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Review

Utilizing Plant Growth-Promoting Rhizobacteria (PGPR) to Advance Sustainable Agriculture

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Abstract: Plant growth-promoting rhizobacteria (PGPR) are beneficial bacteria that play a crucial role in sustainable agriculture by enhancing plant growth through various mechanisms. This review examines the contributions of PGPR in improving nutrient availability, producing phytohormones, providing biocontrol against pathogens, and enhancing abiotic stress tolerance. By reducing the necessity for chemical fertilizers and pesticides, PGPR mitigate environmental impacts, enhance soil health, and support long-term agricultural productivity. However, challenges such as inconsistent performance across various soils, regulatory barriers, and limited farmer awareness, hinder their widespread adoption. Recent advancements in nano-encapsulation technology, genetic engineering, and bioinformatics, present promising solutions for overcoming these obstacles and enhancing PGPR efficacy. The incorporation of PGPR into biofertilizers, biopesticides, and integrated plant management (IPM) offers a sustainable resolution to global agricultural challenges. This review addresses the current state of PGPR research, applications, and future directions for optimizing their use in promoting sustainable agriculture.

Keywords: PGPR; integrated plant management (IPM); sustainable agriculture; biofertilizer; biopesticide; plant fitness tetrahedron; nutrient use efficiency (NUE)

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1. Introduction

Plant growth-promoting rhizobacteria (PGPR) are beneficial bacteria residing in the rhizosphere, the soil region contacted by plant roots [1]. These bacteria play a vital role in promoting plant growth and health through various mechanisms, making them a key component of sustainable agriculture [2,3]. PGPR can promote plant growth directly by improving nutrient acquisition and producing growth-mediating hormones (phytohormones) or indirectly by protecting plants from pathogens (biotic stresses) and mitigating abiotic stresses (such as drought and salinity) [4–6].

Different PGPR have different mechanisms of action. Among them, conserved mechanisms are nutrient solubilization and fixation [7,8], phytohormone production [4,6], biocontrol of pathogens [4–6], and abiotic stress tolerance [5]. Specifically, PGPR enhance nutrient availability by solubilizing phosphorus and fixing atmospheric nitrogen, thus reducing the need for chemical fertilizers, which are not sustainable [9,10]. PGPR produce phytohormones such as auxins, gibberellins, and cytokinins, which stimulate root and shoot development, enhancing overall plant growth [5,6,11,12]. PGPR protect plants from pathogens by producing antimicrobial compounds, competing for resources, and inducing systemic resistance in plants, which can reduce the reliance on chemical pesticides [4,6,9]. These bacteria also help plants withstand abiotic stresses like drought and salinity by enhancing stress response mechanisms and detoxifying harmful substances [4,5,9].

The need for sustainable agricultural practices has become increasingly urgent due to the environmental and health concerns associated with conventional farming methods. Traditional agriculture often relies heavily on synthetic fertilizers and pesticides, which can lead to soil degradation, water pollution, and the development of resistant pest strains. These conventional practices contribute to environmental issues such as eutrophication and biodiversity loss, posing significant threats to ecosystems and human health [9,13]. By integrating PGPR into agricultural practices, farmers can achieve higher crop yields and quality while reducing the environmental impact of farming. This approach aligns with the goals of sustainable agriculture, promoting ecological balance and long-term productivity [9,11].

PGPRs are increasingly recognized as a sustainable alternative or complement to conventional agricultural practices. Their ability to enhance crop productivity while minimizing environmental impacts makes them a promising solution for future agricultural challenges. As research advances, the development of more effective PGPR strains and application methods is expected to further their roles in sustainable agriculture [14].

The integration of PGPR in agricultural practices offers several benefits: (1) Reduced chemical inputs: By improving nutrient availability and providing natural pest control, PGPRs reduce the need for synthetic fertilizers and pesticides, contributing to more sustainable agricultural practices [9,10]. (2) Improved soil health: PGPR enhance soil fertility and structure, supporting long-term agricultural productivity and sustainability [9]. (3) Environmental benefits: The reduction in chemical inputs leads to lower environmental pollution and a smaller carbon footprint, aligning with the goals of sustainable agriculture [11,15]. (4) Additionally, PGPR play a pivotal role in augmenting soil fertility and structure by promoting organic matter breakdown and nutrient cycling, thereby fostering overall soil health [7,9,15].

2. Mechanisms of Action

2.1. Nutrient Solubilization and Fixation

PGPRs play a crucial role in enhancing plant nutrition by solubilizing phosphorus and fixing atmospheric nitrogen, making these essential nutrients more available to plants. Phosphorus is a vital nutrient for plant growth, but it often exists in forms that are not readily accessible to plants. Although the dynamics of inorganic phosphate and PGPR's influence on it are completely different from those of the organic phosphate fraction, some PGPR can solubilize certain types of insoluble phosphates through the production of organic acids like gluconic acid and citric acid. These acids lower the pH and chelate cations bound to the phosphate group, thereby releasing it into a form that plants can absorb [16]. This process could be facilitated by enzymes like phytases and phosphatases, which further aid in the mineralization of organic phosphorus compounds [17]. Recent studies have highlighted the effectiveness of PGPR strains from genera such as *Bacillus*, *Pseudomonas*, and *Enterobacter* in solubilizing phosphate and promoting plant growth [18].

In addition to phosphorus solubilization, PGPR are instrumental in fixing atmospheric nitrogen, a process that converts inert nitrogen gas into ammonia, which plants can incorporate. This biological nitrogen fixation is primarily carried out by diazotrophic bacteria, which possess the nitrogenase enzyme complex capable of reducing atmospheric nitrogen to ammonia [19]. PGPR such as *Azospirillum* and *Rhizobium* are well-known for their nitrogen-fixing capabilities, particularly in association with leguminous plants, where they form symbiotic relationships in root nodules [20]. These interactions not only enhance nitrogen availability but also improve soil fertility and reduce the necessity for chemical nitrogen fertilizers, contributing to more sustainable agricultural practices [19].

2.2. Phytohormone Production

PGPR are known for their ability to produce phytohormones such as auxins, gibberellins, and cytokinins, which play a crucial role in enhancing plant growth and development. Auxins, particularly indole-3-acetic acid (IAA), are among the most studied phytohormones produced by PGPR [4,5]. IAA is primarily produced in the rhizosphere and is instrumental in promoting root elongation, root hair formation, and lateral root development, which collectively enhance the plant's ability to absorb water and nutrients [21,22]. This hormone is produced by various PGPR species, including *Azospirillum*, *Pseudomonas*, and *Agrobacterium*. IAA's production is also considered a key mechanism through which PGPR facilitate plant growth [23].

Gibberellins (GAs) are another group of phytohormones produced by PGPR that significantly influence plant growth. These hormones are involved in promoting seed germination, stem elongation, and flowering. PGPR such as *Bacillus* and *Pseudomonas* species have been reported to produce gibberellins, which can enhance plant growth even under stressful conditions [24,25]. The application of PGPR that produce gibberellins can be particularly beneficial in improving crop yield and resilience to unfavorable stresses, making them a valuable component of sustainable agricultural practices [26].

Cytokinin is another class of phytohormones produced by PGPR that play a vital role in cell division, shoot initiation, and leaf expansion. These phytohormones interact with auxins to regulate various aspects of plant growth and development, including delaying leaf senescence and enhancing chlorophyll production [27,28]. The production of cytokinin by PGPR can lead to improved plant vigor and productivity, as demonstrated in studies involving *Bacillus megaterium* and other cytokinin-producing rhizobacteria [29].

2.3. Biocontrol of Pathogens

PGPR protect plants from pathogens through several mechanisms, including the production of antimicrobial compounds and competition for resources. These bacteria reside in the rhizosphere and play a pivotal role in enhancing plant health by suppressing natural plant diseases. One of the primary mechanisms by which PGPR exert their protective effects is through the production of antimicrobial compounds like antibiotics, siderophores, and enzymes that degrade pathogen cell walls [4,6]. For instance, PGPR like *Pseudomonas* and *Bacillus* species produce antibiotics that inhibit the growth of harmful pathogens, thereby reducing disease incidence in plants [30].

In addition to producing antimicrobial compounds, PGPR compete with pathogens for nutrients and ecological niches, effectively limiting the resources available to harmful microbes [31]. This competition is crucial in the rhizosphere, where nutrients can be scarce, and the ability of PGPR to efficiently utilize these resources can outcompete and suppress pathogenic organisms [32]. By rapidly colonizing plant roots and establishing themselves in the rhizosphere, PGPR can effectively prevent the colonization and proliferation of pathogens, thereby acting as a natural biocontrol agent [33].

Furthermore, PGPR can induce systemic resistance in plants, enhancing their innate immune responses against a broad spectrum of pathogens [4,6]. This induced resistance is often mediated by signaling molecules such as salicylic acid, jasmonic acid, and ethylene, which activate defense pathways in plants, providing them with enhanced protection against future pathogen attacks [34]. The integration of PGPR into agricultural practices not only helps reduce the reliance on chemical pesticides but also contributes to sustainable agriculture by promoting plant health and resilience in an environmentally friendly manner [9].

2.4. Abiotic Stress Tolerance

PGPR play a significant role in helping plants cope with abiotic stresses such as drought, salinity, and heavy metal toxicity. These stresses are exacerbated by climate change and pose significant challenges to agricultural productivity. PGPR mitigate these stresses through different mechanisms such as the production of phytohormones, modulation of antioxidant systems, and enhancement of nutrient uptake [35,36].

In the context of drought stress, PGPR enhance plant tolerance by producing phytohormones like indole-3-acetic acid (IAA) and gibberellic acid, which promote root growth and increase water uptake efficiency [37,38]. Additionally, PGPR can produce

1-aminocyclopropane-1-carboxylate deaminase (ACC), an enzyme that lowers ethylene levels in plants [4]. Since ethylene can inhibit root growth under stress conditions, reducing its concentration helps in maintaining root growth and function during drought [39].

Under salinity stress, PGPR improve plant resilience by enhancing ionic balance and osmotic adjustment. They achieve this by producing osmo-protectants and modulating ion transporters that help maintain a favorable potassium-to-sodium ratio, which is necessary for cellular function under saline conditions [40,41]. PGPR also enhance the antioxidant capacity of plants, reducing oxidative damage caused by salt-induced stress [35].

In the case of heavy metal toxicity in plants and soil, PGPR assist in phytoremediation by secreting chelating agents and enzymes that transform metals into less toxic forms. They are also capable of immobilizing heavy metals in the rhizosphere, which helps prevent these metals from being absorbed by plants [42,43]. This not only protects plants from metal toxicity but also improves soil health by reducing metal bioavailability [44].

3. Applications in Agriculture

3.1. Biofertilizers

A biofertilizer is a formulated product containing one or more living microorganisms (or their latent cells) that, when applied to seeds, plant surfaces, or soil, colonize the rhizosphere or the interior of the plant and promote growth by enhancing the availability, uptake, or use efficiency of nutrients [45]. PGPR have emerged as a promising alternative or complement to synthetic fertilizers, offering a sustainable approach to improve soil fertility and plant growth. These beneficial bacteria are naturally occurring soil microorganisms that colonize plant roots (or other parts of the plant) and promote growth through various mechanisms. Recent studies have shown that PGPR can improve soil biological activity [46,47]. The formulation of PGPR biofertilizers involves isolating effective strains from the rhizosphere, mass-producing them through fermentation, and developing stable formulations such as liquid suspensions, powders, or granules [48].

The application of PGPR biofertilizers can be tailored to different crops and farming practices. Methods such as seed inoculation, soil drenching, foliar sprays, and root dipping are commonly used to deliver PGPR to plants. These applications enhance root colonization, improve nutrient uptake, and protect plants from pathogens [46,49]. PGPR biofertilizers offer several advantages over conventional synthetic fertilizers. PGPR biofertilizers are environmentally sustainable, reducing soil and water pollution while maintaining soil health and fertility [48]. PGPR also improve nutrient efficiency by enhancing the availability of nitrogen, phosphorus, and other essential nutrients, thereby reducing the need for chemical fertilizers [46].

Moreover, PGPR enhance plants' resilience to abiotic stresses by producing stress-relieving compounds like ACC-deaminase and inducing systemic resistance, thereby contributing to healthier plant growth [46,49]. While the initial costs of PGPR biofertilizers may be higher, they can lead to long-term cost savings by reducing the need for chemical inputs and improving crop yields [48].

3.2. Seed Treatments and Soil Amendments

PGPR are applied to crops through various methods, each tailored to optimize their effectiveness in different environments and crop types. One common method is seed inoculation, where seeds are coated with PGPR before planting. This technique promotes early root colonization, leading to improved seedling vigor and nutrient uptake. Seed inoculation has been shown to be particularly effective in enhancing the growth of crops like maize and cowpea, as it facilitates the establishment of a healthy soil microbiome [50].

Another effective method is soil amendment, which involves incorporating PGPR into the soil to improve its fertility and structure. This approach enhances nutrient availability and promotes root growth, making it suitable for various crops, including lettuce and poplar. Recent studies have demonstrated that soil amendments with PGPR can significantly improve plant growth and yield by enhancing nutrient uptake and reducing the need for chemical fertilizers [51].

Additionally, PGPR can be applied through foliar sprays and root dipping, which are particularly useful in environments where soil conditions are suboptimal or where rapid microbial colonization is needed [50]. In addition to triggering induced systemic resistance (ISR), some PGPR can directly inhibit the growth of plant pathogens, even though they were originally isolated from plant root systems [4–6,52].

The effectiveness of PGPR applications varies depending on the crop and environmental conditions. For instance, in hydroponic systems, PGPR have been used to reduce mineral fertilizer use while maintaining or even improving crop yield and quality. This is particularly beneficial in regions where mineral fertilizers are costly or difficult to obtain [53].

4. Challenges and Limitations

4.1. Consistency and Survival

The inconsistent performance of PGPR in different soils and environmental conditions presents a significant challenge to their widespread adoption in sustainable agriculture. One of the primary reasons for this variability is the complex interaction between PGPR and the native soil microbiome. These interactions can influence the colonization and efficacy of PGPR, as native microbes often compete with introduced strains for resources and niches [54]. Additionally, the physiochemical properties of the soil, such as pH, nutrient content, and moisture levels, can affect the survival and activity of PGPR. This makes it difficult to predict their performance across different environments [55].

Another factor contributing to the inconsistent performance of PGPR is the specificity of plant–microbe interactions. Different plant species and even cultivars within a species can exhibit varying responses to the same PGPR strains. This host specificity can result in variable plant growth promotion and disease resistance outcomes, depending on the plant genotype and the PGPR strain used [9]. At the molecular level, this specificity is often mediated by plant pattern recognition receptors (PRRs) that recognize specific molecular patterns associated with microbes (MAMPs or PAMPs). The composition and sensitivity of these PRRs can vary between plant species and cultivars, leading to differential recognition and response to PGPR [56]. For instance, certain plants may have evolved PRRs that are more sensitive to the flagellin or lipopolysaccharides of specific PGPR strains, resulting in a stronger growth-promoting response [57]. Physiologically, the effectiveness of PGPR can be modulated by the plant's hormonal balance and nutrient status. Different plant species and cultivars may have varying baseline levels of phytohormones or different sensitivities to PGPR-produced hormones like auxin or cytokinin. This can result in differential growth responses when exposed to the same PGPR strain [58]. Moreover, environmental stressors such as temperature fluctuations can further complicate the effectiveness of PGPR, as these conditions can alter plant physiology and microbial community dynamics in the rhizosphere [59].

The rhizosphere is the narrow region of soil surrounding plant roots, typically extending a few millimeters from the root surface. This zone is characterized by intense microbial activity due to the presence of root exudates, which serve as a nutrient source for microorganisms [60]. In contrast, the rhizoplane refers to the root surface itself, including the epidermis and mucilage. This zone is in direct contact with soil particles and is the site of intimate plant–microbe interactions [61]. Many PGPR form biofilms on the rhizoplane, creating a protective barrier against pathogens and enhancing nutrient exchange. This natural defense mechanism reduces the need for chemical pesticides [62]. PGPR colonizing the rhizoplane can directly influence plant growth by producing phytohormones like auxins and cytokinins. This promotes sustainable plant growth without reliance on synthetic growth regulators [63]. Beneficial PGPR on the rhizoplane can also outcompete pathogenic microorganisms, providing a natural and sustainable approach to disease control [64]. However, PGPR face several challenges and limitations when applied to the rhizosphere and/or rhizoplane for sustainable agriculture [55]. These include biological constraints such as competition with indigenous microorganisms and potential incompatibility with existing beneficial microbes. Technical constraints involve maintaining PGPR viability during formulation, storage, and application, as well as ensuring consistent rhizoplane colonization. Field-level constraints include unpredictable performance under varying soil and environmental conditions and potential negative interactions with agrochemicals [55]. To address these challenges, several strategies have been proposed, one of which is to select robust PGPR strains that are adaptable to local environmental conditions and compatible with specific crops. This involves screening for PGPR that can withstand stress factors and that have shown effectiveness with local plant species [59]. Additionally, developing advanced formulations that enhance the viability and stability of PGPR during storage, transport, and application can improve their persistence in the soil [55]. Utilizing consortia of different PGPR strains that have synergistic effects can also enhance nutrient acquisition, disease suppression, and stress tolerance [65].

4.2. Compatibility and Interaction

The compatibility of PGPR with target crops and the indigenous soil microbiome is crucial for their successful application in sustainable agriculture. This compatibility ensures that PGPR can effectively colonize plant roots, promote growth, and provide protection against pathogens. One of the primary challenges in achieving this compatibility is the strain specificity of PGPR, as certain strains may only benefit specific plants or perform optimally under particular environmental conditions [53]. This specificity necessitates careful selection of PGPR strains that are well-suited to the target crop and its optimal growing environment.

The interactions between PGPR and the native soil microbiome also play a significant role in determining the effectiveness of PGPR applications. Indigenous microorganisms can compete with introduced PGPR strains for resources and ecological niches, potentially limiting their colonization and persistence in the rhizosphere [54]. It is essential to understand these interactions, as they can influence the overall efficacy of PGPR in promoting plant growth and health. For example, PGPR must be able to survive and proliferate in the presence of native soil microbes to exert their beneficial effects [33].

To address these challenges, it is important to select PGPR strains that are not only effective with the target crop but also compatible with the existing soil microbiome. This involves screening for strains that can thrive in the specific soil conditions and that have demonstrated positive interactions with the target plant species [65]. Additionally, developing formulations that enhance the stability and viability of PGPR during storage and application can improve their performance in diverse environments [66].

4.3. Commercialization and Adoption

The widespread adoption of PGPR technologies faces several significant barriers, including regulatory challenges and a lack of farmer awareness. Regulatory issues are particularly daunting because each country has its own set of regulations governing the use of microbial products in agriculture. These regulations can be complex and costly to navigate, often requiring significant investments in time and resources to ensure compliance. For example, the high costs associated with the development and registration of new biocontrol agents (BCAs) have been identified as a barrier in countries like Australia, where regulatory frameworks demand rigorous evaluation to ensure environmental safety and efficacy [67,68]. This complexity is compounded by the lack of standardized international regulations, which can hinder the global commercialization of PGPR products [33,69].

Alongside regulatory hurdles, it is essential to increase farmer awareness and education about the benefits and applications of PGPR technologies. Many farmers may be unfamiliar with PGPR or lack the knowledge needed to integrate these biological solutions into their current farming practices. This lack of awareness can lead to slow adoption rates, as farmers may perceive chemical fertilizers and pesticides as more reliable and predictable compared to PGPR [68]. Educational programs and workshops highlighting the economic and environmental benefits of PGPR can be crucial in overcoming this barrier, helping farmers understand how to use PGPR effectively to improve crop productivity and sustainability [67,70].

Moreover, the scalability and cost-effectiveness of PGPR strategies are critical for their widespread adoption. PGPR technologies must be adaptable to different crops, environments, and farming practices to be effective. This adaptability requires ongoing research and development to tailor PGPR solutions to specific agricultural contexts [65]. Additionally, efforts must be made to reduce production costs and improve accessibility, particularly for farmers in developing countries. Collaboration among researchers, farmers, governments, and industry stakeholders is essential to develop cost-effective and sustainable PGPR products and practices [65].

5. Advances and Future Directions

5.1. Nano-Encapsulation Technology

Nano-encapsulation offers a promising method to increase the efficacy and stability of PGPR formulations, which can address some of the challenges associated with their application in agriculture. By encapsulating PGPR in nanoparticles, it is possible to protect these beneficial microbes from environmental stressors, such as UV radiation, desiccation, and temperature fluctuations, thereby improving their survival and functionality [71]. This protective mechanism ensures that PGPR can be delivered more effectively to plant roots, enhancing their colonization and promoting better plant growth and resilience [72].

Recent studies have demonstrated the potential of various encapsulation materials, such as alginate, silica nanoparticles, and carbon nanotubes, to improve the delivery and performance of PGPR. For instance, the encapsulation of *Pseudomonas* sp. in alginate beads with salicylic acid and zinc oxide nanoparticles has shown enhanced antifungal activity and superior plant growth-promoting effects on rice seedlings compared to non-encapsulated strains [72]. Similarly, nano-encapsulated *Bacillus subtilis* using sodium alginate, starch, and bentonite has been effective in controlling the proliferation of *Rhizoctonia solani* and increasing bean vegetative growth parameters [73].

The use of nano-encapsulation not only improves the stability and efficacy of PGPR formulations but also allows for the controlled and sustained release of the bacteria into the soil. This ensures a more consistent and prolonged interaction between PGPR and the plant roots, which is crucial for maximizing their growth-promoting effects [73,74]. Moreover, nano-encapsulation can enhance the resilience of PGPR to abiotic stresses, such as drought and salinity, by providing a stable microenvironment that supports their metabolic activity [75].

5.2. Biotechnological Approaches

The integration of genetic engineering and bioinformatics in the development of PGPR strains holds significant promise for enhancing their effectiveness in agriculture. Genetic engineering allows for the modification of PGPR strains to enhance desirable traits such as nutrient solubilization, phytohormone production, and pathogen resistance. By employing techniques such as CRISPR-Cas9, researchers can precisely edit the genomes of PGPR to introduce or enhance specific plant growth-promoting traits, thereby improving their efficacy under various environmental conditions [76,77]. Bioinformatics plays a crucial role in this process by enabling the analysis and interpretation of large genomic datasets, which is essential for identifying genes responsible for beneficial traits in PGPR. Through genome mining and comparative genomics, researchers can uncover biosynthetic gene clusters and regulatory networks that contribute to the plant growth-promoting capabilities of PGPR [78]. This information is invaluable for designing genetically engineered strains that are more robust and effective in promoting plant health and productivity [79].

Moreover, bioinformatics tools facilitate the prediction and modeling of PGPR interactions with plant hosts and soil microbiomes, allowing for the optimization of strain selection and application strategies. By understanding these complex interactions, scientists can develop PGPR strains that are better customized to given crops and environmental conditions, thereby enhancing their performance in the field [80]. This approach not only improves the efficacy of PGPR but also supports sustainable agriculture by lowering the need for chemical fertilizers and pesticides [81].

The use of biotechnological approaches to develop new PGPR strains is a topic of considerable debate, both within and outside the scientific community. For agriculture, genetic modification is not expected to introduce additional regulatory barriers for future applications [82]. In other words, while biotechnological approaches offer significant potential for developing improved PGPR strains, they do introduce additional regulatory considerations. However, these are not necessarily insurmountable barriers, especially given the existing frameworks for GMOs in agriculture. The key will be to balance the potential benefits of engineered PGPR with ensuring their safety and addressing public concerns. Ongoing dialogue between scientists, regulators, and the public will be crucial in navigating this aspect of PGPR development and application.

5.3. Integrated Plant Management (IPM)

Incorporating PGPR into integrated plant management (IPM) strategies offers a comprehensive approach to enhancing crop health and yield while reducing reliance on chemical pesticides. By incorporating PGPR into IPM, farmers can leverage these natural processes to create more resilient agricultural systems that are less dependent on synthetic chemicals, thereby minimizing environmental impact and promoting sustainable practices [32].

Nutrient use efficiency (NUE) is a crucial concept in agriculture that measures how effectively plants utilize available nutrients for growth and yield production. The application of PGPR has been shown to improve NUE in various crops. The integration of PGPR in agricultural practices shows promise in reducing chemical fertilizer requirements by 20–30% while maintaining or even improving crop yields and quality. This approach aligns with sustainable agriculture goals by reducing environmental impacts and potentially lowering production costs [83]. In hydroponic systems, combining 80% mineral fertilizers with PGPR has resulted in yields comparable to 100% mineral fertilizer treatments [53], which further underscores the potential of PGPR to enhance NUE across different agricultural systems. Of note, PGPR should be compatible with chemical fertilizers, contributing to more sustainable agriculture as a practical approach. Currently, PGPR are not an alternative to conventional management but rather a complement that can boost crop yield and reduce environmental impact.

PGPR contribute to IPM by suppressing plant diseases through various mechanisms, including the production of pathogen-antagonizing compounds [6] and the stimulation of systemic resistance in plants [4,6]. These actions not only help control pathogens but also enhance the plant's innate defense responses, making them more resistant to pest attacks [33]. For example, PGPR can produce antibiotics and enzymes that inhibit the growth of harmful microbes, while also triggering plant immune responses that bolster the plant's ability to withstand pest pressures [34].

Moreover, PGPR improve nutrient uptake and root architecture, indirectly contributing to pest management. By enhancing root growth and nutrient acquisition, PGPR help plants become more vigorous and less susceptible to pest infestations. This improved plant health can lead to increased tolerance to pest damage and a reduction in the need for chemical interventions [65].

6. Conclusions

The integration of PGPR into agricultural systems as biofertilizers offers a sustainable alternative or complement to chemical fertilizers, promoting nutrient cycling and improving plant health and yield (Figure 1A). By solubilizing phosphorus and fixing nitrogen, PGPR enhance nutrient availability and uptake, leading to improved plant growth and productivity [18]. Moreover, the use of PGPR can mitigate environmental impacts associated with excessive fertilizer use, such as soil degradation and water pollution, thereby supporting sustainable agriculture (Table 1) [16,20]. PGPR biofertilizers represent a viable alternative or complement to synthetic fertilizers, providing sustainable solutions for enhancing crop productivity and soil health. Their ability to improve nutrient uptake, enhance stress tolerance, and suppress diseases makes them an invaluable tool in the pursuit of sustainable agriculture, particularly as the global demand for food continues to rise [46,48]. As research continues to advance, the development of more effective PGPR strains and formulations will be crucial in maximizing their benefits for crop production and environmental health [17].

Table 1. Potential of PGPR from the soil microbiome for sustainable agriculture.

Functional PGPR Species	Source Isolated From	Beneficial Roles	Mechanisms of Action	Applicable Plants	References
Arthrobacter globiformis	Soil, rhizosphere	Nutrient solubilization, pathogen control	Phosphate solubilization, biocontrol of pathogens	Vegetables, cereals	[84–86]
Azospirillum brasilense	Soil, plant roots	Enhanced root growth, nitrogen supply	Nitrogen fixation, phytohormone production (auxins)	Cereals (e.g., maize, wheat), grasses	[87,88]
Azotobacter chroococcum	Soil, rhizosphere	Nitrogen fixation, soil fertility improvement	Nitrogen fixation, produces growth-promoting substances	Cereals, vegetables	[89,90]
Bacillus amyloliquefaciens	Soil, plant roots	Pathogen suppression, growth enhancement	Antifungal activity, induced systemic resistance	Fruits, vegetables	[4,91–93]
Bacillus cereus	Soil, plant roots	Disease control, plant vigor improvement	Biocontrol of pathogens, induced systemic resistance	Vegetables, cereals	[94–96]
Bacillus subtilis	Soil, plant roots	Disease suppression, nutrient uptake enhancement	Produces antibiotics, induces systemic resistance, solubilizes phosphorus	Vegetables, cereals, legumes	[97,98]
Bacillus thuringiensis	Soil, plant roots	Insect pest suppression, plant protection	Pest control, biocontrol of insects	Vegetables, fruits	[99–102]
Burkholderia cepacia	Soil, rhizosphere	Pathogen control, plant growth promotion	Produces antifungal compounds, competes with pathogens	Vegetables, ornamentals	[103,104]
Enterobacter cloacae	Soil, plant roots	Disease suppression, nutrient enhancement	Phosphate solubilization, biocontrol of pathogens	Vegetables, cereals	[105,106]
Flavobacterium johnsoniae	Soil, rhizosphere	Disease suppression, growth enhancement	Biocontrol of pathogens, growth promotion	Vegetables, cereals	[107–109]
Klebsiella pneumoniae	Soil, rhizosphere	Nitrogen supply, growth enhancement	Nitrogen fixation, growth promotion	Vegetables, cereals	[110,111]
Micrococcus luteus	Soil, plant roots	Nutrient availability, plant growth support	Phosphate solubilization, growth promotion	Vegetables, cereals	[112–114]

Table 1. *Cont.*

Functional PGPR Species	Source Isolated From	Beneficial Roles	Mechanisms of Action	Applicable Plants	References
Paenibacillus macerans	Soil, plant roots	Nutrient availability, growth promotion	Produces enzymes, solubilizes phosphorus	Vegetables, cereals	[115,116]
Paenibacillus polymyxa	Soil, plant roots	Nutrient solubilization, disease suppression	Nitrogen fixation, phosphate solubilization	Cereals, vegetables	[117,118]
Pseudomonas fluorescens	Soil, plant roots, rhizosphere	Disease resistance, improved nutrient acquisition	Produces siderophores and antibiotics, induces systemic resistance	Vegetables, fruits, cereals	[119,120]
Pseudomonas putida	Soil, rhizosphere	Enhanced nutrient uptake, disease control	Siderophore production, biocontrol of pathogens	Vegetables, ornamentals	[121,122]
Pseudomonas stutzeri	Soil, rhizosphere	Nitrogen fixation, disease suppression	Nitrogen fixation, biocontrol of pathogens	Vegetables, cereals	[123–126]
Rhizobium leguminosarum	Soil, legume roots	Symbiotic nitrogen fixation, plant growth promotion	Nitrogen fixation, nodule formation	Legumes (e.g., peas, beans)	[127–129]
Streptomyces griseoviridis	Soil, plant roots	Disease control, enhanced plant health	Produces antibiotics, competes with pathogens	Vegetables, ornamentals	[130–132]
Streptomyces lydicus	Soil, rhizosphere	Disease control, enhanced plant health	Antifungal activity, biocontrol of pathogens	Vegetables, ornamentals	[133–135]

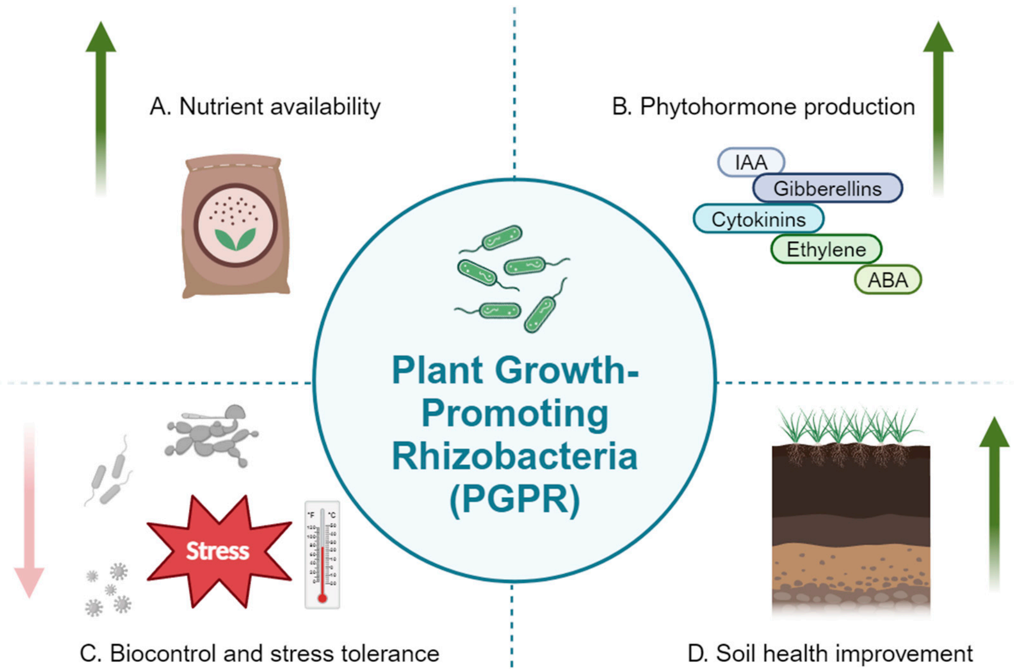

Figure 1. Roles of PGPR in sustainable agriculture. (**A**) Nutrient availability. (**B**) Phytohormone production. Abbreviations: Indole-3-Acetic Acid (IAA); Gibberellins (GA); Abscisic Acid (ABA). (**C**) Biocontrol and stress tolerance. (**D**) Soil health improvement. Created with BioRender.com (accessed on 1 September 2024).

The production of auxins, gibberellins, and cytokinins by PGPR significantly contributes to their ability to promote plant growth and development (Table 1). These phytohormones enhance root and shoot growth, improve nutrient uptake, and increase plant resilience to environmental stresses, which makes PGPR an integral part of modern sustainable agriculture (Figure 1B) [26,136]. As research continues to explore the complex interactions between PGPR-produced phytohormones and plant physiology, the potential for optimizing PGPR applications in agriculture remains promising [137].

The integration of PGPR into agricultural practices offers a sustainable approach to managing abiotic stresses (Figure 1C). By enhancing plant growth and resilience, PGPR contribute to improved crop yields and stability, even under adverse environmental conditions [39,138]. PGPR offer a promising approach to biopesticide development, providing an eco-friendly and effective means of controlling plant diseases and pests (Figure 1C). Their ability to enhance plant resilience and promote growth makes them an invaluable tool in the pursuit of sustainable agricultural practices [65]. As research continues to advance, the development of more effective PGPR strains and formulations will be crucial in maximizing their benefits for stress management in agriculture (Table 1) [139].

The application of PGPR through methods like seed inoculation and soil amendments offers a sustainable approach to improving crop productivity and resilience (Figure 1D). By enhancing nutrient uptake and stress tolerance, PGPR contribute to more sustainable agricultural practices, reducing the reliance on chemical inputs and supporting global food security [9]. While the inconsistent performance of PGPR in different soils and environmental conditions poses challenges, ongoing research and innovation in PGPR selection, formulation, and application strategies hold promise for overcoming these obstacles.

By optimizing PGPR inoculum efficacy in field conditions, researchers and farmers can enhance crop productivity, soil health, and environmental sustainability, contributing to more resilient agricultural systems [9,55]. Despite those promising advancements, further research is needed to optimize nano-encapsulation techniques and assess their long-term impacts on soil health and plant growth. The scalability and cost-effectiveness of these technologies remain challenges that need to be addressed to facilitate their widespread adoption in agriculture [140]. Nonetheless, the integration of nanotechnology with PGPR formulations represents a significant step forward in developing more efficient and sustainable agricultural practices (Table 1) [141].

Ensuring the compatibility of PGPR with target crops and indigenous soil microflora is essential for maximizing their benefits in sustainable agriculture (Figure 2). By selecting appropriate strains and understanding the complex interactions within the soil ecosystem, researchers and practitioners can enhance the effectiveness of PGPR applications, leading to improved crop productivity and resilience (Table 1) [53,54]. While PGPR technologies hold significant potential for improving sustainable agriculture, overcoming regulatory hurdles and increasing farmer awareness are crucial for their widespread adoption. By addressing these challenges, PGPR can become a more integral part of agricultural systems, contributing to enhanced crop productivity and environmental sustainability [49].

Despite these advancements, challenges remain in the large-scale application of genetically engineered PGPR. Regulatory hurdles and public concerns about genetically modified organisms (GMOs) can impede the commercialization of these strains. However, ongoing research and dialogue among scientists, policymakers, and stakeholders are essential to address these issues and realize the full potential of genetic engineering and bioinformatics in developing effective PGPR strains for sustainable agriculture [142,143].

The integration of PGPR into IPM strategies requires the careful selection of compatible strains that can thrive in specific environmental conditions and work synergistically with other IPM components. This approach not only enhances the effectiveness of pest management but also contributes to overall crop productivity and sustainability [65]. As research continues to advance, the development of tailored PGPR formulations and application methods will be crucial in maximizing their benefits within IPM frameworks, ultimately leading to more resilient and productive agricultural systems (Figure 3) [32]. PGPR protect plants from pathogens through a combination of antimicrobial production, resource competition, and induction of systemic resistance. These mechanisms make PGPR a valuable component of integrated pest management strategies, offering a sustainable alternative or complement to chemical-based disease control methods (Table 1) [144]. As research continues to advance, the development of more effective PGPR strains and formulations will be crucial in maximizing their benefits for crop protection and productivity [11].

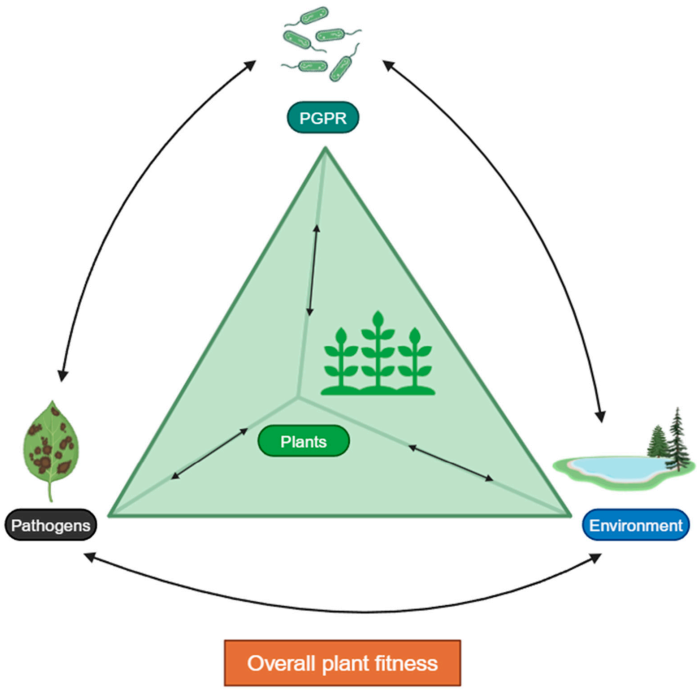

Figure 2. The plant fitness tetrahedron for sustainable agriculture. Adapted from [31]. PGPR play a crucial role in maintaining the health and vitality of plants. Created with BioRender.com (accessed on 1 September 2024).

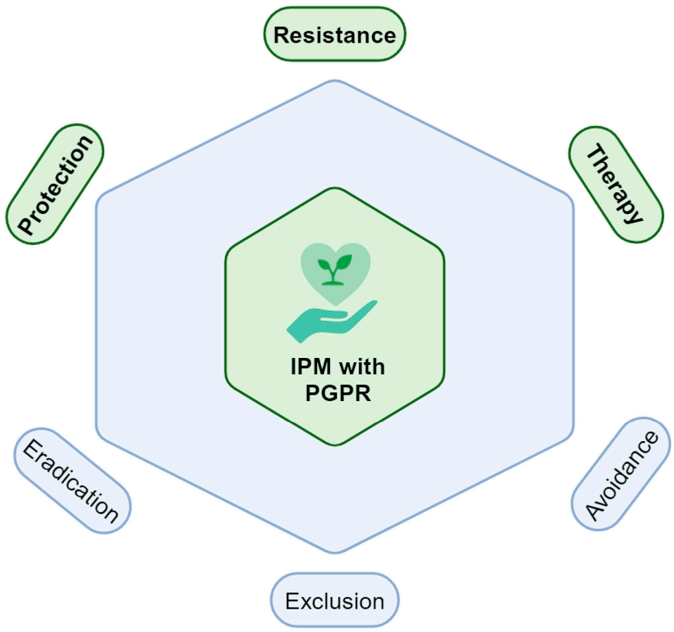

Figure 3. Integrated plant management (IPM) with PGPR. IPM has six directions: protection, resistance, therapy, avoidance, exclusion, and eradication. Directions integrated with PGPR are highlighted in green. Adapted from [31,145]. Created with BioRender.com (accessed on 1 September 2024).

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