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Plant Microbiome in Sustainable Agriculture: From Interaction Mechanisms to Technological Applications and Future Challenges

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Abstract

Introduction: The plant microbiome, comprising dynamic and complex communities of microorganisms including bacteria, fungi, viruses, and archaea, plays a fundamental role in plant health, growth, productivity, and the sustainability of agroecosystems.

Materials and Methods: This comprehensive review is based on a systematic search of peer-reviewed literature published between 2012 and 2026 using PubMed, Scopus, Web of Science, and Google Scholar databases. A total of 53 relevant articles were selected for inclusion.

Results: Microbial communities inhabit various plant compartments including the rhizosphere, phyllosphere, endosphere, and spermosphere. They enhance plant growth through direct mechanisms such as nitrogen fixation, phosphate solubilization, siderophore and phytohormone production, as well as indirect mechanisms including induced systemic resistance (ISR) and biological control. Beyond direct effects, microbiomes are the primary drivers of biogeochemical cycles of nitrogen, phosphorus, carbon, and sulfur in soil, improving soil fertility and carbon sequestration. From an ecological and evolutionary perspective, the plant microbiome acts as a "hologenome," providing phenotypic plasticity and rapid adaptation to environmental changes. Synthetic microbial communities (SynComs) designed based on ecological principles represent one of the most promising approaches for disease management, nutrient acquisition, and stress tolerance enhancement.

Conclusion: Despite significant challenges in commercialization and field application, the transition from chemistry-based to biology-based agriculture, with microbiomes at its core, is imperative. Realizing this vision requires synergy among scientists, farmers, industry, and policymakers to adopt microbiome-aware management strategies.

Keywords: Biogeochemical cycles, Hologenome, Induced Systemic Resistance (ISR), Microbiome engineering, Plant Growth-Promoting Rhizobacteria (PGPR), Plant microbiome, Rhizosphere, Sustainable agriculture, Synthetic Microbial Communities (SynComs)

1. Introduction

In recent decades, the rapidly growing global population and climate change have placed unprecedented pressure on food production systems. Modern agriculture, which heavily relies on chemical fertilizers and pesticides, faces serious challenges including soil structure degradation, biodiversity loss, water resource pollution, and increased greenhouse gas emissions (1). These issues have increasingly highlighted the necessity of transitioning toward more sustainable agricultural systems. In this context, the plant microbiome has emerged as one of the most promising bio-based and sustainable approaches for enhancing agricultural productivity and reducing dependence on chemical inputs (2, 3).

The plant microbiome refers to the vast assemblage of microorganisms (bacteria, fungi, actinomycetes, viruses, and archaea) living in close association with plant tissues and their surrounding environment (4). These microorganisms function as an inseparable part of plant physiology and, through their effects on various processes,

play a determining role in plant health and performance. In other words, the plant together with its associated microbiome forms a "hologenome," which is considered the primary unit of natural selection (5).

The twenty-first century can be considered the era of microbiome discovery and exploitation. Remarkable advances in novel technologies such as Next-Generation Sequencing (NGS), metagenomics, metatranscriptomics, and metabolomics have enabled in-depth study of unculturable microbial communities, providing researchers with a more precise picture of their diversity, structure, and function (6, 7). These new insights have transformed our understanding of the complex mechanisms of plant-microbe interactions and have paved the way for the targeted design and management of microbiomes for agricultural crop improvement (8).

This review article aims to provide a comprehensive overview of the current knowledge regarding the plant microbiome. In this regard, it first describes the main niches of the microbiome (rhizosphere, phyllosphere, endosphere, and spermosphere) and the diverse

mechanisms of beneficial plant-microbe interactions. It then examines the key role of the microbiome in inducing resistance to stresses and the impact of agricultural activities on it. Subsequently, recent advances in microbiome engineering with an emphasis on the design of Synthetic Communities (SynComs) and the role of advanced tools such as artificial intelligence and genome editing are introduced, and finally, the challenges facing the widespread application of these technologies and their future perspective are discussed.

2. Materials and Methods

This article is a narrative review based on a comprehensive and systematic search of peer-reviewed literature. The search was conducted using the following electronic databases: PubMed, Scopus, Web of Science, and Google Scholar. The search covered the period from January 2012 to March 2026. The following keywords and their combinations were used: "plant microbiome," "rhizosphere," "phyllosphere," "endosphere," "spermosphere," "PGPR," "plant growth-promoting rhizobacteria," "induced systemic resistance," "ISR," "synthetic microbial communities," "SynComs," "microbiome engineering," "biogeochemical cycles," "hologenome," and "sustainable agriculture."

The initial search yielded a total of 1,247 records across the four databases. After removing 312 duplicate records, 935 unique records remained for further screening. The screening process was conducted in three stages: (1) Title and abstract screening, in which 657 records were excluded based on irrelevance to the topic; (2) Full-text assessment, in which 217 records were excluded based on the inclusion and exclusion criteria; and (3) Final selection, in which 61 records were critically evaluated for scientific quality, and 8 records were excluded. Finally, 53 articles were selected for inclusion in this review.

Inclusion Criteria: Articles were included if they were peer-reviewed original research articles, review articles, or book chapters; published in English between 2012 and 2026; directly related to the plant microbiome, rhizosphere, phyllosphere, endosphere, spermosphere, PGPR, ISR, SynComs, microbiome engineering, biogeochemical cycles, hologenome, or sustainable agriculture; provided substantial scientific evidence or comprehensive reviews; and were available in full text.

Exclusion Criteria: Articles were excluded if they were non-English publications; conference abstracts, editorials, letters to the editor, or short communications without sufficient data; duplicate publications or overlapping datasets; studies focused solely on non-plant microbiomes without relevance to plant systems; articles with insufficient methodological details or low scientific

quality; or articles published before 2012, unless they were seminal works essential for historical context.

Data from the 53 selected articles were extracted and synthesized narratively. Key information extracted from each article included: author(s), year of publication, study objectives, microbial groups or communities studied, mechanisms of plant-microbe interactions, agricultural management practices, and main findings. The extracted data were then organized thematically into the following sections: (1) major niches of the plant microbiome, (2) mechanisms of beneficial plant-microbe interactions, (3) ecological and evolutionary dynamics, (4) biogeochemical cycles, (5) stress tolerance, (6) impact of agricultural practices, and (7) microbiome engineering and SynComs. This narrative synthesis approach allowed for a comprehensive overview of the plant microbiome and its applications in sustainable agriculture.

3. Main Themes

3.1. Major Niches of the Plant Microbiome

The plant microbiome is a complex and dynamic system in which different plant compartments with varying ecological conditions harbor distinct microbial communities. Understanding these niches is essential for microbiome management and engineering (Fig. 1).

3.1.1. Rhizosphere

The rhizosphere is the region of soil that is directly influenced by plant roots and their metabolic activities (9). This region is ecologically dynamic and nutrient-rich. Plants actively control the microbial population and activity of the rhizosphere through root exudates, including carbohydrates, amino acids, organic acids, and secondary compounds such as flavonoids (10, 11). These exudates serve as food sources and can also act as signaling molecules to attract beneficial microbes and repel pathogens (12).

The rhizosphere harbors one of the densest microbial communities, playing vital roles in nutrient cycling, organic matter decomposition, and root protection against soil-borne pathogens. Plant Growth-Promoting Rhizobacteria (PGPR), which constitute a significant portion of the rhizosphere microbiome, enhance plant growth and health through direct and indirect mechanisms (13). Furthermore, Arbuscular Mycorrhizal Fungi (AMF), which form extensive symbioses with the roots of most plants, establish themselves in this region and, through the development of hyphal networks, greatly enhance the uptake of immobile elements such as phosphorus (14, 15).

3.1.2. Phyllosphere

The phyllosphere refers to the surfaces of above-ground

plant organs including leaves, stems, and flowers, which serve as habitats for various microorganisms (16). Unlike the rhizosphere, which is rich in nutrients, the phyllosphere is an environment with harsher conditions including severe fluctuations in temperature, humidity, and ultraviolet radiation, as well as limited nutrient sources (17). Nevertheless, this surface hosts diverse microbial communities including bacteria, fungi, and yeasts.

The phyllosphere microbiome plays an important role in plant health. These microorganisms can act as protectors against airborne pathogens through competition for space and resources, production of antimicrobial compounds, and induction of plant resistance (18). Additionally, some phyllosphere bacteria are capable of nitrogen fixation, which can contribute to plant nutrition. In recent years, attention to phyllosphere microbiome engineering for disease management and improvement of agricultural crop efficiency has increased (16).

3.1.3. Endosphere and Spermosphere

The endosphere refers to the internal tissues of the plant, which are inhabited by endophytic microorganisms (19). These microorganisms can be bacteria, fungi, or actinomycetes, living within plant tissues without causing disease symptoms. Endophytes enter the plant through roots or aerial organs and can benefit from the protected environment and access to nutrients within plant tissues. They enhance plant growth and resistance through the production of phytohormones, nitrogen fixation, increased nutrient uptake, and production of anti-pathogenic compounds (20). The potential of bacterial endophytes as biological control agents in managing pre- and post-harvest diseases is of great importance.

The spermosphere is the region around the germinating seed that is influenced by seed exudates (21). This region acts as an initial entry point for the establishment of the root and endosphere microbiome. Seeds themselves contain specific microbiomes (seed microbiomes) inherited from the mother plant, which can affect seedling health and performance (22, 23). Strategies such as seed biopriming with beneficial microorganisms are effective methods for early establishment of beneficial microbiomes in growing plants (24).

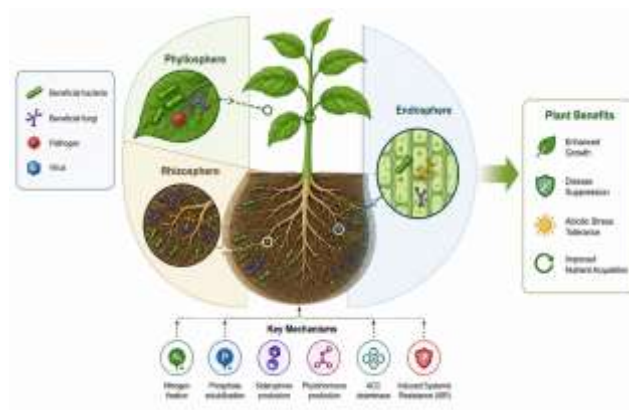


Figure 1. Schematic representation of the main plant microbiome niches, including the phyllosphere, rhizosphere, and endosphere, and their roles in promoting plant growth, enhancing nutrient acquisition, inducing systemic resistance, and improving tolerance to abiotic stresses.

3.2. Mechanisms of Beneficial Plant-Microbe Interactions

Beneficial microorganisms enhance plant growth and health through a wide range of direct and indirect mechanisms.

3.2.1. Nutrient Bioavailability and Nitrogen Fixation

One of the most important roles of the microbiome is improving plant nutrition by increasing the availability of essential nutrients.

Nitrogen Fixation: Some bacteria, known as nitrogen fixers, are capable of converting atmospheric molecular nitrogen (N_2) into ammonia (NH_3), which is usable by plants. The most important of these symbioses is the relationship between bacteria of the genus *Rhizobium* and leguminous plants, which occurs in root nodules (25). In addition, free-living bacteria such as *Azospirillum* are also capable of non-symbiotic nitrogen fixation.

Phosphate Solubilization and Siderophore Production: Despite its abundance in soil, phosphorus is unavailable to plants due to the formation of insoluble compounds with calcium, iron, and aluminum. Phosphate-solubilizing microorganisms release organic acids and phosphatases, converting insoluble phosphorus into a form absorbable by plants. Additionally, many microbes produce siderophores (high-affinity iron-chelating molecules), which sequester iron from the environment and make it available to plants (26).

3.2.2. Phytohormone Production and Growth Regulation

Plant Growth-Promoting Rhizobacteria produce a wide range of phytohormones and hormone-like compounds that influence plant growth and development.

Auxin (Indole-3-Acetic Acid or IAA): Many PGPR strains are capable of producing IAA, which promotes root

elongation and enhances nutrient uptake (27). Furthermore, recent research has shown that some bacteria can regulate root growth and improve colony establishment through catabolism (degradation) of excess auxin in the rhizosphere (28).

Other Hormones: PGPR can also produce cytokinins, gibberellins, and ethylene. Controlling ethylene levels through the production of ACC deaminase, which degrades the ethylene precursor ACC, is one of the most important mechanisms for reducing stress in plants, especially under environmental stress conditions such as salinity and drought (29).

3.2.3. Biocontrol and Induced Systemic Resistance

Beneficial microorganisms play a key role in protecting plants against diseases. This protection occurs through two main pathways:

Direct Biological Control: Through mechanisms such as the production of antimicrobial compounds (antibiotics, lytic enzymes), competition for iron (via siderophores), and competition for attachment sites on the root surface (30).

Induced Systemic Resistance (ISR): An important defense mechanism in which non-pathogenic microbes (such as some PGPR strains and mycorrhizal fungi) prime the entire plant immune system for resistance against subsequent attacks by pathogens and even pests through the induction of hormonal signals such as jasmonate and ethylene (31, 32). This is an efficient and sustainable approach to disease management.

3.3. Ecological and Evolutionary Dynamics of the Plant Microbiome

The plant microbiome is not merely a static assemblage of microorganisms but a dynamic and evolving system influenced by complex ecological and evolutionary processes (4, 5). Understanding these dynamics is essential for predicting microbiome behavior under changing environmental conditions and for designing effective microbial interventions. Plant microbial communities are shaped through processes of host selection, dispersal, diversification, and genetic drift, collectively known as the Ecological Four-Frame Framework (4). Plants actively shape their associated microbiome composition through root exudates, molecular signals, and the physical structure of their tissues, selecting beneficial microbes and repelling pathogens (10, 11). This selective process leads to the formation of specialized microbial communities adapted to the specific ecological niche of each plant (9).

One of the key concepts in microbiome ecology is the principle of context-dependency, according to which microbiome composition and function are strongly influenced by environmental factors such as soil type,

climate, agricultural management, and the presence of other organisms (33, 34). For example, a microbial strain that performs excellently as a growth promoter under greenhouse conditions may perform poorly under field conditions with environmental stresses (drought, salinity, temperature fluctuations) (35). This phenomenon occurs due to changes in microbial interaction networks and plant physiological responses to environmental conditions. Therefore, the success of microbial interventions requires a deep understanding of the ecological resilience of microbial communities and their ability to adapt to changing conditions (3, 36).

From an evolutionary perspective, the plant microbiome is considered a hologenome, in which the plant and its associated microbiome function as a single unit of natural selection (5). This view suggests that changes in the microbiome can serve as a rapid mechanism for plant adaptation to new environmental conditions, as microbes can respond to changes at much faster evolutionary rates than plants (34). In fact, the microbiome acts as a "secondary genome" that provides genetic diversity and phenotypic plasticity to the plant, enabling it to rapidly adapt to new stresses (5). This is particularly critical in the face of climate change, which is occurring at an unprecedented rate (1, 33).

Understanding these ecological and evolutionary dynamics has important implications for microbiome engineering and the development of sustainable agricultural solutions. The design of Synthetic Microbial Communities (SynComs) should be based on ecological principles such as synergy, competition, and niche partitioning to ensure community stability and function over time (37, 38). Furthermore, the long-term success of SynComs requires consideration of their ability to evolve and adapt to changing field conditions (39, 40). Therefore, future approaches in microbiome engineering should focus not only on selecting high-performing strains but also on designing communities that possess ecological stability and evolutionary flexibility (41, 8). Ultimately, integrating ecological and evolutionary biology knowledge with applied approaches will be key to developing next-generation microbiome-based solutions for sustainable agriculture (42, 43).

3.4. Role of Microbiome in Biogeochemical Cycles and Agroecosystem Sustainability

Beyond their direct effects on plant growth and stress tolerance, microbial communities play an indispensable role in driving biogeochemical cycles that underpin the functioning and sustainability of agricultural ecosystems (4, 3). Soil microorganisms are the primary drivers of organic matter decomposition, nutrient mineralization, and soil aggregation, processes that are fundamental to

maintaining soil health and fertility (36). Through the decomposition of crop residues and soil organic matter, microbial communities release essential nutrients such as nitrogen (N), phosphorus (P), and sulfur (S) in plant-available forms, thereby reducing the need for synthetic fertilizers (44). Moreover, the formation of soil aggregates by microbial exopolysaccharides (EPS) and fungal hyphae enhances soil structure, water infiltration, and carbon sequestration, contributing to climate change mitigation (45). Therefore, maintaining a diverse and active soil microbiome is not only critical for crop productivity but also for the long-term sustainability and resilience of agroecosystems (Fig. 2).

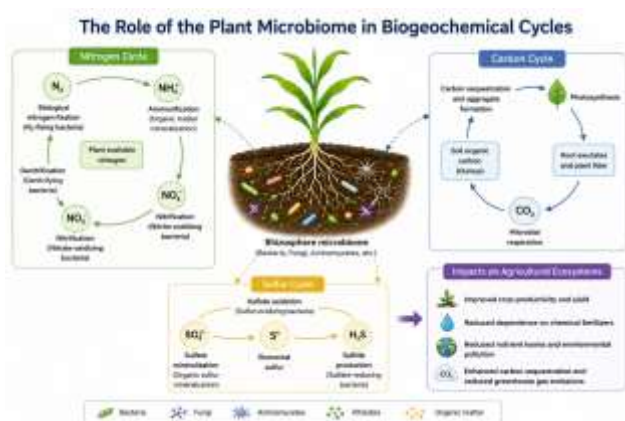


Figure 2. Schematic representation of the role of the soil and rhizosphere microbiome in biogeochemical cycles. Microbial communities regulate key processes such as nitrogen fixation, nitrification, denitrification, and organic matter decomposition, thereby controlling nutrient and carbon cycling and contributing to improved soil fertility and the sustainability of agricultural ecosystems.

The plant microbiome also significantly influences the global nitrogen and carbon cycles. Nitrogen-fixing bacteria, both symbiotic (e.g., *Rhizobium*) and free-living (e.g., *Azospirillum*), contribute substantial amounts of biologically fixed nitrogen to agricultural systems, reducing dependency on energy-intensive synthetic nitrogen fertilizers (25, 2). Additionally, nitrifying and denitrifying microorganisms regulate nitrogen losses through volatilization and leaching, impacting both crop nutrition and environmental quality (44). On the other hand, the rhizosphere microbiome plays a critical role in the carbon cycle by controlling the balance between carbon mineralization and sequestration. Root exudates serve as a major carbon source for soil microbes, fueling microbial activity and promoting the formation of stable soil organic carbon pools (10, 11). This microbial-mediated carbon stabilization is essential for improving soil fertility and mitigating greenhouse gas emissions, particularly under climate change scenarios (1, 33).

Furthermore, agricultural management practices have profound effects on microbial-driven biogeochemical

processes. Long-term application of mineral fertilizers, intensive tillage, and monoculture cropping can disrupt microbial community structure and function, leading to declines in nutrient cycling efficiency and soil organic matter content (44, 46). Conversely, sustainable management practices such as organic amendments, crop rotation, and reduced tillage promote microbial diversity and activity, enhancing nutrient cycling and ecosystem services (47, 48). A comprehensive understanding of plant-microbiome-soil interactions is essential for designing resilient agroecosystems that can withstand environmental stresses while ensuring food security for a growing global population (42, 43).

3.5. Role of Microbiome in Stress Tolerance

With the intensification of climate change, plants face numerous abiotic stresses including drought, salinity, extreme temperatures, and heavy metal pollution. The microbiome plays a vital role in enhancing plant tolerance to these stresses (49, 34).

Drought Resistance: Microorganisms help plants cope with drought through multiple mechanisms. These mechanisms include ACC deaminase production to reduce ethylene levels, secretion of osmolyte-producing compounds such as exopolysaccharides to maintain moisture around roots, alteration of plant gene expression patterns related to drought resistance, and modification of root exudate composition to attract specific microbes (50, 33). Recent research has further demonstrated that plants actively shape their rhizosphere microbiome under drought stress by altering root exudate profiles, thereby recruiting microbes with osmoprotective functions (10, 11). This bidirectional interaction between plants and microbes is critical for maintaining plant productivity under water-limited conditions. Furthermore, the ecological resilience of microbial communities under drought stress is influenced by factors such as soil type, agricultural management, and the presence of native microbial populations (3, 36).

Salinity Resistance: Salinity stress is one of the most significant threats to agricultural production. Salt-tolerant PGPR can improve plant tolerance through several mechanisms, including ACC deaminase production, modulation of plant hormone levels, increased potassium uptake and reduced sodium uptake, as well as altered expression of genes involved in ion transport (Kumawat et al., 2023). ACC deaminase-producing bacteria play a particularly important role in mitigating salinity stress by reducing ethylene levels in plant tissues, thereby preventing growth inhibition (29). Additionally, salt-tolerant PGPR can enhance antioxidant enzyme activities and maintain ionic homeostasis, which are essential for plant survival under high-salinity conditions (13). The

effectiveness of these mechanisms depends on the specific plant-microbe combination and environmental context (35).

Heavy Metal Resistance: Beneficial microbes can help plants tolerate heavy metals and reduce their accumulation in edible tissues through mechanisms such as biostabilization (converting metals to insoluble and non-toxic forms), production of siderophores, and phytochelators (19, 20). Siderophore-producing bacteria not only enhance iron availability to plants but also compete with heavy metal ions for binding sites, thereby reducing metal toxicity (26). Furthermore, endophytic bacteria have been shown to improve plant tolerance to heavy metals by promoting plant growth and modulating metal translocation within plant tissues (20). These mechanisms highlight the potential of beneficial microbes for phytoremediation and safe crop production in contaminated soils.

Common Mechanisms and Future Directions: Collectively, these studies demonstrate that beneficial microorganisms employ a range of common mechanisms—including ACC deaminase activity, EPS production, osmolyte accumulation, phytohormone modulation, and antioxidative defense—to enhance plant tolerance to multiple abiotic stresses. However, the translation of these mechanisms into effective field applications requires a deeper understanding of the ecological and evolutionary dynamics of microbial communities under stress conditions (33, 34). Future research should focus on designing robust microbial consortia that can maintain functionality under diverse environmental conditions while integrating with existing agricultural management practices (35, 41).

3.6. Impact of Agricultural Practices on the Plant Microbiome

Agricultural activities have profound effects on the diversity, structure, and function of microbial communities (Fig. 3).

Fertilization: Long-term application of chemical fertilizers, especially nitrogenous fertilizers, leads to reduced soil microbial diversity, soil acidification, and decreased populations of beneficial microbes such as nitrogen fixers (44). In contrast, organic fertilizers such as compost and vermicompost can increase microbial diversity and activity.

Tillage and Soil Cultivation: Intensive tillage negatively affects the microbiome by disrupting soil structure, reducing organic matter, and destroying the hyphal networks of beneficial fungi such as mycorrhizae. In contrast, conservation tillage (reduced or no-till) and deep tillage can improve rhizosphere microbial structure

and populations (47, 48).

Crop Rotation: Plant diversity in crop rotation increases soil microbial diversity and reduces populations of pathogens specific to a particular crop (46).

Plant Domestication: The process of plant domestication, aimed at selecting desirable agricultural traits (such as high yield and uniformity), has led to a reduction in the diversity of plant-associated microbiomes compared to their wild relatives, a phenomenon known as "domestication footprints on microbial diversity" (51). This suggests that future breeding programs should simultaneously consider selecting traits related to beneficial microbiome recruitment.

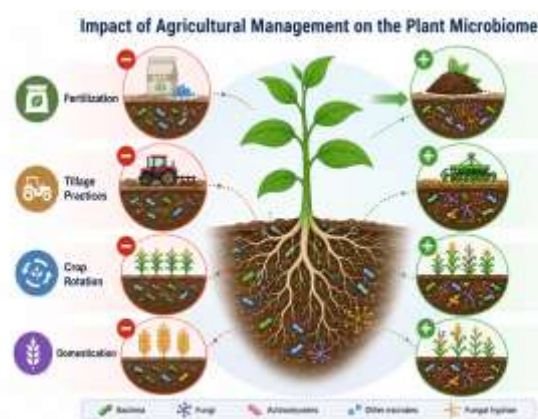


Figure 3. Impact of agricultural management practices on the structure and function of the plant microbiome.

3.7. Microbiome Engineering and Synthetic Communities (SynComs)

With increasing knowledge of the plant microbiome, approaches have shifted from merely studying natural communities toward targeted engineering. The primary goal is to design microbial communities with predefined functions to improve plant growth and resistance (52, 53).

3.7.1. Synthetic Communities (SynComs)

SynComs are assemblages of fully defined microbial strains designed based on ecological and functional knowledge to perform specific tasks (39). The main advantage of SynComs is their simplicity and reproducibility compared to complex natural communities.

Design Principles: Effective SynCom design is based on two main approaches: the "top-down" approach, which begins by selecting key microbes from a complex natural community, and the "bottom-up" approach, which starts with selecting strains with desirable functions (e.g., siderophore production, nitrogen fixation) from culturable collections and combining them (40). SynCom design must be based on competitive and synergistic relationships between strains to ensure community stability and efficiency (37, 38).

Applications: SynComs have been successfully tested for various purposes, including control of soil-borne diseases such as *Fusarium* wilt in banana and cucumber (54, 37), enhanced nutrient uptake (55), and protection of plants against abiotic stresses (18, 56).

3.7.2. Role of Advanced Tools in Microbiome Engineering

Advances in other fields have accelerated microbiome engineering:

Artificial Intelligence (AI) and Machine Learning:

These tools are used to analyze massive metagenomic and metabolomic datasets to identify complex patterns and predict optimal microbial combinations for specific conditions (57). These methods can optimize the SynCom design process.

CRISPR Technology: Genome editing technologies such as CRISPR-Cas have enabled precise genetic modification of microbial strains to enhance their functions (e.g., increased production of a specific metabolite or improved colonization) (58).

Multi-Omics Approaches: Integration of genomics, transcriptomics, proteomics, and metabolomics data provides researchers with a comprehensive and systems-level picture of plant-microbe interactions, which is essential for successful engineering (6, 59).

4. Discussion

The findings of this comprehensive review demonstrate that the plant microbiome represents a transformative frontier in sustainable agriculture. The intricate relationships between plants and their associated microbial communities offer unprecedented opportunities to enhance crop productivity, resilience, and environmental sustainability. However, the translation of these fundamental insights into practical agricultural applications faces several significant challenges that warrant careful consideration.

One of the most critical challenges is the context-dependent nature of plant-microbe interactions (33, 34). While numerous studies have demonstrated the remarkable potential of PGPR and other beneficial microbes under controlled conditions, their performance under field conditions often fails to meet expectations (35). This discrepancy can be attributed to the complex interplay of environmental factors, including soil type, climate, agricultural management practices, and competition with native microbial communities. Addressing this challenge requires a shift from simplistic single-strain approaches toward more sophisticated strategies that consider the ecological and evolutionary dynamics of microbial communities.

The concept of the hologenome, which views the plant and its associated microbiome as a single unit of natural selection, provides a powerful framework for understanding plant adaptation and resilience (5). This perspective suggests that breeding programs should consider not only the plant's genetic potential but also its ability to recruit and maintain beneficial microbial communities. The phenomenon of "domestication footprints on microbial diversity" highlights the unintended consequences of modern breeding practices, which have inadvertently reduced the diversity and functionality of plant-associated microbiomes (51). Future breeding efforts should therefore incorporate microbiome-related traits into selection criteria to develop "microbiome-smart" crop varieties.

The development of synthetic communities (SynComs) represents a promising approach to overcome some of the limitations of single-strain inoculants. By designing communities based on ecological principles such as synergy, competition, and niche partitioning, researchers can create more stable and resilient microbial assemblages (37, 38). The integration of advanced tools such as artificial intelligence, CRISPR technology, and multi-omics approaches further enhances our ability to design and optimize SynComs for specific agricultural applications (6, 57, 58). However, the successful commercialization of SynComs and other microbiome-based technologies requires overcoming significant hurdles, including formulation, shelf-life stability, regulatory approval, and farmer adoption (35, 41, 60).

The role of microbiomes in biogeochemical cycles and carbon sequestration adds another dimension to their importance in sustainable agriculture (3, 4). By enhancing nutrient cycling, improving soil structure, and promoting carbon storage, microbiomes contribute not only to crop productivity but also to climate change mitigation (45). This underscores the need for agricultural management practices that support and enhance soil microbial diversity and activity, such as organic amendments, crop rotation, and reduced tillage (44, 46, 47).

5. Conclusion

The plant microbiome, as a valuable and renewable asset, has revolutionized our approach to agriculture. This comprehensive review has demonstrated that a deeper understanding of the molecular, ecological, and evolutionary mechanisms governing plant-microbe interactions has opened new avenues for enhancing the productivity, sustainability, and resilience of agricultural systems. On one hand, beneficial microorganisms improve plant growth and health through direct mechanisms such as nitrogen fixation, phosphate solubilization, siderophore and phytohormone production, as well as indirect

mechanisms including induced systemic resistance (ISR) and biological control (13, 32). On the other hand, microbiomes play a role far beyond direct plant growth promotion, acting as primary drivers of biogeochemical cycles of nitrogen, phosphorus, carbon, and sulfur in soil, thereby underpinning the long-term sustainability of agroecosystems (44, 45). Through organic matter decomposition, nutrient mineralization, and soil aggregate formation, these microorganisms not only improve soil fertility but also contribute to carbon sequestration, mitigating the effects of climate change (1, 33).

Understanding the ecological and evolutionary dynamics of the plant microbiome reveals that these microbial communities are not static systems but are continuously shaped and adapted to environmental conditions through host selection, dispersal, diversification, and genetic drift (4, 5). This ecological and evolutionary flexibility enables plants to rapidly adapt to new environmental stresses such as drought, salinity, and climate change through their associated microbiome (34, 49). This hologenomic perspective has transformed our understanding of plant evolution and their capacity to cope with environmental challenges, opening new horizons for plant breeding and agroecosystem management (5, 8). However, modern agricultural practices such as excessive use of chemical fertilizers, intensive tillage, and monoculture have had detrimental effects on microbiome diversity and function, leading to the phenomenon of "domestication footprints on microbial diversity," which poses serious challenges to agricultural sustainability (51, 46, 44).

Rapid advances in omics technologies (metagenomics, metatranscriptomics, metabolomics), artificial intelligence, and genome editing herald a future in which we can purposefully engineer and manage microbiomes to reduce dependence on chemical inputs, combat climate change, and ensure food security for a growing global population (6, 57, 58). The design of synthetic communities (SynComs) based on ecological principles such as synergy, competition, and niche partitioning represents one of the most promising approaches in this field. By considering ecological stability and evolutionary flexibility, SynComs can offer effective and sustainable solutions for disease management, nutrient acquisition, and stress tolerance enhancement (37, 38, 39). Despite significant challenges in commercialization and field application—including variable performance under real-world conditions, competition with native microbes, the need for appropriate formulation, and regulatory barriers—it appears that the transition from chemistry-based to biology-based agriculture, with microbiomes at its core, is not only possible but imperative (35, 60, 41). Ultimately, realizing this vision requires synergy among scientists, farmers,

industry, and policymakers to adopt microbiome-aware management strategies and establish supportive regulatory frameworks, thereby taking effective steps toward sustainable food security and the conservation of natural resources for future generations (3, 42, 61).

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References

1. IPCC (Intergovernmental Panel on Climate Change). Climate Change 2025: Impacts, Adaptation and Vulnerability. Cambridge University Press. 2025.
2. Compant S, Cassan F, Sessitsch A. Harnessing the plant microbiome for sustainable crop production. *Nature Reviews Microbiology*. 2025;23(1):1-16. DOI: 10.1038/s41579-024-01079-1
3. Pedrinho A, Mendes LW, Pellegrinetti TA, et al. Integrating plant microbiome for resilient agriculture and a sustainable environment. *Plant and Soil*. 2026. DOI: 10.1007/s11104-026-08578-5
4. Fierer N. Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology*. 2017;15(10):579-590. DOI: 10.1038/nrmicro.2017.87
5. Kouas S, Khan N, Hirsch AM. The Hologenome Hypothesis and Its Application to Plant-Microbe Interactions on an Evolutionary Scale. In: Hurst CJ, editor. *Microbes: The Foundation Stone of the Biosphere*. Springer. 2021. DOI: 10.1007/978-3-030-63512-1_21
6. Kumar U, Raj S, Sreenikethanam A, Maddheshiya R, Kumari S, Han S, et al. Multi-Omics Approaches in Plant-Microbe Interactions Hold Enormous Promise for Sustainable Agriculture. *Agronomy*. 2023;13(7):1804. DOI: 10.3390/agronomy13071804
7. Mmotla K, Sibanyoni NR, Allie F, et al. Exploring the intricacies of plant growth promoting rhizobacteria interactions: an omics review. *Annals of Microbiology*. 2025;75:5. DOI: 10.1186/s13213-025-01793-y
8. Zhang J, Liu W, Wang B, Zhai Q, Bai Y. Plant microbiome regulation for sustainable agriculture. *Current Opinion in Biotechnology*. 2026;98:103444. DOI: 10.1016/j.copbio.2026.103444
9. Mendes R, Garbeva P, Raaijmakers JM. The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiology Reviews*. 2013;37(5):634-663. DOI: 10.1111/1574-6976.12028
10. Li J, Wang B, Ma H, Yang X, Wang T, Zhou G. Root exudates drive plant-microbiome interactions influencing

- the quality of cultivated *Rheum tanguticum* during different growth development stages. *Industrial Crops and Products*. 2025;237:122157. DOI: 10.1016/j.indcrop.2025.122157
11. Tong Y, Zheng X, Hu Y, Wu J, Liu H, Deng Y, et al. Root exudate-mediated plant-microbiome interactions determine plant health during disease infection. *Agriculture, Ecosystems & Environment*. 2024;370:109056. DOI: 10.1016/j.agee.2024.109056
 12. Wang L, Chen M, Lam PY, et al. Multifaceted roles of flavonoids mediating plant-microbe interactions. *Microbiome*. 2022;10:233. DOI: 10.1186/s40168-022-01420-x
 13. Kumawat KC, Sharma B, Nagpal S, Kumar A, Tiwari S, Nair RM. Plant growth-promoting rhizobacteria: Salt stress alleviators to improve crop productivity for sustainable agriculture development. *Frontiers in Plant Science*. 2023;13:1101862. DOI: 10.3389/fpls.2022.1101862
 14. Shi Y, Yang H, Chu M, Niu X, Bao H, Wang N, et al. Plant Microbiome and Mycorrhizal Fungi. In: *Arbuscular Mycorrhizal Fungi in Agriculture - New Insights*. IntechOpen. 2023. DOI: 10.5772/intechopen.107373
 15. Smith SE, Read DJ. *Mycorrhizal Symbiosis*. 5th ed. Academic Press. 2024. DOI: 10.1016/B978-0-12-652840-4.X5000-1
 16. Rangel LI, Leveau JHJ. Applied microbiology of the phyllosphere. *Applied Microbiology and Biotechnology*. 2024;108:211. DOI: 10.1007/s00253-024-13042-4
 17. Sivakumar N, Sathishkumar R, Selvakumar G, Shyamkumar R, Arjunekumar K. Phyllospheric Microbiomes: Diversity, Ecological Significance, and Biotechnological Applications. *Plant Microbiomes for Sustainable Agriculture*. 2020;25:113-172. DOI: 10.1007/978-3-030-38453-1_5
 18. Sarver E, González-Morelo KJ, Christensen KG, et al. Phyllosphere synthetic microbial communities: a new frontier in plant protection. *BMC Plant Biology*. 2025;25:949. DOI: 10.1186/s12870-025-06935-7
 19. White JF, Kingsley KL, Zhang Q, Verma R, Obi N, Dvinskikh S, et al. Review: Endophytic microbes and their potential applications in crop management. *Pest Management Science*. 2019;75:2558-2565. DOI: 10.1002/ps.5527
 20. Morales-Cedeño LR, Orozco-Mosqueda MC, Loeza-Lara PD, Parra-Cota FI, de los Santos-Villalobos S, Santoyo G. Plant growth-promoting bacterial endophytes as biocontrol agents of pre- and post-harvest diseases: Fundamentals, methods of application and future perspectives. *Microbiological Research*. 2021;242:126612. DOI: 10.1016/j.micres.2020.126612
 21. Nelson EB. The seed microbiome: Origins, interactions, and impacts. *Plant and Soil*. 2018;422:7-34. DOI: 10.1007/s11104-017-3289-7
 22. Qi X, Jin D, Olimi E, et al. What do we know about the seed microbiome? *Microbiome*. 2026;14:106. DOI: 10.1186/s40168-026-02390-0
 23. Truyens S, Weyens N, Cuypers A, Vangronsveld J. Bacterial seed endophytes. *Environmental Microbiology Reports*. 2015;7:40-50. DOI: 10.1111/1758-2229.12181
 24. Singh P, Vaishnav A, Liu H, Xiong C, Singh HB, Singh BK. Seed biopriming for sustainable agriculture and ecosystem restoration. *Microbial Biotechnology*. 2023;16:2212-2222. DOI: 10.1111/1751-7915.14322
 25. Maróti G, Kondorosi É. Nitrogen-fixing *Rhizobium-legume* symbiosis: are polyploidy and host peptide-governed symbiont differentiation general principles of endosymbiosis? *Frontiers in Microbiology*. 2014;5:326. DOI: 10.3389/fmicb.2014.00326
 26. Ahmed E, Holmström SJ. Siderophores in environmental research: roles and applications. *Microbial Biotechnology*. 2014;7(3):196-208. DOI: 10.1111/1751-7915.12117
 27. Spaepen S, Vanderleyden J. Auxin and plant-microbe interactions. *Cold Spring Harbor Perspectives in Biology*. 2011;3(4):a001438. DOI: 10.1101/cshperspect.a001438
 28. Roca A, Gorts J, Matilla MA. Bacterial auxin catabolism as a driver of plant growth promotion and rhizosphere colonization fitness. *Microbiological Research*. 2026;305:128431. DOI: 10.1016/j.micres.2025.128431
 29. Gupta A, Bano A, Rai S, Kumar M, Ali J, Sharma S, et al. ACC deaminase producing plant growth promoting rhizobacteria enhance salinity stress tolerance in *Pisum sativum*. *3 Biotech*. 2021;11(12):514. DOI: 10.1007/s13205-021-03047-5
 30. Raaijmakers JM, Mazzola M. Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annual Review of Phytopathology*. 2012;50:403-424. DOI: 10.1146/annurev-phyto-081211-172908
 31. Bakker PAHM, Doornbos RF, Zamioudis C, Berendsen RL, Pieterse CMJ. Induced systemic resistance and the rhizosphere microbiome. *The Plant Pathology Journal*. 2013;29(2):136-143. DOI: 10.5423/PJP.SI.07.2012.0111
 32. Pieterse CM, Zamioudis C, Berendsen RL, Weller DM, Van Wees SC, Bakker PA. Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*. 2014;52:347-375. DOI: 10.1146/annurev-phyto-082712-102340
 33. Afkhami ME, Classen AT, Dice CG, Hernandez DJ, Li VW, Rawstern AH, et al. Unraveling complexity in climate change effects on beneficial plant-microbe interactions: mechanisms, resilience, and future directions. *The New Phytologist*. 2026;249(1):93-113. DOI: 10.1111/nph.70644
 34. Zeng Q, Hu HW, Ge AH, Xiong C, Zhai CC, Duan GL, et al. Plant-microbiome interactions and their impacts on plant adaptation to climate change. *Journal of Integrative Plant Biology*. 2025;67:826-844. DOI: 10.1111/jipb.13863
 35. Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, et al. Plant Growth-Promoting

- Rhizobacteria: Context, Mechanisms of Action, and Roadmap to Commercialization of Biostimulants for Sustainable Agriculture. *Frontiers in Plant Science*. 2018;9:1473. DOI: 10.3389/fpls.2018.01473
36. Heintz-Buschart A, Guerra C, Djukic I, Cesarz S, Chatzinotas A, Patoine G, et al. Microbial diversity-ecosystem function relationships across environmental gradients. *Research Ideas and Outcomes*. 2020;6:e52217. DOI: 10.3897/rio.6.e52217
37. Sun X, Xia R, Xie J, et al. Cooperative Interactions Between *Bacillus* and *Lysobacter* Enhance Consortium Stability and *Fusarium* Wilt Suppression in Cucumber. *Microbial Ecology*. 2025;88:92. DOI: 10.1007/s00248-025-02592-3
38. Wang Z, Wang S, He Q, Yang X, Zhao B, Zhang H, et al. Ecological design of high-performance synthetic microbial communities: from theoretical foundations to functional optimization. *ISME Communications*. 2025;5(1):ycaf133. DOI: 10.1093/ismeco/ycaf133
39. Xu X, Dinesen C, Pioppi A, Kovács ÁT, Lozano-Andrade CN. Composing a microbial symphony: synthetic communities for promoting plant growth. *Trends in Microbiology*. 2025;33(7):738-751. DOI: 10.1016/j.tim.2025.01.006
40. San León D, Nogales J. Toward merging bottom-up and top-down model-based designing of synthetic microbial communities. *Current Opinion in Microbiology*. 2022;69:102169. DOI: 10.1016/j.mib.2022.102169
41. Copeland C, Schulze-Lefert P, Ma KW. Potential and challenges for application of microbiomes in agriculture. *The Plant Cell*. 2025;37(8):koaf185. DOI: 10.1093/plcell/koaf185
42. Panek J, Gryta A, Maj W, Mącik M, Oszust K, Pertile G, et al. Plant–soil–microbiome interactions: mechanisms, advances, and challenges in sustainable agriculture and healthy agroecosystems. *Frontiers in Microbiology*. 2026;17:1762743. DOI: 10.3389/fmicb.2026.1762743
43. Ribeiro RC, Matos JPC, Martins DVdS, et al. Microbial inoculants and root microbiome: a path to sustainable agroecosystem management. *npj Sustainable Agriculture*. 2026;4:51. DOI: 10.1038/s44264-026-00164-7
44. Geisseler D, Scow KM. Long-term effects of mineral fertilizers on soil microorganisms – A review. *Soil Biology and Biochemistry*. 2014;25:54-63. DOI: 10.1016/j.soilbio.2014.03.023
45. Muhammad W, Yu X, Wu J, Yang X, Mo Y, Luo Q, et al. A global meta-analysis reveals coupled biogeochemical and microbial successional trajectories in forest soils. *Forest Ecosystems*. 2026;16:100442. DOI: 10.1016/j.fecs.2026.100442
46. Venter ZS, Jacobs K, Hawkins HJ. The impact of crop rotation on soil microbial diversity: A meta-analysis. *Pedobiologia*. 2016;59:215-223. DOI: 10.1016/j.pedobi.2016.04.001
47. Han J, Zhang Y, Xi H, Mao L, Fang Z, Li C, et al. Agricultural management shapes soil multitrophic communities and biodiversity-ecosystem function relationships in a dryland agroecosystem. *Agriculture, Ecosystems & Environment*. 2026;409:110523. DOI: 10.1016/j.agee.2026.110523
48. Sui J, Wang C, Hou F, Shang X, Zhao Q, Zhang Y, et al. Effects of Deep Tillage on Rhizosphere Soil and Microorganisms During Wheat Cultivation. *Microorganisms*. 2024;12(11):2339. DOI: 10.3390/microorganisms12112339
49. Haider S, Munyaneza V, Zhang W, Ren L, Song H, Ahmad IA, et al. Plant-microbe interactions under drought stress: Unlocking new pathways for sustainable agricultural resilience. *Microbiological Research*. 2026;309:128516. DOI: 10.1016/j.micres.2026.128516
50. Sharma A, Das N, Pandey P, Shukla P. Plant-microbiome responses under drought stress and their metabolite-mediated interactions towards enhanced crop resilience. *Current Plant Biology*. 2025;43:100513. DOI: 10.1016/j.cpb.2025.100513
51. Berg G, Raaijmakers JM. Domestication leaves footprints of microbial diversity. *The ISME Journal*. 2018;12(5):1167-1170. DOI: 10.1038/s41396-017-0028-2
52. Dubey A, Malla MA, Vimal SR, et al. Plant-microbiome engineering: synergistic microbial partners for crop health and sustainability. *Plant Growth Regulation*. 2025;105:1825-1839. DOI: 10.1007/s10725-025-01385-5
53. Panchal K, Sudhir A, Prajapati AS. Engineering the plant microbiome: synthetic community approaches to enhance crop protection. *Frontiers in Plant Science*. 2026;16:1705289. DOI: 10.3389/fpls.2025.1705289
54. Prigigallo MI, Gómez-Lama Cabanás C, Mercado-Blanco J, Bubici G. Designing a synthetic microbial community devoted to biological control: The case study of *Fusarium* wilt of banana. *Frontiers in Microbiology*. 2022;13:967885. DOI: 10.3389/fmicb.2022.967885
55. Zheng L, Zheng Q, Zhang T, Duan K, Zhang R. Engineering rhizosphere synthetic microbial communities to enhance crop nutrient use efficiency. *Synthetic Biology Journal*. 2025;6(5):1058-1071. DOI: 10.12211/2096-8280.2025-075
56. Liu S, Wang S, Zhang J, et al. Host-guided microbiome-metabolite interactions enable cross-kingdom SynComs for disease suppression. *Microbiome*. 2026. DOI: 10.1186/s40168-026-02430-9
57. Ma J, Qiao J, Cao Y, Cheng Z. Harnessing artificial intelligence to decode the rhizosphere microbiome. *aBIOTECH*. 2026;7:100005. DOI: 10.1016/j.abiote.2025.100005
58. Barrangou R, Doudna JA. Applications of CRISPR technologies in research and beyond. *Nature Biotechnology*. 2016;34(9):933-941. DOI: 10.1038/nbt.3659
59. Gehlot P, Yadav J, Meena P, Soni P, Jain T. Genomic insights into plant-microbe interactions. *Current Plant Biology*. 2025;42:100409. DOI: 10.1016/j.egg.2025.100421

60. Patil P, Sarkar A. New Strategies for Commercialization of Microbial Technologies. In: Soni R, Suyal DC, Bhargava P, Goel R, editors. *Microbiological Activity for Soil and Plant Health Management*. Springer. 2021. DOI: 10.1007/978-981-16-2922-8_23

61. Anas M, Falak A, Khattak WA, Soylu S, Iqbal J, Abbasi BA. Regulatory Frameworks and Policy Implications for Next-Generation Fertilizers. In: Fahad S, Saud S, Nawaz T, Fiaz S, Munir I, editors. *Next-Generation Fertilizers for Sustainable Agricultural Practices and Food Security*. Wiley. 2026. DOI: 10.1002/9781394383375.ch12