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MICROBIAL SEED TREATMENTS AND THE SEED MICROBIOME: A NEW PARADIGM FOR ECO-FRIENDLY APPROACHES TOWARDS SUSTAINABLE CROP PRODUCTION

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ABSTRACT
Sustainable agriculture requires environmentally friendly strategies that maintain crop productivity while reducing dependence on synthetic fertilizers and pesticides. Microbial seed treatments have emerged as a promising, low input approach to enhance crop establishment, productivity and resilience. Concurrently, the seed microbiome the community of bacteria, fungi, archaea and other microorganisms associated with seeds has gained recognition as a key regulator of seed germination, seedling establishment, plant growth, nutrient acquisition, disease resistance and the vertical transmission of beneficial microorganisms across generations. This review highlights the role of microbial seed treatments and the seed microbiome in promoting eco-friendly crop production. It discusses the composition and functions of the seed microbiome and examines microbial seed treatment approaches, including seed coating, biopriming, microbial inoculation and microbiome engineering. Beneficial microorganisms improve nutrient mobilization, phytohormone production, biological nitrogen fixation, phosphate solubilization, pathogen suppression and induced systemic resistance, thereby enhancing germination, seedling vigor, nutrient-use efficiency, yield stability and tolerance to abiotic stresses such as drought, salinity, heat and waterlogging. Recent advances in synthetic microbial consortia, next-generation sequencing, multi-omics technologies, artificial intelligence and genome editing have expanded opportunities to optimize microbial selection, colonization and field performance. The review also addresses key challenges, including formulation stability, shelf life, host genotype specificity, environmental variability, biosafety and large-scale field validation. Overall, integrating microbial seed treatments with seed microbiome management offers a sustainable strategy to improve crop productivity, climate resilience and resource use efficiency while minimizing agrochemical inputs. Continued research integrating microbiome science, advanced biotechnology and precision agriculture will facilitate the development of reliable, climate smart seed technologies for sustainable crop production.

KEYWORDS: Seed microbiome, microbial inoculants, seed treatment, plant growth promoting microorganisms, sustainable agriculture, biofertilizers and biocontrol agents

1. INTRODUCTION

Global food demand is rising with population growth toward nearly 10 billion people by midcentury, increasing pressure on agriculture to raise productivity without exhausting land, water and biodiversity (Islam, 2025; McLennon *et al.,* 2021). Conventional gains have relied heavily on synthetic fertilizers and pesticides, but their long-term overuse drives soil degradation, water pollution, biodiversity loss and greenhouse gas emissions, making current production systems environmentally and agronomically unsustainable (Mahmood *et al.,* 2024; Penuelas *et al.,* 2023). At the same time, climate change is already reducing agricultural productivity through higher temperatures, erratic rainfall, drought, floods and expanding pest pressure, with projections of substantial future losses in food production without adaptation (Bibi & Rahman, 2023; Farah *et al.,* 2025; Verma *et al.,* 2025). These converging pressures have intensified interest in ecofriendly biological strategies, the seed microbiome and microbial seed treatments are increasingly viewed as promising tools to support resilient crop establishment, reduce dependence on chemical inputs and advance climate smart sustainable agriculture (Raza *et al.,* 2025; Shah *et al.,* 2021).

In this context, seed treatment technologies have evolved from basic seed dressing and pesticide delivery toward more refined systems such as film coating, pelleting, priming and multifunctional coatings designed to improve planting precision, germination, seedling establishment and early crop protection (Afzal *et al.,* 2020; Sharma *et al.,* 2015). In response, biological seed treatments based on bacteria, fungi, algae and plant derived products are gaining importance as ecofriendly alternatives that support germination, root growth, nutrient acquisition, stress tolerance and disease suppression while reducing dependence on synthetic inputs and better preserving the seed microbiome (Lamichhane *et al.,* 2022; Paulikienė *et al.,* 2025). This transition has encouraged integrated seed enhancement technologies in which priming, coating, pelleting, inoculation and other delivery platforms are combined to place nutrients, bio stimulants and beneficial microorganisms directly in the seed microenvironment, making seed treatment a coordinated biological technical system for sustainable and ecofriendly crop production rather than a simple presowing protective step (Brown *et al.,* 2021; Halmer, 2006; Sharma *et al.,* 2015).

The concept of the seed microbiome has emerged from a shift away from viewing healthy seeds as sterile structures toward recognizing them as biologically active reservoirs of diverse internal and surface associated microorganisms that influence the earliest stages of plant life (Berg & Raaijmakers, 2018; Nelson, 2018; Romão *et al.,* 2025). This recognition has elevated seeds from passive propagules to microbial carriers with ecological and agricultural significance, because seed associated microbes can contribute to germination, seedling establishment, plant vigor and resilience under stress (Qi *et al.,* 2026; Romão *et al.,* 2025; War *et al.,* 2023). Current evidence suggests that these two pathways act together, with vertical transmission providing continuity of core inherited taxa across generations and horizontal acquisition adding ecological flexibility and local adaptation, a framework that underpins growing interest in microbial seed treatments as a foundation for ecofriendly crop production (Frank *et al.,* 2017; Sulesky-Grieb *et al.,* 2024; Zhang *et al.,* 2022).

2. Understanding the Seed Microbiome

2.1 Definition and Composition

Within this paradigm, the seed microbiome refers to the diverse community of microorganisms inhabiting seed surfaces and internal tissues and it functions as an initial inoculum that helps establish plant microbiota across generations (Qi *et al.,* 2026; Shade *et al.,* 2017). Its composition is broad but uneven, with seed associated taxa spanning stable core members and flexible, environment responsive fractions across plant species and samples (Bintarti *et al.,* 2022; Simonin *et al.,* 2022). Bacterial members are typically the most consistently reported component, dominated largely by Proteobacteria, Actinobacteria, Firmicutes and Bacteroidetes, with recurrent genera such as *Pantoea*, *Enterobacter*, *Pseudomonas*, *Acinetobacter*, *Sphingomonas*, *Bacillus*, *Klebsiella* and *Massilia* frequently detected as common or core seed inhabitants (Johnston-Monje *et al.,* 2021; Simonin *et al.,* 2022). Fungal communities are also integral to seed microbiome structure and often include major groups such as *Dothideomycetes*, *Sordariomycetes* and *Tremellomycetes*, with common genera including *Alternaria*, *Fusarium*, *Cladosporium*, *Cryptococcus*, *Davidiella*, *Aspergillus*, *Penicillium* and *Wallemia*, indicating that fungi are not incidental contaminants but persistent members of seed associated communities (Bintarti *et al.,* 2022; Johnston-Monje *et al.,* 2021; Wassermann *et al.,* 2019). Seed associated microorganisms are commonly discussed as endophytes because many persist inside seed tissues and can be vertically transmitted to the next generation, although horizontal acquisition from other plant compartments or the environment also contributes to community assembly (Samreen *et al.,* 2021; Shade *et al.,* 2017).

2.2 Origin of Seed Microbiota

The origin of seed microbiota is now understood as a composite process in which seeds inherit part of their microbiome from parental tissues while also acquiring microbes from surrounding environments, rather than assembling from a single source alone (Abdelfattah *et al.,* 2023; Rochefort *et al.,* 2021; Shade *et al.,* 2017). Maternal or vertical transmission occurs through internal plant pathways, including vascular connections to developing seeds and can also involve floral compartments that package endophytic microbes into internal seed tissues or onto seed surfaces (Abdelfattah *et al.,* 2023; Prado *et al.,* 2020; Sulesky-Grieb *et al.,* 2024). Evidence for this inherited route is strong, with multigenerational studies identifying stable bacterial and fungal members transmitted from seed to seed, including rice and bean systems in which a restricted but persistent core microbiota was maintained across generations. Soil is particularly influential because sterile substrate experiments in *Setaria viridis* produced progressively less diverse seed microbiota, while seedling assembly studies showed that soil contributed far more taxa to emerging seedlings than seeds did once both communities encountered each other (Rochefort *et al.,* 2021; Rodríguez *et al.,* 2020). Overall, current evidence indicates that seed microbiota arises through the interaction of maternal transmission, environmental acquisition and recruitment from both floral and soil microbiomes, with their relative contributions varying by host species, developmental stage and ecological context (Abdelfattah *et al.,* 2023; Kim *et al.,* 2022; Nelson, 2018).

2.3 Methods for Studying Seed Microbiomes

Methods for studying the seed microbiome increasingly combine culture dependent and culture independent workflows because no single approach captures both cultivable function and full community diversity (Wassermann *et al.,* 2020). Culture dependent methods remain important for activating dormant seed microbes, isolating bacterial and fungal strains, preserving them and experimentally confirming physiological traits that sequencing alone cannot validate (Bergmann *et al.,* 2022; Liu *et al.,* 2022). In parallel, culture independent approaches based on next generation sequencing have transformed microbiome analysis by detecting difficult to culture taxa directly from seed material and by surveying genes, transcripts and metabolites in situ (Boers *et al.,* 2019; Su *et al.,* 2012). To identify which seed associated microbes are active rather than merely present, meta transcriptomics profiles community RNA and links taxa to expressed functions under changing environmental conditions, often revealing biologically important responses that DNA based methods miss, though it remains analytically complex and less widely adopted (Liu *et al.,* 2021; Shakya *et al.,* 2019). Metabolomics adds a complementary functional layer by measuring community associated metabolites or predicting metabolic outputs from paired sequencing data, helping connect microbiome composition to biochemical activity, although cost, metadata quality and experimental complexity still limit broad standardization and cross study comparison (Kumar *et al.,* 2024; Mallick *et al.,* 2019). Together, these methods support a multiomics, experimentally grounded view of seed microbiomes that is essential for designing microbial seed treatments for ecofriendly crop production (Beghini *et al.,* 2021; Wassermann *et al.,* 2020). The major physiological and biochemical mechanisms through which microbial seed treatments enhance early stress adaptation are summarized in **Figure 1**.

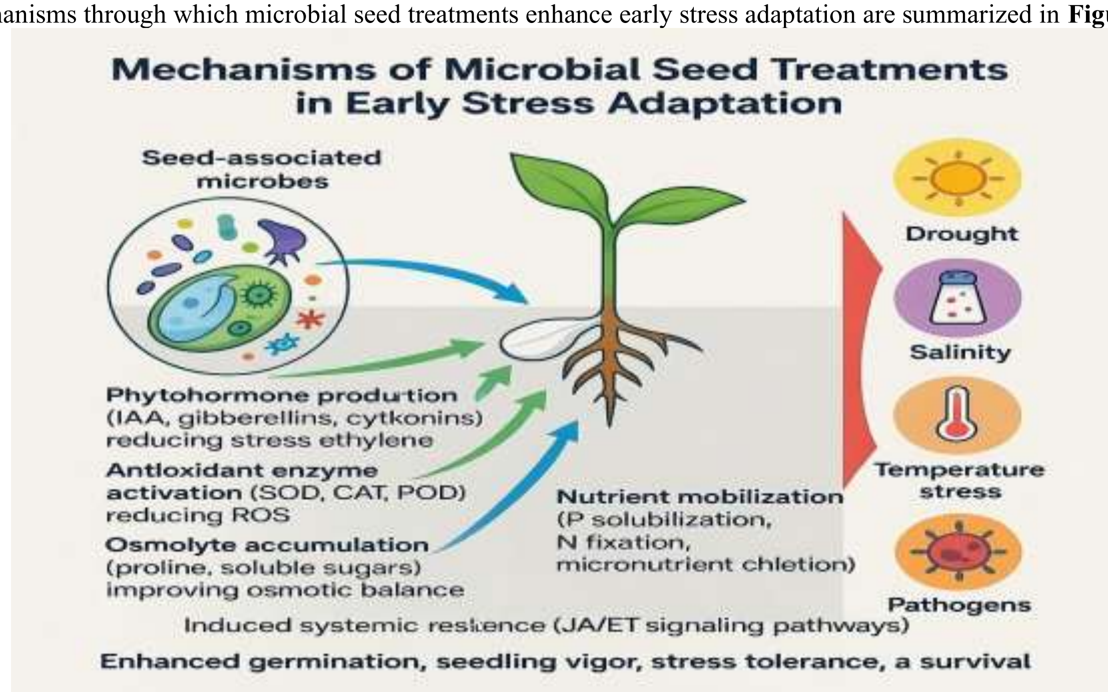

Figure 1. Mechanisms of microbial seed treatments in early stress adaptation

3. Microbial Seed Treatments: Concepts and Types

3.1 Definition and Principles

Microbial seed treatments in the seed microbiome paradigm refer to the application of living beneficial microorganisms to seeds by inoculation, coating, dressing, soaking, pelleting, film coating, slurry application or biopriming so they colonize the spermosphere, rhizosphere or plant interior during germination and early growth, thereby improving nutrient acquisition, seed vigor, stress tolerance and protection from seed and soilborne pathogens (Mitra *et al.,* 2021; Wassermann *et al.,* 2020). A major class is biofertilizer based seed treatment, in which formulations containing single strains or consortia are selected for nutrient mobilizing and growth promoting traits, especially Rhizobium, Azotobacter, Azospirillum and other phosphate solubilizing microorganisms (Aloo *et al.,* 2022; Khan *et al.,* 2023; Timofeeva *et al.,* 2023). Rhizobium is used not only as a classical nitrogen fixer but also as a seed applied phosphorus mobilizing inoculant, with field evidence showing that a Rhizobium strain increased labile inorganic phosphorus by 14% and maize grain yield by 696 kg ha−1 while replacing 50% of recommended phosphate fertilizer (Beltran-Medina *et al.,* 2023). Azotobacter and Azospirillum are repeatedly identified as seed biopriming agents that support biological nitrogen fixation, nutrient uptake, germination, growth promotion, disease resistance and drought tolerance and some strains also act as phosphate solubilizing bacteria (Mitra *et al.,* 2021; Thomas & Singh, 2019). Evidence also supports combining microbes, since seed treatments that pair Trichoderma with Pseudomonas or other beneficial taxa can reduce root rot and wilt while improving vigor under field conditions, although broader reviews note that field performance still varies with strain choice, formulation, host, soil and environment (Sain *et al.,* 2023; Singh *et al.,* 2023).

3.2 Bio-fertilizer Based Treatments

In this newer seed microbiome framework, endophytic microbial inoculants are attractive, Endophyte based microbiome engineering also appears promising at the seed stage because floral or seed associated inoculation can place beneficial bacteria directly into developing seeds, potentially avoiding some colonization limitations seen with conventional coating or biopriming, although this approach remains less developed than standard seed treatment systems (YILDIRIM *et al.,* 2025). Seed applied Synods can directly modulate seed microbiota composition and abundance and in one seedling engineering study they contributed about 80% of the seedling microbiota, showing that abundance on the seed strongly shapes later colonization and priority effects in seedlings and the rhizosphere (Arnault *et al.,* 2024). Delivery technology is therefore central: seed coating applies microbial inoculants to the seed surface with binders and sometimes fillers, allowing precise, low dose, scalable delivery, while the main coating formats include seed dressing, film coating and seed pelleting depending on seed traits and the intended biological function (Rocha *et al.,* 2019). Film coating is especially useful when minimal changes in seed size and shape are desired and maize studies using Hydroxypropyl methylcellulose (HPMC) and dextrin based films showed preserved seed appearance, successful rhizosphere colonization and improved seedling growth after consortium delivery (Priyadharshini *et al.,* 2022). By contrast, pelleting is better suited to improving handling, sowing uniformity and placement of small or irregular seeds and newer pelleting systems increasingly integrate biological agents, biodegradable materials and controlled release concepts for more resilient crop establishment (Bozdar *et al.,* 2026). Overall, the evidence supports a shift from single strain, loosely formulated inoculation toward endophyte aware, consortium based and technologically protected seed delivery platforms that more deliberately shape the seed microbiome for ecofriendly crop production (Arnault *et al.,* 2024; Balla *et al.,* 2022; Ma, 2019).

4. Interaction Between Microbial Seed Treatments and the Native Seed Microbiome

Microbial seed treatments interact with the native seed microbiome as biological invasion events whose success depends on host filtering, resident community resistance and the inoculant's ability to establish during early seedling development (Poppeliers *et al.,* 2023; Rybakova *et al.,* 2017). Colonization is highly dynamic rather than uniform, because seedborne or introduced microbes shift across tissues and growth stages and successful strains differ in their ability to occupy leaves, roots and rhizosphere habitats (Arnault *et al.,* 2025; Novak *et al.,* 2026). In seed based Synthetic Community studies, inoculant abundance on the seed strongly influenced seedling colonization, some taxonomic groups were consistently better colonizers than others and community coalescence outcomes remained difficult to predict because both mass effects and niche based interactions mattered (Arnault *et al.,* 2024). Mechanistically, these beneficial networks appear to rely on niche partitioning, cross feeding and cooperation among strains, while overly competitive or chemically incompatible consortia are less stable in the presence of native communities (Garrido-Sanz & Keel, 2025; Velte *et al.,* 2025). The impact on rhizosphere recruitment can be substantial even when direct persistence is low, because seed inoculation can modify initial sperm sphere assembly, generate priority effects, alter host physiology and exudation and thereby redirect which resident bacteria and fungi are later recruited around roots (Arnault *et al.,* 2024; Francioli *et al.,* 2025). Evidence is mixed on the magnitude of seed to rhizosphere transmission itself, with some systems showing low direct SynComs contribution to the mature rhizosphere while others show seedborne bacteria surpassing soil as a dominant rhizosphere source, indicating that outcomes are strongly context, strain and host dependent (Arnault *et al.,* 2024; Garrido-Sanz & Keel, 2025). Overall, microbial seed treatments work best not as simple single strain additions but as ecological interventions that must be compatible with the native seed microbiome, able to survive early competitive filters and capable of steering resilient plant beneficial networks that shape later rhizosphere assembly (Kampouris *et al.,* 2025; Kong & Liu, 2022; Park *et al.,* 2023).

5. Mechanisms of Plant Growth Promotion

In this framework, microbial seed treatments promote plant growth chiefly through direct mechanisms that increase nutrient availability and modulate plant hormonal balance during germination and early root establishment (Fiodor *et al.,* 2023; Lopes *et al.,* 2021; Sharma *et al.,* 2025). A central mechanism is biological nitrogen fixation, in which seed or root colonizing diazotrophs reduce atmospheric N_2 to ammonia via nitrogenase, thereby supplying plant available nitrogen and helping reduce synthetic N fertilizer demand (Fanai *et al.,* 2024; Granada *et al.,* 2018; Lopes *et al.,* 2021). This function is agronomically meaningful in inoculation studies, with maize associated Plant Growth Promoting Rhizobacteria (PGPR) showing positive tests for N_2 fixation together with phosphate solubilization and auxin production and one strain contributing up to 30.5% of maize N requirement before anthesis and 25.5% at ear harvest under reduced fertilizer input (Kuan *et al.,* 2016). Comparable evidence from diazotrophic Pseudomonas shows that biologically fixed nitrogen can account for 21–35% of plant nitrogen in sugarcane while also improving physiological performance, supporting the view that seed delivered or root establishing inoculants can couple nutrition with vigor enhancement (Singh *et al.,* 2024). In screening and consortium studies, many isolates simultaneously express P and K solubilization with nitrogen fixation and hormone production and mixed phosphorus solubilizing consortia enhanced maize growth, soil phosphatase activity and rhizosphere Proteobacteria abundance by 16.07–69.10% (Fiodor *et al.,* 2023; Luo *et al.,* 2024). Endophytic phosphate solubilizing bacteria likewise increased Chinese fir seedling height, stem diameter, biomass and soil available P and K, indicating that mineral mobilization can translate into measurable plant nutrient uptake and growth gains (Chen *et al.,* 2021). Among these, auxins are the most consistently linked to seed responses: many isolates produce indole3acetic acid, auxin producing strains are routinely selected in seed biopriming screens and available evidence suggests auxins are especially involved in stimulating seed germination and early seedling growth (Fiodor *et al.,* 2023; Luo *et al.,* 2024; Moreno-Valencia *et al.,* 2024). Cytokinins and gibberellins add complementary effects by shaping cell division, shoot development and germination physiology; bacteria are known to produce both hormones and inoculated sugarcane showed increased cytokinin levels while broader inoculation studies note microbial gibberellin synthesis as a mechanism improving germination (Lopes *et al.,* 2021; Orozco-Mosqueda *et al.,* 2023; Singh *et al.,* 2024). Overall, the evidence supports microbial seed treatments as ecofriendly tools that integrate nitrogen fixation, phosphorus and potassium mobilization and auxin, cytokinin and gibberellin mediated signaling to strengthen early plant growth while reducing reliance on chemical fertilizers (de Andrade *et al.,* 2023; Hyder *et al.,* 2023; Timofeeva *et al.,* 2023).

Microbial seed treatments enhance early plant performance by coupling siderophore mediated iron acquisition, 1-aminocyclopropane-1-carboxylate (ACC) deaminase–mediated stress relief and broader nutrient mobilization functions that reshape the seedling microbiome toward improved nutrient capture and growth. Siderophore producing inoculants chelate Fe^{3+}, increase iron bioavailability and can supply iron to plants either through Siderophore uptake, ligand exchange or rhizosphere reservoirs formed in microbial biofilms, with field and controlled studies showing improved Fe nutrition, chlorosis relief, biomass and yield under iron limiting or alkaline conditions (Aloo *et al.,* 2022; Gao *et al.,* 2022; Ranjan *et al.,* 2024; Tan *et al.,* 2025). ACC deaminase positive bacteria complement this by hydrolyzing ACC, the immediate precursor of ethylene, into α-ketobutyrate and ammonia, thereby lowering stress ethylene and sustaining seed germination, root elongation and seedling growth under salinity and other abiotic stresses (Penrose & Glick, 2003; Saleem *et al.,* 2007; Sarkar *et al.,* 2018). Nutrient mobilization extends beyond iron, because seed or soil applied beneficial bacteria solubilize phosphorus, zinc and potassium, increase available soil nutrient pools, modify root architecture and raise nutrient uptake efficiency, including maize increases of up to 34% in nitrogen uptake efficiency and 25.43% in potassium uptake efficiency without phosphorus fertilizer (Cheng *et al.,* 2025; Devi *et al.,* 2023). Together, these findings support the view that microbial seed treatments act as multifunctional microbiome engineering tools that integrate iron scavenging, ethylene regulation and nutrient solubilization to reduce dependence on synthetic fertilizers while improving crop nutrition and resilience in ecofriendly production systems (Aloo *et al.,* 2022; Ferreira *et al.,* 2019; Fiuzi *et al.,* 2024) . The contribution of different microbial mechanisms to nutrient-use efficiency is summarized in **Table 1**.

Nutrient	**Microbial mechanism**	**Plant response**	**Agronomic benefit**	**References**
Nitrogen (N)	Biological N fixation	Enhanced N assimilation	Reduced fertilizer requirement	(Bhattacharyya & Jha, 2012)
Phosphorus (P)	Phosphate solubilization	Improved root uptake	Higher biomass & yield	(Richardson *et al.,* 2009; Vessey, 2003)
Iron (Fe)	Siderophore production	Increased micronutrient availability	Stress tolerance	(Hayat *et al.,* 2010)
Multiple nutrients	Root architecture modulation	Increased root surface area	Improved NUE under stress	(Nawaz *et al.,* 2021)

Table 1. Contribution of microbial seed treatments to nutrient-use efficiency

6. Seed Microbiome Mediated Disease Suppression

Microbial seed treatments and the seed microbiome represent a new ecofriendly paradigm for crop production because seeds can be used to deliver beneficial microbes that establish early, shape subsequent plant associated communities and reduce reliance on chemical inputs through disease suppression and improved plant resilience. They also control seedborne pathogens by direct antagonism, including antibiosis and antifungal metabolite production such as fengycin, bacillomycin, surfactin and related compounds, as shown for *Bacillus* and *Paenibacillus* associated systems suppressing Fusarium and other seedling pathogens (Romão *et al.,* 2025; Xun *et al.,* 2023) . In parallel, these microbes induce systemic resistance through JA/ET and SA-linked defense signaling, thereby extending protection beyond the seed surface and strengthening seedling immunity against diverse phytopathogens (Panchal *et al.,* 2026; Poonguzhali *et al.,* 2025; Romão *et al.,* 2025). Effective disease suppression also depends on biofilm formation and niche occupation, because stable colonization of seed and root microsites limits pathogen establishment and formulation advances can enhance microbial persistence and biofilm supported attachment on seeds (Rocha *et al.,* 2019; Romão *et al.,* 2025; Singh *et al.,* 2023). Evidence from seed microbiome engineering and synthetic consortia further suggests that cooperative, functionally complementary communities can provide more stable pathogen suppression than single strains, although field consistency, strain compatibility and formulation stability remain important translational constraints (Compant *et al.,* 2025; Xun *et al.,* 2023; Zholdasbek *et al.,* 2026) . The principal mechanisms involved in seed microbiome-mediated disease suppression are summarized in **Table 2**.

Disease suppression mechanism	**Microbial trait**	**Target pathogens**	**Mode of action**	**Key references**
Competitive exclusion	Rapid colonization	Damping-off pathogens	Niche occupation, nutrient competition	(Nelson, 2018; Walsh *et al.,* 2021)
Antimicrobial production	Antibiotics, VOCs	Soil-borne fungi & bacteria	Cell wall disruption, quorum sensing inhibition	(Compant *et al.,* 2005)
Induced systemic resistance (ISR)	JA & ET signaling	Broad-spectrum pathogens	Immune priming without fitness cost	(Pieterse *et al.,* 2014)
Endophytic defense activation	Defense gene modulation	Chronic pathogens	PR proteins, phenylpropanoid pathway	(Shahzad *et al.,* 2018; Truyens *et al.,* 2015)

Table 2. Disease suppression mechanisms mediated by microbial seed treatments

7. Influence on Seed Germination and Seedling Establishment

Microbial seed treatments and the seed microbiome improve seed germination and seedling establishment by creating early plant–microbe associations that increase germination speed and uniformity, strengthen seedling vigor and support better use of available resources during emergence (Cardarelli *et al.,* 2022; Fiodor *et al.,* 2023; Singh *et al.,* 2023). These effects appear to arise from nutrient mobilization, phytohormone regulation and stress buffering, with seed associated microbes improving nutrient uptake and hormonal balance during the earliest growth stages (Adeboye *et al.,* 2025; Mbah *et al.,* 2025; Yang *et al.,* 2025). Seed applied inoculants also enhance early root development and seedling growth, as seen in rice where combined biopriming increased germination to 94% and root length to 17.63 cm and in soybean where PGPR based formulations significantly improved root length and seedling vigor index (Marinković *et al.,* 2025; Monika *et al.,* 2025). Vertical transmission and deliberate microbiome modification add a longer-term dimension, because inherited or engineered seed microbiota can shape progeny traits, while altered seed microbiomes have improved stand establishment and mature biomass even when direct germination gains were limited in some crops (Mitter *et al.,* 2017; YILDIRIM *et al.,* 2025). Overall, the literature supports microbial seed treatments as an ecofriendly strategy for more uniform crop establishment and improved early nutrient acquisition, although responses remain crop, strain and environment dependent and field performance is not always consistent (Romão *et al.,* 2025; Singh *et al.,* 2023; Xu *et al.,* 2026). The major microbial groups, their transmission routes and functional roles during seed germination and seedling establishment are summarized in **Table 3**. The process through which seed-associated microorganisms influence rhizosphere microbiome assembly via priority effects is illustrated in **Figure 2**.

Microbial group	**Mode of transmission**	**Key functional roles**	**Mechanisms involved**	**Representative references**
Bacteria (PGPR)	Vertical & horizontal	Germination, seedling vigor	Phytohormone production (IAA, GA), ROS modulation	(Backer *et al.,* 2018; Nelson, 2018)
Endophytic bacteria	Vertical	Stress tolerance, early growth	ACC deaminase activity, osmolyte induction	(Shahzad *et al.,* 2018; Truyens *et al.,* 2015)
Fungal endophytes	Vertical	Biomass accumulation	Improved water-use efficiency, nutrient uptake	(Harman, 2011)
Seed epiphytes	Horizontal	Protection during germination	Competitive exclusion, antimicrobial compounds	(Barret *et al.,* 2015; Mitra *et al.,* 2021)

Table 3. Role of the seed microbiome in plant establishment and early development

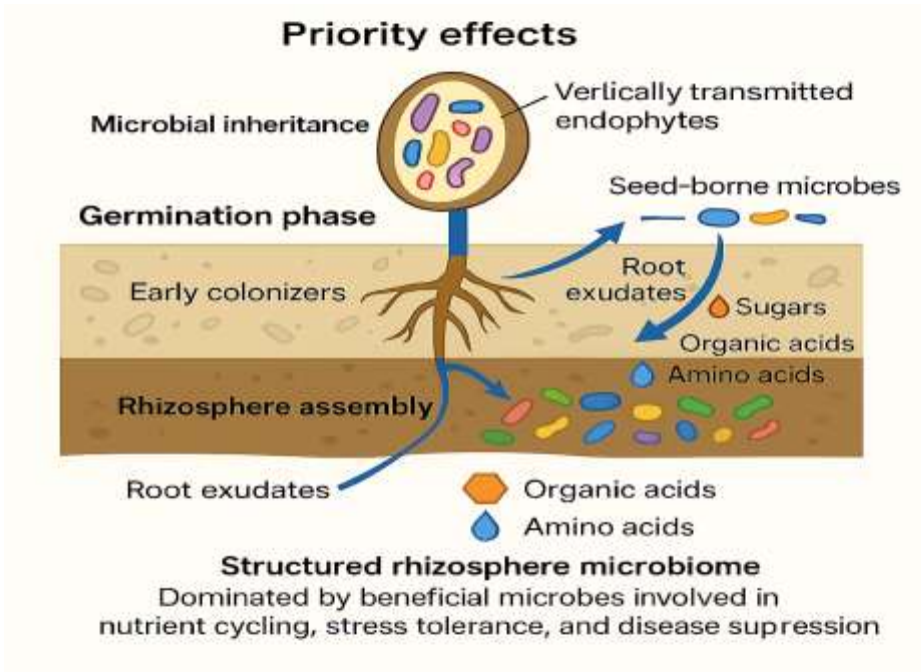

Figure 2. Seed-driven assembly of the rhizosphere microbiome through priority effects

8. Microbial Seed Treatments in Major Cropping Systems

Microbial seed treatments are being applied across major cropping systems as an ecofriendly strategy to improve establishment, nutrient use, stress tolerance and disease management, with the strongest documented use in cereals such as rice, wheat and maize, legumes such as soybean, chickpea and groundnut and several oilseed and horticultural crops (Cardarelli *et al.,* 2022; Sarkar *et al.,* 2021). In cereals, seed inoculation and biopriming have increased productivity and stress resilience in rice, improved establishment and agronomic performance in wheat and enhanced maize germination, seedling growth, grain yield, rhizosphere functioning and drought or salinity tolerance depending on the microbial strain and formulation (Di Salvo *et al.,* 2018; Naik *et al.,* 2020; Ocwa *et al.,* 2024) . Maize specific evidence further shows that Bacillus, Azospirillum and Pseudomonas based treatments can act as both biofertilizers and biopesticides, raise grain yield by up to 14.3% in saline soil and more under selected Bacillus treatments and sometimes reduce disease severity through induced defense responses, although performance remains species and environment dependent (Huo *et al.,* 2024; Ocwa *et al.,* 2024). In legumes, pre sowing bacterial treatments have accelerated germination and improved yield and grain quality in soybean and pea, while microbial consortia or Bacillus biopriming increased nodulation, root growth, seedling vigor and disease suppression in soybean, chickpea and groundnut (Eliseeva *et al.,* 2025; Javed *et al.,* 2023; Kampa *et al.,* 2025). Oilseed crops are also represented, with canola and sunflower among the major responsive systems, sunflower showing higher chlorophyll, carbohydrate, protein and mineral status and sesame included among seed and soilborne pathos systems addressable by microbial consortia, whereas plantation crop evidence is not directly represented here and remains a gap (Cardarelli *et al.,* 2022; Kampa *et al.,* 2025; Naik *et al.,* 2020). Across systems, the paradigm is reinforced by evidence that microbial inoculants can support yields with lower external inputs and often limited nontarget disruption of resident soil microbiota, but field consistency, crop–microbe compatibility and formulation quality still determine whether benefits translate reliably at scale (de Jesus Boaventura *et al.,* 2023; Díaz-Rodríguez *et al.,* 2025; Jaramillo-López *et al.,* 2024).

9. Advances in Seed Microbiome Engineering

Advances in seed microbiome engineering are shifting microbial seed treatments from empirical inoculation toward predictive, ecofriendly crop management by combining seed coating and biopriming with host mediated selection, endophyte introduction, environmental manipulation and genome informed screening of seed associated taxa (Yang *et al.,* 2025; Zhang *et al.,* 2026). A central innovation is the use of synthetic communities (SynComs) and designer microbiomes, which assemble robust colonizers and functionally complementary strains to improve colonization, persistence, nutrient acquisition, stress tolerance and disease suppression more consistently than single inoculants (De Souza *et al.,* 2020; Fouad *et al.,* 2026; Shayanthan *et al.,* 2022). Seed based SynComs delivery is especially attractive because seeds provide an early entry point and priority effects that can redirect microbiome assembly, with experimental inoculations showing that introduced SynComs can dominate seedling microbiota and reshape rhizosphere recruitment (Arnault *et al.,* 2024; Xu *et al.,* 2026). This design logic is expanding toward programmable or designer microbiomes, where Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/Cas, CRISPR interference, RNA based tools, quorum sensing modules, biosensor circuits and metabolic engineering are used to modify microbial functions or host recruitment traits for more stable beneficial performance under field stress (Adhikary *et al.,* 2026; Portal-Gonzalez *et al.,* 2025; Yadav *et al.,* 2026). These capabilities align with precision agriculture because sensors, remote sensing, drone imaging, variable rate application and metadata rich decision systems can guide where, when and how microbial seed treatments are deployed and iteratively refined across environments (Fouad *et al.,* 2026; Panchal *et al.,* 2026; Vompe *et al.,* 2026) . Emerging approaches for microbial seed delivery and microbiome engineering are summarized in **Figure 3**.

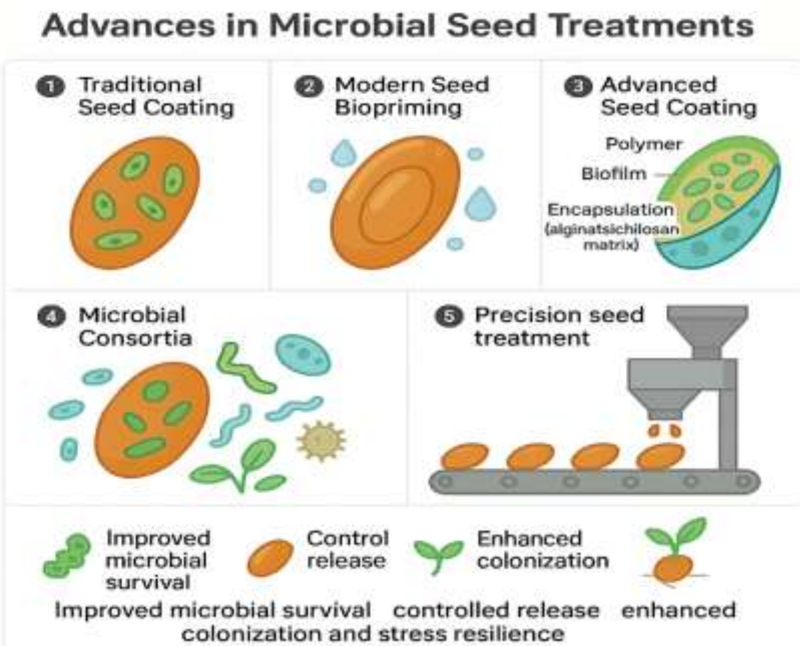

Figure 3. Advances in microbial seed treatment technologies and delivery systems

10. Challenges and Limitations

Microbial seed treatments and the seed microbiome represent a promising ecofriendly crop strategy, but their main limitations are variable field performance, uncertain establishment in heterogeneous agroecosystems and incomplete ecological understanding of how introduced microbes interact with seeds, soils and host plants (Compant *et al.,* 2025; Xu *et al.,* 2026; Yang *et al.,* 2025). Performance is often inconsistent because laboratory gains do not reliably translate to farms, where dynamic soil conditions, native microbial competition and environmental heterogeneity rapidly alter inoculant activity and persistence (Panchal *et al.,* 2026; Singh *et al.,* 2023) . Environmental influences such as temperature, precipitation, elevation, soil pH, texture organic matter, tillage, crop rotation and local terroir reshape seed associated communities and strongly condition whether beneficial inoculants survive and function after sowing (Romão *et al.,* 2025) . Microbial survival and establishment remain central bottlenecks because inoculants can lose viability during storage, seed treatment, transport or field exposure and introduced strains often fail to maintain stable populations against already adapted resident microbiota (O'Callaghan, 2016; Panchal *et al.,* 2026; Yang *et al.,* 2025) . Responses are also host specific, since seed microbiome assembly can depend on plant species, cultivar, genotype, developmental stage and preexisting microbiome context, making strain performance difficult to generalize across crops (Adeboye *et al.,* 2025; Singh *et al.,* 2023; Yao *et al.,* 2026). Broader agricultural practices further complicate outcomes because pesticides, fertilizers and other seed treatments can reduce microbial diversity or alter recruitment of both beneficial and pathogenic taxa during early establishment (Romão *et al.,* 2025). Important knowledge gaps persist in seed microbiome ecology, especially around transmission routes, intracellular and heritable endophytes, dormancy–germination signaling, functional specificity, long term effects on plant and soil microbiomes and interactions with fertilizers or pesticides (Singh *et al.,* 2023; Vompe *et al.,* 2026; Xu *et al.,* 2026). Progress appears to depend on standardized validation pipelines, multisite field testing, reproducible microbiome characterization, data driven strain selection and interdisciplinary coordination among researchers, industry, policymakers and farmers before seed microbiome technologies can become reliable at scale (David & Parthasarathi, 2026; Hanif *et al.,* 2024; Vompe *et al.,* 2026).

11. Future Perspectives

Future progress in microbial seed treatments and the seed microbiome is moving toward next generation biological seed treatments that use seed coating, biopriming, encapsulation, microbial consortia and protective polymers to deliver beneficial microbes precisely at sowing while improving survival, colonization and early functional engagement with the host. This transition is increasingly being driven by multiomics approaches, because genomics, transcriptomics, proteomics, metabolomics, epigenomics and high throughput culturing now provide deeper resolution of seed microbe interactions, microbial functions and the chemical signals needed to design more effective inoculants and engineered communities. A parallel priority is building climate resilient microbiomes, since microbiome engineering, stress adapted consortia and climate smart crop frameworks appear to improve nutrient cycling, stress resilience and yield stability under drought, salinity, heat and other climate related constraints. Breeding is also shifting toward microbiome-based selection, where plant genotypes are developed for microbiome supportive traits, beneficial signaling chemistry and improved compatibility with vertically transmitted or reintroduced seed endophytes, including microbes sourced from non-domesticated relatives. In this framework, microbial seed technologies support sustainable and carbon conscious farming by reducing agrochemical dependence, improving nutrient use efficiency, restoring soil biological function, fitting circular bioeconomy models and contributing to climate change mitigation goals alongside food security. Integration with smart farming technologies is becoming equally important, with AI, machine learning, advanced phenotyping, drones, hyperspectral imaging and precision guided microbial seed coatings expected to improve prediction, targeting and field scale adaptation of microbiome interventions. Even so, the evidence remains clear that broad adoption will depend on solving persistent problems in field reliability, microbial persistence, ecological predictability and regulatory translation through data driven strain selection, continuous monitoring and interdisciplinary collaboration.

12. CONCLUSION

In conclusion, seed microbiomes appear to be a previously underused biological resource because seed associated microbes shape germination, seedling vigor, long term resilience and plant adaptability, yet their agricultural potential has only recently become a major focus of microbiome science. Microbial seed treatments, including coating and biopriming, can improve crop establishment, nutrient acquisition, stress tolerance and disease protection while reducing dependence on synthetic fertilizers, fungicides and pesticides, making them a credible ecofriendly alternative within integrated crop management rather than a complete one to one replacement for agrochemicals. This value proposition is strengthened by broader evidence that beneficial microbes can raise yields and resource use efficiency through nutrient solubilization, nitrogen fixation, phytohormone production and biocontrol functions, while helping agriculture respond to soil degradation, climate stress and the environmental costs of chemical intensive farming. The next major advance is the integration of microbiome science with biotechnology and precision agriculture, where multiomics, synthetic communities, CRISPR enabled engineering, sensors, drones and machine learning guided prediction can support more reliable, crop and environment specific microbiome interventions. Even so, largescale adoption still depends on solving persistent problems in colonization, field inconsistency, formulation stability, storage, regulation and farmer trust, which remain the main barriers between experimental promise and routine farm use. Future efforts should therefore prioritize microbiome engineering, standardized multisite field validation and commercialization pipelines that improve formulation quality, scalability and economic returns, while aligning researchers, industry, breeders and farmers around practical deployment in sustainable and climate resilient cropping systems.

REFERENCE:

1. Abdelfattah, A., Tack, A. J., Lobato, C., Wassermann, B., & Berg, G. (2023). From seed to seed: the role of microbial inheritance in the assembly of the plant microbiome. *Trends in Microbiology*, *31*(4), 346-355.
2. Adeboye, K. A., Fayose, C. A., Ayangbenro, A. S., Oyetunde, O. A., Awopegba, T. M., Adeleke, B. S., Daniel, I. O., & Boerner, A. (2025). Harnessing microbial communities to enhance seed germination: a review of opportunities and challenges. *Discover Agriculture*, *3*(1), 258.
3. Adhikary, K., Selim, S., Sarkar, R., Ganguly, K., Das, J., Almuhayawi, M. S., Alruhaili, M. H., Gattan, H. S., & Karak, P. (2026). Synthetic microbiomes in bioengineered rhizospheres: new frontiers for climate-resilient agriculture. *Frontiers in Microbiology*, *17*, 1780132.
4. Afzal, I., Javed, T., Amirkhani, M., & Taylor, A. G. (2020). Modern seed technology: Seed coating delivery systems for enhancing seed and crop performance. *Agriculture*, *10*(11), 526.
5. Aloo, B. N., Tripathi, V., Makumba, B. A., & Mbega, E. R. (2022). Plant growth-promoting rhizobacterial biofertilizers for crop production: The past, present, and future. *Frontiers in Plant Science*, *13*, 1002448.
6. Arnault, G., Colaert-Sentenac, L., Marais, C., Sarniguet, A., Barret, M., & Simonin, M. (2025). Synthetic community inoculation on seeds revealed its transient colonization capacity but legacy effects on plant microbiota assembly. *bioRxiv*, 2025.2003. 2028.645722.

7. Arnault, G., Marais, C., Préveaux, A., Briand, M., Poisson, A.-S., Sarniguet, A., Barret, M., & Simonin, M. (2024). Seedling microbiota engineering using bacterial synthetic community inoculation on seeds. *FEMS Microbiology Ecology*, *100*(4), fiae027.
8. Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., & Smith, D. L. (2018). Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science*, *9*, 1473.
9. Balla, A., Silini, A., Cherif-Silini, H., Chenari Bouket, A., Alenezi, F. N., & Belbahri, L. (2022). Recent advances in encapsulation techniques of plant growth-promoting microorganisms and their prospects in the sustainable agriculture. *Applied Sciences*, *12*(18), 9020.
10. Barret, M., Briand, M., Bonneau, S., Préveaux, A., Valière, S., Bouchez, O., Hunault, G., Simoneau, P., & Jacques, M.-A. (2015). Emergence shapes the structure of the seed microbiota. *Applied and Environmental Microbiology*, *81*(4), 1257-1266.
11. Beghini, F., McIver, L. J., Blanco-Míguez, A., Dubois, L., Asnicar, F., Maharjan, S., Mailyan, A., Manghi, P., Scholz, M., & Thomas, A. M. (2021). Integrating taxonomic, functional, and strain-level profiling of diverse microbial communities with bioBakery 3. *elife*, *10*, e65088.
12. Beltran-Medina, I., Romero-Perdomo, F., Molano-Chavez, L., Gutiérrez, A. Y., Silva, A. M., & Estrada-Bonilla, G. (2023). Inoculation of phosphate-solubilizing bacteria improves soil phosphorus mobilization and maize productivity. *Nutrient Cycling in Agroecosystems*, *126*(1), 21-34.
13. Berg, G., & Raaijmakers, J. M. (2018). Saving seed microbiomes. *The ISME Journal*, *12*(5), 1167-1170.
14. Bergmann, G. E., Heitmann, S. J., Busby, P. E., & Leveau, J. H. (2022). Characterization of seed mycobiota using culture-dependent and culture-independent approaches. In *Microbial Environmental Genomics (MEG)* (pp. 65-78). Springer.
15. Bhattacharyya, P. N., & Jha, D. K. (2012). Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology*, *28*(4), 1327-1350.
16. Bibi, F., & Rahman, A. (2023). An overview of climate change impacts on agriculture and their mitigation strategies. *Agriculture*, *13*(8), 1508.
17. Bintarti, A. F., Kearns, P. J., Sulesky-Grieb, A., & Shade, A. (2022). Abiotic treatment to common bean plants results in an altered endophytic seed microbiome. *Microbiology Spectrum*, *10*(2), e00210-00221.
18. Boers, S. A., Jansen, R., & Hays, J. P. (2019). Understanding and overcoming the pitfalls and biases of next-generation sequencing (NGS) methods for use in the routine clinical microbiological diagnostic laboratory. *European Journal of Clinical Microbiology & Infectious Diseases*, *38*(6), 1059-1070.
19. Bozdar, B., Ahmed, N., Meghwar, M. R., Zhu, Z., Talpur, A., & Li, Z. H. (2026). Seed Pelleting Technologies: Paving the Way for Resilient and Sustainable Future Farming. *Food and Energy Security*, *15*(1), e70193.
20. Brown, V. S., Erickson, T. E., Merritt, D. J., Madsen, M. D., Hobbs, R. J., & Ritchie, A. L. (2021). A global review of seed enhancement technology use to inform improved applications in restoration. *Science of the Total Environment*, *798*, 149096.
21. Cardarelli, M., Woo, S. L., Rouphael, Y., & Colla, G. (2022). Seed treatments with microorganisms can have a biostimulant effect by influencing germination and seedling growth of crops. *Plants*, *11*(3), 259.
22. Chen, J., Zhao, G., Wei, Y., Dong, Y., Hou, L., & Jiao, R. (2021). Isolation and screening of multifunctional phosphate solubilizing bacteria and its growth-promoting effect on Chinese fir seedlings. *Scientific reports*, *11*(1), 9081.
23. Cheng, Y., Shi, X., Narayanan, M., Li, Z., Li, Y., & Ma, Y. (2025). Enhancing nutrient uptake efficiency in Zea mays: The role of plant growth-promoting bacteria in modifying root characteristics and mobilizing soil nutrients. *Journal of the Science of Food and Agriculture*, *105*(9), 5030-5039.
24. Compant, S., Cassan, F., Kostić, T., Johnson, L., Brader, G., Trognitz, F., & Sessitsch, A. (2025). Harnessing the plant microbiome for sustainable crop production. *Nature Reviews Microbiology*, *23*(1), 9-23.
25. Compant, S., Duffy, B., Nowak, J., Clément, C., & Barka, E. d. A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Applied and Environmental Microbiology*, *71*(9), 4951-4959.
26. David, E. M., & Parthasarathi, T. (2026). Soil microbial processes shaping seed performance: linking soil microbiomes to sustainable agriculture. *Frontiers in Microbiology*, *17*, 1797362.
27. de Andrade, L. A., Santos, C. H. B., Frezarin, E. T., Sales, L. R., & Rigobelo, E. C. (2023). Plant growth-promoting rhizobacteria for sustainable agricultural production. *Microorganisms*, *11*(4), 1088.
28. de Jesus Boaventura, K., Da Silva, C. M., & Silva, S. D. (2023). Building soil fertility: Embrapa and the agronomic development for the "conquest" of the Brazilian Cerrado (1975-95). *História Agrária: revista de agricultura e história rural*(89), 247-278.
29. De Souza, R. S. C., Armanhi, J. S. L., & Arruda, P. (2020). From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. *Frontiers in Plant Science*, *11*, 1179.

30. Devi, S. P., Ranjithkumar, R., Djearamane, S., Tey, L.-H., Wong, L. S., Kayarohanam, S., Arumugam, N., Almansour, A. I., & Perumal, K. (2023). Organic Remobilization of zinc and phosphorus availability to plants by application of mineral solubilizing bacteria Pseudomonas aeruginosa. *Heliyon*, *9*(11).
31. Di Salvo, L. P., Cellucci, G. C., Carlino, M. E., & de Salamone, I. E. G. (2018). Plant growth-promoting rhizobacteria inoculation and nitrogen fertilization increase maize (Zea mays L.) grain yield and modified rhizosphere microbial communities. *Applied Soil Ecology*, *126*, 113-120.
32. Díaz-Rodríguez, A. M., Parra Cota, F. I., Cira Chávez, L. A., García Ortega, L. F., Estrada Alvarado, M. I., Santoyo, G., & de Los Santos-Villalobos, S. (2025). Microbial inoculants in sustainable agriculture: advancements, challenges, and future directions. *Plants*, *14*(2), 191.
33. Eliseeva, L., Eliseev, I., & Mikhailova, N. (2025). The effect of treatment of legume seeds with bacterial preparations on crop formation. BIO Web of Conferences,
34. Fanai, A., Bohia, B., Lalremruati, F., Lalhriatpuii, N., Lalmuanpuii, R., & Singh, P. K. (2024). Plant growth promoting bacteria (PGPB)-induced plant adaptations to stresses: an updated review. *PeerJ*, *12*, e17882.
35. Farah, A. A., Mohamed, M. A., Musse, O. S. H., & Nor, B. A. (2025). The multifaceted impact of climate change on agricultural productivity: A systematic literature review of SCOPUS-indexed studies (2015–2024). *Discover Sustainability*, *6*(1), 397.
36. Ferreira, M. J., Silva, H., & Cunha, A. (2019). Siderophore-producing rhizobacteria as a promising tool for empowering plants to cope with iron limitation in saline soils: a review. *Pedosphere*, *29*(4), 409-420.
37. Fiodor, A., Ajijah, N., Dziewit, L., & Pranaw, K. (2023). Biopriming of seed with plant growth-promoting bacteria for improved germination and seedling growth. *Frontiers in Microbiology*, *14*, 1142966.
38. Fiuzi, A., Hassanzadehdelouei, M., & Madani, A. (2024). Synergistic effects of microbial inoculation, different forms of iron application, and phosphorus on wheat growth and nutrient uptake in alkaline soil. *Journal of Plant Nutrition*, *47*(18), 2972-2988.
39. Fouad, N., Elzayat, E. M., Amr, D., El-Khishin, D. A., Radwan, K. H., Youssef, A., Khalaf, A. A., Ahmed, H. A., Radwan, E. H., & Tawkaz, S. (2026). Rhizosphere Microbiome Engineering for Climate-Smart Agriculture: From Synthetic Consortia to Precision Decision Support. *Microorganisms*, *14*(5), 1138.
40. Francioli, D., Kampouris, I. D., Kuhl-Nagel, T., Babin, D., Sommermann, L., Behr, J. H., Chowdhury, S. P., Zrenner, R., Moradtalab, N., & Schloter, M. (2025). Microbial inoculants modulate the rhizosphere microbiome, alleviate plant stress responses, and enhance maize growth at field scale. *Genome Biology*, *26*(1), 148.
41. Frank, A. C., Saldierna Guzmán, J. P., & Shay, J. E. (2017). Transmission of bacterial endophytes. *Microorganisms*, *5*(4), 70.
42. Gao, B., Chai, X., Huang, Y., Wang, X., Han, Z., Xu, X., Wu, T., Zhang, X., & Wang, Y. (2022). Siderophore production in pseudomonas SP. strain SP3 enhances iron acquisition in apple rootstock. *Journal of applied microbiology*, *133*(2), 720-732.
43. Garrido-Sanz, D., & Keel, C. (2025). Seed-borne bacteria drive wheat rhizosphere microbiome assembly via niche partitioning and facilitation. *Nature Microbiology*, *10*(5), 1130-1144.
44. Granada, C. E., Passaglia, L. M., De Souza, E. M., & Sperotto, R. A. (2018). Is phosphate solubilization the forgotten child of plant growth-promoting rhizobacteria? *Frontiers in Microbiology*, *9*, 2054.
45. Halmer, P. (2006). Seed technology and seed enhancement. XXVII International Horticultural Congress-IHC2006: International Symposium on Seed Enhancement and Seedling Production 771,
46. Hanif, M. S., Tayyab, M., Baillo, E. H., Islam, M. M., Islam, W., & Li, X. (2024). Plant microbiome technology for sustainable agriculture. *Frontiers in Microbiology*, *15*, 1500260.
47. Harman, G. E. (2011). Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. *New Phytologist*, *189*(3).
48. Hayat, R., Ali, S., Amara, U., Khalid, R., & Ahmed, I. (2010). Soil beneficial bacteria and their role in plant growth promotion: a review. *Annals of microbiology*, *60*(4), 579-598.
49. Huo, Q., Gong, M., Jiang, Y., Yang, X., Kong, M., He, J., Zhang, Q., Song, J., Li, X., & Han, W. (2024). Microencapsulated microbial seed coating could improve soil environment and maize grain yield in saline soil. *Plants*, *13*(22), 3139.
50. Hyder, S., Rizvi, Z. F., los Santos-Villalobos, S. d., Santoyo, G., Gondal, A., Khalid, N., Fatima, S. N., Nadeem, M., Rafique, K., & Rani, A. (2023). Applications of plant growth-promoting rhizobacteria for increasing crop production and resilience. *Journal of plant nutrition*, *46*(10), 2551-2580.
51. Islam, S. (2025). Agriculture, food security, and sustainability: a review. *Exploration of Foods and Foodomics*, *3*, 101082.
52. Jaramillo-López, P. F., Romero, J. B., Sarabia, M., Fonteyne, S., Saldivia-Tejeda, A., Verhulst, N., Vestergård, M., & Larsen, J. (2024). Non-target effects of pesticide and microbial seed treatments in maize and barley on the resident soil microbiota under conservation agriculture. *European Journal of Soil Biology*, *122*, 103653.

53. Javed, S., Ismail, S., AL, D., & SS, M. (2023). Effect of Microbial Consortia Inoculation and Chemical Fertilizers on Growth Parameter and Nodulation of Soybean (Glycine max L. merill.) and Chickpea (Cicer arietinum L.). *International Journal of Plant & Soil Science*, *35*(22), 779-790.
54. Johnston-Monje, D., Gutiérrez, J. P., & Lopez-Lavalle, L. A. B. (2021). Seed-transmitted bacteria and fungi dominate juvenile plant microbiomes. *Frontiers in Microbiology*, *12*, 737616.
55. Kampa, R., Vittal, R., Basha, S. A., Pushpavalli, S., & Bokka, V. (2025). Plant Growth-Promoting Microbial Consortia for Effective Biocontrol of Groundnut Collar Rot and Chickpea Wilt. *Plant Pathology*, *74*(4), 1121-1141.
56. Kampouris, I. D., Kuhl-Nagel, T., Behr, J. H., Sommermann, L., Babin, D., Francioli, D., Zrenner, R., Kublik, S., Schloter, M., & Ludewig, U. (2025). Selective recruitment of beneficial microbes in the rhizosphere of maize affected by microbial inoculants, farming practice, and seasonal variations. *Environmental Microbiome*, *20*(1), 69.
57. Khan, A., Singh, A. V., Gautam, S. S., Agarwal, A., Punetha, A., Upadhayay, V. K., Kukreti, B., Bundela, V., Jugran, A. K., & Goel, R. (2023). Microbial bioformulation: a microbial assisted biostimulating fertilization technique for sustainable agriculture. *Frontiers in Plant Science*, *14*, 1270039.
58. Kim, H., Jeon, J., Lee, K. K., & Lee, Y.-H. (2022). Longitudinal transmission of bacterial and fungal communities from seed to seed in rice. *Communications Biology*, *5*(1), 772.
59. Kong, Z., & Liu, H. (2022). Modification of rhizosphere microbial communities: a possible mechanism of plant growth promoting rhizobacteria enhancing plant growth and fitness. *Frontiers in Plant Science*, *13*, 920813.
60. Kuan, K. B., Othman, R., Abdul Rahim, K., & Shamsuddin, Z. H. (2016). Plant growth-promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PloS one*, *11*(3), e0152478.
61. Kumar, B., Lorusso, E., Fosso, B., & Pesole, G. (2024). A comprehensive overview of microbiome data in the light of machine learning applications: categorization, accessibility, and future directions. *Frontiers in Microbiology*, *15*, 1343572.
62. Lamichhane, J. R., Corrales, D. C., & Soltani, E. (2022). Biological seed treatments promote crop establishment and yield: a global meta-analysis: Biological seed treatments promote crop establishment and yield: a global meta-analysis. *Agronomy for Sustainable Development*, *42*(3), 45.
63. Liu, S., Moon, C. D., Zheng, N., Huws, S., Zhao, S., & Wang, J. (2022). Opportunities and challenges of using metagenomic data to bring uncultured microbes into cultivation. *Microbiome*, *10*(1), 76.
64. Liu, Y.-X., Qin, Y., Chen, T., Lu, M., Qian, X., Guo, X., & Bai, Y. (2021). A practical guide to amplicon and metagenomic analysis of microbiome data. *Protein & cell*, *12*(5), 315-330.
65. Lopes, M. J. d. S., Dias-Filho, M. B., & Gurgel, E. S. C. (2021). Successful plant growth-promoting microbes: inoculation methods and abiotic factors. *Frontiers in Sustainable Food Systems*, *5*, 606454.
66. Luo, D., Shi, J., Li, M., Chen, J., Wang, T., Zhang, Q., Yang, L., Zhu, N., & Wang, Y. (2024). Consortium of phosphorus-solubilizing bacteria promotes maize growth and changes the microbial community composition of hizosphere soil. *Agronomy*, *14*(7), 1535.
67. Ma, Y. (2019). Seed coating with beneficial microorganisms for precision agriculture. *Biotechnology advances*, *37*(7), 107423.
68. Mahmood, H., Hassan, M. S., Meraj, G., & Furqan, M. (2024). Agriculture's role in environmental sustainability: a comprehensive review of challenges and solutions. *Challenges in Sustainability*, *12*(3), 178-189.
69. Mallick, H., Franzosa, E. A., Mclver, L. J., Banerjee, S., Sirota-Madi, A., Kostic, A. D., Clish, C. B., Vlamakis, H., Xavier, R. J., & Huttenhower, C. (2019). Predictive metabolomic profiling of microbial communities using amplicon or metagenomic sequences. *Nature communications*, *10*(1), 3136.
70. Marinković, J., Miljaković, D., Červenski, J., Vasiljević, M., Đorđević, V., Tamindžić, G., & Miladinović, J. (2025). Synergistic Effect of PGPR and Nutrient Complex on Soybean Seed Germination and Initial Seedling Growth. *Agriculture*, *15*(19), 2022.
71. Mbah, C. E., Sunbare-Funto, O. J., Ajibade, O. A., & Oyawoye, O. M. (2025). Microbial allies in seeds: pioneering sustainable solutions for crop productivity and resilience.
72. McLennon, E., Dari, B., Jha, G., Sihi, D., & Kankarla, V. (2021). Regenerative agriculture and integrative permaculture for sustainable and technology driven global food production and security. *Agronomy Journal*, *113*(6), 4541-4559.
73. Mitra, D., Mondal, R., Khoshru, B., Shadangi, S., Mohapatra, P. K. D., & Panneerselvam, P. (2021). Rhizobacteria mediated seed bio-priming triggers the resistance and plant growth for sustainable crop production. *Current Research in Microbial Sciences*, *2*, 100071.
74. Mitter, B., Pfaffenbichler, N., Flavell, R., Compant, S., Antonielli, L., Petric, A., Berninger, T., Naveed, M., Sheibani-Tezerji, R., & Von Maltzahn, G. (2017). A new approach to modify plant microbiomes and traits by introducing beneficial bacteria at flowering into progeny seeds. *Frontiers in Microbiology*, *8*, 11.

75. Monika, K., Bastian, D., Palathingal, V. F., Rashmi, C., & Revi, S. (2025). Comparative Efficacy of Microbial Biopriming on Germination Kinetics and Seedling Vigor in Rice (Oryza sativa L.). *Microbiology Research Journal International*, *35*(12), 101-107.
76. Moreno-Valencia, F. D., Plascencia-Espinosa, M. Á., Morales-García, Y. E., & Muñoz-Rojas, J. (2024). Selection and effect of plant growth-promoting bacteria on pine seedlings (Pinus montezumae and Pinus patula). *Life*, *14*(10), 1320.
77. Naik, K., Mishra, S., Srichandan, H., Singh, P. K., & Choudhary, A. (2020). Microbial formulation and growth of cereals, pulses, oilseeds and vegetable crops. *Sustainable Environment Research*, *30*(1), 10.
78. Nawaz, H., Hussain, N., Ahmed, N., & Alam, J. (2021). Efficiency of seed bio-priming technique for healthy mungbean productivity under terminal drought stress. *Journal of integrative agriculture*, *20*(1), 87-99.
79. Nelson, E. B. (2018). The seed microbiome: origins, interactions, and impacts. *Plant and Soil*, *422*(1), 7-34.
80. Novak, S. D., Aguirre, K. A., Neher, W. R., & Torres, A. M. (2026). Bacterial endophytes journey from the seed to the seedling: an analysis of community structural shifts and bacterial localization during colonization. *BMC Plant Biology*.
81. O'Callaghan, M. (2016). Microbial inoculation of seed for improved crop performance: issues and opportunities. *Applied microbiology and biotechnology*, *100*(13), 5729-5746.
82. Ocwa, A., Ssemugenze, B., & Harsányi, E. (2024). Seed treatment with Bacillus bacteria improves maize production: a narrative review. *Acta Agraria Debreceniensis*(1), 105-111.
83. Orozco-Mosqueda, M. D. C., Santoyo, G., & Glick, B. R. (2023). Recent advances in the bacterial phytohormone modulation of plant growth. *Plants*, *12*(3), 606.
84. Panchal, K., Sudhir, A., & Prajapati, A. S. (2026). Engineering the plant microbiome: synthetic community approaches to enhance crop protection. *Frontiers in Plant Science*, *16*, 1705289.
85. Park, I., Seo, Y.-S., & Mannaa, M. (2023). Recruitment of the rhizo-microbiome army: assembly determinants and engineering of the rhizosphere microbiome as a key to unlocking plant potential. *Frontiers in Microbiology*, *14*, 1163832.
86. Paulikienė, S., Benesevičius, D., Benesevičienė, K., & Ūksas, T. (2025). Seed treatment: Importance, application, impact, and opportunities for increasing sustainability. *Agronomy*, *15*(7), 1689.
87. Penrose, D. M., & Glick, B. R. (2003). Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting rhizobacteria. *Physiologia plantarum*, *118*(1), 10-15.
88. Penuelas, J., Coello, F., & Sardans, J. (2023). A better use of fertilizers is needed for global food security and environmental sustainability. *Agriculture & Food Security*, *12*(1), 5.
89. Pieterse, C. M., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C., & Bakker, P. A. (2014). Induced systemic resistance by beneficial microbes. *Annual review of phytopathology*, *52*(1), 347-375.
90. Poonguzhali, G., Rajendran, L., Manoranjitham, S., Raja, P., Vinothkumar, B., & Saravanakumari, K. (2025). Seed microbiome in crop disease management. *Israel Journal of Plant Sciences*, *1*(aop), 1-14.
91. Poppeliers, S. W., Sánchez-Gil, J. J., & de Jonge, R. (2023). Microbes to support plant health: understanding bioinoculant success in complex conditions. *Current opinion in microbiology*, *73*, 102286.
92. Portal-Gonzalez, N., Wang, W., He, W., & Santos-Bermudez, R. (2025). Engineering plant holobionts for climate-resilient agriculture. *The ISME Journal*, *19*(1), wraf158.
93. Prado, A., Marolleau, B., Vaissière, B. E., Barret, M., & Torres-Cortes, G. (2020). Insect pollination: an ecological process involved in the assembly of the seed microbiota. *Scientific reports*, *10*(1), 3575.
94. Priyadharshini, C., Gnanachitra, M., Balachandar, D., & Jayanthi, D. (2022). Assessment of shelf-life and efficacy of the seed-coating delivery system of biofertilizers in maize. *International Journal of Plant & Soil Science*, *34*(22), 548-558.
95. Qi, X., Jin, D., Olimi, E., Chen, X., & Cernava, T. (2026). What do we know about the seed microbiome? *Microbiome*, *14*(1), 106.
96. Ranjan, R., Singh, R., Yadav, A., & Yadav, G. (2024). Response of Nitrogen, Phosphorus and Potassium on Nutrient Content and Uptake by Mungbean (Vigna radiata L.). *International Journal of Environment and Climate Change*, *14*(2), 392-397.
97. Raza, A., Khare, T., Zhang, X., Rahman, M. M., Hussain, M., Gill, S. S., Chen, Z. H., Zhou, M., Hu, Z., & Varshney, R. K. (2025). Novel strategies for designing climate-smart crops to ensure sustainable agriculture and future food security. *Journal of sustainable agriculture and environment*, *4*(2), e70048.
98. Richardson, A. E., Barea, J.-M., McNeill, A. M., & Prigent-Combaret, C. (2009). Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. In: Springer.
99. Rocha, I., Ma, Y., Souza-Alonso, P., Vosátka, M., Freitas, H., & Oliveira, R. S. (2019). Seed coating: a tool for delivering beneficial microbes to agricultural crops. *Frontiers in Plant Science*, *10*, 1357.
100. Rochefort, A., Simonin, M., Marais, C., Guillerm-Erckelboudt, A.-Y., Barret, M., & Sarniguet, A. (2021). Transmission of seed and soil microbiota to seedling. *Msystems*, *6*(3), 10.1128/msystems. 00446-00421.

101. Rodríguez, C. E., Antonielli, L., Mitter, B., Trognitz, F., & Sessitsch, A. (2020). Heritability and functional importance of the Setaria viridis bacterial seed microbiome. *Phytobiomes Journal*, *4*(1), 40-52.
102. Romão, I. R., do Carmo Gomes, J., Silva, D., & Vilchez, J. I. (2025). The seed microbiota from an application perspective: an underexplored frontier in plant–microbe interactions. *Crop Health*, *3*(1), 12.
103. Rybakova, D., Mancinelli, R., Wikström, M., Birch-Jensen, A.-S., Postma, J., Ehlers, R.-U., Goertz, S., & Berg, G. (2017). The structure of the Brassica napus seed microbiome is cultivar-dependent and affects the interactions of symbionts and pathogens. *Microbiome*, *5*(1), 104.
104. Sain, S. K., Dewasi, H., & Singh, A. (2023). Combined application of effective Trichoderma, Pseudomonas and arbuscular mycorrhiza spp. reduced soil-borne diseases and boosted growth in cotton. *Egyptian Journal of Biological Pest Control*, *33*(1), 94.
105. Saleem, M., Arshad, M., Hussain, S., & Bhatti, A. S. (2007). Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. *Journal of industrial Microbiology and Biotechnology*, *34*(10), 635-648.
106. Samreen, T., Naveed, M., Nazir, M. Z., Asghar, H. N., Khan, M. I., Zahir, Z. A., Kanwal, S., Jeevan, B., Sharma, D., & Meena, V. S. (2021). Seed associated bacterial and fungal endophytes: Diversity, life cycle, transmission, and application potential. *Applied Soil Ecology*, *168*, 104191.
107. Sarkar, A., Ghosh, P. K., Pramanik, K., Mitra, S., Soren, T., Pandey, S., Mondal, M. H., & Maiti, T. K. (2018). A halotolerant Enterobacter sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Research in microbiology*, *169*(1), 20-32.
108. Sarkar, D., Singh, S., Parihar, M., & Rakshit, A. (2021). Seed bio-priming with microbial inoculants: A tailored approach towards improved crop performance, nutritional security, and agricultural sustainability for smallholder farmers. *Current Research in Environmental Sustainability*, *3*, 100093.
109. Shade, A., Jacques, M.-A., & Barret, M. (2017). Ecological patterns of seed microbiome diversity, transmission, and assembly. *Current opinion in microbiology*, *37*, 15-22.
110. Shah, A., Nazari, M., Antar, M., Msimbira, L. A., Naamala, J., Lyu, D., Rabileh, M., Zajonc, J., & Smith, D. L. (2021). PGPR in agriculture: A sustainable approach to increasing climate change resilience. *Frontiers in Sustainable Food Systems*, *5*, 667546.
111. Shahzad, R., Khan, A. L., Bilal, S., Asaf, S., & Lee, I.-J. (2018). What is there in seeds? Vertically transmitted endophytic resources for sustainable improvement in plant growth. *Frontiers in Plant Science*, *9*, 24.
112. Shakya, M., Lo, C.-C., & Chain, P. S. (2019). Advances and challenges in metatranscriptomic analysis. *Frontiers in genetics*, *10*, 904.
113. Sharma, K., Singh, U., Sharma, P., Kumar, A., & Sharma, L. (2015). Seed treatments for sustainable agriculture-A review. *Journal of Applied and Natural Science*, *7*(1), 521.
114. Sharma, N., Mahawar, L., Mishra, A., & Albrectsen, B. R. (2025). Microbial Contributions to Plant Growth and StressTolerance: Mechanisms for Sustainable Plant Production. *Plant Stress*, 100966.
115. Shayanthan, A., Ordoñez, P. A. C., & Oresnik, I. J. (2022). The role of synthetic microbial communities (SynCom) in sustainable agriculture. *Frontiers in Agronomy*, *4*, 896307.
116. Simonin, M., Briand, M., Chesneau, G., Rochefort, A., Marais, C., Sarniguet, A., & Barret, M. (2022). Seed microbiota revealed by a large-scale meta-analysis including 50 plant species. *New Phytologist*, *234*(4), 1448-1463.
117. Singh, P., Singh, R. K., Li, H.-B., Guo, D.-J., Sharma, A., Verma, K. K., Solanki, M. K., Upadhyay, S. K., Lakshmanan, P., & Yang, L.-T. (2024). Nitrogen fixation and phytohormone stimulation of sugarcane plant through plant growth promoting diazotrophic Pseudomonas. *Biotechnology and Genetic Engineering Reviews*, *40*(1), 15-35.
118. Singh, P., Vaishnav, A., Liu, H., Xiong, C., Singh, H. B., & Singh, B. K. (2023). Seed biopriming for sustainable agriculture and ecosystem restoration. *Microbial Biotechnology*, *16*(12), 2212-2222.
119. Su, C., Lei, L., Duan, Y., Zhang, K.-Q., & Yang, J. (2012). Culture-independent methods for studying environmental microorganisms: methods, application, and perspective. *Applied microbiology and biotechnology*, *93*(3), 993-1003.
120. Sulesky-Grieb, A., Simonin, M., Bintarti, A. F., Marolleau, B., Barret, M., & Shade, A. (2024). Stable, multigenerational transmission of the bean seed microbiome despite abiotic stress. *Msystems*, *9*(11), e00951-00924.
121. Tan, T., Xu, Z., Tao, L., Sun, X., Xie, J., Miao, Y., Zhang, N., Xun, W., Beauregard, P. B., & Kovács, Á. T. (2025). Siderophore-mediated iron enrichment in the biofilm matrix enhances plant iron nutrition. *Cell Reports*, *44*(11).
122. Thomas, L., & Singh, I. (2019). Microbial biofertilizers: types and applications. In *Biofertilizers for sustainable agriculture and environment* (pp. 1-19). Springer.
123. Timofeeva, A. M., Galyamova, M. R., & Sedykh, S. E. (2023). Plant growth-promoting soil bacteria: nitrogen fixation, phosphate solubilization, siderophore production, and other biological activities. *Plants*, *12*(24), 4074.
124. Truyens, S., Weyens, N., Cuypers, A., & Vangronsveld, J. (2015). Bacterial seed endophytes: genera, vertical transmission and interaction with plants. *Environmental Microbiology Reports*, *7*(1), 40-50.

125. Velte, J. M., Mudiyanselage, S., Hofmann, O. F., Lee, S. T., Huguet-Tapia, J., Miranda, M., & Martins, S. J. (2025). Interactions between native soil microbiome and a synthetic microbial community reveals bacteria with persistent traits. *Msystems*, *10*(9), e00921-00925.
126. Verma, K. K., Song, X. P., Kumari, A., Jagadesh, M., Singh, S. K., Bhatt, R., Singh, M., Seth, C. S., & Li, Y. R. (2025). Climate change adaptation: challenges for agricultural sustainability. *Plant, Cell & Environment*, *48*(4), 2522-2533.
127. Vessey, J. K. (2003). Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil*, *255*(2), 571-586.
128. Vompe, A. D., Hamidizade, M., López, M. M., O'Connor, E., Kaur, L., Hockett, K. L., & Bull, C. T. (2026). Translational microbiomes in agriculture: microbial communities as tools to effect host and system health for improved crop production. *Applied and Environmental Microbiology*, e01704-01725.
129. Walsh, C. M., Becker-Uncapher, I., Carlson, M., & Fierer, N. (2021). Variable influences of soil and seed-associated bacterial communities on the assembly of seedling microbiomes. *The ISME Journal*, *15*(9), 2748-2762.
130. War, A. F., Bashir, I., Reshi, Z. A., Kardol, P., & Rashid, I. (2023). Insights into the seed microbiome and its ecological significance in plant life. *Microbiological Research*, *269*, 127318.
131. Wassermann, B., Cernava, T., Müller, H., Berg, C., & Berg, G. (2019). Seeds of native alpine plants host unique microbial communities embedded in cross-kingdom networks. *Microbiome*, *7*(1), 108.
132. Wassermann, B., Rybakova, D., Adam, E., Zachow, C., Bernhard, M., Müller, M., Mancinelli, R., & Berg, G. (2020). Studying seed microbiomes. In *The Plant Microbiome: Methods and Protocols* (pp. 1-21). Springer.
133. Xu, X.-Y., Wang, C.-L., Xu, J.-Y., Dong, C.-J.-H., Tan, C., He, Y.-X., Hu, H.-W., Shu, K., Dai, C.-C., & Chen, Z.-H. (2026). Seed-microbiome interactions: Mechanistic insights and utilization toward seed performance for sustainable agriculture. *Plant Communications*.
134. Xun, W., Ren, Y., Yan, H., Ma, A., Liu, Z., Wang, L., Zhang, N., Xu, Z., Miao, Y., & Feng, H. (2023). Sustained inhibition of maize seed-borne Fusarium using a Bacillus-dominated rhizospheric stable core microbiota with unique cooperative patterns. *Advanced Science*, *10*(5), 2205215.
135. Yadav, J., Gehlot, P., Soni, P., & Jain, T. (2026). Plant microbiome engineering: from inoculation to genome editing. *Frontiers in Microbiology*, *17*, 1781381.
136. Yang, P., Lu, L., Condrich, A., Muni, G. A., Scranton, S., Xu, S., Xia, Y., & Huang, S. (2025). Innovative approaches for engineering the seed microbiome to enhance crop performance. *Seeds*, *4*(2), 24.
137. Yao, Y., Zhao, L., Zhang, Y., Duan, A., Yang, Y., Wang, A., Xue, C., Zhang, J., & Zhao, M. (2026). Comparative analysis of the seed microbiome in four major oilseed crops (rapeseed, sunflower, soybean, sesame) reveals host-specific assembly and potential application of seed core microbes. *Frontiers in Plant Science*, *17*, 1721916.
138. YILDIRIM, K. C., Orel, D. C., Okyay, H., Gürsan, M. M., & Yildiz, G. (2025). Enhancing seed quality and plant growth through modification of seed microbiome with beneficial endophytic bacteria. *Scientia Horticulturae*, *354*, 114531.
139. Zhang, J., Liu, W., Wang, B., Zhai, Q., & Bai, Y. (2026). Plant microbiome regulation for sustainable agriculture. *Current Opinion in Biotechnology*, *98*, 103444.
140. Zhang, X., Ma, Y.-N., Wang, X., Liao, K., He, S., Zhao, X., Guo, H., Zhao, D., & Wei, H.-L. (2022). Dynamics of rice microbiomes reveal core vertically transmitted seed endophytes. *Microbiome*, *10*(1), 216.
141. Zholdasbek, A., Tekebayeva, Z., Kulzhanova, K., Abzhalelov, A., Bekshin, Z., Yevneyeva, D., Saylau, M., Li, X., Tan, Z., & Wang, Z. (2026). Microbiome and plant relationship: a symbiosis against phytopathogens. *Frontiers in Plant Science*, *17*, 1722279.