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REVIEW

Fungi for Future Farming: Enhancing Nutrient Uptake and Stress Resilience in Sustainable Development Era

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ABSTRACT: Plant growth-promoting fungi (PGPF) are a diverse group of non-pathogenic fungi that benefit host plants through multiple mechanisms. With the growing global emphasis on sustainable agriculture, research has increasingly focused on understanding fungal ecology and its role in enhancing plant growth and development. PGPF contributes significantly by facilitating nutrient acquisition, solubilizing minerals, producing growth hormones, and transferring essential elements from the soil to plants. PGPF have been proposed as biofertilizers, bio-stimulants, and/or biocontrol agents for a variety of plant species in earlier research findings. Modern biotechnological tools can help uncover plant-PGPF interactions, facilitating the development of crop-specific bioinoculants. This review critically evaluates PGPF as drivers of sustainable agriculture by bridging mechanistic insights with field-level applications. Unlike previous descriptive reviews, this study integrates nutrient acquisition, stress resilience mechanisms, and real-world efficacy under varying environmental conditions. We highlight the role of PGPF in climate-resilient cropping systems and circular bioeconomy frameworks, including waste valorization and biofertilizer development. Furthermore, we identify key limitations such as host specificity, environmental variability, and scalability challenges. Finally, future research directions including omics-driven inoculant design and microbiome engineering are proposed. This review provides a novel, integrative perspective on the application of PGPF in sustainable agriculture.

KEYWORDS: Bio-stimulants; microorganisms; nutrient acquisition; PGPF; sustainable agriculture; stress management

1 Introduction

Since 2010, the global population has exceeded 7 billion and continues to rise rapidly. With an annual increase of approximately 83 million people, projections indicate that by 2050, the population will reach 9.7 billion—24% higher than in 2023 [1]. To meet the growing food demand, agricultural production must increase by 25–70% over current levels [2]. Intensifying agriculture is often considered a solution to this challenge. One promising approach involves harnessing plant growth-promoting microorganisms (PGPMs), which naturally inhabit the rhizosphere and enhance plant productivity. The rhizosphere is the

soil region surrounding plant roots with the greatest biological activity [3]. However, pathogenesis-related (PR) proteins such as Phytoalexins, and plant defensive chitinase are a few examples of active defense mechanisms that plants have against pathogen attacks, as well as cell wall fortification and build-up of such sub-stances [4]. Furthermore, PR-gene expression can be induced by several plant pathogen-derived chemicals. The biocontrol approach has piqued the interest of experts due to its environmentally friendly defense against plant diseases and safety features [5]. Plant growth promoting fungi (PGPF) are soil fungi that dwell in the root zone and are either directly or indirectly involved in encouraging plant growth by secreting a variety of inhibitory and antagonistic compounds into the rhizosphere [6].

According to Hawksworth and Lucking, fungi are an essential component of the plant microbiome and range in species from 2.2 to 3.8 million [7]. They also generate a large amount of volatile organic compounds (VOCs), which are important in the network of interactions between two organisms [8,9]. Fungi are the only organisms to produce dozens to hundreds of various VOCs, including alcohols, aldehydes, acids, ethers, esters, ketones, hydrocarbons, terpenes, and sulfur compounds [10]. PGPF promotes plant development through multiple mechanisms, making it difficult to attribute their effects to a single pathway. Mineral solubilization, phytohormone synthesis, volatile organic compound generation, microbial enzyme utilization, increased nutrient uptake, abiotic stress amelioration, and phytopathogen suppression are just a few direct and indirect methods. An ideal PGPF formulation should be cost-effective, work with currently available application technologies, protect biological actives from stress, ensure viability, remain unaffected after storage in ambient conditions, and ensure microbiological actives in the field [11].

Despite extensive research on PGPF, a critical gap exists between laboratory-based mechanistic studies and their performance under field conditions. Environmental variability, soil heterogeneity, and microbial competition often limit the reproducibility of experimental findings. Microorganisms also inhabiting the rhizosphere can affect plant growth through a range of direct and indirect mechanisms (Table 1). Moreover, the integration of PGPF into climate-resilient agriculture and circular bioeconomy systems remains underexplored. Therefore, this review aims to bridge these gaps by critically synthesizing mechanistic understanding with applied outcomes and identifying future research priorities.

Table 1: List of potential PGPF in plant nutrition enhancement.

PGPF Strains	Improvement	Plant Species	References
Beauveria bassiana	Enhanced spike production Strengthen the root sett	Wheat Sugarcane	[12,13]
Purpureocillium lilacinum	Improved yield	Tomato	[14]
Metarhizium brunneum	Biomass, leaf area, nitrogen, and phosphorus were increased	Potato	[15]
Beauveria bassiana, *Isaria fumosorosea*, *Metarhizium brunneum*	Positive impact on survival, growth, health, length, and cabbage's dry mass	Cabbage	[16]
Syncephalastrum racemosum; *Paecilomyces lilacinus*	Enhanced cucumber yield, promoted root and shoot length	Cucumber	[17]
Beauveria bassiana; *Metarhizium brunneum*	Growth promotion	Faba bean	[18]
Beauveria bassiana; *Purpureocillium lilacinum*	Improvement of plant growth	Cotton	[19]
Metarhizium robertsii	Plant root development and root hair proliferation	Switchgrass, Haricot beans	[20]
Metarhizium anisopliae	Enhanced plant height, root length, and dry weight of the shoot and root	Tomato	[21]

Table 1: *Cont.*

PGPF Strains	Improvement	Plant Species	References
Clonostachys rosea	A better emergence process and time	Carrot, Onion	[22]
Trichoderma harzianum	30% more seedlings emerged. Decreased *F. verticillioides* and *fumonisin* incidence and increased field emergence Enhanced establishment of plant stands	Cucumber, Maize, Rice	[23–25]
T. viride	A rise in the weight of new shoots	Arabidopsis, Tomato	[26]
Fusarium oxysporum	Both fresh and dry shoots increased by 85%	Arabidopsis, Tobacco	[27]
Aspergillus spp.	Increased fresh, dry biomass, and shoot length	Cucumber	[28]
Fusarium spp.	Lengthened roots, fresh roots, and dried roots	Indian spinach	[28]
Penicillium spp.	Longer and more biomass-producing roots	Sesame	[29]
T. longibrachiatum	Increased soluble sugar and protein content	Wheat	[30]
Pochonia chlamydosporia	Hastened blossoming process	Tomato	[31]
Phoma sp.	Root-shoot growth, incresed crop production	Cucumber	[32]
Exophiala sp.	Drought and salinity-induced plant growth	Cucumber	[33]
Chaetomium globosum	Biomass and root-shoot development	Capsicum	[34]
Cladosporium sp.	Increased root-shoots, chlorophyll, soluble carbohydrates	Tobacco	[35]

2 Plant Growth Promoting Fungi

The microorganisms that reside in the rhizosphere can influence plant growth in a variety of ways, both direct and indirect (Table 1). Plant interactions with a range of microorganisms, particularly rhizosphere bacteria and fungi, can result in changes in plant metabolism and an increase in plant vigor, growth, and development as well as stress tolerance [36]. The PGPF is a type of rhizospheric fungi that colonizes plant roots and stimulates plant growth [37]. Nonpathogenic saprotroph fungi are a broad group of organisms. According to the published literature, most true fungi classified as PGPF belong to the phylum Ascomycota (*Aspergillus*, *Aureobasidium*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Exophiala*, *Penicillium*, *Trichoderma*, *Fusarium*, *Gliocladium*, *Phoma*, *Phomopsis*, *Purpureocillium*), but a small number [38]. For example, cucumbers exhibit systemic resistance to various diseases due to colonization by PGPF species [39]. PGPF are soil-dwelling non-pathogenic saprophytes that aid many crop plants by protecting them from disease and promoting plant growth [40,41].

Current literature shows a strong bias toward well-studied genera such as *Trichoderma*, *Aspergillus*, and *Penicillium*, while many ecologically significant fungi remain underexplored. This bias may limit our understanding of the full potential of fungal diversity in sustainable agriculture. Additionally, Table 1 reveals that most studies focus on a narrow range of crops, indicating a need for broader crop-specific investigations.

Factors such as temperature, pH, soil type, moisture, and microbial diversity influence the effectiveness of fungal biofertilizers [42]. Numerous biological control agents create a variety of antibiotics or non-specific metabolites that, through a process known as antibiosis, either suppress or eradicate harmful bacteria. When combined with cell wall-degrading enzymes, these antibiotics synergistically inhibit various plant pathogens [43]. It is commonly known that the *Penicillium*, *Gliocladium*, and *Trichoderma* species produce a wide array of antibiotics and treat disease in various ways [44].

Another tactic used by biological control agents to lessen plant disease is mycoparasitism [45]. Additionally, the high iron affinity of the siderophore produced by the PGPF and the intense competition

for iron in the rhizosphere should have an impact on the iron feeding of other soil species, such as plant diseases [46]. *Aspergillus*, *Piriformospora*, *Fusarium*, *Penicillium*, *Phoma*, *Rhizoctonia*, and *Trichoderma* are well-known nonpathogenic fungal genera that promote various plant characteristics beneficial for increased yields [19,47]. Endophytes, ectomycorrhizas (EcM), arbuscular mycorrhizae (AMF), yeasts, *Trichoderma* sp., and several avirulent strains of phytopathogens such as *Fusarium oxysporum*, *Cryphonectria parasitica*, and *Muscodor albus* are some examples of PGPF exhibiting BCA activity [48]. These helpful fungi have been created in vast quantities and used extensively to treat plant disease [49]. Thus, the use of plant-beneficial microorganisms in agriculture as biofertilizers, biopesticides, and for phytoremediation is of great interest [50,51].

The identification of PGPF began with rhizosphere fungi. According to recent studies, phyllosphere fungi have PGPF potential. The phyllosphere, which is made up of plant above-ground surfaces, is one of the most prevalent microbial homes on Earth. Fungi in the phyllosphere can work with plants to help them develop and survive environmental obstacles [52].

Plant growth promotion by PGPF is a complex process that is not always explained by a single mechanism. Both direct and indirect mechanisms are known to influence plant growth and development for agricultural improvement. Direct growth promotion occurs when fungi produce chemicals or make nutrients readily available to plants. On the other hand, PGPF demonstrates fungal ability to manage plant diseases and alleviate stress, which are two of the most important indirect techniques for stimulating plant development (Fig. 1). A specific PGPF may influence plant growth and development by using one or more of these methods [53].

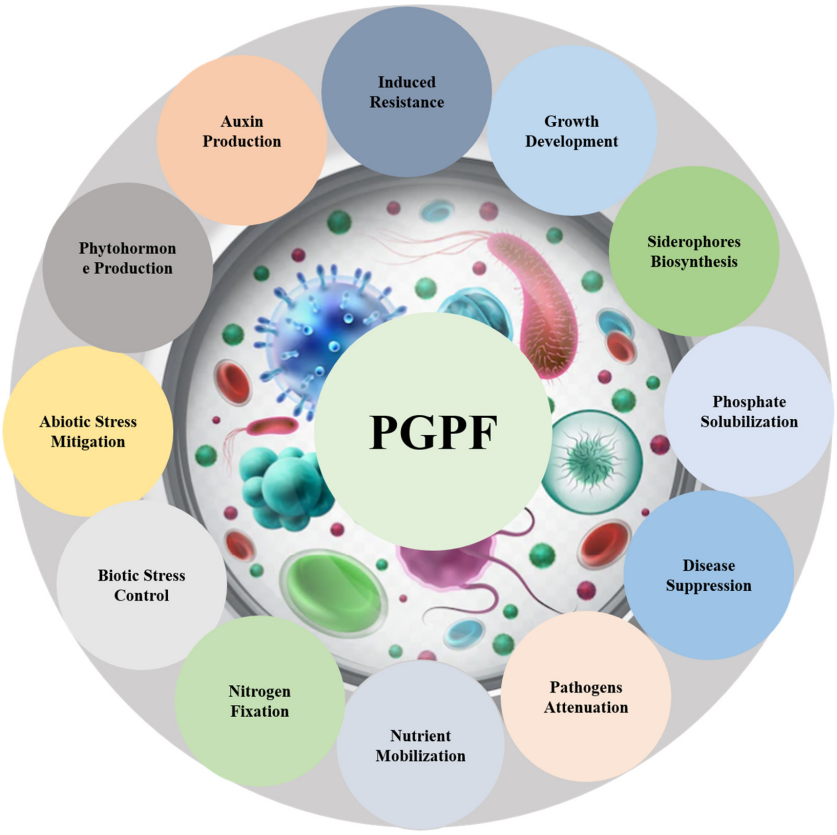

Figure 1: Beneficial interaction between plant and plant growth promoting fungi (PGPF) for enhanced and sustainable plant growth.

In addition to promoting plant growth and development, numerous microorganisms that co-exist in contact with plant roots have been successfully employed to induce resistance in host plants against the encroaching phytopathogens [54]. Non-pathogenic, naturally occurring saprophytes called plant growth-promoting fungi serve to maintain soil fertility, which in turn promotes plant development and triggers the first line of defense against pathogen infections [53,55]. The ability of PGPF in case of roots to colonize the soil is thought to be the first and most important mechanism for preventing pathogen infection. It also helps to intake nutrients, which promotes plant growth [53,56]. Because of the profoundly beneficial benefits of PGPF in agriculture, researchers have focused their attention on the application of PGPF for the induction of resistance and improvement of plant growth by activating induced systemic resistance (ISR) in plants [56,57].

3 Potential Mechanisms Involved in PGPF Activities for Plant Growth

3.1 Siderophore Production

Due to the poor availability of iron in the environment, fungi produce microbial iron chelators known as siderophore production (Fig. 2). Phenolates, hydroxamates, and polycarboxylates are the three groupings that are introduced. It controls the synthesis of aromatic compounds, antibiotics, cytochromes, siderophores, vitamins, toxins, porphyrins, pigments, and nucleic acids [58]. Microbes producing siderophores are advantageous to plants because they can prevent the spread of plant diseases. It is possible that fungi make hydroxamate siderophores, which are stable down to pH-2.0, due to their ability to synthesize organic acids [59]. In fungus, ornithine has both hydroxylated and alkylated bases [60].

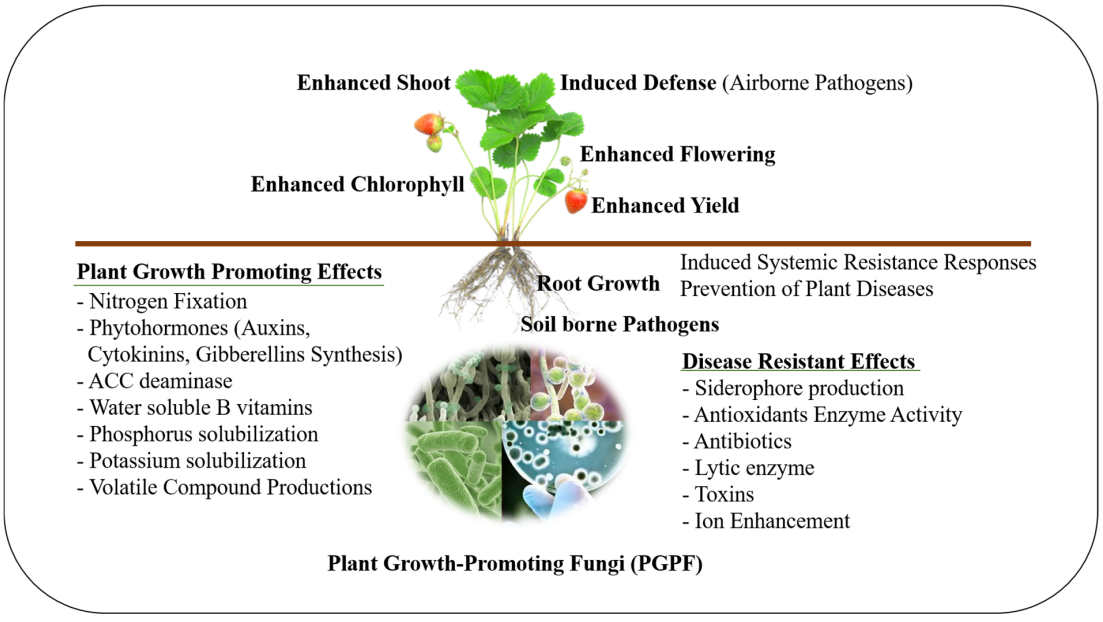

Figure 2: Multifaceted enhancement of plant growth and defense responses through PGPF during mitigation of biotic and abiotic stress conditions.

3.2 Antibiotics Production

Antibiotics are substances that can either kill or stop the growth of germs, the disease-causing microbes, and are active at extremely low concentrations. They are chemical substances that are produced as an essential part of the life process of an organism. Cephalosporin, fusaric acid, and penicillin are among the

many antibiotics produced from fungi that have antibacterial and antifungal properties and are widely used as medications throughout the world. Fungal endophytes have been documented to develop using novel antibacterial, anticancer, antifungal, anti-inflammatory, antimalarial, and antiviral compounds [61].

3.3 Chitinase Production

The chitinase enzyme has drawn increased interest because of its many biotechnological applications, particularly in agriculture for the biocontrol of threatening insects and pathogenic fungi [62]. Chito-oligomers produced by the enzymatic hydrolysis of chitin are used in a wide range of industries, including medical, agricultural, and industrial uses, for their anti-fungal, antihypertensive, and antibacterial qualities as well as to improve food quality [63]. Recent evidence also demonstrated that CaEch1-mediated mitophagy regulates vegetative growth, conidiation, appressorium formation, and pathogenicity in *Colletotrichum camelliae*, highlighting the importance of fungal cellular regulation in host–fungus interactions [64].

3.4 Induced Systemic Resistance

Increased plant defenses against a variety of pests and pathogens are known as induced resistance (IR) [65]. The physical and mechanical strength of the cell wall was increased, and the physiological and biochemical responses of the host were changed by the plant growth promoting rhizosphere, which in turn induced ISR in plants. It triggers the defense mechanisms like proteins connected to peroxidase, chitinase, and pathogenicity [66].

3.5 Plant Growth Regulators (PGR) Production

Several PGPF have been found to be able to produce IAA *in vitro*. For instance, *Rhodosporidiobolus paludigenum* and *Cryptococcus flavus* isolated from rice leaves [67] found to produce IAA. *R. graminis* and *R. mucilaginosa* are the first endophytic yeast strains found in *Populus* species [68]. They can enhance squash, pepper, and tomato plant development and fruit production due to their ability to produce IAA which is evidenced from previous research [34]. Further, different endophytic filamentous fungus species, including *F. oxysporum* and *P. chrysogenum* isolated from tea [69], have been found to be capable of producing Giberellic acid *in vitro*. *Aspergillus clavatus* [70], *Gliomastix murorum* [33], *Penicillium citrinum* [71], *Phoma glomerata* [72], or *Aspergillus niger* [73] boost plant height by producing GA3, GA4, and GA7.

Although these mechanisms are well documented, their effectiveness is highly context dependent. Environmental conditions, soil microbiome composition, and host plant specificity significantly influence the expression and efficiency of these mechanisms. Furthermore, interactions among mechanisms (e.g., nutrient solubilization and ISR) may result in synergistic or antagonistic effects, which are not yet fully understood.

3.6 Molecular Signaling and Cross-Kingdom Communication in PGPF Interactions

Recent studies have demonstrated that plant growth-promoting fungi (PGPF) establish sophisticated molecular communication systems with host plants through signal molecule exchange and regulatory networks. Signaling compounds such as flavonoids, strigolactones, lipochitooligosaccharides, fungal elicitors, and volatile organic compounds (VOCs) are involved in the establishment of plant–fungus symbiosis and activation of downstream defense and growth pathways [9,10,53,56,57]. These signaling interactions regulate nutrient acquisition, root architecture modification, stress adaptation, and induced systemic resistance.

In addition, several symbiosis-related genes are differentially regulated during plant–fungus interactions. Genes associated with nutrient transporters, phytohormone biosynthesis, antioxidant enzymes, defense-related proteins, and stress-responsive pathways play essential roles in enhancing plant growth

and tolerance under adverse environmental conditions [74–77]. Recent transcriptomic and metabolomic studies have further improved understanding of fungal-mediated molecular regulation in plants [78–82].

Emerging evidence also highlights the role of small RNAs (sRNAs) in cross-kingdom communication between fungi and plants. Fungal-derived sRNAs can suppress host immune responses by targeting plant defense genes, whereas plant-derived sRNAs may regulate fungal pathogenicity and colonization processes. These findings provide new insights into the molecular basis of plant–fungus interactions and offer promising opportunities for microbiome engineering and precision agriculture.

4 Applications and Efficacies of PGPF in Promoting Plant Health

4.1 Nitrogen Availability

Direct nitrogen transfer to plants occurs through the synthesis of ammonia. Cereals, such as wheat and rice, are the principal sources of this process. Within the roots of these plants, fungi like *Trichoderma harzianum* and *T. gammii*, as well as *Aspergillus niger*, contribute to the production and transportation of ammonia [83]. This ammonia synthesis and transfer play a crucial role in supporting plant growth and development. Additionally, other fungi like *Penicillium chrysogenum* and *P. crustosum* found in the roots of maize plants have also been associated with ammonia production, further enhancing shoot and root length, as well as overall plant biomass [84]. This direct nitrogen transfer mechanism facilitated by ammonia synthesis is vital for ensuring optimal nutrient availability and promoting healthy plant growth.

PGPF has been proven to enhance the plant's nitrogen (N) uptake capacity across various crops, with rice being a particularly notable example. Studies have demonstrated that the yeast *Rhodotorula mucilaginosa*, isolated from lesser bulrush (*Typha angustifolia*), can substantially improve rice plant growth while increasing the nitrogen content within their tissues [85]. Moreover, in the case of rice, specific isolates of the filamentous fungus *Phomopsis liquidambari* have been found to boost plant nitrogen content by promoting the decomposition of below-ground straw and facilitating nitrogen transformation processes [86]. These findings highlight the significant role played by PGPF in enhancing plant nitrogen uptake, ultimately contributing to improved growth and nutrient assimilation in crops such as rice.

4.2 Phosphate Solubilization and Phosphorus Availability

Plant growth-promoting fungi play a crucial role in phosphate solubilization, thereby enhancing plant nutrient availability (Fig. 2). These fungi possess the ability to release organic acids, such as citric acid, oxalic acid, and gluconic acid, which facilitate the solubilization of insoluble phosphate compounds present in the soil. The organic acids produced by these fungi lower the pH in the rhizosphere, creating an acidic environment that promotes the release of phosphate ions from insoluble minerals. Additionally, some plant growth-promoting fungi produces enzymes like phosphatases, which break down organic phosphorus compounds into simpler forms that can be readily absorbed by plant roots. By solubilizing phosphate and making it more accessible to plants, these fungi contribute to improved phosphate uptake, leading to enhanced plant growth, root development, and overall nutrient utilization.

Several instances have been identified where plant growth-promoting fungi have proven beneficial in enhancing phosphorus availability and promoting the growth of various vegetable crops. For instance, in the case of chillies, the filamentous fungus *Xylaria regalis*, isolated from *Thuja plicata*, has been shown to increase phosphorus content in seedling tissues and enhance the size of stems and roots [87]. Similarly, in maize yeasts *Candida railenensis* and *Cryptococcus flavus* have demonstrated significant potential in promoting plant growth and increasing shoot phosphorus content [88]. In wheat, the filamentous fungi *Trametes versicolor* and *Serendipita indica* have exhibited the ability to substantially enhance grain yield [89].

Additionally, in rice, *Phomopsis liquidambari* has been found to enhance phosphorus uptake and utilization, while also influencing microbiota patterns [90]. Furthermore, the filamentous fungus *Talaromyces pinophilus* has been discovered to enhance phosphorus uptake and promote plant development, even in industrial crops such as oil palm. These findings underscore the diverse roles that plant growth-promoting fungi can play in optimizing phosphorus availability and facilitating the growth of various crops.

4.3 Acquiring Iron

PGPF enhances iron acquisition and availability, ensuring adequate micronutrient supply for plant growth and development. PGPF enhances iron uptake by solubilizing insoluble iron compounds, making them more accessible to plants. This solubilization is facilitated by the release of organic acids, siderophores, and other compounds that chelate and mobilize iron. Siderophore production is another strategy employed by certain fungi, as these molecules bind to iron and enhance its uptake by plants. Additionally, PGPF can promote root growth and development, leading to increased surface area and root exudation, which enhances iron acquisition. Moreover, some PGPF can induce systemic responses in plants, such as the upregulation of iron acquisition-related genes or the production of iron-chelating compounds within the plant itself [91,92].

4.4 Additional Nutrient Acquisition

The disease resistance, mechanical stability, and nutritional value of a crop are all impacted by potassium (K) deficiency. In this regard, the solubilization of K by microbes is an effective substitute for providing plants with this element [93,94]. Various agricultural crop-isolated fungi can solubilize K *in vitro*. Zn-solubilizing microorganisms, which have been explored as potential plant growth-promoting elements, can be found in the soils of a variety of different crops [95]. As demonstrated by the presence of *Serendipita indica* in lettuce, which has enhanced the Zn concentration in their tissues, chlorophyll content, and plant development, whereas several species of the genus Penicillium have been reported as efficient zinc-solubilizing fungi capable of mobilizing insoluble zinc compounds through the production of organic acids and other metabolites [96], which increases the nutrient acquisition of plants [97]. In contrast, the fungus *Neotyphodium coenophialum* in *Festuca arundinacea* can increase both the plants uptake of K, Ca, and Mg and its growth [98].

Despite promising results, several limitations hinder the large-scale application of PGPF. These include host specificity, inconsistent field performance, environmental variability, and competition with native microbial communities. Addressing these challenges is essential for successful commercialization and field adoption. The potential of PGPF to reduce the detrimental effects of abiotic stresses has been examined in several studies, which are summarized in Table 2.

Table 2: Screened PGPF in stress mitigation with salient features.

PGPF	Plant Species	Activities of PGPF under Stress Conditions	References
Fusarium oxysporum	Mint	Promote plant growth and enhance host tolerance to drought stress.	[99]
Trichoderma spp.	*Cucumis sativus*	(i) Suppresses *Fusarium* nematode complex through the production of volatile and nonvolatile organic compounds, ceratoplatanin-like small molecules, glucanases and chitinases. (ii) Produce growth hormone and promote plant growth.	[100]

Table 2: *Cont.*

PGPF	Plant Species	Activities of PGPF under Stress Conditions	References
Cunninghamella bertholletiae	*Solanum lycopersicum*	(i) Reduce symptoms of salinity, drought and heavy metal stresses by modulating the physiochemical apparatus, enhanced expression of SlCDF3 and SlICS genes. (ii) Reduce the expression of SlACCase, SlAOS, SlGRAS6, SlRBOH, SlRING1, SlTAF1, and SlZH13 genes.	[74]
Glomus lamellosum or *G. etunicatum*	*Cinnamomum migao*	(i) Alleviate drought stress by increasing CAT activity. (ii) Higher water content in leaves and higher fresh and dry weight. (iii) Lower malondialdehyde (MDA) content.	[101]
Ampelomyces sp.	*S. lycopersicum* var. Better Boy	Enhance drought stress tolerance and promote plant growth.	[102]
Lecanicillium lecanii	*S. lycopersicum*	Induce systemic resistance against biotic stress caused by Myzus persicae through strongly upregulated the salicylic acid associated genes and moderately upregulated the jasmonic acid associated genes.	[103]
G. etunicatum	*Juglans regia*	Alleviate drought stress and increase fresh weight, leaf number and N, P and Zn content in leaves.	[104]
G. mossae with *G. etunicatum*	*J. regia*	Lighten drought stress. Decrease leaves abscission and increase N, P and Zn content in leaves.	[105]
Pseudomonas veronii	*Sesamum indicum* L.	Mitigate waterlogging-stress related damage and enhance lant growth.	[106]
Pseudomonas	*Triticum aestivum*	Alleviate heavy metal stress and reduce Catalase (CAT), glutathione reductase (GR), Superoxide dismutase (SOD), proline and MDA levels.	[107]
P. fluorescens with biochar or compost or their combination	*C. sativus*	Reduce the effect of abiotic stress and enhance plant growth.	[108]
Alternaria sp. or *T. harzianum*	*S. lycopersicum* var. Rutger	(i) Increasing salt and drought stress tolerance by lowering the content of ROS in plants. (ii) Improve photosynthetic rate, root and shoot biomass and water use efficiency.	[109]
T. virens	*Brassica juncea*	Genetic transformation of an endochitinase gene 'ech42' enhanced tolerance to Alternaria blight.	[110]
G. intraradices (*Rhizophagus irregularis*)	*S. lycopersicum*, and *Lactuca sativa*	Increase drought tolerance.	[111]
T. asperellum	*Popular*	Enhanced tolerance to salt stress (200 mMNaCl) via 1-Aminocyclopropane-1-carboxylate deaminase.	[30]
T. harzianum	*S. melongena*	(i) Reduce salt stress through increasing proline and phenolics. (ii) Improved plant growth. (iii) Increase phosphorous content.	[112]
T. harzianum and *F. pallidoroseum*	*Oryza sativa*	(i) Alleviate severe drought stress via greater induction of antioxidant enzymes (SOD, CAT, POD). (ii) Promote plant growth and production.	[113]
Chaetomium globosum or *P. resedanum*	*Capsicum annum*	Improve growth under salinity stress.	[114]
G. intraradices	*L. sativa*	Increased mycorrhizal colonization with strigolactone production in a dose-dependent manner, which resulted in arbuscular mycorrhizal fungi (AMF)-induced growth promotion under salt stress.	[115]

Table 2: *Cont.*

PGPF	Plant Species	Activities of PGPF under Stress Conditions	References
Phoma glomerata and *Penicillium* sp.	*C. sativus*	(i) mprove plant biomass and related growth parameters under sodium chloride and polyethylene glycol induced salinity and drought stress. (ii) Modulated stresses through down-regulated abscisic acid, altered jasmonic acid, and elevated salicylic acid contents.	[116]
T. virens	*Nicotiana tabacum*	Enhanced cadmium tolerance via Glutathione S-transferases.	[117]
T. atroviride	*Pennisetum glaucum*	Improved resistance to biotic stress caused by *Sclerospora graminicola* through β-1,3-Glucanase.	[118]
G. mosesseae	*Fragaria* × *ananassa*	(i) Reduce drought stress by slowing down the reduction of Chl a + b. (ii) Inhibit the decomposition of carotenoids.	[119]
Piriformospora indica	*Brassica rapa* subsp. *pekinensis*	(i) Improve drought tolerance by stimulating antioxidant activities such as increasing peroxidase, CAT and SOD activities in leaves. (ii) Increase lateral root development and root-shoot growth.	[75]
T. harzianum	*Theobroma cacao*	(i) Alleviate drought stress. (ii) Increase osmolyte concentration and plant growth.	[120]
Phoma spp.	*Pinus tablaeformis*	(i) Delayed the onset of the drought response Increase the activity of CAT and SOD. (ii) Improve the content of proline, chlorophyll and water in leaves.	[121]
G. mosseae or *G. versiforme* or *G. diaphanum*	*Poncirus trifoliata*	Alleviate drought stress by higher enzyme activity and lower CAT activity in soil.	[122]
T. atroviride	Lemon	Endochitinase enhanced resistance to biotic stress caused by *Phoma tracheiphila* and *Botrytis cinerea.*	[123]
T. harzianum	*T. cacao*	Increase plants tolerance against drought stress via gene expression change.	[76]
G. intraradices	*Lycopersicum esculentum*	Alleviate drought stress and improve plant growth parameters.	[124]
T. atroviride	Poplar and black spruce	An endochinase gene increased resistance to *Melampsora medusae* in poplar and to *Cylindrocladium floridanum* in black spruce.	[125]
T. atroviride	*O. sativa*	*Increased resistance to Rhizoctonia Solani and Magnaporthe grisea* via Endochitinase, *N* acetyl-β-hexosaminidase and glucanase.	[40]
Funneliformis mosseae (*G. mosseae*)	Grapevine	(i) Greater tolerance to water stress. (ii) Greater foliar growth. Higher concentration of P in the leaves. (iii) Increase in water potential at dawn. (iv) Higher carbon assimilation rates.	[126]

5 PGPF in Biotic and Abiotic Stress Management

In natural environments, plants are often exposed to multiple stresses simultaneously, and PGPF-mediated responses are interconnected. The integration of biotic and abiotic stress responses represents a critical area for advancing sustainable crop protection strategies. Due to the sessile nature, plants are subjected to a range of biotic (pathogens and insects) and abiotic (drought, salinity, high and low temperature, waterlogging, UV radiation and heavy metals) throughout their life cycle. Most of the cases, plants face

multiple stresses in combination of different biotic and abiotic stresses at a time which restricts their growth, development and thereby reduces the production. Management of biotic and abiotic stresses in crop plants is essential for a better crop yield. To secure food production, a diverse range of chemicals including fertilizers, fungicides, and pesticides have been used since the green revolution which poses a negative impact on ecosystem and increase the risk of new diseases and pests. Therefore, it is important to include ecofriendly approaches, and biological control is one of them as a potential tool. PGPF has been used as a biofertilizers and biocontrol agent which has shown its potential impact on controlling the abiotic and biotic stresses [127].

5.1 PGPF in Biotic Stress Management

Insects and pathogens are one of the most threats for crop production. A diverse range of biocontrol agents has been reported to improve plant resistance to pathogens. PGPF such as *Beauveria bassiana*, *Chaetomium globosum*, *Cladosporium oxysporum*, *Colletotrichum gloeosporioides*, *Epichloë typhina*, *Fusarium oxysporum*, *Moesziomyces bullatus*, *Pichia anomala*, *Trichoderma* species, *Penicillium chrysogenum*, and *Sarocladium strictum* showed their potentiality to suppress a diverse range of pathogens in crop plant [127–130]. Trichoderma spp. has shown its potential impact in suppressing the growth of diverse pathogens including *F. oxysporum*, *R. solani*, *P. aphanidermatium*, *F. culmorum*, *Gaeumannomyces graminis* var. *tritici*, *Sclerotium rolfsii*, *Phytophthora cactorum*, *Botrytis cinerea* and *Alternaria* spp. [130]. *Pseudomonas* spp. has shown lower infection rate in Acacica due to the endophyte *F. oxysporum* [131]. *Serependita indica* could develop symbiotic relationships with a range of crops which showed the suppression of other pathogens [132]. Other studies showed the antagonistic relationships with pathogenic fungus in cotton and tomato plants [133,134].

Plant associated endophytic fungi has been used against insect herbivores as well [127,135]. *Beauveria bassiana* has been reported as one of the most common endophytes in several crops including cocoa, tomato, potato, date palm, banana and poppy [12]. *B. bassiana* has been used to biocontrol agents against stem gall wasp, corn berer, berry borer, banana weevil and cotton aphid [135]. *B. bassianas* showed lower damage with higher fitness, infestation and better growth against the two-spotted spider mite with a significant reduction of survival rates [136,137]. Foliar spray of *Metarhizium brunneum* on melon and *Cucumis melo* showed reduction in leaf worm [138]. There are some other endophytic fungi such as *Aspargillus parasiticus*, *Lecanicillium lecanii*, *Acremonium strictum*, Metarhizium brunneum and *Fusarium* spp. have been used as a biocontrol agent against a diverse range of insect herbivores in diverse range of crops [139].

5.2 PGPF in Abiotic Stress Management

Abiotic stresses such as salinity, drought, heat, cold, UV radiation, waterlogging, and heavy metals impair the growth and development of plants. Plants implicate a diverse range of molecular and physiological mechanisms to adapt to the adverse environmental conditions [114]. The symbiotic relationships between endophytes and host plants contribute to the plant adaptation to the environmental stimuli. Several studies have been carried out to apply the PGPF to reduce the negative impact of abiotic stresses which have been summarized as a tabular format (Table 2). Table 2 demonstrates that many PGPF species simultaneously confer tolerance to both biotic and abiotic stresses, indicating overlapping regulatory pathways and multifunctional roles. The application of endophytic fungi such as *Epichole* sp. has shown its role in improving the plant tolerance against drought stresses, heavy metals, waterlogging stress, salinity stresses in *Hordeum vulgare*, *Lolium perenne*, *Hordeum brevisubulatum*, *Lolium arundinaceum*, *Fescus*, ryegrass, and wheat [140–143]. Other endophytic fungi such as *Penicillium roqueforti*, *P. citrnum*, *Aurobassium pullunts*,

T. harzianum, *P. chrysohenum*, *Chaetomium globosum*, *Clonostachys rosea*, *Ampelomyces* sp., *Pilidium* sp., *Plectosphaerella* sp., and *Dothideomycetes* sp. have been used to mitigate the abiotic stresses [144–146].

5.3 PGPF Mediated Stress Mitigation Mechanisms

To mitigate the negative impact of biotic and abiotic stresses in plants, plants activate and modify several physiological and molecular mechanisms. Changes in morphological traits in both above and below ground level, hormonal regulations, activation of defense pathway, production of metabolites, and changes in gene expression are the common underlying mechanisms that plant apply for better adaptation with or without costing the growth. PGPF are involved in plant responses by supporting the plant growth and assisting the plant defense systems either directly and/or indirectly. In addition to increasing the competition for foods, space and mycoparasitism with the insects and pathogens, PGPF positively regulates the plant underlying tolerance responses which are shown in Fig. 3.

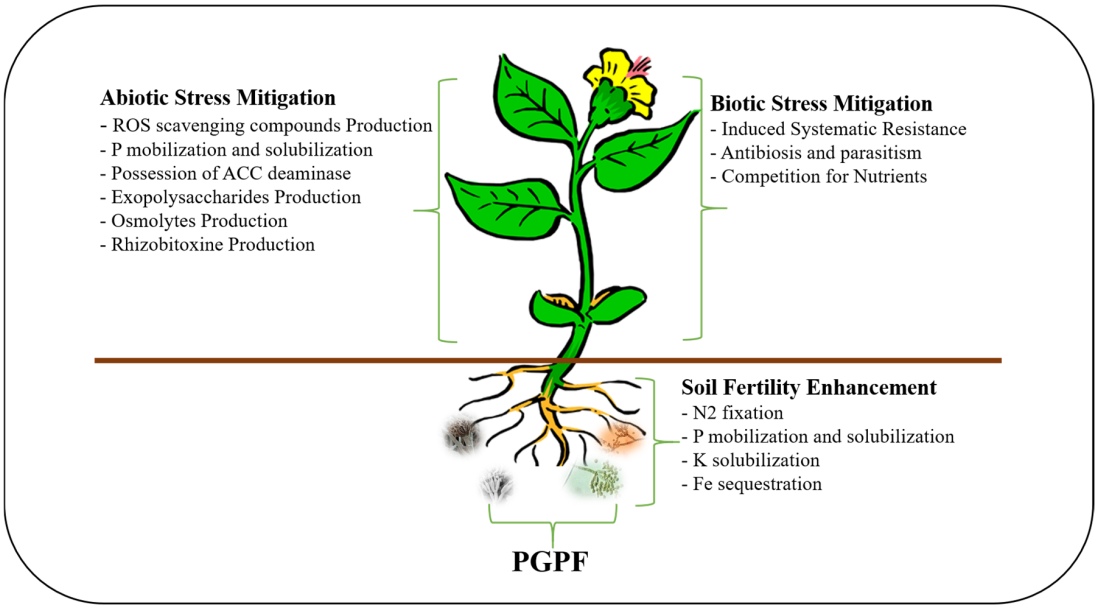

Figure 3: Mechanistic insights of biotic and abiotic stress management through PGPF.

Plant growth regulators or phytohormone regulate plant responses to biotic and abiotic stresses which activate the downstream signaling pathway to activate the defense systems in plants. A diverse range of PGPF has been reported to have the ability to synthesize the phytohormone [78]. Production of phytohormone at rhizosphere changes the root system's architecture including the development of root hairs, increase the lateral roots, root length and root biomass which positively regulates the plant growth under both biotic and abiotic stresses [147]. Increase in synthesis of IAA, ABA, and suppression of ethylene has been reported to support the plant tolerance against biotic and abiotic stresses.

Increase in primary and secondary metabolites are one of the major mechanisms of plants against biotic and abiotic stresses. Secondary metabolites including alkaloids, phenols, flavonoids, peptides, setroides and terpenoids play major roles in plant resistance to biotic stresses [148]. Some PGPF can synthesize secondary metabolites having antifungal and antibacterial properties which inhibit the fungal and bacterial pathogens from infection. Besides the production of metabolites, PGPF are involved in production of enzymes and antioxidative compounds such as CAT, POD, SOD, osmolytes and prolines which mitigate the negative impact of reactive oxygen species generated due to the biotic and abiotic stresses [149].

Systemic acquired resistance (SAR) and tolerance to biotic and abiotic stresses are among the most widely utilized mechanisms by which plants adapt to environmental challenges [150]. SAR is a long lasting and broad-spectrum biotic stress resistance against the secondary infection [78]. PGPF play roles in activation of SAR in host plants by a several ways including increasing the phytohormone (JA, SA, MeSA, ET), gene expression (pathogenesis related genes), phenols, peroxidase, enzymatic activation (SOD, POD, polyphenol oxidase) and defense related protein (PR-1) [78–82].

Changes in gene expression levels are another underlying tolerant mechanism against biotic and abiotic stress conditions. PGPF are involved in modulating the gene expression pattern in host plants which positively regulates the plant tolerance level. Genes related to hormonal pathway, positive association with plant defense, activation in priming and systemic acquired resistance/tolerance, and enzymatic activation are positively regulated by plant associated fungal endophytes [77].

Maintaining the plant growth under biotic and abiotic stress conditions is one of the major concerns. PGPF are involved in nutrient acquisition, nutrient uptake, nutrient transfer and nutrient availability during the biotic and abiotic stresses which sustain plant growth and development with a minimum or negative impact due to stress [151]. Nitrogen, phosphorus, calcium, magnesium, and iron have been reported to be increased due to the symbiotic relationships which positively influence the plant adaptation to biotic and abiotic stresses. Supporting the plant's growth under biotic and abiotic stresses positively increases the plant's adaptability.

6 Potential Application of PGPF in Circular Bioeconomy

The prospect of plant growth-promoting fungi (PGPF) within the context of circular bioeconomy holds significant promise for sustainable agricultural practices and the efficient utilization of resources. PGPF are beneficial fungi that form symbiotic relationships with plants, promoting their growth, enhancing nutrient uptake, and providing protection against various stresses. In a circular bioeconomy, the focus is on creating closed-loop systems that minimize waste, maximize resource efficiency, and promote regenerative processes. PGPF can play a vital role in this framework by improving nutrient cycling, reducing the need for synthetic fertilizers, and enhancing soil health and fertility. By harnessing the potential of PGPF, farmers can optimize their crop yields while reducing environmental impacts, contributing to the development of a more sustainable and resilient agricultural sector.

Despite their potential, the large-scale implementation of PGPF within circular bioeconomy systems faces several challenges, including economic feasibility, formulation stability, and regulatory constraints. Lifecycle assessment and cost–benefit analyses are required to evaluate their long-term sustainability. Additionally, policy support and industry adoption will play critical roles in scaling up these technologies. Support of the circular bioeconomy and sustainable agriculture approaches depends on absolutely necessary plant growth-promoting fungus (PGPF). By combining biological systems into industrial and agricultural output, biocontrol perspectives and circular bioeconomy seeks to maximize resource efficiency and hence reduce waste [152,153]. By enhancing nutrient absorption, phytohormone producing, and soilborne pathogen control PGPF including species of *Trichoderma*, *Penicillium*, and *Aspergillus*—increases plant development. By means of biofertilizers and biopesticides developed from these fungi, dependency on chemical inputs can be minimized and environmental damage can be limited. PGPF also helps to value organic waste by turning agricultural waste into bioactive molecules that increase soil fertility [154]. Complementing ideas of turning biomass waste into profitable agricultural inputs, they enhance soil structure and encourage carbon sequestration. Moreover, in biorefineries combining PGPF with other microbial consortia could help to produce biopolymers and biofuels, therefore complete the nutrient cycle

in agroecosystems [155]. Thus, using PGPF in agriculture is a sensible approach to support ecological resilience as well as for sustainable food production. Furthermore, the use of PGPF aligns with the principles of circularity by promoting the recycling and reuse of organic waste materials, such as agricultural residues and byproducts, which can serve as substrates for fungal growth and subsequent plant stimulation. The integration of PGPF into circular bioeconomy strategies represents a promising avenue for achieving sustainable and resource-efficient agriculture, fostering a harmonious relationship between plant health, environmental stewardship, and economic viability.

7 Challenges and Future Perspective

In natural ecosystems, plants interact with both mutualistic and pathogenic fungi. A key concern is how invading pathogens influences these beneficial interactions. Furthermore, it is still difficult to identify the native fungi from the environment, and many fungal species remain undocumented. Microbes screening, production, marketing, and commercialization are major obstacles to the use of microbial inoculants. Identification of microbiome interactions, diversity, effects on environmental stressors, and mechanism of action are required at the field and laboratory levels (Fig. 4). Future eco-friendly and efficient inoculants must be created using cutting-edge technologies like meta-proteomics, nanotechnology, and rhizoengineering.

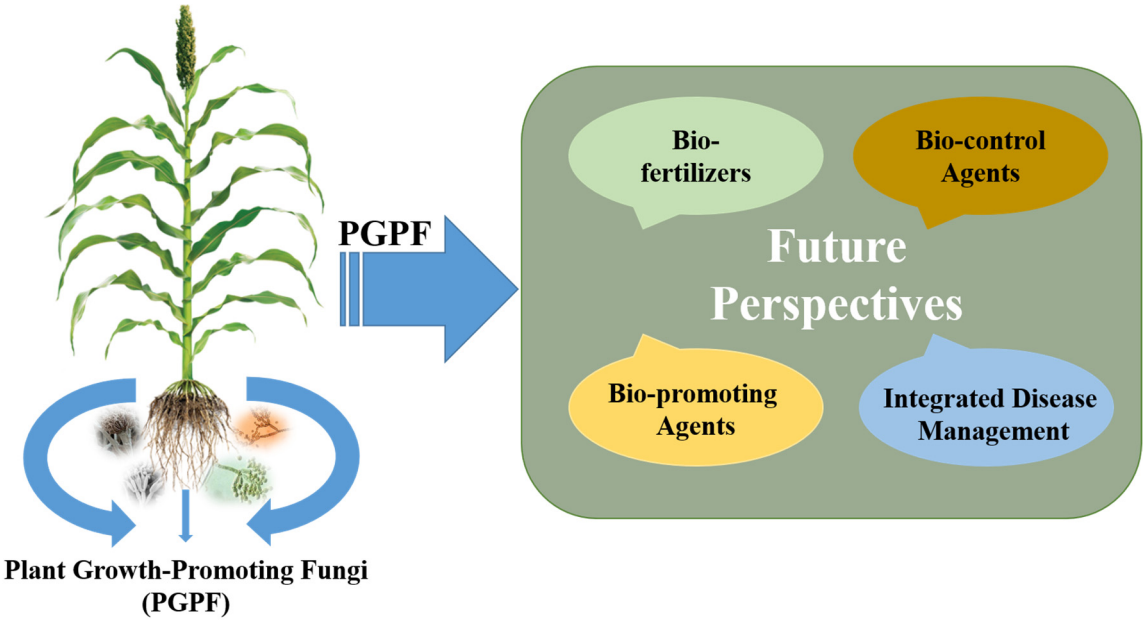

Figure 4: Future direction and prospects concerning PGPF for crop protection and improvement.

Another important challenge limiting the large-scale application of PGPF is the instability of fungal colonization under diverse environmental conditions. Native soil microbial communities often compete with introduced fungal inoculants for ecological niches and nutrient resources, thereby reducing colonization efficiency and persistence. Environmental factors including soil pH, temperature fluctuations, salinity, drought stress, and moisture variability also influence fungal survival and effectiveness in field conditions [42,149,156,157]. Climate change-related stresses may further alter microbial community dynamics and plant–fungus interactions. Therefore, future studies should focus on developing environmentally adaptable and stress-resilient fungal inoculants with improved colonization stability and field persistence [158–160].

Endophytes-fungi have already been investigated as a unique source of fungal metabolites with a variety of possible uses in the medical area and as microorganisms that can help plants be more resilient to environmental challenges [161]. Despite these benefits, certain endophytes can coexist with the host plants for several cycles in a dormant state before manifesting indications of illness [162]. When the host (i.e., the plant tissue) becomes conductive to the development of illness, this relationship eventually alters [163]. In this context, abiotic stresses such as heat and water deficits, whether occurring individually or in combination, can significantly influence both the host plant and the pathogen, thereby affecting disease development and severity [164].

Microbial communities including living biomass and necromass are crucial to ecosystem stability and the rice—*Stropharia rugosoannulata* rotation paradigm for sustainable agriculture. Fungal necromass may maximize agricultural soil carbon sequestration in response to climate change and soil carbon accumulation, but further research is needed. These results offer new insights into sustainable agriculture plans that balance yield and environmental protection [164]. Another study highlights the function of plant-microbe signaling which produces strigolactones, phytohormones, and flavonoids in creating the microbial environment and increasing plant resistance. How genetics and next-generation sequencing can improve precision agriculture is also highlighted. Genotype-microbiome interactions, innovative microbial consortia, and precision agricultural system microbiome management should be studied to improve plant health and yield [165,166]. For plants to acquire nutrients, be able to tolerate stress, and maintain their overall health, the plant microbiome, which can be found in the rhizosphere, phyllosphere, and endosphere, is necessary. With conventional inoculants and synthetic biology, microbiome engineering increases food availability and drought resistance. Microbiome improvements and M genes aid agricultural resilience, but climate change worsens them. M gene studies to breed disease resistance and microbiome engineering's environmental and agronomic implications are highlighted in this study. We conclude with rice microbiome engineering studies and approaches to sustainably boost agricultural output and reduce environmental impact [158].

Nanomaterials enhance hydration, nourishment, and active ingredient distribution. Nano-materials control hormones, photosynthesis, and antioxidants. Antibacterial and protective qualities increase plant immune responses and microbial-plant symbiosis [159], making plants more disease- and pest-resistant. Nanoparticles have health and environmental effects, and this report suggests eco-friendly ways to reduce risks. Nanotechnology, smart technologies, and precision agriculture could transform agriculture. This study illuminates nanomaterial R&D's future, enabling a more resilient agricultural system [160].

While studies on free-living fungi and plant performance are limited, it is well established that root-associated fungi form mutualistic relationships with plants. Fungi in the rhizosphere performs essential biogeochemical cycles that are necessary to supply plants with food sources and hence increase crop productivity. Despite these advantages, little is known about how microorganism's function in a natural setting when numerous biotic and abiotic stressors are present at once. The potential to use diverse plant/microorganism combinations in specific crops, most notably tomato, has already permitted the identification of microbial species that may be exploited to improve tolerance and resilience to a state of stress. These effects are species-specific [156,157].

To establish a clear and actionable research agenda for advancing plant growth-promoting fungi (PGPF) in sustainable agriculture, future research should focus on several key priorities. First, long-term, multi-environment field validation is essential to bridge the gap between controlled experimental outcomes and field-level performance, as most current studies remain limited to greenhouse or short-term trials despite demonstrating significant improvements in plant growth and physiological traits [167,168]. Second, integrated multi-omics approaches (metagenomics, transcriptomics, and metabolomics) should

be prioritized to elucidate complex plant–fungus–microbiome interactions. Recent evidence shows that PGPF regulate primary and secondary metabolites, antioxidant systems, and stress-responsive pathways, thereby enhancing plant tolerance to drought and salinity stress [169,170]. Third, future studies should emphasize the development of synthetic microbial consortia, as mixed inoculations and native fungal communities often outperform single-strain applications by improving nutrient uptake, osmotic regulation, and stress resilience under adverse environmental conditions [168,171]. Fourth, scalable formulation and delivery systems, including nano-enabled carriers and stress-tolerant inoculants, must be optimized to enhance shelf-life, colonization efficiency, and field applicability. Additionally, the integration of PGPF into precision agriculture and climate-smart farming systems through data-driven microbiome management is crucial for maximizing productivity under changing climatic conditions [172,173]. Finally, host specificity and functional diversity of fungal strains should be systematically investigated, as different PGPF species exhibit variable effects on plant physiology, antioxidant activity, and stress mitigation depending on environmental conditions and host genotype [171,173]. Addressing these research priorities will facilitate the transition of PGPF from experimental systems to scalable, field-ready solutions for sustainable and climate-resilient agriculture.

Recent studies on fungal stress adaptation mechanisms, including BdUth1-associated pathways, have provided important insights into fungal survival, cellular homeostasis, and environmental adaptability under stress conditions [171–173]. Understanding these molecular regulatory pathways may improve the development of stress-tolerant fungal inoculants for sustainable agricultural applications [158–160]. The construction of synthetic fungal microbiota based on functional complementarity has emerged as a promising strategy for sustainable agriculture. Combining fungal strains possessing complementary traits such as nutrient solubilization, phytohormone production, stress tolerance, antioxidant activity, and pathogen suppression may provide more stable and efficient plant growth promotion than single-strain inoculants [158,165,168,171]. Such multifunctional microbial consortia can improve nutrient cycling, ecological stability, and plant resilience under complex environmental conditions. Future research should therefore prioritize the rational design of crop-specific fungal consortia using systems biology and microbiome engineering approaches.

8 Conclusion

Plant growth-promoting fungi holds significant potential for sustainable agriculture, enhancing plant growth and productivity in an eco-friendly and cost-effective manner. Understanding of many biochemical, physiological, and ecological aspects of plant-microbe interactions has advanced, and a considerable body of research has been developed; this suggests a relevant function to increase plant tolerance and resilience. While the mechanisms governing plant defenses in response to beneficial microbes remain partially understood, the functional potential of plant-associated microbiota warrants further exploration. For some crop cultivars where diseases have overcome genetic resistance, the introduction of beneficial plant-associated microbes to increase plant resistance may also be helpful. There are various elements that influence the plant microbiome and its interactions, which are extremely diverse. The importance of the rhizospheric microbiota, which includes fungi that promotes plant growth and is good for plant development and yield, is underscored by scientific research. Current breakthroughs in molecular and bioinformatics technologies have enabled the identification of beneficial fungal species that can stimulate the growth of their host plants via a variety of mechanisms. Precision farming, which strives to reduce input while increasing output by using targeted action and monitoring environmental variables, should be the major goal of farming in the future via PGPF. It is therefore vital to investigate the fundamental

mechanisms of plant-microbe interactions to incorporate microbes in the development of sustainable agricultural techniques for crop protection and improvement.

This review demonstrates that plant growth-promoting fungi represent a key component of sustainable and climate-resilient agriculture by integrating nutrient efficiency, stress tolerance, and ecological sustainability. However, bridging the gap between laboratory research and field application remains a major challenge. Future research should prioritize scalable, crop-specific inoculant development supported by advanced omics technologies and precision agriculture. The integration of PGPF into circular bioeconomy systems offers a promising pathway toward sustainable food production and environmental conservation.

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