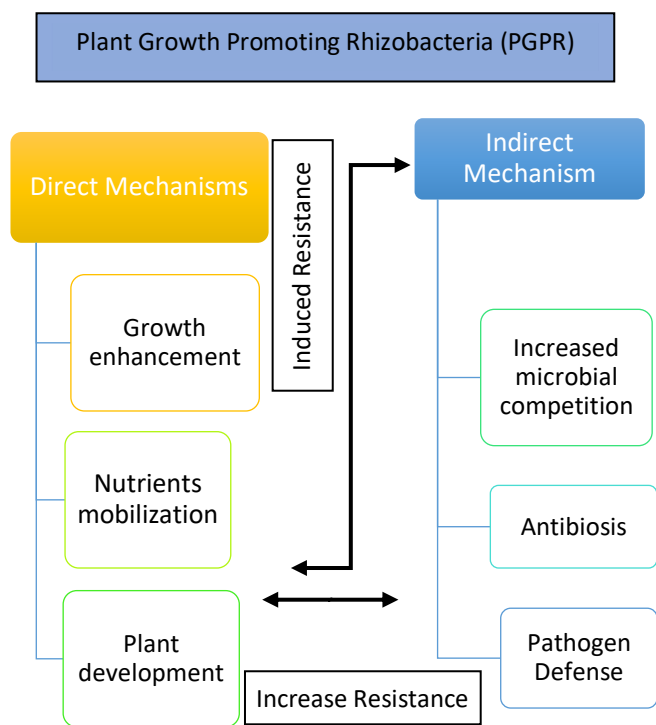


Figure 3. Overview of the main interactions between plant growth-promoting rhizobacteria (PGPR)

which prepares the plant's immune system to respond more efficiently to a broad spectrum of root and foliar pathogens. Furthermore, *Pseudomonas spp.* can release volatile organic compounds (VOCs), which function as signaling molecules to trigger ISR in host plants (Zhu et al., 2022). This microbial antagonism is additionally supported by mechanisms including parasitism, competition for nutrients and niches within the rhizosphere, and the synthesis of secondary metabolites with antimicrobial characteristics. These encompass hydrogen cyanide, siderophores, antibiotics, and lytic enzymes such as chitinases, gluconates, and proteases (Gupta et al., 2015). Together, these diverse strategies emphasize the ecological importance of *Pseudomonas spp.* in advancing sustainable crop production and strengthening plant resilience (Gupta et al., 2015). Collectively, these multifaceted strategies highlight the ecological significance of *Pseudomonas spp.* in promoting sustainable crop production and enhancing plant resilience.

Nevertheless, a continuing challenge in utilizing these beneficial microbes involves developing efficient and dependable delivery systems for field applications. Improving the biocontrol effectiveness of PGPR through genetic engineering provides a potential solution, with encouraging implications for environmentally sustainable agricultural practices. Table 1 presents an overview of the direct and indirect mechanisms of PGPR and their roles in enhancing plant health and productivity.

1.3. Key traits and functional mechanisms of Plant Growth-Promoting Rhizobacteria (PGPR)

Expanding upon the general mechanisms of microbial inoculants, this section examines in more detail the particular functional characteristics that characterize PGPR and their interactions with host plants. Soil bacterial communities, especially those possessing high adaptability, can multiply rapidly and utilize a diverse range of organic substrates as nutrient sources. Numerous bacteria maintain close associations with soil particles and frequently establish dynamic interactions with plant root systems (Adesemoye & Ugoji, 2009). Kloepper and Schroth initially coined the term plant growth-promoting rhizobacteria (PGPR) to characterize soil-inhabiting bacteria that colonize plant roots following inoculation and subsequently promote plant growth (Figueiredo et al., 2010).

A crucial factor affecting the effectiveness of biofertilizers is their colonization efficiency, which is intimately connected to the application method. Most biofertilizers are provided as carrier-based formulations and are commonly administered through seed treatment, root dipping, or direct soil application (Thomas & Singh, 2019). Nevertheless, the success of any delivery approach fundamentally relies on the inoculant's capacity to establish itself efficiently within the rhizosphere (Singh et al., 2021). For PGPR to operate optimally, they must withstand the initial seed inoculation, multiply in the spermosphere, which denotes the narrow zone of soil that encircles a germinating seed, where dynamic biological and chemical interactions take place, attach to root surfaces, and actively colonize the expanding root system (Tallapragada & Seshachala, 2012). Inability to colonize host plant roots is commonly identified as a major reason for the inconsistent performance of PGPR under field conditions (Sindhu et al., 2019).

Table 1. Functional mechanisms of plant growth-promoting rhizobacteria (PGPR)

Mechanism Type	Function	Examples	Role in Plant Growth
Direct	Phosphate solubilization	<i>Pseudomonas fluorescens</i> , <i>Bacillus spp.</i>	Improves phosphorus uptake
	Siderophore production	<i>Pseudomonas spp.</i>	Enhances iron acquisition
	Phytohormone synthesis	<i>Pseudomonas putida</i>	Stimulates root and shoot development
Indirect	Antibiosis (e.g., antibiotics)	<i>Pseudomonas aeruginosa</i>	Suppresses pathogens
	ACC deaminase production	<i>Pseudomonas spp.</i> , <i>Burkholderia spp.</i>	Reduces ethylene-induced stress
	Lytic enzyme production	<i>Pseudomonas spp.</i> , <i>Bacillus spp.</i>	Degrades pathogen cell walls
	ISR induction	<i>Pseudomonas fluorescens</i> , <i>P. chlororaphis</i>	Primes plant immune response

Successful colonization relies on a combination of microbial characteristics, including motility, chemotactic responses to root exudates, pili or fimbriae formation, specific surface adhesion molecules, the capacity to metabolize root exudates, and quorum sensing for coordinated gene expression (Arora et al., 2010). Research utilizing mutants with modified expression of these characteristics has been crucial in determining their functions in colonization (Dorjey et al., 2017). Furthermore, the utilization of rRNA-targeted molecular probes has allowed researchers to track rhizobacterial metabolic activity, demonstrating that microbial populations near the root apex display the highest levels of activity (Priya et al., 2021).

The rhizosphere is acknowledged as a highly active ecological niche, distinguished by intensive microbial activity surrounding plant roots. This area accommodates the highest density of bacterial communities, allowing them to efficiently metabolize a wide spectrum of root-derived compounds (Adesemoye & Ugoji, 2009). It is calculated that microbial colonies occupy roughly 15% of the root surface area (Govindasamy et al., 2011). Between 5% and 30% of a plant's photosynthates are discharged into the rhizosphere as sugars and other organic compounds, which function as energy

sources for microbial populations (Etesami & Adl, 2020). The consequent microbial metabolism improves nutrient transformation processes, thus enhancing the absorption of mineral nutrients by plant roots (Adesemoye & Ugoji, 2009).

Within the framework of sustainable agriculture, PGPR serve an essential role by increasing crop yields, enhancing soil fertility, promoting beneficial microbial associations, improving microbial biodiversity, and controlling plant pathogens (Singh et al., 2022). Table 2 outlines the various plant growth-regulating functions carried out by different PGPR strains, along with the nature of their interactions within the plant system.

Numerous strains of beneficial soil microorganisms have been identified for their capacity in rhizosphere management to enhance plant yield and are currently being employed in biotechnology to advance food security and agricultural sustainability. The majority of well-established PGPR groups belong to the genera *Acinetobacter*, *Azospirillum*, *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Burkholderia*, *Frankia*, *Serratia*, *Bradyrhizobium*, *Rhizobium*, *Thiobacillus*, *Pseudomonas*, and *Bacillus* (Adesemoye & Ugoji, 2009; Etesami & Adl, 2020; Figueiredo et al., 2010; Singh et al., 2021; Thomas & Singh, 2019).

Table 2. Impact of different strains of plant growth-promoting rhizobacteria (PGPR) on plant growth.

		Plant Growth-Rhizobacteria	
Symbiotic N ₂ -fixing strains	Source	Plant growth regulation	References
<i>Rhizobium undicola</i> ; <i>R. leguminosarum</i> , <i>Bradyrhizobium</i> , <i>Sinorhizobium meliloti</i> , <i>Rhizobium</i> spp. <i>Mesorhizobium</i>	Nodules of aquatic legume <i>Neptunia oleracea</i> , <i>Pisum sativum</i> , <i>Trifolium alexandrinum</i> L., <i>Cicer arietinum</i> L., <i>Trigonella foenumgraecum</i> L., <i>Medicago sativa</i> L., <i>Indigofera</i> spp. Birdsfoot trefoil (<i>Lotus corniculatus</i>)	Indole acetic acid (IAA), ACC deaminase, exopolysaccharides N ₂ fixation Volatile antifungal compounds, protease, ammonia, hydrogen cyanide (HCN), phosphorus solubilization, and siderophore production,	Alemneh et al. (2020) Bhattacharjee et al. (2012)
Free-living PGPR strains	Source	Plant growth regulation	References
<i>Bacillus subtilis</i> , <i>B. cereus</i> , <i>B. amyloliquefaciens</i> , <i>Bacillus</i> sp., <i>B. megaterium</i> .	Rhizospheres of paddy (<i>Oryza sativa</i>), Common bean (<i>Phaseolus vulgaris</i> L.), <i>Catharanthus roseus</i> , roots of sweet potato (<i>Ipomoea batatas</i> (L.) Lam.), diseased roots of soybean (<i>Glycine max</i> L. Merrill)	IAA, Gibberellic acid (GA ₃), siderophore production, phosphorus solubilization, ACC deaminase, phosphatases, phytases, HCN, cellulases, zinc solubilization, organic acids, lytic enzymes, oxalate oxidase, potassium, and zinc solubilization	Kumar et al. (2017)
<i>Pseudomonas fluorescens</i> , <i>Pseudomonas putida</i> , <i>Pseudomonas Aeruginosa</i> , <i>Pseudomonas</i> spp.	Rhizospheres of paddy (<i>Oryza sativa</i>), common bean (<i>Phaseolus vulgaris</i> L.), <i>Catharanthus roseus</i> , roots of sweet potato (<i>Ipomoea batatas</i> (L.) Lam.), diseased roots of soybean (<i>Glycine max</i> L. Merrill)	IAA, siderophore production, ACC deaminase, phosphorus solubilization, HCN, exopolysaccharides, ammonia, antifungal compounds	Ali et al. (2014)
Asymbiotic N ₂ -fixing strains	Source	Plant growth regulation	References
<i>Azospirillum lipoferum</i> , <i>A. brasilense</i> , <i>Azotobacter chroococcum</i>	Soils, rhizosphere of <i>Catharanthus roseus</i> , <i>Triticum aestivum</i> , and <i>Hordeum vulgare</i>	IAA, GA ₃ , siderophore production, and protease activity	Kumar et al. (2014)

Through direct or indirect means, these PGPR groups can enhance nutrient concentration and accessibility in the rhizosphere. *Pseudomonas* spp. have achieved recognition for their plant growth-promoting activities, establishing them as an eco-friendly alternative to potentially hazardous chemical fertilizers (Adesemoye & Ugoji, 2009; Choi et al., 2008; Dorjey et al., 2017; Molina et al., 2020; Nadeem et al., 2014; Otieno et al., 2015; Panpatte et al., 2016). Additionally, they facilitate plant growth by strengthening resistance to environmental stresses and providing nutritional advantages to host plants.

Within these, *Pseudomonas* spp. has surfaced as one of the most efficient and environmentally beneficial PGPR owing to their extensive range of growth-promoting characteristics. Their utilization is progressively acknowledged as a sustainable substitute to synthetic chemical fertilizers, which present environmental and health risks (Choi et al., 2008; Dorjey et al., 2017; Molina et al., 2020; Nadeem et al., 2014; Otieno et al., 2015; Panpatte et al., 2016). Beyond enhancing nutrient acquisition, *Pseudomonas* spp. strengthens plant tolerance to diverse environmental stresses and contributes to the comprehensive nutritional support and vitality of host plants (Adesemoye & Ugoji, 2009).

2. Functional diversity of biofertilizers

2.1. Plant Growth-Promoting Biofertilizers (PGPB): roles and applications

Comprehensive research endorses the utilization of biofertilizers formulated with cultivated microbial strains recognized for their plant growth-promoting characteristics, especially in improving nutrient absorption by plants and enhancing soil fertility. These microbial consortia operate either directly or indirectly to provide essential nutrients for plant development (Zainuddin et al., 2022). In oil palm cultivation, biofertilizer application has demonstrated considerable benefits, especially in enhancing plant growth performance and nutrient uptake efficiency (Khotimah et al., 2019). Growth parameters, including plant height and stem thickness, have shown notable improvement under biofertilizer treatment. Seedlings treated with microbial inoculants displayed considerably greater vertical growth compared to untreated controls (Tang & Al Qahtani, 2020). Similarly, enhanced stem girth in treated seedlings indicated more vigorous growth patterns (Zainuddin et al., 2019). These improvements are not restricted to physical development but also demonstrate enhanced nutrient assimilation capabilities (Keni et al., 2023).

Experimental findings additionally confirmed that seedlings subjected to biofertilizer treatments experienced enhanced growth over time (Peng et al., 2022). For example, root elongation per seedling improved considerably within a four-week experimental period when compared with plants under synthetic or control treatments, indicating that strains like *Pseudomonas aeruginosa* may function effectively as biological growth enhancers (Parvin, Govender, et al., 2020). Statistical analysis verified that the treatments generated significant variations ($p < 0.05$) in seedling stem diameter, emphasizing the effectiveness of biofertilizer application (Peng et al., 2022).

Despite some variation between treatment outcomes, biofertilizer usage favorably influenced biomass accumulation, including the fresh and dry weights of both leaves and roots (Rebitanim et al., 2020). Pot trials also demonstrated that microbial extracts contributed to extended leaf development compared to non-treated controls (Parvin, Rahman, et al., 2020). Additionally, studies indicate that endophytic colonization by beneficial microbes may promote the biosynthesis of essential compounds such as thiamine, which contributes to oil palm growth (Duhan & Kataria, 2022).

Previous research has consistently recognized *Pseudomonas* spp. as one of the most powerful and promising PGPR genera, especially for application in rhizosphere-based biocontrol strategies (Panpatte et al., 2016). *Pseudomonas aeruginosa*, specifically, is acknowledged for producing growth-promoting compounds, establishing it as a viable biofertilizer candidate. Beyond enhancing plant growth, *Pseudomonas* strains can activate systemic resistance in plants, providing protection against a broad range of bacterial, fungal, and viral pathogens (Ahmad & Khan, 2010; Molina et al., 2020). These findings collectively emphasize the diverse advantages of incorporating biofertilizers in oil palm agriculture, particularly advancing sustainable production practices.

To optimize effectiveness, biofertilizer formulations are commonly customized based on microbial strain compatibility and crop-specific requirements. PGPR are typically isolated from plant-associated niches such as the rhizosphere or rhizoplane, where their growth-enhancing characteristics can be utilized (Singh et al., 2021). Many PGPR are recognized to produce specific phytohormones that control plant development. For instance, *Azospirillum brasilense* and *Pseudomonas fluorescens* are efficient producers of IAA, a major auxin involved in root elongation and cell division (Panpatte et al., 2016). Gibberellins, which promote stem elongation and seed germination, are generated by strains of *Bacillus subtilis* and *Azotobacter chroococcum* (Goswami et al., 2016). Furthermore, microbes such as *Pseudomonas putida* and *Klebsiella pneumoniae* contribute to ethylene modulation by producing ACC deaminase, which assists in alleviating ethylene-induced stress in plants. Various bacterial genera have been recognized as capable of promoting plant growth (Khan et al., 2019). They also offer protective functions by generating bioactive compounds such as siderophores, antibiotics, and hydrogen cyanide, and by activating ISR, collectively controlling phytopathogens and improving plant health (Beneduzi et al., 2012).

2.2. Classification and functional types of biofertilizers

Biofertilizers are biological formulations containing beneficial microbial inoculants, commonly comprised of artificially cultivated microorganisms within organic carriers. When administered to seeds, plant surfaces, or soil, they establish themselves in the rhizosphere or within internal plant tissues (Basu et al., 2021). These active or dormant microbial populations colonize their respective niches and promote plant development by enhancing nutrient availability and uptake efficiency (Figueiredo et al., 2010). The effectiveness of a biofertilizer largely relies on selecting the

suitable type for the target crop, considering various environmental variables such as soil structure, pH levels, and the specific ecological conditions of the plant niche. Consistent and proper application is essential for achieving long-term gains in crop productivity (Nosheen et al., 2021).

In certain cases, biofertilizer formulations may incorporate multiple microbial strains to optimize synergistic effects. For instance, dual inoculations involving arbuscular mycorrhizal fungi (AMF) such as *Glomus fasciculatum* alongside *Bradyrhizobium* sp. (for *Vigna* spp.) and *Pseudomonas striata* or *Penicillium variabile* have been demonstrated to considerably enhance nutrient uptake and overall yield performance (Sammauria et al., 2020). For a bioinoculant to be efficient, it must satisfy several criteria, including compatibility with soil conditions, high viable cell counts per gram, cost-effective production, extended shelf life, high organic matter and moisture retention capacity, and the ability to maintain microbial viability during storage and field application (Basu et al., 2021). Nevertheless, even when these physical and chemical attributes are optimized, whether in liquid or carrier-based formulations, the fundamental challenge remains achieving consistent and robust rhizosphere colonization for successful commercial application (Arora et al., 2010).

Biofertilizers can be classified based on their microbial composition, functional traits, and mechanisms of action. Common types encompass nitrogen-fixing organisms (N-fixers), potassium-solubilizing microbes (K-solubilizers), phosphorus-solubilizing bacteria (P-solubilizers), and other rhizobacteria recognized to support plant growth (Fig. 4) (Maçik et al., 2020; Nosheen et al., 2021; Singh et al., 2021). The principal objectives of biofertilizer use include advancing plant development, improving biological nitrogen fixation, and supporting key nutrient cycles within the agroecosystem.

Nitrogen-fixing microbes transform atmospheric nitrogen (N_2) into biologically available forms, such as ammonium (NH_4^+) and nitrate (NO_3^-), which can be readily absorbed by plants (Singh et al., 2019). Following nitrogen, phosphorus is the second most crucial nutrient affecting plant growth. Biofertilizers containing phosphate-solubilizing bacteria convert insoluble forms of phosphorus, such as HPO_4^{2-} and $H_2PO_4^-$, into plant-available forms through mechanisms including organic acid production, ion exchange, and chelation (Nosheen et al., 2021). Biofertilizers may also be utilized to improve the availability of micronutrients such as sulphur, zinc, and iron, which are crucial for various physiological and metabolic functions in plants (Thomas & Singh, 2019).

Biofertilizers that promote the solubilization and mobilization of essential micronutrients, specifically phosphorus, sulphur, zinc, and iron, serve a crucial role in improving nutrient bioavailability and uptake in plants. Phosphate-solubilizing microorganisms (PSMs), including species from the *Pseudomonas* and *Bacillus* genera, are recognized to transform insoluble phosphate compounds into soluble forms through mechanisms such as organic acid production, thus making phosphorus more accessible to plant roots. Similarly, sulphur-oxidizing bacteria such as *Thiobacillus* spp. convert elemental sulphur and other sulphur-containing compounds into sulfate, the form absorbable by plants.

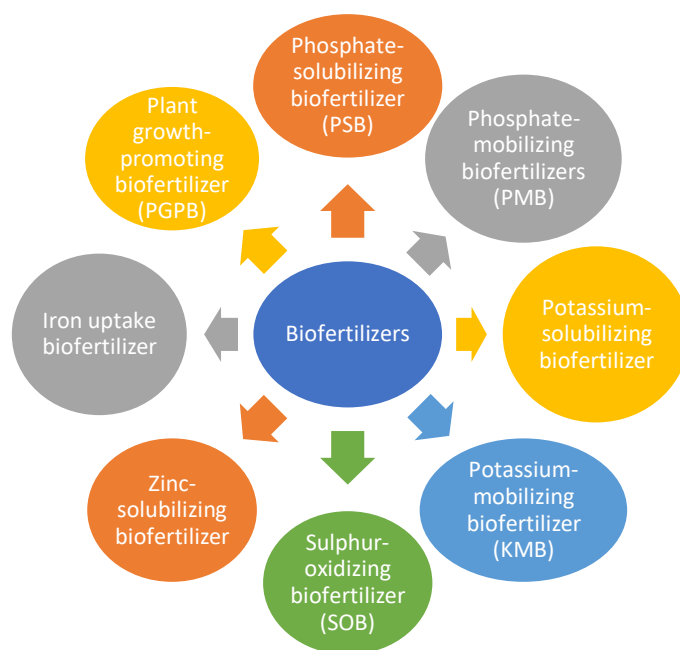


Figure 4. Functional classification of biofertilizers used in traditional agricultural farming systems

Moreover, zinc- and iron-solubilizing microbes, such as *Pseudomonas* and *Azospirillum*, contribute to micronutrient availability by secreting organic acids and siderophores. In Figure 4, the classification of the various biofertilizers applied in traditional agricultural production systems has been compiled. These biofertilizer compounds improve the chelation and mobilization of zinc and iron, facilitating their uptake under nutrient-limiting conditions. When applied collectively, these biofertilizers function synergistically to enhance plant nutrition, support vigorous growth, and increase crop productivity. Together, their application contributes substantially to the advancement of sustainable and resource-efficient agricultural practices.

2.3. Nitrogen-fixing microorganisms and their agricultural importance

Plant growth-promoting microorganisms (PGPMs) demonstrate multifaceted effects through essential functional mechanisms such as atmospheric nitrogen fixation, phosphorus solubilization, and the synthesis of bioactive compounds that promote growth (Umesha et al., 2018). Among these, nitrogen-fixing bacteria, especially rhizobial species, are well recognized for their capacity to improve legume productivity and are particularly valuable in low-input farming systems, including those implemented by smallholder and marginal farmers (Ghaffari et al., 2018). Species such as *Pseudomonas fluorescens* and *Pseudomonas putida* have been thoroughly investigated for their beneficial characteristics, including their ability to synthesize auxins and gibberellins, solubilize phosphate, and enhance nutrient assimilation (Mishra et al., 2020; Zboralski & Fillion, 2020). Furthermore, *Pseudomonas* spp. is acknowledged for its capacity to produce siderophores, release ACC deaminase, and affect ethylene levels, a significant hormone involved in plant stress signaling. These biochemical characteristics assist in reducing abiotic

stress in plants grown under suboptimal environmental conditions (Mahmud & Chong; Syafiq et al., 2021).

Nitrogen (N), a macronutrient essential to plant metabolism and structural development, is vital for the synthesis of amino acids, nucleic acids, and chlorophyll (Singh et al., 2021). While nitrogen gas (N₂) comprises the majority of atmospheric nitrogen, it is chemically inert and not easily absorbed by plants (Chu et al., 2021). Plants mainly obtain nitrogen in biologically available forms such as ammonium (NH₄⁺) and nitrate (NO₃⁻), which are generated through microbial nitrification and subsequently converted or lost via denitrification or anaerobic ammonia oxidation (Xiong et al., 2021). Various microbes perform biological nitrogen fixation, classified as free-living, symbiotic, endophytic, or associative (Singh et al., 2021).

Free-living diazotrophs such as *Azotobacter*, *Beijerinckia*, *Anabaena*, *Tolypothrix*, *Cylindrospermum*, and *Derxia* are capable of fixing atmospheric nitrogen without establishing direct symbiotic associations with host plants (Nosheen et al., 2021a). These bacteria are autonomous microorganisms that inhabit soil, water, or other environments without forming symbiotic relationships with host organisms, yet still contribute to processes such as nitrogen cycling. Beyond enhancing nitrogen availability, they secrete exopolysaccharides and phytohormones that improve soil structure and plant health. For example, *Azotobacter* species are recognized for generating substantial quantities of exopolysaccharides and displaying strong nitrogen-fixing capacity under diverse environmental conditions (Gauri et al., 2012). Likewise, other free-living bacteria, such as *Beijerinckia* and *Clostridium*, have demonstrated potential in promoting crop growth through nitrogen fixation and other plant-beneficial mechanisms (Nunes Oliveira et al., 2017). Additionally, free-living cyanobacteria are extensively utilized in flooded rice systems to provide supplemental nitrogen (Syiem et al., 2017).

Symbiotic and endophytic bacteria are microorganisms that reside within plant tissues. Symbiotic bacteria establish mutualistic relationships with the host, frequently in specialized structures such as root nodules, while endophytic bacteria inhabit internal plant parts without causing damage and may provide benefits such as enhanced nutrient acquisition or stress resistance. By dwelling within plant tissues, they can participate in mutualistic, commensal, or occasionally parasitic interactions (Tipton et al., 2019). Among these, *Rhizobium* spp. and related genera, including *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, and *Allorhizobium*, are especially effective at forming nodules on legume roots, where nitrogen fixation occurs (Nosheen et al., 2021). Other organisms, such as *Frankia*, *Anabaena azollae*, and *Trichodesmium*, are capable of initiating nodule formation in non-leguminous woody species such as *Casuarina*, *Myrica*, *Rubus*, and *Alnus* (Ballhorn et al., 2017; Zhong et al., 2019).

Associative nitrogen-fixing bacteria form relationships similar to symbiotic species but remain primarily localized within the rhizosphere. These bacteria colonize root surfaces and may occasionally penetrate root tissues. Notable examples include *Acetobacter diazotrophicus*, *Herbaspirillum*,

Azoarcus, *Alcaligenes*, *Bacillus*, *Enterobacter*, *Klebsiella*, and *Pseudomonas* spp., all of which display nitrogen-fixing and plant growth-promoting capabilities (Singh et al., 2021; Thomas & Singh, 2019). Despite the abundance of nitrogen in the environment, it remains inaccessible to plants in its molecular form due to its strong triple bond, emphasizing the importance of microbial mediation in nitrogen availability (Singh et al., 2019). Moreover, *Pseudomonas stutzeri* CSP03 and *Pseudomonas fluorescens* have demonstrated the capacity to promote rapid vegetative growth through nitrogen-fixation abilities and other plant-beneficial traits. These findings emphasize the potential role of *Pseudomonas* spp. in supporting nitrogen fixation under diverse agricultural conditions. Although *Pseudomonas*-based inoculants have shown considerable promise, additional research is needed to improve strain compatibility, ensure consistent survival across varied soil environments, and develop effective strategies for large-scale commercialization. Nitrogen-fixing microorganisms are functionally classified according to their ecological associations into free-living, symbiotic, and associative symbiotic groups (Fig. 5).

2.4. Phosphate and potassium solubilizing microbes: mechanisms and efficiency

Restricted phosphorus availability represents a major constraint on crop yield, as it negatively impacts both physiological and biochemical processes in plants and soil (Wang et al., 2020). Phosphorus deficiency can lead to

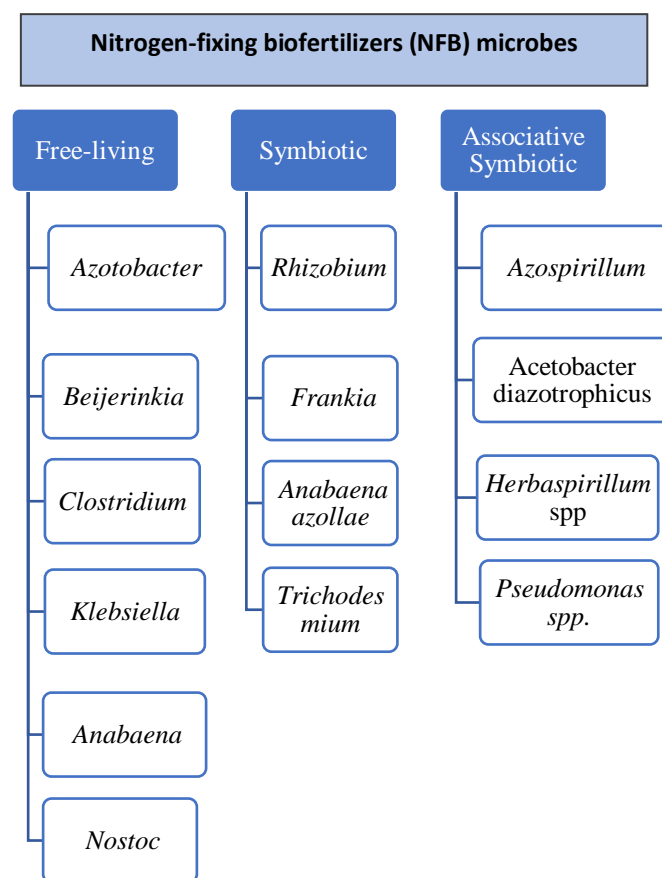


Figure 5. Functional classification of nitrogen-fixing microorganisms based on their ecological associations: free-living, symbiotic, and associative symbiotic groups

stunted growth, delayed maturity, poorly developed root systems, and diminished yield due to its crucial role in energy transfer, nucleic acid synthesis, and overall metabolic function (Khalisha et al., 2022). While agricultural soil typically contains considerable amounts of phosphorus, much of it occurs in insoluble forms. In response, certain microorganisms have developed mechanisms to either mobilize or solubilize phosphate, thus enhancing its availability to plants (Khan et al., 2019).

Phosphate solubilization mainly occurs through microbial activity that involves the secretion of organic acids, protons, and specific enzymes. These processes transform insoluble phosphate compounds into forms that are bioavailable for plant uptake. This function is essential to plant development, as phosphorus is a key component of vital biomolecules, including nucleic acids, coenzymes, phospholipids, nucleotides, phytin, and phosphorylated sugars (Singh et al., 2021).

Phosphate-solubilizing bacteria hydrolyze both organic and inorganic insoluble phosphorus compounds into soluble forms, while phosphate-mobilizing microorganisms improve phosphorus availability through solubilization and mineralization of soil-bound phosphorus (Zahran, 2009). Various soil bacteria have been recognized for their capacity to transform insoluble phosphorus compounds into plant-available forms. Strains of *Pseudomonas*, *Agrobacterium*, and *Bacillus Circulans* are well recognized for their phosphate-solubilizing capacity. Other efficient genera include *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Kushneria*, *Paenibacillus*, *Ralstonia*, *Rhizobium*, *Rhodococcus*, and *Serratia* (Maçik et al., 2020).

Bacillus and *Pseudomonas* species are among the principal microbial groups acknowledged for their efficient phosphate-solubilizing capabilities, mainly through the utilization of specialized biochemical mechanisms such as the production of organic acids and chelating agents (Fig. 6) (Alaylar et al., 2019). These microorganisms break down phosphate compounds and release metabolites that contain complexing or mineral-dissolving compounds, such as gluconic acid, keto-gluconic acid, malonic acid, glutamic acid, oxalic acid, and malic acid, which transform insoluble phosphate into plant-available soluble forms (Chen et al., 2016; Gupta et al., 2015; Liu et al., 2019). Species of *Pseudomonas*, including *Pseudomonas striata*, *Pseudomonas fluorescens*, *Pseudomonas stutzeri* CSPO3, and *Pseudomonas rathonis*, are especially efficient at solubilizing phosphorus compounds. These compounds are intimately connected to numerous plant metabolic activities, signal transduction pathways, energy transfer processes, and other crucial physiological functions (El-Sayed et al., 2014; Otieno et al., 2015; Yasmin et al., 2016).

Potassium is among the primary macronutrients vital for plant growth and development. A shortage of potassium in plants results in impaired photosynthesis, decreased enzyme activation, poor water regulation, and weakened resistance to both abiotic and biotic stresses. These limitations ultimately lead to restricted growth and reduced crop productivity (Khalisha et al., 2022).

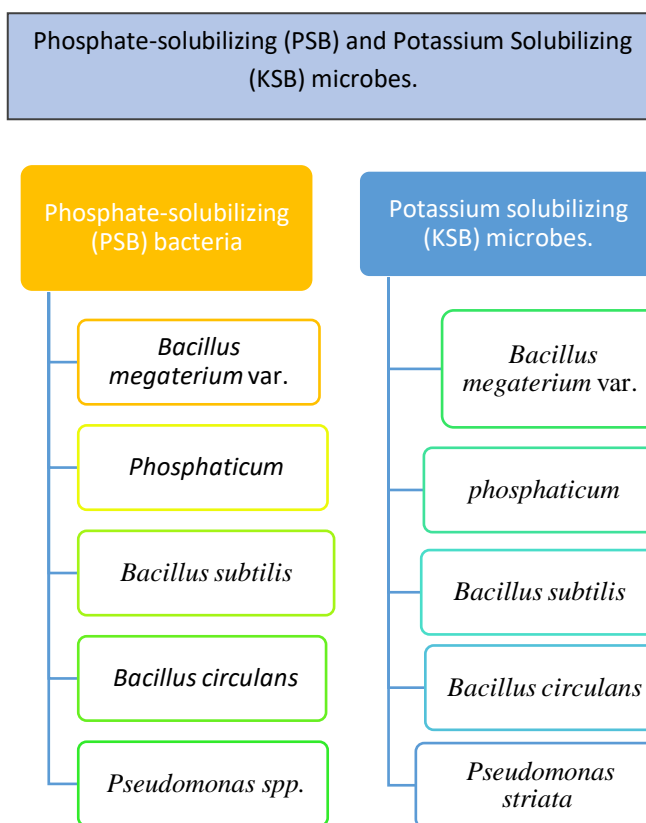


Figure 6. Representative microbial types and strain examples involved in phosphorus and potassium solubilization

The solubilization of potassium in natural soils mainly occurs through the weathering of minerals such as feldspar, mica, and illite, a process enabled by various mechanisms. Microbial activity serves a central role in this transformation. Soil microbes release organic acids, protons, and chelating agents that solubilize mineral-bound potassium into soluble K^+ ions, which are easily absorbed by plants (Das & Pradhan, 2016). Since more than 90% of the soil's potassium occurs in the form of insoluble rocks and silicate minerals, specific microbial strains can considerably improve the direct uptake of potassium by plants (Gupta et al., 2015).

Figure 6 details the specific microbial groups and strains that contribute to the solubilization of phosphorus and potassium. Biofertilizers represent one of the most valuable innovations in agricultural science, providing a sustainable alternative to commercially synthesized potassium fertilizers (Kumar et al., 2017). Various mechanisms, such as acid generation, chelation, acidolysis, complexolysis, and exchange reactions, have been linked with the solubilization of insoluble potassium by different bacterial and fungal strains (Nosheen et al., 2021). Different microbes, including *Bacillus Circulans*, *Bacillus Edaphicus*, *Burkholderia* sp., *Acidithiobacillus Ferrooxidans*, *Arthrobacter* sp., *Paenibacillus Mucilaginosus*, *P. frequentans*, *Cladosporium* sp., *Aminobacter* sp., *Sphingomonas* sp., *Paenibacillus glucanolyticus*, *Enterobacter hormaechei*, and *Pseudomonas* spp., exhibit these mechanisms (Kumar et al., 2018). The most prevalent bacteria utilized to solubilize potassium include *Pseudomonas*, *Gluconacetobacter*, *Bacillus*, and *Acinetobacter*. These organisms can extract potassium from insoluble minerals such as orthoclase, mica, and illite (Fig. 6) (Singh et al., 2021).

2.5. Phosphate-potassium-mobilizing microbes: mechanisms and efficiency

Phosphate-mobilizing microorganisms, also referred to as P-mobilizers, can improve phosphorus uptake by transferring and mobilizing insoluble phosphate from deeper soil layers to the root cortex (Nosheen et al., 2021). Most P-mobilizers are fungi. *Arbuscular mycorrhizae*, a well-recognized example of P-mobilizing fungi, penetrate plant roots to expand the effective surface area and stimulate metabolic processes, thus enhancing phosphorus availability under nutrient-deficient conditions (Fig. 7) (Taktek et al., 2015). The hyphal structures of these fungi enable such mechanisms by extending into the soil and making nutrients accessible to plants (Sammauria et al., 2020). Furthermore, mycorrhizal fungi are acknowledged for their functions in enhancing soil quality, improving soil aeration and water dynamics, strengthening plant tolerance to drought and heavy metals, and decreasing susceptibility to root diseases and herbivory (Thomas & Singh, 2019).

Mycorrhizal fungi are extensively classified into two categories: *endomycorrhizal* and *ectomycorrhizal* fungi. *Arbuscular mycorrhizae*, the most prevalent type of endomycorrhiza, establishes intracellular associations within plant roots. The genera are regarded as *arbuscular mycorrhizal fungi* (AMF): *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Sclerocystis*, and *Scutellospora* are extensively recognized as AMF (Maçik et al., 2020).

Mobilization of potassium (K) is crucial for maintaining plant health, especially in potassium-deficient soils. Potassium occurs in several forms: soluble, exchangeable, non-exchangeable, and mineral-bound. Nevertheless, only the soluble and exchangeable forms are easily available for plant uptake. Root-soil interactions and microbial activity in the rhizosphere serve a vital role in releasing potassium from less available sources such as feldspar, mica, and illite (Naorem et al., 2021). Figure 7 shows the representative microbial genera and species that are engaged in the mobilization or solubilization of phosphate and potassium.

In field applications, biofertilizers such as Symbion-K, Biosol-K, and K Sol B are commonly administered through soil drenching, basal application during sowing, or furrow placement near the root zone. These formulations, frequently containing *Frateuria aurantia*, operate by colonizing the rhizosphere and secreting organic acids that solubilize insoluble potassium-bearing minerals such as feldspar, mica,

and illite, thus improving potassium availability and enhancing crop performance (Fig. 7) (Maçik et al., 2020; Meena et al., 2016). The mobilization of potassium through the production of organic acids is a well-established mechanism, in which microbial isolates reduce the surrounding pH to promote the solubilization of otherwise unavailable potassium sources (Jha, 2017). For example, the application of potassium-mobilizing bacteria (KMB), including *Pseudomonas pseudoalcaligenes*, *Bacillus mucilaginosus*, and *Bacillus pumilus*, improves the bioavailability of insoluble potassium present in soil (Meena et al., 2016).

2.6. Microbial solubilization of micronutrients: Zinc (Zn), Iron (Fe), and Sulphur (S)

Beyond macronutrients, various microbial species improve the bioavailability of essential micronutrients such as zinc, iron, and sulphur, which are vital for diverse metabolic and physiological functions in plants (Kathpalia & Bhatla, 2018). Microorganisms can enhance micronutrient content in crop grains through multiple mechanisms, including siderophore production, secretion of organic acids and phenolic compounds, modification of root morphology and anatomy, upregulation of micronutrient uptake genes, and phytase activity (Singh et al., 2021). While plants require micronutrients only in trace amounts (approximately 100 mg kg⁻¹ dry weight), these elements serve crucial roles in numerous cellular and metabolic processes, including energy metabolism, gene regulation, signal transduction, and hormone perception (Kumawat et al., 2019). The utilization of microorganisms capable of promoting plant uptake of nutrients such as iron, phosphorus, and silicon becomes a fundamental part of enhancing plant growth and yield (Figueiredo et al., 2010). Different microorganisms can solubilize various micronutrients, and bacteria such as *Pseudomonas spp.* possess several strains that can utilize diverse mechanisms to solubilize more than one micronutrient simultaneously (Kumar et al., 2017).

2.5.1. Sulphur-oxidising microorganisms and their role in soil sulphur cycling

Micronutrient deficiencies, particularly of sulphur (S), can considerably impede crop yield. To tackle this, chemical fertilizers are frequently formulated with known concentrations of essential nutrients such as nitrogen (N), phosphorus (P), potassium (K), and sulphur (S) (Kumar et al., 2017). Sulphur deficiency in plants results in impaired nitrogen metabolism, chlorosis, decreased oil content, and ultimately low yields (Meena, 2018). According to researchers, sulphur is regarded as the fourth essential macronutrient in crop production, following nitrogen, phosphorus, and potassium in significance (Matraszek-Gawron & Hawrylak-Nowak, 2019). Inorganic sulphur compounds can be oxidized by a broad range of sulphur-oxidizing bacteria, which act on sulphur in its reduced or partially oxidized forms (Singh et al., 2021). *Thiobacillus spp.* is a well-investigated genus of sulphur-oxidizing microbes. Species such as *T. thiooxidans* and *T. thioparus* transform sulphur into plant-available sulphates, thus improving plant nutrition (Nosheen et al., 2021).

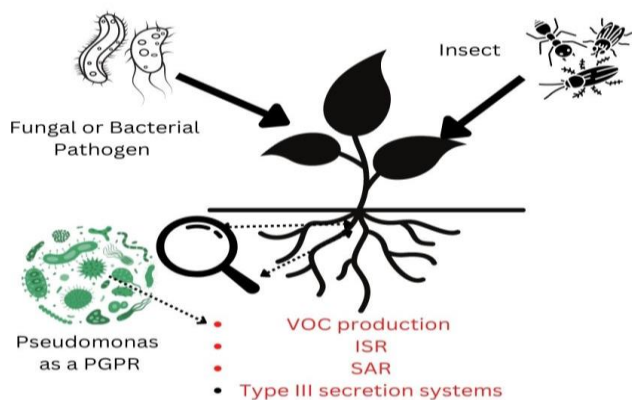


Figure 7. Schematic representation of signalling mechanisms in *Pseudomonas* spp.

Solubilization of sulphur occurs through various mechanisms utilized by different microbes. These include: (i) the mineralization of high molecular weight sulphur compounds into smaller units, which can subsequently be converted into sulphates; (ii) microbial immobilization, involving the transformation of inorganic sulphur compounds into organic forms; and (iii) oxidation, whereby chemoautotrophic and photosynthetic microorganisms transform substances such as hydrogen sulphide, sulphite, and thiosulphate into sulphates (SO_4^{2-}) from elemental sulphur (Maçik et al., 2020). Microorganisms capable of oxidizing sulphur belong to bacterial genera such as *Xanthobacter*, *Alcaligenes*, *Bacillus*, and *Pseudomonas* (Singh et al., 2019). The application of these microorganisms as constituents of biofertilizers provides a promising and sustainable approach to improve sulphur nutrition, especially in soils affected by sulphur deficiency.

2.5.2. Zinc-solubilizing microbes: mechanisms and agricultural potential

Zinc (Zn) is a crucial plant micronutrient that mainly occurs in insoluble forms within the soil. Its availability must be improved through biochemical processes enabled by microorganisms. Zinc solubilization refers to the microbial dissolution of insoluble zinc compounds (e.g., ZnO , ZnCO_3 , $\text{Zn}_3(\text{PO}_4)_2$) into soluble Zn^{2+} ions that plants can absorb. This is mainly accomplished by zinc-solubilizing bacteria (ZSB), including *Pseudomonas*, *Bacillus*, and *Azospirillum spp.*, which secrete organic acids like gluconic, citric, and oxalic acid. These acids reduce the pH of the rhizosphere and chelate zinc ions, thus increasing zinc solubility (Kamran et al., 2017; Nosheen et al., 2021; Saravanan et al., 2004). The process of mobilization of zinc from soluble forms in the soil to plant roots that are otherwise unable to access is additionally supported by mycorrhizal fungi, especially AMF. Their mycelial networks connect nutrient-deficient zones around roots with distant nutrient-rich regions, improving both zinc mobilization and uptake (Maçik et al., 2020).

In numerous plants, zinc serves several crucial functions. It plays a central role in the metabolism of carbohydrates, proteins, and auxin to regulate carbonic anhydrase activity, which is essential for carbohydrate fixation in plants (Sindhu et al., 2019). *B. subtilis*, *Thiobacillus thiooxidans*, and *Saccharomyces spp.* are examples of microorganisms capable of solubilizing zinc when applied as biofertilizers (Kumar et al., 2017). Another significant function of zinc is its role as an enzyme cofactor and metal activator (Singh et al., 2021). Nevertheless, despite being present in various soluble forms, zinc may remain inaccessible to plants under certain conditions (Saravanan et al., 2004). Zinc deficiency can adversely affect grain yield, root development, pollen formation, and water uptake and transport. It may also lead to slower shoot growth, impaired membrane integrity, decreased leaf size, chlorosis, and increased susceptibility to light, heat, and fungal diseases (Nosheen et al., 2021).

To enhance zinc availability in soil for improved plant growth, microbial genera such as *Pseudomonas spp.*, *Rhizobium spp.*, *Azospirillum spp.*, and *Bacillus spp.*, along with bacterial strains like *Klebsiella*, *Arthrobacter*, and fungal

genera such as *Penicillium* and *Aspergillus*, are regarded as suitable candidates for use as zinc-solubilizing biofertilizers (Maçik et al., 2020; Shaikh & Saraf, 2017; Sindhu et al., 2019). *Pseudomonas* species, including *Pseudomonas fragi* EPS1 and *Pseudomonas aeruginosa* ZSB-22, have shown the capacity to solubilize complex forms of zinc compounds such as zinc carbonate (ZnCO_3) when applied to soil. The zinc-solubilizing potential of these strains can be assessed by comparing the zinc concentrations in the roots of treated plants against those grown under untreated control conditions (Kamran et al., 2017).

2.5.3. Siderophore-producing microbes and iron acquisition in plants

Although iron is the fourth most abundant element on Earth, it is not easily assimilated by either bacteria or plants (Gupta et al., 2015). Iron commonly occurs in the form of amorphous and crystalline iron oxides, in soil and minerals, which are poorly soluble (Singh et al., 2021). To address this limitation, microbes have evolved various iron uptake strategies, including the production of siderophores. Siderophore production is a crucial microbial mechanism that promotes the solubilization and uptake of micronutrients, especially iron (Fe), which is frequently present in insoluble forms in the soil.

Siderophores are low-molecular-weight, high-affinity iron-chelating compounds released by microorganisms under iron-deficient conditions. These compounds capture Fe^{3+} from the surrounding environment, making it bioavailable for microbial and plant use (Prasad et al., 2019; Singh et al., 2019). Specific membrane receptors facilitate the uptake of siderophore-bound iron, improving plant iron nutrition, promoting growth, and contributing to pathogen suppression (Singh et al., 2021). Based on their chemical structure and functional groups involved in iron binding, siderophores are commonly classified into four major types: catecholates, hydroxamates, carboxylates, and mixed-type siderophores (Gupta et al., 2015; Zboralski & Fillion, 2020). Catecholates, such as enterobactin produced by *Escherichia coli*, contain catechol groups with exceptionally high Fe^{3+} binding affinity (Prasad et al., 2019). Hydroxamates, extensively synthesized by soil bacteria and fungi, utilize hydroxamic acid groups for chelation; examples include pyoverdine from *Pseudomonas aeruginosa* and ferrioxamines from *Streptomyces spp.* (Singh et al., 2019). Carboxylate-type siderophores, produced by genera such as *Rhizobium* and *Azotobacter*, employ carboxylic and hydroxyl groups to mobilize iron in acidic or organic matter-deficient soils (Gupta et al., 2015). Siderophore-producing bacterial strains have been linked with both plant growth promotion and biocontrol. Various plant growth-promoting rhizobacteria, including *Aeromonas*, *Azadirachta*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces spp.*, are regarded as promising candidates for application in iron-deficient environments (Jha & Saraf, 2015).

3. Biofertilizer potential and agronomic significance of *Pseudomonas spp*

3.1. The genus *Pseudomonas spp.* as effective Plant Growth-Promoting Rhizobacteria (PGPR)

The relationships between plant roots and soil microorganisms have been acknowledged for many decades, especially in connection with biofertilizers, which contain living or dormant microbes capable of displaying various PGPR functions. These biofertilizers are progressively considered as sustainable alternatives to chemical fertilizers. Following an assessment of multiple functional microbial groups, our research study focused on the PGPR activity in the genus *Pseudomonas*, which is a complex group distinguished by its diverse plant growth-promoting properties.

Pseudomonas spp. is considered one of the most efficient rhizobacterial genera, producing beneficial effects on characteristics such as plant height, bulb diameter, leaf area, chlorophyll content, photosynthesis rate, and root development, all in an environmentally friendly manner (Basu et al., 2021).

The genus *Pseudomonas* includes numerous species of Gram-negative, aerobic, heterotrophic bacteria that inhabit a broad range of environments, including soil, water, animals, and plant surfaces such as tobacco leaves (Adesemoye & Ugoji, 2009). *Pseudomonas spp.* distinguishes itself among PGPR due to its remarkable capabilities in root colonization, nitrogen fixation, phytohormone production, phosphate solubilization, hydrogen cyanide (HCN) production, exopolysaccharide and siderophore secretion, and solubilization of potassium and zinc. Furthermore, this genus is recognized for its capacity to form biofilms, structured microbial communities embedded in a self-produced extracellular matrix adhering to surfaces such as plant roots, and for its tolerance to various abiotic stresses, antioxidant activities, and synergistic interactions with other beneficial microbial communities (Dorjey et al., 2017).

Sustainable agriculture output is more likely to be accomplished through the extensive use of biofertilizers rather than chemical inputs. PGPR, such as *Pseudomonas spp.*, also provide chemical-free alternatives to conventional crop protection strategies (Thomas & Singh, 2019).

Table 3. PGPR activity, mechanism, and benefits of different strains of *Pseudomonas* bacteria

Type of PGPR activity	Mechanism	Significant Strain(s)	Benefits	Reference(s)
Nitrogen fixation (N)	Captures atmospheric nitrogen and converts it into plant-available forms.	<i>Pseudomonas stutzeri</i> CSP03, <i>Pseudomonas fluorescens</i> , <i>Pseudomonas putida</i> .	<ol style="list-style-type: none"> 1. Improves plant vegetative growth. 2. Enhances the production of plant hormones. 3. Contributes to disease Management. 	El-Sayed et al. (2014) Nosheen et al. (2021)
Phosphorus solubilization (P)	Solubilizes insoluble phosphorus compounds	<i>Pseudomonas striata</i> , <i>Pseudomonas fluorescens</i> , <i>Pseudomonas stutzeri</i> CSP03, <i>Pseudomonas rathonis</i>	<ol style="list-style-type: none"> 1. Regulates plant metabolism. 2. Facilitates energy transfer. 3. Contributes to photosynthesis. 4. Aids signal transduction. 	Otieno et al. (2015) El-Sayed et al. (2014) Sandhya et al. (2010) Yasmin et al. (2016) Sammauria et al. (2020) Mehnaz (2016)
Potassium solubilization (K)	Releases potassium from potassium-bearing minerals in soils into accessible forms.	<i>Pseudomonas spp.</i>	<ol style="list-style-type: none"> 1. Essential for enzyme activation. 2. Supports protein synthesis and photosynthesis 	Liu et al. (2022)
Zinc solubilization (Zn)	Solubilizes complex forms of zinc in soil	<i>Pseudomonas spp.</i> such as <i>Pseudomonas fragi</i> (EPS1), <i>Pseudomonas aeruginosa</i> (ZSB-22),	<ol style="list-style-type: none"> 1. Improves yield and root development. 2. Supports pollen formation and water transport 	Kamran et al. (2017)
Phytohormones production IAA, cytokinin, gibberellins)	<ol style="list-style-type: none"> 1. Produces hormones that promote root and shoot growth. 2. Improves nutrient availability and crop yield. 	<i>Pseudomonas</i> BA-8, <i>Pseudomonas putida</i> , <i>Pseudomonas putida</i> PHP03, <i>Pseudomonas stutzeri</i> CSP03, <i>Pseudomonas stutzeri</i> P3	<ol style="list-style-type: none"> 1. Enhances root growth. 2. Increases nutrient uptake 3. Boosts crop yield 4. Improves tolerance to abiotic stress. 	El-Sayed et al. (2014) Backer et al. (2018)

Efficient colonization of the rhizosphere by beneficial *Pseudomonas* strains is crucial for ensuring their effectiveness in field conditions. Various studies have shown that *Pseudomonas* spp. can enhance plant growth through the production of siderophores and phytohormones, which result in significant increases in leaf area and plant height (Muniroh et al., 2019).

Regarding plant protection against both biotic and abiotic stress, *Pseudomonas* species display strong potential. Various strains are capable of alleviating stress through multiple mechanisms, including the production of nutrient enzymes, volatile organic compounds, antibiotics, biosurfactants, iron-chelating compounds, and by competing for favorable nutritional sites (Arora et al., 2010; Gupta et al., 2015; Thomas & Singh, 2019). Economically important crops such as maize and rice typically have limited capacity to accumulate osmo-protectant enzymes. Nevertheless, when inoculated with *Pseudomonas pseudoalcaligenes* and *Pseudomonas aeruginosa*, these crops develop the capacity to biosynthesize proline and glycine-betaine, which function as osmo-protectants and provide tolerance to saline stress (Jha, 2019). As a mutualistic genus, *Pseudomonas* can also establish synergistic associations with mutualistic bacteria or fungi, leading to enhanced uptake of macro- and micronutrients, improved hormone production, and greater resilience to environmental stressors (Singh et al., 2021). Due to these characteristics, *Pseudomonas*-based biofertilizers are extensively used across various regions. For example, *Pseudomonas fluorescens* is utilized in Vietnam as a nitrogen fixer, in Cuba as a phosphate solubilizer, and in Sri Lanka as a phytostimulator (Maçik et al., 2020; Mehnaz, 2016). Similarly, *Pseudomonas striata* and *Pseudomonas azotoformans* are used in India and Sweden, respectively, for their phosphate-solubilizing and phytostimulatory capabilities (Maçik et al., 2020; Mehnaz, 2016). In Sweden and Argentina, *Pseudomonas chlororaphis* is applied as a biocontrol agent (Mustafa et al., 2019). The extensive application and well-documented effectiveness of *Pseudomonas* spp. emphasize their significant role in improving plant growth and development. Table 3 presents an overview of the different *Pseudomonas* strains and their associated PGPR activities.

Microbial signaling represents a fundamental component of PGPR activity. Various strains of *Pseudomonas* spp. release volatile organic compounds (VOCs) that suppress pathogenic diseases (Ortiz-Castro et al., 2009). Beyond their function as biocontrol agents (BCAs), members of the *Pseudomonas* genus can also activate systemic resistance (ISR) by stimulating plant immune responses through the recognition of pathogen-associated molecular patterns (PAMPs), which serve as the primary line of defense against pathogens (Zhu et al., 2022). Therefore, the *Pseudomonas* genus is not only highly valued for its PGPR activities but is also extensively utilized in the biocontrol of pathogens such as *Gaeumannomyces graminis* var. *tritici*, *Rhizoctonia solani*, *Erwinia carotovora* var. *carotovora*, *Pythium ultimum*, and *Fusarium oxysporum* (Quan et al., 2010). Various *Pseudomonas* strains, including *Pseudomonas aeruginosa*, are capable of establishing symbiotic relationships with plants as endophytes and rhizosphere colonizers, thus enhancing plant health through suppression of pathogenic bacteria and strengthening of plant resistance to disease (Singh et al., 2021).

Figure 7 represents a graphical depiction of the signalling mechanisms of *Pseudomonas* spp. For instance, the synthesis of antibiotics such as pyoluteorin and 2,4-diacetylphloroglucinol can safeguard cucumber plants against pathogens. The release of HCN suppresses certain phytopathogenic fungi, while the breakdown of extracellular chitin and laminarin by microbial enzymes can decompose fungal mycelia. Furthermore, malic acid can attract beneficial soil bacteria such as *Bacillus subtilis* to the root zone, an interaction that contributes to plant protection against foliar pathogens (Gray & Smith, 2005). Various *Pseudomonas* strains are also capable of activating systemic acquired resistance (SAR), ISR, and hydrogen cyanide production as part of their VOC response, which collectively inhibit the development of pathogenic diseases (Zhu et al., 2022).

In addition, the formation of various organic acids such as citric acid, oxalic acid, tartaric acid, and lactic acid by *Pseudomonas* spp. enhances the solubilization of nutrients, making them more accessible for plants' root uptake from the soil (Sammauria et al., 2020). The effectiveness of *Pseudomonas* spp. in controlling pathogens and promoting plant growth is closely linked to their ability to colonise and persist in the rhizosphere competitively, a trait referred to as rhizo-competence (Zboralski & Fillion, 2020). Further in-depth research is needed to better understand the efficiency of PGPR mechanisms and the signaling processes of *Pseudomonas* spp., in order to optimize their application for plant stress management. Figure 8 presents a comprehensive overview of the diverse PGPR mechanisms exhibited by *Pseudomonas* spp., with particular emphasis on their functional roles as biofertilizers.

3.2. Functional role of *Pseudomonas fluorescens* in plant growth and soil health

Pseudomonas fluorescens is a prevalent gram-negative, rod-shaped bacterium, plentiful in soil and water, recognized for its exceptionally adaptable metabolism. While it is an obligate aerobe, certain strains can employ nitrate as the terminal electron acceptor during cellular respiration in the absence of oxygen (Scales et al., 2014).

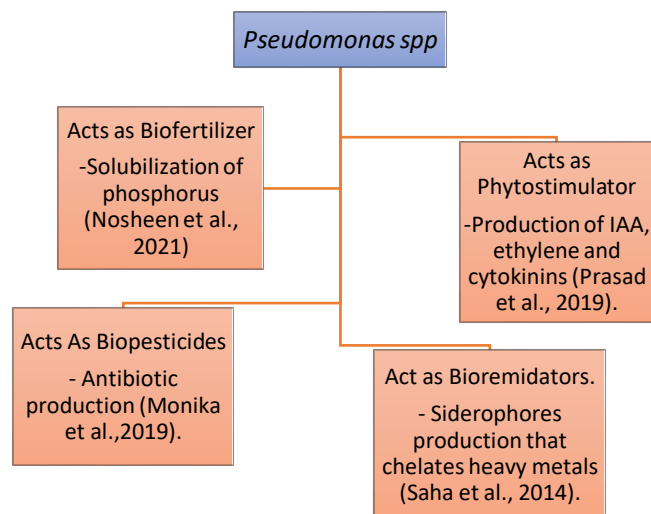


Figure 8. Overview of plant growth-promoting rhizobacteria (PGPR) mechanisms exhibited by different *Pseudomonas* spp., including their roles as biofertilizers

Table 4. Effects of *P. fluorescens* on various plants as a bioinoculant

Plant Name	Experimental Condition	Mechanism	Management Condition	Plant Responses	References
Wheat	Nursery Pots	Synthesis of EPS and phosphorus solubilization	Abiotic stress (drought)	Increased biomass production, relative water content, and nutrient uptake	Khan et al. (2019)
Rice	Laboratory, greenhouse, and field conditions.	Accumulation of stress-related metabolites (chaperonin 60)	Normal conditions.	Improved plant growth parameters, seedling vigour, and metabolite accumulation for stress tolerance	Kandasamy et al. (2009)
Marigold	Not specified	Not specified	Not specified	Increased shoot fresh weight, root dry weight, number of leaves, and number of nodes.	Bonilla et al. (2014)
Pea	Not specified	Enhanced ACC deaminase production.	Abiotic Stress (water deficit)	Improved shoot growth, earlier flowering, and higher grain yield	Arshad et al. (2008)
Tomato	Not specified	Increased ACC-deaminase activity	Abiotic Stress (salinity)	ACC deaminase-producing strains improved salinity tolerance compared to mutants deficient in ACC deaminase	Ali et al. (2014)

As a member of the PGPR group, *P. fluorescens* serves a vital role in the activation of systemic resistance, biological control of diseases, and promotion of plant growth. *P. fluorescens* has demonstrated the capacity to sequester cadmium ions, thus reducing their toxic effects on barley plants in soil remediation ([Prasad et al., 2019](#)). The *P. fluorescens* WCS365 strain, initially isolated from a potato, is acknowledged as an efficient root colonizer and has shown effectiveness in controlling tomato foot and root rot caused by fungal pathogens ([Kamilova et al., 2008](#)). It also generates antibiotic compounds that are active against root pathogens such as *Agrobacterium tumefaciens* and *Ralstonia solanacearum* ([Choi et al., 2008](#)).

Most research on *P. fluorescens* has emphasized its potential as an environmental bacterium capable of improving plant health through various antimicrobial and growth-promoting mechanisms ([Scales et al., 2014](#)). For example, rice seeds treated with the *P. fluorescens* KH-1 strain displayed significant improvements in growth parameters compared to untreated controls ([Kandasamy et al., 2009](#)). The vigor index analysis demonstrated that KH-1 treatment considerably improved root and shoot lengths. Treated seedlings recorded higher wet (1025.2 mg) and dry (806.4 mg) weights than the control group, which recorded 490.6 mg and 249.4 mg, respectively ([Kandasamy et al., 2009](#)). Additionally, *P. fluorescens* strain B16 has been documented to considerably enhance the growth of cucumber (*Cucumis sativus*) and barley (*Hordeum vulgare*) under both greenhouse and field conditions ([Choi et al., 2008](#)).

Furthermore, *Pseudomonas fluorescens* strains can generate several antifungal antibiotics, such as 2,4-diacetylphloroglucinol, which controls black root rot in

tobacco and take-all disease in wheat, and pyoluteorin, which suppresses Pythium-induced disease in cress ([Antoun, 2013](#)) by activating defense-related enzymes such as peroxidase (POD) and polyphenol oxidase (PPO), *Pseudomonas fluorescens* and *Bacillus spp.* They have been linked with improved control of *Fusarium* diseases ([Singh et al., 2021](#)). *P. fluorescens* displays highly versatile metabolic capabilities that enable it to flourish in diverse environments, including soil, rhizospheres, and plant surfaces, thus contributing to its resilience and effectiveness in plant disease suppression ([Scales et al., 2014](#)). Strains of *P. fluorescens* are recognized to generate powerful, broad-spectrum antifungal compounds effective against various phytopathogens. This genus is regarded as one of the most promising groups of PGPR due to its rapid growth, simple nutritional requirements, capacity to utilize a wide range of organic substrates, and strong motility. [Table 4](#) lists the beneficial impacts of *Pseudomonas fluorescens* on plant growth and health, based on its mechanisms of action and the specific conditions under which it is applied.

3.3. Functional role of *Pseudomonas aeruginosa* in plant growth and soil health

Following *P. fluorescens*, *Pseudomonas aeruginosa* displays vigorous plant growth-promoting and biocontrol characteristics, especially under stress conditions. It demonstrates a broad range of antibiotic mechanisms and PGPR factors, which contribute to its extensive spectrum of effectiveness as a biofertilizer ([Parvin, Govender, et al., 2020](#)). *P. aeruginosa* is a widespread bacterium capable of surviving under varied environmental conditions. It is recognized for its pearlescent appearance and a distinctive grape-like or tortilla-like odor. It develops well at temperatures ranging

from 25°C to 37°C, and its capacity to grow at 42°C differentiates it from many other *Pseudomonas* species (Diggle & Whiteley, 2020).

P. aeruginosa generates rhamnolipids, a type of secondary metabolite with strong surface and interfacial activity. These biosurfactants are extensively utilized in the petroleum industry, environmental remediation, agriculture, and other fields due to their high effectiveness and ease of production (Das et al., 2014). Additionally, *P. aeruginosa* produces pyocyanin, a powerful bacterial pigment with the capacity to disrupt the electron transport chain in fungi, thus displaying strong antifungal activity (DeBritto et al., 2020). Moreover, polyhydroxyalkanoate (PHA) accumulation by *P. aeruginosa*, which contributes to biofilm formation, serves a significant role in stress tolerance. PHA co-mobilization has been well established to improve microbial resilience under adverse conditions (Nadeem et al., 2016).

Most of the growth-promoting effects attributed to *Pseudomonas aeruginosa* are shown through improvements in nutrient uptake, plant biomass, and physiological parameters. For instance, inoculation with *P. aeruginosa* has been demonstrated to improve phosphorus and nitrogen

uptake in wheat plants, resulting in increased chlorophyll content, total soluble protein, and overall biomass production (Islam et al., 2014). The plant growth-promoting capacity of *P. aeruginosa* as a PGPR has also been assessed through its effects on various growth indicators in three test crops (Adesemoye & Ugoji, 2009). In tea rhizosphere soil, the strain *Pseudomonas aeruginosa* RTE4 was discovered to enhance plant growth by solubilizing tricalcium phosphate (46 g mL⁻¹), generating hydrolytic enzymes, and producing indole acetic acid (74.54 g mL⁻¹) (Chopra et al., 2020). Additionally, treatment with *P. aeruginosa* UPMP3 considerably increased leaf size, stem thickness, and plant height by 20–40% in palm oil seedlings, compared to synthetic fertilizer and untreated control groups, which demonstrated limited development (Parvin, Govender, et al., 2020). Furthermore, *P. aeruginosa* has demonstrated potential for bioremediation and growth promotion in wheat under zinc-induced oxidative stress. This effect is accomplished by improving nutrient availability, activating the antioxidant defense system, and decreasing zinc uptake by the plant (Islam et al., 2014).

Table 5. Effect of *Pseudomonas aeruginosa* on various plants as a bioinoculant

Plant Name	Experiment Condition	Management Condition	Mechanism	Plant Responses	References
Maize	Pots	Abiotic Stress (water tension)	Formation of EPS and activation of antioxidant enzymes.	Increased relative water content, protein, sugar level, and total plant biomass.	Naseem and Bano (2014)
Okra	Pots	Abiotic Stress (water tension)	Production of EPS.	Increased water and moisture content in the soil.	Yadav et al. (2018)
Wheat	Pots	Abiotic Stress (presence of heavy metal)	Synthesis of indole-3-acetic acid (IAA), siderophore production, and phosphorus (P) solubilization.	Increased total soluble protein, biomass, and phosphorus and nitrogen uptake.	Islam et al. (2014)
Chir-pine	-	Pathogen stress (<i>Macrophomina phaseolina</i>)	Production of siderophores, IAA, and root colonization.	Enhanced plant growth and biomass. Enhanced antifungal and antibacterial effect	Singh et al. (2021)
Pea	Pots and field	Pathogen stress (<i>Sclerotinia sclerotiorum</i>)	Induced systemic resistance.	Increased plant growth and yield	Jain et al. (2015)
Sunflower	Pots	Pathogen stress (<i>Macrophomina Phaseolina</i>)	Production of biosurfactants (Antibiosis).	Improved plant growth	Tewari and Arora (2016)
Green gram	-	-	Production of PGRs and secondary metabolites biosynthesis.	Regulation of various plant processes, including cell expansion, cell division, root formation, and growth rate	Ahemad and Khan (2010)

Successful colonization by *Pseudomonas aeruginosa* is advantageous for decreasing the incidence of plant diseases and improving crop yields across a broad range of agricultural systems. For example, the antifungal activity against *Sporisorium scitamineum* and enhanced sugarcane growth have been connected to the presence of colonization-associated genes, such as *minCDE*, *lysC*, and *yjbB*, in the genome of *P. aeruginosa* B18 (Singh et al., 2021). Among the various *Pseudomonas* species, *P. aeruginosa* serves a crucial role as a biological control agent against *Ganoderma* in oil palm plantations (Parvin, Rahman, et al., 2020). Research has demonstrated that endophytic *P. aeruginosa* isolated from healthy oil palm roots displays significant in vitro inhibitory effects against *G. boninense* (Siddiqui et al., 2021).

Moreover, the biocontrol effectiveness of *P. aeruginosa* RTE4 has been proven against two foliar fungal pathogens of tea. This strain displayed considerable antagonistic activity, with growth inhibition (GI) values of 36.6% and 56.8% against *C. invisium* and *F. solani*, respectively (Chopra et al., 2020). The RTE4 strain generates di-rhamnolipid, a biosurfactant composed of fatty acids and two rhamnose sugar units. This compound improves nutrient mobilization, promotes root colonization, and controls plant pathogens. These findings support the potential application of di-rhamnolipid from *P. aeruginosa* RTE4 as a large-scale biological alternative to chemical fertilizers (Chopra et al., 2020). The plant growth-promoting effects of *P. aeruginosa* as a bioinoculant across various crops are summarized in Table 5.

3.4. Functional role of *Pseudomonas putida* in plant growth and soil health

Another notable species, *Pseudomonas*, is acknowledged for its metabolic adaptability and environmental resilience, making it a valuable bioinoculant in various soil systems (Molina et al., 2020). *P. putida* can endure environmental challenges through mechanisms such as protein and peptide secretion and trafficking, protein modification and repair, protein folding and stability, and the degradation of proteins, peptides, and glycopeptides (Svenningsen et al., 2015). Due to its exceptional ability to metabolize organic contaminants, *P. putida* has been characterized as a "laboratory workhorse" for research on bacteria-mediated soil remediation processes (Moore et al., 1987). Research has documented that inoculating cotton plants with *P. putida* demonstrated improved germination rates and enhanced growth parameters, including plant height, dry weight, and fresh weight under alkaline and high-salinity conditions. These improvements were attributed to increased uptake of potassium, magnesium, and calcium ions, along with decreased absorption of sodium ions (Singh et al., 2021).

Strains of the genus *Pseudomonas putida* are typical inhabitants of the rhizosphere and freshwater environments, exhibiting a remarkable capacity to metabolize a diverse array of biogenic and xenobiotic compounds (Fernández et al., 2015). Among its notable strains is *P. putida* KT2440, which colonizes plant roots and establishes a mutualistic relationship with its host plant (Ramos-González et al., 2005). Another example is *P. putida* PCL1444, which can effectively utilize root exudates, degrade naphthalene in the rhizosphere, and prevent naphthalene-induced seed damage, thus enabling normal plant growth (Arora et al., 2010).

The rhizosphere denotes the outermost layer of plant roots, where bacteria flourish by utilizing nutrients released from the roots. In exchange, microbes such as *Pseudomonas putida* enhance plant growth and protect against disease-causing pathogens (Zhu et al., 2022). Due to these beneficial characteristics, *P. putida* is commonly utilized in bioengineering research to develop biopesticides and improve plant health, as it contributes to promoting plant development (Ramos-González et al., 2005).

Pseudomonas putida can form commensal relationships with plants, involving a series of functions encoded by core genes that promote nutrient mobilization, pathogen suppression, and efficient niche colonization (Fernández et al., 2015). For instance, *P. putida* BSP9, isolated from the rhizosphere of *Brassica juncea*, has shown the capacity to generate indole acetic acid, siderophores, and phosphate-solubilizing activity, as well as being an effective biosurfactant producer (Mishra et al., 2020). The *P. putida* KT2440 strain has also been demonstrated to reduce abiotic stress damage in plants grown under high salinity, making it a suitable PGPR candidate for inoculation programs to improve salt tolerance in citrus cultivation (Ramos-González et al., 2005). Certain *P. putida* strains possess accessory genes providing specific biodegradative capabilities, enabling their use in rhizoremediation to eliminate pollutants from plant root environments (Molina et al., 2020). Inoculation with *P. putida* has been documented to improve ethylene regulation and promote quorum sensing, thus facilitating the coordinated expression of beneficial PGPR traits (Gray & Smith, 2005). The production of gibberellic acid by *P. putida* strains has been associated with enhanced root-adhering soil weight, greater soil aggregate stability, and improved maize growth (Singh et al., 2021). Furthermore, inoculation with *P. putida* KT2440 decreased chloride accumulation in roots under 90 mM NaCl stress by 24.6% compared to non-inoculated plants. This was accompanied by increases in root and shoot length, dry biomass, tiller number, spikelet formation, and grain yield in wheat (Ramos-González et al., 2005).

Two *Pseudomonas putida* strains have been demonstrated to effectively decrease the severity of cotton vascular wilt caused by *Fusarium oxysporum* f. sp. *vasinfectum*. In *Gladiolus grandiflorus* L., co-inoculation with *P. putida* and *Thiobacillus thiooxidans* in the presence of vermicompost and elemental sulphur improved phytoremediation efficiency (Mani et al., 2016). Under field conditions, *Pseudomonas putida* suppressed the fungal growth of *Macrophomina phaseolina* in chickpeas (Gupta et al., 2015). The *P. putida* KT2440 strain considerably stimulates oxylipin production, compounds closely associated with enhanced plant defense against diseases and insect pests (Zhu et al., 2022). The incorporation of *P. putida* as a biofertilizer not only improves crop yield but also preserves long-term soil health, making it a promising alternative to synthetic fertilizers. By promoting a balanced and resilient rhizosphere, *P. putida* contributes to sustainable agricultural practices, enhancing productivity while reducing environmental impact. The growth-promoting effects of *Pseudomonas putida* as a bioinoculant across various plant species are summarized in Table 6.

3.5. Functional role of *Pseudomonas stutzeri* in plant growth and soil health

Pseudomonas stutzeri is discovered in both terrestrial and marine environments. In soil, it has been recognized in the rhizosphere of cordgrass and other extensively cultivated plants such as wheat, barley, and rice. In marine habitats, it resides in silt and the water column (Lalucat et al., 2006).

The nitrogen-fixing strain *Pseudomonas stutzeri* is regarded as a model organism for denitrification, a process that serves an important role in agricultural production and nitrogen cycling (Figueiredo et al., 2010). For instance, *Pseudomonas stutzeri* A1501 has been demonstrated to improve nitrogen fixation in rice (Jha, 2019). Plants hosting *Pseudomonas stutzeri* can facilitate the conversion of nitrous oxide into inert nitrogen. Therefore, integrating this bacterial characteristic into crops could assist in reducing atmospheric nitrous oxide levels (Nadeem et al., 2016). Additionally, *Pseudomonas stutzeri* exhibits the capacity to metabolize a broad range of substrates, making it a promising candidate for applications in bioremediation and wastewater treatment (Lalucat et al., 2006).

The growth-promoting mechanisms of *Pseudomonas spp.* encompass the production of growth regulators (phytohormones), mineral solubilization, siderophore

production, phosphate solubilization, and protection against both biotic and abiotic stresses. Key mechanisms involve enzymes such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase and chitinase, as well as the synthesis of osmolytes and exopolysaccharides (Singh et al., 2021). Improved biofilm-forming capacity and a strong chemotactic response to root exudates are thought to contribute to the ability of *Pseudomonas stutzeri* to enhance soybean growth under saline stress (Lami et al., 2020). Remarkably, this characteristic was further enhanced in highly saline environments, demonstrating the adaptability of the bacterium to challenging conditions. Under salt stress, *P. stutzeri* has also been demonstrated to enhance seed germination, plant growth, and overall plant health (Shang et al., 2021). Isolated strains such as MJL19 and XL272 have exhibited strong chemotaxis toward soybean root exudates and superior biofilm-forming ability, both independently and in collaboration with *Bacillus velezensis* SQR9, leading to greater biomass production compared to single-species biofilms (Lami et al., 2020; Sun et al., 2021).

Pseudomonas stutzeri can endure exposure to toxic metals, a characteristic linked with the accumulation of specific proteins in the cell wall (Nadeem et al., 2016).

Table 6. Effect of *Pseudomonas putida* on various plants as a bioinoculant

Plant Name	Experiment Condition	Mechanism	Management Condition	Plant Responses	References
Sunflower	Pots	Production of EPS	Abiotic stress (water tension)	Increased biomass, plant vitality, and proportion of root tissue to soil adhered to roots	Sandhya et al. (2009)
Maize	Pots	IAA production, gibberellic acid production, siderophore production, ammonia production, and P-solubilization	Abiotic stress (water tension)	Increased root-adhering soil and soil aggregate firmness at normal weight diameter	Sandhya et al. (2010)
Wheat	Pots	Increased gibberellin production	Abiotic stress (water tension)	Increased antioxidant activity	Kang et al. (2014)
Soybean	Pots	Amplified IAA production and P-solubilization.	Abiotic stress (salinity)	Enhanced phosphorus and nitrogen acquisition Nodule formation and root system development	Egamberdieva et al. (2017)
Maize	Laboratory	-	Pathogen stress (<i>Fusarium verticillioides</i>)	Inhibition of fungal growth and colonisation	Niu et al. (2017)
Pea	-	Amplified ACC deaminase production.	Abiotic stress (water tension)	Enhanced shoot growth, pod flowering, and grain yield	Arshad et al. (2008)
Cherry trees	-	Enhanced rhizosphere colonization.	Normal conditions.	Improved plant growth, fruit yield, fruit set, and vegetative growth.	Tang et al. (2021)

Strains generating exopolysaccharides have displayed considerable potential for treating heavy metal-contaminated water (Coelho da Costa Waite et al., 2020). In nitrogen-deficient conditions, nitrogen-fixing microbes in root nodules improve nitrogen uptake in leguminous plants (Shang et al., 2021). The nitrogen-fixing rice-associated strain *Pseudomonas stutzeri* A15 possesses three distinct nitrate reductase systems, allowing the conversion of nitrate to nitrite via three physiologically distinct pathways: nitrate assimilation, nitrate respiration, and nitrate dissimilation (Pham et al., 2017). Due to these PGPR characteristics, *P. stutzeri* A15 considerably enhanced the growth of rice seedlings compared to uninoculated controls (Lami et al., 2020). Overall, *P. stutzeri* is a versatile PGPR, combining multiple plant growth-promoting characteristics, including high colonization efficiency, IAA production, ammonia (NH₃) release, phosphate solubilization, hydrogen cyanide (HCN) production, antimicrobial activity, strong performance under saline stress, chemotactic responsiveness to root exudates, and robust biofilm synthesis. These attributes make it a promising candidate as a bioinoculant (Lami et al., 2020; Pham et al., 2017).

4. Future outlook and challenges

During the past decade, PGPR has attracted considerable attention due to the rhizosphere's vital role as an ecological niche in maintaining biosphere functions. This has stimulated

comprehensive research to clarify the mechanisms by which PGPR interact with plants in the rhizosphere. Pathogenic diseases continue to be a major factor decreasing agricultural productivity and crop quality, establishing conditions conducive for contamination and spoilage. As a component of PGPR, beneficial microbes generate phytohormones and bioactive compounds that serve as antibiotics under stress conditions, contributing to induced systemic resistance. For biofertilizer development, microorganisms from various bacterial and fungal groups, including *Rhizobium*, *Pseudomonas*, *Bacillus*, *Klebsiella*, *Azotobacter*, *Azospirillum*, and *Azomonas*, can colonize the rhizosphere and enhance plant growth without adverse environmental effects (Zainuddin et al., 2022). Efficient rhizosphere management demands careful consideration of inoculant formulation and delivery methods, as well as soil and crop management practices. These microbes improve nutrient availability, produce growth-promoting compounds, and reinforce plant defenses against diseases. By combining multiple biological functions, complex biofertilizer formulations can be developed to address plant growth and protection comprehensively. Significantly, after three to four years of consistent biofertilizer application, nutrient availability and the persistence of introduced beneficial microbes in the soil may be adequate to maintain plant growth, representing an environmentally sustainable cultivation strategy (Nosheen et al., 2021).

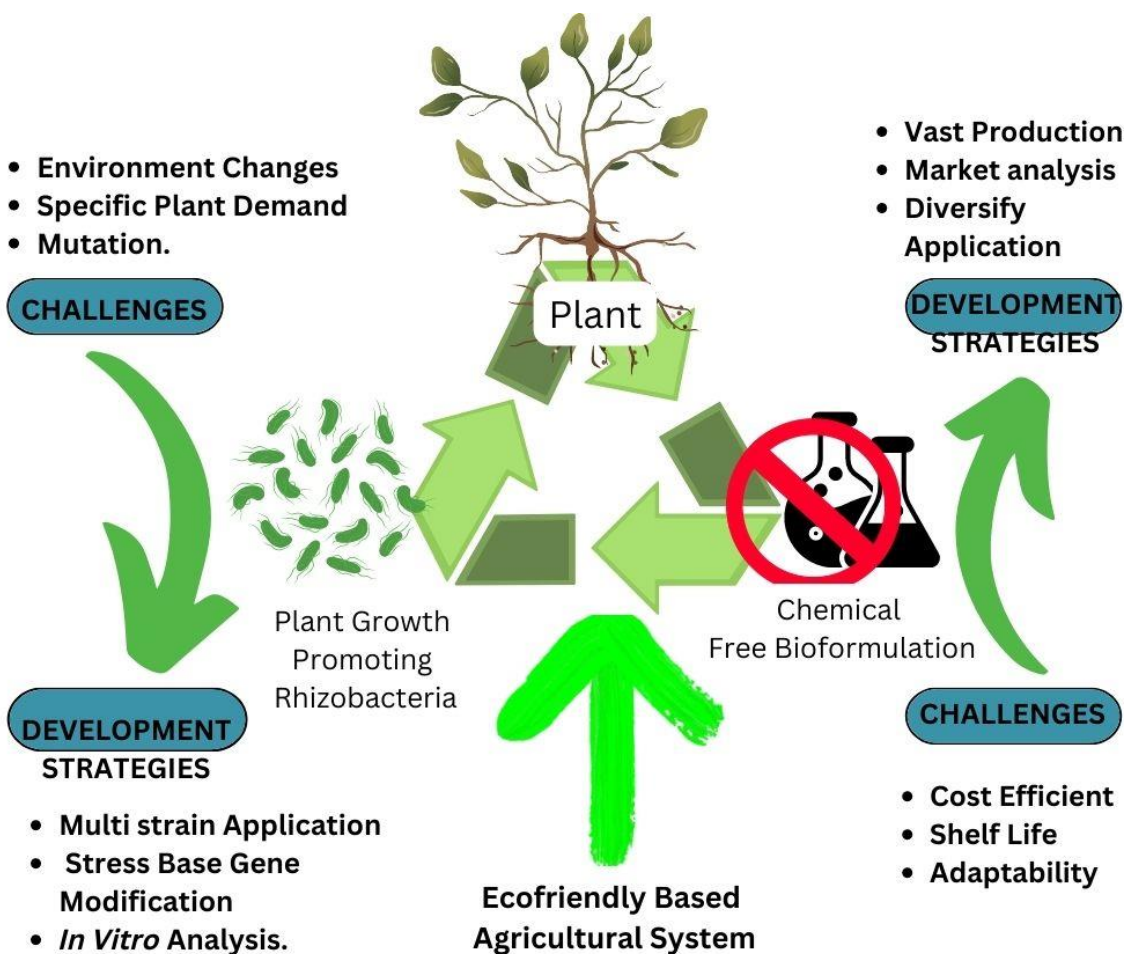


Figure 9. Strategies for research and development towards the successful commercialization of the bioformulation industry.

Despite these benefits, commercialization encounters challenges. Regulatory concerns and public perception of genetically modified organisms (GMOs) can hinder adoption. Clear and comprehensive policies governing biofertilizer production, distribution, and use are crucial to support widespread implementation. Functions in PGPR inoculants, combining well-characterized strains with complementary functions, are especially promising as they can target multiple pathogens, utilize diverse modes of action, and adapt to spatial or temporal variability in the field. Nevertheless, the inoculant industry must address key formulation challenges, including prolonging shelf life, maintaining high viable cell counts, protecting inoculants from adverse soil conditions, ensuring ease of application, and keeping costs low. Additional research is required on scalable production methods and advanced formulation strategies to create biofertilizers that are stable, effective, safe, and economically viable. Accomplishing these goals will require strong collaboration between farmers, microbiologists, biotechnologists, industrial stakeholders, and agriculturists. Figure 9 illustrates the strategies that can be implemented to support the commercial application of the biofertilizer industry.

5. Conclusion

This review emphasizes the crucial role of *Pseudomonas* spp. as multifunctional plant growth-promoting rhizobacteria (PGPR), with proven potential to improve crop productivity and resilience under varied environmental conditions. These bacteria facilitate plant growth through direct mechanisms such as nitrogen fixation, phosphate and potassium solubilization, siderophore production, and phytohormone synthesis, as well as indirect mechanisms including induced systemic resistance (ISR), pathogen suppression, and biofilm formation. Strains such as *P. fluorescens*, *P. aeruginosa*, *P. putida*, and *P. stutzeri* have shown strong effectiveness in nutrient acquisition, stress tolerance (e.g., salinity), and biocontrol of phytopathogens. Their adaptability and extensive metabolic activities make them promising candidates for integrated nutrient management and long-term soil health enhancement. The review achieves its objective by highlighting the importance of understanding biofertilizer types and mechanisms to advance sustainable and eco-friendly agricultural practices. As viable alternatives to synthetic agrochemicals, *Pseudomonas*-based biofertilizers provide cost-effective and environmentally responsible solutions. Practical evidence confirms their effectiveness: *P. aeruginosa* UPMP3 enhanced growth parameters in oil palm seedlings beyond those accomplished with chemical fertilizers, while *P. putida* KT2440 reduced salt stress in citrus crops by improving nutrient uptake and decreasing chloride accumulation. Future research should focus on the clarification of strain-specific genomic traits, optimization of bioformulations, and large-scale field trials to ensure consistent performance. An emphasis on connecting laboratory findings with real-world applications will be essential to promoting the successful adoption of *Pseudomonas*-based bioinoculants in sustainable farming systems.

Acknowledgment

This work was supported by a research grant FRGS 5540305. The authors express their gratitude to the Ministry of Higher Education Malaysia (MOHE) and Universiti Putra Malaysia for providing financial support for this research.

Declaration of Competing Interest

The authors declare that no competing financial or personal interests may appear to influence the work reported in this paper.

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