



REVIEW

Advances in PGPR-Mediated Plant-Pathogen Control for Food Security and Ecosystem Stability

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ABSTRACT: This review focused on the role of plant growth-promoting rhizobacteria (PGPR) in enhancing plant growth and protecting against pathogens, highlighting their mechanisms of action, ecological benefits, and challenges. PGPR mediate plant growth through several mechanisms, including nutrient acquisition, production of antimicrobial compounds and induction of systemic resistance. These mechanisms are critical in improving crop yields, especially under stressful conditions. This review examines the molecular mechanisms of PGPR-mediated plant pathogen control, cellular mechanisms of PGPR in plant pathogen control, ecological and environmental benefits of PGPR application. Despite their potential, PGPR application is limited by environmental variability, inconsistent efficacy, and challenges in formulation and commercialization. The review discusses these challenges and also provides solutions. Additionally, the review outlines the latest advancements in PGPR strain selection and their genetic modifications for enhanced resilience and biocontrol efficacy. PGPR are particularly crucial in addressing global food security challenges, exacerbated by climate change, and the need for sustainable agricultural practices. PGPR have been shown to increase crop yields by 20%–30% in drought-prone regions and reduce pesticide use by up to 50%, contributing to more sustainable farming. As research advances, PGPR can play a key role in reducing chemical input dependency and promoting long-term agricultural sustainability. This review examines the role of PGPR in pathogen control and highlights their potential to enhance agricultural sustainability.

KEYWORDS: Agricultural biocontrol; crop disease resistance; environmental sustainability; PGPR; plant-pathogen management; sustainable agriculture

1 Introduction

Plant-pathogen interactions represent a critical dimension of agricultural science, greatly influencing crop productivity and ecosystem stability [1]. The constant co-evolution of plants and pathogens—including bacteria, fungi, viruses, and nematodes—has shaped the trajectory of agricultural systems for centuries. Plant diseases caused by these pathogens continue to threaten food security significantly, reducing yields and adversely affecting crop quality globally [2]. Estimates suggest that plant diseases contribute to approximately 30% of annual crop losses globally, resulting in direct economic losses exceeding \$200 billion annually, with staple crops such as wheat, maize, and rice being particularly vulnerable. These losses not only affect food availability but also have far-reaching consequences on farmers' livelihoods, especially in developing regions [3]. In addition to direct yield reductions, plant diseases also contribute to the degradation of ecosystem services, such as soil fertility, carbon sequestration, and water regulation, thus threatening the stability of ecosystems and the agricultural systems dependent on them. Maintaining plant health is crucial



for ensuring ecosystem stability [4]. Healthy plants provide critical services, including nutrient cycling, habitats for biodiversity, and support for the physical structure of soils, which are essential for long-term ecological and agricultural sustainability. For instance, plants contribute to soil aeration and water retention, enhance biodiversity by providing food and shelter for other organisms, and facilitate carbon sequestration, which helps mitigate climate change [5]. However, plant diseases can disrupt these vital functions, leading to a cascade of ecological imbalances. Pathogenic attacks on plants result in several symptoms, ranging from root rot, blight, wilting, and stunted growth to complete plant death. These effects undermine plant health and hinder the plant's ability to perform ecosystem functions. Consequently, plant diseases represent a double-edged sword, threatening both the productivity of crops and the stability of the ecosystems that support them [6,7].

Conventional strategies for managing plant diseases have traditionally relied on chemical pesticides and fertilizers. While these methods have been effective in controlling certain plant pathogens, they have several significant drawbacks [8]. For example, the widespread use of chemical treatments can result in environmental degradation, including soil and water contamination, and the development of resistance in pathogens [9]. Pesticide resistance, in particular, has become a growing concern, with several pathogen species evolving mechanisms to evade chemical control, making management even more difficult. Additionally, chemical inputs often disrupt the delicate balance of beneficial soil microbes, negatively affecting soil health and plant growth [10]. Thus, the need for sustainable and eco-friendly alternatives to chemical pesticides has never been more urgent. In this context, plant growth-promoting rhizobacteria (PGPR) have emerged as a promising solution, offering an environmentally friendly and cost-effective approach to disease management [11]. PGPR are a diverse group of microorganisms that colonize the rhizosphere of plants and promote plant growth through a variety of mechanisms. These bacteria enhance plant growth and development by increasing nutrient availability, producing phytohormones, and protecting plants from pathogens through direct and indirect mechanisms [12]. One of the key roles of PGPR in plant health is their ability to induce systemic resistance in plants, making them more resistant to a broad spectrum of pathogens. PGPR can also produce a range of antimicrobial compounds, including antibiotics, volatile organic compounds (VOCs), and hydrolytic enzymes, which help inhibit pathogen growth [13]. Moreover, PGPR can outcompete harmful pathogens in the rhizosphere for space and resources, thus reducing the likelihood of infection. These multifaceted benefits of PGPR make them powerful agents in enhancing plant resistance to diseases, thus reducing the need for chemical pesticides and supporting sustainable agricultural practices [14].

The significance of PGPR in modern agriculture cannot be overstated, particularly in the context of global challenges such as climate change, population growth, and food security [15]. The world's population is projected to reach 9.7 billion by 2050, placing immense pressure on agricultural systems to produce sufficient food. Climate change is expected to exacerbate existing challenges, with more frequent and severe droughts, floods, and temperature extremes placing additional stress on crops, making them more vulnerable to pathogens [16]. In this context, PGPR offer a sustainable solution, as they are eco-friendly, cost-effective, and capable of enhancing plant growth and pathogen resistance. In addition to promoting plant health, PGPR contribute to soil fertility by increasing nutrient availability and enhancing soil microbial diversity, which are crucial for long-term agricultural sustainability [17]. Several plant pathogens have been successfully managed using PGPR. For example, *Pseudomonas fluorescens*, a widely studied PGPR, has been shown to control soilborne pathogens such as *Fusarium* species, *Pythium* spp., and *Rhizoctonia solani* by producing antibiotics and competing for space in the rhizosphere [18]. Similarly, *Bacillus subtilis* and *Bacillus thuringiensis* have demonstrated efficacy in controlling foliar pathogens, including *Alternaria* spp., *Botrytis cinerea*, and *Xanthomonas* spp., through lipopeptide and VOC production. Furthermore, PGPR also enhance

resistance to viral pathogens, such as Tobacco mosaic virus, by inducing systemic acquired resistance (SAR) in plants. The ability of PGPR to reduce the severity of diseases caused by these pathogens is crucial for maintaining crop productivity and reducing the reliance on chemical pesticides [19,20].

The global impact of plant diseases on crop productivity is vast and multifaceted. It is estimated that plant pathogens are responsible for 20%–30% of global crop losses, with some crops suffering up to 50% yield loss in regions heavily affected by diseases [21]. For example, the wheat yellow rust epidemic in 2010 resulted in an estimated yield loss of 9 million metric tons, while rice blast disease, caused by *Magnaporthe oryzae*, results in an annual global rice production loss of 10%–30%. These losses contribute to the growing food insecurity in many parts of the world, particularly in developing countries where agriculture plays a central role in the economy [22,23]. Moreover, plant diseases affect biodiversity by reducing the population sizes of native plant species, which can have cascading effects on ecosystems. The decline of plant species due to pathogen pressure disrupts the food web and decreases habitat availability for other organisms, leading to further biodiversity loss [24]. In the context of food security, the importance of PGPR cannot be overstated. With increasing pressure to enhance agricultural productivity, PGPR offer an innovative approach to disease management that is both environmentally sustainable and effective. By enhancing plant resistance to pathogens, PGPR reduce the need for chemical pesticides, thereby promoting healthier soils, reducing water contamination, and preventing pesticide resistance development [25]. PGPR application has been shown to improve crop yields by 10%–30% in various agricultural systems, making them a valuable tool for farmers worldwide [26,27]. Additionally, PGPR support rhizosphere health by improving soil structure, increasing nutrient cycling, and promoting microbial diversity. These benefits contribute to the long-term sustainability of agricultural ecosystems, ensuring that crops can withstand the challenges posed by climate change and the increasing demand for food [17,28]. The direct and indirect mechanisms through which PGPR augment plant growth promotion and plant protection against pathogens are illustrated in Fig. 1.

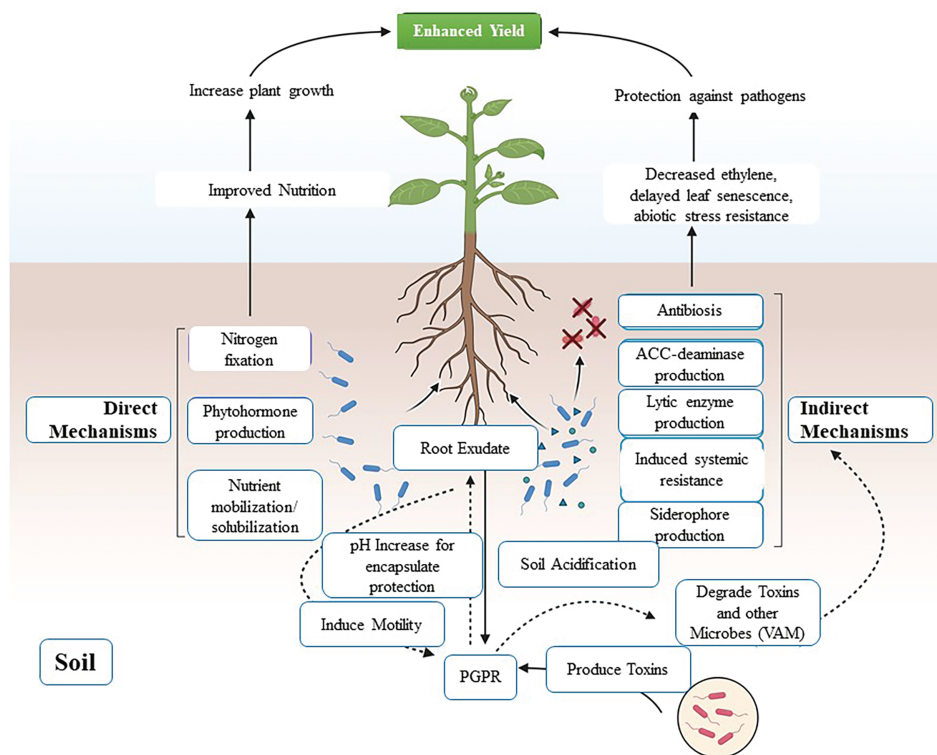


Figure 1: Illustrates the direct and indirect mechanisms through which PGPR augment plant growth promotion and provide protection against pathogens

This review aims to provide a comprehensive overview of the molecular and ecological mechanisms underlying PGPR-mediated plant-pathogen control, with an emphasis on the types of pathogens that PGPR are effective against. It also explores the current state of research on PGPR application in agriculture, identifying key PGPR strains used for managing plant diseases, and discussing the challenges and future directions for their widespread use. Additionally, this review examines the potential of PGPR to enhance plant resistance to a wide range of pathogens and their role in promoting sustainable agricultural practices, highlighting their potential to reduce reliance on chemical pesticides and fertilizers. By synthesizing current research and offering insights into future developments, this review contributes to the advancement of PGPR-based solutions in agriculture, helping to ensure global food security and the stability of ecosystems in the face of ongoing environmental challenges.

2 Molecular Mechanisms of PGPR-Mediated Plant-Pathogen Control

PGPR benefit plants through several molecular and biochemical mechanisms, each contributing to the plant's enhanced resistance to pathogens. These mechanisms enable PGPR to function as natural biocontrol agents, reducing the need for chemical pesticides and enhancing the sustainability of agricultural practices [29,30]. A key aspect of PGPR-mediated disease resistance is the induction of systemic resistance in plants, production of antimicrobial compounds, modulation of plant hormones, and formation of biofilms that aid in pathogen suppression (Fig. 2). PGPR mediates pathogen suppression through various mechanisms [13]. These include competition for nutrients and space in the rhizosphere, the production of antimicrobial compounds such as antibiotics and volatile organic compounds (VOCs), and the activation of plant immune responses such as Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR) [31]. Biofilm formation further enhances PGPR colonization and pathogen suppression [29]. Fig. 2 summarizes these mechanisms. Understanding these processes at the molecular level offers critical insight into how PGPR can be effectively utilized in crop protection and sustainable farming.

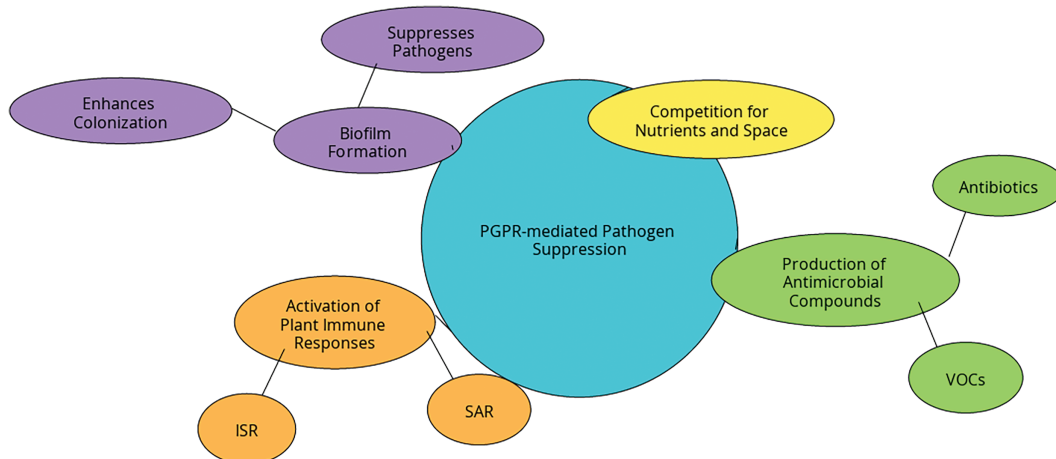


Figure 2: The flowchart illustrates the various mechanisms through which plant growth-promoting rhizobacteria (PGPR) mediate pathogen suppression

In addition to the general concepts described, certain antimicrobial compounds produced by PGPR strains are essential for suppressing pathogens. For example, *Pseudomonas aeruginosa* and *Pseudomonas fluorescens* produces phenazines, which exhibit a strong antimicrobial activity by disrupting pathogen cellular functions and inhibit biofilm production and leading to inhibiting the colonization of the pathogen [32,33].

Another well-known PGPR, *Bacillus subtilis*, synthesizes lipopeptides, such as surfactin, that exhibit broad-spectrum antimicrobial activity by destabilizing microbial cell membranes [34,35]. *Pseudomonas chlororaphis* produces volatile organic compounds (VOCs), such as 2,4-diacetylphloroglucinol (DAPG), which inhibit pathogen growth by causing cellular damage to plant pathogens. Additionally, HCN prevents the growth of insects, microbes and other plant diseases. It is produced from glycine by HCN synthase in a variety of *Pseudomonas* species. According to the majority of fluorescent *Pseudomonads* a few species of the genus *Chromobacterium*, *Burkholderia*, and some *Rhizobia*, reported for cyanide synthesis in the bacteria [36]. PGPR like *Trichoderma harzianum* secrete hydrolytic enzymes (e.g., chitinase and β -1,3-glucanase), which degrade fungal cell walls and reduce pathogen virulence. PGPR also activate plant immune responses, including the induction of Systemic Acquired Resistance (SAR) or Induced Systemic Resistance (ISR). These reactions occur when plant receptors identify PGPR-associated molecular patterns (PAMPs). This results in the activation of signaling pathways, such as calcium influx, MAPK signaling, and the generation of reactive oxygen species (ROS). These pathways then activate genes linked to defense and improve the plant's resistance to infections [37,38].

PGPR-ISR is one of the most widely studied mechanisms by which PGPR confer protection against plant pathogens. ISR refers to the enhanced defense of a plant against pathogens that is triggered by an initial interaction with beneficial microorganisms, such as PGPR, leading to a plant-wide immune response [14]. This defense response occurs without the need for the pathogen to directly infect the plant, thus enhancing the plant's resistance to subsequent pathogen attacks. The molecular basis of ISR involves the activation of the plant's innate immune system, which includes both local and systemic responses that prepare the plant for future pathogen challenges [39,40].

At the core of ISR is the interaction between PGPR and plant immune receptors, particularly pattern recognition receptors (PRRs) that detect pathogen-associated molecular patterns (PAMPs). PRRs are part of the plant's immune system and are responsible for recognizing conserved microbial features such as flagellin, chitin, or lipopolysaccharides [41,42]. When PGPR interact with plant roots, they often produce signaling molecules, including PAMPs, that are recognized by these receptors. The binding of PGPR-derived PAMPs to PRRs triggers a cascade of signaling events that activate the plant's immune response [14,43]. These events are often mediated by mitogen-activated protein kinase (MAPK) pathways, calcium signaling, and reactive oxygen species (ROS) generation, all of which contribute to the activation of defense genes. This process induces the production of pathogenesis-related (PR) proteins, which include enzymes such as chitinases and glucanases, capable of degrading pathogen cell walls and inhibiting pathogen growth [44,45].

Research has shown that PGPR can activate ISR in many plant species. For example, in *Arabidopsis thaliana*, treatment with *Pseudomonas fluorescens* induces ISR against *Pythium ultimum* by activating genes involved in the defense response [46]. Similarly, in tomato plants, *Bacillus subtilis* application induces ISR, leading to increased resistance to *Fusarium oxysporum* and other soilborne pathogens. The magnitude of ISR activation can vary depending on the PGPR strain, plant species, and pathogen type. Quantitative studies suggest that PGPR application can reduce disease incidence by up to 40% in some crops, providing a robust alternative to chemical pesticide use [47,48].

Another key mechanism by which PGPR protect plants from pathogens is through the production of antimicrobial compounds. These compounds are produced by PGPR as part of their natural defense strategies against competing microorganisms in the rhizosphere [18]. PGPR synthesize a variety of antimicrobial compounds, including antibiotics, enzymes, and VOCs, all of which play a role in pathogen suppression. The production of these compounds is often species-specific, and the effectiveness of PGPR as biocontrol agents can be linked to the types of antimicrobial compounds they produce [49].

Antibiotics produced by PGPR include compounds such as phenazines, which are produced by *Pseudomonas* species, and bacillomycin, produced by *Bacillus* species. These antibiotics are toxic to a broad spectrum of plant pathogens, including fungi, bacteria, and viruses [50]. For example, *Pseudomonas fluorescens* produces phenazines, which inhibit the growth of *Fusarium* spp. and other soilborne pathogens. Similarly, *Bacillus subtilis* produces a range of lipopeptides, including surfactin and iturin, which exhibit strong antifungal activity against pathogens such as *Rhizoctonia solani* and *Alternaria solani* [51]. In addition to antibiotics, PGPR also produce hydrolytic enzymes, such as chitinases, glucanases, and proteases, which break down the cell walls of pathogens and inhibit their growth. Enzyme production is often induced by PAMPs, which are detected by plant PRRs, further enhancing the plant's immune response [52,53].

VOCs are another class of antimicrobial compounds produced by PGPR that play an important role in pathogen suppression. VOCs, including aldehydes, alcohols, ketones, and terpenes, are emitted by PGPR into the surrounding environment and can act in many ways to inhibit pathogen growth [54]. For instance, *Pseudomonas putida* and *Bacillus amyloliquefaciens* produce VOCs such as 2,3-butanediol and acetoin, which inhibit the growth of fungal pathogens such as *Fusarium* spp. and *Botrytis cinerea*. VOCs can also affect the growth of bacterial pathogens by disrupting their cell membranes and inhibiting their ability to form biofilms. The production of these antimicrobial compounds by PGPR represents a key mechanism in their ability to suppress pathogen growth and promote plant health [20,55].

In addition to antimicrobial compound production, PGPR can modulate plant hormone signaling to enhance plant growth and defense responses. Plant hormones, including auxins, cytokinins, and ethylene, play central roles in regulating various aspects of plant growth, development, and stress responses. PGPR can influence the levels and activity of these hormones, thus improving plant health and resistance to pathogens [13,56].

Auxins, such as indole-3-acetic acid (IAA), are among the most important plant hormones involved in regulating root development. PGPR are known to produce IAA, which can promote root growth and increase the plant's ability to absorb water and nutrients [57,58]. Additionally, IAA can influence the plant's defense response by modulating the expression of defense-related genes. For example, *Pseudomonas putida* produces IAA, which enhances root growth and increases the plant's resistance to root pathogens such as *Pythium* spp. and *Rhizoctonia* spp. Cytokinins, another group of plant hormones, are involved in promoting cell division and differentiation [59]. PGPR can produce cytokinins, which enhance plant growth and improve pathogen resistance by modulating the plant's immune response [60]. In *Arabidopsis* plants treated with *Bacillus amyloliquefaciens*, cytokinin production was linked to increased resistance to *Fusarium* spp. by enhancing the expression of defense genes [61].

Ethylene, a plant hormone involved in stress responses and pathogen defense, can also be modulated by PGPR. PGPR can produce ethylene or enhance its production in plants, which in turn activates the plant's defense response against pathogens [62]. For example, *Pseudomonas fluorescens* can stimulate ethylene production in plants, which activates the expression of defense-related genes and increases resistance to various pathogens. Conversely, PGPR can also modulate ethylene levels to prevent overactivation of defense responses that could harm plant growth [63].

Biofilm formation is another critical mechanism through which PGPR suppress plant pathogens and enhance root colonization. Biofilms are clusters of bacteria encased in a self-produced extracellular matrix that protects the bacteria from environmental stressors and enhances their ability to compete with other microorganisms [64]. In the rhizosphere, PGPR form biofilms on plant roots, creating a physical barrier that protects plants from pathogen colonization. This biofilm formation is especially important for soil-borne pathogens, which must invade the root system to cause disease [64]. The formation of biofilms by PGPR allows them to outcompete pathogens for space and nutrients, thereby preventing pathogen establishment.

For example, *Pseudomonas fluorescens* and *Bacillus subtilis* form biofilms that reduce the ability of *Fusarium* spp. and *Rhizoctonia solani* to colonize plant roots [65].

The impact of biofilms extends beyond competition with pathogens. Biofilms also help PGPR maintain a stable and long-lasting presence in the rhizosphere, increasing their effectiveness as biocontrol agents. In addition, biofilms enhance the ability of PGPR to survive under nutrient-limited conditions and help them resist environmental stresses, such as desiccation and changes in pH. Furthermore, biofilm formation by PGPR can stimulate plant immune responses, further enhancing plant resistance to pathogens [66,67].

Conclusively, PGPR utilize a multifaceted array of molecular mechanisms to protect plants from pathogens. These mechanisms include the induction of systemic resistance, production of antimicrobial compounds, modulation of plant hormone signaling, and biofilm formation [13]. Each of these mechanisms contributes to enhanced pathogen resistance, reduced disease symptoms, and growth maintenance. Understanding these mechanisms is essential for optimizing PGPR use in agricultural systems to provide a sustainable alternative to chemical pesticides and contribute to the overall health and productivity of crops [39,68]. As research continues to uncover the complexity of PGPR interactions with plants and pathogens, these beneficial microorganisms will likely play an increasingly important role in integrated pest management strategies and sustainable agricultural practices worldwide [69].

3 Cellular Mechanisms of PGPR in Plant-Pathogen Interaction

The cellular mechanisms through which PGPR mediate plant-pathogen interactions are a fundamental area of study in plant biology, as they offer insights into how beneficial microorganisms can protect plants from a variety of pathogens. These mechanisms involve complex signaling pathways, interactions with the plant's immune system, and modifications to the root environment, which enhance plant resistance to soil-borne pathogens [18,70]. Specifically, PGPR initiates pathogen suppression through various cellular mechanisms. Upon recognition of PAMPs by plant receptors, several defense responses are activated, including MAPK signaling, calcium signaling, and ROS production. These responses trigger the induction of systemic resistance, which enhances plant immunity across the whole plant [71]. Additionally, PGPR directly inhibit pathogen growth and compete for resources in the rhizosphere. The ability of PGPR to improve plant health is underpinned by their influence on plant immune signaling, enhancement of root defense mechanisms, and modulation of the rhizosphere microbiome. These interactions collectively contribute to plant growth promotion and disease suppression, providing a sustainable alternative to chemical pesticides and fertilizers (Table 1) [72,73].

PGPR strains have demonstrated significant potential in managing various plant diseases by targeting diverse pathogens and employing multiple mechanisms of action. For instance, *Pseudomonas fluorescens* effectively controls soilborne pathogens like *Ralstonia solanacearum*, *Rhizoctonia solani*, in *Fusarium ox-ysporum* in tomatoes by producing antibiotics (phenazines), excluding pathogens competitively, and activating systemic resistance [74]. Similarly, *Bacillus amyloliquefaciens* suppresses bacterial and fungal pathogens such as *Botrytis pelargonii* and *Alternaria alternata* in crops like peppers, thus reducing disease severity by up to 50% through lipopeptide production, systemic resistance induction, and niche competition [74,75]. Other notable rhizobacteria include *Bacillus*, *Pseudomonas*, and *Serratia* lead to disease reduction in potatoes against *Phytophthora infestans* through antibiosis, and, indirectly, through the induction of plant defense systems [76]. Additionally, strains like *Bacillus velezensis* (SM-39), and *Bacillus cabrialesii* (SM-93) demonstrate effective pathogen control against *Fusarium* spp., *Macrophomina phaseolina*, and *Rhizoctonia solani* in *Triticum aestivum* [77]. *Pseudomonas* strain IALR1619 also exhibit significant reductions in disease severity, leveraging antifungal compound production, suppress *Pythium ultimum* in *Cucumis sativus* [78]. Collectively, these PGPR strains exemplify the promise of eco-friendly alternatives

to chemical pesticides, offering sustainable solutions for integrated pest management by reducing disease severity and promoting plant health.

Table 1: Summary of plant growth-promoting rhizobacteria (PGPR) strains and their effectiveness against plant pathogens

PGPR strain	Target pathogen(s)	Crop(s)	Mechanisms of action	Reference
<i>Pseudomonas fluorescens</i> VSMKU3054	<i>Ralstonia solanacearum</i> , <i>Rhizoctonia solani</i> , <i>Fusarium oxysporum</i>	<i>Lycopersicon esculentum</i>	Antibiotic production (phenazines), competition, systemic resistance activation	Suresh et al. 2021 [74]
<i>Bacillus amyloliquefaciens</i>	<i>Botrytis pelargonii</i> , <i>Alternaria alternata</i>	<i>Capsicum annuum</i>	Hydrolytic enzymes, Lipopeptide production, systemic resistance induction, space competition	Kazerooni et al. 2021 [75]
<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Rahnella</i> , and <i>Serratia</i>	<i>Phytophthora infestans</i>	<i>Solanum tuberosum</i>	Antibiosis, and (or) indirectly, through the induction of plant defense systems	Daayf et al. 2003 [76]
<i>Bacillus velezensis</i> (SM-39), <i>Bacillus cabrialesii</i> (SM-93)	<i>Fusarium</i> spp., <i>Macrophomina phaseolina</i> , and <i>Rhizoctonia solani</i>	<i>Triticum aestivum</i>	Production of antibiotics, competition, biofilm formation	Mulk et al. 2022 [77]
<i>Pseudomonas</i> strain IALR1619	<i>Pythium ultimum</i>	<i>Cucumis sativus</i>	Antagonism via VOCs, competition, siderophore production	Amaradasa et al. 2024 [78]
<i>Bacillus subtilis</i> , <i>Pseudomonas aeruginosa</i>	<i>Rhizoctonia solani</i> , <i>Fusarium oxysporum</i>	<i>Lycopersicon esculentum</i>	Root growth induction, nutrient uptake improvement, catalase enzyme, lipase enzyme and indole acetic acid production	Akintokun et al. 2016 [79]
<i>Bacillus pumilus</i>	<i>Fusarium</i> spp., <i>Rhizoctonia</i> spp.	<i>Glycine max</i>	Lipopeptide and siderophore production, root colonization competition	Dobrzynski et al. 2023 [80]
<i>Bacillus Amyloliquefaciens</i> , <i>Bacillus Pumilus</i>	<i>Fusarium oxysporum</i>	<i>Oryza sativa</i>	Expression of defense-related genes. Modulates microbial community structures, enhances microbial network stability, and boosts the resistance of rice seedlings against blight	Jiang et al. 2024 [81]
<i>Pseudomonas chlororaphis</i>	<i>Pythium aphanidermatum</i>	<i>Solanum lycopersicum</i>	Organic amendments to enhance sustainability of growing media such as potting soil by increasing its disease suppressiveness	Postma et al. 2019 [82]
<i>Bacillus velezensis</i> X5-2, <i>Bacillus megaterium</i> X6-3, <i>Pseudomonas orientalis</i> X2-1P <i>Bacillus subtilis</i>	<i>Xanthomonas campestris</i> pv. <i>campestris</i> (Xcc)	<i>Brassica napus</i>	The isolates act against pathogen via secondary metabolites, produces phenazine-1-carboxylic acid, benzoic acid, organic compounds and lipopeptides	Jelusic et al. 2021 [83]
<i>Bacillus subtilis</i>	<i>Alternaria solani</i>	<i>Solanum tuberosum</i>	Plant immunity induction, strong antifungal activity, antifungal compound production, competition	Zhang et al. 2020 [84]
<i>Bacillus velezensis</i> LBUM279, <i>Bacillus subtilis</i> LBUM979	<i>Botrytis cinerea</i>	<i>Cannabis sativa</i> L.	Hydrolytic enzyme and antibiotic production, competition	Balthazar et al. 2022 [85]

The plant immune system plays a crucial role in recognizing and responding to pathogen attack. When plants are exposed to pathogens, they rely on sophisticated signaling pathways to activate defense responses that inhibit pathogen growth and limit infection [86]. One of the most well-established pathways involved in plant immune responses is the mitogen-activated protein kinase (MAPK) cascade. MAPKs are a family of enzymes that transduce external signals into a range of intracellular responses, ultimately leading to the activation of genes that promote plant defense [87]. When PGPR are introduced to plants, they can trigger MAPK signaling pathways by delivering microbe-associated molecular patterns (MAMPs), such as flagellin or chitin, which are recognized by the plant's PRRs. This recognition initiates a signaling cascade that activates a broad array of defense mechanisms, including ROS production, defense-related protein synthesis, and SAR induction [88,89].

In addition to MAPK signaling, calcium signaling is another essential mechanism that mediates plant immune responses. The interaction between PGPR and plant roots can lead to calcium ion (Ca^{2+}) elevation in plant cells, which acts as a secondary messenger in plant immune signaling [90]. Increased cytosolic Ca^{2+} levels activate various downstream signaling components, including calcium-dependent protein kinases (CDPKs), which in turn activate further immune responses. Calcium signaling is particularly important in the activation of genes involved in pathogen defense, such as those encoding PR proteins, antimicrobial compounds, and cell wall-modifying enzymes. For instance, *Pseudomonas fluorescens* stimulates calcium influx in plant roots, which enhances plant resistance to pathogens like *Pythium* spp. and *Rhizoctonia solani* [91,92].

ROS, including hydrogen peroxide (H_2O_2) and superoxide anions (O_2^-), are another class of signaling molecules that play a pivotal role in plant defense. PGPR can trigger ROS generation in plants as part of the initial immune response to pathogen invasion. ROS not only act as signaling molecules to activate further defense responses, but they also have direct antimicrobial properties that help limit pathogen growth [93]. ROS accumulation in plant cells creates an oxidative burst, which is associated with pathogen growth inhibition through membrane damage and enzyme inactivation. Additionally, ROS are involved in cell wall reinforcement through the cross-linking of lignin and other cell wall components, thus fortifying the plant's physical defenses [94]. In *Arabidopsis thaliana* treated with *Bacillus subtilis*, ROS production has been linked to enhanced resistance to *Fusarium oxysporum* and *Botrytis cinerea*, demonstrating the role of ROS in PGPR-mediated pathogen defense [95].

Cross-talk between PGPR and plant immune systems further amplifies plant resistance to pathogens. PGPR can induce both local and systemic immune responses in plants, which are coordinated by intricate networks of signaling pathways [89]. For example, when PGPR such as *Pseudomonas fluorescens* or *Bacillus subtilis* interact with plant roots, they activate a combination of local responses at the infection site and systemic responses throughout the plant [96]. This interaction primes the plant to respond more rapidly and effectively to subsequent pathogen attacks. Studies have shown that PGPR can induce both PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI) in plants, which are two complementary arms of the immune system. PTI is triggered by the recognition of conserved microbial signatures, such as flagellin, while ETI is activated when the plant detects specific microbial effectors that are secreted and enter plant cells. The simultaneous activation of both PTI and ETI results in a stronger and more coordinated immune response, allowing the plant to fend off a broader range of pathogens [14,97].

PGPR-mediated root defense is another critical aspect of their ability to protect plants from soil-borne pathogens. The root system is often the first site of pathogen attack, as soilborne pathogens must infiltrate the root tissues to cause disease [98]. PGPR can enhance root defense through several mechanisms, including resource competition, antimicrobial compound secretion, and root environment modification. One of the most important roles of PGPR in root defense is their ability to outcompete pathogens for space and

nutrients in the rhizosphere, thus preventing pathogen colonization [14,29]. For instance, *Bacillus subtilis* and *Pseudomonas fluorescens* are known to produce antifungal metabolites and compete with pathogens such as *Fusarium* spp. and *Rhizoctonia solani* for available niches in the root zone [96].

Furthermore, PGPR can improve root health by promoting root growth and development, which enhances the plant's ability to resist pathogen attack. PGPR promote root growth through the production of phytohormones, including auxins, cytokinins, and gibberellins [18]. These hormones stimulate cell division, elongation, and differentiation in root tissues, leading to the development of a more extensive root system. A larger root mass increases the plant's ability to take up water and nutrients, making it more resistant to drought and nutrient stress, which are often predisposing factors for pathogen infection [99,100]. Moreover, enhanced root growth enables plants to maintain better root health, reducing their susceptibility to root-borne pathogens. In *Arabidopsis* and tomato plants treated with *Pseudomonas* and *Bacillus* strains, root growth was significantly enhanced, resulting in increased resistance to root rot diseases caused by *Pythium* and *Fusarium* species [101,102].

The rhizosphere is a dynamic environment that hosts a diverse microbial community, including both beneficial and harmful microorganisms. PGPR play a pivotal role in shaping the rhizosphere microbiome, which in turn influences plant health and disease resistance. PGPR can alter the composition and diversity of the rhizosphere microbiota by promoting the growth of beneficial microorganisms while inhibiting the growth of pathogens [18,103]. One of the key ways PGPR influence the rhizosphere microbiome is by producing antimicrobial compounds that selectively inhibit pathogen growth. This antagonistic interaction between PGPR and harmful pathogens helps maintain a balanced microbial community in the rhizosphere, thereby preventing harmful pathogens from dominating [29]. For example, *Bacillus amyloliquefaciens* produces lipopeptides, which inhibit the growth of *Fusarium oxysporum* and *Rhizoctonia solani*, while promoting the growth of beneficial bacteria that support plant growth [104].

PGPR also interact with other beneficial microorganisms, such as mycorrhizal fungi and nitrogen-fixing bacteria, to enhance plant health. Mycorrhizal fungi form symbiotic relationships with plant roots, improving nutrient uptake, particularly phosphorus, while also enhancing pathogen resistance through the production of antifungal compounds [105]. PGPR can facilitate these symbiotic relationships by promoting mycorrhizal colonization of plant roots and stimulating the production of mycorrhizal spores [106]. Similarly, PGPR can interact with nitrogen-fixing bacteria, such as *Rhizobium* spp., which form nodules on legume roots and provide essential nitrogen to the plant. These interactions between PGPR, mycorrhizal fungi, and nitrogen-fixing bacteria enhance plant growth and resistance to pathogens, contributing to overall plant health and ecosystem stability [107].

Antagonistic interactions between PGPR and harmful pathogens are a key feature of PGPR's role in plant disease suppression. PGPR not only compete with pathogens for space and nutrients but also directly suppress pathogen growth through the production of antimicrobial compounds, VOCs, and enzymes [108]. These interactions have been studied extensively regarding soilborne pathogens, where PGPR such as *Pseudomonas fluorescens* and *Bacillus subtilis* have been shown to reduce pathogen colonization and suppress disease symptoms. For example, *Pseudomonas fluorescens* produces phenazines, which inhibit the growth of *Fusarium* spp., while *Bacillus subtilis* secretes iturin, which suppresses the growth of *Rhizoctonia solani* [109]. These antagonistic interactions are often complemented by the PGPR's ability to induce plant immune responses, further enhancing disease resistance [108,110].

Thus, PGPR exert their beneficial effects on plants through a variety of cellular mechanisms that involve intricate interactions with the plant's immune system as well as rhizosphere microbiome modulation and root defense enhancement. The ability of PGPR to trigger immune signaling pathways, promote root health, and outcompete pathogens in the rhizosphere is central to their role in plant pathogen control [111,112].

Understanding these cellular mechanisms at a deeper level provides valuable insights into how PGPR can be utilized as a sustainable and effective tool for enhancing plant health and managing plant diseases. Continued research into PGPR-mediated mechanisms of pathogen control will lead to more targeted and efficient applications of PGPR in agriculture, ultimately contributing to the development of more resilient and sustainable agricultural systems [113].

4 Ecological and Environmental Benefits of PGPR Application

The application of PGPR in agriculture offers numerous ecological and environmental benefits that are increasingly recognized as essential for promoting sustainable farming practices. PGPR provide a promising alternative to chemical inputs, contributing to a reduction in the reliance on chemical pesticides and fertilizers [114,115]. By fostering plant growth, enhancing disease resistance, and improving soil health, PGPR help maintain or even increase crop productivity while minimizing negative environmental impacts. The integration of PGPR into agricultural systems holds significant promise for addressing pressing environmental concerns such as soil degradation, water contamination, and the loss of biodiversity, thereby contributing to long-term ecosystem stability [116,117].

One of the primary benefits of PGPR application is the reduction of chemical inputs in agricultural systems. Chemical pesticides and fertilizers have long been the mainstay of modern agriculture, helping to protect crops from pests and diseases while ensuring high yields [118]. However, the widespread and excessive use of these chemicals has led to several environmental issues, including soil degradation, water contamination, and the development of pesticide resistance in pathogens and pests. PGPR offer an eco-friendly alternative to these chemicals by enhancing plant health, promoting nutrient uptake, and protecting crops from pathogens naturally [119]. For instance, PGPR such as *Pseudomonas fluorescens* and *Bacillus subtilis* reduce the need for chemical pesticides by inducing systemic resistance in plants and outcompeting pathogens in the rhizosphere. Studies have demonstrated that PGPR use can lead to a reduction in pesticide application by up to 30%–50%, thus decreasing the environmental burden associated with pesticide use [120,121].

The environmental impact of reduced pesticide use is significant, particularly in terms of improving soil and water quality. Pesticide runoff from agricultural fields is a major source of water pollution, affecting aquatic ecosystems and contaminating drinking water sources [122]. The accumulation of pesticides in the soil can also disrupt soil microbial communities, leading to a decline in soil fertility and the development of resistant pest populations. By reducing the need for chemical pesticides, PGPR helps mitigate these environmental risks [123]. PGPR application has been associated with improved soil health, including increased microbial diversity and activity, which are essential for maintaining soil fertility and structure. For example, PGPR such as *Rhizobium* spp. and *Azospirillum* spp. promote nitrogen fixation in the soil, reducing the need for synthetic nitrogen fertilizers [18]. This not only reduces the environmental footprint of agriculture but also promotes the sustainability of farming systems by enhancing nutrient cycling and improving soil organic matter content [124].

PGPR also contributes significantly to sustainable agricultural practices, such as organic farming and integrated pest management (IPM). In organic farming, the use of synthetic chemical inputs is restricted, and PGPR can serve as valuable tools for managing plant diseases, improving nutrient availability, and promoting plant growth without resorting to chemical fertilizers or pesticides [125]. For instance, *Trichoderma* spp., a well-known PGPR, has been used extensively in organic farming systems to control soilborne pathogens and improve plant growth. In IPM systems, PGPR are often integrated with other biocontrol agents, such as natural predators or parasitoids, to provide a holistic approach to pest and disease management [108]. The use of PGPR in these systems not only reduces the reliance on chemical inputs but also promotes the

health and stability of agroecosystems by maintaining a balanced microbial community and enhancing plant resilience to environmental stress [126].

The role of PGPR in promoting sustainable agriculture goes beyond disease control and nutrient management. PGPR also plays a crucial role in improving soil health, which is fundamental for the long-term sustainability of agricultural systems. By enhancing the activity of beneficial soil microorganisms, PGPR contributes to the overall health of the rhizosphere, promoting the decomposition of organic matter, enhancing nutrient cycling, and improving soil structure [127,128]. For example, PGPR such as *Bacillus amyloliquefaciens* and *Pseudomonas putida* stimulate the activity of soil enzymes involved in the breakdown of organic materials, which helps recycle nutrients and improve soil fertility. Additionally, PGPR application increases soil organic carbon content and improves soil aggregation, both of which are critical for maintaining soil structure and preventing erosion [121].

The long-term benefits of PGPR for ecosystem stability are also evident in their ability to promote biodiversity. Biodiversity is essential for the resilience and functioning of ecosystems, as it enhances ecosystem services such as pollination, pest control, and nutrient cycling. PGPR application has been shown to have positive effects on soil biodiversity, particularly by promoting the growth of beneficial microorganisms and enhancing microbial community structure [26]. PGPR can alter the composition of the rhizosphere microbiome by stimulating the growth of beneficial bacteria and fungi while suppressing the growth of harmful pathogens [29]. For example, *Pseudomonas* spp. increases the diversity of soil bacteria by promoting the growth of other beneficial microbes and suppressing pathogenic species such as *Fusarium* spp. and *Rhizoctonia solani*. This shift in microbial community composition can enhance plant health and resilience to disease, contributing to the overall biodiversity of the soil ecosystem [18].

The impact of PGPR on soil biodiversity goes beyond bacteria and fungi because it can also influence the abundance and diversity of other soil organisms, such as earthworms and nematodes, which play key roles in soil health and nutrient cycling [129]. Studies have shown that PGPR application can increase earthworm populations, which in turn improve soil structure and nutrient availability. PGPR such as *Bacillus subtilis* have been shown to stimulate the growth of beneficial nematodes, which help control root-damaging pests and enhance soil health. By promoting the activity and diversity of these soil organisms, PGPR contributes to the overall health and resilience of soil ecosystems, enhancing their capacity to withstand environmental stresses such as drought or pathogen invasion [130,131].

Beyond the rhizosphere, PGPR also promote biodiversity at the ecosystem level. By enhancing plant health and promoting sustainable agricultural practices, PGPR help maintain the balance of ecosystems, including agroecosystems, wetlands, and forest ecosystems [132]. For example, PGPR can enhance the establishment and growth of native plants in disturbed ecosystems, such as agricultural fields or degraded lands, thereby contributing to habitat restoration and ecosystem recovery [133]. The increased plant growth resulting from PGPR application can also lead to enhanced carbon sequestration, further contributing to ecosystem stability by mitigating climate change. In agroecosystems, PGPR can help maintain biodiversity by reducing the need for chemical inputs, which can harm non-target species such as pollinators, birds, and beneficial insects [134].

The contribution of PGPR to ecosystem balance and resilience is particularly important regarding climate change, which poses significant challenges to agriculture and biodiversity. Climate change is expected to exacerbate the frequency and intensity of extreme weather events, such as droughts, floods, and temperature extremes, which can severely affect crop productivity and ecosystem functioning [135]. PGPR can help mitigate the impacts of these stresses by enhancing plant resilience to environmental fluctuations and improving soil health. By promoting drought tolerance, improving nutrient availability, and enhancing pathogen resistance, PGPR can help plants withstand the negative effects of climate change,

thus contributing to the resilience of agricultural systems and ecosystems [136,137]. The ecological and environmental benefits of PGPR application are profound and multifaceted. By reducing the reliance on chemical pesticides and fertilizers, PGPR help mitigate the environmental risks associated with conventional agricultural practices, including water contamination, soil degradation, and pesticide resistance [101]. The use of PGPR in sustainable farming systems contributes to the health of the soil ecosystem by promoting biodiversity, enhancing nutrient cycling, and improving soil structure [138]. Moreover, PGPR play a crucial role in promoting long-term ecosystem stability by enhancing plant health, reducing the environmental impact of farming, and contributing to the resilience of ecosystems in the face of climate change [139]. The integration of PGPR into agricultural systems offers a promising pathway for achieving more sustainable and environmentally friendly agricultural practices, ensuring food security and ecosystem health for future generations [140].

5 PGPR in Pathogen Control for Major Crops

PGPR have emerged as a significant tool for managing plant pathogens across various crops, offering both direct and indirect benefits in pathogen control. These beneficial microorganisms play a critical role in protecting crops against soil-borne and foliar pathogens, as well as in enhancing disease resistance in perennial crops and those vulnerable to climate change-induced stresses [141]. The integration of PGPR into agricultural systems offers a sustainable alternative to chemical pesticides, thus reducing environmental impacts while promoting plant health and ecosystem stability. Their application has proven effective in managing major plant diseases caused by fungi, bacteria, and viruses, demonstrating their broad utility across different crop types and environmental conditions [137,142].

PGPR have shown significant efficacy in the control of soil-borne pathogens. Soil-borne pathogens like *Fusarium* spp., *Pythium* spp., and *Rhizoctonia solani* are responsible for considerable crop losses, particularly in crops such as tomatoes, cucumbers, and rice. PGPR can suppress the growth of these pathogens through several mechanisms, including the production of antibiotics, competition for nutrients and space, and the induction of systemic resistance in plants [143]. For instance, *Pseudomonas fluorescens* has been extensively studied for its ability to control Fusarium wilt in tomatoes and cucumbers. For example, one field study demonstrated a 40–60% reduction in disease severity in tomato plants treated with *P. fluorescens* compared to that of the untreated controls [144]. This reduction in disease incidence is primarily attributed to the antibiotic production by *P. fluorescens*, including phenazines and 2,4-diacetylphloroglucinol, which directly inhibit the growth of *Fusarium* spp. [145]. Similarly, *Bacillus subtilis* has been successfully used to control *Rhizoctonia solani* in soybean and rice, with reductions in root rot symptoms of up to 50%. These PGPR outcompete the pathogen for space and nutrients, while also producing lipopeptides that have direct antifungal activity [146].

PGPR also play a crucial role in controlling foliar pathogens, which are responsible for a variety of destructive diseases in crops. Foliar pathogens, such as *Xanthomonas* spp. (causing bacterial spot), *Phytophthora infestans* (causing late blight), and downy mildew, can cause severe damage to crops like tomatoes, peppers, and potatoes [21]. The use of PGPR in managing these diseases has proven highly effective in reducing reliance on chemical pesticides. For example, *Bacillus subtilis* has been widely applied for managing bacterial leaf spot caused by *Xanthomonas* spp. in peppers and tomatoes [109]. In a field trial, the application of *B. subtilis* led to a 30%–50% reduction in bacterial spot incidence, significantly lowering the need for chemical bactericides. In addition to its direct antibacterial activity, *B. subtilis* also enhances plant immune responses, priming the plant for a quicker and more robust response to pathogen attack [147]. Similarly, *Trichoderma harzianum*, a well-known PGPR, has been used to control *Phytophthora infestans*, the causal agent of late blight in potatoes and tomatoes. Specifically, *T. harzianum* competes with

the pathogen for space on the leaf surface and produces hydrolytic enzymes that degrade the pathogen's cell wall, effectively reducing disease severity. Additionally, the use of PGPR to manage foliar pathogens not only reduces disease incidence but also promotes plant growth by enhancing nutrient availability and improving overall plant health.

In perennial crops, PGPR enhance disease resistance, making them a valuable tool in the management of long-lived crops such as fruit trees, vines, and woody perennials. Perennial crops are particularly vulnerable to repeated pathogen infections due to their long life cycle, making effective pathogen control crucial for maintaining productivity [148]. For example, in grapevines, *Pseudomonas putida* and *Bacillus amyloliquefaciens* have been used to reduce *Phytophthora* spp. infections, a common cause of root rot. In field trials, the application of these PGPR resulted in a 25%–40% reduction in disease incidence, improving both plant health and yield [149]. In apple orchards, *Bacillus subtilis* has been employed to control *Venturia inaequalis*, the fungus responsible for apple scab. A study showed that *B. subtilis* applications reduced apple scab severity by up to 50%, leading to healthier trees and higher fruit yield. Thus, PGPR not only protect against pathogens but also promote plant growth, improve nutrient uptake, and enhance the overall health of perennial crops, which is crucial for their long-term productivity and resilience [150].

The role of PGPR in controlling pathogens in crops affected by climate change-induced stress is becoming increasingly important. Climate change is expected to intensify the frequency and severity of extreme weather events, such as droughts, floods, and temperature extremes, which can weaken plant defenses and exacerbate pathogen susceptibility [151]. PGPR offer a promising solution to mitigate the effects of these stresses, while also improving plant resilience to pathogen outbreaks. For example, *Azospirillum brasilense* and *Bacillus* spp. have been used to enhance drought tolerance in crops like maize and wheat. In maize, *Bacillus* spp. significantly improved root development and water uptake, leading to a 20%–30% increase in plant growth under water-limited conditions [152]. Similarly, *B. pumilus* improved wheat growth under heat stress, reducing yield losses by approximately 25% compared to that of the non-inoculated plants. These PGPR not only enhance drought tolerance but also help reduce pathogen infections that tend to proliferate under stressed conditions [153]. In one study, *Pseudomonas fluorescens* reduced the severity of *Fusarium* spp. infections in wheat plants exposed to heat stress, with a 30%–40% reduction in disease symptoms compared to that of the untreated controls [154].

PGPR also contribute to pathogen control by enhancing plant immune responses under abiotic stress conditions [155]. The ability of PGPR to induce SAR and ISR in plants enhances the plant's ability to resist pathogens even during environmental stresses. For example, *Pseudomonas fluorescens* and *Bacillus subtilis* can prime plants to activate their defense mechanisms more rapidly upon pathogen attack, thereby improving disease resistance [156]. In a study on soybean, *B. subtilis* application led to a 50% reduction in *Fusarium* root rot under drought conditions, demonstrating the combined effect of PGPR in both stress tolerance and disease control [157].

Finally, PGPR offer significant benefits for pathogen control across major crops, ranging from soil-borne pathogens such as *Fusarium* and *Rhizoctonia* to foliar disease-causing pathogens like *Xanthomonas* and *Phytophthora infestans* [158]. Through mechanisms such as nutrient competition, antimicrobial compound production, and plant immunity induction, PGPR reduce the incidence and severity of diseases, leading to improved plant health and higher yields (Fig. 3). PGPR application has been shown to improve both crop yields and pathogen management in several crops [159]. Fig. 3 illustrates the impact of PGPR on crop yield and disease severity. The application of PGPR in perennial crops helps protect against long-term infections and promotes resilience in fruit trees, vines, and other long-lived crops. Moreover, PGPR is a valuable tool for managing crops affected by climate change-induced stresses, improving drought tolerance, and mitigating pathogen outbreaks under extreme weather conditions [148,160]. As research continues to

uncover the full potential of PGPR in pathogen control, their widespread adoption in sustainable agriculture will contribute to the development of more resilient and environmentally friendly farming systems, thereby reducing reliance on chemical pesticides and improving crop productivity.

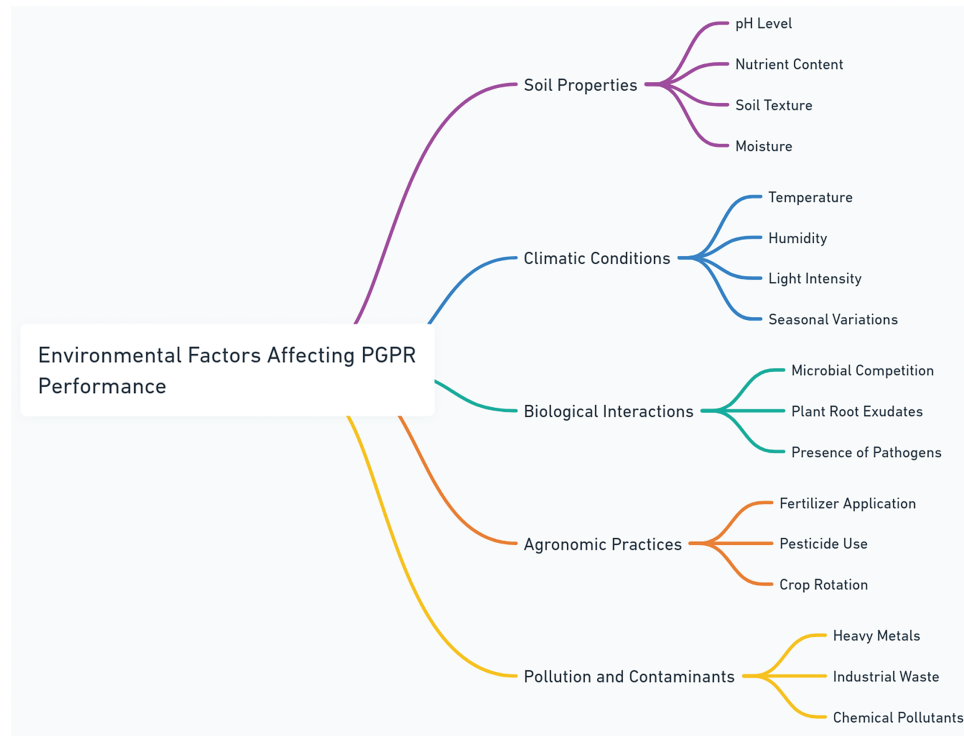


Figure 3: The performance of plant growth-promoting rhizobacteria (PGPR)-based treatments is influenced by various environmental conditions

6 Challenges and Limitations in PGPR Application

While PGPR offer promising solutions for pathogen control and sustainable agriculture, there are several challenges and limitations in their widespread application. These challenges range from variability in efficacy to difficulties in scaling up production and overcoming regulatory barriers. Understanding these limitations is essential for optimizing PGPR use in agricultural systems and ensuring that their benefits are realized in diverse field conditions [108,161].

One of the primary challenges in PGPR application is the variability in their efficacy across different environments (Fig. 3). Environmental factors, including soil pH, temperature, and moisture levels, influence PGPR performance [162]. Fig. 3 presents a mind-map summarizing these factors and their impact on PGPR efficacy.

Environmental conditions such as temperature, humidity, and soil pH can significantly impact the survival and activity of PGPR in the field (Table 2). For instance, PGPR strains that thrive in temperate climates may not perform well in tropical or arid environments [163]. In a study on *Pseudomonas fluorescens* application to control Fusarium wilt in tomatoes, the treatment efficacy varied by region, with a 40% reduction in disease severity in temperate climates but only a 15% reduction in tropical climates. Similarly, soil properties such as texture, organic matter content, and pH can influence the effectiveness of PGPR [144]. Soils with low organic matter or high salinity may not support the growth of certain PGPR strains, leading to

reduced pathogen suppression. For example, in saline soils, the performance of *Bacillus subtilis* in controlling *Rhizoctonia solani* was significantly lower, with a 20% reduction in disease severity compared to a 50% reduction in non-saline soils [164].

Table 2: Environmental and soil factors affecting PGPR efficacy

Environmental /Soil factor	Impact on PGPR efficacy	Example	Reference
Soil type	Soil texture and structure affect PGPR colonization and activity. Loamy soils typically support better PGPR growth compared to sandy or clay-rich soils.	PGPR efficacy reduced in compacted, clay-rich soils.	Adeniji et al. 2024 [165]
Soil pH	PGPR efficacy is often pH-dependent, with most strains preferring neutral or slightly acidic conditions. Extreme pH levels (either acidic or alkaline) can inhibit PGPR activity.	<i>Bacillus amyloliquefaciens</i> was evaluated under low pH and compared to its activity in neutral pH.	Chowdhury et al. 2022 [166]
Temperature	PGPR strains have optimal temperature ranges. High or low temperatures can reduce microbial survival and activity. Extreme heat or cold can significantly reduce their biocontrol effectiveness.	<i>Bacillus subtilis</i> XZ18-3 is most effective at 25°C–30°C.	Yi et al. 2022 [167]
Soil moisture	Adequate moisture is essential for PGPR activity. High moisture promotes PGPR survival and pathogen suppression, while drought can hinder their colonization and pathogen management.	PGPR efficacy increased under moderate moisture.	Liu et al. 2022 [168]
Soil salinity	High salinity stresses PGPR, reducing their colonization and activity. PGPR adapted to saline conditions can still be effective under moderate salinity stress.	<i>Pseudomonas putida</i> reduced Fusarium wilt severity in saline soils.	Ahmad et al. 2024 [169]
Organic matter content	Soils rich in organic matter support greater PGPR colonization by providing nutrients and favorable conditions. Low organic matter reduces PGPR viability and pathogen control.	PGPR were more effective in soils with high organic content.	Das et al. 2014 [170]
UV radiation	High UV radiation negatively impacts the survival and effectiveness of PGPR, particularly those applied to the surface. PGPR formulations often include protectants like UV-absorbing compounds to improve stability.	PGPR strains like <i>Bacillus subtilis</i> are more stable when encapsulated.	Balla et al. 2022 [171]

While the efficacy of PGPR is often influenced by environmental conditions, several strategies can be employed to mitigate these challenges including microencapsulation and controlled-release formulations. In microencapsulation, PGPR are encapsulated in protective coatings, has been shown to enhance the survival and activity of PGPR under stressful environmental conditions [172,173]. This technique offers protection from UV radiation, extreme temperatures, and soil desiccation, ensuring that PGPR can persist in the rhizosphere and maintain pathogen-suppressing activity. Additionally, controlled-release formulations (CRFs) allow for the gradual release of PGPR over time, providing sustained protection against pathogens and improving the long-term efficacy of PGPR applications. These formulations also help to synchronize PGPR activity with the plant's growth cycle, further optimizing their performance [174,175].

Plant pathogen diversity also complicates PGPR use in pathogen control. Different PGPR strains exhibit varying levels of effectiveness against different pathogens. While some PGPR are effective against a wide range of pathogens, others are more specific in their activity [137]. For example, *Trichoderma harzianum* suppresses a wide range of fungal pathogens, including *Phytophthora infestans* and *Fusarium oxysporum*, but may not be effective against bacterial pathogens such as *Xanthomonas* spp. [176]. In contrast, *Pseudomonas fluorescens* is more effective against bacterial pathogens but may offer limited control over fungal diseases. The strain-specific nature of PGPR means that choosing the right PGPR for the target pathogen is crucial for successful disease management [177]. Additionally, environmental stress factors, such as drought, may reduce the effectiveness of PGPR by impairing their ability to induce systemic resistance in plants. Thus, the variability in PGPR efficacy highlights the need for tailored approaches that take into account environmental and pathogen-specific factors [137].

Another major challenge in the widespread use of PGPR in agriculture is the scaling up of production and PGPR application on a commercial scale [178]. The mass production of PGPR strains that are effective, stable, and economically viable remains a significant hurdle. While PGPR can be cultured in laboratory settings, scaling up production to meet the demands of large-scale agricultural use requires considerable investment in infrastructure, technology, and resources [179]. The cost of producing PGPR at a commercial scale is often high, and the quality of the product can vary between batches. For example, a study on the mass production of *Bacillus subtilis* for use in tomato disease control found that while the product was effective at small-scale trials, large-scale production led to inconsistent results, with some batches showing reduced efficacy due to variations in microbial concentration and formulation stability [162,180].

The formulation of PGPR products also poses challenges. PGPR formulations must be stable under varying environmental conditions, such as changes in temperature, humidity, and soil pH. Many PGPR strains are sensitive to desiccation, UV radiation, and extreme temperatures, which can compromise their viability during storage and application [181]. For instance, *Pseudomonas fluorescens* strains may lose up to 50% of their viability when stored for extended periods at ambient temperatures. To ensure the stability of PGPR formulations, protective agents such as cryoprotectants, stabilizers, and encapsulation techniques are often used [182]. However, these add to the cost of production and may not always provide long-term stability, particularly in the field where conditions can fluctuate. Inconsistent formulations and reduced stability can undermine the efficacy of PGPR-based treatments, leading to poor results when applied to crops [183].

In addition to these technical challenges, there are significant regulatory and commercialization barriers that hinder the widespread adoption of PGPR in agriculture. Regulatory frameworks for PGPR-based biocontrol agents vary widely across regions, and many countries do not have established guidelines for their registration and use [162]. Unlike chemical pesticides, which are subject to extensive regulation and testing, PGPR products are often considered to be "natural" and may not fall under the same regulatory scrutiny. This lack of clear regulatory standards can create uncertainty for producers and consumers alike. For instance, in

some regions, PGPR products may not be registered as biocontrol agents, which limits their market access and restricts their use in commercial agriculture [183,184].

The regulatory process for registering PGPR-based products can also be lengthy and expensive. In the European Union, for example, the registration of biocontrol products can take several years and require extensive testing to ensure safety and efficacy [185]. This regulatory delay can prevent farmers from accessing effective PGPR treatments in a timely manner, particularly when facing an outbreak of a plant pathogen. Moreover, the cost of registration and testing can be prohibitive for small-scale producers, limiting the availability of PGPR products on the market [186]. The lack of standardized guidelines for PGPR also presents challenges in ensuring the quality and consistency of PGPR products. Without clear regulations, manufacturers may produce substandard products that fail to meet efficacy and safety standards, undermining consumer confidence in PGPR as a viable biocontrol solution [187].

In addition to regulatory challenges, economic and market barriers further complicate the commercialization of PGPR products. Despite the growing demand for sustainable agricultural practices, the market for PGPR-based biocontrol agents remains a niche, with limited consumer awareness and acceptance [185]. Farmers may be hesitant to adopt PGPR-based products due to concerns about their effectiveness, ease of use, and cost compared to that of conventional chemical pesticides. Additionally, the upfront costs of PGPR products may be higher than those of synthetic chemicals, particularly for small-scale farmers who may not see immediate returns on their investment [188]. Furthermore, the lack of widespread education and training on the use of PGPR in agriculture can limit their adoption. For instance, in some regions, farmers may lack awareness of PGPR-based treatments and may continue to rely on chemical inputs due to established practices and marketing efforts by pesticide companies [189]. Overcoming these economic and market barriers requires not only greater awareness and education but also the development of cost-effective and user-friendly PGPR products that can compete with traditional chemical inputs [190].

7 Future Directions and Outlook

The future of PGPR as biocontrol agents and agricultural tools is promising, with several areas of research requiring further exploration to optimize their use in diverse agricultural systems. Advances in PGPR strain selection, integration with other biocontrol strategies, applications in precision agriculture, and the necessity for large-scale trials are all critical factors for realizing the full potential of PGPR in sustainable farming [108]. These areas of research offer valuable opportunities to improve pathogen management, increase crop yields, and minimize environmental impacts, aligning with the growing demand for eco-friendly agricultural practices [191].

Advances in PGPR strain selection represent one of the most crucial areas for enhancing PGPR effectiveness in agricultural applications. The isolation and identification of PGPR strains with superior biocontrol capabilities are essential for optimizing their performance in diverse environmental conditions. Consequently, various techniques are employed for isolating effective PGPR strains, including culture-based methods, molecular tools, and high-throughput screening techniques [192,193]. However, culture-based methods, while still widely used, often fail to capture the full diversity of PGPR populations in the rhizosphere. More advanced molecular techniques, such as 16S rRNA gene sequencing and metagenomics, enable researchers to identify novel PGPR strains with potential biocontrol properties from complex microbial communities [194]. High-throughput screening of microbial libraries also allows the rapid assessment of the antimicrobial potential of different PGPR strains, facilitating the selection of the most effective candidates. For example, screening *Bacillus* species for their ability to suppress *Fusarium* spp. led to the identification of strains that reduce disease severity in crops like tomatoes by up to 50% [195,196].

Genetic engineering has also emerged as a promising tool to enhance the properties of PGPR strains. Through genetic modifications, researchers can introduce traits that improve their biocontrol potential, such as enhanced production of antimicrobial compounds, increased resistance to environmental stressors, or improved root colonization [197]. A notable example is the genetic engineering of *Pseudomonas fluorescens* to overexpress antifungal compounds like phenazines, which significantly enhances its ability to suppress soil-borne pathogens such as *Fusarium* spp. In addition, genetic engineering can be used to optimize PGPR strains for specific environmental conditions, such as high salinity or extreme temperatures, expanding their applicability across diverse agricultural systems [198]. More recently, the study of Liu et al. [199] revealed that *Bacillus subtilis* (HS3) and *Bacillus mycoides* (EC18) are rhizospheric bacteria with plant growth-promoting activity. The CRISPR-Cas9 system was employed to investigate the plant-microbe interaction mechanisms of these isolates and their role in biocontrol. Their results demonstrated that fengycin and surfactin contribute to the antifungal activity of *B. subtilis*, which also emits several volatile organic compounds, including 2,3-butanediol, promoting plant growth. Confocal laser scanning microscopy of the GFP-labeled strain revealed that HS3 selectively colonizes root hairs of *Lolium perenne* in a hydroponic system. Finally, they concluded that the CRISPR-Cas9 system developed for these environmental isolates is broadly applicable and will aid in elucidating *Bacillus* and other plant-microbe interaction. The application of genetic engineering to PGPR represents an exciting frontier for improving the efficacy and resilience of biocontrol agents [200]. Similarly, synthetic microbial communities (SMC) have emerged as a promising strategy for plant disease management, leveraging the collective capabilities of multiple microbial species. Advances in omics technologies and tools such as artificial intelligence have significantly improved the design and efficiency of SMCs, enabling synergistic interactions that can effectively control phytopathogens. However, the complexity of plant-associated systems, along with the numerous variables influencing SMC performance, presents challenges in developing a universal biocontrol approach. Future research should focus on refining the design principles and addressing the critical considerations for the successful application of SMCs in plant disease management [201].

Integrating PGPR with other biocontrol strategies is another key avenue for enhancing pathogen management in agriculture. Combining PGPR with other biocontrol agents, such as biopesticides and mycorrhizal fungi, can provide synergistic effects that improve disease suppression and plant health [202]. Biopesticides, such as *Beauveria bassiana* and *Trichoderma harzianum*, are fungal-based agents that have been successfully used in conjunction with PGPR to target a wide range of pathogens. For example, *Trichoderma* spp. and *Pseudomonas fluorescens* have been shown to work together in suppressing *Rhizoctonia solani*, with combined applications leading to a 40–60% reduction in disease severity compared to single-agent treatments [203,204]. Using PGPR with mycorrhizal fungi is another promising strategy, as mycorrhizal fungi enhance nutrient uptake and increase plant resistance to root pathogens, while PGPR suppress pathogenic microbes in the rhizosphere [205]. This combination improved plant growth and yield by 20–30% in crops such as maize and wheat. Integrating PGPR with other biocontrol agents, such as mycorrhizae and biopesticides, not only improves pathogen control but also enhances soil health and biodiversity, thus supporting sustainable agricultural practices (Fig. 4) and offering a promising approach for enhancing pathogen management [108]. Fig. 4 illustrates how these agents can work synergistically to improve pathogen control.

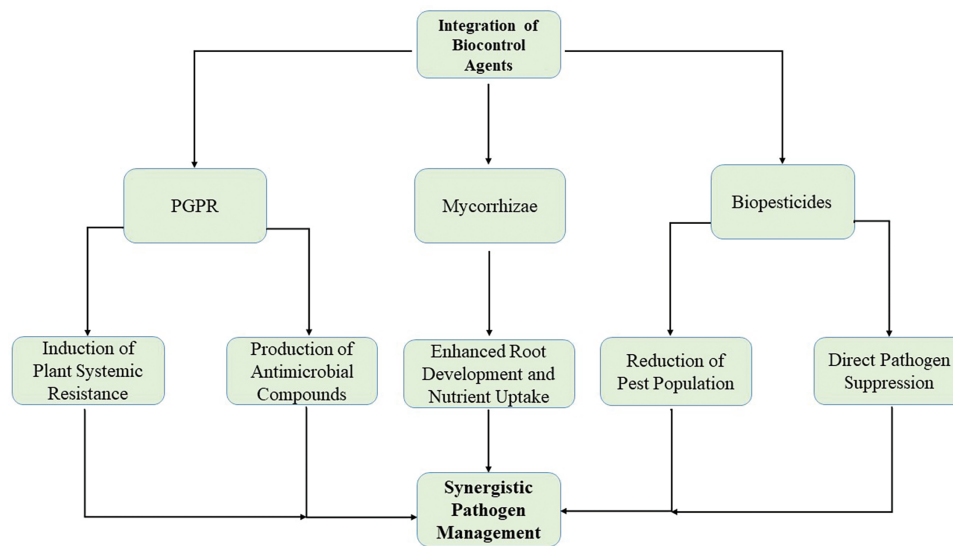


Figure 4: Integrating plant growth-promoting rhizobacteria (PGPR) with other biocontrol agents offers a promising approach to enhancing pathogen management

PGPR's potential in precision agriculture represents an innovative approach to enhancing crop management and optimizing resource use. Precision agriculture leverages advanced technologies, such as remote sensing, drones, and sensor networks, to monitor and manage agricultural processes with high precision [206]. In the context of PGPR application, these technologies can be used to track PGPR distribution, monitor plant health, and identify areas with high pathogen pressure. For instance, drones equipped with multispectral imaging can detect plant stress caused by pathogen infection, allowing for the targeted application of PGPR in areas where they are most needed. Additionally, sensor networks can be used to monitor soil conditions, such as moisture, pH, and temperature, to determine the optimal conditions for PGPR survival and activity [206,207]. By combining PGPR with precision agriculture technologies, farmers can improve disease management while minimizing resource inputs, leading to more efficient and sustainable farming practices. For example, the use of PGPR combined with precision irrigation systems has been shown to increase water use efficiency by 15%–25% in crops such as rice and wheat, while simultaneously enhancing pathogen resistance [208].

While much progress has been made in the development and application of PGPR, large-scale field trials are essential for evaluating the effectiveness of PGPR-based treatments in real-world agricultural settings. Many studies on PGPR efficacy have been conducted in controlled greenhouse conditions or small-scale field trials, but the performance of PGPR in larger, more variable environments remains an uncertainty [209]. Large-scale trials across different agroecological zones are necessary to assess the impact of PGPR on crop productivity, disease resistance, and soil health under diverse field conditions. For example, trials in both temperate and tropical regions have shown varying levels of PGPR effectiveness, with some strains performing better in cooler climates and others excelling in hotter environments [210]. These trials provide valuable insights into the environmental factors that influence PGPR performance, allowing researchers to identify the most effective PGPR strains for specific crops and regions. Furthermore, large-scale trials help to determine the optimal application rates and timings for PGPR, ensuring that they provide consistent and sustainable benefits in the field [205].

Collaboration between researchers, farmers, and policymakers is essential for the successful implementation of PGPR-based solutions at the farm level. Researchers must continue to generate evidence on the efficacy and environmental benefits of PGPR, while farmers require practical information on how to integrate PGPR into their farming systems. Policymakers play a key role in supporting the adoption of PGPR by establishing clear regulatory frameworks and providing incentives for the use of biocontrol agents. For example, in the European Union, the use of PGPR-based products has been supported through regulatory reforms that streamline the registration process for biocontrol agents [211]. Similarly, government initiatives to promote sustainable farming practices, such as subsidies for organic farming, can encourage the adoption of PGPR-based treatments. Collaboration between these stakeholders is crucial for translating scientific research into practical solutions that can benefit farmers, improve crop yields, and promote environmental sustainability.

8 Conclusion

In conclusion, PGPR offer substantial benefits in managing plant pathogens and enhancing agricultural productivity. PGPR contribute to pathogen control through multiple mechanisms, including nutrient competition, antimicrobial compound production, and systemic resistance induction in plants. Additionally, PGPR not only suppress pathogens but also enhance plant health by improving root growth, nutrient uptake, and resilience to abiotic stresses like drought, thus further enhancing crop productivity. Despite these advantages, several challenges remain, including variability in PGPR efficacy due to environmental factors and pathogen species, as well as difficulties in scaling up production and ensuring formulation stability. Additionally, regulatory barriers and the need for widespread adoption present obstacles to the commercial use of the PGPR. However, ongoing research into strain selection, genetic engineering, and the integration of PGPR with other biocontrol strategies is expected to improve their performance and expand their use in diverse agricultural systems. PGPR play a critical role in addressing global food security challenges by enhancing crop resilience and reducing dependence on chemical inputs. As climate change exacerbates environmental stresses, PGPR's ability to improve disease resistance and promote growth under stressful conditions is increasingly valuable. PGPR have been shown to increase crop yields in drought-prone regions and reduce chemical pesticide use, thus contributing to sustainable agricultural practices and improved environmental outcomes. Conclusively, PGPR offer a promising solution for managing plant diseases, improving crop yields, and supporting sustainable agriculture. As research continues to optimize their use and overcome existing challenges, PGPR can significantly contribute to global food security and environmental sustainability, making them an integral part of the future of agriculture.

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