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Review Article

The Multifaceted Roles of Microorganisms in Promoting Sustainable Plant Growth in Agriculture

Yakubu Iliya Appollm[1,5], Norida Mazlan[2,4]*, Dzarifah Mohamed Zulperi[1], and Noraini Md Jaafar[3]

[1]*Department of Plant Protection, Faculty of Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia*
[2]*Department of Agriculture Technology, Faculty of Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia*
[3]*Department of Land Management, Faculty of Agriculture, Universiti Putra Malaysia. 43400 Serdang, Selangor, Malaysia*
[4]*Laboratory of Climate-Smart Food Production, Institute of Tropical Agriculture and Food Security, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia*
[5]*Department of Agricultural Education, Federal College of Education (Tech), Gombe, Gombe State, Nigeria*

ABSTRACT

Sustainable agricultural productivity increasingly relies on plant growth-promoting microorganisms (PGPMs), which include plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF). These beneficial microbes enhance crop growth by improving nutrient acquisition through processes such as nitrogen fixation, phosphate solubilization, and the synthesis of phytohormones. As a result, they help reduce the need for chemical fertilizers and pesticides. Additionally, PGPMs mitigate plant pathogens by producing antimicrobial compounds, inducing systemic resistance, and competing for ecological niches, resulting in significant reductions in disease incidence and severity. However, despite their demonstrated effectiveness in controlled environments, the performance of PGPMs in real-world agricultural systems is often inconsistent, with efficacy declining by 30-50% due to factors such as abiotic stressors, ecological incompatibilities, and reduced microbial viability. To overcome these challenges, this review presents a strategic framework focused on strain-specific adaptation to local soil and climate conditions, optimized co-inoculation strategies, and omics-guided selection of resilient microbial consortia. These approaches aim to bridge the gap between laboratory success and field performance, enhancing the stability and reliability of PGPM-based solutions. By identifying and addressing

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E-mail addresses:
appollmiliya@yahoo.com (Yakubu Iliya Appollm)
noridamz@upm.edu.my (Norida Mazlan)
dzarifah@upm.edu.my (Dzarifah Mohamed Zulperi)
j_noraini@upm.edu.my (Noraini Md Jaafar)
*Corresponding author

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critical barriers to PGPM adoption, this review seeks to advance microbial technologies that promote sustainable farming, improve crop quality, and ensure global food security despite climate variability.

Keywords: Disease suppression, microbial inoculation, PGPMs, plant growth, sustainable agriculture

INTRODUCTION

The global population's continuous growth necessitates increased food production. However, sustaining this demand using conventional methods such as, chemical fertilizers presents financial and environmental challenges (Asghari et al., 2020). Agrochemical companies promote these practices, but their reliance on non-renewable fossil fuels and associated health concerns raises doubts about long-term viability. In contrast, farmers are increasingly adopting biopesticides for their affordability and effectiveness as biocontrol agents (Hulot & Hiller, 2021). To mitigate the negative impacts of agrochemicals in agriculture, plant growth-promoting microorganisms (PGPMs) have emerged as an environmentally friendly and sustainable alternative (Etesami, 2020).

Biocontrol agents (BCAs), including microorganisms such as *Azotobacter* sp., *Cyanobacteria*, fungi, and algae, show promise in enhancing agricultural productivity (Mensah et al., 2018). Notable examples include *Azospirillum*, *Bacillus*, *Rhizobium*, and *Trichoderma*. These PGPMs function as BCAs by converting nitrogen into plant-usable forms and improving the solubilization of key soil nutrients like phosphorus and potassium. Bhat et al. (2019) demonstrated that these microorganisms produce siderophores to enhance iron uptake and act as phytostimulants by influencing plant hormone levels. Additionally, Khan et al. (2020) reported that PGPMs indirectly serve as biopesticides by inducing systemic resistance against phytopathogens. When applied to soil, biofertilizers colonize the rhizosphere and internal plant structures, increasing nutrient accessibility and improving soil properties (Chatterjee et al., 2017). This eco-friendly approach supports sustainable development and environmental protection, offering a viable alternative to chemical fertilization (Etesami, 2020). Furthermore, PGPMs or biofertilizers can act as biocontrol agents through indirect mechanisms, such as enhancing plant vigor and enabling competition between plant growth-promoting rhizobacteria (PGPR) and pathogens in the root zone (Saeed et al., 2021). By colonizing plant roots, seedlings, or seed surfaces, BCAs improve growth by making essential nutrients available and enhancing soil physical, chemical, and biological conditions through microbial exudates that facilitate nutrient uptake (Chatterjee et al., 2017).

This article explores the mechanisms by which PGPM inoculation enhances plant growth, the influence of inoculation techniques on microbial effectiveness, and the role of PGPMs in suppressing disease development by antagonizing plant pathogens. It also lays a foundation for future research on sustaining plant-beneficial microbe interactions. The uniqueness of this review lies in its practical framework for sustainable agriculture tailored to diverse environmental conditions, integrating recent advances in PGPM applications, including innovative inoculation techniques and their synergistic effects.

The reliance of chemical fertilizers on non-renewable fossil fuels poses significant environmental and health risks (Hulot & Hiller, 2021). In contrast, plant growth-promoting microorganisms (PGPMs) offer a sustainable alternative by enhancing nutrient cycling and reducing pesticide use (Etesami, 2020). Comparative studies reveal substantial variability in the efficacy of PGPMs, with field experiments demonstrating inconsistent crop yields. For instance, *Azospirillum* increased maize yields by 15–20% under optimal conditions (Al-Tammar & Khalifa, 2022), but its effectiveness declined by 30% under water stress (Asghari et al., 2020). This inconsistency presents a significant challenge to large-scale adoption, influenced by specific bio-ecological factors. To address these variations, targeted research is needed to connect PGPM mechanisms, such as nitrogen fixation and biocontrol, to sustainability outcomes like yield consistency and reduced chemical inputs.

PGPMs function through various mechanisms that promote agricultural sustainability. Nitrogen fixation contributes to yield stability but is affected by soil pH and moisture levels. However, there is a critical gap in understanding the long-term stability of nitrogen release under field conditions. Phosphate solubilization improves soil health, with its effectiveness influenced by soil type and microbial density. Nevertheless, its performance is limited by pH-dependent efficacy, highlighting the need for targeted strain selection. In terms of biocontrol, PGPMs help lower chemical inputs by suppressing pathogen loads, with the method of inoculation playing a vital role. A current gap exists in understanding how PGPMs interact or synergize with existing pathogens. Also, phytohormone production enhances plant stress tolerance and is influenced by crop genotype and stress type, but the underlying molecular interaction pathways remain inadequately explored.

To provide holistic synthesis and guide future research, this review adopts a conceptual framework that integrates validated PGPM mechanisms and highlights critical knowledge gaps, particularly in translating laboratory-based efficacy into field performance. This framework also forms the basis for the thematic structure of the review outlined below.

ADVANCING PGPM APPLICATION: A CONCEPTUAL FRAMEWORK TO OVERCOME PRACTICAL BARRIERS

The widespread adoption of plant growth-promoting microorganisms (PGPMs) faces three major barriers: ecological mismatches, technological limitations, and regulatory inconsistencies. First, incompatibility between soil, plants, and microbes is a significant challenge, as microbial efficacy can decrease by up to 20% when inoculants are applied to different soil types (Brown et al., 2020). Second, access to advanced technologies, particularly omics-based tools, is uneven; about 30% of developing regions lack access to

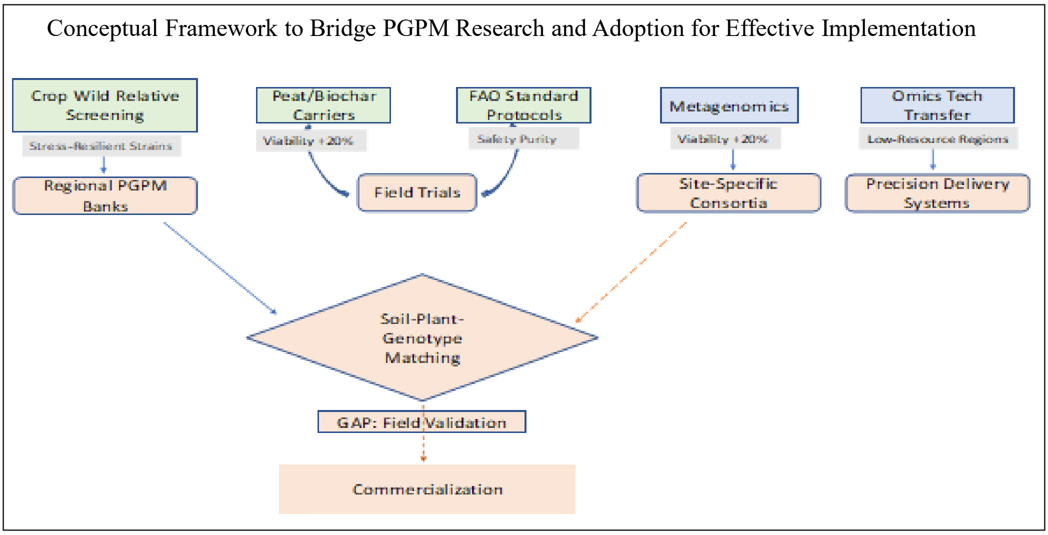

Figure 1. Integrated PGPM implementation framework. Green nodes: short-term priorities; blue nodes: long-term strategies. Dashed arrows indicate key research gaps (e.g., field validation of omics-guided consortia). Framework informed by FAO (2017); Muller et al. (2022)

these innovations (Reis et al., 2024). Finally, the lack of globally standardized protocols for evaluating inoculant purity, shelf-life, safety, and genetic stability undermine regulatory confidence and hampers market scalability. To address these constraints, we propose a dual-phase implementation framework (Figure 1) consisting of Short-term priorities and Long-term strategies:

Short-Term Priorities

1. Develop enhanced carrier materials, such as peat-based microcapsules, to improve microbial viability during storage and delivery.
2. Initiate regionally adapted PGPM screening programs, focusing on crop wild relatives, to identify stress-resilient strains.
3. Standardize evaluation protocols for assessing safety, microbial purity, and genetic stability before commercialization (FAO, 2017).

Long-Term Strategies

1. Utilize metagenomics and omics-guided selection to create site-specific PGPM consortia tailored to specific crop genotype and soil environments.
2. Expand molecular biology and omics infrastructure in low-resource regions through global technology transfer programs.

3. Integrate PGPMs into precision agriculture platforms for real-time, targeted delivery based on field conditions (Muller et al., 2022).

This framework highlights the importance of utilizing microbial diversity from crop wild relatives, which have developed superior phytostimulant traits, including improved nutrient uptake and drought tolerance. It also stresses the essential role of environmental compatibility, particularly soil characteristics and plant genotype in determining the survival and effectiveness of plant growth-promoting microorganisms (PGPM). While this approach is promising, its successful implementation will require a careful balance between agricultural productivity and ecological conservation, especially in areas rich in biodiversity.

PLANT GROWTH-PROMOTING MICROORGANISMS (PGPMS)

Plant growth-promoting microorganisms (PGPMs), encompassing plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF), serve as beneficial biofertilizers, biocontrol agents, and decomposers (Dhawi, 2023). The term "rhizobacteria" was coined by Kloepper and Schroth (1978) to describe soil bacteria that colonize plant roots, enhance growth, and protect against disease. In 1980, they further defined "plant growth-promoting rhizobacteria" (PGPR) to characterize these microbes. To qualify as PGPR, a bacterial strain must fulfill at least two of the following criteria: effective root colonization, plant growth promotion, or disease suppression. PGPR can exist as endophytes within plant tissues or as rhizospheric bacteria on root surfaces, depending on their host interaction. Endophytic PGPR colonize the apoplastic region, while rhizospheric PGPR inhabits the root surface or superficial intercellular spaces (Vandana et al., 2021). Several symbiotic and nitrogen-fixing bacteria, including *Rhizobium*, *Azospirillum*, *Azotobacter*, *Mycobacterium*, *Bacillus*, *Serratia*, *Xanthomonas*, *Proteus*, *Pseudomonas*, and *Clostridium*, are recognized as PGPR. These microorganisms convert nitrogen into plant-usable forms.

In contrast, plant growth-promoting fungi (PGPF) includes beneficial species such as *Aspergillus*, *Penicillium*, *Fusarium*, *Trichoderma*, *Rhizoctonia*, and *Talaromyces*. Their hyphal networks and enzymatic capabilities enable them to degrade organic matter, solubilize nutrients, and stabilize soil aggregates (Corbu et al., 2023). PGPMs colonize the root zone and enhance plant growth through mechanisms such as nitrogen fixation, production of indole-3-acetic acid (IAA) and siderophores, phosphate solubilization, increased resistance to biotic and abiotic stresses, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, quorum sensing (QS), and disease suppression (Cortivo et al., 2017).

Multiple studies indicate that PGPMs differ in their functional capabilities. *Trichoderma* improves phosphate solubilization, increasing tomato growth by 25% in acidic soils

(Tripathi et al., 2020), while *Azotobacter* is excellent at nitrogen fixation in microaerobic conditions, increasing wheat yields by 18% (Meena et al., 2017). Contradictions do arise, however, since strain-related siderophore synthesis varies by 40% under drought stress (Syed et al., 2023), suggesting limitations specific to the soil. Given that field observations show a 15–20% reduction in efficacy after a year (Mukhtar et al., 2017), research on long-term nutrient retention is lacking. A prolonged, strain-targeted study is necessary to improve long-term effects.

PLANT GROWTH-PROMOTING MECHANISMS OF PGPMS

This section discusses the mechanisms by which Plant Growth-Promoting Microorganisms (PGPMs) enhance crop growth, highlighting both direct and indirect processes. These mechanisms, influenced by factors such as soil type, host genotype, and plant developmental stage, play a crucial role in increasing agricultural yields (Brown et al., 2020). Direct mechanisms include nutrient acquisition through nitrogen fixation and phosphate solubilization, alongside the production of growth-promoting compounds like indole-3-acetic acid (IAA) and siderophores. Indirect mechanisms involve biocontrol activities that protect plants from phytopathogens (Elekhtyar, 2015).

Together, these mechanisms enhance plant vigor, nutrient uptake, and disease resistance. Their effectiveness has been demonstrated across a variety of crops, highlighting their importance in promoting sustainable agriculture (Kumar et al., 2022; Singh et al., 2019).

Biological Fixation of Nitrogen

Nitrogen is a crucial component of proteins and chlorophyll, essential for photosynthesis and plant growth. However, intensive agricultural practices often deplete soil nitrogen reserves, highlighting the need for microbial solutions (Saritha & Tollamadugu, 2019). Nitrogen-fixing bacteria, such as *Azotobacter* sp., *Rhizobium* sp., and *Azospirillum* sp., tackle this issue by converting atmospheric nitrogen into forms usable by plants, like nitrates and amines, through the nitrogenase enzyme and its FeMo cofactor (Meena et al., 2017). This microbial process not only maintains soil fertility but also adapts well to varying environmental conditions. The effectiveness of nitrogen-fixing microbes differs significantly among species and ecosystems. For instance, *Azotobacter* can boost maize yields by 18% in microaerobic soils (Al-Tammar & Khalifa, 2022), but its effectiveness drops by 30% in water-stressed conditions (Asghari et al., 2020). In contrast, Rhizobium-legume systems achieve stable nitrogen fixation through specialized oxygen-regulation mechanisms, such as the production of leghemoglobin, which protects nitrogenase activity (Reis et al., 2024). These physiological differences highlight the importance of selecting specific strains based on context, especially in arid regions where fluctuations in moisture and oxygen can significantly impact microbial function. Table 1 summarizes the agronomic performance and stress adaptation mechanisms of major nitrogen-fixing PGPM strains, highlighting their yield benefits and limitations under field conditions.

Table 1
Performance and stress tolerance of key nitrogen-fixing PGPM strains

Strain	Optimal Condition	Yield Increase	Stress Tolerance Mechanism	Key Limitations	Reference
Azotobacter sp.	Microaerobic soils	18%	EPS production maintains hydration	30% decline under drought	Al-Tammar & Khalifa (2022)
Rhizobium sp.	Legume symbiosis	25%	Leghemoglobin protects nitrogenase from O_2	Host-specific	Poria et al. (2022)
Azospirillum brasilense	Well-drained soils	15–20%	ACC deaminase reduces ethylene stress	Sensitive to salinity (>6 dS/m)	Bashan & de-Bashan (2023)
Bradyrhizobium japonicum	Soybean symbiosis	22%	Heat-shock proteins (HSPs) stabilize enzymes	Low persistence in acidic soils	Reed & Glick (2023)
Paenibacillus polymyxa	Wide pH range (5–9)	12%	Biofilm formation enhances drought resistance	Competes poorly with native flora	Kumar et al. (2022)

PGPM = Plant Growth-Promoting Microorganisms; EPS = Exopolysaccharides; ACC = 1-Aminocyclopropane-1-Carboxylate. Data represent field-scale observations under optimal vs. stressed conditions

Phosphate Solubilization

Phosphorus is essential for energy transfer and plant development, but its availability is often restricted due to fixation as insoluble inorganic phosphates in soils and losses through runoff and leaching (Tripathi et al., 2020). Phosphate-solubilizing microorganisms, such as*Rhizobium* sp., *Bacillus* sp., and *Azotobacter* sp., utilize various biochemical strategies to enhance phosphorus availability. These microbes secrete organic acids, including gluconic and citric acid, which chelate metal cations (Ca^{2+}, Fe^{3+}, Al^{3+}) and release bound phosphate ions (Mukhtar et al., 2017). The acidification of the rhizosphere not only solubilize phosphorus but also increases the availability of other micro-nutrients. Furthermore, these microorganisms produce enzymes like Phytase and acid phosphatase, which mineralize organic phosphorus compounds from plant residues and soil organic matter. The *pqq* gene cluster is vital as it regulates gluconic acid production, a key factor in solubilization efficiency (Tripathi et al., 2020). Collectively, these processes convert inaccessible phosphorus into plant-available forms, enhancing nutrient uptake and reducing reliance on chemical fertilizers.

Production of Siderophores

Siderophores are vital for iron acquisition in iron-limited environments, commonly found in calcareous and high-pH soils. These low molecular weight compounds, produced by microorganisms such as *Pseudomonas* sp. and *Trichoderma* sp., have a very high affinity for ferric iron (Fe^{3+}), with formation constants exceeding 10^{30} (Syed et al., 2023). The structural diversity of siderophores (e.g., pyoverdines, catecholates, hydroxamates) allows different microbial species to thrive in various ecological niches within the rhizosphere. Specific siderophores, like pyoverdine and catechol-based compounds, facilitate iron uptake through specialized transport systems encoded by genes such as *fepA* and *fhuA* (Meena et al., 2017). In addition to their nutritional role, siderophores enhance plant health by sequestering iron from potential pathogens, thereby limiting their growth and virulence (Syed et al., 2023). This iron competition creates selective pressure in the rhizosphere, favoring beneficial organisms over pathogens. The dual role of siderophores-promoting plant iron nutrition while suppressing pathogens, highlights the sophisticated biocontrol capabilities of beneficial microbes and their potential to reduce reliance on pesticides.

Production of Phytohormones

Plant growth-promoting microorganisms significantly affect plant physiology through the production of various phytohormones, creating a complex signaling network that coordinates growth and stress responses. These microbial-derived hormones, including auxins, cytokinins, gibberellins, and abscisic acid, function at much lower concentrations than synthetic plant growth regulators while causing significant physiological changes (Chakraborty et al., 2021). Notably, indole-3-acetic acid (IAA), synthesized via the indole-3-pyruvate pathway in microbes such as *Pseudomonas* sp. and *Trichoderma* sp., plays a crucial role. The *ipdC* gene, which encodes indole-3-pyruvate decarboxylase, is essential in this process, directly impacting root architecture by stimulating lateral root formation and root hair development (Chakraborty et al., 2021). This morphological adaptation greatly increases the root surface area, enhancing nutrient and water acquisition. Additionally, cytokinins synthesized by PGPMs, produced through *ipt* gene activity, help modulate plant stress responses by upregulating key regulatory genes such as *DREB* and *MYB* (Singh et al., 2019). These hormonal interactions enSable plants to optimize growth under both favorable and stressful conditions, showcasing the sophisticated regulatory capacity of plant growth-promoting microorganisms (PGPMs). The balanced production of multiple phytohormones by microbial communities helps maintain plant homeostasis, preventing excessive vegetative growth or premature senescence often associated with synthetic hormone applications.

Production of Antibiotics and Enzymes

Microbial biofertilizers, including *Pseudomonas*, *Bacillus*, and *Streptomyces* spp., are well-known for their antagonistic effects against phytopathogens, primarily through the production of various secondary metabolites. These metabolites, which include antibiotics and cell wall-degrading enzymes, not only directly suppress pathogens but also induce systemic resistance in host plants (Kumar et al., 2022). For instance, *Pseudomonas* spp. produces 2,4-diacetylphloroglucinol (2,4-DAPG), an antibiotic regulated by the *phl* gene cluster, that effectively inhibits fungal pathogens. Similarly, *Bacillus* spp. secretes hydrolytic enzymes, such as chitinases and β-glucanases, regulated by the *chi* and *bgl* genes, which disrupt fungal cell walls. *Streptomyces* spp. also contributes by producing antibiotics like streptomycin, whose biosynthesis is modulated by quorum-sensing pathways to enhance effectiveness.

However, relying too heavily on single-strain biocontrol agents can lead to pathogen resistance. For example, repeated applications of 2,4-DAPG-producing *Pseudomonas* have resulted in *Fusarium oxysporum* populations developing *phl*-resistance genes, with a reported threefold increase in resistance after multiple inoculation cycles (Daigham et al., 2024). To mitigate this issue, we recommend rotating plant growth-promoting microorganisms (PGPMs) with distinct and complementary mechanisms. For instance, combining the chitinase activity of *Bacillus* with the antibiotic production of *Streptomyces* can strategically diversify approaches, reducing selective pressure, maintaining long-term efficacy, and promoting sustainable disease management.

Indole Acetic Acid Production

Bacillus species, especially *Bacillus thuringiensis*, are well-known for their ability to produce indole-3-acetic acid (IAA), a key phytohormone in the auxin group. The biosynthesis of IAA in these microorganisms typically occurs through the tryptophan-dependent pathway, where tryptophan is converted into IAA via intermediates such as indole-3-pyruvate. This conversion is facilitated by indole-3-pyruvate decarboxylase, encoded by the *ipdC* gene, which is crucial for enhancing IAA production. IAA functions to promote root elongation, lateral root formation, and cell division, thereby improving water and nutrient uptake—critical processes for developing a strong root system, particularly in nutrient-poor or stressed soils. Research on the *B. thuringiensis* strain RZ2MS9 has demonstrated that the IAA produced by the bacteria stimulates the expression of plant genes related to growth, nutrient transport, and stress tolerance. Moreover, the improved root architecture fosters better seedling establishment, resulting in enhanced biomass accumulation and increased crop yields. When combined with other beneficial traits such as phosphate solubilization or nitrogen fixation, IAA production significantly enhances the overall effectiveness of plant growth-promoting microorganisms (PGPMs). Thus, IAA-producing strains like *B. thuringiensis* present a promising strategy for minimizing reliance on synthetic agrochemicals and promoting environmentally sustainable farming practices (Figueredo et al., 2023).

Hydrogen Cyanide Production

Beneficial microorganisms such as *Pseudomonas* sp., *Bacillus* sp., and *Trichoderma* sp. produce hydrogen cyanide (HCN) as a sophisticated biocontrol mechanism. Regulated by the *hcnABC* gene cluster, these microbes inhibit pathogenic organisms by disrupting cytochrome oxidase activity, thereby impairing their energy metabolism (Khoso, 2023). This natural pesticide action is further enhanced by the microbial release of ammonia (NH_3), a byproduct of amino acid degradation that serves dual purposes in soil ecosystems. The released NH_3 is rapidly converted to plant-available ammonium (NH_4^+) and simultaneously raises soil pH, creating conditions favorable for many crops. This pH modification can improve nutrient availability while suppressing acid-loving pathogens (Khoso, 2023). The combined effects of HCN and NH_3 offer a comprehensive approach to plant health management: HCN directly suppresses pathogens, while NH_3 enhances soil fertility and indirectly controls disease through environmental modification.

Zinc Solubilization

Zinc availability is a critical limiting factor in agricultural systems worldwide, despite its essential role in numerous enzymatic processes and protein synthesis. Plant growth-promoting microorganisms (PGPMs) tackle this challenge through various solubilization pathways. *Trichoderma* sp., *Providencia* sp., and *Anabaena* sp. secrete organic acids, particularly citric acid, to chelate zinc ions from insoluble compounds like ZnO. Additionally, their production of siderophores offers another pathway for zinc mobilization (Kumar, Sindhu et al. 2022). The efficiency of these systems is enhanced by high-affinity zinc transporters encoded by the *znuABC* genes, which facilitate plant uptake of the solubilized zinc. This microbial-mediated zinc cycling is particularly significant in alkaline soils, where conventional zinc fertilizers often fail. The resulting improvement in zinc nutrition not only boosts crop yields but also enhances nutritional quality, which is crucial for addressing human micronutrient deficiencies through bio-fortification (Kumar, Sindhu et al. 2022).

These mechanisms illustrate how PGPMs create integrated systems for promoting plant growth. The HCN/NH_3 systems provide both nutrition and protection, while zinc solubilization addresses a common micronutrient limitation. Importantly, these processes occur simultaneously in the rhizosphere, yielding synergistic benefits that surpass those achieved through single-mechanism approaches. The effectiveness of these natural systems suggests significant potential for reducing synthetic inputs in agriculture while maintaining or improving productivity. Figure 2 illustrates the interconnections of these diverse mechanisms in promoting plant growth, emphasizing the multifunctional role of PGPMs in agricultural systems. This system-level understanding is essential for developing effective microbial inoculants that perform reliably across various field conditions.

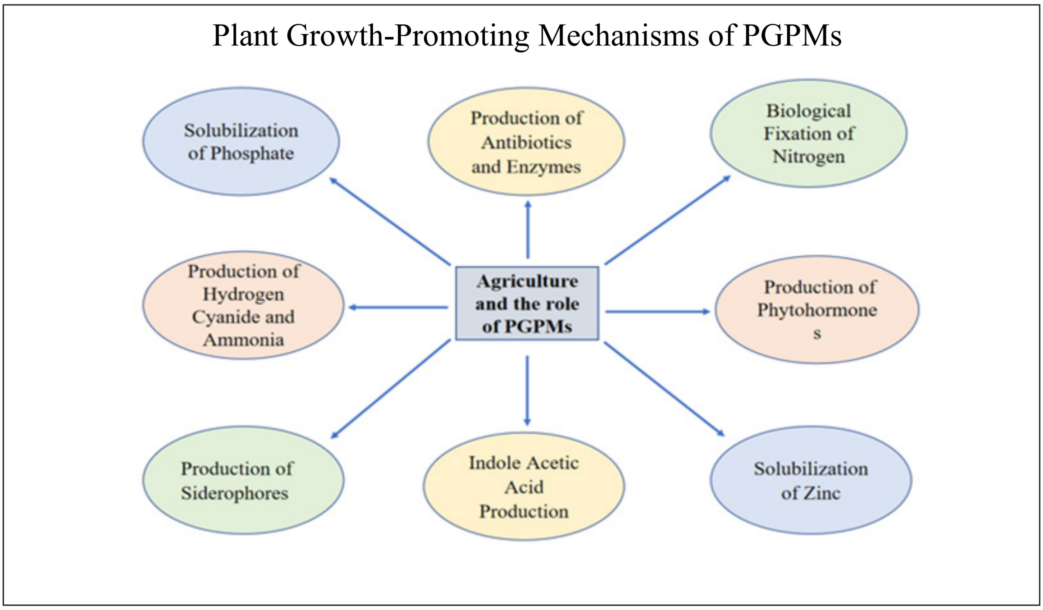

Figure 2. Plant growth-promoting mechanisms of PGPMs (PGPR and PGPF). The figure highlights key mechanisms such as nutrient solubilization (phosphate, zinc), biological nitrogen fixation, siderophore production, and synthesis of phytohormones (e.g., Indole Acetic Acid), antibiotics, and enzymes

These processes enhance plant growth, improve nutrient uptake, and increase resistance to pathogens, contributing to sustainable agriculture by boosting yield and reducing reliance on chemical inputs (Elekhtyar, 2015; Kumar et al., 2022; Singh et al., 2019).

APPROACH FOR SUCCESSFUL PLANT INOCULATION WITH PGPMS IN AGRICULTURE

Inoculation techniques are pivotal in ensuring the successful establishment, persistence, and growth-promoting activities of plant growth-promoting microorganisms (PGPMs) in the rhizosphere when introduced to host plants (Hernández-Montiel et al., 2017). These microorganisms enhance plant growth by inducing systemic resistance, producing growth regulators, and solubilizing nutrients. PGPMs can be applied individually or in mixtures via leaves, seeds, seedlings, roots, or soil. Such inoculations enable colonization of the plant interior or rhizosphere, promoting growth and improving adaptability to abiotic stress. For instance, inoculation with *Trichoderma* sp. through seed treatment or soil application has demonstrated significant suppression of plant diseases and enhancement of plant growth. Dual inoculation with *Trichoderma harzianum* and *Azotobacter chroococcum* has proven more effective as a combined strategy for biological control in plant protection (Lopes et al., 2021). To optimize success, the following factors should be considered:

Proximity to Rhizosphere

Rhizosphere, with exudates of roots being present, enables colonization and activity of PGPMs such as *Pseudomonas* and *Bacillus* spp., enhancing plant growth through increased solubilization of nutrients and plant protection (Hernández-Montiel et al., 2017). Due to the low microbial mobility, inoculation near the root zone is necessary to achieve successful colonization. As they carry microorganisms on their cuticle or inside them, *Steinernema* and *Heterorhabditis* nematodes also facilitate PGPM transmission to allow root-targeted delivery (Hernández-Montiel et al., 2017; Knox et al., 2007). PGPM efficiency is enhanced, and farm-based sustainable food production is increased through combining nematode-delivery assisted with traditional inoculation techniques such as seed coating and soil drenching, as elaborated by Backer et al. (2018).

Inoculum Density and Method

The efficacy of plant growth-promoting microorganisms (PGPMs) inoculation depends on inoculum density, application method, and root colonization, which are influenced by microbial proliferation, soil conditions, and plant physiological state. For instance, applying solutions of *Trichoderma ghanense* and *Trichoderma tomentosum* at 10^9 conidia/mL significantly enhanced rye seedling growth in both grassland and arable soils. This can be achieved through seed inoculation or soil drenching, where *Trichoderma* is mixed with water and applied around plant bases during seedling and panicle initiation stages. Soil drenching with *Trichoderma* improves soil pH, nutrient uptake, and protection against root diseases (Msimbira & Smith, 2020).

The decline in microbial populations after inoculation poses a significant challenge to the efficacy of plant growth-promoting microorganisms (PGPMs). Research indicates that viability can decrease by up to 50% within 60 days due to environmental stressors (Msimbira & Smith, 2020). This decline results from both biotic factors, such as competition with native microbiota, and abiotic challenges, including fluctuations in soil pH and moisture extremes. Consequently, careful selection of site-adapted strains is essential (Etesami, 2020).

The choice of inoculation method also plays a critical role in outcomes. For example, seed inoculation can enhance rice germination by 20% (Ullah et al., 2017), while soil drenching with *Trichoderma* can boost tomato yields by 30% (Hernández-Montiel et al., 2017). Furthermore, root inoculation can achieve 40% greater rhizosphere colonization in cucumbers (Gouda et al., 2020). Emerging technologies, such as micro-encapsulation, show particular promise, demonstrating 15% greater efficacy than liquid inoculants in tomato systems (Hernández-Montiel et al., 2017). However, to maintain field performance, it is crucial to optimize inoculum densities and develop strain-specific delivery protocols tailored to the specific crop and environmental conditions.

Single Vs. Co-Inoculation

Inoculation can involve a single isolate or co-inoculation with multiple isolates. Co-inoculation entails the simultaneous application of several microorganisms, promoting synergistic interactions that enhance efficacy. Research demonstrates that co-inoculation stimulates root development, boosting growth and productivity across various plant species (Asghari et al., 2020; Bakhshandeh et al., 2020; Lopes et al., 2018; Samaddar et al., 2019;). For example, Khan et al. (2023) compared single inoculation with *Trichoderma* sp. to co-inoculation with arbuscular mycorrhizal fungi (AMF) on tomato (*Solanum lycopersicum* L.) growth. The results showed that co-inoculation significantly improved plant development and nutrient absorption compared to single inoculation, highlighting the benefits of microbial synergy. Co-inoculated plants also exhibited enhanced growth parameters, including greater plant height, root length, and chlorophyll content, suggesting a synergistic effect on plant development.

Co-inoculation strategies show significant but context-dependent synergies. When *Trichoderma* is combined with arbuscular mycorrhizal fungi (AMF), tomato growth increases by 35% under optimal conditions with co-inoculation, more than double the 15% improvement observed with single inoculation (Khan et al., 2023). However, this advantage drops to just 5% under severe drought stress, highlighting critical limitations in stress adaptation. This variability in performance likely arises from three factors: (1) microbial competition for limited resources, (2) host-specific compatibility issues, and (3) insufficient expression of stress-responsive traits in sub-optimal consortia (Bakhshandeh et al., 2020).

Emerging omics approaches are shedding light on these interactions. Guzmán-Guzmán et al. (2024) found a 25% upregulation of antifungal genes in *Trichoderma*-PGPR combinations, indicating molecular pathways that facilitate synergy. However, a translational gap persists; although laboratory studies demonstrate promise, there is still limited field validation of these mechanisms. To tackle this issue, the following strategy is recommend:

Targeted Consortia Design

Where pairing microbes with complementary stress-response traits enhances plant resilience in adverse environments. For example:

- Drought-tolerant *Pseudomonas* species, which produce exopolysaccharides and ACC deaminase, when combined with nitrogen-fixing *Azospirillum brasilense*, are less effective under water scarcity and improve crop performance in arid conditions (Bashan et al., 2023).
- Salinity-resistant *Bacillus subtilis*, known for expressing osmolyte synthesis genes, paired with phosphate-solubilizing *Rhizobium*, helps mitigate salt stress in legumes (Etesami & Maheshwari, 2023).

Molecular Screening

Omics technologies, such as genomics and transcriptomics, facilitate the identification of strains with strong symbiotic potential and stress resilience through:

- CRISPR-based editing of *Bradyrhizobium japonicum* has enhanced its nitrogenase activity under heat stress (Reed et al., 2023).
- Metagenomic profiling of root microbiomes has uncovered *Paenibacillus polymyxa* strains with upregulated biofilm-related genes (*epsB*, *pelA*), contributing to improved drought tolerance (Kumar et al., 2023).

Condition-Specific Formulations

Tailored inoculants are designed to address specific agroecological challenges. For example:

- Under optimal conditions, high-performance consortia, such as *Azotobacter chroococcum* and *Trichoderma harzianum*, enhance nutrient uptake and promote plant growth (Singh et al., 2023).
- In stressed environments, specialized blends, like HCN-producing *Pseudomonas* combined with siderophore-producing *Streptomyces*, effectively suppress soil-borne pathogens, particularly in saline soils (Elekhtyar et al., 2023).

INOCULATION TECHNIQUES

Various techniques, including seed, root, soil, and foliar inoculation, are employed to introduce beneficial microorganisms to plants. Seed inoculation is the most widely used method, whereas foliar inoculation is the least common (Arora et al., 2020). The efficacy of microbial inoculation can be influenced by the composition and quantity of root exudates, as well as environmental stresses during plant growth. Seed inoculation involves applying beneficial microorganisms directly to seeds before planting, while soil inoculation disperses them throughout the soil. In contrast, root inoculation targets the plant roots specifically. The different inoculation methods used in screening trials are illustrated in Figure 3.

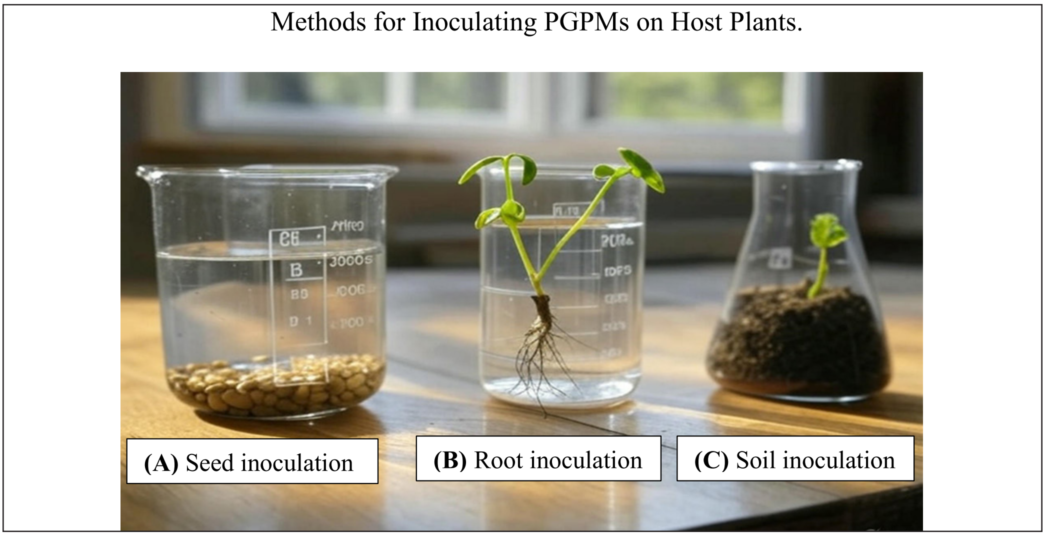

Figure 3. Methods for inoculating PGPMs on host plants.

The figure illustrates three key methods for inoculating PGPMs on host plants: (a) seed inoculation, where seeds are soaked in a microbial suspension to enhance germination and early seedling growth; (b) root inoculation, where seedling roots are submerged in microbial solutions to ensure direct colonization of the rhizosphere and facilitate nutrient uptake; and (c) soil inoculation, where microbial formulations are applied to the soil, promoting rhizosphere activity and disease suppression.

These techniques have been shown to improve plant growth, nutrient absorption, and pathogen resistance, supporting sustainable agriculture (Arora et al., 2020).

Seed Inoculation

Microbial inoculation methods, one of which involves immersing seeds in a solution of microorganisms with a defined concentration, and secretion occurs when carbohydrates and amino acids are released during seed germination (Lopes et al., 2018). This process has been shown to improve biomass production in species such as *Cicer arietinum* L. (Khan et al., 2019) and *Oryza sativa*. The inoculum remains dormant in the soil until it is activated by the growing root tips, which helps maintain effective cell density under field conditions. Additionally, *Pseudomonas fluorescens* was found to improve vigor, biomass, and water stress tolerance in *Vigna radiata* (Ullah et al., 2017).

Soil Inoculation

Soil inoculation delivers PGPMs directly into the soil through irrigation, soil addition, or microcapsules (Hernández-Montiel et al., 2017; Lopes et al., 2021). Soil soaking places the microorganism solution near host roots (Lopes et al., 2018) to promote critical functions such as phosphate solubilization and phytohormone synthesis (Gouda et al., 2018). For *Brachiaria brizantha,* soil soaking with *Burkholderia pyromania* and *Pseudomonas fluorescens* promoted growth, while seed inoculation did not, due to a reduction in allelochemicals (Lopes et al., 2018). Soil inoculation with *Bacillus* increased nodule formation and development of *Cicer arietinum* L. compared to seed inoculation. The addition of PGPRs to the soil improved the growth of *Ranunculus asiaticus* by increasing nutrient and water absorption (Lopes et al., 2021). Inoculation via soil with *Pseudomonas putida* in microcapsules improved the development of *Lycopersicum esculentum* by providing gradual release and improved root colonization (Hernández-Montiel et al., 2017).

Root Inoculation

Root inoculation, which involves immersing seedling roots in a suspension of plant growth-promoting microorganisms (PGPM), offers a direct and effective method for delivering beneficial microbes to the rhizosphere. This technique ensures close contact between the inoculum and the root surface, enhancing both root colonization and microbial establishment. Research shows that root inoculation can lead to up to 40% higher rhizosphere colonization compared to seed coating (Gouda et al., 2020), significantly improving the consistency and effectiveness of plant growth promotion. Additionally, this method allows for the standardization of seedling size, enabling uniform inoculation of plants at similar developmental stages.

However, manual root inoculation can be labor-intensive, which limits its scalability in commercial agriculture. Fortunately, advancements in automated seedling dip systems, like those used in nurseries, have decreased labor costs by 25%, providing a practical balance between efficiency and affordability (Backer et al., 2018). These developments underscore the potential for integrating precision inoculation technologies to enhance the large-scale application of PGPMs in sustainable crop production systems. Table 2 below summarizes the impact of various PGPM inoculation techniques on plant growth parameters.

Table 2 outlines the impact of different PGPMs and their inoculation methods on various crops, demonstrating notable enhancements in plant growth, yield, and stress resilience. The effectiveness of these techniques varies based on the specific PGPM and the targeted plant.

The functions of PGPR and PGPF are to improve plant development, leading to increased production while maintaining environmental safety. They do this by producing phytohormones such as IAA, ABA, cytokinins, and ethylene, which facilitate processes like cell division, elongation, seedling emergence, and flower/fruit development (Meena et al., 2017). In addition to hormone production, PGPR and PGPF contribute to phosphate solubilization, nitrogen fixation, siderophore generation, and the synthesis of essential vitamins like niacin and biotin (Cortivo et al., 2017). Studies have shown that specific

Table 2
Effects of PGPM inoculation techniques on plant growth

PGPM	Plant	Inoculation Type	Effect of Inoculation	Reference
PGPR consortium	*Triticum aestivum* (wheat)	Soil application	Enhanced wheat productivity and nitrogen use efficiency with PGPR and nitrogen doses.	Gaspareto et al. (2023)
Pseudomonas fluorescens, *Bacillus licheniformis*	*Amaranthus hybridus(smooth pigweed)*	Soil application	Reduced plant stress and increased production with co-inoculation and seaweed bio-stimulant.	Ngoroyemoto et al. (2020)
Pseudomonas putida	*Lycopersicon esculentum (tomato)*	Soil microcapsules, liquid medium	Increased growth and yield with microcapsule and liquid medium inoculation.	Hernández-Montiel et al. (2017)
Rhizobial	*Oryza sativa (rice)*	Seed, root	Improved plant growth with seed inoculation.	Ullah et al. (2017)
Bacillus subtilis, *Pseudomonas putida*	*Cucumis sativus* (cucumber)	Soil application	Enhanced root growth and yield with combined inoculation and seaweed extracts.	Kakbra (2024)
Pseudomonas burkholderia	*Brachiaria brizantha (signal grass)*	Seed, soil	Improved plant development with seed inoculation.	Lopes et al. (2018)

species like *Klebsiella sp., B. spumilus, Acinetobacter sp.*, and *B. subtilis* enhance maize productivity through nitrogen fixation, phosphate solubilization, and IAA production (Kuan et al., 2016). Biofertilizers containing *B. mojavensis, B. subtilis, B. pumilus*, and *B. pseudomycoides* increased sweet maize yield and improved grain protein and fiber content (Katsenios et al., 2022). Furthermore, *Trichoderma* rhizosphere-competent varieties have equally expressed effectiveness in promoting plant growth, enhancing nutrient uptake, accelerating seed germination, and activating plant defense mechanisms. Numerous studies have reported the functions of PGPR and PGPF on plant growth, as highlighted in Tables 3 and 4.

Table 3 summarizes the effect of various PGPRs on different crops, highlighting their notable contributions to plant growth, nutrient uptake, and stress resilience. Observations indicate that PGPR can enhance root development, improve disease resistance, and promote crop yield, supporting their role as biological agents.

Table 3
PGPR and their impact on plant growth

PGPR	Crop	Observation	Reference
Azospirillum sp., *Azoarcus sp.*	*Triticum aestivum* (wheat)	Improved root growth, stress tolerance, and reduced nitrogen losses.	Bashan & de-Bashan (2023)
Bacillus subtilis	*Solanum lycopersicum* (tomato)	Enhanced growth and yield via nutrient uptake and disease resistance.	Souza et al. (2015)
Flavobacterium johnsoniae, *Pseudomonas putida*, *Azotobacter chroococcum*	*Triticum aestivum* (wheat)	Improved bacterial growth and seed germination under salt stress.	Rai et al. (2018)
Azospirillum brasilense	*Zea mays* (maize)	Enhanced root development and nutrient absorption, increasing yields.	Al-Tammar & Khalifa (2022)
Rhizobium leguminosarum	*Pisum sativum* (pea)	Increased nitrogen fixation, biomass, and yield.	Poria et al. (2022)
Enterobacter cloacae	*Oryza sativa* (rice)	Promoted growth under saline conditions via stress tolerance.	Katsenios et al. (2022)
Serratia marcescens	*Glycine max* (soybean)	Improved seed germination and early seedling growth.	Reed & Glick (2023)

Table 4
PGPF and their impact on plant growth

PGPF	Crop	Observation	Reference
Pleurotus tuber-regium, *Lentinus squarrosulus*, *Ganoderma sp.*	*Triticum aestivum* (wheat), *Solanum lycopersicum* (tomato)	Enhanced growth via siderophore production, phosphate solubilization, and enzyme activities.	Kumar et al. (2022)
Trichoderma harzianum	*Solanum lycopersicum* (tomato)	Improved growth and fungal pathogen resistance.	Aamir et al. (2023)
Penicillium chrysogenum	*Solanum lycopersicum* (tomato)	Promoted growth through phosphate solubilization and growth-promoting substances.	Adedayo & Babalola (2023)
Aspergillus chevalieri	*Solanum lycopersicum* (tomato)	Protected against *Alternaria solani*, enhancing growth and health.	Daigham et al. (2024)
Penicillium olsonii	*Nicotiana tabacum* (tobacco)	Enhanced salt tolerance and reduced fertilizer needs.	Tarroum et al. (2022)
Trichoderma spp.	*Arabidopsis thaliana (*thale-cress)	Potentiated antifungal and growth-promoting traits with PGPR.	Guzmán-Guzmán et al. (2024)

Table 4 presents various PGPF and their observed effects on different crops, highlighting significant impacts on plant growth, nutrient uptake, and stress tolerance. The findings highlight the potential of PGPF as effective biological agents.

The growth enhancement is demonstrated by increased plant material production, promoted lateral root development, higher yields, improved seed germination rates, and better growth parameters. *Azospirillum* sp., *Azoarcus* sp and *Bacillus* sp highly improved root development, ability to withstand unfavorable conditions, reduced losses in N, and disease resistance in wheat and tomato. Similarly, *Trichoderma* sp has shown beneficial effects on multiple plant species, including tomato and Arabidopsis, suggesting its versatility in promoting growth across different plant types. Likewise, the application of *Trichoderma harzianum* has led to improvements in yield quality parameters, such as improved salt tolerance in tobacco. In addition, *Trichoderma* sp. and *Pleurotustuber-regium*, *Lentinus squarrosulus*, and *Ganoderma* sp., have demonstrated disease protection capabilities, providing resistance against various plant pathogens. Consequently, overall findings suggest that the application of PGPMs can be a promising strategy for enhancing plant growth, improving yield, and protection against plant diseases across various crop species. Despite the proven benefits of PGPMs, their large-scale adoption remains limited.

CONCLUSION

Plant growth-promoting microorganisms (PGPMs) play a crucial role in achieving sustainable crop production and enhancing soil health. By improving nutrient uptake and activating plant immune responses such as induced systemic resistance and antibiosis PGPMs can reduce reliance on chemical fertilizers and pesticides by 40–60% (Kumar et al., 2022). This reduction supports ecological balance, fosters soil biodiversity, and aligns with organic farming principles. However, the real-world adoption of PGPMs is still limited due to practical challenges. One major issue is strain resilience; studies have shown that microbial populations can decline by up to 50% after inoculation, highlighting the need for better delivery systems and formulations (Msimbira & Smith, 2020). Additionally, farmer education is essential pilot programs in Malaysia saw a doubling of PGPM uptake when paired with training modules (Lopes et al., 2021). Policy support also plays a significant role in adoption rates, as evidenced in India, where subsidies for biofertilizers resulted in a 25% increase in PGPM use (Saritha & Tollamadugu, 2019).

To bridge the gap between laboratory efficacy and field performance, future research should focus on advancing co-inoculation techniques that utilize complementary microbial strains and employ molecular omics to better understand plant–microbe–soil interactions. At the same time, developing low-cost, user-friendly inoculation technologies tailored for smallholder contexts will be vital. Implementing these strategies can unlock the full potential of PGPMs, contributing to sustainable agriculture and long-term food security.

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