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Review

Plant Growth-Promoting Microorganisms as Biocontrol Agents: Mechanisms, Challenges, and Future Prospects

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Abstract: The escalating threats posed by plant pathogens and the environmental repercussions of conventional agrochemicals necessitate sustainable agricultural solutions. This review focuses on plant growth-promoting microorganisms (PGPMs) such as bacteria, filamentous fungi, and yeasts, which play a pivotal role as biocontrol agents. These organisms enhance plant growth and resilience through nutrient solubilization, phytohormone production, and antagonistic activities against pathogens, offering a dual benefit of disease suppression and growth enhancement. However, the effective application of PGPMs faces challenges, including variability in field performance, survival and colonization under field conditions, and regulatory hurdles. This paper discusses these challenges and explores recent advances in utilizing these bioagents in sustainable agriculture, underscoring the importance of integrated pest management systems that reduce chemical inputs, thus promoting ecological balance and sustainable farming practices.

Keywords: biocontrol agents; environmental impact; integrated pest management; PGPM; phytopathogens; plant growth-promoting microorganisms; sustainable agriculture

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1. Introduction

Agriculture faces significant challenges due to the increasing prevalence of plant pathogens and the adverse environmental impacts of synthetic agrochemicals [1–3]. Plant diseases are responsible for considerable crop losses, often reducing yields by 21–30% in significant crops worldwide [4]. Traditional chemical-based pest and disease management approaches are ultimately unsustainable and pose severe risks to human health and the environment [5,6]. This has driven the quest for alternative, eco-friendly solutions to agricultural productivity challenges [7,8].

Among promising alternatives, plant growth-promoting microorganisms (PGPMs), including bacteria, filamentous fungi, and yeasts, have garnered considerable attention for their dual role as biocontrol agents and plant growth enhancers [3,8–10]. PGPMs affect plants in many ways, including making nutrients more available, creating phytohormones, and stopping pathogens by building systemic resistance or creating antimicrobial metabolites [11–13]. Notably, plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF) have demonstrated the ability to improve stress tolerance and crop yield while minimizing environmental impact [14–17].

Though less studied than bacteria and filamentous fungi, yeasts exhibit significant potential as biocontrol agents and plant growth promoters. Some types of yeast make antibiotics, enzymes that break down cell walls, and plant growth regulators. These help plants fight soil-borne fungal pathogens and stay healthy [18–21]. Their rapid growth and adaptability to diverse environments also position them as viable candidates for sustainable agricultural practices [22,23].

This review explores the mechanisms by which PGPMs, such as bacteria, filamentous fungi, and yeasts, contribute to sustainable agriculture. It includes their role in nutrient cycling, pathogen suppression, and resilience against biotic and abiotic stresses. It also highlights recent advances in their application and the challenges associated with scaling these biological solutions to field conditions.

Numerous experimental studies provide strong evidence of the positive impacts of PGPMs on crop productivity and health. For example, *Bacillus subtilis* and *Pseudomonas fluorescens* have been shown to significantly reduce the incidence of Fusarium wilt in tomatoes, achieving yield increases of up to 25% under greenhouse conditions [24]. In another field trial, applying *Trichoderma harzianum* on cucumber resulted in a 31% yield increase and significant suppression of *Rhizoctonia solani*-induced damping-off [25]. Similarly, *Saccharomyces cerevisiae* has been demonstrated to reduce postharvest decay in apples caused by *Penicillium expansum* while enhancing fruit firmness and shelf life [26]. Mycorrhizal fungi, such as *Rhizophagus irregularis*, have shown up to a 40% enhancement in phosphorus uptake and a 20% increase in maize grain yield under low-input conditions [27]. These examples underscore the practical utility of PGPMs in sustainable agriculture and advocate for their integration into crop management strategies.

2. Study Selection Criteria

This review included peer-reviewed research articles, including experimental studies, field trials, and meta-analyses, focusing on the efficacy of PGPMs such as bacteria, filamentous fungi, and yeasts in agricultural settings. Eligible studies specifically examined recognized PGPMs like *Bacillus subtilis*, *Pseudomonas fluorescens*, *Trichoderma harzianum*, and *Saccharomyces cerevisiae*. They provided precise quantitative measurements of plant growth parameters (e.g., height, biomass, yield) and/or disease suppression effectiveness. Only studies published in English within the last 20 years were considered to maintain accuracy and ensure that recent advancements were covered.

In contrast, this review excluded non-peer-reviewed sources (e.g., grey literature, opinion pieces, and reviews lacking original data), studies unrelated to plant–microbe interactions for agricultural applications, or those without precise experimental controls or data on microbial application and plant response. Studies in non-agricultural contexts, such as bioremediation, or those reporting redundant or duplicated data already included in other selected studies, were also excluded.

3. Plant Growth-Promoting Rhizobacteria (PGPR), Filamentous Fungi, Yeasts, and Rhizobacteria as Promising Biocontrol Agents

Biological control strategies utilizing microorganisms have emerged as effective and sustainable alternatives to chemical pesticides in managing plant diseases [28,29]. Plant growth-promoting rhizobacteria (PGPR), filamentous fungi, yeasts, and rhizobacteria have shown significant promise due to their diverse mechanisms of action, adaptability, and compatibility with eco-friendly agricultural practices [12,30].

3.1. Plant Growth-Promoting Rhizobacteria (PGPR)

PGPR are beneficial bacteria that colonize plant roots and promote growth through direct and indirect mechanisms [31–34]. These bacteria enhance nutrient availability by solubilizing nutrients, stimulate lateral root development for increased nutrient uptake, and produce a variety of phytohormones such as indole-3-acetic acid (IAA), gibberellins, and cytokinins to regulate plant growth and development [35–40].

Bacillus subtilis and *Pseudomonas fluorescens* are well-studied PGPR strains known for suppressing pathogens like *Phytophthora capsici* and *Fusarium oxysporum* in crops under greenhouse and field conditions [24]. The ability of PGPR to adapt to various environmental conditions and their synergistic interactions with host plants highlight their potential as sustainable tools for disease management and crop productivity enhancement [41,42].

3.2. Fungi as Biocontrol Agents

PGPF, such as *Trichoderma* and *Aspergillus* species, are well known for their biocontrol potential. These fungi improve nutrient acquisition, particularly phosphorus solubilization, and enhance root health by producing bioactive compounds [43]. Additionally, PGPF are crucial in inducing systemic resistance and competing with pathogens for space and nutrients in the rhizosphere.

Trichoderma species have been extensively documented for their ability to manage soil-borne fungal pathogens such as *Rhizoctonia solani* and *Fusarium graminearum* while also promoting plant growth by modulating phytohormonal pathways [44]. Their capacity to withstand abiotic stresses further enhances their application in sustainable agriculture [14,45].

3.3. Yeasts as Biocontrol Agents

Although underexplored, yeasts, unlike bacteria and fungi, exhibit unique traits that make them effective biocontrol agents and plant growth promoters [46]. These include rapid growth, production of antimicrobial metabolites, and induction of plant defence mechanisms [47,48]. Yeasts such as Saccharomyces cerevisiae and Candida oleophila exhibit biocontrol capabilities by outcompeting fungal pathogens for nutrients, secreting cell wall-degrading enzymes like chitinases and glucanases, and inducing plant defence responses [19] (Table 1).

Moreover, yeasts have been reported to enhance the rhizosphere's microbial diversity and improve plant resilience against biotic and abiotic stresses [49–51]. Their adaptability to varied environmental conditions and ability to colonise plant surfaces make them a promising component of integrated disease management strategies [52–54].

Table 1. Yeast species with plant-beneficial properties and their known effects.

Yeast Species	Plant-Beneficial Effect(s)	Reference
Saccharomyces cerevisiae	Auxin production, biofilm formation, antifungal metabolite production	[19]
Candida oleophila	Nutrient competition, secretion of chitinases and glucanases, colonization of plant surfaces	[55]
Metschnikowia fructicola	VOC production, inhibition of *Botrytis cinerea*, postharvest disease control	[56]
Pichia anomala	Mycoparasitism, production of antifungal enzymes, enhancement of plant immunity	[57]

Note: VOC = volatile organic compound.

3.4. Rhizobacteria and the Phytomicrobiome

Rhizobacteria, as a subgroup of plant growth-promoting rhizobacteria (PGPR), establish dynamic interactions with plant roots and the surrounding microbiome. They enhance nutrient uptake, promote root growth, and provide protection against pathogens through the secretion of antimicrobial compounds and volatile organic compounds

(VOCs) [34,58–60]. The co-evolution of rhizobacteria with host plants has led to highly specialized and efficient symbiotic relationships, enabling them to suppress pathogens while supporting plant growth [61].

The rhizosphere microbiome, including rhizobacteria, plays a critical role in disease suppression through competitive exclusion and niche colonization. For example, *Pseudomonas* species have been widely studied for their ability to produce siderophores that deprive pathogens of essential iron, thereby reducing their proliferation [62].

4. Biocontrol Mechanisms of PGPMs

Plant growth-promoting microorganisms (PGPMs) exhibit diverse biocontrol strategies, each adapted to their unique biology [63–65]. These include bacteria such as PGPR, filamentous fungi, yeasts, and rhizobacteria, which interact with plants and pathogens through both direct and indirect mechanisms. The biocontrol potential of plant growth-promoting microorganisms stems from their ability to suppress pathogens and enhance plant defenses through various direct and indirect mechanisms [12,42]. The mechanisms employed by filamentous fungi and yeasts involve competition for nutrients and space, secretion of antimicrobial compounds, and induction of plant defense responses.

Plant growth-promoting rhizobacteria (PGPR). These beneficial bacteria protect plants by producing antimicrobial compounds, competing for nutrients, and by causing induced systemic resistance (ISR). For example, *Pseudomonas fluorescens* produces phenazines and pyrrolnitrin to suppress fungal pathogens while promoting plant growth via VOCs like 2,3-butanediol. PGPR employ several biocontrol strategies that directly or indirectly protect plants from pathogens. These include antibiosis, where PGPR produce antimicrobial compounds such as antibiotics, hydrogen cyanide, and secondary metabolites that inhibit pathogen growth, as seen in *Pseudomonas fluorescens* producing phenazines and pyrrolnitrin to suppress fungal pathogens [66]. Another mechanism is siderophore production, where iron-chelating compounds deprive pathogens of essential iron in the rhizosphere, effectively limiting their growth, which is particularly crucial in iron-deficient soils [62]. PGPR also cause ISR by producing elicitors that activate the jasmonic acid (JA) and ethylene signaling pathways, priming plants to defend themselves against future pathogen attacks [67]. Nutrient competition is another key strategy, as PGPR rapidly colonize the rhizosphere and efficiently utilize root exudates, giving them a competitive advantage over harmful microorganisms [59]. Lastly, PGPR release VOCs, such as 2,3-butanediol and acetoin, which act as antimicrobial agents and enhance plant growth [68].

Plant growth-promoting fungi (PGPF). Filamentous fungi, in particular, contribute to biocontrol through various physical and biochemical mechanisms. Mycoparasitism involves fungi, such as *Trichoderma* and *Aspergillus* species, directly attacking pathogenic fungi by secreting lytic enzymes, such as chitinases and glucanases, that degrade their cell walls [43]. Additionally, fungi compete for space and nutrients by colonizing the rhizosphere or root surfaces, excluding pathogens from infecting plant tissues [44]. Similar to PGPR, fungi can cause ISR by activating plant defense pathways, particularly through the salicylic acid (SA) and JA signaling cascades, which strengthen the plant's ability to resist pathogens. Filamentous fungi also produce antimicrobial compounds, such as gliotoxin and harzianic acid, which inhibit spore germination and mycelial growth [55]. Moreover, they enhance nutrient uptake by solubilizing phosphorus and mobilizing other nutrients, thereby improving plant vigor and indirectly reducing susceptibility to pathogens [38].

Yeasts exhibit distinctive biocontrol mechanisms through their ability to colonize plant surfaces and produce bioactive compounds. They compete for space and nutrients, with species like *Saccharomyces cerevisiae* and *Candida oleophila* occupying niches on plant surfaces and preempting colonization by pathogens [56]. Yeasts also produce antifungal metabolites, including diffusible and volatile compounds such as β-1,3-glucanase, chitinases, and organic acids, suppressing fungal pathogens like *Botrytis cinerea* and *Penicillium expansum* [57]. Additionally, they induce host resistance by enhancing plant immune responses through the expression of defense-related genes, aiding plants in combating pathogens effectively [69]. Some yeasts form biofilms on plant surfaces, creating physical barriers that hinder pathogen entry [19]. Although less commonly than fungi, specific yeasts exhibit mycoparasitic behavior by attaching to and degrading fungal hyphae [70].

Rhizobacteria. As a specialized subset of PGPR, rhizobacteria employ targeted mechanisms to suppress pathogens and promote plant health. They form biofilms that protect plant roots and create competitive microenvironments unfavorable to pathogens [58]. By secreting plant hormones such as IAA and gibberellins, rhizobacteria stimulate root growth and enhance plant resistance to stress [61]. Additionally, they interfere with quorum-sensing signals of pathogens, thereby inhibiting their virulence [71]. Some rhizobacteria degrade toxins produced by pathogens, neutralizing their harmful effects on plants [72]. Like PGPR, they also mobilize nutrients by solubilizing phosphorus and enhancing nitrogen fixation, improving plant nutrition and reducing the impact of pathogens [66]. These diverse mechanisms highlight the multifaceted roles of PGPR, filamentous fungi, yeasts, and rhizobacteria in protecting plants and promoting growth. Their adaptability and effectiveness make them invaluable for sustainable integrated pest and disease management systems. These biocontrol agents offer promising solutions to enhance agricultural productivity while maintaining ecological balance by reducing reliance on chemical inputs and integrating seamlessly into natural ecosystems.

5. Challenges of Employing PGPR, Filamentous Fungi, Yeasts, and Rhizobacteria as Biocontrol Agents

While PGPMs have shown immense potential as biocontrol agents, their widespread adoption faces significant challenges [8,12,73]. These challenges stem from biological, environmental, and regulatory factors unique to each group.

The field performance and widespread adoption of PGPR encounter several challenges that underscore the complexity of their application in agriculture. One significant issue is the variability in field performance, as the effectiveness of PGPR is influenced by environmental factors such as soil type, moisture, temperature, and crop species, making it difficult to achieve consistent outcomes under diverse field conditions [71]. Another challenge is the survival and colonization of PGPR, as these microorganisms must effectively establish themselves on plant roots and persist in the rhizosphere while competing with native microbes and enduring environmental stressors. Additionally, ensuring their viability during storage, transportation, and application adds another layer of complexity [74]. The strain-specific efficacy of PGPR further limits their applicability, as certain strains are often effective only for specific crops or pathogens, reducing their utility across a wide range of agricultural settings [38]. However, this specificity can also be regarded as an advantage, particularly regarding biosafety and regulatory compliance. Targeted interactions reduce the likelihood of unintended effects on non-target organisms and ecological systems, making safety assessments more straightforward and predictable. Moreover, the precision offered by strain-specific PGPR aligns well with integrated pest management (IPM) strategies that emphasize customized and environmentally sound approaches. Future research should leverage this specificity to design highly tailored microbial formulations while exploring methods to broaden the host range or deploy microbial consortia that combine strain specificity with greater versatility.

Despite the growing interest in microbial-based products, regulatory frameworks remain a significant bottleneck. In the European Union, microbial biostimulants are regulated under the Fertilising Products Regulation (EU) 2019/1009, which explicitly excludes their use as Plant Protection Products (PPPs). PPPs are governed separately under Regulation (EC) No 1107/2009, which entails a more stringent and complex authorization process [75,76]. This bifurcation challenges product developers, as the same microorganism may be subject to different regulatory pathways depending on its intended use. The situation is particularly impactful in Southern EU countries, where the agricultural sector represents a significant market for microbial PPPs. The dual regulatory approach often leads to confusion and delays in commercialization, discouraging innovation and limiting the adoption of these eco-friendly solutions. Streamlined policies and clearer guidelines are needed to support the integration of microbial biocontrol agents into mainstream agricultural practice.

Regulatory barriers present significant challenges, as developing and registering PGPR-based products necessitates extensive testing to meet safety and efficacy standards, resulting in delays in commercialization and increased costs [77]. Additionally, PGPR must be compatible with various agricultural inputs, such as fertilizers, pesticides, and irrigation practices. However, this compatibility is not always assured, which can restrict their integration into existing farming systems [78]. PGPR encounter several hurdles, including variability in field performance and colonization under natural conditions. Regulatory frameworks also impact their application but remain an underexplored area. While safety and efficacy testing are essential, the complexity and duration of regulatory procedures often hinder commercialization and discourage broader adoption [77]. Addressing these challenges is vital for maximizing the potential of PGPR in sustainable agriculture.

Recent advancements provide several solutions to the key limitations faced in PGPR applications. Microencapsulation technologies and carrier-based formulations have effectively extended microbial viability and enhanced root adherence to improve field performance and colonization. Consortia formulations combining multiple PGPR strains—or PGPR with fungi—are being developed to address strain specificity, thereby increasing both host range and efficacy. Omics tools, including genomics and metabolomics, are now utilized to screen and engineer PGPR with improved traits such as stress resilience and bioactive metabolite production. On the regulatory front, pilot frameworks for microbial inoculants in Europe and Asia are beginning to recognize biostimulants as distinct from synthetic agrochemicals, streamlining registration. Alongside precision application techniques, these approaches signify substantial progress in integrating PGPR into mainstream sustainable farming systems.

5.1. Challenges of Employing Fungi

The effectiveness of fungal biocontrol agents, such as *Trichoderma*, is influenced by several challenges that affect their practical application. Environmental sensitivity plays a critical role, as their efficacy depends on factors like temperature, pH, and soil moisture, which can vary significantly under field conditions, potentially limiting their success in diverse environments. Additionally, many fungal formulations have a limited shelf life and are highly sensitive to storage conditions, complicating their transportation and long-term usability. Another concern is the potential for pathogen resistance, where fungal pathogens may develop resistance to biocontrol fungi, diminishing their effectiveness over time. The field application of fungi also presents challenges, as their successful establishment and colonization require precise environmental conditions that are often difficult to replicate outside of controlled settings. Furthermore, there is a risk of non-target effects, where fungal biocontrol agents might inadvertently impact beneficial soil microbes or local biodiversity if not carefully managed, emphasizing the need for cautious and targeted application. These challenges highlight the importance of advancing formulation technologies and application strategies to optimize the use of fungal biocontrol agents in sustainable agriculture.

5.2. Challenges of Employing Yeasts

Yeasts, while promising biocontrol agents, face several challenges that limit their broader application. Their potential remains underexplored compared with bacteria and fungi, as limited research has been conducted to fully understand their mechanisms and applications in biocontrol systems [19]. Additionally, many yeasts are transient in soil environments, meaning they often fail to persist long enough to provide lasting biocontrol effects, which raises concerns about their environmental sustainability [79]. The host range of yeast biocontrol agents is another limitation; their effectiveness is often restricted to specific pathogens or crops, reducing their versatility and applicability across diverse agricultural systems [69]. Scaling up the production of yeast-based biocontrol products presents further challenges, as maintaining efficacy and cost-effectiveness can be difficult due to their complex growth requirements, including specialized nutrients and conditions [79]. Furthermore, potential pathogenicity of some yeast strains poses risks to human health, emphasizing the importance of careful strain selection and rigorous safety testing to ensure their suitability for agricultural use [80]. Addressing these challenges is essential for realizing the full potential of yeasts as biocontrol agents in sustainable agriculture.

5.3. Challenges of Employing Rhizobacteria

Rhizobacteria, as promising biocontrol agents, face several challenges that can hinder their effectiveness in agricultural applications. One major constraint is their ability to survive and remain active under diverse environmental conditions, including extreme pH, temperature, and salinity, which can significantly limit their biocontrol activity [81]. Additionally, rhizobacteria must compete with native soil microorganisms, which can antagonize their establishment and reduce their activity within the rhizosphere [72]. Another limitation is their dependency on host plants, as many rhizobacteria exhibit high host specificity, restricting their use across a wide range of crops [61]. Furthermore, the complexity of developing effective formulations poses a significant challenge, as these formulations must ensure the viability of rhizobacteria during storage, transportation, and application without compromising their efficacy [82]. Regulatory and market barriers further complicate their adoption, as strict regulations and skepticism about their economic viability among farmers can delay widespread acceptance [77]. Despite these obstacles, advancements in microbial formulations, microbial consortia use, and genetic tools to enhance rhizobacterial efficacy offer promising solutions. Addressing these challenges is essential to fully harness the potential of rhizobacteria and other microbial biocontrol agents in promoting sustainable agriculture and reducing reliance on chemical inputs (Table 2).

Table 2. Challenges and limitations of PGPMs.

Microorganism	Challenges
PGPR	Field performance variability, survival in diverse conditions, regulatory hurdles
Filamentous fungi	Environmental sensitivity, short shelf life, pathogen resistance, field application complexities
Yeasts	Transient soil presence, limited host range, scale-up challenges, safety concerns
Rhizobacteria	Competition with native microbes, host specificity, formulation stability

5.4. Proposed Solutions and Future Directions

While the challenges associated with PGPM application—such as strain specificity, environmental variability, and regulatory constraints—are well documented, several emerging strategies offer potential solutions:

1. Formulation Advancements: Encapsulation techniques, such as alginate beads and biochar-based carriers, can enhance microbial survival during storage and improve field persistence. These formulations provide protection from environmental stress and enable controlled release of microbes [74].
2. Consortia Development: Employing microbial consortia instead of single strains can broaden functional range, improve colonization, and provide synergistic effects on plant growth and disease suppression. Combining bacteria with fungi or yeasts helps ensure performance across variable soil and crop conditions [73].
3. Genomics and Omics Technologies: Whole-genome sequencing and transcriptomics allow for the identification of genes responsible for biocontrol and plant growth-promoting traits. These tools can guide the selection or genetic improvement of strains with enhanced adaptability and effectiveness [83].
4. Precision Agriculture and Microbiome Engineering: Advances in precision agriculture enable targeted application of PGPMs based on soil health indicators and crop phenology. Additionally, microbiome engineering techniques, such as synthetic microbial communities, are being developed to shape plant-associated microbiota for improved outcomes [84].
5. Regulatory Streamlining and Policy Support: Harmonizing global regulatory frameworks and recognizing microbial products under integrated pest and nutrient management policies would reduce commercialization barriers. Europe's shift toward recognizing microbial biostimulants separately from PPPs marks a significant step, but broader implementation and clarity are required [77].

By integrating these approaches, future efforts can overcome current bottlenecks and fully harness the potential of PGPMs for sustainable and resilient agriculture.

6. Rhizosphere Competence and Biocontrol Mechanisms

PGPR. These bacteria thrive in the rhizosphere by utilizing root exudates such as organic acids, sugars, and amino acids. Their ability to form biofilms enhances survival and competitiveness, and PGPR exhibit exceptional rhizosphere competence, a critical factor for their effectiveness as biocontrol agents. These bacteria thrive in the rhizosphere by utilizing a variety of root exudates, including organic acids, sugars, and amino acids, as energy sources [35,85,86]. Their ability to form robust biofilms on root surfaces enhances their survival and competitiveness in the soil environment [58]. This biofilm formation not only provides a physical barrier against pathogens but also ensures a steady supply of nutrients for the bacteria, allowing them to produce antimicrobial compounds and induce systemic resistance in plants. Moreover, the rapid colonization capabilities of PGPR enable them to outcompete native soil microorganisms, further strengthening their role in plant protection [66] (Table 2).

PGPF. Filamentous fungi, such as *Trichoderma* and *Aspergillus* species, also demonstrate strong rhizosphere competence. Their ability to form extensive hyphal networks enables them to colonize large areas of the rhizosphere efficiently, creating a physical and biochemical barrier against soil-borne pathogens [43]. These fungi produce a wide range of lytic enzymes, such as chitinases and glucanases, which degrade the cell walls of pathogenic fungi, further asserting their dominance in the rhizosphere. Additionally, PGPF improve nutrient cycling by solubilizing phosphorus and releasing plant-available nutrients, thus fostering a healthy root environment that indirectly suppresses pathogens [38] (Table 3).

Yeasts. Although yeasts are less commonly associated with the rhizosphere than PGPR and filamentous fungi, some species have demonstrated moderate rhizosphere competence. They can colonize root surfaces by utilizing sugars and organic acids from root exudates [19]. Their rapid growth and ability to produce antifungal metabolites and biofilms make them effective in protecting plants under certain conditions [47,54,87]. However, their transient presence in soil ecosystems often limits their long-term effectiveness [88–90]. Despite this limitation, their potential to interact synergistically with other microorganisms in the rhizosphere enhances their role as part of integrated biocontrol strategies [42,91,92] (Table 3).

Rhizobacteria. As a specialized subset of PGPR, rhizobacteria employ targeted mechanisms to suppress pathogens and promote plant health. They form biofilms that protect plant roots and create competitive microenvironments unfavorable to pathogens [81]. By secreting plant hormones such as IAA and gibberellins, rhizobacteria stimulate root growth and enhance plant resistance to stress [61]. Additionally, they interfere with quorum-sensing signals of pathogens, thereby inhibiting their virulence [71]. Some rhizobacteria degrade toxins from pathogens, neutralizing their harmful effects on plants [72]. Like PGPR, they also mobilize nutrients by solubilizing phosphorus and enhancing nitrogen fixation, thus improving plant nutrition and reducing the impact of pathogens [66]. These diverse mechanisms highlight the multifaceted roles of PGPR, filamentous fungi, yeasts, and rhizobacteria in protecting plants and promoting growth. Their adaptability and effectiveness make them invaluable for sustainable integrated pest and disease management systems. By reducing reliance on chemical inputs and integrating seamlessly into natural ecosystems, these biocontrol agents offer promising solutions to enhance agricultural productivity while maintaining ecological balance (Table 3).

Table 3. The mechanisms of antagonism for each group.

Microorganism Group	Mechanisms of Antagonism	References
PGPR	Antibiosis: Producing antibiotics and secondary metabolites to inhibit pathogens.	[66]
	Siderophore production: Depriving pathogens of iron through chelation.	[62]
	ISR: Activating jasmonic acid and ethylene signaling pathways in plants.	[67]
	Nutrient competition: Rapidly colonizing the rhizosphere to outcompete pathogens.	[93]
	Volatile organic compounds: Releasing antimicrobial and growth-promoting compounds.	[94]
Filamentous Fungi	Mycoparasitism: Secreting enzymes like chitinases and glucanases to degrade pathogens.	[43]
	Competition: Occupying space and resources to exclude pathogens.	[44]
	ISR: Triggering plant defenses via salicylic acid and jasmonic acid pathways.	[95]
	Antimicrobial compounds: Producing bioactive substances like gliotoxin to suppress pathogens.	[55]
	Nutrient enhancement: Solubilizing phosphorus and improving root nutrient uptake.	[38]

Table 3. *Cont.*

Microorganism Group	Mechanisms of Antagonism	References
Yeasts	Nutrient and space competition: Colonizing plant surfaces to block pathogens.	[56]
	Antifungal metabolites: Producing enzymes like β-1,3-glucanase and organic acids.	[57]
	Induced host resistance: Enhancing plant immune responses to combat pathogens.	[69]
	Biofilm formation: Creating physical barriers on plant surfaces.	[19]
	Mycoparasitism: Occasionally degrading fungal pathogens directly.	[70]
Rhizobacteria	Biofilm formation: Protecting plant roots and creating a competitive microenvironment.	[58]
	Secretion of plant hormones: Enhancing root growth and overall plant health.	[61]
	Quorum-sensing interference: Disrupting pathogen communication to inhibit virulence.	[71]
	Toxin degradation: Neutralizing harmful substances produced by pathogens.	[72]
	Nutrient mobilization: Solubilizing phosphorus and enhancing nitrogen fixation.	[66]

ISR, induced systemic resistance.

7. Integration of Rhizosphere Competence into Biocontrol Mechanisms

The rhizosphere serves as the primary battleground for the interaction between plants, beneficial microorganisms, and pathogens [96,97]. The competence of PGPR, filamentous fungi, yeasts, and rhizobacteria to establish, survive, and function effectively in this dynamic environment is pivotal to their biocontrol success. Their ability to outcompete pathogens, form protective biofilms, and enhance nutrient availability underscores their value in integrated pest management systems. Improving the understanding of their rhizosphere dynamics through advanced molecular tools and field studies could pave the way for more consistent and effective applications in sustainable agriculture [98–100].

8. Endophytic and Exophytic Traits of Microorganisms in Biocontrol

Microorganisms exhibit diverse colonization strategies that significantly contribute to their roles as biocontrol agents. These strategies are broadly categorized into endophytic (internal colonization of plant tissues) and exophytic (surface colonization) modes [101–104]. PGPR, filamentous fungi, yeasts, and rhizobacteria possess unique endophytic and exophytic traits, enabling them to effectively suppress pathogens, enhance plant health, and promote sustainable agriculture. Understanding and leveraging these traits can optimize the application of microbial biocontrol agents in crop management systems [102,105,106].

PGPR as Endophytes. Species such as *Bacillus subtilis* and *Pseudomonas fluorescens* colonize internal plant tissues, including roots, stems, and leaves, without causing harm. As endophytes, they produce antimicrobial compounds (e.g., lipopeptides and phenazines) to suppress internal pathogens and induce systemic resistance by activating the SA and JA pathways [95]. Additionally, endophytic PGPR improve nutrient uptake and mitigate abiotic stresses, such as drought and salinity, by producing stress-alleviating compounds like exopolysaccharides [107].

As Exophytes. PGPR also form biofilms in the rhizosphere, using root exudates to support colonization, including sugars and organic acids, as energy sources. They rapidly colonize root surfaces, forming biofilms that act as protective barriers against pathogens. PGPR also produce siderophores, which chelate iron and limit its availability to pathogens and release volatile organic compounds (VOCs) with antimicrobial and plant growth-promoting effects [94]. These traits make PGPR crucial components of sustainable pest management strategies.

Mycorrhizal Fungi. Arbuscular mycorrhizal fungi (AMF), in particular, establish symbiotic relationships with plant roots, functioning both endophytically (within cortical cells) and exophytically (through external hyphal networks). These fungi are pivotal in improving plant phosphorus, nitrogen, and micronutrient uptake, while also enhancing water use efficiency and tolerance to abiotic stressors. Field-based research has validated their significant role in yield and quality improvements across multiple crops. For example, in maize and tomato systems, AMF inoculation has consistently enhanced biomass production and nutrient density [27,108].

Beyond nutritional effects, AMF influence crop quality traits such as antioxidant accumulation, sugar content, and shelf life. In strawberries and lettuce, for instance, AMF symbiosis has been linked to higher phenolic and carotenoid levels, contributing to both nutritional and commercial value [109,110]. These effects are particularly pronounced under field conditions that are low in fertility or subject to water stress, demonstrating the adaptability and ecological relevance of AMF. Their integration into biofertilizer strategies offers an avenue for sustainable yield enhancement with minimal environmental impact.

Fungi as Endophytes. *Trichoderma* and *Piriformospora* indica are well known for their endophytic capabilities. They colonize root cortical cells and vascular tissues, producing lytic enzymes (e.g., chitinases and glucanases) to degrade pathogen cell walls [111,112]. Endophytic fungi also release secondary metabolites like harzianic acid and gliotoxin, which inhibit pathogen growth. Furthermore, they prime systemic defenses, enabling plants to combat various pathogens [43]. Their ability to enhance nutrient uptake, especially phosphorus solubilization, further supports plant health and productivity.

As Exophytes. Fungi like *Trichoderma* colonize root surfaces, forming a protective barrier that prevents pathogen invasion. They compete with pathogens for space and nutrients while secreting antimicrobial compounds that directly inhibit pathogen growth. Their exophytic activity complements their endophytic colonization, providing comprehensive protection against soil-borne pathogens like *Fusarium oxysporum* and *Rhizoctonia solani* [44].

Yeasts as Endophytes. Some yeast species, such as *Pichia*, can colonize internal plant tissues and produce antimicrobial enzymes, like β-1,3-glucanase, which suppress fungal pathogens. As endophytes, yeasts can improve internal microbial balance, enhance nutrient acquisition, and contribute to plant stress tolerance [19,113–115].

As Exophytes. Yeasts mainly colonize external surfaces such as leaves, fruits, and roots. They form biofilms that physically block pathogen attachment and secrete antifungal metabolites to suppress pathogens like *Botrytis cinerea*. Yeasts such as *Candida oleophila* and *Saccharomyces cerevisiae* effectively manage postharvest diseases, demonstrating their potential as exophytic biocontrol agents [56,116–118].

Rhizobacteria. These organisms show dual traits: internally, they promote nutrient uptake and stress tolerance; externally, they compete effectively with pathogens. Certain rhizobacteria, such as *Azospirillum* and *Bradyrhizobium*, act as endophytes by colonizing plant roots and internal tissues. These bacteria enhance nutrient availability through nitrogen fixation and phosphorus solubilization while also suppressing pathogens by producing antimicrobial compounds. Their ability to interact with host plants at the molecular level enables them to modulate stress responses and improve overall plant health [58].

Rhizobacteria thrive as exophytes in the rhizosphere, forming dense populations by utilizing root exudates. Their biofilm formation protects plant roots from pathogen colonization, while their production of siderophores and VOCs inhibits pathogen growth. By competing effectively with native soil microbes, rhizobacteria establish themselves as dominant players in the rhizosphere, ensuring effective biocontrol and nutrient cycling [62].

Endophytes target internal pathogens and enhance systemic resistance, while exophytes form the first line of defense by occupying plant surfaces and suppressing external pathogens. Together, these traits ensure robust biocontrol and contribute to the sustainability of agricultural systems. Future research should focus on developing microbial consortia that combine the strengths of endophytic and exophytic microorganisms, maximizing their synergistic effects for enhanced efficacy in diverse agroecosystems [45,62,119,120] (Figure 1).

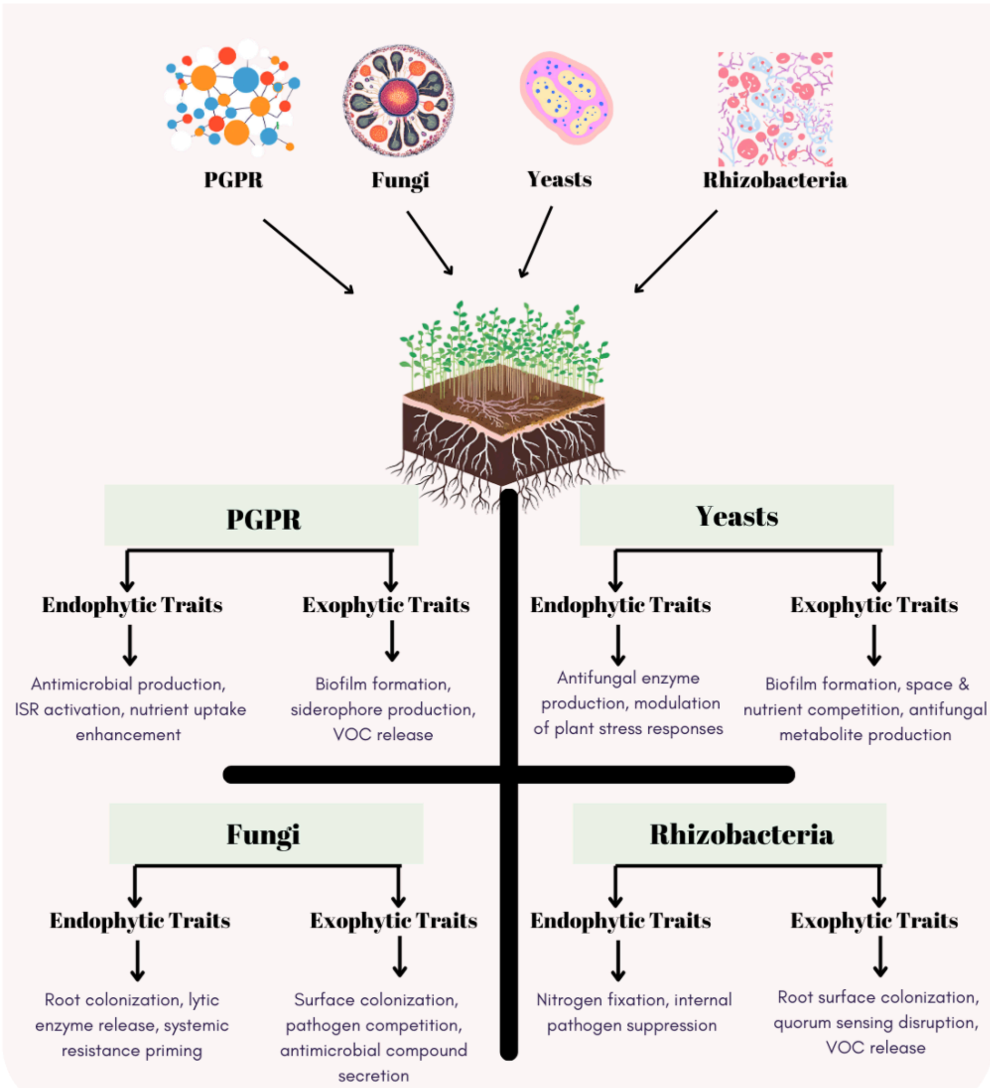

Figure 1. Endophytic and exophytic traits of microorganisms. VOC, volatile organic compounds. ISR, induced systemic resistance.

9. Yeasts and Their Role in Plant Growth Promotion

Yeasts have emerged as promising PGPMs due to their ability to produce plant growth regulators (PGRs) and support plant health in diverse environments. These regulators, including auxins, cytokinins, gibberellins, and ethylene, play critical roles in modulating plant physiological processes, enhancing growth, and improving stress resilience.

Auxins. Auxins, such as IAA (Table 4), are among the most prominent PGRs produced by yeasts. For example, species like *Rhodotorula* and *Saccharomyces cerevisiae* synthesize IAA in response to tryptophan exuded by plant roots. Auxins like IAA facilitate root elongation and branching, thus enhancing water and nutrient absorption by plants, which contributes to improved growth and overall health [19]. Enhanced root systems are particularly beneficial in stress-prone soils, such as saline or drought-affected regions [121,122].

Table 4. Plant growth regulators (PGRs) produced by yeasts.

PGR	Function	Yeast Example
Auxins (IAA)	Promote root elongation and branching	*Rhodotorula*, *Saccharomyces cerevisiae*
Cytokinins	Stimulate cell division and shoot growth	*Candida*, *Pichia*
Gibberellins	Enhance stem elongation, seed germination, and flowering	*Debaryomyces hansenii*
ACC Deaminase	Reduces ethylene levels, alleviating stress-induced growth inhibition	Various yeast species

ACC, 1-aminocyclopropane-1-carboxylic acid.

Cytokinins. Certain yeasts in the genera *Candida* and *Pichia* are known to secrete cytokinins, which promote above-ground biomass accumulation and delay senescence in plants, thus enhancing yield potential [123,124].

Gibberellins. Yeasts such as *Debaryomyces hansenii* produce gibberellins, which regulate stem elongation, seed germination, and flowering. These hormones are particularly valuable in promoting growth under suboptimal environmental conditions, such as low light or nutrient deficiency [13,125].

Ethylene modulation. While ethylene is a key stress-response hormone in plants, excessive ethylene production can negatively impact growth. Plant growth-promoting yeasts help mitigate this by producing ACC deaminase, an enzyme that lowers ethylene levels by breaking down its precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) [120]. This activity alleviates stress-induced growth inhibition, particularly under salinity or drought stress.

Production of secondary metabolites. In addition to PGRs, yeasts produce secondary metabolites such as organic acids, amino acids, and volatile organic compounds (VOCs) that stimulate plant growth indirectly. These compounds can alter root architecture, enhance nutrient solubilization, and promote beneficial interactions with other microbes in the rhizosphere [126–128]

Synergistic effects. Yeasts often work synergistically with other PGPMs, such as rhizobacteria and fungi, amplifying their growth-promoting and biocontrol effects. For instance, yeasts can enhance the bioavailability of nutrients and provide an ideal environment for microbial consortia by modifying root exudates and rhizosphere conditions [14,128,129].

10. Conclusions

The application of PGPMs, including yeasts, filamentous fungi, rhizobacteria, and PGPR, represents a sustainable alternative to chemical inputs in agriculture. These microorganisms demonstrate a wide array of mechanisms—such as the production of antimicrobial compounds, competition for nutrients, and induction of systemic resistance—that effectively suppress plant pathogens while promoting growth. Additionally, their ability to function as endophytes and exophytes allows them to provide multi-layered protection, with endophytes colonizing internal plant tissues to enhance systemic resistance and nutrient uptake and exophytes forming protective barriers on plant surfaces. Yeasts, with their capacity to produce plant growth regulators (PGRs) like auxins, gibberellins, cytokinins, and ethylene-modulating enzymes, further expand the potential of PGPMs to enhance crop resilience and productivity.

Despite their immense promise, challenges such as environmental variability, limited field efficacy, and formulation stability must be addressed to ensure consistent performance. The transient nature of certain microorganisms, such as yeasts, and their dependence on specific environmental conditions can limit their broad applicability. Similarly, regulatory hurdles and farmers' adoption barriers remain significant obstacles to large-scale implementation.

11. Future Prospects

The future of sustainable agriculture strongly hinges on the effective integration of plant growth-promoting microorganisms (PGPMs) into crop production systems. While numerous microbial biopreparations have been developed—primarily targeting PGPR, *Trichoderma* spp., and certain yeasts—their widespread adoption remains limited by inconsistent field results, regulatory complexity, and knowledge gaps. To move forward, efforts should focus on both enhancing existing formulations and introducing new strains identified through advanced screening and genomic approaches.

First, it is essential to stimulate innovation around existing microbial products by optimizing their delivery systems (e.g., encapsulation, seed coatings) and combining them with compatible agronomic practices. Second, introducing new microbial candidates through microbiome mining, synthetic consortia development, and functional validation under diverse field conditions will diversify the available toolbox for farmers. Incorporating microbial consortia with complementary functions (e.g., nutrient mobilization, ISR, pathogen suppression) will increase efficacy and stability.

Third, regulatory harmonization—particularly recognizing microbial biopreparations as distinct from synthetic pesticides—can accelerate market entry and farmer adoption. Public–private partnerships and policy incentives could help scale production and reduce the cost barriers that currently limit accessibility for smallholders.

Lastly, future research should emphasize field-based validation, crop specificity, and formulation stability to bridge the gap between laboratory success and agricultural relevance. Integrating PGPMs into digital agriculture platforms and precision farming tools may further optimize their timing, dosage, and synergy with crop development stages.

These steps will not only enhance the credibility and reliability of microbial solutions but also reinforce their role in achieving global food security, reducing chemical inputs, and maintaining ecosystem health.

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