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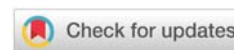
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Review Article

The Seed Microbiome: Microbial Hashes for Plant Wellbeing

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Abstract

Seeds harbour diverse and unique microbial communities that significantly influence seed quality, germination, seedling health, and overall plant resilience. The seed microbiome is shaped by both vertical transmission (from parent plants) and horizontal transmission (from the surrounding environment), with microbial colonization highly dependent on floral pathways, microbial composition, and seed structure. However, the mechanisms governing microbial transmission, their functional roles, and their impact on plant development remain poorly understood. This gap in knowledge limits the ability to harness beneficial microbial interactions for improving germination success and plant health. This review explores the sources and transmission routes of the seed microbiome, emphasizing its role in germination, plant nutrition, disease resistance, and stress tolerance. Additionally, it highlights the dynamic establishment of microbial communities during seedling development and their long-term influence on plant health and longevity. Understanding the complex interactions within the seed microbiome is crucial for leveraging its potential in sustainable agriculture. By uncovering these microbial relationships, future research can pave the way for microbiome-based strategies to enhance crop productivity, resilience, and ecological sustainability.

Introduction

Seeds, holding the blueprint for the next generation, play a critical role in plant survival and growth. In agriculture, they initiate new crop cycles, but in natural ecosystems, they go beyond reproduction, enabling dispersal, adaptation, and establishment in new environments [1]. Nonetheless, a variety of obstacles must be overcome by both germinating seeds and seedlings, including fungal diseases, predators, and drought [2]. Even after developing roots, they can suffer from resource limits and inappropriate settings. This “seed-to-seedling transition” is a critical bottleneck in plant life, impacting both natural populations and agricultural success [3]. The microorganisms linked to seeds can originate from various plant organs. They can be transmitted to the seeds via gametes or vascular connections, which results in the establishment of microbes in the embryo and endosperm. Additionally, the source of the microorganisms may be the reproductive meristems [4,5]. Potential endophytes can typically enter plant

tissue through stomata, lenticels, regions where lateral roots arise, radicals, root hairs, and wounds that spontaneously form as a result of plant growth [6]. Throughout their life cycle, plants pick up a variety of bacteria from a variety of sources, and the majority of these germs are passed down through their seeds to the following generation. Variations in plant species, seed development, geographic location, and the existence of additional plant diseases can all affect the microbial makeup of seeds [7], some of which sources may include soil, rhizosphere, and phyllosphere. Plants negotiate a complicated network of interactions with their environment throughout their existence. The microbial communities that are closely related to plants are one of the most interesting subsets of the biotic players. The term “microbiota” refers to the collective term for these microscopic allies that constantly interact with their plant hosts, pertaining to their growth, resilience, and overall health [8].

Across diverse plant lineages, the seed microbiome varies widely, with the number of microbial genera ranging from

a few to thousands [9]. This variation partly stems from the evolutionary journey of plants themselves, with speciation, domestication, and breeding leaving a lasting mark on their microbial companions [10,11]. Studies exploring the “phylosymbiosis” of seed microbiomes reveal a clear link between plant lineage and the specific microbial community it harbours [12]. The microscopic ecosystem that exists inside seeds has enormous power to influence the life and health of plants. The seed microbiota is a varied community of microorganisms that serves as the initial inoculum for the plant’s overall microbiome, hence altering the plant’s fitness throughout its life cycle. It’s interesting to note that the microbes that dwell inside and around seeds, referred to as the seed microbiota, might affect the vigour of the seed in agricultural contexts as well as its suitability for human consumption [7,12]. The seed microbiome has not received as much attention as other plant compartments, such as the phyllosphere, endosphere, and rhizosphere, despite substantial advancements in research in these areas [13]. The dynamic assembly processes of this essential microbial community have come to light, in part due to a recent spike in interest in reproductive organs and early plant life stages [14]. The importance of seeds is often neglected, even with the recent wave of microbiome investigations [15,16]. A deeper comprehension of the relationships between plants and microbes requires acknowledging seeds as important participants in this ecosystem, capable of having a substantial impact on the composition, organization, and functionality of the plant microbiome [7]. Hence considering the above reflectance about seed microbiome we found out that although seed holds an enormous microbiome but still have limited information about acquisition, interaction, and its effect on seed germination and plant growth this review aims to establish a hypothesis about the seed microbiome that by utilizing beneficial seed-associated microbes can enhance seed germination, support plant establishment, and promote sustainable agricultural practices.

Plant and microbe interaction

Plants and microbes interact at every stage of their life cycles, and seeds are no exception. Relationships that are intimate or casual have an impact on the developing “seed microbiome.” It is important to consider seeds in the context of the plant microbiome since the microbial community is dynamic and continues to exist in later stages of plant growth [17]. Numerous chances for contact arise during development because of the diversity and number of microorganisms and the different niches that plants offer. Crucially, the microbial communities interacting with seeds and seedlings during these vulnerable stages shape their trajectories. These interactions influence plant populations and community dynamics in natural systems and ultimately determine the success or failure of crops in agriculture. Understanding these interactions is vital for ensuring the resilience of plant life in both natural and managed environments [7] (Figure 1). Spermatophytes, conquering land during the Devonian period, relied on seeds for survival, dispersal, and protection. But their success wasn’t solo – symbiotic relationships with microbes played a crucial role [18]. These microbial communities, residing within (endophytes) and on (epiphytes) seeds, form a diverse and functional “seed microbiome” that has long been overlooked [7,19]. Early perceptions of seed-borne microbes as solely pathogenic led to widespread sterilization practices, impacting beneficial populations and potentially leaving plants vulnerable [20,21]. However, studies like the symbiosis between fungi and tall fescue challenged this notion, highlighting the potential benefits of these microbial partners [22]. However, new studies have uncovered an amazing symbiotic tale that emphasizes the vital roles these microbes play in plant life. We now understand that the seed microbiome is a significant reservoir of beneficial microorganisms that influence processes such as seed dormancy, germination, environmental adaptation, disease resistance, and growth promotion [23], in contrast to old beliefs that prioritized seed sterilization. Studies on

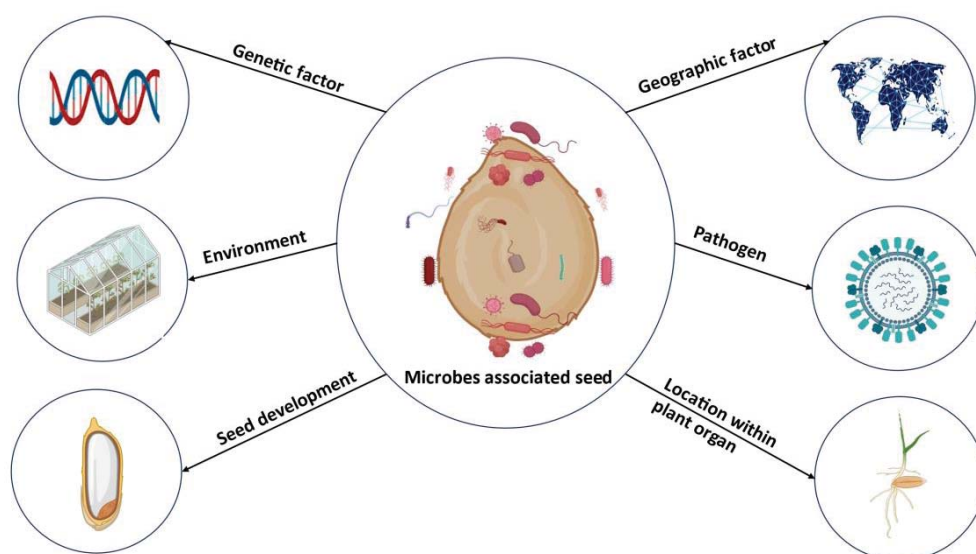


Figure 1: Factors affecting microbes associated with seeds.

the seed microbiome are still behind those on other plant compartments, such as the rhizosphere, despite this expanding knowledge because of their intimate host-microbe connections and potential for vertical transmission [24]. The identity of these dominant players varies greatly, both between different plant species and even within seeds of the same plant. Seeds, often overlooked, play a critical role not only in plant health but also in the entire agri-food system. Interestingly, they harbour their own unique communities of microorganisms, known as the seed microbiota, which significantly impact both seed quality and seedling development [25].

Effect of domestication on seed microbe

Plant domestication has reshaped seed traits and microbiomes, affecting germination, plant health, and resilience. With seeds providing up to 70% of human nutrition, understanding their microbial interactions is crucial [26,27]. Domestication-driven changes in seed size, metabolites, and reproduction influence these communities, shaping crop performance and sustainability [28]. The double-leash framework suggests that artificial selection alters plant-microbe interactions, impacting microbial diversity. Domesticated plants show species loss, replacement, or gain due to trait changes, as seen in wheat. Agricultural practices further shape microbiome assembly, influencing plant health and resilience. Seeds, acting as a key transmission route for beneficial microbes, provide an excellent model to study domestication's impact on microbiomes. Seed microbiomes, typically low in alpha diversity, are shaped by host-to-microbe interactions before dispersal. Domestication alters seed-related traits, such as size and chemical composition, influencing microbial colonization [29]. Microorganisms colonize seeds via the anthosphere (flowers), rhizosphere (roots), and phyllosphere (leaves). Changes in flowering traits, root structure, and plant immunity affect microbial connectivity. Domesticated crops, often having shorter life cycles, may experience reduced microbial exchange between roots and seeds.

Seed size, chemical composition, and secondary metabolites influence microbiome composition and function. Larger seeds, a common domestication trait, affect water uptake, seed exudate release, and microbial interactions in the spermosphere. Reduced secondary metabolites in domesticated seeds may alter pathogen survival and beneficial microbe transmission. Additionally, grafting, a common practice in fruit tree domestication, influences microbial connectivity between plant compartments, potentially affecting seed microbiome assembly [30].

Microbial acquisition in seeds: Horizontal vs. vertical transmission

Seeds serve as the first inoculum for the plant microbiota because they facilitate the transfer of microbes from one generation of plants to the next. Research has shown that bacteria linked to seeds not only perform comparable tasks to those of bacteria found in the rhizosphere, but they can also swiftly spread beneficial microbial communities through seeds, increasing the host plant's capacity to compete [31]. In any event, the diversity of microorganisms in seeds and their interactions with them can foster novel avenues for plant-microbe interaction research [32].

There are two primary ways that plants obtain their microbial communities: from their parents vertically and from the environment horizontally (Figure 2). Both of these mechanisms could have a major influence on the development of the seed microbiome, even though their relative significance is still up for discussion. It's interesting to note that the particular route the bacteria take to get at the seed determines the transmission mode – horizontal vs. vertical. There are three primary channels:

Internal route

The xylem vessels or nonvascular tissues, i.e. meristematic tissues of the mother plant, are the route by which microbes



Figure 2: Microbial transmission pathway.

enter the seed. Unless external bacteria (plant pathogens, for example) infiltrate these tissues, this can be regarded as vertical transmission [33]. These microorganisms have been identified in the endosperm, embryo, and seed coat, among other seed compartments. It has been observed that *Sophora davidii*-isolated endophytic seed-associated bacteria are vertically transferred to the following generation of plants [32]. Research indicates that the promotion of plant growth induced by bacteria associated with seeds is especially effective in unfavourable growth conditions. This is mainly due to the improvement of tolerance to abiotic stresses like drought and metalloids, as well as the enhancement of hydrolytic enzyme production [34].

Floral pathway

The stigma of the mother plant serves as a conduit for microbes to colonize the seed, indicating that although this entails acquiring the environment, the plant has the ability to choose which microorganisms go to the seed and therefore affect vertical transmission [35]. Microbes can attach themselves to seeds through the floral pathway, changing their makeup and possibly affecting the health of the plant. Research on a range of plants, including rice, apple tree, pumpkin, and grapes has revealed similarities between the microbial communities found in their flowers and seeds. These findings point to the floral pathway as a major avenue for transmission [36]. The mechanism, efficacy, and specificity of this transmission are significantly influenced by the closeness of flowers to growing seeds. The floral route seems to be less selective and more open, which may favour non-specialized microorganisms that do not have close pathogenic or symbiotic connections with the host plant, which is opposite to the vascular system. Intriguingly, in common beans, even transmission across non-host plants has been documented via the floral channel [37].

Flowers have a secret role in influencing the microbial communities of seeds, even though their vivid colours and enticing fragrances draw pollinators. Beyond their ability to draw in beneficial pollinators, floral characteristics can play a major role in the transfer of a variety of microorganisms to growing seeds. Expanding upon studies conducted by McArt, et al. (2014) [38] regarding the effects of these characteristics on plant pathogen dissemination may also observe their broader impact on non-pathogenic microbiota. Microbial establishment within flowers is influenced by various factors, including floral lifetime and age, style length and morphology, and even nectar features, including sugar content, antimicrobial capabilities, and reactive oxygen species. Still, the complex relationship between seed microbiome composition and floral characteristics could not be comprehended. To go further, additional basic research and experiments are required. An important field of study is examining the makeup and effectiveness of microbial transmission between plants with different floral characteristics. We can learn a great deal about how certain characteristics favour or select microorganisms that will make up the future generation by directly examining the composition of the seed microbiome across such a wide range of genotypes. Therefore, while the floral pathway offers

a fascinating approach for microbial colonization of seeds, factors like flower lifetime and dispersal techniques may limit the effectiveness of this pathway for non-specialized bacteria [13]. Various routes within the seed result in different microhabitats. Microbes can live in storage tissues (endosperm or perisperm), on the seed coat, or on the surface of the embryo (e.g., embryonic axis and cotyledons). The features and resources that are specific to each microhabitat influence the microbial communities that flourish there [39].

External pathway

The seed surface is directly contaminated by microbes from fruits, threshing residues, or the surrounding area; this is mainly seen as horizontal transfer.

Microbial diversity within the seed

Elucidating the seed surface

Studies on the seed microbiome have long overlooked the possible importance of bacteria living on the seed surface in favour of concentrating mostly on the interior endophytic population [17]. This caused a void in our knowledge regarding the origin of the microorganisms colonizing seedlings during germination – from the external or inside seed microbiome.

This mystery was solved by Links, et al. [40], who conducted a groundbreaking study in which they explicitly examined the epiphytic bacterial and fungal communities of *Triticum* and *Brassica* seeds. They discovered that, although endophytic bacterial communities in each plant genus were unique and dominated by Proteobacteria, the epiphytic bacterial communities were surprisingly large and similar, with up to 10⁸ bacterial genomes per gram of seed. What's more, the epiphytic fungal communities were dominated by known plant pathogens like *Phoma*, *Alternaria*, and *Fusarium*. This suggests that the external seed microbiome may be more important than previously believed and that species filtering can also occur in this microbial group [7].

Microorganisms known as “seed epiphytes” are those that grow on the surfaces of seeds and so occupy a little space at the interface between the seed and the atmosphere [41]. The community structure of the seed microbiome may be shaped by interactions between microorganisms, such as competition and facilitation, as a result of the restricted area on the seed surface and the shortage of nutrition supply. Dispersal and local factors also control epiphytic microbial seed colonization [42]. The subsequent horizontal mode of transmission and concurrent with the seed surface. Microbes residing in the rhizosphere or on the seed coat are often where horizontal transmission has been documented [43].

The interesting domain of fungi, known as the mycobiome, is still relatively unexplored in studies of plant microorganisms, despite bacteria frequently taking centre stage [44]. Similar to how they affect the human gut, fungi are important for plant health and function even though they are very small compared to bacteria [44].

Fungi such as *Epichloe* symbionts and mycorrhizal partners are important cohorts for plants, whose roles in their physiology and health are critical [45]. Although the relationship between fungal imbalances and plant disease is still unknown, the plant mycobiome, a hidden world of fungal communities, holds immense potential for sustainable agriculture. Various and mutually advantageous fungi called mycorrhizal fungi penetrate plant roots, providing vital nutrients like phosphorus and strengthening defences against infections [45]. Conversely, *Epichloe* and grasses develop an obligatory endophytic symbiosis in which the plant systemically infects the reproductive and vegetative organs of successive generations. These fungi are potential biofertilizers for sustainable agriculture because, in addition to promoting growth, they also produce alkaloids that increase stress resilience and discourage herbivores [46].

In today's dynamic agricultural environment, plants face a range of biotic and abiotic stressors. Stress-exposed plants were shown to have both constitutive and inducible defence systems induced. Under stress, plants produce more phenolics and superoxide radicals to quench enzymes as a significant defence mechanism. There are many more fungi that assist plants. According to studies by Xia, et al. [47] and *Penicillium*, *Aspergillus*, *Fusarium*, *Phoma*, and *Trichoderma*, among others, these species either directly create or regulate plant hormones that promote growth. Abiotic stresses, including salt and drought, are also lessened in large part by fungal symbionts [41]. A synergistic effect is possible. The development and yield of plants may be further enhanced if these helpful fungi are combined with useful bacteria [48]. Nevertheless, it is indisputable that these fungal communities have potential advantages for agriculture.

Seeds endophytes

The endophytic seed microbiome is a diverse consortium of bacteria and fungi found in seeds that is essential to the growth and health of plants [33]. Though historically thought to be purely advantageous or neutral, a more complex picture is beginning to emerge, acknowledging the context-dependent character of their interactions with plants [33]. Endophytes can infiltrate the roots or other portions of a plant during growth and are not limited to seeds. Unlike epiphytic bacteria, endophytic microorganisms form a robust and long-lasting relationship with their host plants [43]. The majority of the bacteria that make up the seed microbiome are Proteobacteria, Bacteroidetes, Firmicutes, and Actinobacteria [49]. These phyla are plausible candidates for seed colonization since they are widely found in soil and aquatic settings. However, selection is important because different plant species, genotypes, developmental phases, geographic regions, and even the presence of pathogens affect the different bacterial species [49].

The interesting fact indicates that within some plant species, specific bacterial endophytes exhibit extraordinary conservation, suggesting that they may comprise the core seed microbiome that is passed on to seedlings [40]. Some seed endophytes may have originated from maternal plants, as indicated by their differentiation from the soil microbiota [50].

Studies have shown that both soil recruitment and non-host-specific assembly mechanisms are present in the assembly process, although their exact nature is still unknown [51]. Endophytes can colonize a variety of plant organs, potentially migrating from the endosphere to flowers and eventually seeds or vice versa, emerging from roots and into the rhizosphere [52]. This adds still another level of intricacy to the situation. This complex union involving bacteria, soil, and seeds emphasizes the need for more study to fully understand the web of relationships [53].

Fungal endophytes also inhabit seeds, with *Epichloe* and *Neotyphodium* being well-studied examples in Poaceae, offering protection against pathogens [40]. But now that ascomycete and basidiomycete yeasts and fungi have interclasped, the fungal world offers a far greater diversity. Studies on Brassicaceae seeds show that basidiomycete Tremellomycetes and ascomycetes such as Eurotiomycetes, Leotiomycetes, Sordariomycetes, and Dothideomycetes predominate [54]. Curiously, a large number of these species are also frequently found in soil, including *Fusarium*, *Alternaria*, and *Aureobasidium*, which also commonly suggest potential horizontal transmission. Indeed, studies suggest local conditions may play a stronger role than host genotypes in shaping fungal seed microbiomes.

Moreover, studies indicate that the fungal seed microbiome may be significantly shaped by local site factors as opposed to host genotypes. Though their precise location inside seeds is yet unknown, these fungi most likely live on and within the seed coat, where they may play a role in generational transmission both vertically and horizontally. A more profound understanding can be drawn from the dynamic interactions within the seed microbiome by transcending the oversimplified concepts of mutualism and pathogenicity. This information is essential for maximizing the positive effects of microorganisms while reducing the negative effects of unfavourable partners [7].

Classification of microbes across various plant species

Microorganisms play essential roles in plant health, growth, and productivity. These microbes, which include bacteria, fungi, archaea, and other microorganisms, colonize various plant parts, such as the rhizosphere (soil around the roots), phyllosphere (aerial parts, especially leaves), and endosphere (internal tissues), which can be clearly visualised from Table 1. Understanding the functional categories of these microbes is crucial for harnessing their potential to improve agricultural practices and promote sustainable food production [62]. This essay will explore the diverse functional roles of microbes in different plant species, focusing on rice, maize, wheat, and soybean, highlighting their contributions to plant growth, nutrient acquisition, disease resistance, and stress tolerance.

Role of microbes in rice

Rice, a staple food for a significant portion of the world's population, benefits immensely from its associated microbiome. Rice fields harbor a diverse array of microbes, each contributing to the overall health and productivity of

Table 1: List of microorganisms obtained from different parts of crop plants.

Crop	Organisms isolated from plant part	Organisms isolated	Reference
Wheat	Rhizosphere	<i>Azotobacter</i> , <i>Azospirillum</i> , <i>Pseudomonas</i> , <i>Acetobacter</i> , <i>Burkholderia</i> and <i>Bacillus</i>	[55]
Soyabean	Epiphytic and Endophytic Bacteria	<i>Pseudomonas</i> , <i>Ralstonia</i> , <i>Enterobacter</i> , <i>Pantoea</i> , and <i>Acinetobacter</i> isolates displayed plant growth-promoting characteristics.	[56]
<i>Phaseolus vulgaris</i>	Bacteria were isolated from the reproductive tissues of various bean genotypes grown in field conditions.	Two were identified as <i>Bacillus</i> spp., and one was identified as <i>Pseudomonas fluorescens</i>	[57]
Wheat and canola	Seed	The bacterial strains recognized as <i>Pantoea agglomerans</i> exhibited antagonistic characteristics towards an isolate of fungus (<i>Alternaria</i> sp.)	[58]
Poaceae weed species <i>Avena fatua</i> and <i>Echinochloa crus-galli</i>	Seeds	The most common fungi were <i>Alternaria</i> , <i>Fusarium</i> , <i>Cladosporium</i> , and <i>Sarocladium</i> . Some <i>Fusarium</i> isolates, particularly <i>F. sporotrichioides</i> and <i>F. culmorum</i> , showed the ability to infect and damage <i>E. crus-galli</i> seeds in lab tests.	[59]
Maize	Root and leaf apoplastic fluid	<i>Alcaligenes</i> sp. MZ895490, <i>Bacillus amyloliquefaciens</i> MZ895491	[60]
Sorghum	Sorghum root	<i>Acinetobacter pittii</i> , <i>Bacillus licheniformis</i> , <i>Bacillus</i> sp., <i>Pseudacidovorax intermedius</i> , and <i>Acinetobacter baumannii</i> strains	[51]
Bamboo	Bamboo rhizosphere soil samples	<i>Azotobacter</i> , <i>Azospirillum</i> , and <i>Beijerinckia</i>	[61]

the plant. These functional categories include nitrogen fixers, which convert atmospheric nitrogen into a usable form for the plant, and nitrifiers, which convert ammonia into nitrates, further enhancing nitrogen availability [62,63]. Methanogens and methane oxidizers play a crucial role in the methane cycle, with methanogens producing methane in anaerobic conditions and methane oxidizers consuming it, thereby reducing greenhouse gas emissions. Plant-growth regulators, phosphate-dissolving microbes, and sulfur oxidizers contribute to nutrient mobilization and availability, ensuring that rice plants have access to essential elements. Decomposers and nutrient recyclers break down organic matter, releasing nutrients back into the soil for plant uptake. The composition of these microbial communities is influenced by various factors, including chemical, physical, and climatic conditions and agricultural management practices. For instance, water-saturated soil conditions can diminish the symbiotic relationship between mycorrhizal fungi and rice roots. Studies have shown that organically cultivated soils are enriched with plant-growth-promoting genera like *Anabaena*, *Azospirillum*, and *Rhodobacter*. Inoculating rice plants with beneficial microbes such as *Azospirillum* can promote early tillering and improve reproductive performance [64]. Furthermore, microbial consortia, such as those containing *Pseudomonas*, *Azospirillum*, and cyanobacteria, have been developed to enhance nutrient uptake, growth, and grain yield in rice.

Role of microbes in maize

Maize, another globally important crop, also relies on a diverse microbiome for its growth and health. The maize rhizosphere hosts various microbial communities, including Proteobacteria, Bacteroidetes, and Actinobacteria [65]. Key functional categories of microbes associated with maize include nitrogen fixers, phosphate solubilizers, and plant growth-promoting rhizobacteria (PGPRs). Genera such as *Azospirillum*, *Azotobacter*, *Acetobacter*, *Pseudomonas*, *Paraburkholderia*, *Herbaspirillum*, and *Rhizobium* have been reported to exhibit PGPR effects on maize. These PGPRs enhance plant growth through various mechanisms, such as improving nutrient availability, producing phytohormones, and acting as biocontrol agents. For instance, *Azospirillum lipoferum* has been shown to increase plant height and underground biomass,

while *Pseudomonas fluorescens* and *P. putida* can enhance aerial dry matter. Specific bacterial strains, such as *Paraburkholderia nodosa* NB1 and *Burkholderia cepacia* PB3, have demonstrated comparable effects on maize biomass and improved nitrogen and phosphorus use efficiencies compared to chemical fertilization [66]. These findings suggest that incorporating beneficial bacteria into integrated nutrient management strategies can reduce the reliance on chemical fertilizers. However, some microbial strains, such as *Serratia nematodiphila* C46d, have shown poorer maize nutrient uptake and use efficiency compared to other single-strain treatments (2020). The interactions among different functional rhizobacteria are also crucial, as compatibility among strains can enhance their beneficial effects on maize [66].

Role of microbes in wheat

Wheat, a staple cereal crop worldwide, also benefits from its associated microbiome, which includes a diverse array of bacteria and fungi. These microbes colonize various plant parts, including stems, leaves, roots, seeds, spikes, and the rhizosphere [67]. The functional categories of microbes in wheat encompass plant growth-promoting rhizobacteria (PGPRs), biocontrol agents, and microbes involved in stress mitigation. PGPRs, such as *Caulobacter*, *Devosia*, and *Rhizobium*, enhance plant growth through mechanisms like IAA production, nitrogen fixation, and biocontrol of pathogens [68]. In particular, *Paraburkholderia phytofirmans* strain PsJN has been shown to improve photosynthetic rate, water use efficiency, chlorophyll content, grain yield, and nutrient levels in wheat under drought conditions. Microbes also play a role in mitigating biotic stresses, with several bacterial biocontrol agents inhibiting fungal pathogens like *Fusarium graminearum* by secreting antifungal metabolites [67]. For example, *Pseudomonas piscium* secretes phenazine-1-carboxamide, which affects the fungal histone acetyltransferase, inhibiting fungal growth. Additionally, microbes assist in mitigating abiotic stresses such as drought, salinity, and temperature extremes. For instance, phenazine-producing bacteria in the rhizosphere of dryland-grown wheat enhance drought resistance. Certain fungal endophytes also improve seed germination and seedling growth under heat and drought stress. The composition of the

wheat microbiome is influenced by various factors, including anthropogenic activities, edaphic conditions, environmental stresses, host genotype, and growth stage [67].

Role of microbes in soybean

Soybean, a crucial legume crop, relies on a diverse microbiome for nutrient acquisition, growth promotion, and stress tolerance [56]. The soybean rhizosphere hosts a variety of microbial communities, with Proteobacteria, Actinobacteria, Firmicutes, and Acidobacteria being the dominant phyla. Key functional categories include nitrogen fixers, phosphorus solubilizers, and microbes involved in nutrient cycling. Genera such as *Bradyrhizobium*, *Streptomyces*, *Arthrobacter*, *Nitrobacter*, and *Burkholderia* are commonly found in the soybean rhizosphere. These microbes contribute to plant growth through various mechanisms, such as nitrogen fixation via nodulation and enhanced nutrient availability. The functional diversity of the soybean rhizosphere microbiome is influenced by soil properties, with phosphorus being a significant factor. Additionally, the relative abundance of functional categories, such as carbohydrate metabolism, amino acid metabolism, and sulfur metabolism, plays a critical role in the overall health and productivity of soybean plants [69]. Soil microbial communities help plants acquire carbon through metabolic pathways. Soybean-nodulating rhizobia help with nitrogen fixation and increases yield. The microbes also produce sulphur metabolic genes and enzymes to protect soybean plants from stress during the biosynthesis of thiamine [69].

Effect of seed microbiome

Effect of seed microbiome on seed germination

A variety of biotic and abiotic factors, such as soil microbes, soil-borne pathogens, pests, weeds, granivores, herbivores, and microbial endophytes, including seed-borne pathogens, can affect the germination of seeds. Among biotic factors, bacterial endophytes, which are microbes that live in the rhizosphere and penetrate the germinating seed, may be essential in influencing germination and sharing a mutualistic relationship with the host seedlings [70].

Like the rhizosphere, the spermosphere is a zone that surrounds seeds and is potentially the site of interactions between soil microbes, germinating seeds, and seed microbes [7]. The microbiota that inhabits this zone, while typically fleeting as individual organisms, can have a long-lasting impact on seed germination and seedlings [71]. More recently, studies have shown that microbes in the seed spermosphere and endosphere, which are less studied than other groups of symbionts, can enhance plant growth during both abiotic and biotic stress [33]. Involving bacteria, soil, and seeds emphasizes the need for more study to fully understand the web of relationships [33].

Nonetheless, the function of the seed microbiome and its possible uses have not received much attention in research. In nutrient-poor soils and under stressful circumstances, seed-associated bacteria have been demonstrated to support the establishment, growth, and development of host plants'

seedlings [72]. According to reports, endophytes and epiphytes attached to seeds have a major impact on plant growth and seed germination. It has been demonstrated that seed epiphytic fungi like *Fusarium* sp. and *Penicillium* sp. improve seed germination in the rainy tropics [73]. Thus, genetic and metabolic diversity can be found in the spermosphere and endosphere of seeds, according to research conducted on these microbial communities utilizing contemporary metagenomics [74].

Microorganisms carried by seeds are more than just things that live on seeds. According to research, they serve as microscopic defenders, shielding seeds from harmful environmental stressors as well as diseases and predators. However, their advantages go well beyond germination. These microbial allies have the power to encourage plant development and even function as organic biocontrol agents for dangerous plant illnesses. "Priority effect" is a concept that they use to shape the root microbiome as they colonize the roots, effectively providing them an advantage in creating a healthy community surrounding the plant. Additionally, by generating a variety of compounds that foster an environment conducive to the success of the seed, these beneficial microorganisms aid in the germination and storage of seeds [32]. Microorganisms are important for maintaining plant health in the early phases of growth and can live on and inside the seed. Essential activities like nutrition intake, redox homeostasis, secondary metabolism modulation, defence against pathogens, growth promotion, antioxidant activity, and hormone generation and modulation are all aided by the seed microbiota in plants. The early growth and development of plants depend on the seed microbiome. Its extreme susceptibility to alterations in the abiotic conditions of the forest, however, emphasizes the significance of essential beneficial symbioses that are essential to the life cycle of forest plants. These microbes have the ability to favourably affect how plants react to environmental stress, indicating that the microbiota can preserve plant adaptability in stressful situations [34].

A plant's first microbiome is formed at the critical stage of seed germination by a mix of horizontal inheritance from the surrounding environment and vertical inheritance from the parent plant [75]. The spermosphere, a dynamic zone of microbial activity, develops around the seed as it takes in water and releases nutrient-rich exudates [7]. For the plant and the microbial community, it has gathered, the critical stage from seed to seedling, which has a significant impact on the plant's fitness, is a delicate time. Both agricultural systems and the maintenance of natural ecosystems depend on this stage [54].

The future of the developing plant is influenced by interactions inside these microbial olos, which are driven by competition for resources. Studies reveal that the soilborne diseases that susceptible seedlings face can be prevented by the seed microbiome [76]. Additionally, by releasing phytohormones like cytokinin, which aid in breaking dormancy, the microbiome can even promote germination [77]. In addition to acting as the plant's first inoculum, these microbes help prevent microbial invasion. However, much

remains to be discovered regarding the ways in which this early microbial community affects seedling establishment and ultimately contributes to the mature plant microbiome [17].

Seed harbours diverse microbial communities, their ultimate fate and impact on plants are highly intricate. Both temporary inhabitants (seed-borne) and possible long-term spouses (seed-transmitted) can be thought of in relation to the bacteria. They must be able to invade the plant and outcompete soil microorganisms in order to persist during seedling growth [78].

The spermosphere, a nutrient-rich area that develops surrounding the seedling shortly after germination, is initiated. Since seed-borne bacteria are close by and have access to resources, this particular environment may give them a competitive advantage. Nevertheless, because most seed-borne bacteria are not present in root samples, research indicates that soil type dominates in determining the composition of the spermosphere's bacterial population. In order to precisely track seed-borne microorganisms, this emphasizes the necessity for more thorough research utilizing unsterilized seeds and cutting-edge methods. Plant exudates present a dynamic environment for microorganisms in the spermosphere, regardless of their place of origin. Barret, et al. [54], have shown that rapid growth "copiotrophs" are more prevalent during germination because efficient resource acquisition and utilization are essential for survival.

Effect of seed microbiome on plant nutrition, health, productivity, and seed quality: Several microorganisms can be used to increase productivity in plants by using a consortium of different beneficial microorganisms [79]. The diversity and dynamics of the seed microbiota are important for plant health and productivity because they influence root symbiosis, plant nutrition and growth, seed germination and seedling phenotypes, and phytopathogen inhibition [7]. It can be very beneficial to implement innovative alternatives to enhance plant health, productivity, and seed quality. This is especially important to ensure food security, as improved seed quality alone can increase rice crop output by 5% – 20% [61].

A plant's first microbiome is formed at the critical stage of seed germination by a mix of horizontal inheritance from the surrounding environment and vertical inheritance from the parent plant [13]. The spermosphere, a dynamic zone of microbial activity, develops around the seed as it takes in water and releases nutrient-rich exudates [7]. The transition from seed to seedling is a critical stage for both the plant and its microbial community, significantly influencing the plant's fitness. This delicate period plays a vital role in the overall development of the plant. Both agricultural systems and the maintenance of natural ecosystems depend on this stage [49]. Nutrient solubilization can be improved by seed-associated bacteria such *Pantoea* sp., *Citrobacter* sp., *Bacillus* sp. and *Flavobacterium* sp. [80]. The capacity of endophytic *Bacillus* species to raise the levels of N, P, and K in infected plants was ascertained in the year 2018 by Ribeiro, et al. [81]. It has also been demonstrated that endophytic strains of *Priestia megaterium*, *Lecanicillium* sp., *Pseudomonas bijjeensis*,

and *Aspergillus terreus* enhance the concentration of zinc and NPK content in plants that are injected. Inoculating plants with fungi endophytes enhances their growth and grain output when the plants are starved of nutrients [82].

In order to prevent detrimental effects on their internal metabolism, symbiotic bacteria, and fungi have developed defence mechanisms that include the synthesis of siderophores, organic acids, and exopolysaccharides [60]. Additionally, bacteria use strategies including colonization and biofilm formation on the root surface to thwart plant uptake [83]. The subsequent generations of *Noccaea caerulea* seeds grown in soils rich in metals inherit a core microbiome [84]. By causing metabolic and physiological changes that favour metal accumulation in plants without affecting critical metabolism, this core microbiome helps plants better withstand the severe circumstances of polluted soils [74]. Similarly, soil acidity majorly limits *Rhizobium* survival thereby reducing nodulation. In addition, it results in deficiencies of minerals like Potassium, Magnesium, Molybdenum, and Calcium, and also causes aluminium toxicity which also affects nodulation and in turn causes productivity loss in pulses. Through their impact on numerous physiological and biochemical processes, mutualistic relationships between microorganisms and plants are crucial for increasing plant fitness [72]. Thus, seed microbiomes both safeguard farms and increase their output.

For a crop to be established successfully, these microorganisms have a major impact on seed vigor and early seedling growth [85]. In contrast to other plants, a variety of leguminous species have the ability to create root nodules in symbiosis with soil bacteria known as rhizobia, which fix nitrogen. Although rhizobia is the super-dominant group, a variety of bacteria inhabit the endosphere of healthy nodules, which functions as a nitrogen-fixing organ [86]. The species shared by rhizosphere soil, nodules, and seeds comprise the core microbiota of nodules when taking into account all plant organs [32].

Numerous studies have been done on the use of seed endophytes as biocontrol agents and in phytoremediation, and the literature on the subject focuses on using seed-associated microorganisms to boost host plant growth. The quality and endophytic contents of seeds have a positive correlation. For instance, because of its greater germination % and strong robustness, a superior-grade seed lot is typically regarded as disease-free [43]. Endophytic bacteria have been widely employed in sustainable agriculture as biocontrol agents, biofertilizers, and inducers of abiotic stress tolerance during the past few decades. An important component of the positive plant-microbe interaction that leads to several processes that promote plant growth is the successful colonization of the host plant by endophytes. Many phenomena, including attachment, entrance, motility, transmission, and proliferation of endophytic populations within the host plant, are included in colonization [85].

Through a variety of processes, including nitrogen fixation, phosphate and potassium solubilization, siderophore

synthesis, and mechanisms that enable multiple nutrients to be absorbed by plants, endophytic bacteria contribute to the growth of plants [52]. Additionally, they promote plant growth through the production of various phytohormones, such as auxins, and gibberellins, which have been shown to positively influence rice seedling establishment under submergence [70] or even by strengthening plants' resistance to biotic stresses. For instance, seed endophytes can produce subtilomycin, which binds to flagella to influence the plant defence induced by the flagellin peptide. Alternatively, they can accumulate PR1 protein, which triggers the WRKY53 gene expression through the jasmonic acid and ethylene signalling pathway and activates Mitogen-Activated Protein Kinases (MAPKs) signaling [87]. Microorganisms can supplement and lessen the use of agrochemicals by ensuring more effective plant protection and, consequently, contributing to a healthier environment [61]. Microorganisms do this through their ability to synthesize secondary metabolites with direct biocontrol activities or by inducing plant systemic resistance [19].

According to Shahzad, et al. [74], bacterial endophytes that are carried by seeds also influence endogenous phytohormones. Furthermore, by producing the catalyst ACC deaminase (1-aminocyclopropane-1-carboxylate) of an ethylene precursor in higher plants, some plant growth-promoting bacterial endophytes can reduce ethylene levels [88]. This demonstrates the significance of seed microbiota as a source of endophytic bacteria in the nodules of the next generation of plants.

Studies have shown that the microbial diversity in seeds was high, comparable to that of the rhizosphere soil, but significantly higher than that found in nodule samples (nodules, nodule fermentation broth, and passaged nodules). This is in contrast to some previously published studies that found only a small number of bacterial and/or fungal species in seeds [89]. Furthermore, endophytes can generate phytohormones such as gibberellin-like molecules, auxins, cytokinins, ethylene, and abscisic acid that promote plant growth [57]. As a result, in 2021, Samreen, et al. [43], said seed microbiome is important in influencing seed quality. However, according to Truysens, et al. [33], the seed microbiome is only made up of a small number of microbial species that appear to have evolved through co-selection with the host plant species and give unique growth characteristics necessary for plant survival [43].

Endophytic microorganisms have been shown to benefit the host in a number of ways, including increasing biomass, growth rate, and availability of phosphorus, zinc, and potassium. They can also fix atmospheric nitrogen, produce a variety of phytohormones, and increase resistance to abiotic stressors. As a result, there is increasing interest in the function of these microbiomes, particularly those related to seeds, as they are essential to the plant life cycle maturity. The quality and endophytic contents of seeds have a positive correlation. For instance, because of its greater germination % and strong robustness, a superior-grade seed lot is typically regarded as disease-free. It was confirmed that tall fescue seedlings from seeds removed before reaching physiological maturity have lower endophytic fungal infection rates. Furthermore, fewer

seeds germinate when harvested before they reach maturity [43].

These microorganisms affect crop productivity in a number of ways, such as by helping to regulate the availability and uptake of nutrients and encouraging plant stress tolerance [90]. Nonetheless, due to difficulties in researching non-culturable microorganisms, the majority of research has concentrated on the functional roles of particular microbial groupings (such as particular species or genera) [91]. Mycorrhiza-forming fungi and bacteria that fix nitrogen are two examples [92]. Beyond single groups, a comprehensive knowledge of this system emphasizes the vital connections between various microbial groups, giving rise to the idea of the plant microbiome. The term "ecological community of microorganisms" connected with a plant was coined by Lederberg and McCray [93]. Similar to the human microbiome, the function and impact of the plant microbiome depends on our ability to comprehend the interactions within it.

According to Boon, et al. [94], the word "microbiome" has been used to refer to a variety of microbial communities found in diverse hosts or habitats, stressed the functional significance of these interactions by proposing that the microbiome be defined by the collection of genes present, rather than merely concentrating on taxonomy, which makes it possible to apply the idea of the microbiome to plants and highlight the crucial roles that various microbial groups play in relation to them [94].

Effect of seed microbiome on stress mitigation

In reaction to environmental challenges, plants can control seed endophytes and pass them on to their progeny. Plants use these bacteria both during the establishment stage and during their whole life cycle. This response is triggered by a variety of climate-related factors, which make it easier for microorganisms to be recruited from the environment to help them adapt to stressful situations [80]. Furthermore, plant growth-promoting rhizobacteria's genes for hormone production are influenced by stressors that affect the rhizosphere and soil, including acidic pH, osmotic stress, and root exudates [71].

Vertical or horizontal transfers of microorganisms can improve a plant's ability to adapt to unfavourable environmental conditions. They are essential in reducing the effects of climate change on the regeneration of native forests, especially when it comes to advantageous symbiotic relationships that occur when plants are still in their juvenile stages [34]. However, because of the accumulation of many pressures brought on by climate change, it is difficult to analyse plant responses to specific abiotic stresses. In these situations, microbial relationships become essential for promoting plant establishment and growth. For example, endophytic *Bacillus* species can withstand multiple stresses, have characteristics that aid in the growth of plants, and use different strategies to fight phytopathogens [95]. Stress-tolerant plants like *S. davidii* grown in arid areas, as well as quinoa, Agave, and forage species with high-stress

resilience, have been reported to be colonized by Firmicutes [96].

Effect of seed microbiome in mitigating abiotic stresses

Temperature stress: Heat stress has a direct effect on plant performance due to high temperatures and direct UV exposure, which impacts seed germination and plantlet establishment. Extreme and quick temperature changes rank among the most harmful abiotic stimuli that affect the growth of forest plants [97]. Temperature affects water transport in heat-stressed plants and is crucial for the enhancement of seed germination. Similarly, heat-induced water evapotranspiration causes a constant decrease in soil water content and plant availability in soils subjected to high temperatures. In order to withstand heat stress, plants have developed physiological and anatomical adaptations. These adaptations mainly include the production of suitable solutes that cause molecular modifications that result in osmotic adjustment and the restoration of redox equilibrium [98]. *Pseudomonas* and *Trichoderma* are examples of beneficial bacteria that can increase the expression of Heat Shock Proteins (HSPs) and help preserve the integrity of proteins. Plant organs, including seeds, seedlings, and adult plants, can interact directly with microorganisms that produce heat shock proteins (HSPs). The beneficial effects of microorganisms that enhance growth and overall metabolic activity in response to heat stress include improved nutrient availability and water balance, which can be attributed to increased root growth or improved absorption surface [99].

Plant hormones like ABA and jasmonate can be modulated by microbes to change their physiological state and cause metabolic reactions that increase a plant's ability to withstand stress [99]. Plant growth-promoting bacteria can be microbially primed to protect against the harmful effects of extended heatwaves. By raising levels of ACC deaminase, indole-3-acetic acid (IAA), gibberellic acid, and the synthesis of kinetin and exopolysaccharides, heat-tolerant strains of *Bacillus safensis* reduce the harmful effects of heat stress in inoculated plants. Plant tolerance is mostly increased by soil fungi like *Trichoderma koningii*, which do this by producing more antioxidants [100]. By enhancing the expression of genes linked to heat stress tolerance, arbuscular mycorrhizal fungus also helps inoculated plants tolerate heat stress better. According to Bilal, et al. [58], endophytic fungi like *Penicillium funiculosum* and *Paecilomyces formosus* might enhance the physiological responses of plants under drought and high-temperature stress; similarly, Anandakumar, et al. (2020) [101] showed that *Glomus intraradices* and *Rhizobium* were found to stimulate defence in blackgram against *Spodoptera litura*, resulting in the production of a significant number of defence compounds.

Low temperatures have a detrimental impact on plant metabolism, which hinders the development and survival of plants. Low temperatures significantly inhibit seed germination and plantlet establishment throughout the early stages of plant development. In plants growing under cold stress, reduced leaf expansion and chlorosis are frequently seen, which might indirectly affect photosynthesis and change the activity

of vital enzymes [102]. By generating antifreeze proteins, cryoprotectants, and osmo protectants to guard against cellular damage brought on by low temperatures, psychrophilic bacteria increase plant tolerance to cold stress. Additionally, microorganisms can produce phytohormones that improve plants' physiological responses to cold stress; additionally, microbe activity stimulates metabolic pathways linked to low-temperature tolerance [34]. Plant-associated psychrophilic bacteria are capable of sustaining essential plant processes at low temperatures, such as phytohormone synthesis, nutrition solubilization, and biocontrol [34]. According to Wu, et al. [103], *Bacillus* species that have been isolated from plant rhizospheres on the Qinghai-Tibetan Plateau exhibit the potential to adapt to cold environments and stimulate the growth of *T. aestivum* seedlings.

Similar to this, when used in tandem, psychrotolerant *Pseudomonas* sp. and *Curtobacterium* sp. encourage development under cold stress [49]. By activating particular transcription factors, a bacterial consortium made up of *Bacillus cereus*, *B. subtilis*, and *Serratia* sp. reduces the damage caused by cold stress [59]. Psychrophilic *Bacillus* species primarily reduce the effects of cold stress by expressing genes related to the metabolism of phytohormones. Additionally, mycorrhizal fungi enhance plant growth in cold stress conditions by enhancing growth, photosynthesis, osmotic potential, antioxidant defense mechanisms, and accumulating protective compounds [34]. In *Vaccinium corymbosum* that has been infected, fungal endophytes like *Penicillium rubens* and *Penicillium bialowiezense* have the ability to alter gene expression, leading to increased photochemical efficiency and decreased oxidative stress in comparison to uninoculated plants [15].

Salt stress: Although there are some parallels between salt and water stress, it is best to look into each one independently in order to fully comprehend how each affects different plant species and how best to manage them in different settings. Such a distinct analysis improves understanding of the management of plant species under various environmental circumstances. One of the most complex types of stress is salt stress, which modifies plant osmotic balance and causes ionic toxicity, oxidative stress, and nutritional imbalances by affecting water availability. It primarily hinders water absorption and interferes with vital enzymatic processes, which negatively impacts seed germination and seedling growth [34]. Certain microorganisms secrete phytohormones that help plants flourish by reducing the effects of salt stress and enhancing the availability of nutrients [104]. Halotolerant plant growth-promoting rhizobacteria (HTPGPR) are advantageous microorganisms that can be used to lessen the detrimental effects of soil salinity on crops. According to Zhang, et al. [105], salt stress also throws off hormone balance, antioxidant activity, and ionic equilibrium, and causes reactive oxygen species (ROS) to be released into the environment, which damages important biomolecules including proteins and DNA.

Closure of stomata lowers carbon dioxide absorption and lowers total plant metabolism; high salt concentrations usually inhibit plant development [18]. According to Tewari and

Sharma [106], salinity in the soil causes notable changes in the diversity of microorganisms, which in turn affects the quantity of advantageous bacteria that are essential for promoting plant growth. Salinity suppresses vital genes related to central metabolism and compromises proteins linked to chaperones, elongation factors, and cell division in salt-sensitive bacteria, among other effects on soil microorganisms [34]. Additionally, salinity prevents the synthesis of essential bacterial surface molecules required for plant contact, which in turn prevents rhizobial colonization in the rhizosphere. However, stress from salinity encourages the formation of halotolerant strains that may play a part in boosting plant growth [57]. Arbuscular mycorrhizal fungi are an example of a symbiotic microbe that selectively increases potassium (K) uptake while reducing sodium uptake, increasing plant resistance to salinity stress. In addition, these microbes improve nutrient and water intake, strengthen plant defences against phytopathogens, and control protein expression to mitigate the effects of salt. According to recent research, mycorrhizal fungi can help plants that are under salt stress [34]. Beneficial bacteria protect plant tissues from harm caused by salt by assisting in the reduction of ROS buildup. Microorganisms associated with seeds contribute to soil health by improving soil structure, nutrient cycling, and organic matter decomposition. This, in turn, improves the soil's ability to retain water and its overall nutrient status [107]. Furthermore, under salt-stress circumstances, inoculating *Zelkova serrata* with *F. mosseae* boosts photosynthetic rates and raises the concentration of magnesium (Mg), potassium (K), and phosphorus (P) in the leaves [59].

Drought stress: The detrimental effect on agricultural productivity worldwide is caused by drought stress. There are significant effects of drought stress on plant physiology and metabolism [108]. In order to minimize the effects of the drought, microbial inoculation is an appropriate and affordable technique [108]. Arunthavasu, et al. [109] conducted experiments and found that, in comparison to uninoculated controls, bacteria increased stress-related metrics such as total phenolic content, proline accumulation, and the activity of antioxidant enzymes (peroxidase, catalase, and polyphenol oxidase) as well as plant growth. Plant growth is significantly hampered by drought, mostly due to the obstruction of gas exchange. Stomatal closure is the main way that plants adapt to water constraints by reducing the amount of water lost through transpiration. This process invariably results in a decrease in the absorption of carbon and, as a result, in the production of biomass as a whole [74]. As a result of this quick response, the bulk flow of water-soluble nutrients from the soil is also reduced, which reduces nutrient uptake and utilization and exacerbates the negative effects of drought [110]. On the other hand, under extended water stress, stomatal closure is usually associated with metabolic limitations that cause photosynthetic rates to be downregulated because ribulose-1,5-bisphosphate synthesis is limited [111].

According to a recent concise summary, soil microorganisms can help plants conserve water and recover from it. This highlights the potential of soil microorganisms as resources for the creation of biological methods that support plant

growth [34]. As a result, microbes have a direct impact on how plants react to temporary or chronic water shortages. By producing osmo protectants and other suitable solutes, root-associated microorganisms can improve plant performance in water-deficient environments [112]. These solutes are essential for preserving intracellular water balance and preventing dehydration by stabilizing proteins and cellular structures [34]. Additionally, endophytic bacteria can enhance abscisic acid (ABA) levels, influencing plant metabolism and aiding adaptation to water deficiency-induced stress [55]; similarly, Umapathi, et al., in the year (2024) [108], isolated different drought-tolerant bacteria and also found out that these bacteria produce a large number of plant growth promoting factors like IAA, GA, protein and proline which protects the plant under drought conditions. Furthermore, under conditions of water scarcity, the development of microbial symbioses increases the production of genes linked to stress, which generally boosts plant performance. Analogously, modifications in the synthesis of antioxidant enzymes such as peroxidase, catalase (CAT), and superoxide dismutase (SOD) can scavenge reactive molecules [105]. By increasing the root absorption surface, the beneficial root-associated fungus can also improve plant water availability; similarly, by controlling stomatal opening and shutting, microbes can either directly or indirectly enhance water utilization [34].

Effect of seed microbiome in mitigating biotic stresses

Different microorganisms after isolation and characterization have been found to be beneficial against specific diseases like wise endophytic bacteria isolated from cotton were beneficial against cotton root rot disease [7]; likewise, Barret, et al. [54], reported that native isolates of *Trichoderma* and *Bacillus* spp. effectively inhibits the mycelial growth of *Fusarium oxysporium* f.sp *clavus* than control. Many bacterial and fungal endophytes that are spread through seeds contain substances that either directly stop the growth of pathogens or indirectly increase the resilience of plants to pathogenic invasions [113]. Priyanka, et al. [114] found that endophytes were also found to be effective against damping off in the nursery of cucumber and also found that *Pythium aphanidermatum* was effective in growth-promoting when compared to control and *Pseudomonas aeruginosa* showed the antifungal property. *Epichloe festucae* was found to contain several indole compounds, a sesquiterpene, and diacetamide by Yue, et al. [115]. Furthermore, several organic acids generated by seed-borne endophytic *Bacillus amyloliquefaciens* strongly suppressed pathogenic *Fusarium oxysporum*'s development in vitro and promoted systemic resistance in tomato plants, according to Shahzad, et al. [34]. Plant development and resistance against *F. graminearum* were significantly boosted by the endophytes *Paenibacillus* sp., *Pantoea* sp., and *Bacillus* sp. that were identified from wheat seeds by Herrera, et al. [116]. Additionally, a lot of work is done to increase the productivity and survival of perennial ryegrass by using *Epichloe* grass endophytes. The resistance of turfgrasses infected with *E. festucae* to the two main leaf spot pathogens, *Sclerotinia homeocarpa* and *Laetisaria fuciformis*, was much higher than that of non-inoculated turfgrasses [94]. But it's still unclear

if endophyte-derived compounds, secondary metabolites produced by plants after endophyte inoculation or competition between harmful microorganisms are responsible for this increased defence mechanism.

It is interesting to note that and also in addition to acting as antagonists against pathogenic microbes, seed endophytes also improve plant tolerance, mitigate abiotic stress, and promote seed germination. These effects are probably caused by their capacity to produce siderophores, ACC deaminase (1-aminocyclopropane-1-carboxylate), and secondary metabolites [34]. Furthermore, the use of bacterial endophytes that promote plant growth in seed form could aid in the phyto- and bioremediation of contaminated soil. When tobacco plants were inoculated with seed endophytes under Cd stress, Mastretta, et al. [117], showed that this greatly improved plant growth and biomass, reduced Cd toxicity, and increased tolerance over uninoculated plants. After inoculating grasses with seed-borne endophytes that can solubilize phosphorus and produce indole-3-acetic acid (IAA), siderophores, ACC deaminase, and acetone, Truysens, et al. [33] found increased phytoremediation of the grasses. Additionally, they came to the conclusion that planting Cd-tolerant seed-borne endophytes in Cd-contaminated areas during phytoextraction and phyto-stabilization had advantages: endophyte inoculation greatly enhanced plant growth in non-exposed plants, while inoculation increased Cd uptake under Cd stress conditions without impairing plant growth. These results demonstrate the endophyte microorganisms' potential for phytoremediation [34].

In plant tissues, seed-borne bacterial endophytes use direct or indirect processes to improve plant development and growth, as well as to make plants more resilient to biotic and abiotic challenges [34]. By releasing plant hormones, controlling or inhibiting phytopathogens to protect the plant, improving soil structure, and bioremediating contaminated soils by securing hazardous metals and breaking down xenobiotic mixes, they promote plant growth. Additionally, endogenous phytohormones are modulated by bacterial endophytes carried by seeds [46]. Spermatophytes rely on seeds to complete their life cycle; these seeds can wait for ideal growth circumstances to occur before germinating into new plants [7]. According to Rodriguez, et al. [118] and other studies, seed-borne bacterial and fungal endophytes probably help preserve seeds and promote seed germination in soil. Seed-borne endophytes are especially significant since they are passed down vertically between plant generations, guaranteeing their existence in the following generation of seedlings and providing their progeny with beneficial endosymbionts [13]. By encouraging mutualism, which improves both plant survival and microbial proliferation, this vertical transmission reduces the ability of microbial pathogens to support plant growth and development. Additionally, bacterial and fungal endophytes that are carried by seeds help host plants by generating. Seed endophytes can form endospores, which shield the seed from external changes [52]. They can also preserve other characteristics, like cell motility and phytase activity, which allow them to move freely within the plant and enter seeds before they harden. Studies

on biodiversity in seed-borne endophytes have, however, been comparatively scarce [59].

Conclusion and future prospect

Seeds are always surrounded by and also carry within a large number of small microorganisms in the form of epiphytes and endophytes respectively. These tiny partners, known as the seed microbiome, are influenced by both plant lineage and human interventions like domestication have left their mark, suggesting a long history of co-evolution. These microorganisms can be transmitted to the seeds through different other sources like soil, air, and other plant parts like phyllosphere, rhizosphere, or maybe plant endophytes. Microbes reach seeds through two main routes: vertical transmission from parent plants, often via flowers, and horizontal transmission from the environment through air, soil, and insects. Within the seed, distinct microbial populations with specific functions reside in different microhabitats. Hence, we can say that when passed from parent fungal transmission is typically more successful than bacterial transmission, but bacteria are generally more prevalent. On the other hand, fungal abundance is generally constant, although bacterial transmission success varies significantly per species. Germination triggers a critical interaction between the seed microbiome and the environment, shaping the seedling microbiome. More research is needed to understand the specific roles of different bacterial groups and their complex interactions with plants. The diverse communities of bacteria and fungi living on and within seeds play crucial roles in plant health, from germination and growth to disease resistance and adaptation to varied climatic conditions but still, the mechanisms involved during these processes are the main research areas to be carried out. Additionally, advanced techniques are required to explore the vast diversity of unculturable bacteria within the seed microbiome as well as their mode of action. By unlocking the secrets of this hidden world within seeds, we can unlock new avenues for promoting plant health, enhancing agricultural productivity, and ultimately ensuring the well-being of both plants and the ecosystems they sustain.

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