Review

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Review paper

Plant-Microbe Interactions in the Rhizosphere and the Role of Root Exudates in Chemical Signaling and Microbiome Engineering

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Abstract: Microbial interactions within the rhizosphere are fundamental to plant health, influencing nutrient availability, stress tolerance, and pathogen resistance. Beneficial microbes, such as plant growth-promoting microbes (PGPM) including bacteria and mycorrhizal fungi, enhance plant resilience through mechanisms like nutrient solubilization, phytohormone production, and pathogen suppression via antimicrobial compounds and siderophores. Root exudates, composed of sugars, organic acids, and secondary metabolites, act as chemoattractants that shape the rhizosphere microbiome by recruiting beneficial microbes. Stress conditions alter exudate composition, enabling plants to attract specific microbes that aid in stress mitigation. The dynamic interactions between plants and microbes are central to sustainable agriculture, as they can reduce dependency on chemical fertilizers and pesticides. Advancements in microbiome engineering have led to the development of synthetic microbial communities (SynComs) tailored to enhance plant productivity and disease resistance. Recent studies have highlighted the potential of engineered microbiomes to establish stable, beneficial microbial consortia that support plant growth under diverse environmental conditions. This review will discuss the role of microbial interactions in plant health, the influence of root exudates on microbiome composition, and the emerging potential of SynComs in optimizing plant-microbe associations for sustainable agriculture.

Keywords: Rhizosphere; Root exudates; Chemical signaling; SynComs; Microbial engineering

1. Introduction

Climate change is increasingly threatening the ecosystem, agriculture, and global food security [1]. Rising temperatures, extreme weather events, water scarcity, and the depletion of natural resources are placing unprecedented pressure on agricultural systems [2]. Farmers have aimed to address agriculture's challenges through chemical fertilizers, pesticides, monocultures, and genetically modified crops. While these practices are often effective in the short term, they have contributed to soil degradation and erosion, loss of biodiversity, the development of pest and disease resistance, and undermining long-term sustainable systems [3]. Ensuring resilient agricultural systems moving into the future will require more than a singular focus on increasing yields [4]. The future of food security depends on the crop's ability to continue to thrive in such conditions, a priority for farmers, policymakers, consumers, and researchers alike.

Soil health plays a critical role in this shift. The plant roots and soil microorganisms' interactions, particularly in the rhizosphere, are a key factor in mitigating stressors that impact plant health and productivity [5]. The term "rhizosphere" was coined by German agronomist Lorenz Hiltner in 1904, describing the soil zone immediately surrounding the plant root, teeming with microorganisms influenced by chemicals released by roots [6]. Over a century of research has deepened our understanding of the rhizosphere and aimed to further define these root exudates and how they interact with and influence the soil microbiota. Sugars, organic acids, and secondary metabolites, synthesized and released into the soil through plant roots, influence the soil environment and act as a chemoattractant [7]. These chemical signals facilitate mutualistic relationships between plants and beneficial microorganisms, including plant-growth promoting bacteria (PGPB) and mycorrhizal fungi. These plant-microbe interactions can reduce the effects of biotic and abiotic stressors, increase nutrient uptake, and ultimately increase the resiliency of plants [8].

In recent years, microbiome engineering has emerged as a promising approach to enhancing plant-microbe interactions and improving agricultural outcomes. Fertilizing plants with beneficial microbes' dates to the late 18th century, although the first commercial biofertilizer was released in 1895 [9]. The term "SynCom", referring to synthetic microbial communities, was first employed in 2019 [10]. Engineering microbial communities are a valuable tool in climate-smart agriculture. By customizing microbial communities to meet the needs of crops in particular environments, SynComs offer a strategy for developing more resilient agricultural systems capable of withstanding the challenges posed by climate change [11].

Despite significant progress in understanding plant-microbe interactions and microbiome engineering, there remain avenues for further research and field testing. Further studies are needed to refine our understanding of root exudates and the role of soil microorganisms in plant stress mitigation. Identifying the most beneficial microbial strains for particular cultivars and environments, as well as the long-term effects of engineering microbial communities on ecosystem stability, is a critical step forward.

2. Search Methodology:

To compile relevant literature for this review, a systematic search strategy was employed using multiple academic and research-oriented platforms. Primary sources were identified through databases including PubMed, Scopus, and ScienceDirect, using combinations of keywords such as "plant-microbe interactions," "root exudates," "synthetic microbial communities," "rhizosphere microbiome," "plant stress tolerance," and "microbiome engineering." Boolean operators (AND, OR) were applied to refine and broaden searches where necessary. To improve readability and clarity, select sections of the draft were restructured using an AI-powered language platform, which assisted in refining grammar, enhancing coherence, and maintaining an academic tone without altering the original meaning or content. Only peer-reviewed articles, conference proceedings, and credible reviews published in English between [2020] and [2025] were considered, with supporting referencing to seminal papers across all dates. Studies were selected based on relevance, scientific rigor, and contribution to the current understanding of microbiome-driven plant responses.

3. Microbial Interactions in Plant Microbiomes

3.1. Composition and Dynamics of Microbial Communities in the Rhizosphere and Endosphere

The plant microbiome is a community of microorganisms that live in and around plants, forming a dynamic microbial ecosystem [12]. Like the human microbiome, it plays a crucial role in supporting its host by interacting with the surrounding soil, air, and water. Plant-associated microorganisms include bacteria, fungi, viruses, and some algae, and these are found in all plant tissues. Microbe-microbe and microbe-plant interactions occurring from the microbial presence in plants are involved in regulating plant health and vigor [13].

The plant microbiome is divided into three main domains- endosphere, rhizosphere, and phyllosphere. The endosphere consists of microorganisms living inside plant tissues, either within or between cells [14], and includes the plant's vasculature and seeds. The phyllosphere consists of microbes that inhabit the plant's aerial parts, such as leaves and stems [15]. The rhizosphere is the region in the soil surrounding the plant's roots, where microbes interact closely with plant and soil components [6]. The microbes survive within the plant as endophytes or on outer surfaces as epiphytes [16], and colonization involves the formation of biofilms of different genera and species. The composition of a plant's microbiome is influenced by factors such as species, age, health, genetics, and soil conditions. Even two plants of the same species can host different microbial communities based on their environment [17–19]. These microbial colonization zones differ in environmental factors, such as nutrient sources from the plant's metabolites and exposure to environmental conditions [20–22]. These variations partly explain the differences in microbial composition, diversity, and abundance between the different plant habitats.

3.2. The Rhizosphere: A Hotspot for Microbial Activity with the Plant

The rhizosphere is the zone around plant roots where complex microbial communities inhabit the rhizoplane and soil particles because of the nutritional values of root-released metabolites [6]. The rhizosphere is enriched with organic materials of high and low molecular weight from the plant and products from microbes and other fauna in this space (e.g., nematode and larval waste products). Certain compounds in root exudates, such as sugars, amino acids, and organic acids, serve not only as chemoattractants that draw soil microbes to the root but also support microbiome formation [23]. The rhizosphere microbial density, up to 10^{12} cells/g soil, and diversity, up to 30,000 distinct prokaryote species, is orders of magnitude higher than the surrounding bulk soil [24,25]. Within the rhizosphere, microbes intensively compete for space, water, and nutrition. Plants may allocate up to 40% of their photosynthetically derived carbon as exudates into the rhizosphere, consisting primarily of various compounds such as amino acids, complex sugars, and organic acids [26]. Increased availability of nutrients through the dissolution of minerals in the soil promotes the growth of both microbes and the plant host [27–30]. Plant growth also may be enhanced by microbial volatiles such as butanediol [27,31,32]. The production of auxins and cytokines or the control of ethylene levels can further dictate plant morphology and growth [33].

The rhizosphere's chemical variety includes factors that regulate the morphology and function of both the plant and the microbes. Cell signaling factors that govern biofilm formation for the microbes are important. This vital structure offers high survival value to several stresses. Rhizosphere communication can be classified into three major types: microbe-to-microbe, plant-to-microbe, and microbe-to-plant signaling.

Microbe-to-Microbe Signaling: Microorganisms communicate via quorum sensing (QS), using autoinducers like N-acyl homoserine lactones (AHLs) in Gram-negative bacteria and peptides in Gram-positive species [34]. QS regulates biofilm formation, chemotaxis, and virulence, facilitating coordinated microbial behavior [35]. Additionally, volatile organic compounds (VOCs), like alkanes, ketones, alkene, terpenoids, and sulfurs [36], and inorganic compounds (VICs), like nitric oxide (NO), hydrogen sulfide (H_2S), ammonia, hydrogen cyanide (HCN), and carbon dioxide (CO_2) [37], mediate long-distance interactions. However, their perception by microbial cells remains poorly understood [38]. Other signaling molecules, such as trehalose and thiamine, play roles in microbial symbioses, promoting survival in nutrient-limited environments [39].

Plant-to-Microbe Signaling: Plants release diverse root exudates, including flavonoids, strigolactones, and organic acids, which shape microbial communities and facilitate beneficial interactions [40]. For instance, strigolactones stimulate mycorrhizal colonization under nutrient deficiency [41], while flavonoids in legume exudates promote rhizobial infection and nitrogen fixation [42]. These signaling compounds also influence nutrient cycling, promoting phosphorus solubilization and microbial chemotaxis.

Microbe-to-Plant Signaling: Rhizosphere microbes impact plant development, immunity, and stress responses through microbe-associated molecular patterns (MAMPs), QS molecules, and phytohormone production [43,44]. MAMPs, such as lipopolysaccharide, peptidoglycans, flagellin, and chitin, stimulate the systemic development of tolerance to abiotic and biotic stresses in the plant [45]. Beneficial microbes induce systemic resistance (ISR) and modulate plant hormonal balance, enhancing to biotic and abiotic stress tolerance. Additionally, microbial VOCs can promote plant growth and nutrient uptake [46], though the underlying mechanisms require further study.

3.3. Key Roles of Beneficial Microbes in Maintaining Plant Health

Plant-associated microorganisms influence plant growth in various ways and can be categorized as beneficial, deleterious, or neutral based on their interactions with the host [47]. Among these, plant growth-promoting microorganisms (PGPM) play a crucial role in enhancing plant health and development [48–51] (Figure 1). The majority of beneficial microbes are bacteria, commonly referred to as plant growth-promoting rhizobacteria (PGPR), which colonize plant roots and support growth through various direct and indirect mechanisms [52,53]. First introduced by Kloepper et al. (1978) [54], PGPR includes free-living, symbiotic, and endophytic bacteria that facilitate plant growth. These microbes can be further classified into symbiotic PGPR, such as *Rhizobium* and *Frankia*, which establish mutualistic associations with plants, and free-living PGPR, like *Pseudomonas* and *Bacillus*, which inhabit the rhizosphere without forming specialized structures [55]. In addition to PGPR, other beneficial microbes, including arbuscular mycorrhizal fungi (AMF) and rhizobia, contribute to plant health by improving nutrient uptake and stress tolerance [56,57], with AMF soil amendments commercially available. These microbes interact in various ways, ranging from antagonism to mutualism, with some species exhibiting positive co-occurrence while others display negative co-occurrence patterns [58,59].

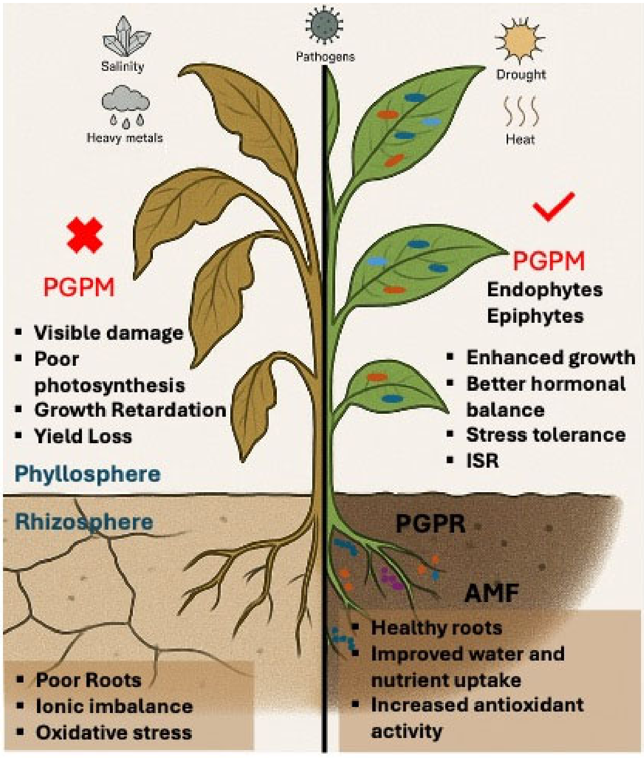

Figure 1. Contrasting plant health outcomes in the presence and absence of beneficial microbes in response to biotic and abiotic stressors. PGPM – Plant Growth Promoting Microorganisms, PGPR – Plant Growth Promoting Rhizobacteria, AMF – Arbuscular Mycorrhizal Fungi, ISR – Induced Systemic Resistance .

PGPR promote plant growth through direct mechanisms, including nitrogen fixation, phosphate solubilization, and the production of phytohormones such as auxins, gibberellins, and cytokinin [60–63]. Some PGPR enhance nutrient availability by secreting siderophores that chelate iron, making it more accessible to plants [64,65]. Additionally, these beneficial microbes modulate root architecture, enhance water uptake, and help plants cope with abiotic stress factors like salinity, drought, and heavy metals by producing osmoprotectants and antioxidant enzymes [57]. Well-documented plant-beneficial rhizosphere microbiomes include rhizobia symbiosis, which provides nitrogen, and mycorrhizal associations, which facilitate phosphorus acquisition [66,67]. Several biotic and abiotic factors, such as temperature, soil moisture, pH, root exudate composition, and mineral concentrations, significantly influence the interaction between rhizobacteria and plant roots, thereby affecting colonization efficiency [68].

Apart from direct benefits, PGPR and other beneficial microbes contribute to plant health through indirect mechanisms by suppressing pathogens and inducing plant defense responses [69,70]. These microbes compete with phytopathogens for nutrients and space, produce antimicrobial compounds, and activate ISR in plants. Some PGPR synthesizes lipopeptides and antibiotics that inhibit pathogen growth or disrupt quorum-sensing signals essential for virulence [45]. Additionally, PGPRs volatile organic compounds (VOCs) enhance plant immunity and promote systemic resistance [71]. The colonization process of PGPR follows four key steps: (i) chemotactic signal recognition, (ii) attachment to the root surface, (iii) evasion of plant immune defenses, and (iv) biofilm formation on the root surface [72]. These microbes can also establish biofilm-like structures composed of multi-bacterial communities in the rhizosphere, further strengthening plant-microbe interactions and enhancing plant resilience and productivity.

4. Role of PGPR in Stress Management

PGPR are essential in enhancing plant resilience to both abiotic and biotic stresses [73]. Recent studies have highlighted the diverse plant-microbe interactions and their importance in nutrient acquisition, hormone signaling, pathogen inhibition, and more. These beneficial rhizospheric plant-bacteria interactions are increasingly recognized as a critical component of sustainable stress management in agricultural systems [74].

In biotic stress, PGPR can help suppress the negative impacts of weeds, pathogens, and pests [75–77]. PGPRs exert biocontrol by competing with pathogenic microbes for root interaction sites and nutrients, effectively reducing the number of pathogens by releasing secondary metabolites such as antibiotics that inhibit the growth of other bacteria and fungi [78]. Beyond direct antagonism, PGPR can also induce systemic resistance in plants. It occurs when rhizobacteria mimic pathogen-associated molecular patterns (PAMPs), effectively priming the plant's immune system for a heightened response without the cost of a full immune response [79,80]. It can enhance defenses without depleting energy stores and reducing plant growth. The process of ISR involves PGPR triggering plant immune responses through recognition of microbial cell surface elements or metabolites that resemble PAMPs, leading to faster and stronger defense reactions upon subsequent pathogen attack [81].

PGPR also offers significant advantages in mitigating the impacts of abiotic stresses on plants [82]. As Earth's climate warms and weather patterns shift, drought is an increasing risk to agriculture [83]. PGPR helps mitigate the effects of drought by influencing the rate of water uptake through the roots, inducing gene expressions, producing biofilms that reduce water loss, and influencing the production of plant hormones to enhance water use efficiency [84]. Flooding, on the other hand, has a significant impact on the rhizobacteria community, while PGPR can increase flood tolerance by reducing ethylene content in the soil and improving soil aeration, structure, and permeability [85]. Extreme temperatures also pose a significant threat to agricultural productivity, while PGPR can induce thermotolerance by improving growth through plant hormone production, increasing nutrient acquisition, and increasing plant biomass [86]. PGPR can increase cold tolerance through mechanisms that control defense responses and accelerate cell division [87]. Irrigation practices increase soil salinity and reduce plant productivity. Bacteria in these soils adapt more rapidly than plants under this evolutionary pressure, producing osmoregulators that have knock-on benefits to host plants [88]. These actions collectively improve plant vigor under stress conditions (Figure 2).

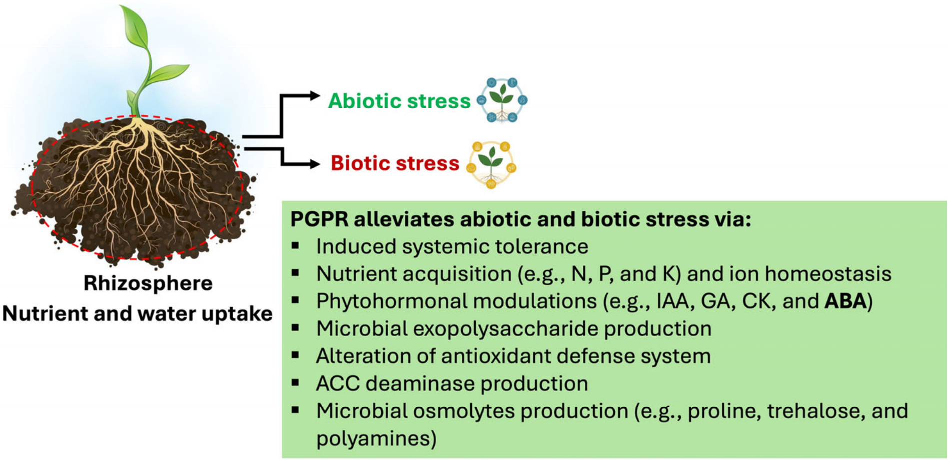

Figure 2. Mechanisms of PGPR to alleviate abiotic and biotic stress. IAA: Indole-3-acetic acid, GA: Gibberellins, CK: Cytokinin, ABA: Abscisic acid, ACC: 1-amino-cyclopropane-1-carboxylic acid**.**

5. Role of Root Exudations in Rhizospheric Microbial Interactions

Root exudates play a pivotal role in shaping the composition and function of soil microbial communities by providing a diverse array of organic compounds, such as sugars, amino acids, and organic acids, which serve as nutrient sources and signaling molecules for soil microbes [89,90]. The chemical composition of these exudates determines their specific effects on microbial community structure; for example, carboxylic acids can increase the prevalence of *Actinobacteria* and facilitate carbon mobilization, while amino acids may favor *Proteobacteria* and influence dissolved organic carbon dynamics [89]. The addition of root exudates has been shown to shift bacterial and fungal community structures, often promoting fast-growing, copiotrophic taxa and altering microbial diversity, with some exudate types (like sugars) reducing diversity while still driving significant compositional changes [91–94]. Root exudate diversity is a crucial factor, as higher exudate diversity can enhance soil microbial biomass and diversity, sometimes negating the effects of plant diversity on microbial properties [95]. Plants dynamically adjust their exudation patterns daily and throughout different growth stages, tailoring microbial recruitment to meet changing nutrient demands and optimize plant growth [96].

Furthermore, root exudates influence the rhizosphere and the bulk soil, stimulating the growth of beneficial bacteria such as *Paenarthrobacter* and rhizobia and causing shifts in alpha and beta diversity over time [93]. Environmental factors, such as temperature and soil type, modulate the impact of root exudates on microbial communities, with exudates and temperature shaping microbial diversity, community structure, and network dynamics [91,97,98]. These interactions can also affect biogeochemical processes, such as carbon and nutrient cycling, and even the mobility of elements like arsenic in paddy soils by altering the abundance of specific microbial functional groups [89,94,97]. In summary, as first documented by Lorenz Hiltner in 1904, root exudates are key drivers of soil microbial community assembly and function; more recent studies have systematically categorized root exudates and resulting microbial composition, diversity, and environmental context, which collectively determine the structure and metabolic potential of the soil microbiome as overview in Table 1.

Table 1. Summary of Root Exudate Functions, Chemical Classes, and Effects on Plant-Microbe Interactions.

Role/Function of Root Exudates	Chemical classes involved	Microbiome Engineering/ Signaling Mechanism	Impact on Microbiome or Plant Health	References
Modulate rhizosphere microbiota under stress	Carbohydrates, phenolics, organic acids, amino acids, proteins, polysaccharides	Alter microbial nutrition, quorum-sensing, defense signaling	Enhanced plant-microbe interactions, stress mitigation	[99]
Systemic root-to-root signaling	Acylsugars, glycosylated azelaic acid	SIREM: local microbial colonization triggers systemic exudate changes	Microbiome-driven soil conditioning, altered metabolite exudation	[100]
Link plant hormone signaling to exudate profile	Amino acids (asparagine, ornithine, tryptophan), others	Jasmonic acid pathway alters exudate composition	Shifts in bacterial/archaeal community, defense response modulation	[101]
Interspecific plant interaction	Flavonoids (taxifolin), other exudates	Exudates from one plant recruit beneficial microbes in neighbor	Disease-suppressive microbiome, improved plant fitness	[102]
Allelopathy and nutrient mobilization	Primary and secondary metabolites, allelochemicals	Exudates mediate plant-plant and plant-microbe communication	Microbiome manipulation, targeted disease mitigation	[103]
Influence soil microbial diversity	Organic acids, sugars, phytohormones	Exudate composition shapes microbial membership and function	Altered metabolite production, potential for microbiome management	[94]
Recruitment of beneficial microbiota	Organic acids, chelators, antimicrobials	Modify soil pH, solubilize nutrients, attract PGPR/mycorrhiza	Alleviation of plant stress, improved nutrient uptake	[8]
Manipulation of root microbiome	Malate, citrate, γ-aminobutyric acid	Altered transporter expression changes exudate release	Significant shifts in root microbiome composition	[104]
Initiate and modulate root-microbe dialogue	Various root-secreted chemicals	Signal symbiosis with rhizobia/mycorrhiza, maintain microbial diversity	Evolutionary shaping of soil microbial communities	[7]
Facilitate beneficial rhizobacterial colonization	Organic acids, amino acids, sugars, flavonoids, volatiles	Serve as nutrients, signals, antimicrobials for rhizobacteria	Enhanced colonization, sustainable plant growth and health	[23]

Microbial communities in the rhizosphere engage in cooperative and competitive interactions, with root exudates as a primary driver of these dynamics. Cooperative interactions include mutualistic associations, such as those between PGPR and AMF, which exchange nutrients and metabolites to enhance plant growth, nutrient acquisition, and stress resistance [105–108]. These beneficial microbes often form multi-species biofilms and communicate through signaling molecules like quorum-sensing compounds, coordinating behaviors such as biofilm formation, antibiotic production, and nutrient exchange [106,109]. Conversely, competition arises as microbes compete for limited space, nutrients, and host-derived resources. Root exudates can selectively recruit beneficial microbes while deterring pathogens by releasing antimicrobial or allelopathic compounds, shaping the rhizosphere community in favor of plant health [109–111]. Competitive interactions are further characterized by the production of specialized metabolites, such as lipopeptides and siderophores, which inhibit competitors or restrict their access to essential nutrients [109]. The balance between cooperation and competition is crucial for microbial community stability and plant health. Cooperative networks, including trophic relationships among bacteria, fungi, and protists, enhance community resilience and plant physiological functions, while competitive dynamics can increase resistance to species invasion but may reduce resilience to environmental changes [107,111,112]. Understanding and harnessing these interactions is key to developing sustainable agricultural strategies that promote beneficial microbial consortia and suppress pathogens.

Root exudates are central in fostering microbial consortia that synergistically enhance plant growth, defense, and stress adaptation. Specific compounds in root exudates act as chemical signals, stimulating PGPR to produce phytohormones such as auxins and cytokinins, which directly support plant development and vigor [94,113–115]. Regarding plant defense, root exudates can trigger ISR, where PGPR receiving these exudates in turn stimulate plant immune responses, priming the plant against pathogens and pests. This preemptive activation of defense pathways is a key mechanism by which exudate-driven microbial consortia enhance plant resilience to biotic threats like plant-parasitic nematodes [116]. For example, exudate-mediated recruitment of beneficial bacteria such as *Bacillus* and *Pseudomonas* has been shown to suppress soil-borne pathogens and induce systemic resistance in crops [102,113]. The study shows that root exudates, modulated by treatment with beneficial microbes like *Pseudomonas chlororaphis* PA6, selectively enrich beneficial rhizobacteria such as *Pseudomonas* and *Lactobacillus* [113]. This exudate-mediated recruitment enhances systemic resistance and supports suppression of foliar pathogens like *Botrytis cinerea*, ultimately promoting plant health. As well as [102] study demonstrates that in a tomato-potato-onion intercropping system, root exudates, particularly taxifolin, promote the recruitment of beneficial *Bacillus spp*. in the tomato rhizosphere. These bacteria suppress *Verticillium dahliae* and induce systemic resistance, highlighting exudate-mediated microbiome shaping as a key strategy for disease suppression. Plants also dynamically alter their exudation profiles in response to abiotic stresses like drought and salinity, attracting microbes that confer stress tolerance. For instance, root-secreted flavonoids can recruit AMF that improve water uptake under drought, while certain organic acids in exudates help mitigate metal toxicity in contaminated soils [94,114,117]. The study [117] highlights that root exudates from *Haloxylon* species under drought conditions distinctly shape rhizosphere microbial communities. Specifically, *H. ammodendron* and *H. persicum* differ in exudate composition, sugars, and fatty acids vs. steroids and terpenoids, leading to recruitment of microbial taxa that enhance nutrient cycling and stress resilience, underscoring exudate-mediated microbiome assembly as a key survival strategy in arid environments [117]. The composition and diversity of root exudates are thus crucial in shaping the structure and function of rhizosphere microbial communities, enabling plants to adapt to changing environmental conditions.

Root exudate's chemical composition and secretion rate profoundly influence microbial interactions in the rhizosphere. Different plant species and even genotypes within the same species exude distinct compounds that shape microbial community structure. For example, sorghum genotypes with high-organic-acid or high-sugar exudates foster different soil microbial memberships and metabolic functions, impacting the production of plant-relevant metabolites and phytohormones [94].[96] A study [96] shows that *Arabidopsis thaliana* alters its root exudation over developmental stages to shape soil microbial communities. Fast-growing stage exudates enhanced nutrient mineralization and microbial functional potential more than slow-stage exudates, suggesting plants actively modulate exudates to recruit beneficial microbes that meet their nutrient needs during rapid growth. The concentration of specific compounds, such as sugars and jasmonic acid, has been shown to significantly affect rhizosphere bacterial communities at various plant developmental stages of maize, with different sugars influencing community composition at different times [118]. Root exudates also facilitate microbial succession, where early colonizers modify the rhizosphere environment, paving the way for secondary colonizers with complementary functions [119]. A study [119] reveals that *Avena barbata* follows a developmental program of root exudation, releasing aromatic organic acids, like nicotinic, shikimic, salicylic, cinnamic, and indole-3-acetic, that selectively recruit microbes with matching substrate preferences. This chemically driven interaction guides predictable microbial community assembly, highlighting a plant-regulated mechanism to shape beneficial rhizosphere microbiomes for enhanced fitness. Moreover, through plant-microbe feedback loops systemically alter root exudation patterns through mechanisms such as systemically induced root exudation of metabolites (SIREM), where local microbial colonization triggers changes in exudate composition elsewhere in the root system, further influencing microbial assembly and soil conditioning [100]. Understanding how root exudates influence microbial assembly and function is crucial for developing strategies to enhance plant health and productivity, such as breeding/engineering crops with optimized exudate profiles or manipulating exudate chemistry to promote beneficial microbial consortia and suppress disease.

Chemoattraction is a fundamental mechanism by which root exudates shape rhizospheric microbial communities, as many beneficial microbes use chemotaxis to move toward specific root-derived compounds such as sugars, organic acids, amino acids, and nucleosides, enabling efficient colonization and the establishment of mutualistic interactions [120–123]. For instance, nucleosides in root exudates have been shown to induce strong chemotactic responses in both beneficial bacteria like *Bacillus* and *Pseudomonas* and certain pathogens, highlighting the double edge of chemoattraction in recruiting both helpful and harmful microbes [120]. The specific composition of root exudates, which varies among plant species and even within different root regions, acts as a selective force, guiding the assembly and spatial distribution of microbial communities in the rhizosphere [119,124]. Key attractants such as arginine and other amino acids can be particularly important in establishing microbial community structure, as demonstrated in *Casuarina equisetifolia*, where arginine attracted beneficial strains that closely resembled the natural forest community [121]. Advanced experimental approaches, such as real-time monitoring of chemotaxis and high-throughput sequencing, have revealed that the interplay between chemoattraction, microbial colonization, and plant signaling is central to the dynamic assembly and function of rhizospheric microbial communities, ultimately impacting plant health and ecosystem stability [113,125].

6. Impact of Abiotic and Biotic Stress on Root Exudates

Abiotic and biotic stresses such as drought, salinity, and pathogen attack significantly alter the quantity and composition of root exudates, modulating plant-microbe interactions in the rhizosphere. Under drought and salinity, plants often increase the exudation of osmoprotectants, organic acids, and signaling molecules, which attract beneficial microbes capable of stress mitigation. Microbes such as PGPR, endophytes, and AMF alleviate these stresses through multiple mechanisms: they enhance nutrient uptake, regulate ion homeostasis, and produce phytohormones like abscisic acid, cytokinin, and indole-acetic acid, which help maintain plant growth under adverse conditions [126,127]. Some microbes, such as sulfur-oxidizing bacteria, can reduce toxic ion accumulation and increase antioxidant levels, thereby improving plant tolerance to moderate salinity and drought [128]. This study [128] demonstrates that inoculation with sulfur-oxidizing bacteria (*Halothiobacillus halophilus*) enhances *Plantago coronopus* tolerance to drought and moderate salinity by improving sulfur uptake, reducing toxic ion accumulation, and boosting antioxidant responses. Others, like phosphorus-solubilizing and drought-adaptive microbes, promote the accumulation of osmolytes (e.g., proline, glycine betaine, sugars) and reduce oxidative damage by enhancing antioxidant enzyme activity, leading to improved water retention, photosynthetic efficiency, and reduced lipid peroxidation[129–131]. Microbial exopolysaccharides also play a protective role by improving soil structure and water retention and shielding roots [132]. For biotic stress, beneficial microbes can induce systemic resistance, modulate plant immune responses, and outcompete pathogens for root exudate-derived resources, thereby reducing disease incidence [126]. These microbe-mediated mechanisms alleviate the direct effects of abiotic and biotic stresses and contribute to the dynamic feedback between root exudation patterns and rhizosphere community assembly, ultimately enhancing plant resilience and productivity under challenging environmental conditions [128,133]. Under pathogen attack [18,134], root exudate composition changes significantly, and it is found that these modifications can lead to the recruitment of beneficial microbes like *Pseudomonas* and *Bacillus* [135]. For instance, barley plants grown in split root systems, infected with *Pythium ultimum*, and simultaneously exposed to *P. fluorescens* secrete phenolic-enriched exudates that inhibit fungal spore germination and activate genes related to the production of antibiotics in the bacterium [136].

Abiotic stressors, such as drought, also significantly impact root exudation. Drought increases the root release of abscisic acid (ABA) and organic osmolytes, including proline, glycine betaine (GB), trehalose, and pinitol, which mitigate oxidative stress and influence rhizospheric microbial dynamics [137–139]. These compounds protect plants and shape microbial communities by selectively favoring drought-tolerant bacteria [140]. Investigating the effects of exogenous GB plant treatments on bacterial interactions in the rhizosphere can provide critical insights into how plants adapt their microbiome under water-limited conditions.

The challenge of nutrient acquisition, especially in calcareous soils, is addressed by root exudate components [141] such as carboxylates acting as metal-chelating agents that can sequester toxic metals as well as solubilize nutrients such as P for plant uptake [142]. Rhizobacteria also produce chelates that may broker nutrient transport to the host plant, thus it is increasingly recognized that plants select for their microbiomes. A primary example of this is the secondary metabolite DIMBOA in maize root exudates acting as an allelochemical and a chemoattractant for *P. putida* KT2440 to promote root colonization [143].

The role of root exudates in microbial interactions is well known; however, studying these complex multi-species interactions under controlled conditions remains challenging. The rhizosphere is a highly dynamic and heterogeneous environment where spatial and temporal variations in root exudation patterns affect microbial responses. Traditional in vitro studies fail to replicate the complexity of in situ root-microbe interactions, leading to incomplete or oversimplified conclusions, and synthetic growth media may not fully support the metabolic diversity of rhizospheric microbes, limiting the reproducibility of interactions observed in natural settings. Advanced techniques such as microfluidic platforms, stable isotope probing, and metagenomics are being developed to capture the real-time impact of root exudates on microbial communities. However, integrating these approaches to dissect the functional significance of multi-species interactions remains an ongoing challenge in microbial ecology.

7. Engineering Plant-Microbe Interactions for Sustainable Agriculture

One of the most exciting developments in agricultural microbiology is the construction of SynComs designed to enhance specific plant traits, such as drought tolerance, nutrient use efficiency, and disease resistance. These SynComs are assembled from functionally compatible microbial strains selected based on genomic and phenotypic traits, such as the ability to fix nitrogen, solubilize phosphorus, or produce phytohormones. For instance, PGPR strains like *Bacillus*, *Pseudomonas*, and *Azospirillum* are commonly included in drought-focused SynComs due to their ability to produce osmoprotectants, exopolysaccharides, and ACC deaminase, which modulate plant stress responses [144,145]. Such engineered communities can enhance root development, increase water use efficiency, and maintain photosynthetic activity under water-deficit conditions, when applied to crops.

For example, a SynCom derived from the rhizosphere of the xerophyte *Haloxylon ammodendron* significantly improved maize drought tolerance in both greenhouse and field trials by increasing stomatal conductance, photosynthetic rate, and proline content, while reducing transpiration and modulating stomatal density and xylem structure, with the authors reporting up to a 700% increase in water use efficiency under their test conditions [146]. Similarly, a four-species SynCom (SPMX), *Stenotrophomonas rhizophila*, *Xanthomonas retroflexus*, *Microbacterium oxydans*, and *Paenibacillus amylolyticus*, in Arabidopsis demonstrated that emergent community properties, such as synergistic biofilm formation, were essential for enhanced drought survival, sustained chlorophyll content, and activation of abscisic acid (ABA) signaling, effects not observed with individual strains alone [147]. In maize, SynCom inoculation of naturally occurring, highly abundant bacteria from the sugarcane root and stalk core microbiomes reduced yield loss, lowered leaf temperature, improved turgor maintenance, and accelerated recovery after rehydration, likely through improved sap flow and water usage, while also recruiting additional beneficial microbes from the soil and seed microbiome [148].

In addition to improving drought resilience, engineered SynComs have been shown to influence plant gene expression and hormone signaling pathways, priming the plant for better growth and resistance. For example, transcriptomic analyses in soybean revealed that SynCom application systemically regulates nitrogen and phosphorus signaling networks at the transcriptional level, with significant upregulation of auxin-responsive genes and other growth-related pathways, ultimately leading to increased nutrient acquisition and yield [149]. Advances in high-throughput screening and metagenomics have enabled the functional screening and assembly of SynComs based on their ability to modulate plant signaling and metabolic networks, allowing for the prediction and optimization of microbe-microbe and microbe-host interactions [150]. Metabolomics and RNA-seq approaches have further demonstrated that SynComs can induce broad changes in plant hormone signaling, including auxin, jasmonic acid, and abscisic acid pathways, which are central to plant stress responses and development [151,152]. Importantly, these SynComs are often tailored to the host plant genotype and local soil conditions, as shown by the functional assembly of root-associated microbial consortia that consistently promoted growth and nutrient efficiency across different field sites, highlighting their ecological compatibility and effectiveness[153]. Some of these examples are given in Table 2.

Table 2. Effects of SynComs on Plant Stress Resilience**.**

Crop/Plant Species	Stress Type	SynCom Composition/Source	Observed Effects on Stress Resilience	References
Mesembryanthemum crystallinum / *Medicago sativa* (alfalfa)	Heavy metals (As, Cd, Cu, Zn)	Metal-resistant rhizobacteria & endophytes	Improved growth, physiology, reduced metal accumulation, safe for nutraceutical use	[154]

Neopallasia pectinata	Drought	*Bacillus, Protomicromonospora, Streptomyces*	Enhanced biomass, resistance-related substances under mild/moderate drought, supports restoration	[155]
Maize	Drought	*Pseudomonas* sp. (FUM1, 3, and 6), *Bacillus* sp. (FUM2), and *Peribacillus* sp. (FUM5)	Increased water use efficiency, stomatal conductance, photosynthesis, drought tolerance	[146]
Tomato	Drought	*Bacillus velezensis*, *Pseudomonas spp*., *Glutamicibacter halophytocola*, and *Leclercia sp*.	Improved water stress response, xylem development, altered rhizosphere community	[156]
Maize	Drought	Plant-beneficial SynCom (unspecified)	Reduced yield loss, lower leaf temperature, better turgor, faster recovery, improved productivity	[148]
Banana (Musa acuminata)	Biotic and abiotic	Endophytic SynComs (probiotic)	Increased resilience, growth promotion, potential for sustainable production	[157]
Brachypodium distachyon	Drought	15-member SynCom (5 phyla, rhizobiome-derived)	Enhanced drought resilience, better recovery, osmoprotectant production, root colonization	[158]
Rice	Arsenic (As)	*Pseudomonas sp., Achromobacter sp., Delftia sp., Enterobacter sp., Advenella sp., Flavobacterium sp., Duganella sp., Stenotrophomonas sp., Ochrobactrum sp., Phyllobacterium sp., Comamonas*	Improved growth, antioxidant defense, polyamine metabolism, reduced As toxicity	[159]

sp., Oerskovia sp., *and Rhizobium sp*

8. Potential for Developing Stress-Tolerant Crops via Microbial Inoculants

Microbial inoculants, comprising either single strains or multi-species consortia, represent a sustainable and environmentally friendly alternative to chemical fertilizers and pesticides, as they can promote plant growth and resilience without the ecological drawbacks of agrochemicals [160]. These bioinoculants can be formulated to help crops tolerate various abiotic stresses, including drought, salinity, heavy metal toxicity, and temperature extremes, by enhancing nutrient uptake and improving physiological responses such as photosynthesis and stomatal conductance [161,162]. The ability of microbes to modulate root architecture, improve osmotic balance, and detoxify reactive oxygen species (ROS) enables plants to maintain cellular homeostasis during stress, as seen in tomato plants where microbial inoculation led to improved biochemical stress markers and hormonal profiles under water deficit [161,162]. Furthermore, microbial inoculants often produce phytohormones such as indole-3-acetic acid (IAA), gibberellins, and cytokinins, which regulate growth and development even under suboptimal conditions, supporting plant adaptation and productivity during environmental challenges [162].

In the case of salinity stress, inoculants containing halotolerant PGPR can enhance ion homeostasis by increasing the K^+/Na^+ ratio in plant tissues, as demonstrated in spring mungbean, maize, wheat, and other crops. These inoculants reduce Na^+ accumulation and promote K^+ uptake, improving growth, yield, and stress tolerance [163–166]. In scenarios of cold or heat stress, certain microbes are known to produce protective proteins and enzymes, such as heat shock proteins and antioxidant enzymes, that stabilize cellular structures and mitigate oxidative damage [150,167,168].[169,170] These functional attributes make microbial inoculants a powerful tool for developing climate-resilient agriculture, as they consistently improve plant physiological and biochemical responses to multiple abiotic stresses, including salinity, drought, and temperature extremes [150,171]. Moreover, integrating microbial technologies with advanced breeding strategies or CRISPR-based gene editing in plants holds promise for amplifying the benefits of plant-microbe interactions [172–174]. While direct research on combining these approaches is still emerging, the demonstrated ability of microbial inoculants to modulate stress-responsive genes and physiological pathways suggests strong potential for developing “microbe-smart” crop varieties that are better equipped to respond to environmental challenges [149,175].

9. Challenges and Opportunities in Translating Lab Findings to Field Applications

It is significantly challenging to translate the promising results of engineered microbial inoculants and SynComs from laboratory and greenhouse settings to real-world field applications. Field environments are highly complex and variable, leading to inconsistent performance of introduced microbes compared to controlled conditions. Field conditions differ greatly from lab settings due to variations in soil type, climate, and agricultural practices, all of which influence the establishment, survival, and efficacy of microbial inoculants [176–179]. Native microbial communities in the soil can outcompete or inhibit introduced strains, making it difficult for inoculants to establish and persist as they do in controlled environments [180]. The beneficial effects observed in the lab often do not translate directly to the field, with outcomes varying widely depending on local environmental factors and the presence of indigenous microbes. Microbial interactions in the field are more complex, and competitive or synergistic dynamics may differ from those seen in the lab, leading to unpredictable results. Maintaining the viability and effectiveness of microbial inoculants during storage, transport, and application at scale remains a technical challenge. There is a need for improved formulations and delivery methods to enhance the survival and activity of inoculants in diverse field conditions with integration of metatranscriptomics, a set of techniques used to study gene expression of microbes within natural environments, and other novel techniques [107,181,182]. Co-creating inoculant strategies with farmer input and integrating multidisciplinary approaches can help tailor solutions to specific field conditions, improving adoption and effectiveness. Advances in predictive modeling, smart delivery systems, and the selection of plant genotypes that interact well with beneficial microbes offer promising avenues for overcoming current barriers.

To address these challenges, research increasingly focuses on identifying microbial “core taxa” that are stable across environments and capable of establishing robust associations with the host plant [183]. Adaptive field trials, multi-location experiments, and long-term studies are essential to evaluate the performance and persistence of microbial inoculants under real-world conditions. Also, standardized protocols, improved formulation technologies (e.g., encapsulation and carrier materials), and regulatory frameworks that support bioinoculants commercialization are required. Besides, these various technologies, like microbial engineering with digital agriculture and precision farming, can be integrated to develop microbes for sustainable agriculture. Remote sensing tools, machine learning, and soil microbiome diagnostics can help in site-specific recommendations of microbial products, enhancing their efficacy and adoption. Public-private partnerships, farmer engagement, and interdisciplinary collaborations will be crucial in scaling up microbial technologies and ensuring their alignment with sustainable agricultural practices.

10. Knowledge Gaps and Future Directions

Despite significant advances in understanding plant-microbe interactions in the rhizosphere, several critical knowledge gaps remain. The precise mechanisms by which the rhizosphere microbiome modulates root metabolism and exudation, and how plants fine-tune these complex belowground interactions, are still largely unexplored, particularly regarding long-distance and systemic signaling processes such as SIREM (systemically induced root exudation of metabolites) [100]. The chemical communication that leads to defense priming and induced systemic resistance is not yet fully understood, especially the linkage between below- and above-ground plant physiological processes and the specific metabolites involved in these signaling events [184]. While root exudates are known to play a pivotal role in shaping the rhizosphere microbiome and mediating plant-microbe associations, the diversity and functional specificity of exudate compounds, as well as their roles in microbial recruitment, nutrition, and signaling, require further elucidation [99,185]. Additionally, the initial steps of chemotactic recruitment of beneficial rhizobacteria to root exudates and the identification of key chemoeffectors and their cognate chemoreceptors remain incomplete, limiting our ability to engineer or manipulate these interactions for improved plant health [122]. There is also a need for integrative, multi-omics approaches and advanced imaging technologies to unravel the dynamic and multitrophic interactions within the rhizosphere, and to translate this knowledge into practical strategies for microbiome engineering and sustainable agriculture [186,187].

Future research in plant-microbe interactions within the rhizosphere should focus on unraveling the intricate metabolic and chemical signaling networks that govern root exudate-mediated microbiome assembly and function. Advancements in high-resolution metabolomics, multi-omics integration, and gene-editing technologies will be essential for dissecting the diversity and specificity of root exudate compounds and their roles in recruiting beneficial microbes or deterring pathogens [103,184]. Investigating systemically induced root exudation processes, such as SIREM, and the long-distance signaling mechanisms between roots and shoots will provide deeper insights into how plants fine-tune their belowground interactions in response to environmental cues and microbial colonization [72,188]. Additionally, future directions should include the development of targeted microbiome engineering strategies, leveraging synthetic microbial communities, host-mediated selection, and ecological engineering, to enhance plant resilience, productivity, and sustainable disease management in agricultural systems. Understanding and harnessing interkingdom signaling and multitrophic interactions in the rhizosphere will be pivotal for designing next generation biofertilizers, biopesticides, and sustainable crop management practices.

11. Conclusions

Plant-microbe interactions in the rhizosphere are mediated through a complex web of chemical signaling, with root exudates playing a central role in modulating the composition and function of the soil microbiome. These exudates, composed of a diverse range of primary and secondary metabolites, serve as both nutrients and signaling molecules. They attract beneficial microbes that enhance plant defense and facilitate interspecific plant interactions, thereby suppressing disease and improving plant fitness. Recent studies have highlighted the dynamic and bidirectional nature of these plant-microbe interactions, where the rhizosphere microbiome can induce systemic changes in root exudate profiles and influence soil conditioning and plant health. Microbiome engineering for sustainable agriculture requires the advancement of technologies and high throughput methods to dissect the metabolic crosstalk and multitrophic interactions within the rhizosphere.

A comprehensive understanding of root exudate-mediated signaling and the underlying molecular mechanisms is necessary to promote its use in crop improvement. This understanding is necessary to advance the current practice of isolating candidate microbes from disparate sources and inoculating plants of agricultural significance to test for enhanced plant growth, resilience, and disease management. The SynCom solution for sustainable agriculture aims to engineer a non-native plant microbiome that harnesses the benefits associated with each constituent species in the inoculation milieu, requiring intensive, multifactorial experimental designs to understand the contributions of each probiotic to the host plant individually, as well as collectively. A similar concerted effort will be needed from the broader research community for SynComs to compete with synthetic chemicals.

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