

Review

Microbial Utilization to Nurture Robust Agroecosystems for Food Security

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Abstract: In the context of anthropogenic evolution, various sectors have been exploited to satisfy human needs and demands, often pushing them to the brink of deterioration and destruction. One such sector is agrochemicals, which have been increasingly employed to achieve higher yields and bridge the gap between food supply and demand. However, extensive and prolonged use of chemical fertilizers most often degrades soil structure over time, resulting in reduced yields and consequently further exacerbating the disparity between supply and demand. To address these challenges and ensure sustainable agricultural production, utilization of microorganisms offers promising solutions. Hence, microorganisms, particularly effective microorganisms (EMs) and plant growth-promoting microbes (PGPMs), are pivotal in agricultural biomes. They enhance crop yields through active contribution to crucial biological processes like nitrogen fixation and phytohormone synthesis, making vital nutrients soluble and acting as natural enemies against pests and pathogens. Microbes directly enhance soil vigor and stimulate plant growth via the exudation of bioactive compounds. The utilization of EMs and PGPMs reduces the need for chemical inputs, leading to lower costs and reduced environmental pollutants. Furthermore, beneficial soil microflora produces growth-related metabolites and phytohormones that augment plant growth and support stress resilience. Microbes also help plants tolerate various abiotic stresses, including metal stress, salt stress, and drought stress, through various mechanisms. Understanding the interactions and activities of microorganisms provides valuable insights into their potential use to manage stress in plants. Thus, by leveraging the full potential of microorganisms, we can develop healthier agroecosystems that contribute sustainably to meet the growing global food demands.

Keywords: agroecology; microbiome; PGPMs; plant growth regulators; stress tolerance



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1. Introduction

In the pursuit of a luxurious lifestyle, humans have driven anthropogenic evolution, resulting in widespread industrialization. Concurrently, the global population has been growing exponentially, raising significant concerns regarding food security. To address these challenges, a revolution unfolded in the early 1970s with the introduction of agrochemicals, aimed at enhancing crop yields and productivity. The primary objective of using these agrochemicals was to alleviate the miseries faced by the growing population by ensuring an ample food supply [1]. This rather led to heavy reliance of crop productivity on synthetic agrochemicals, creating new threats for contemporary agroecosystems. The non-judicious usage of these chemicals not only deteriorated agroecosystems but also led

to contamination of water bodies [2]. Excessive use of agrochemicals and their ensuing accumulation can cause them to become part of the food chain, thereby negatively impacting living organisms. Moreover, the runoff of these chemicals from agroecosystems during flooding exacerbates the deterioration of the situation [3].

Moreover, prolonged and indiscriminate usage of industrial fertilizers can also disturb the microecology of the soil, leading to disruptions in the nutrient cycle. In such circumstances, it becomes crucial to safeguard soil microbial diversity from the adverse impacts of commercial fertilizers [4]. In a review by Meena, et al. [5], it was noted that the WHO has recorded three million cases of agrochemical poisoning in developing nations. The extended, intensive, and indiscriminate use of agrochemicals has negatively impacted soil biodiversity, agricultural sustainability, and food safety, leading to long-term detrimental effects on nutritional security, as well as human and animal health. Many of these agrochemicals disrupt soil microbial functions and biochemical processes. Changes in the diversity and composition of beneficial microbial communities can negatively impact plant growth and development by either reducing nutrient availability or increasing the incidence of diseases. The decline in microflora and disruption of nutrient cycling hinder the ability of plant roots to access essential nutrients, leading to decreased plant development, yield, and overall production [6,7]. Apart from that, industrial fertilizers also have detrimental effects on underground diversity, which is essential for ecosystem sustainability. Therefore, it is imperative to prioritize the adoption of natural agricultural practices to preserve and restore degraded soil fertility and the environment [8]. This has led to a renewed interest in organic farming, a cropping system that involves minimal or no chemical usage, and instead relies on substitutive techniques that promote sustainable crop productivity. This approach includes the use of organic manures, which not only enhance the physiochemical properties of agricultural land but also serve as a nutrient source [9,10].

Another sustainable option is to advance crop productivity and mitigate agrochemical pollution through the exploitation of PGPMs. A review by de Andrade, et al. [11] highlighted the potential of rhizospheric bacteria for promoting sustainable agriculture. These microbes possess various abilities to promote plant growth, both directly and indirectly. They support host plants by enhancing nutrient availability, stimulating higher phytohormone production, mitigating their effects, inducing systemic resistance to protect against phytopathogens, and improving root and shoot development. Additionally, PGPRs (plant growth-promoting rhizobacteria) help the host alleviate abiotic stresses by modulating enzymes and proteins, detoxifying the plant from harmful impacts. Utilizing these microbes is a crucial strategy in sustainable agriculture, as they reduce the need for synthetic fertilizers and pesticides while promoting plant growth and health and enhancing soil fertility. These microbes offer a novel and cost-effective approach by not only enhancing agronomic efficiency and reducing the production costs of agrochemicals but also acting as a more effective alternative to industrial fertilizers. Additionally, their use helps in minimizing the pollution triggered by the hefty use of agrochemicals [12]. Microbial communities consisting of fungi and bacteria are employed as inoculants to primarily promote host growth via diverse mechanisms. These mechanisms include secretion of exopolysaccharides, nitrogen fixation, chelation of iron, solubilization of phosphate and potassium, biocontrol capabilities, breakdown of organic matter, and production of siderophores [13]. For instance, the bacterium *Azospirillum*, which exists as a free-living organism, has a significant contribution to nitrogen fixation and increasing soil nitrogen levels. As a result, it contributes to enhancing the overall performance of non-leguminous crops [14,15]. Certain species, like *Pseudomonas putida* and *Pseudomonas fluorescens*, indirectly contribute to host plant growth by inhibiting phytopathogens and promoting nitrogen and phosphate solubilization and assimilation [16,17]. *Azospirillum* and *Azotobacter* are highly operative in stimulating the release of phytohormones and other growth-related metabolites, thereby boosting vegetative growth [18,19]. Phosphorus-solubilizing bacteria play a key role in making phosphate accessible to plants. Phosphate is a vital soil nutrient that typically exists in a complex and unattainable form [20,21]. In a contemporary investigation on eggplants, it was noticed that

Bacillus mucilaginosus and *Bacillus megaterium* significantly improved the solubilization of potassium and phosphorus, consequently boosting the growth attributes of the host plant. Additionally, co-inoculation with multiple organisms compared to single-strain inoculation may further enhance agronomic attributes by providing diverse benefits to host plants (Figure 1) [22–24].

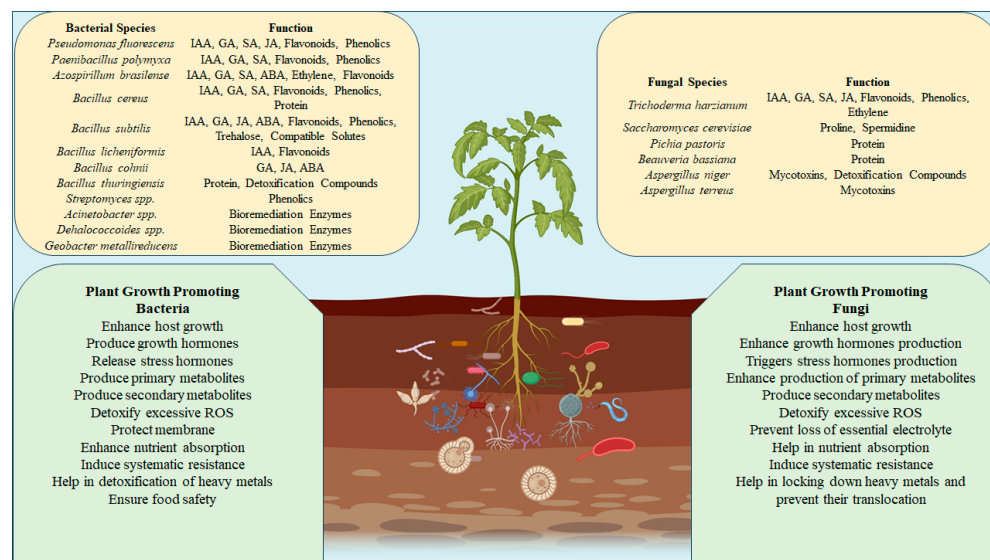


Figure 1. Bacterial and fungal metabolites in support of plant growth and development.

2. Promoting Sustainability and Crop Productivity through Microbial Interactions

With an increase in societal awareness, farmers in developed and technologically advanced countries are transitioning their farming methods towards organic practices [25]. Consumers who opt for organic crops are typically well-educated, affluent, environmentally conscious, and prioritize their health. While organic farming holds the promise of enhancing the environment and food quality along with the sustainability of the agricultural framework, it may not be sufficient to satisfy the rising demands for food [26].

Significant scientific research is currently underway to explore the optimal utilization of agricultural resources aimed at increasing output through biological techniques, rather than relying on chemical methods [27]. Researchers have been actively considering the implementation of organic agroecosystems using EMs to enhance production while maintaining environmental sustainability [28]. These microorganisms are vital for driving the biogeochemical nutrient cycle and mitigating the use of industrial fertilizers. For instance, the widespread use of plant and animal manures, along with distinctive microbial species such as fungi and bacteria, promotes overall crop growth and yields [2]. By enhancing processes like photosynthesis, nitrogen fixation, synthesis of phytohormones and stress-related metabolites, vitamin and enzyme production, decomposition, release of bioactive compounds, drought tolerance, and biocontrol mechanisms against pests, the formulated EMs ensure the well-being of crops. Consequently, EMs improve the diversity of microflora and fauna, adding to the improvement of resilient farming [18,29,30].

Furthermore, microorganisms have a pivotal role in preserving a balanced agroecosystem by facilitating interactions between biotic and abiotic components through ecological associations, as well as mineral biogeochemical cycling [31]. In soils, microbes are essential for sustaining the balance of organic and inorganic nutrients, which is closely related to the stoichiometric C:N ratio [32]. The C:N ratio reflects the abundance of carbon (C), nitrogen (N), and phosphorus (P) in the soil, playing a key role in sustaining microbial activity and, consequently, soil health and crop productivity. The decomposition of organic matter leads to an increased carbon-to-nitrogen ratio, which revitalizes microbial diversity and activity [32,33]. These microorganisms are also crucial for nutrient cycling processes, including nitrification, nitrogen fixation, and the mobilization of phosphorus and other

essential elements. Imbalances in the C:N ratio can disrupt these microbial activities, leading to inefficient nutrient cycling and potential soil deficiencies, which may decrease soil fertility [34]. However, a high C ratio may restrict nitrogen availability for plants, whereas a low ratio could result in excess nitrogen, potentially causing environmental problems such as leaching or volatilization [35]. Similarly, phosphorus availability, which is regulated by microbial activity, is crucial for maintaining the optimal C:N ratio that supports overall soil fertility and plant growth [36]. Soil microorganisms metabolize organic compounds, ensuring the maintenance of soil organic carbon exceeding critical levels, which aids in soil particle retention, enhances water holding capacity, and reduces soil erosion [37,38]. The decay of organic substances leads to a greater carbon-to-nitrogen ratio, revitalizing microbial diversity [39–41]. Microbes also contribute to the production of soil-available NH_4^+ and NO_3^- through nitrification and nitrogen fixation processes. Microbial enzymes such as “nitrogenase” cleave the diazo bond to yield NH_4^+ , while bifurcated processes (nitritification/nitrosification and nitrataion/nitrification) oxidize NH_4^+ and NO_3^- . Meanwhile, the designated microorganisms are proficient in breaking down phosphorus-containing compounds and making them available through the secretion of organic acids. They also facilitate the chelation and liberation of other vital elements such as K^+ , Mg^{+2} , Ca^{+2} , Mn^{+2} , and trace elements [42–46]. These mineral biogeochemical cycles are predominantly carried out by potential microorganisms, which can be influenced by various interactions with the biotic community (microbe–microbe, microbe–plant, or microbe–animal/human) as well as abiotic elements [31]. Host plants also benefit from beneficial associations with microbes, including symbiosis, mutualism, amensalism, commensalism, and photo-cooperation. Conversely, these interactions can also exert adverse effects on phytopathogens through their antagonistic nature. These interactions represent fundamental aspects of the beneficial activities exhibited by PGPMs [47–49]. In short, organic approaches prioritize environmental preservation, food quality, and consumer health, while EMs, composed of helpful microorganisms, perform a critical function in promoting nutrient cycling, improving crop growth and yield, and maintaining a balanced agroecosystem. Hence, the use of EMs and their interactions with the host plant and other soil microbiomes hold significant potential for advancing sustainable agriculture and meeting the increasing demands for food.

3. Exploiting the Potential of Microbes

Microbes possess unique traits that are often absent in higher organisms but are extremely valuable in agricultural ecosystems. With their distinct biological and physiochemical compatibility, these microorganisms are commonly co-inoculated, formulated, and utilized as EMs in agricultural practices. The role of EMs as PGPMs [50,51] is also crucial in nitrogen fixation, synthesis of siderophores, release of ACC deaminase and exogenous phytohormones, solubilization of biologically important elements like nitrogen, carbon, and phosphorus, and improvement of soil features. They also contribute by enhancing photosynthetic efficiency, synthesizing growth regulators, monitoring soil diseases, and promoting the digestion of lignin in the soil [50,52,53].

Direct actions such as soil amelioration, production of phytohormones, and enhancement of soil fertility by mobilizing mineral components are important contributions of microorganisms in agriculture, while indirect actions involve the production of bioactive compounds that inhibit or kill phytopathogens, acting as biocontrol agents, ultimately augmenting the growth and yield of the host species and maintaining a healthy agroecosystem [54,55]. Hence, PGPMs can serve as viable alternatives to pesticides and insecticides. Agricultural lands with low organic phosphorus content face challenges in terms of bioavailability. Phosphate-solubilizing microorganisms (PSMs) are instrumental in solubilizing the insoluble form of phosphate (PO_3) and improving its accessibility for plant uptake [56,57]. The phosphate-solubilizing abilities of bacteria like *Bacillus* and *Pseudomonas*, together with fungal species like *Aspergillus* and *Penicillium*, can be augmented through genetic modification or co-inoculation practices to enhance their in situ performance [58,59].

The known PGPMs can be sorted into three distinct groups, i.e., plant growth-promoting bacteria (PGPB), plant growth-promoting rhizobacteria (PGPRs), and vesicular-arbuscular mycorrhizal fungi (AMF) [60,61]. PGPRs like *Chryseobacterium humi* and *Pseudomonas reactans*, as well as AMF like *Rhizophagus irregularis*, contribute to soil fertility enhancement, ultimately improving crop productivity and development [31,62]. Various inputs such as manure, chemical fertilizers, organic biofertilizers, and molasses can be combined with EMs. By utilizing a microbial consortium composed of PGPRs, fertilizers and insecticides can be replaced, reducing pollutants and contaminants and lowering input costs without compromising yield [63]. Mutualistic N₂-fixing partners like *Mesorhizobium*, *Sinorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Rhizobium*, and *Allorhizobium* contribute positively to plant growth and yield [64,65]. The N₂-fixing bacteria such as *Enterobacter*, *Klebsiella*, *Azospirillum*, and *Pseudomonas* colonize the rhizosphere and also function as N₂ fixers for host plants [66], while PGPB such as *Bacillus subtilis* and *Pseudomonas fluorescens* produce plant growth-promoting chemicals [67,68]. *Bacillus amyloliquefaciens* promotes host plant growth while protecting against *Fusarium oxysporum* [69]. Co-inoculated *Azospirillum brasilense* and *Bacillus subtilis* effectively improve host growth attributes through modulation of metabolite production and acting as biocontrol agents [70]. Likewise, PGPB (*Pseudomonas*) and AMF enhance the nutritional value (sugar and vitamin contents) and quality of tomatoes by improving flowering and fruiting [31]. Among AMF, *Glomus fasciculatum* has a substantial impact on the growth of *Zea mays* [71]. These fungal isolates produce alkaline and acid phosphatases that solubilize phosphorus, making it accessible to plants. Soil actinomycetes yield antibiotics and ectoenzymes that hinder phytopathogens, thereby promoting the plant's physiological development [72]. Numerous microbial strains from different genera have been observed to protect plants from various stresses (Figure 2), with PGPR isolates, in particular, showing antagonistic effects against phytopathogens [73].

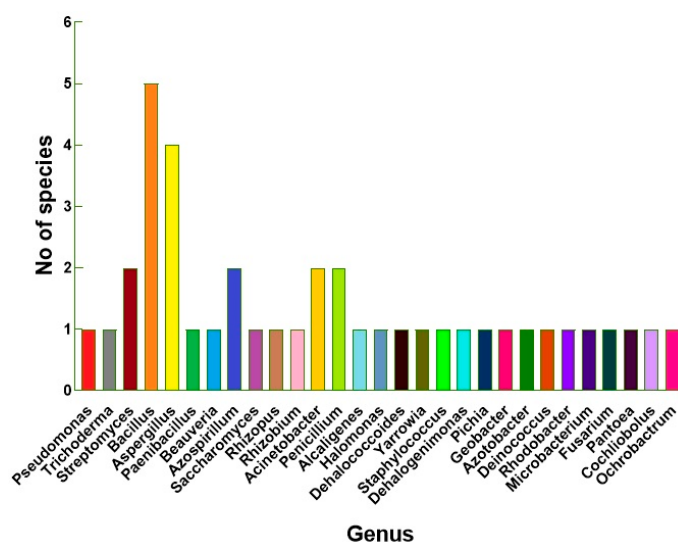


Figure 2. Microbial species and genera that promote plant growth.

3.1. Metabolite Synthesis and Ethylene Regulation

One key aspect of PGPMs is the synthesis of growth-related metabolites. For example, *Staphylococcus arlettae* is perceived to stimulate host root and shoot growth, resulting in higher yield and productivity, with increased levels of gibberellic acid (GA), indole acetic acid (IAA), and salicylic acid (SA) [74]. Similarly, the endophytic fungi, W11 strain, also demonstrated the proficiency to synthesize phytohormones and growth-related metabolites while colonizing maize roots, thereby augmenting host plant growth attributes [75], while strains such as *Pantoea conspicua* and *Acinetobacter bouvetii* produce higher quantities of important metabolites, including GA, IAA, SA, sugar, phenolics, flavonoids, and proline.

These metabolites not only enhance host growth attributes but also assist in stress mitigation during harsh environmental conditions [76,77].

Ethylene, at lower concentrations, dictates plant growth, senescence, and stress tolerance. However, elevated concentrations of ethylene can have undesirable effects on roots in host plants [78]. In plants, ACC (1-aminocyclopropane-1-decarboxylate) acts as an antecedent to ethylene production. The enzyme ACC deaminase metabolizes ACC, inhibiting ethylene production as an ethylene precursor [79]. Microbes possessing ACC deaminase production properties actively absorb ACC and metabolize it into NH_3 and α -ketoglutarate, thereby reducing ethylene production in host plants. Actinomycetes, for instance *Streptomyces* sp. and *Microbispora* sp., secrete the phytohormone IAA and the stress-alleviating ACC deaminase, helping to alleviate stressful conditions. They are commonly used as co-inoculants and are frequently reported to relieve stress in host plants [80,81].

3.2. Important Metal Solubilizers and Mobilizers

In sugarcane and sunflowers, potential microbes demonstrate the power to produce siderophores, solubilize phosphate (PO_4), and fix nitrogen (N_2), which in turn promote host growth [76,82–84]. These microbes serve as efficient bioinoculants, producing phytohormones, for example, GA, IAA, ethylene, and cytokinins [76,82–84]. In some cases, single microbial cultures may face challenges from the competitiveness and aggressive actions of native soil microflora, resulting in a decline in their population [85–87]. Some of these PGPMs can enhance resistance against salinity stresses. Soil salinity poses a significant barrier to crop development and overall well-being, particularly in coastal areas. For instance, a *Bacillus flexus* strain demonstrated increased salinity resistance in crops [88]. The inoculation of *Enterobacter* sp. UPMR18 improved the germination rate, growth parameters, and total chlorophyll content of okra plants by enhancing salt tolerance [89]. Meanwhile, some of the EMs can help shift the equilibrium and promote crop growth by improving and maintaining the physicochemical properties of the soil. Model EMs, including *Pseudomonas*, *Bacillus*, *Serratia*, *Streptomyces*, and *Stenotrophomonas*, as well as fungi like *Ampelomyces*, *Coniothyrium*, and *Trichoderma*, have shown improvements in crop health [90,91].

In the rhizosphere, EMs can establish symbiotic relationships. Plant roots exude organic acids, carbohydrates, amino acids, and active enzymes, acting as a food source for beneficial microorganisms [92]. In return, these microbes release amino acids, nucleic acids, vitamins, and hormones to benefit the plant [93]. Disease-suppressive agroecosystems harbor a significant number of antibiotic-producing microorganisms, including *Penicillium*, *Aspergillus*, *Trichoderma*, and *Streptomyces* [94]. Soils rich in yeasts, lactic acid-producing bacteria, and fermenting fungi like *Rhizopus* and *Aspergillus*, usually referred to as “zymogenic soils”, exhibit excellent physical characteristics and have enhanced water storage capacity [95]. Bacterial endophytes play a beneficial role in fixing nitrogen in the soil and rendering it available to the plants. They also exude plant growth-promoting hormones to facilitate their host plants under normal and stressful conditions [96].

Essentially, beneficial microbes have a crucial impact on enhancing and preserving the physicochemical characteristics of the soil, thereby promoting crop growth, production, and health. The establishment of symbiotic relationships in the rhizosphere allows for the exchange of nutrients between plants and beneficial bacteria, contributing to the plants' well-being. Disease-suppressive agroecosystems harbor antibiotic-producing microorganisms, and soils rich in zymogenic organisms exhibit excellent physical characteristics and enhanced water storage capacity. Bacterial endophytes provide additional benefits by fixing nitrogen and secreting plant growth-promoting hormones to assist host plants under normal and stressful conditions. Overall, these microbial interactions and activities offer valuable opportunities for improving crop cultivation and ensuring sustainable agricultural practices.

4. Biotic Stress and PGPMs

Biotic stresses that are caused by a range of organisms, including pathogenic bacteria and pests, pose a substantial threat to global agricultural productivity and food security [97]. Conventional farming practices, which are predominantly dependent on chemical pesticides and fertilizers, have adversely affected the environment and resulted in the emergence of resistant strains [98,99]. As a response, the demand for sustainable agriculture has reached a critical point, driving research into more environmentally friendly alternatives. As a general approach to sustainable farming, PGPMs have exhibited potential in enhancing both plant yield and resilience against diverse biotic stresses (Table 1). Through their intrusion into the rhizosphere and a multitude of advantageous effects, PGPMs establish symbiotic partnerships with plants [100]. These results encompass the solubilization of vital elements like phosphorus and iron, enhancing the accessibility of nutrients to plants (Figure 3). Additionally, PGPMs can generate other phytohormones such as auxins, cytokinins, and GAs that play a pivotal role in governing plant growth and stress responses. Through the alteration of stress-responsive gene expression, PGPMs enhance the plant's capacity to adeptly manage biotic stress factors [12].

Table 1. PGPMs and their role in biotic stress alleviation.

No.	Name of Microbial Species	Stress	References
1	<i>Pseudomonas fluorescens</i>	Plant pathogens, soil-borne diseases	[101]
2	<i>Trichoderma harzianum</i>	Plant pathogens, soil-borne diseases, abiotic stress	[102]
3	<i>Streptomyces</i> spp.	Antibiotic production, pathogenic bacteria	[103]
4	<i>Bacillus thuringiensis</i>	Insect pests, nematodes	[104]
5	<i>Aspergillus oryzae</i>	Aflatoxin contamination	[105]
6	<i>Paenibacillus polymyxa</i>	Plant pathogens, nematodes	[106]
7	<i>Beauveria bassiana</i>	Insect pests	[107]
8	<i>Azospirillum brasilense</i>	Plant growth promotion, induced systemic resistance	[108]
9	<i>Streptomyces venezuelae</i>	Antibiotic production, pathogens	[109]
10	<i>Bacillus cereus</i>	Plant growth promotion, induced systemic resistance	[110]

Another effect of PGPMs on plants is their ability to induce systemic resistance, commonly abbreviated as ISR (induced systemic resistance). This ISR entails priming the plant's immune system for a quick and efficient response when confronted with potential disease threats [111]. The accretion of pathogenesis-related (PR) proteins and secondary metabolites has also been evidenced during this heightened defensive response, including antimicrobial substances that hinder pathogen growth and infection [112]. For PGPMs to be effectively employed in sustainable agriculture, a pivotal requirement is their capacity to function as a biocontrol agent against phytopathogens. This aspect holds significant importance, as certain PGPMs exhibit antagonistic traits that effectively thwart the proliferation and colonization of infections [113]. The synthesis of antifungal and antibacterial compounds, resource and space competition, as well as the activation of plant-mediated defense mechanisms, are among the contributing elements to this antagonistic interaction. Harnessing these biocontrol capabilities offers a practical approach to reduce dependency on chemical pesticides and mitigate adverse environmental impacts [114,115].

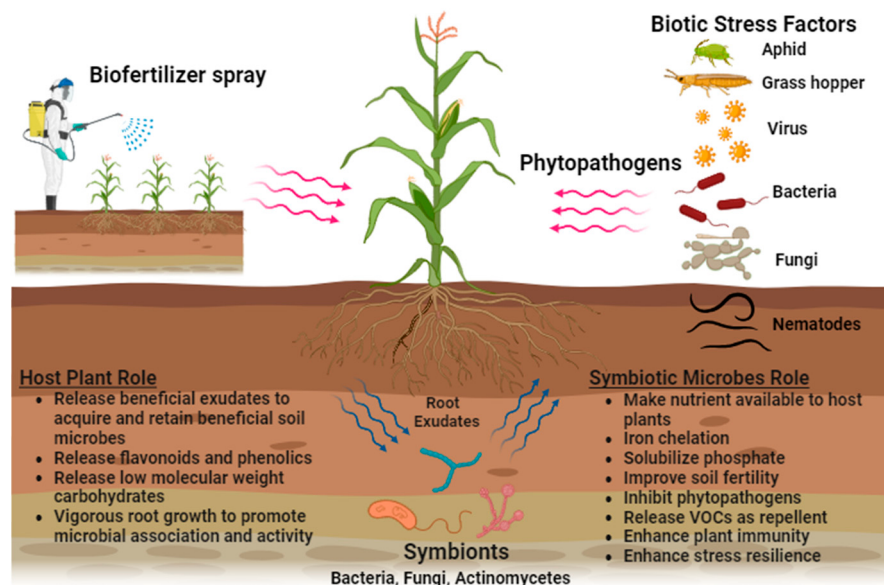


Figure 3. Role of plant growth-promoting microbes (PGPMs) in maintaining plant health under biotic stress.

Plant-parasitic nematodes, diminutive worms that inflict substantial damage to crops worldwide, lead to significant financial losses within the realm of agriculture [116,117]. Conventional strategies for managing these worms rely on chemical nematicides, despite their potential adverse effects on the environment and non-target organisms [106]. The utilization of Plant PGPMs as an ecologically sound and sustainable solution for nematode control has witnessed an upsurge in popularity in recent times. Beyond fostering plant growth, PGPMs also possess the capability to manage nematode populations through a variety of methods [117,118]. Eliciting systemic resistance within plants stands as a primary strategy employed by PGPMs to counter nematode infestations. Upon root colonization by PGPMs, plants activate their defense mechanisms, leading to the accumulation of defensive chemicals that are of paramount importance in protection [119,120]. Among these mechanisms, the presence of PR proteins that impede nematode growth and reproduction, along with phytohormones like SA and jasmonate, is noteworthy. This fortifies the plant's immune system, thereby reducing root penetration and feeding ability of nematodes [121,122].

Certain PGPMs exhibit the capability to synthesize antimicrobial compounds and secondary metabolites that exert toxicity against parasitic nematodes. These substances directly influence the survival and growth of nematodes, potentially disrupting their life cycles and diminishing their virulence. Moreover, specific PGPMs produce volatile organic compounds (VOCs) that act as repellents, deterring nematodes from entering the root zone [123,124]. The rhizosphere (soil area encompassing plant roots) establishes a dynamic milieu where PGPMs and nematodes contend for nutrients. Additionally, these PGPMs can curtail the proliferation and establishment of nematode populations by outcompeting them for essential nutrients and the limited space available [125,126]. Sharing the same ecological niche, nematodes find it challenging to thrive, leading to a decrease in their ability to infect and harm plant roots. Moreover, enhancements in plant growth and root system structure resulting from PGPMs can augment plants' resistance to nematode infestations, alongside their direct suppressive effects on nematodes. Meanwhile, a robust and extensively developed root system offers heightened resilience against nematode-induced harms, enabling quicker recovery from stress triggered by nematode activity [127].

Due to substantial crop damage and adverse economic repercussions, insects/pests persist as a grave threat to global agricultural productivity. Conventional approaches to pest control, predominantly reliant on chemical pesticides, not only jeopardize the environment but also foster the emergence of insect populations resistant to these chemicals [128]. Due to heightened endeavors of discovering environmentally friendly and sustainable

solutions to these challenges, PGPMs have emerged as a robust biocontrol strategy against insects/pests. Through the induction of systemic resistance, PGPMs intricately contribute to enhancing plant defenses against insects/pests [129]. Upon successful root colonization, PGPMs trigger intricate immunological responses within plants, including the production of defensive chemicals and signaling molecules [130]. By enabling an improved and rapid response to subsequent insect attacks, this systemic defensive priming diminishes crop losses caused by pests. Many PGPMs possess the capacity to generate secondary metabolites and insecticidal compounds that directly impact insects/pests. These substances might disrupt the insect's neurological system, inhibit its feeding, or influence its growth and development. To safeguard beneficial insects and non-target organisms, PGPM-mediated natural pesticides endorse a targeted and selective approach to pest control [131].

Insects/pests can either be drawn towards or repelled by the VOCs emitted by PGPMs. The presence of these VOCs can reduce pest-related harms by diverting them away from vital crops. Conversely, specific VOCs exert an opposing influence, acting as repellents to deter pests from feeding on plants [132]. Utilizing VOCs generated by PGPMs enables the manipulation of insect behavior and interference with their life cycles. These VOCs also increase plant resistance against insect predation [119]. Plants fortified by PGPMs develop extensive root systems, enhancing their resilience against insect feeding and ability to recover from damage. Furthermore, PGPMs within the rhizosphere influence the soil microbiome, fostering a diverse and harmonious ecosystem that indirectly contributes to managing insects/pests [133].

5. Abiotic Stress and PGPMs

Abiotic stresses, encompassing extreme temperatures, drought, salinity, and heavy metal exposure, have significantly disrupted global agricultural production. These stresses negatively influence plant growth and development, leading to substantial economic losses. Numerous PGPMs have been reported to play crucial roles in different abiotic stresses (Table 2). These PGPMs secrete a diverse range of bioactive compounds, including phytohormones, enzymes, and secondary metabolites during stress that are vital in facilitating plant growth and improving stress tolerance (Figure 4).

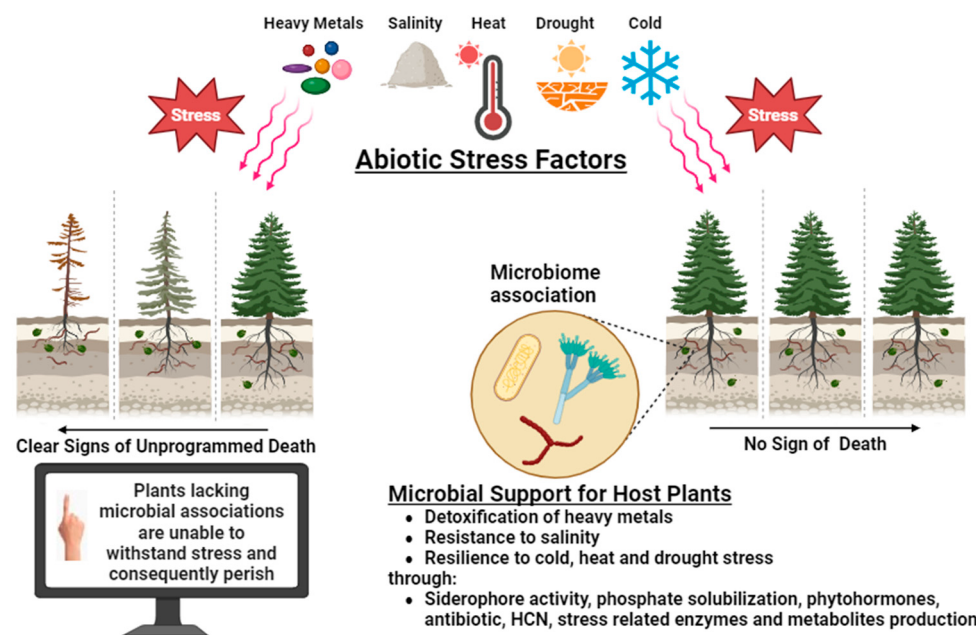


Figure 4. Mechanisms of plant growth-promoting microbes (PGPMs) in mitigating abiotic stress.

Table 2. PGPMs and their role in abiotic stress alleviation.

No.	Name of Microbial Species	Stress	References
1	<i>Bacillus subtilis</i>	Drought stress, salinity, heavy metals	[134]
2	<i>Saccharomyces cerevisiae</i>	Oxidative stress, heavy metals	[135]
3	<i>Azospirillum brasilense</i>	Drought stress, salinity, nutrient deficiency	[136]
4	<i>Rhizopus</i> sp.	Heavy metals	[137]
5	<i>Rhizobium</i> spp.	Nitrogen deficiency, salinity	[138]
6	<i>Streptomyces</i> spp.	Antibiotic production, pathogenic bacteria	[103]
7	<i>Aspergillus oryzae</i>	Aflatoxin contamination	[105]
8	<i>Acinetobacter bouvetii</i>	Heavy metals	[76]
9	<i>Penicillium radicum</i>	Heavy metals	[137]
10	<i>Alcaligenes eutrophus</i>	Heavy metals, organic pollutants	[139]
11	<i>Halomonas elongate</i>	Salinity, osmotic stress	[140]
12	<i>Bacillus licheniformis</i>	Salinity, drought stress	[141]
13	<i>Dehalococcoides</i> spp.	Chlorinated solvents, bioremediation	[142]
14	<i>Bacillus coagulans</i>	Abiotic stress, heat resistance	[143]
15	<i>Yarrowia lipolytica</i>	Salinity	[144]
16	<i>Staphylococcus arlettae</i>	Heavy metals	[74]
17	<i>Enterobacter</i> spp.	Heavy metals, organic pollutants	[145]
18	<i>Acinetobacter</i> spp.	Hydrocarbon degradation, organic pollutants	[146]
19	<i>Dehalogenimonas</i> spp.	Chlorinated solvents, bioremediation	[147]
20	<i>Pichia pastoris</i>	Oxidative stress, protein expression stress	[148]
21	<i>Bacillus cohnii</i>	Salinity, alkalinity	[149]
22	<i>Geobacter metallireducens</i>	Heavy metals, organic pollutants	[150]
23	<i>Enterobacter</i> sp. EB-14	Drought	[151,152]
24	<i>Azotobacter</i> spp.	Nutrient deficiency	[153]
25	<i>Deinococcus geothermalis</i>	Thermal stress, radiation resistance	[154]
26	<i>Rhodobacter sphaeroides</i>	Light stress, photosynthesis	[155]
27	<i>Penicillium roqueforti</i>	Heavy metals	[156]
28	<i>Microbacterium</i> sp. EB-65	Drought	[151,152]
29	<i>Fusarium proliferatum</i>	Heavy metals	[137]
30	<i>Aspergillus fumigatus</i>	Heavy metals	[137]
31	<i>Pantoea conspicua</i> and <i>A. niger</i>	Heavy metals	[77]
32	<i>Aspergillus niger</i>	Heavy metals	[157]
33	<i>Aspergillus terreus</i>	Salinity	[144]
34	<i>Cochliobolus</i> sp.	Salinity	[158]
35	<i>Enterobacter cloacae</i> strain EB-48	Drought	[151,152]
36	<i>Ochrobactrum</i> sp. EB-165	Drought	[151,152]

Phytohormones play a crucial role in stimulating plant growth and managing stress effectively. Microbial production of phytohormones modifies the physiology of the host and enhances its defense system, contributing to stress tolerance. For instance, *Penicillium roqueforti* modulates IAA in wheat plants. *P. roqueforti* has shown the proficiency to provoke resilience in wheat plants by limiting the transportation of soil heavy metals to

the plants [156]. Other strains like *Fusarium proliferatum*, *Aspergillus fumigatus*, *Penicillium radicum*, and *Rhizopus* sp. have been identified for their capacity to reduce metal stress and enhance host growth attributes [137]. In the case of chromate stress, the rhizobacterium MT4 strain of *Staphylococcus arlettae*, found in the rhizosphere of *Malvestrum tricuspadatum* L., has demonstrated the proficiency to release plant growth regulators and primary and secondary metabolites. Hence, it is considered a suitable choice for chromate stress relief. Similarly, MT4 has the ability to increase the relative growth rate and net assimilation of sunflower plants under chromate stress conditions. The underlying mechanism reveals that it reduces the uptake of chromate by the host, enhancing the host's antioxidant system and regulating the phytohormones. The ameliorated antioxidant system is evident through lower peroxidase activity, increased reactive oxygen species (ROS) scavenging, higher phenol accumulation, and decreased ROS generation [74]. In experiments with *S. lycopersicum* (tomato), *Aspergillus niger* has been found to reduce metal uptake and translocation to aerial parts. This isolate also facilitates the release of IAA, proline, flavonoids, phenols, ascorbic acid oxidase (AAO), catalase (CAT), and lower molecular weight carbohydrates and proteins to alleviate metal stress. Furthermore, *A. niger* upregulates stress-responsive genes (*SIGSH1* and *SIPCS1*) to bolster immune responses to metal (cadmium and chromium) exposure, allowing the host to chelate these metals and mitigate their toxicity [157]. A combination of *Pantoea conspicua* and *A. niger* can relieve metal stress in host plants via the generation of stress-related phytohormones and metabolites. *P. conspicua* transforms metals into stable and biologically unavailable forms, preventing their absorption by the host roots and avoiding toxicity. Meanwhile, *A. niger* immobilizes metals in its hyphae, preventing their translocation to aerial parts and reducing their toxic effects [77]. Similarly, *Acinetobacter bouvetii* mitigates metal and oxidative stresses in the host by strengthening its antioxidant system. This strain modulates the host's antioxidant system, leading to efficient ROS scavenging and lower ROS accumulation, facilitating robust growth of the host plant [76].

5.1. Salinity Stress

Salinity is recognized as one of the most detrimental abiotic stress factors, leading to significant annual losses in crop production. Recent research underscores the role of endophytes in mitigating salt stress. For instance, *Yarrowia lipolytica*, as an endophyte, potentially exhibits higher antioxidant activity and produces elevated levels of indole-3-acetamide (IAM), IAA, total flavonoids, and phenolics. This strain has been confirmed to augment the agronomic characteristics of maize plants under salt stress [144]. Similarly, *Aspergillus terreus* has been proven to promote the growth characteristics of *Pennisetum glaucum* under saline conditions. Increased colonization by this endophyte leads to enhanced chlorophyll content, higher fresh and dry biomass production, as well as greater shoot and root length under 100 mM NaCl stress conditions. Additionally, greater levels of stress-related metabolites and osmolytes have been recorded, contributing to stress alleviation [144]. Another endophyte, *Cochliobolus* sp., has been evidenced to alleviate salt stress by colonizing the host plant and modulating phytohormones and stress-related responses. Meanwhile, LC-MS/MS analysis of *Cochliobolus* sp. extracts disclosed the existence of salinity stress relievers such as chlorogenic acids, calycosin, pinocembrin, wogonin, and diadzein [158]. Hence, it can be inferred that endophytic fungi can serve as valuable tools for salt stress management in crops and offer promising prospects for sustainable agriculture in salinity-affected areas.

5.2. Drought Stress

Drought stress significantly limits crop production, and various strategies such as conventional breeding and genetic engineering are exercised to tackle this menace. In the current era, the interaction between plants and endophytic bacteria has gained attention as a promising approach for agricultural improvement. Endophytic bacteria residing within plant tissues have proven to be remarkably effective in improving host growth characteris-

tics during drought stress conditions. These bacteria inhabit intercellular and intracellular spaces and produce a range of compounds that facilitate plants in coping with detrimental environmental factors, including drought [159]. Nitrogen fixation, phosphorus solubilization, nutrient acquisition, siderophore production, synthesis of other phytohormones, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity are among the plant-growth beneficial attributes [159]. These endophytic bacteria participate in boosting root length and density, thereby improving drought tolerance. Moreover, they aid in the formation of drought-resilient substances, namely ACC deaminase, abscisic acid, IAA, and diverse volatile compounds. Endophytic bacteria indirectly enhance relative water content, osmotic adjustment, and antioxidant activity in plants [160]. In general, these bacteria continue to exhibit drought resilience and plant growth-enhancing capabilities even under harsh drought conditions, resulting in increased plant proliferation and yield. Consequently, the integration of drought-enduring and plant growth-boosting endophytic bacteria has been emphasized as a natural and environmentally friendly approach for intensifying drought survivability in plants [161].

Several pivotal endophytic bacteria, namely *Microbacterium* sp. EB-65, *Enterobacter cloacae* strain EB-48, *Enterobacter* sp. EB-14 and *Ochrobactrum* sp. EB-165 exhibit the ability to confer drought stress resistance to a non-stay green and senescent sorghum genotype [151,152]. The application of these isolates during seed treatment has demonstrated a significant improvement in plant development, with remarkable rises in root length, root dry weight, and root surface area under drought stress in a sterile soilrite mix. Rhizobacterial endophytes improved relative water content (RWC), osmotic adjustment in leaves, and cell membrane stability index (MSI) of the host plants by expressing drought-responsive genes (*sbP5CS2* and *sbP5CS1*) under drought stress [151].

Biotechnology provides a promising solution through plant growth-promoting microorganisms (PGPs) like endophytic and rhizospheric bacteria. These microorganisms colonize the rhizosphere, improving nutrient uptake, solubilizing phosphorus, inducing osmolyte accumulation, regulating stress-responsive genes, and modifying root morphology, leading to enhanced stress responses and overall plant development [162,163]. Inoculating plants with PGP microorganisms enhances their resistance to various abiotic stressors like drought, salinity, and metal toxicity. Identifying endophytic and rhizospheric bacterial strains that offer cross-protection against multiple stressors would significantly benefit agricultural productivity amid changing climatic conditions. Several genera, including *Streptomyces*, *Serratia*, *Pseudomonas*, *Paenibacillus*, *Lysinibacillus*, *Klebsiella*, *Enterobacter*, *Burkholderia*, *Bacillus*, *Azotobacter*, *Azospirillum*, and *Arthrobacter*, consist of phosphate-solubilizing microorganisms crucial for improving plant yield and soil health [163].

Drought stress also restricts the growth of cool-season grasses. Inoculating timothy plants (*Phleum pratense* L.) with the endophytic microorganism *Bacillus subtilis* strain B26 enhances drought resistance and improves plant tolerance. Strain B26 effectively colonizes timothy plants, positively influencing plant development with significant increases in shoot and root biomass, improving photosynthesis, and enhancing stomatal conductance [164]. Endophyte colonization of plants leads to enhanced metabolic functions, resulting in increased levels of sugars (sucrose and fructose) and essential amino acids (glutamic acid, asparagine, and glutamine) in shoots and roots [165]. Moreover, non-protein gamma-aminobutyric acid is elevated in both stressed and control plants. *Bacillus subtilis* B26, an endophytic bacterium, plays a key role in promoting plant growth during drought conditions by regulating osmolyte accumulation in roots and shoots. This knowledge can be used to develop microbial agents that boost the productivity of grass species, including fodder crops and cereals, under challenging environmental conditions [164].

Azospirillum spp., a group of beneficial bacteria, enhances plant development by producing phytohormones like GA, IAA, and ABA [166]. These bacteria can alleviate various stressors in plants. In a study on maize plants subjected to drought stress and ABA and GA synthesis inhibitors (fluridone and prohexadione-Ca), *Azospirillum* inoculation fully restored the reduced plant growth caused by drought stress and inhibitors [167]. The

presence of the bacterium reversed the negative effects of the inhibitors on relative water content in drought-stressed plants. Inhibitor treatments leading to increased ABA levels resulted in reduced growth, whereas GAs produced by *Azospirillum* contributed to stress reduction. This study suggests that both ABA and GAs are essential for *Azospirillum*'s effectiveness in mitigating plant water stress [167,168]. In general, the utilization of endophytic bacteria offers a promising and environmentally friendly approach for boosting drought tolerance in crops and enhancing crop yield under water scarcity [169,170].

5.3. Cold Stress

Cold or low-temperature stress is particularly significant in temperate and high-altitude environments, exerting a profound impact on plant development and agricultural productivity [171]. The need for sustainable approaches to enhance plants' cold stress tolerance is increasingly urgent, given the more frequent extreme cold episodes attributed to global climate shifts [172]. Cold stress commonly leads to cellular dehydration and interference with water uptake in plants. PGPMs are of paramount importance in osmotic regulation by producing osmoprotectants and compatible solutes that aid in preserving cellular water balance and shielding against cellular harm during cold stress [173]. Under cold stress, plant cells accumulate ROS, leading to oxidative damage. PGPMs can enhance a plant's cold stress resilience by releasing antioxidants like superoxide dismutase and catalase. These antioxidants effectively scavenge ROS, providing protection against oxidative stress and bolstering the plant's capacity to endure cold stress [174]. Furthermore, PGPMs have the capacity to incite the development of heat shock proteins, which hold a critical position in stabilizing proteins and sustaining cellular functions amid cold stress conditions [173]. Within plants, PGPMs possess the power to alter the expression of cold-responsive genes, thereby activating multiple stress-related pathways [175]. This gene regulation empowers plants to establish a more effective defense against cold stress and adapt to challenging conditions. Cold stress often hinders plant nutrient absorption and assimilation [176]. In this regard, PGPMs can enhance nutrient accessibility in the root zone by solubilizing complex nutrient forms, consequently enhancing nutrient uptake and utilization efficiency for plants confronted with cold stress [138]. In regions prone to frost and subfreezing conditions, PGPMs can mitigate plant freezing damage [177]. The PGPMs promote the formation of ice crystals outside the plant cells, thereby averting the development of ice within the cells [178]. This mechanism minimizes cellular damage and provides protection to plants against frost-induced harm [178,179].

5.4. Heat Stress

Heat stress is increasingly common due to climate change, and has already been reported to detrimentally impact crop productivity [180]. The urgency to develop sustainable approaches for enhancing plant resilience to heat stress is heightened as climate change leads to more frequent and intense heat waves. Heat-stressed plants often suffer from water loss and cellular dehydration [181]. In this context, PGPMs play a crucial role in regulating osmotic balance by producing osmoprotectants and compatible solutes. These substances help maintain cellular water balance, thereby mitigating heat-induced water deficits [182,183]. Heat stress activates the buildup of ROS within plant cells, resulting in oxidative damage. PGPMs can augment plant heat stress tolerance by engineering antioxidants like catalase and superoxide dismutase. These antioxidants efficiently scavenge ROS, offering resistance against oxidative stress and encouraging the plant's proficiency to endure heat stress [179,183]. Moreover, PGPMs have the ability to stimulate the production of heat shock proteins, which perform a major role in stabilizing proteins and safeguarding cells from the effects of heat stress [184]. Heat shock protein 70 (Hsp70), functioning as a molecular chaperone, is a type of heat shock protein that PGPMs can induce plants to produce. Under heat stress, Hsp70 expedites proper protein folding and prevents protein accretion, thereby stabilizing cellular functionality [185]. Within plants, PGPMs possess the capacity to alter the expression of heat-responsive genes, thereby initiating various

stress-related pathways. This gene regulation empowers plants to establish a more efficient defense against heat stress and adapt to elevated temperatures. Heat stress often impedes the assimilation and deployment of nutrients by plants. PGPMs, through nitrogen solubilization, can enhance nutrient availability in the rhizosphere, consequently improving nutrient uptake and utilization efficiency in plants facing heat stress [185,186]. Moreover, PGPMs can mitigate the detrimental effects of high temperatures in plants by promoting cellular defense mechanisms. Through the modulation of specific enzymes and metabolic pathways, PGPMs enhance cellular integrity and minimize heat-induced damage [187].

6. Conclusions

The rummage of a more comfortable lifestyle and the resultant rise in industrial development has extremely transmuted agricultural practices, greatly relying on synthetic agrochemicals to fulfill the needs of an expanding global population. This dependence has led to remarkable environmental and health issues, such as soil degradation, water adulteration, and disturbances in soil microbial communities. As a result, there is a rising movement towards adopting sustainable agricultural practices as a remedy to these challenges. Organic farming and the incorporation of plant growth-promoting microorganisms (PGPMs) offer promising alternatives to conventional chemical fertilizers and pesticides. These microorganisms (encompassing a diverse range of bacteria and fungi) play a vital role in enhancing plant growth, improving soil health, and counteracting the detrimental effects of chemical pollution. Their contributions are crucial in nutrient cycling, soil fertility, and improving crop productivity through promoting beneficial microbial interactions, enhancing nutrient availability, and increasing stress tolerance. The significance of PGPMs in addressing both biotic and abiotic stresses highlights their critical role in sustainable agriculture. Biotic stresses, such as those imposed by pathogenic bacteria, pests, and plant-parasitic nematodes, pose considerable threats to agricultural productivity. Microorganisms, including *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Trichoderma harzianum*, have emerged as potent biocontrol agents, enhancing plant resilience through systemic resistance induction, antagonistic interactions, and competition for resources. These microbes not only strengthen plant defenses against diseases but also reduce the dependency on chemical pesticides, thereby promoting environmental sustainability. Abiotic stresses like drought, salinity, cold, and heat further challenge crop production. PGPMs such as *Azospirillum brasilense*, *Bacillus amyloliquefaciens*, and *Aspergillus niger* exhibit remarkable potential in alleviating these stresses. They do so by producing beneficial compounds such as phytohormones, antioxidants, and osmoprotectants that enhance plant growth and stress tolerance. For instance, *Yarrowia lipolytica* and *Cochliobolus* sp. have demonstrated efficacy in managing salinity stress, while *Penicillium roqueforti* and *Fusarium proliferatum* revealed resilience against metal stress. Likewise, *Microbacterium* sp., *Enterobacter cloacae*, and *Bacillus subtilis* contribute to improved drought resistance and plant growth under arid conditions. The assimilation of PGPMs into agricultural practices represents a multifaceted approach to overpowering biotic and abiotic stressors. Their ability to enhance nutrient availability, transform stress-responsive genes, and strengthen plant defenses underlines their potential as a foundation for sustainable agriculture. Continuous investigation and application of these microorganisms are essential for developing resilient crop varieties and securing global food supply among the growing challenges posed by climate change and environmental degradation.

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