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Review

Plant Growth-Promoting Microbes for Resilient Farming Systems: Mitigating Environmental Stressors and Boosting Crops Productivity—A Review

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Abstract: This review delves into the role of plant growth-promoting microbes (PGPMs) in sustainable agriculture by enhancing soil health, improving plant stress tolerance, and controlling diseases. PGPMs, which include bacteria, fungi, and other microorganisms, are increasingly recognized as important contributors to promoting eco-friendly agricultural practices. Their ability to improve nutrient availability, stimulate plant growth, and protect crops from environmental stressors makes them a cornerstone for resilient and efficient farming systems. By reducing dependency on synthetic fertilizers and pesticides, PGPMs play a vital role in preserving environmental resources, minimizing greenhouse gas (GHG) emissions, and combating climate change's negative impacts. This article thoroughly explores the complex interactions between PGPMs, soil nutrients, plant pathogens, and abiotic stressors. It also examines how these interactions influence phytohormone production and signaling pathways, ultimately impacting crop growth and development. Furthermore, this review discusses how PGPMs enhance nutrient uptake, modulate plant immune responses, and improve stress resilience, offering a holistic understanding of their multifaceted contributions to farming. By synthesizing current research and highlighting future directions, this review underscores the potential of PGPMs to revolutionize agricultural activities, ensuring food security and environmental sustainability in the face of global challenges.

Keywords: microorganisms; biotic stress; abiotic stress; sustainability; disease control

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1. Introduction

Traditional agricultural techniques use chemicals such as fertilizers and pesticides to boost output, posing a danger to agriculture-related ecosystems via contamination of food and soil deterioration as the overuse of chemical fertilizers can encourage soil deterioration, reducing the soil's fertility in the long run [1]. This is because an excessive amount of nutrients can disrupt the natural balance of soil microorganisms, leading to a loss of soil structure and soil health. Salt accumulation from fertilizers also leads to soil salinity, reducing the soil quality for plant cultivation. The excess use of fertilizers and pesticides could also cause ecotoxicity, including water pollution, as agricultural chemicals can seep into water bodies and lead to water pollution. Pesticides and fertilizers can contaminate groundwater and surface water, affecting aquatic life and rendering water unhygienic for consumption by humans. Runoff of nitrogen and phosphorus nutrients can lead to eutrophication and initiate algal blooms that decrease oxygen in water bodies and kill aquatic animals [2]. Loss of biodiversity can occur, where pesticide use can be toxic to non-target organisms, including beneficial insects, birds, and other wildlife. This can disrupt food chains and reduce biodiversity, leading to ecosystem imbalances. Monocropping activities, which are often associated with chemical-based farming, can also reduce genetic diversity and render crops more vulnerable to pests and diseases [3]. So, there is a dire need to transition towards sustainable agriculture techniques to address all these issues. One way to do that is to use plant growth-promoting microbes (PGPMs) instead of traditional chemicals to help restore the microbial communities within the soil. These microbes reside in the soil and relate to the rhizosphere of the plants, where they enhance host crops' development via diversified direct and indirect actions [4].

Soil comprises a dynamic ecology full of microbiota and organisms such as bacteria, fungi, protists, and animals. These organisms are important in plant growth, nutritional regulation, and biological control. They reside in the root zone and endo-rhizosphere of crops, where they assist plant development through several direct and indirect activities [5]. The phyto-microbiome (plant-associated microorganisms) can form competitive, abusive, or neutral relationships with plants, influencing agricultural productivity [6]. Scientists have recently investigated the use of beneficial plant growth-promoting rhizobacteria (PGPR) to suppress phytopathogens and enhance plant development. PGPRs are a subclass of PGPMs that comprise a wide range of microorganisms linked with various plant species and provide plant advantages, such as growth promotion and stress mitigation [7].

Many plant diseases are emerging that threaten the environment and all living organisms [8]. One of the critical issues associated with climate change is the development of new races and diseases, which are fast-spreading and threatening food security [9]. As a result, there is a greater interest in effective and long-term alternatives to traditional pesticides. Currently, new crop protection strategies are focused on decreasing dependence on traditional pesticides and the mandatory adoption of integrated pest management (IPM) concepts as addressed in many nations' legislations [10].

Significant work has been conducted to prove the possible application of PGPR as bioagents and replacements for chemical fertilizers and pesticides/fungicides [11,12]. Biological control is seen as a potential option, and a diverse range of microbial biocontrol agents (BCAs) for treating bacterial and fungal infections has been produced in recent decades. *Bacillus* spp., *Pseudomonas* spp., and *Streptomyces* spp. are among the microorganisms that have received the most investigation [13]. Biological control of plant diseases is most often characterized as the direct or indirect suppression of a disease or the causal organism by another microorganism (antagonist) or collection of organisms [14]. The organism that benefits the plant is called the biological control agent [15]. A broader description includes specific metabolites that can effectively manage the disease, such as those extracted from interactions with plants or plant extracts. They include antibiotics, signaling chemicals, or chemicals with attractant properties (e.g., pheromones) and are frequently referred to as biopesticides [16].

Inducing plant resistance is another option for controlling plant diseases to avoid pesticide health and environmental hazards. Induced resistance (IR) is a physiological condition of increased defensive ability induced by specific environmental triggers, in which the plant defenses are strengthened in the face of future biotic attacks by phytopathogens. This increased resistance helps combat the attacks of various diseases and pests [17]. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are the two most well-known types of induced resistance, which may be distinguished depending on the elicitor's habits and the activated pathways [18]. As we care more about microorganisms' role in enhancing plant growth, we will focus more on ISR. Ref. [19] believed that ISR does not directly contribute to the plant's defensive system; rather, it improves the plant's physiological condition, allowing it to respond more efficiently to biotic stress. The Genus Pseudomonas is among the effective PGPR microbes that have the potential to induce ISR in plants [20]. SAR involves the increase in salicylic acid or pathogenesis-related protein levels while ethylene and jasmonate regulate the pathways in ISR [21].

However, the direct and indirect interactions among different PGPMs and factors affecting plant growth need deep clarification and interpretation. Therefore, the current review article will focus on the crosstalk among PGPMs and several influential factors on plant growth, hence obtaining practicable tools for enhancing the efficacy of beneficial microbes to sustain the different resources in agriculture.

2. PGPMs' Mechanisms of Action

To understand rhizobacteria-mediated ISR, it is essential to identify bacterial processes involved in ISR induction, signaling, and expression. The use of PGPR in agriculture aims to stimulate plant growth and improve plant health, and it could also be used as a biocontrol agent. Different mechanisms of action have been proposed to illustrate precisely how these microorganisms could perform that role, as depicted in Figure 1. PGPR could influence plant growth via (i) direct routes when they reside within the plant and secrete different substances that have a direct effect on plant metabolisms, such as the secretion of phytohormones, phosphate solubilization, and N_2 fixation, and (ii) indirect routes, which in this case could be called biocontrol mechanisms that could involve the secretion of antibiotics, lytic enzymes, and competition with pathogenic microorganisms for space and available nutrients [22,23].

2.1. Direct Mechanisms

2.1.1. Phytohormone Production

A wide variety of phytohormones, i.e., auxins, gibberellins, cytokinin, abscisic acid, and ethylene, could be produced from PGPR [24]. A defensive state in plants ranging from phyto-stimulation to complete plant immunity could be reached and facilitated by IAA, which is a signaling molecule in bacteria [25]. The concentrations of gibberellin and auxin in maize leaves were increased due to inoculation with PGPR [26]. It was found that isolating PGPR from stressed conditions could induce tolerance to stressed plants. Additionally, PGPR could modify growth inhibitors and phytohormone production. For instance, when wheat was inoculated with isolates from plants that exhibited water stress, induced tolerance to water stress was observed in the inoculated wheat plants, as was increased production of abscisic acid and decreased accumulation of gibberellic acid, indole acetic acid, and trans-zeatin riboside [27].

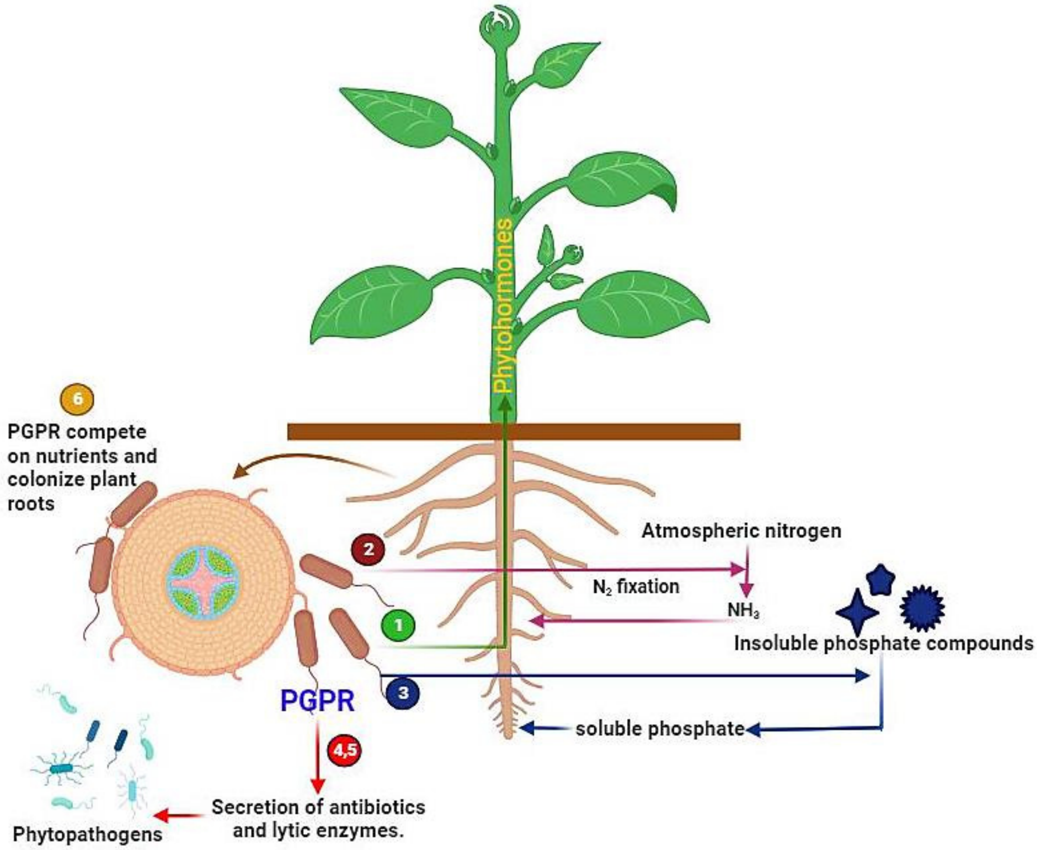

Figure 1. PGPR offer direct and indirect mechanisms to stimulate plant growth and control phytopathogens. (1) Production of phytohormones, (2) N_2 fixation, (3) phosphate solubilization, (4) secretion of antibiotics, (5) lytic enzymes secretion, and (6) competition for space and nutrients.

2.1.2. Solubilization of Phosphate

PGPR are classified into several types, one of which is phosphate-solubilizing rhizobacteria (PSRB) that are recognized for promoting plant growth through increasing P and N uptake and might be utilized as biofertilizers to restore soil health [28]. Gram-negative PSRB strains outnumbered gram-positive PSRB strains. According to [29], rhizodeposition suppresses the activity of gram-positive bacteria, whereas it promotes gram-negative bacteria and makes them motile. Furthermore, root exudates attract gram-negative bacteria; thus, their number increases around plant roots; as a result, plants benefit by absorbing beneficial plant growth promotion substances secreted by those bacteria, while the number of gram-positive bacteria around roots decreases owing to oxygen deficiency. Good PSRB could be selected, relying on their effectiveness in producing organic acids (gluconic and keto gluconic acids) in the growth plates [30]. Those organic acids in the soil chelate the cations linked to phosphate via their carboxyl and hydroxyl groups [31]. Ref. [32] pointed out the use of *Bacillus* sp. and *Arthrobacter* sp. as two phosphates solubilizing stress tolerant rhizobacteria that were isolated from tomato rhizosphere as efficient plant growth promoting rhizobacteria solubilizing insoluble phosphates, such as aluminum and ferric phosphate, under different stress conditions viz. salt, pH, and temperature stress.

Phosphate-solubilizing bacteria (PSB) are multifunctional and comprise a range of species, including *Pseudomonas putida*, *Burkholderia cepacia*, *Pantoea agglomerans*, and *Microbacterium laevaniformans*, among which the *Pseudomonas putida* strain P13 is highly effective in insoluble phosphate solubilization [33].

The biochemical mechanisms of phosphate solubilization are mainly organic acid production and phosphatase activity. Organic acids, such as gluconic acid, are formed via fermentation pathways using gluconolactonase and gluconokinase [34]. Phosphatases such as alkaline phosphatase and acid phosphatase hydrolyze organic phosphorus compounds, thus liberating inorganic phosphate. A comparison between different phosphate-solubilizing PGPMs could be summarized in Table 1 [35].

Table 1. Comparison between most common phosphate-solubilizing PGPMs.

Genus	Species	Mechanism	Advantages
Bacillus spp.	*Bacillus subtilis* *Bacillus megaterium*	Species of Bacillus solubilize phosphate primarily through the production of organic acids such as gluconic acid and citric acid. The acids chelate cations complexed with phosphate, making them available for plant absorption.	*Bacillus* spp. are robust and can resist various environmental conditions. They also produce other plant growth-promoting substances, such as indole-3-acetic acid (IAA) and siderophores.
Pseudomonas spp.	*Pseudomonas fluorescens*, *Pseudomonas putida*	Secretion of organic acids and enzymes like phosphatases. The enzymes degrade organic phosphorus compounds and release inorganic phosphate.	*Pseudomonas* spp. are effective in the induction of systemic resistance in plants and provide the double benefits of nutrient solubilization and disease suppression.
Rhizobium spp.	*Rhizobium leguminosarum*, *Rhizobium radiobacter*	Rhizobium species solubilize phosphate through organic acid production and phosphatase release. Rhizobia are best known for nitrogen fixation but also contribute to solubilizing phosphate.	*Rhizobium* spp. form symbiotic relationships with legumes, which enhance both nitrogen and P availability.
Aspergillus spp.	*Aspergillus niger*, *Aspergillus flavus*	Facilitate the solubilization of phosphate through the excretion of organic acids and enzymes. The fungi secrete a broad spectrum of enzymes capable of breaking down complex organic phosphorus compounds.	*Aspergillus* species efficiently solubilize phosphate from organic sources and can be included in biofertilizer formulations.

The phoD gene encoding alkaline phosphatase is most widely used as a biomarker for PSB [36]. Metagenomic research has shed light on phosphate-solubilizing bacteria's diversity and functional potential in different environments. For instance, research on Vietnamese agricultural soils showed the predominance of bacterial phyla Proteobacteria, Actinobacteria, and Firmicutes, which are phosphate-solubilizing. The occurrence of the phoD gene was in accordance with phosphatase activity, suggesting that the bacteria could make phosphorus more available in the soil [36]. One more study concerning *Pseudomonas asiatica* JP233 confirmed its potential to modify the rhizosphere microbial community and promote plant growth by stimulating genes responsible for soil phosphorus cycling [37].

2.1.3. Nitrogen Fixation

The conversion of atmospheric nitrogen (N) into ammonia (NH_3), a form available for growing plants, is known as N fixation. When this process happens by microorganisms, it is called biological N_2 fixation (BNF) [27]. Many genera have been proven to fix N_2, including non-symbionts (microorganisms that fix nitrogen independently of a host plant such as Bacillus, Corynebacterium, Pseudomonas, and Xanthobacter) and symbionts, i.e., form mutualistic associations with specific plants, often legumes, such as Rhizobia. The

Rhizobiaceae family (α-proteobacteria) includes members that can realize mutualistic symbiosis leading to atmospheric nitrogen fixation with the roots of the members of the family Leguminaceae. Nodule formation, where the Rhizobia colonize host plants intracellularly, results from a complicated host–symbiont relationship. The metalloenzyme responsible for nitrogen fixation comprises two components: (1) dinitrogenase reductase, which acts as the iron protein, and (2) dinitrogenase, in which a metal cation is used as a cofactor. High-reducing-power electrons are generated by dinitrogenase reductase, which dinitrogenase utilizes to reduce N_2 to NH_3 [38]. In other cases, bacteria could fix nitrogen; however, they cannot form nodules on plant roots, which could also increase crop yield as they can reduce N_2 into NH_3, such as in wheat plants, thus playing a significant role in N nutrition [39]. For instance, adding the nitrogen-fixing *Azospirillium* spp. has increased crop yield [40,41].

2.2. Indirect Mechanisms

2.2.1. Antibiotic Secretion

Antibiotics could be identified as low-molecular-weight compounds that act as toxins if used at low concentrations of less than 10 ppm, which could kill other organisms [42]. The bacteria that secrete antibiotics are either bactericidal (kill other bacteria) or bacteriostatic (suppress the growth of other bacteria) [43]. They achieve their role by altering the structure of cell membranes, impacting the formation of pathogen cell walls, and preventing the development of initiation compounds on the ribosome's small subunit [44]. Ref. [45] reported the potential of some bacterial isolates (*Bacillus cereus*, *Bacillus megaterium*, *Pseudomonas libanensis*, *Pseudomonas putida*, and *Flavobacterium* spp.) that were secluded from the chili plant rhizosphere to significantly suppress the growth of *Pythium myriotylum*, the causal agent of post-emergence damping-off in chili pepper in vitro. Moreover, when chili seeds were treated with the previously mentioned bacterial isolates, significant suppression of the damping-off disease occurred, PGP traits were improved, and the seed germination percentage was enhanced compared to the control. Antibiotics are responsible for this antagonistic activity since different antibiotics have been found and described in earlier investigations. Antibiotic synthesis damages fungal cell membranes and inhibits oomycetes from forming zoospores.

A specific class of antibiotics secreted by microorganisms is called cyclic lipopeptides (CLPs or CLiPs). CLPs are bioactive natural secondary metabolite compounds with promising application potential [46]. They are produced by certain bacteria such as *Pseudomonas*, *Streptomyces*, and *Bacillus* spp. by non-ribosomal peptide synthetases and show a wide range of bioactivity, including antibacterial, antifungal, anti-oomycete, antiviral, and anticancer effects [47]. A peptide part is attached to a fatty acid tail [48]. The cyclic peptide portion of lipopeptides is responsible for their interactions with biological targets, while the lipid portion contributes to their stability and membrane-targeting abilities [49]. CLP production by bacteria is most relevant in competitive interactions with other coexisting bacteria, fungi, and oomycetes and during interactions with protozoan predators, thus explaining their antimicrobial nature.

Some of the most important cyclic lipopeptides are those secreted from *Pseudomonas* spp. Ps-CLPs could also be used as biosurfactants due to their structure, which contains a fatty acid tail that lowers their surface tension, such as pseudofactin, orfamide, and viscosin [50]. These CLPs have different modes of action. Some of these CLPs cause a significant malfunction in the plasma membranes of plant pathogens due to their insertion within the membranes, causing transmembrane pores to allow Ca^{2+} and H^+ ions to influx while allowing K^+ ions to efflux, leading to cell death [51], as shown in Figure 2. However, some lipopeptides are considered phytotoxins, such as syringomycin, syringopeptin 22A, and syringopeptin 25A, as they are vital in enhancing the virulence of their producing pathogens. They could also show antimicrobial efficacy against some fungi and gram-positive bacteria [47].

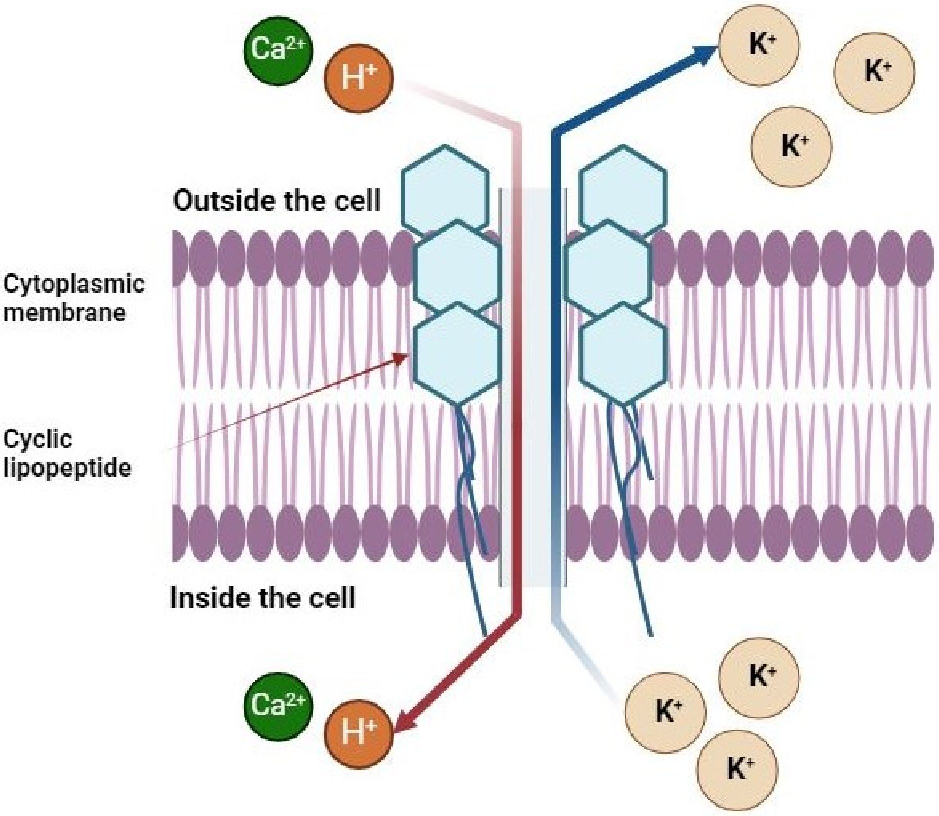

Figure 2. Mechanism of action of some cyclic lipopeptides showing transmembrane pore formation, allowing Ca^{2+} and H^+ ions to influx while allowing K^+ ions to efflux.

2.2.2. Competition

Numerous microorganisms exist in the plant rhizosphere; some are considered beneficial, while others are phytopathogenic for plants. The presence of PGPR in the rhizosphere of plants attracted by their root exudates allows them to contest with other biota on available root exudates and nutrients to colonize plant roots, protecting them against phytopathogens in what is known as rhizosphere competence [52]. This competence is influenced by the efficacy of certain PGPR in colonizing the root surface efficiently and remaining at population density levels adequate to improve plant growth. This explains the importance of the physical occupation of PGPR in infection sites on plant roots, enabling them to suppress soil phytopathogens [53]. Ref. [7] stated that *Pythium aphanidermatum* and *Bipolaris maydis* were suppressed in the maize rhizosphere due to the presence of *Pseudomonas fluorescens* PJ0210 which competes with the pathogens for sources of nourishment such as glucose and asparagine.

The most commonly known microbes that compete with plant pathogens in the soil are *Bacillus* spp., *Pseudomonas* spp., and *Trichoderma* spp., especially *T. harziaum*.

2.2.3. Secretion of Lytic Enzymes

Another biocontrol feature of PGPRs is their ability to secrete hydrolytic enzymes. The secretion of hydrolytic enzymes such as chitinases, proteases, lipases, β-1,3 glucanases, and cellulases from different PGPRs degrade the glycolytic linkages in cell walls of phytopathogenic bacteria and fungi [54]. Those lytic enzymes negatively impact plant pathogens, as they could stop their multiplication and inhibit their growth. Soil-borne phytopathogens viz. *F. oxysporum*, *R. solani*, *P. ultimum*, and *S. rolfsii* could be controlled by the hydrolytic enzymes secreted by PGPR like *B. subtilis*, *B. cereus*, *B. thuringiensis*, and *S. marcescens* [55].

Bacillus subtilis produces an enzyme that degrades chitin called chitinase, where chitin is a significant component of fungal cell walls. The enzymatic activity undermines the structural integrity of the fungal cell wall, leading to cell lysis and eventual cellular death [56]. *Pseudomonas fluorescens* secretes glucanase, which hydrolyzes the β-glucans in fungal pathogens' cell walls. The enzyme's activity destabilizes the cell wall structure, making the fungi susceptible to environmental stresses and leading to their death [57].

Cellulase production was one of the weapons of Trichoderma harzianum, an enzyme that hydrolyzes cellulose in the cell walls of fungal pathogens. The cellulose degradation weakens the fungal cells' structural integrity, causing their lysis [56].

These PGPMs employ their lytic enzymes to control plant pathogens effectively, inducing improved plant health and reducing the incidence of diseases. Their ability to hydrolyze fungal cell walls is one of the key mechanisms of their biocontrol activity.

3. PGPMs and Plant Diseases Crosstalk

Arbuscular mycorrhizal fungi (AMF) and *Trichoderma* spp. regulate stem rust of wheat biologically. The results revealed that both biological agents significantly decreased disease measures, activated polyphenol oxidase and peroxidase enzymes, raised total phenols, and enhanced yield and growth traits [52]. Ref. [58] obtained two novel compounds from thirteen metabolites extracted from a *T. longibrachiatum* culture. Some compounds were able to cause a 75% disease reduction in vivo at a concentration of 500 µg/mL, while other compounds caused a 68% disease reduction at a concentration of 125 µg/mL, showing that *Trichoderma* spp. are capable of enhancing plant defenses by various mechanisms [59]. A recent study discovered that PGPR, isolated from the plant root zone, was used for medicinal purposes and applied to rice plants infected with the causal agent of sheath blight. *Rhizoctonia solani* resulted in noticeable increases in germination, seedling strength, and dry weight. Furthermore, PGPR strains result in reduced relative lesion length, the lowest disease incidence, delayed sclerotia development, and the highest grain production per pot. Plants also showed increased activity of several defense enzymes, indicating induced systemic resistance [60]. The biocontrol potential of sugar beet root rot and damping-off caused by *Sclerotium rolfsii* was investigated by using different *Bacillus* spp. isolates [61]. Results showed that sugar beet seeds treated with *Bacillus* spp. exhibited remarkable depression in damping-off disease with increases in plant biomass and the length of roots and shoots. In vitro, results revealed that *P. fluorescens* showed the most inhibition among other tested bioagents to *R. solanacearum*. The growth promotion of potato plants and biocontrol efficacy results showed different levels of biocontrol against brown rot disease when applying the bioagents individually [62]. In a study aiming at suppressing *Fusarium oxysporum* f.sp. ciceris, the causal agent of chickpea wilt, using bacterial strains isolated from the rhizosphere of healthy plants growing in wilt-infected soil, 90% of them inhibited the growth of the pathogenic fungus. Some isolates colonized plant roots and removed the pathogen's mycelia, suppressing disease and improving root morphology. The levels of several defense enzymes, such as peroxidase, phenylalanine ammonia-lyase, and polyphenol oxidase, were also elevated [63].

The biological control of root rot in beans caused by *Rhizoctonia solani* was investigated by [64]. Results showed that using the wild-type *Pseudomonas strain* CMR12a against two aggressive isolates of *R. solani*, AG 2-2 and AG 4 HGI, caused significant disease reduction due to the production of phenazine and cyclic lipopeptide; however, Pseudomonas mutants lacking phenazine and cyclic lipopeptide production were utterly unable to control the disease. In a study to control grapevine trunk disease caused by *Neofusicoccum luteum* using an endophytic *Pseudomonas poae* strain, ref. [65] reported that using *P. poae* isolate BCA17 caused a significant reduction in the biomass of the pathogenic fungus and also reduced the germination of the spores. They also detected the presence of an unknown cyclic lipopeptide that could be involved in the biocontrol activity of *P. poae* (BCA17), especially since it was not detected in the non-antagonistic strain's (JMN13) diffusible compounds.

In general, PGPMs showed potential disease control for many other diseases such as bacterial blight of rice caused by *Xanthomonas oryzae*, Fusarium wilt of many crops caused by *Fusarium oxysporum*, and Phytophthora root rot of several plants caused by *Phytophthora* spp. through different mechanisms, including A: the production of antimicrobial compounds: *Pseudomonas* spp. produce a range of secondary metabolites with antimicrobial properties. Some of these metabolites include antibiotics like pyrrolnitrin, phenazines, and pyoluteorin. These compounds inhibit the growth of pathogenic bacteria and fungi by disrupting their cellular membranes and interfering with their metabolic processes [66]. B: siderophore production: in this respect, these bacteria can produce siderophores, which are iron-chelating agents. By sequestering iron from their environment, Pseudomonas spp. restrict the supply of this vital nutrient to pathogenic microorganisms, thus suppressing their growth [67]. C. lytic enzymes: *Pseudomonas* spp. secrete lytic enzymes like glucanases and chitinases that degrade the cell constituents of fungal pathogens. This enzyme activity not only suppresses pathogen growth but also facilitates the degradation of fungal cell walls, resulting in pathogen lysis [57]. D. induction of systemic resistance: pseudomonas spp. can induce systemic acquired resistance (SAR) and induced systemic resistance (ISR) in plants. The process includes the induction of plant defense responses throughout the organism, rendering it more resistant to a wide range of pathogens. The biosynthesis of signal molecules, including salicylic acid, jasmonic acid, and ethylene, plays a key role in this process [66]. E. resource competition: *Pseudomonas* spp. compete with pathogens for space and nutrients in the rhizosphere (root area). This competitive exclusion prevents pathogen establishment and growth, protecting the plant [67].

4. PGPMs and Plant Nutrition Crosstalk

4.1. Enhancing Soil Fertility

Soil fertility in agriculture is concerned mainly with the soil's chemical composition and physical features in various origins and climate zones [68]. The importance of soil bioactivity is generally overlooked. The cause of this disparity is a lack of a concept of how soil bioactivity and chemical and physical qualities are connected and how agronomic management approaches impact them [69]. To obtain helpful knowledge about the soil system, researchers must examine the soil biological components included in sustainable agricultural production in terms of the different interactions occurring among plants, microbes, and other soil traits.

In plant nutrition, an intricate symbiosis exists between plants and PGPMs, which are beneficial microorganisms pivotal to the growth and well-being of plants. PGPMs contribute significantly to plant nutrition by facilitating the uptake of essential nutrients, enhancing soil structure, and safeguarding plants against diseases [70]. The beneficial PGPMs, including bacteria, fungi, and other microorganisms, work harmoniously with plants to promote their growth and overall health. By colonizing the root systems of plants, they help improve nutrient uptake, increase resistance to diseases, and enhance stress tolerance. In addition, they also play a key role in breaking down organic matter, releasing essential nutrients such as nitrogen, phosphorus, and potassium for plant use [71]. Soil fertility is the backbone for better crop growth and establishment. Soil traits must match the needs of plants to achieve optimal nutrient availability [72]. Excess fertilizers and inappropriate irrigation can damage soil and disturb its biological and chemical components [73,74]. As a result, soil structure deteriorates, bulk density increases, and organic matter, soil porosity, and biological activity decrease [75]. PGPMs have received much interest for mitigating these negative impacts and improving soil fertility. Developing soil organic matter, improving soil aggregation, improving nutrient uptake, and enhancing micronutrient availability are all activities of PGPMs that contribute to soil fertility [76].

PGPMs serve as biofertilizers by enhancing nutrient availability. They achieve this through bio-fixating atmospheric nitrogen and solubilizing soil minerals like phosphorus and potassium. Some rhizobacteria can assist in producing siderophores, which improve iron absorption. Additionally, PGPMs act as phyto-stimulators, directly encouraging plant growth by influencing the metabolism of phytohormones such as auxin, cytokinins, abscisic acid, gibberellins, and ethylene reduction [77]. PGPMs improve soil fertility by encouraging the development of soil organic matter (SOM). PGPM inoculation significantly enhances soil with low levels of SOM. These microbes contribute to the plentiful addition of ammonium (NH^{4+}) derived from soil, as well as the regulation of microbial transformations of N and the sustainment of the carbon (C)-to-nitrogen (N) ratio in soil [78]. Generally, soil with low SOM gives higher yields once inoculated with PGPMs [79]. Aggregation of soil granules is important for maintaining fertility via adjusting water retention and movement. Some PGPRs generate exopolysaccharides (EPSs), aiding in soil aggregation and productivity [80]. It has been discovered that EPS-producing PGPR improve crop output for soils subjected to salt and drought stress [81].

Arable lands contain about 25,000 species of fungus [82], representing about 20% of total microbial biomass [83], while AMF comprises 5–50% [84]. AMF are helpful microbes that originate symbiotic relationships with the root systems of plants. AMF function practically in plant nutrition by regulating the dynamics of C, P, and N [85]. AMF mycelia penetrate deep into the soil, assisting in C nutrient recycling and improving soil texture [84]. The plant benefits substantially from C because fungal hyphae increase soil access. These structures have an outstanding surface-area-to-volume ratio compared to root hairs and can spread up to 8.0 cm past nutrient-depleted regions around roots [86]. Ref. [87] reported that the “AM pathway” is used by AMF, allowing them to collect P from soil and quickly distribute it to cortical cells in the root, boosting phosphorus availability. AMF also produces glomalin protein, hydrophobin protein, and mucilage, all of which aid in soil aggregation and fertility [74,88]. Colonization of AMF influences bacterial populations since AMF exudates provide a substrate for bacterial development [89]. It has been observed that the compounds emitted by AMF alter the number and behavior of different species of fungus and bacteria [90]. AMF colonization is also important for nitrogen absorption and the stimulation of amino and organic acids in plant shoots and roots [74,91].

4.2. Facilitators of Macro- and Micronutrients

Despite severe environmental dangers, approximately 50% of the world’s population uses synthetic fertilizers to raise food [74,92]. China, India, and the USA are the world’s leading fertilizer consumers, consuming about 50.2, 21.7, and 20.8 million tons of N, P, and K fertilizers. Demand for fertilizer is predicted to rise to fulfill food requirements, although the increased fertilizer consumption may cause environmental issues [93]. Hence, PGPMs are an important substitute for increasing soil availability and absorption of macro- and micronutrients.

4.2.1. Macronutrients

Macronutrients are elements that plants receive in large quantities from the soil. Each element has a specific function in promoting plant development [94]. Plants rely on various macronutrients, including N, P, and K, to perform essential physiological functions such as protein synthesis, photosynthesis, and enzyme activation. N is essential for various physiological processes, including enzyme activation, protein synthesis, and photosynthesis. P is a primary macronutrient for nucleic acids, plant growth, and metabolic pathways [95]. K is the most prevalent cation involved in various physio-biochemical events, such as enzyme activation and osmoregulation. Also, these nutrients are necessary for sustaining critical activities in plants, such as energy transmission, cation–anion equilibrium, and stress tolerance [94]. Sulfur (S) is a component of methionine and cysteine, and it is needed for plant metabolism and growth [96].

Microbes play a distinctive act in nutrient absorption from soil. PGPMs aid in the availability of these nutrients by secreting organic acids and enzymes that help release soil minerals [97]. These microorganisms are critical in establishing adequate nutrient balances and optimal nutrient absorption by plants, resulting in less use of synthetic fertilizers [76]. Consequently, the number of commercially available biofertilizers for different crops is growing [98]. Soil generally contains about 0.1–0.6% N, equating to 2000–12,000 kg N ha-1 according to the soil type [99]. One method to reduce the reliance on chemical nitrogen fertilizers is through biological nitrogen fixation (BNF). BNF accounts for about 60% of Earth's fixed nitrogen. Hence, it is essential to enhance BNF in agriculture to satisfy the increasing global food production needs. Studies show that utilizing BNF leads to a 25% decrease in chemical fertilizer application [97]. Plants prefer nitrate (NO_3) and ammonium (NH^{4+}) soil N, which they obtain from organic and inorganic sources. Because atmospheric N can only be available to plants that can form symbiotic relationships with N-fixing bacteria via the BNF system, the other plants must depend on other sources of N. Consequently, inorganic N fertilizers have traditionally been used to improve agricultural yield [100]. According to the estimations of [101], N fertilizer consumption will reach 119.2 metric tons in 2020, with a progressive increase in the following years.

Legumes are essential in the agricultural system, accounting for up to fifty percent of the worldwide acreage [102]. Pulse crops can fix approximately 16.4 Tg of N yearly, representing 77% of N [103]. PGPMs with BNF capacity are considered suitable for nitrogenous fertilizers [104]. According to [105], BNF generates around 200 million tons of N annually. Although symbiotic fixation accounts for most of the N input in soil, free-living or symbiotic fixation also contributes significantly to N input in most terrestrial ecosystems, particularly those with a low density of symbiotic N-fixing plants [106]. Bacillus, Azotobacter, Klebsiella, and Clostridium are free N fixers that fix BNF [107]. *Azospirillum* species fix N at a rate of 52 mg N g^1 malate [108]. Symbiotic fixation of N by the cyanobacterium *Anabaena azollae* in conjunction with the water fern Azolla has been used as a biofertilizer for nearly one thousand years and can fix up to 0.6 tons of N per ha yearly [109].

The P amount in typical soils is only around 0.05% since it is fixed inorganically, in addition to forming organic compounds, of which about 0.1% is accessible to plants [110]. Universally, P deficiency roughly affects about 5.7 billion hectares of arable land [111]. Phosphate fertilizers, like N fertilizers, are not entirely available for plants; most P in soils exists in two forms: inorganic and insoluble ($Ca_3(PO_4)_2$) and organic and insoluble/soluble (phytate and nucleic acid) [95]. Phosphate-solubilizing bacteria (PSB) and AMF are well known in that they benefit crops by diverting the insoluble state of P to an accessible one [112]. Beneficial bacteria species include Rhodococcus, Gordonia, Arthrobacter, Bacillus Chryseobacterium, Phyllobacterium, Serratia, Pseudomonas, Xanthomonas, Enterobacter, Pantoea, Delftia, Xanthobacter, Rhizobium, and Klebsiella are sold as an inoculant in several countries [98]. Penicillium and Aspergillus are the most common PGPF taxa [113]; although, Rhizoctonia and Trichoderma strains [114,115] have also been discovered as P solubilizes. Organic P compounds were shown to be the primary P source in soil, representing 30.0–65.0% of total P in soil. According to test plants, such an amount is not readily mineralized in soil. For example, it cannot obtain phytate (My inositol hexakisphosphate), accounting for up to 80% of organic P [116]. Numerous rhizospheric bacteria make phytase, hence removing P from phytate, and have been found to help with phosphate solubilization [117]. Ref. [95] tested eight bacterial genera for their phosphorus solubilization ability: Acinetobacter, Pseudomonas, Massilia, Bacillus, Arthrobacter, Stenotrophomonas, Ochrobactrum, and Cupriavidus. Acinetobacter exhibited significant potential in solubilizing phosphorus, making it a promising candidate for enhancing soil fertility and quality. As per [118], phosphorus-solubilizing bacteria can dissolve inorganic phosphorus through the secretion of small molecule organic acids, thereby altering soil properties and indirectly influencing the microbial community in the rhizosphere. Ref. [119] studied the effectiveness of bacteria such as *Bacillus thuringiensis*, *Pseudomonas pseudoalcaligenes*, and *Enterobacter cloacae* in mobilizing plant-unavailable phosphorus, whether in organic (phytin) or inorganic (calcium phosphate) form.

The worldwide concern is not P supply but K supply [120]. Soil K has four forms: structural, solution, exchangeable, and fixed. The most challenging form accessible to K by plants and microorganisms is the structural form followed in an orderly, fixed, and exchangeable manner, and the easiest is the solution form. Some rhizospheric bacteria produce organic acids, which solubilize the “non-exchangeable” form of K in soils [121]. Pseudomonas, Acidithiobacillus, Burkholderia, Paenibacillus, and Bacillus bacteria solubilize K-containing minerals in soil and deliver soluble K to plants [122–124]. Potassium-solubilizing bacteria (KSB) exhibited a noticeable increase in P and K availability. It has been reported that different K-rich soils contained *Spergillus terreus* and *Aspergillus niger* [125]. Similarly, Ref. [126] proved *Aspergillus niger's* potential as a biofertilizer source for K.

Sulfate (SO_4), which is taken up by the roots, is the most significant supply of S for plants; nevertheless, aerial parts may also absorb ambient sulfur dioxide (SO_2) [94]. SO_4 constitutes $< 5\%$ of total S in soil [127], while $>95\%$ remains unavailable since it binds to organic molecules [128]. S concentration changes over time and is governed by the equilibrium among immobilization, mineralization, S exogenous supply, and plant uptake [129]. The pH of the soil is the most important physiological factor regulating SO_4 adsorption [130]. Adsorption is frequently more advantageous at a low pH and diminishes with increasing pH [131]. Bio-oxidation of decreased sulfur compounds to sulfate has been seen in a diverse spectrum of sulfur-oxidizing prokaryotes, including domain archaea and bacteria [132]. It has been documented that sulfur-oxidizing bacteria have significant potential for affecting S absorption in plants [133–135]. Further, issues were reported on AMF-aided S uptake [136,137].

4.2.2. Micronutrients

Most research focused on the relationship between PGPMs and the intake of iron (Fe) and zinc (Zn) as micronutrients. Fe is required for physiological actions such as respiration, photosynthesis, and the generation of chlorophyll [138]. The ferrous (Fe^{2+}) form is the appropriate form of Fe for plant absorption [139]. The insoluble Fe^{3+} (ferric) form of Fe predominates in soil, with concentrations ranging from 7000 to 500,000 mg kg^{-1}. Both plants and bacteria need about 1–10 M soluble Fe to function normally [140]. Fe deficiency and decreased plant availability represent a significant danger to agroecosystems. Thus, an exogenous supply of Fe, whether in inorganic or chelated forms, has now been adopted as a practice in crop fertilization [141,142]. Irrational use has a deleterious influence on plant development [143]. With Fe deficiency, siderophores generated by rhizospheric bacteria perform a distinctive role in crop health programs [144]. Ref. [145] found that a siderophore obtained from the Chryseobacterium C138 bacteria remarkably stimulated the formation of chlorophyll while boosting tomato yield.

Zn is required for several critical plant metabolic processes. Crop yields and quality are reduced in soil with low Zn concentration. About 30% of the world's arable lands suffer from Zn availability [70]. Because 96–99% of inorganic Zn is transformed into various insoluble forms within seven days of application, depending on soil type and physicochemical processes [146], it cannot fulfill plant demands. Organic acids produced via rhizospheric bacteria aid metal solubility. Exploiting PGPR in Zn absorption has recently been advocated as a sustainable technique to address plant demands, particularly in Zn-deficient soil [147–149]. Ref. [150] demonstrated the remarkable potential of AMF in improving the availability of Zn in plant rhizospheres.

5. PGPMs, Phytohormones, and Stresses Crosstalk

Understanding the mechanisms by which PGPMs adjust phytohormones in response to stresses is crucial for realizing their potential in sustainable agriculture. Abiotic stressors [151,152], such as drought [153], salinity [154], and harmful temperatures [155], offer considerable difficulties to plant growth and output. Various studies have verified the helpful impact of PGPMs on different crops, such as chickpeas [156], *Ranunculus asiaticus* [157], pepper [158], tomato [159], and Gerbera [160].

Rhizobacterial species have been shown to mitigate drought stress in tomato [161] and pepper [162] seedlings. *Achromobacter piechaudii* ARV8 increased seedling weights and decreased ethylene production under salt-stressed conditions [163]. Salty soil significantly impacts seeds' germination, the most important part of crop growth. Salt-tolerant bacteria that produce phytohormones (gibberellins and auxins) should be exploited as inoculants for cultivated crops in salinity conditions to enhance plant growth [162,163].

Microbe-mediated mitigation of unfavorable temperatures has been studied in the field of climate change. Heat stress in sorghum seedlings can be mitigated by Pseudomonas AKM-P6 [164]. Trichoderma and Bacillus inoculant are appropriate techniques for improving maize resistance to cold-stress conditions during early growth [165]. These microorganisms directly and indirectly benefit plants through diversified modes, including biofilm formation, exopolysaccharide, siderophores synthesis, and phytohormone production [166,167]. Phytohormones are natural products accountable for the growth of plants [168]. Some PGPMs can modulate phytohormones since PGPMs reduce the impact of stress on plants via the production of phytohormones such as gibberellin, auxin, cytokinin, jasmonic acid, ethylene, and abscisic acid (ABA), [156,169–171]. The growth-promoting compounds produced by plant growth-promoting microorganisms are briefly depicted in Table 2.

Auxins (IAA) gained from microbes are valuable in systemizing cell division, shoot growth, vascular tissue development, and root properties [190,191]. Pseudomonas spp. boost pepper growth by stimulating auxin accumulation [158]. Also, the Endophytic Strain Bacillus subtilis 26D increases auxin in potato [192]. It has been confirmed that bacterial IAA can enhance the root surface area in inoculated plants [193]. Bacillus subtilis LK14 produces auxin and increases plant biomass and levels of chlorophyll in tomato plants [194]. Auxin production promotes deep root anchoring and improves nutrient and water acquisition from the soil, increasing growth and reducing nutrient and water-deficit stress [195]. Under dry conditions, seed treatment of clover with auxin-generating *Bacillus megaterium* and *Pseudomonas putida* increased plant biomass [193]. A germination study on soybean illustrated that individual inoculation with each of *T. longibrachiatum*, *T. simmonsii*, and *B. megaterium*, or triple inoculation with *B. cereus*, *B. megaterium*, and *T. simmonsii*, are the best treatments for seed germination and promoting K uptake and seedling growth through auxin production under stressed or non-stressed conditions [162]. Auxins have been demonstrated to increase plant tolerance to heavy metal stress, which may be attributed to increased plant biomass, which improves the phytoextraction of metals from soil [196].

Table 2. Growth-promoting compounds produced by plant growth-promoting microorganisms.

Microorganism	Plant	Growth Regulator/Nutrient	References
Azotobacter	Mustard, barseem, wheat, sugarcane,	IAA, siderophore, ammonia	[172]
Pantoea dispers	*Pinus sylvestris*	P-solubilization, IAA, siderophores	[173]
Bacillus spp.	Mustard and tomato	IAA, siderophore	[174]
Pseudomonas	Indian mustard	Siderophores, IAA, P-solubilization	[175]
Brevibacillus sp.	*Trifolium repens*	IAA	[176]
Xanthomonas sp.	*Brassica napus*	IAA	[177]
Brevibacterium sp.	*Hordeum vulgare*	P-solubilization	[178]
Bacillus subtilis	*Brassica juncea*	IAA, P-solubilization	[179]
Pseudomonas fluorescens	*Glycine max*	IAA, siderophore, P-solubilization	[180]
Azotobacter chroococcum	In vitro	Gibberellin, kinetin, IAA	[181]
Kluyvera ascorbata	Tomato, canola, and Indian mustard	siderophore	[182]
Bacillus, Pseudomons,	*Trigonella graecum*	P-solubilization, IAA	[183]
Pseudomonas putida	Mung bean	Siderophore	[184]
Variovorax paradoxus, Rhodococcus sp.	Indian mustard	IAA, siderophores	[185]
Bradyrhizobium	Chickpea	IAA, siderophores, HCN	[186]
Mesorhizobium	Mustard, barseem, wheat, sugarcane elc.	IAA, siderophore, ammonia, HCN	[172]
Rhizobium spp.	*Sesbania procumbens*, *Crotalaria* sp.	IAA, siderophores	[187,188]
Rhizobium cicero Rhizobacteria	Chickpea	Siderophore	[189]

Through cytokinin production, PGPMs can boost plant growth and nutrient absorption and augment systemic resistance and stress tolerance [161,162,193]. PGPM-induced cytokinin promotes root growth, vascular cambium activity, and apical dominance and stimulates cell division, cell enlargement, and tissue expansion [197]. Zeatin-riboside content in shoots and roots of potatoes was enhanced due to inoculation with cells *B. subtilis* 26D [192]. *Pseudomonas* spp. and Bacillus may produce phytohormones (auxins and cytokinin), promoting crop growth development [198]. *B. subtilis* IB-22 generates zeatin-ribosides and may induce a 10-fold increase in cytokinin accumulation in lettuce [199]. *Citricoccus zhacaiensis* and *Bacillus amyloliquefaciens*, which produce cytokinins, increased root and shoot biomass in tomato plants [161]. Oriental Thuja plants inoculated with cytokinin-producing *Bacillus subtilis* strains were more resistant to drought stress [200]. Cytokinin generated by PGPMs raises abscisic acid levels, which causes stomata to close during drought, minimizing water loss through the leaves [201]. A previous study found that inoculating soybeans with *Bradyrhizobium japonicum* and *Azospirillum brasilense* maintained leaf membrane stability under drought but was not enough to maintain leaf water content. Co-inoculation of *B. japonicum* and *A. brasilense* alleviated drought stress by maintaining better plant growth, suggesting greater drought tolerance [202].

Furthermore, PGPMs enhance plant growth by boosting gibberellins, enhancing seed germination, and promoting the formation of stems, leaves, flowers, and fruits [197]. Using *Rhodobacter sphaeroides* SIR03 produces gibberellin in sesame seedlings [203]. Inoculation with *Penicillium* species during salt stress stimulated shoot growth in cucumber plants due to increased secretion of active gas [204]. *Penicillium resedanum* LK6 produces gibberellins and improved *Capsicum annuum* growth under salinity, drought, and heat stress. During abiotic stressors, this endophyte treatment significantly boosted shoot length, biomass, chlorophyll content, and photosynthesis [205]. *Penicillium strains* generate gibberellins; GA1, GA3, GA4, and GA7 structures have been discovered as growth hormones generated by *Penicillium strains* as a salt stress resistance response [206]. Surprisingly, the Pseudomonas putida H-2-3 is also capable of secreting gibberellin under drought and salty conditions, hence increasing plant development in soybeans [207].

Jasmonic acid (JA) is one of the significant growth regulators of plant innate immunity. Transcription of jasmonate-biosynthesis genes was stimulated in potato leaves due to supplying *B. subtilis* 26D [192]. *Pseudomonas putida* H-2-3 increased JA levels in soybean [207]. Application endophyte *Sphingomonas* sp. LK11 bacteria enhanced the development characteristics of tomato [208] and JA and ABA in soybean [209] under salty and drought stresses.

Another essential phytohormone that protects plants from stress and regulates their growth is abscisic acid (ABA) [196,210,211]. ABA-producing bacteria under drought conditions, namely *Bacillus licheniformis* and *Pseudomonas fluorescens*, stimulated grapevine growth [212]. Maize tolerance for a water deficit was enhanced with inoculation by *Azospirillum lipoferum* owing to enhanced ABA content and shrinking of GA and ABA synthesis inhibitors [213]. Similarly, *Arabidopsis thaliana* tolerance to drought stress was improved by *Azospirillum brasilense* because of the raised ABA level [214]. Following *Pseudomonas fluorescens* inoculation, genes related to the ABA pathway were highly activated in sensitive rice cultivars, augmenting their drought resistance [215].

Ethylene is an important plant hormone that regulates plant activities such as germinating seeds, ripening fruits, and plant senescence. It is also produced in plants as a reaction to various environmental stressors [216,217]. As a result, ethylene produced under stressful conditions is frequently referred to as “stress ethylene” [216,218]. The ethylene released during stress can cause decay, reduced growth of roots and stems, and gene expression, accelerating crop senescence and minimizing yield [219]. It is interesting to note that 1-aminocyclopropane-1-carboxylic acid (ACC) functions as a precursor for ethylene formation [171,216,220]. Among the various potential ways for improving plant development under drought, the most likely is a change in endogenous ethylene accumulation caused by the PGPMs [171,193]. Many microorganisms reduce ethylene content in stressed circumstances via enzymatic conversion of ACC to alfa ketobutyrate and ammonia [193]. Numerous research studies have confirmed the efficacy of ACC deaminase-stimulating PGPMs in alleviating stress in agricultural plants such as tomato [193], pea [221], rice [222,223], and maize [224], as shown in Table 3.

Table 3. Microorganisms enhance plants' resistance to abiotic and biotic stresses.

Microorganism	Kind of Stress	Plant	References
Rhizobacterial	Drought	*Capsicum annuum*	[162]
Achromobacter piechaudii	Salinity	*Capsicum annuum*	[163]
Pseudomonas AKM-P6	Heat stress	*Sorghum bicolor*	[164]
Trichoderma and *Bacillus*	Cold stress	*Zea mays*	[165]
Penicillium sp.	Salinity	*Cucumis sativus*	[204]
Penicillium resedanum	Salinity, drought, and heat stress	*Capsicum annuum*	[205]
Pseudomonas putida	Drought and salinity	*Glycine max*	[206]
Azospirillum brasilense	Drought	*Arabidopsis thaliana*	[207]
Pseudomonas fluorescens	Drought	*Oryza sativa*	[209]
Mucor sp.	Heavy metal toxicity	*Arabidopsis arenosa* (L.)	[225]
Chaetomium globosum	Salinity	*Chrysanthemum morifolium*	[226]
Arbuseular mycorrhiza	Drought	*Leymus chinensis* and *Hemarthria altissima*	[227]
Bacillus sp. SLS18	Heavy metal toxicity	*Solanum nigrum* (L.), *Sorghum bicolor* L.	[228]
Trichoderma hamatum DIS 219b	Drought	*Theobroma cacao* (L.)	[229]
Pseudomona indica	Osmotic stress	*Capsicum annum* (L.)	[230]
Sinorhizobium meliloti	Drought stress	*Medicago sativa* (L.)	[231]
Pseudomonas koreensis	Heavy metal toxicity	*Miscanthus sinensis*	[232]
Bacillus subtilis Z-12, *Bacillus aryabhattai* Z-48	Salinity	*Brassica rapa* sub sp. *Rapa*	[233]
Rhizobacteria	Biotic stress	*Vigna radiata*	[234]

6. Biofilm-Forming PGPMs

Plant growth-promoting microorganisms (PGPMs) that are biofilm-forming are of utmost significance to enhance plant health and productivity. PGPMs produce biofilms, intricate bacterial communities encased in a matrix of self-produced polymeric compounds. Biofilms confer several advantages, including enhanced resistance to environmental stresses, improved nutrient uptake, and protection against pathogens [235].

Biofilm formation is the result of different mechanisms, including adhesion to plant surfaces as PGPMs that promote plant growth and are biofilm producers stick to the plant surfaces, such as leaves and roots, by secreting adhesins, surface proteins that enable them to adhere. This initial adhesion plays a significant role in biofilm development and subsequent colonization of plant surfaces. Extracellular polymeric substances (EPSs) are synthesized following the adhesion of PGPMs. They consist of polysaccharides, proteins, and nucleic acids. EPSs constitute the matrix of the biofilm, thus conferring structural strength and resistance to environmental stresses. Biofilm formation is typically regulated by quorum sensing, a cell-to-cell communication mechanism allowing bacteria to behave concertedly based on their population density. Quorum sensing involves the production and sensing of signal molecules known as autoinducers, which regulate the expression of biofilm formation genes [235].

PGPMs that are biofilm producers enhance nutrient acquisition by providing a greater surface area for the uptake and release of nutrients from organic matter. For example, PGPMs like *Bacillus subtilis* and *Pseudomonas fluorescens* can solubilize phosphate and produce siderophores, which chelate iron and make it available to plants, as mentioned above.

Biofilms present a defense against plant pathogens by inhibiting their colonization and growth on the surface of plants. The EPS matrix can suppress the attachment of pathogens and destroy their virulence factors. Moreover, biofilm-producing PGPMs may also secrete antimicrobial metabolites, e.g., antibiotics and lytic enzymes, which directly inhibit pathogens' growth [236].

Overall plant fitness: biofilm-forming PGPMs contribute to plant fitness by promoting plant growth, enhancing stress tolerance, and increasing nutrient acquisition. PGPMs can secrete plant hormones such as auxins and cytokinins that trigger root and shoot development. PGPMs enhance the antioxidant defense system of the plant and induce high resistance against abiotic stresses, i.e., drought and salt stress.

7. PGPMs' Commercialization and Challenges in Formulating Viable Inoculants

The growing interest in sustainable agriculture and integrated management of environmental resources has led to the expansion of biofertilizers, which has positively impacted the biofertilizer market in many regions around the world [237]. Demand for biofertilizers, especially microbe-based ones, has increased significantly in Spain, Italy, and Germany. Recent marketing research has revealed that the volume of biofertilizer trading reached USD 2.02 billion in 2022 and is expected to reach USD 5.02 billion by 2030, according to [238]. North America has the largest share of the biofertilizer market at 35.2%, followed by Europe at 28.9% [239]. Microbes that solubilize and mobilize nutrients are the most dominant in the biofertilizer market, such as the genera *Azotobacter* and *Azospirillum*. As for fungi, the genera *Pencillum*, *Trichoderma*, and *Aspergillus* are the most widespread [240,241].

7.1. Bioformulations

Bioformulations are a biologically active mixture of microbial biomass, metabolites, and a carrier substance [242]. These formulations can be divided into solids, liquids, metabolites, cell-free culture supernatant (CFCS), and encapsulated forms [243].

7.1.1. Solid Formulations

Solid formulations provide a nutritious and protected environment for microbes. This formulation is in the form of granules that can be spread and dispersed in water with the carrier materials. This type of formulation faces important challenges, including sediments at the bottom of the containers used to spray biofertilizers and the lack of complete homogeneity. Also, the release of microbes from this type of formulation is slow, which may change the conditions surrounding the microbes in terms of temperature and humidity, which ultimately affects the formulation's effectiveness and the stability of microorganisms in it [169,244].

7.1.2. Liquid Formulations

Liquid formulations are aqueous biomass suspensions in water, oils, or Schisler24. This type of formulation is characterized by its homogeneity and the rapid release of microbes. It provides stability to the microbes but faces challenges during the transportation, handling, and storage process, affecting the microbes' vitality and activity [245].

7.1.3. Metabolites

Secondary metabolites of some microorganisms can be used as growth regulators and stimulants. These metabolites also facilitate nutrients and activate plant defense systems against various pests. Using microbes that produce metabolites as bio-inoculators improves plant growth and productivity [243]. However, this type of formulation faces challenges, the most important of which is the failure to ensure proper solubility and the inability to spread while maintaining the biological activity of the metabolites [245].

7.1.4. Cell-Free Culture Supernatant (CFCS)

This formulation consists of metabolic materials that do not contain any microbial cells, such as enzymes and others. However, this type faces many challenges that hinder its spread, including the fact that these formulations are affected by heat and light, which affects their effectiveness when used. This type is also more susceptible to microbial contamination during storage and handling and is expensive [245,246].

7.1.5. Encapsulated Formulation

There are limitations to solid and liquid formulations, such as microbial viability and long-term storage. However, encapsulation technology has allowed microbes to remain active for a long time and has facilitated the application process [247]. The encapsulation process also helps control the release of microbes and their metabolites into the soil, which improves the area around the plant roots and activates free beneficial microbes inside the soil, which improves soil structure [248]. The encapsulation process is made of polymeric materials that allow the exchange of gases, nutrients, and metabolites, which maintains the vitality of microbes inside the capsule [243]. Currently, no information is available to help understand the effects of encapsulated formulations on soil and water, which may lead to unintended changes in soil structure or interference with nutrient cycling [249].

8. Potentials, Strategies, and Limitations for the Application of PGPMs in Agriculture

Plant growth-promoting microorganisms (PGPMs) hold great potential in agriculture. They can significantly enhance plant growth by solubilizing both organic and inorganic compounds, increasing water uptake, solubilizing nutrients, fixing nitrogen, and producing phytohormones. Additionally, certain PGPMs can suppress plant pathogens and biologically control root pathogens, reducing the need for chemical pesticides. These microorganisms also help plants tolerate abiotic stresses such as drought, salinity, and extreme temperature, contributing to more sustainable farming practices [250,251]. Several strategies exist for applying PGPMs in agriculture. These include inoculating seeds, soil, or plant roots with beneficial microorganisms. Inoculation involves directly applying beneficial microorganisms to seeds, soil, or plant roots [251,252]. This can be implemented as follows:

- Seed treatment: coating seeds with microbial inoculants before planting. Microbial seed coating involves using a binder, and sometimes a filler, combined with inoculant. This process can be performed with essential mixing equipment (e.g., cement mixer) or more advanced machinery (e.g., fluidized bed). Binders and fillers help extend the survival of the microorganisms. The most common types of seed coatings are seed dressings, film coatings, and pelleting. This technique has been tested on over 50 plant species with seeds of varying dimensions, shapes, textures, and germination types, including cereals, vegetables, fruits, pulses, and other legumes. Studies have utilized various species of plant growth-promoting bacteria, Rhizobia, Trichoderma, and, to a lesser extent, mycorrhizal fungi [253];
- Soil inoculation: applying microorganisms directly to the soil to establish beneficial microbial communities. Available in liquid (suspension), solid (powder and granular), and paste forms. Polyvinylpyrrolidone (PVP) is commonly used as a vehicle for liquid inoculants. For solid inoculants, the microbial strain is mixed with solid carriers such as peat, rock phosphate, charcoal, and coconut peat. When using peats, particles with diameters between 0.35 and 1.2 mm are preferred [254];
- Root inoculation: introducing microorganisms to seedling roots to enhance nutrient uptake and growth. Soaking new plant roots in PGPMs just before planting or repotting is a great way to help plants deal with transplant shock;

However, there are limitations to the application of PGPMs in agriculture. Environmental conditions such as soil type, temperature, and moisture can influence the effectiveness of these microorganisms, making it challenging to achieve consistent results. Many of these approaches are not feasible on a large scale because of the amount of microbial inoculum needed, particularly in broad-acre crops [255]. The development and commercialization of PGPM-based products can also face regulatory hurdles. Additionally, the cost of production and application of PGPMs can be a limiting factor for widespread adoption.

9. Conclusions and Future Prospects

Agricultural soils are rich environments with microorganisms, some of which are harmful and could cause plant diseases, while others are serviceable and improve plant growth. PGPMs are considered members of the beneficial microbes present in the soil. Understanding the mechanisms by which PGPMs could increase crop yield is crucial for sustainable agriculture. These mechanisms include the (1) production of phytohormones that lead to an induction of tolerance to plants under stress conditions and an increase in the defensive state in plants. (2) Phosphate solubilization, as they can produce organic acids that calculate the cations linked to phosphate, making it available for plants. (3) Fixation of nitrogen, which happens when symbiotic or non-symbiotic bacteria convert atmospheric nitrogen into ammonia to be available for plants. (4) Secretion of antibiotics that kill or inhibit phytopathogen growth. (5) Competition with plant pathogens for macro- and micronutrients and space. (6) Lytic enzyme secretion to lyse and degrade the cell walls of plant pathogens. PGPMs could also mitigate the negative impacts caused by the increased use of fertilizers, irrigation, and deep tillage by developing soil organic matter, enhancing nutrient uptake, and increasing micronutrient availability. They have also been shown to alleviate abiotic stressors such as drought, salinity, and harmful temperatures. Due to these rationales, the integration of PGPMs in agricultural practices emerges as a crucial imperative for achieving sustainability objectives and safeguarding the integrity of environmental bio-systems.

Developing PGPM products by exploiting industrial technologies is significant in supporting agriculture sustainability, specifically in stressed environments. In this area, substantial scientific attempts should be adopted to raise the efficacy of PGPMs and include them as a significant practice in nutrition, irrigation, and protection management for more resilient and efficient farming systems. Potential research would emphasize realizing molecular and physiological mechanisms and improving application practices. Continuous research, innovation, and application of these microorganisms are needed for building resilient crop varieties, also giving security to the worldwide food chain amongst the agriculture challenges of climate change and environmental stressors.

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