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Review

Microbial Allies in Seeds: Pioneering Sustainable Solutions for Crop Productivity and Resilience

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Abstract: Seeds form the foundation of plant life, underpinning agricultural sustainability. The seed microbiome, a community of microorganisms associated with seeds, influences seed health, germination, and plant growth by serving as the initial inoculum for microbial communities that enhance plant productivity. These microorganisms, including epiphytes and endophytes, promote plant growth through improved nutrient uptake, hormonal modulation, and stress tolerance. The seed microbiome's diversity and functionality are shaped by vertical and horizontal transmission routes, reflecting dynamic interactions between plants and their environment. Recent advances in sequencing technologies have revealed the microbiome's potential to enhance disease resistance and adaptability to environmental challenges. Utilizing microbial inoculation and biological priming can harness the microbiome's benefits, reducing chemical inputs while improving crop productivity. These strategies emphasize the microbiome's role in promoting seedling health and shaping plant morphology. Insights into seed microbiota dynamics offer opportunities to bolster crop resilience, address food security, and mitigate climate change impacts through sustainable agricultural practices. Exploring the ecological and functional interactions of seed-associated microorganisms is pivotal for fostering innovative strategies to enhance plant performance and sustainability in agriculture.

Keywords: Seed microbiome; endophytes; epiphytes; microbial diversity; sustainable agriculture; microbial inoculants.

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1. Seeds: The Vital Foundation of Ecosystems and Agriculture

1.1 Seeds: The Foundation of Life and Agriculture

All angiosperms and gymnosperms (cycads, ginkgos, conifers, and gnetophytes) rely mostly on their seeds for reproduction, and it maintains continuation across numerous generations. Plants distribute (spread) over the globe via their seeds (Crang *et al.*, 2018). Seeds are composed of the integuments of the ovule which grow into the seed's coat, likewise the developing embryo's cotyledons [the endosperm] which retain their nutritional supplies. Given that seeds are encased in a protective covering, they may be resistant to unfavorable climatic conditions like drought and cold as well as transportation by water, wind, or animal hair, all of which may improve the plant's reproductive rate (Crang *et al*., 2018).

The three components of the spermatophyte seed are as follows: The embryo, or growing sporophyte, which is the most important part of the seed. It is made up of many cotyledons that resemble leaves (gymnosperms), eudicotyledons, or monocotyledons, as well as a hypocotyl that connects the cotyledons to the root crown (Kosal, 2023).

The seed coat, also known as the testa, develops from the integument(s), and serves as the only layer of defense for the embryo in seeds discharged from dehiscent fruit; nevertheless, seeds in fleshy or indehiscent dry fruits may lose this layer or have it considerably changed. The seed coat has two properties that enable the seed to mature, dry up, and reach a dry, dormant state: water resistance and delayed germination. Desiccated seeds often germinate when they are exposed to favorable conditions, such as the proper soil moisture, temperature, and aeration. During sprouting, seeds absorb a significant amount of water, which plays a critical role in activating metabolic processes essential for germination. As depicted in Figure 1, the seed comprises three primary elements: the seed coat, embryo, and cotyledons. This visual representation effectively highlights the intricate organization of these components, which play distinct yet interconnected roles in the life cycle of a plant. Depending on the species, germination can follow one of two primary pathways: hypogeal germination, where the cotyledons remain underground and epigeal germination, where the cotyledons are pushed above ground. Figure 2 illustrates these contrasting germination types in eudicotyledons, highlighting their developmental differences (Linkies *et al*., 2010; Crang *et al*., 2018). The morphology of seeds is a crucial aspect of plant biology, as it encompasses the structural components that facilitate germination and growth (Cárdenas-Hernández *et al*., 2020; Boesewinkel and Bouman, 1984; Smith and Doe, 2020 and Seed Parade).

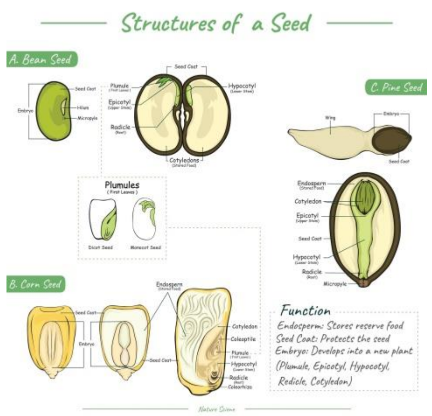

Figure 1. General seed morphology, illustrating the seed coat, embryo, and cotyledons.

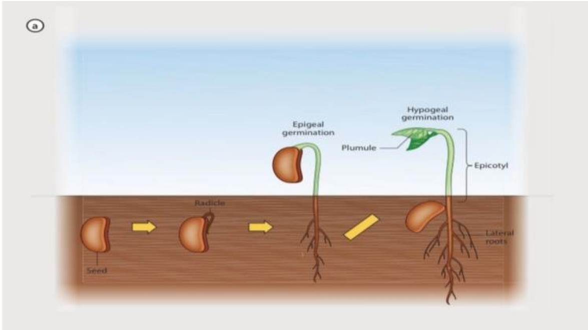

Figure 2. Hypogeal versus epigeal germination in eudicotyledons, emphasizing the developmental differences (Crang *et al*., 2018).

1.2 The Critical Role of Seeds in Agriculture and Ecosystems

Seeds have long been a cornerstone of human civilization, catalyzing the transition from nomadic lifestyles to settled agricultural societies. This shift laid the groundwork for the rise of complex societies, the establishment of trade routes, and the cultivation of essential crops for sustenance. While seeds have undoubtedly shaped our survival and progress, their significance extends beyond agriculture. In many cultures, they symbolize heritage and identity, forming the basis of rituals and traditions. For example, the Māori proverb, "Kohikohi ngā kākano, whakaritea te pārekereke, kia puāwai ngā hua," emphasizes the deep respect and care required in planting and harvesting, illustrating the profound relationship between seeds and cultural practices (Hanson *et al*., 2015; McMillan-Webster, 2022).

Biologically, seeds are the foundation of plant reproduction, containing not only the embryo but also essential nutrients that support early growth. These stored resources ensure that seedlings can survive until they establish the necessary systems for photosynthesis. From an evolutionary perspective, seeds provide plants with the ability to adapt to fluctuating environments. Through dormancy, seeds can withstand unfavorable conditions and only germinate when environmental factors are optimal. This dormancy is regulated by factors such as desiccation and growth hormones, allowing plants to preserve their genetic potential for future generations (Bareke, 2018; Long *et al*., 2015; Waterworth *et al*., 2015). The seed also serves as a bridge between generations, acting as a generative unit that carries the genetic material of the mother plant to the next generation. This ability to transmit genetic information makes seeds vital to both ecological stability and agricultural production (Waterworth *et al*., 2015).

Economically, seeds play a pivotal role in agricultural systems by influencing crop yields and, consequently, the livelihoods of farmers. High-quality seeds are crucial for maximizing productivity, particularly for smallholder farmers who rely on the success of their crops to support their families. However, the seed production industry has seen increasing consolidation, with large companies like Monsanto, Syngenta, and Corteva controlling a significant share of the global market. This concentration not only shapes pricing and innovation but also has implications for accessibility, as smaller farmers may struggle to afford premium seeds (De Bruin, 2023; Sanders, 2024). In parallel, the availability of improved seed varieties promotes sustainable agricultural practices by reducing dependence on chemical inputs like fertilizers and pesticides, fostering environmental sustainability while maintaining high productivity levels (Shah, 2019; Rehman *et al*., 2022; Qaim, 2020).

Yet, this system is not without its challenges. The loss of agricultural biodiversity, accelerated by the rise of commercial agriculture, poses a serious threat to food security and cultural heritage. The dominance of a narrow range of high-yield crop varieties has led to the erosion of plant species that once formed the foundation of global diets. This decline in biodiversity not only jeopardizes the availability of diverse, nutritious foods but also undermines cultural traditions tied to these plants (Tscharntke *et al*., 2012; Heywood, 2011). As a result, the conservation of seeds and the promotion of plant diversity have become urgent priorities to safeguard both food security and ecological balance. Ethnobotany, a field focused on the relationship between cultures and native plants, underscores the need to preserve both biodiversity and cultural heritage. By conserving a diverse range of seeds, we ensure agricultural resilience, protect ecosystems from climate change, and uphold the invaluable connections between plants and people (Singh *et al*., 2015; Srivastav *et al*., 2021).

In recent years, synthetic seed technology has emerged as a powerful tool for plant breeders and tissue culture researchers. This innovative approach enables the mass production of high-quality plant varieties, offering solutions for scaling up plant production. Synthetic seeds also help address challenges posed by conventional seed systems, such as weed germination, by preventing the growth of unwanted species. As a result, synthetic seeds reduce the need for herbicide applications, cutting both costs and treatment frequency, ultimately making agriculture more efficient and sustainable (Reddy *et al*., 2012; Bogdanović *et al*., 2015).

1.3 Seed Microbes: Nature's Hidden Power

The process of making seeds constitutes the most crucial stage in a plant's life cycle. A new crop cycle is initiated in agricultural systems using seeds. Seeds are frequently grown uniformly over a large area of land, handled and processed in large quantities, and produced cheaply. In the environment, seeds aid in spreading, adaptation, and survival in new habitats alongside beginning the life cycle and reproducing the species (Nelson, 2018). Gymnosperm and angiosperm plants both create progeny through the growth of seeds, which are essentially young plants enclosed in a seed coat.

Microbes engage in interactions with seeds as a plant grows. Whether friendly or intimate, these encounters all change the seed microbiome in unique ways that may affect later developing phases (Hardoim *et al*., 2015). The following ought not to be shocking considering the ubiquity of bacteria and the several advantageous microbial homes that plants provide. Thus there may be a direct link between the emergence of the seed microbiome and each of the various microbial communities that are vital to the plant microbiome (Nelson, 2018).

Microorganisms can enter seeds naturally by the penetration of nectarthodes (the stigma style of flowers), paternally through pollen grains, or maternally through the route where carbohydrates are transported to the seed's outer layer from the leaves. Interestingly, for several wild plant species, there are additional means of transmission besides horizontal from the environment, such as vertical from the parents and members of the plant microbiome, or even via way of a bird's or any livestock digestive tract. Certainly, the seed coat is where microorganisms are concentrated, however following germination; they may also be detected on cotyledon and root hypocotyl embryos (Berg and Raaijmakers, 2018).

With an emphasis on contagious pathogens of plants, adequate standards for the quality and purity of seeds have been established at the national and international levels (e.g., the International Seed Federation (ISF), and International Seed Health Initiative (ISHI)). Healthy seeds were once regarded to be "sterile," but that notion has recently changed. Because of this, many phytosanitary techniques have been created and developed over time, including thermal, mechanical, biological, Physical, and chemical treatments for cleansing seedlings (Berg and Raaijmakers, 2018).

The first theory on the presence of microorganisms in seeds was based on research on a harmful fungus, which claimed that seeds without microorganisms were a better indicator of seed quality. Consequently, physical and chemical modifications to agricultural seeds are increasingly often used. Even though some microbial species were lost as a result of these activities, plants might become more sensitive to and reliant on chemicals like pesticides and fertilizers to make up for the functions that the natural seed microbiome has lost (Abdelfattah *et al*., 2022).

Although the focus of past research has been on the microbiomes that influence mature plants, the germination of seeds and the development of seedlings are influenced by environmental conditions that have an impact on plant populations and agricultural output. To be able to regulate plant health outcomes (i.e., seedlings' health), it is crucial to comprehend the factors that affect a plant's microbiome composition during its early life stages (Walsh *et al*., 2021).

2. Seed Microbiome Components

2.1 Seeds and Their Microbial Sidekicks

The study of the fungi, bacteria, and oomycetes microbiomes connected to seeds and other plant parts has significantly increased during the past couple of decades. As a result, there have been several excellent recent assessments of these microbiomes. A large portion of seed microbiomes' present knowledge, especially the endophytic microbiome, is based on research that used a variety of mainly domesticated plant species. Thus, the discovery of a considerably wider variety of microorganisms found in seed microbiomes, especially non-cultivable species, has, however, been made possible by recent developments in sequencing technologies. This has greatly increased our knowledge of the richness and purpose of these communities of microorganisms. These fresh discoveries have significant effects on agriculture and the breeding of plants (Nelson, 2018).

It's important to understand the difference between endophytic and epiphytic microbiota when talking about seed microbiomes (i.e., microbes that inhabit the interior organs of seeds and are vertically passed on to offspring seedlings). The microorganisms that colonize seed surfaces, which may or may not internalize inside seed tissues, and which are transported either horizontally or vertically make up the endophytic microbiota (Bacon and White, 2016; Nelson, 2018; Kumar *et al*., 2017).

Even though endophytes and epiphytes can switch places, this differentiation is made because the endophytic microbiota frequently originates from various seed tissues or external sources as opposed to epiphytic bacteria. Contrary to those linked to the seed coat, which is predicted to be much more diverse and disseminated horizontally, microorganisms connected to the developing embryo and endosperm are more inclined to be transported vertically (Barret *et al*., 2016).

2.1.1 Endophytes

De Bary coined the word "endophyte" in 1866, and referred to it as “Every living organism that grows within a plant's tissues”. To better categorize endophytes, they are now separated into two groups based on the types of organisms (fungi and bacteria) and interactions (Obligatory or facultative relationship with the host plant) they exhibit (Khare *et al*., 2018). These endophytic microbes either originated from seed microbial populations or through the rhizosphere.

Research on the plant microbiome, for instance, has significantly improved the situation by showing that these communities of microorganisms are more flexible and consist of genetic material that codes for certain traits beneficial to their plant hosts. Through vertical seeding, endophytes can penetrate host plant tissues and colonize them. Interestingly, these endophytic microbes are necessary for plants' health, growth, and variety. Moreover, throughout the stages of their life cycle, they have been shown to persist inside of their host asymptomatically (Rana *et al*., 2020). As illustrated in Figure 3, the root microbiome composition encompasses the rhizosphere, rhizoplane, and internal endophytic microbiota (Gaiero *et al*., 2013), emphasizing the intricate interactions among different classes of endophytes in enhancing plant resilience and overall health.

Plants and endophytes may interact in a pathogenic or mutualistic way. However, these microorganisms support the host's defense under a variety of difficult biotic and abiotic circumstances. By fixing atmospheric nitrogen, synthesizing plant hormones, siderophores, hydrogen cyanide, and ammonia, as well as serving as a form of biocontrol against various plant pathogens, endophytic microorganisms significantly contribute to their host's development and promotion (Rana *et al*., 2020).

Namely, the three classes of endophytic bacteria that have received the greatest attention and study are *Proteobacteria, Firmicutes*, and *Actinobacteria*. The listed genera *Bacillus, Pseudomonas, Fusarium, Burkholderia, Rhizobium, and Klebsiella* are those that are most prevalent among the majority of leguminous and non-leguminous plants (Rana *et al*., 2020). Similarly, four different categories of fungal endophytes (FE) are known based on their symbiotic needs (Rodriguez *et al*., 2009).

Class 1 endophytes known as clavicipitaceous fungi are found in several kinds of grasses that grow during the cool season and have the potential to spread vertically through their seeds. Many plants have class 2 endophytes colonizing their shoots, roots, and rhizomes both horizontally and vertically. Class 3 endophytes are horizontally distributed and have a wide variety of hosts with limited colonization of the shoot. Additionally, the class 3 endophytes are also effective in shielding the host crops from various biotic and abiotic dangers, like diseases and insect pests as well as drought. Interestingly, class 4 endophytes are horizontally transferred solely in the roots. (Sampangi-Ramaiah *et al*., 2020; Manasa *et al*., 2020; Waller *et al*., 2005; Hardoim *et al*., 2008; Rho *et al*., 2018a).

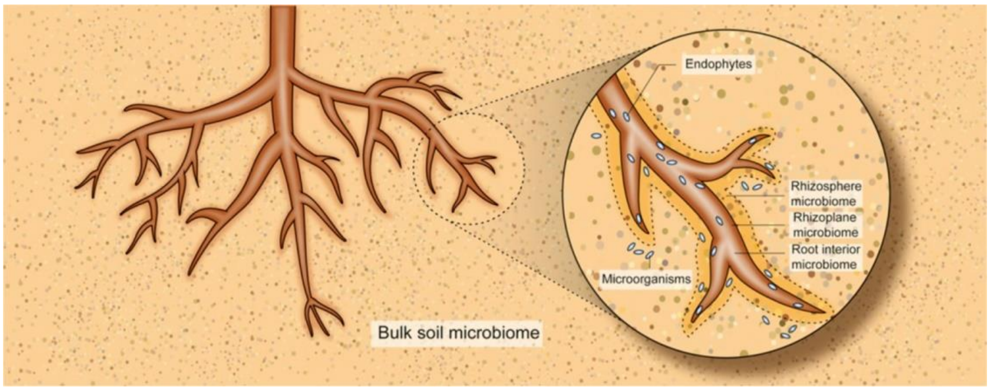

Figure 3. Root microbiome composition: rhizosphere, rhizoplane, and internal endophytic microbiota (Gaiero *et al.,* 2013).

2.1.2 Epiphytes

These are bacteria that can survive and reproduce on plant surfaces. As opposed to endophytic bacteria, epiphytes can be washed off of leaves or eliminated using UV light or chemical surface treatment. The majority of epiphytic bacteria are generally not harmful to the plants they live on, but occasionally they can have positive or negative effects (Sahu *et al*., 2020; Compant *et al*., 2021; Gomes *et al*., 2018).

Similar to the epiphytes, "rhizobacteria" and "phyllobacteria" are terms used to describe all bacteria associated with plants' external structures such as roots and leaves (Gnanamanickam and Immanuel, 2007). It was not known until recently if a seed bacterium that was amplified during germination and could be transmitted to seedlings originated from the endophytic or epiphytic microbiomes since the epiphytic seed microbiome was rarely expressly taken into consideration in investigations of the seed microbiome (Nelson, 2018).

For instance, Links *et al*. (2014) revealed that various endophytic bacterial communities (such as species of *Telluria, Massilia, Xanthomonas, Pseudomonas, and Pantoea*) were found in every single plant genus, and Proteobacteria predominated these communities, as they had in earlier studies. This was done as a component of a study that was designed primarily to look at the kinds of epiphytic bacterial and fungal communities connected to certain *Triticum* and *Brassica* plants. Despite this, the numbers of epiphytic bacteria were comparable and significant (Links *et al*., 2014). Interestingly, widely recognized plant disease species from the genera *Fusarium, Phoma, Pyrenophora, Alternaria,* and *Leptosphaeria* dominated the epiphytic fungal communities enclosing the two plant genera. This discovery suggests that the seed microbiome of epiphytic plants may be more important than previously assumed and that species screening that occurs in endophytic microbes may also occur in epiphytic microbes (Porras-Alfaro and Bayman, 2011; Johnston-Monje *et al*., 2021).

It is now understood that epiphytic bacteria have evolved adaptable mechanisms for growing and reproducing on leaf surfaces, allowing them to withstand environmental factors such as water scarcity, UV radiation, irradiation, variable temperatures, and changes in the supply of nutrients. The display of aggregates that resemble biofilms composed of various bacterial species, yeast, and filamentous fungi is one of the fascinating techniques. The other main bacterial epiphyte subgroups are equally fascinating since they harm advantageous plant pathogens to increase crop yield and cause frost damage and severe bacterial plant illnesses (Gnanamanickam and Immanuel, 2007). Gnanamanickam and Immanuel, (2007) study also provides detailed descriptions of four distinct species of epiphytic bacteria. The majority of them are bacteria that can induce ice to form on plants, biological disease-controlling agents, disease-causing epiphytic bacteria, and bacteria that can create biofilms.

2.2 The Silent Supporters: Revealing Seed Microbiome Roles

As a result of interactions between microorganisms in the environment (such as soil or threshing residues) and the surface of the seed, seeds have traditionally been thought of as a passive route for microbial transmission. Seeds operate as the first inoculum for the plant microbiota because they are a method for transmitting bacteria from one generation of plants to the following.

The concept of "germ-free plants" was created as a result of seed surface sterilization methods, which were once employed in reductionist methods to investigate the interactions among specific plant-microbial strains. Seed-surface cleansing does not ensure seed sterility because seeds have the potential to emit a variety of antimicrobial chemicals that impede the culture-dependent identification of microorganisms (Shade *et al*., 2017).

Research on seed microbiomes is primarily driven by the need to gain a better insight into how microorganisms that seeds acquire during development and germination can improve the makeup and functioning of the whole plant microbiome alongside the implications of these microbial interactions on plant ecology and function. Nonetheless, despite the increased focus on microbiome research, seeds are rarely mentioned as an important part of the plant microbiome and a potential major influence in influencing the assembly, structure, and function of the plant microbiome except for some noteworthy exceptions, (Schlaeppi and Bulgarelli (2015); Turner *et al*., (2013); Van der Heijden and Hartmann (2016); Berg *et al*., (2015); Lebeis (2015); Rout (2014); and Mitter *et al*., 2016).

To sum up, growing interest in the seed microbiome has led to the publication of multiple reviews on the subject recently (Truyens *et al*., 2015; Nelson, 2018; Rodriguez *et al*., 2018). In addition to crop plants like Alfalfa (*Medicago sativa*), rice (*Oryza sativa*), maize (*Zea mays*), tobacco (*Nicotiana tabacum*), coffee (*Coffea spp.*), quinoa (*Chenopodium quinoa*), common beans (*Phaseolus vulgaris*), grapevine (*Vitis vinifera*), barley (*Hordeum vulgare*), and pumpkin (*Cucurbita pepo*), many species of surface-sterilized seeds have been discovered to contain bacteria (Frank *et al*., 2017). The enormous cardon cactus (*Pachycereus pringlei*) and the Norway spruce (*Picea abies*) are two examples of this. Moreover to the coat, endosperm, and embryonic tissues, bacteria have been discovered in some seed constituents (Frank *et al*., 2017). Truyens *et al*. discovered that bacteria found in seeds frequently belong to one of many genera, including *Micrococcus, Staphylococcus, Pantoea, Bacillus, Pseudomonas, Paenibacillus, and Acinetobacter* (Truyens *et al*., 2015).

2.3 Microbial Contributions: Building Plant Health and Resilience

Despite being essential to the continuation of life on Earth, a great deal of microorganisms, including those that live on and in human bodies as well as those that are found in soil, oceans, and the atmosphere, are unknown to us. However, it’s important to note that molecular technologies, like metagenomics, are gradually making it easier to identify bacteria in situ, similarly, culture-based methods have enabled in-depth examinations of such microorganisms. Thus, using this technique, the microbiomes, or microbial communities, of various sites have been studied to comprehend their ecological role (Turner *et al.*, 2013).

When it comes to plants, microbiomes can improve the genetic and metabolic abilities of their hosts, supplying or facilitating many crucial life-supporting processes like nutrient intake, immune system control, and tolerance to biotic and abiotic stress (Cordovez *et al*., 2019). Similarly, Brader *et al.* (2014) confirmed that numerous bacteria that interact closely with plants create secondary metabolites that are necessary for nutrient absorption (Brader *et al*., 2014). Table 1 highlights the critical role of soil-borne microorganisms in mitigating abiotic stress in plants. Additionally, Table 2 highlights the enhanced plant growth-promoting traits resulting from microbial inoculation.

The essential microbial processes that enable the enhancement of plant development, including increased intake of nutrients from the soil, ability to withstand abiotic stressors, production of hormones, as well as indirect pathogen defense, are generally attributed to a group of microbes known as Plant growth-promoting microorganism (PGPM) (Schlaeppi and Bulgarelli, 2015). Many helpful microbes aggressively colonize plants, resulting in a diverse range of interactions between plants and microbes. Some of these interactions are helpful to the plant, but not all of them. Certainly, the plants act as a source of nutrients or as a niche habitat where the bacteria can grow (Vurukonda *et al*., 2018). Figure 4 illustrates the vital roles of PGPMs in enhancing nutrient acquisition and plant resilience.

Prominent among the microbes associated with plants are the microbes associated with the root areas of the plant. Several studies abound indicating the benefits of Plant Growth Promoting Rhizobacteria (PGPR) (Ajibade *et al*., 2023; Kumar *et al*., 2022).

Table 1. Demonstrates how soil-borne microorganisms reduce abiotic stress in plants.

MICROBES	AIM PLANT SPECIES	STRESS REDUCTION	THE STRATEGY OF EFFECT AND TOLERANCE	REFERENCES
Pseudomonas aeruginosa	Wheat	Zinc toxicity	Boost soluble protein uptake, nutrition absorption, and plant development.	Islam *et al*., 2014
Enterobacter intermedius MH8b	*Sinapis alba*	Zinc toxicity	ACC Deaminase, Phosphorous-solubilization	Płociniczak *et al*., 2013
Photobacterium spp	*Phragmites australis*	Hg toxicity	Mercury reductase, IAA	Mathew *et al*., 2015
Burkholderia and Bacillus	*Capsicum annum*	Salt	increased prolinei synthesis	Pawaskar, 2023
Glomus fasciculatum	*Phragmites australis*	Salt	Carbohydrate accumulation	Gao *et al*., 2020
Bacillus subtilis	*Lactuca sativa*	Salt	Signaling by cytokinins and biomass production	Mainardi and Bidoia, 2023
Pseudomonas chlororaphis 06	*Arabidopsis*	Drought	synthesis of a volatile molecule	Cho *et al*., 2018

thaliana

Table 2. Illustrates improved plant growth-promoting characteristics brought on by microbial inoculation.

PLANTS	BENEFICIAL MICROBES	TRAIT FOR PROMOTING PLANT GROWTH	REFERENCES
BIOINOCULANTS/BIOFERTILIZER			
Lens culinaris var. PL	*Chryseobacterium sp.*	the dissolution of phosphate	Singh *et al.*, 2018
Sarracenia species	*Endophytic diazotrophic bacteria*	fixation of nitrogen	Sexton *et al.*, 2020
Zea mays	*Bacterial endophytes (specifically Bacillus and Brevibacillus)*	Increases the productivity and quality of crop	ALKahtani *et al.*, 2020
RESPONSE TO STRESS			
Black pepper	*Bacillus Licheniformis*	Drought stress resistance	Lim and Kim, 2013
Oryza sativa	*Bacillus pumilis strain JPVS11*	tolerant of salt	Kumar *et al.*, 2021
Avicennia marina	*Halomonas sp.*	hefty metal strain	Mukherjee *et al.*, 2019

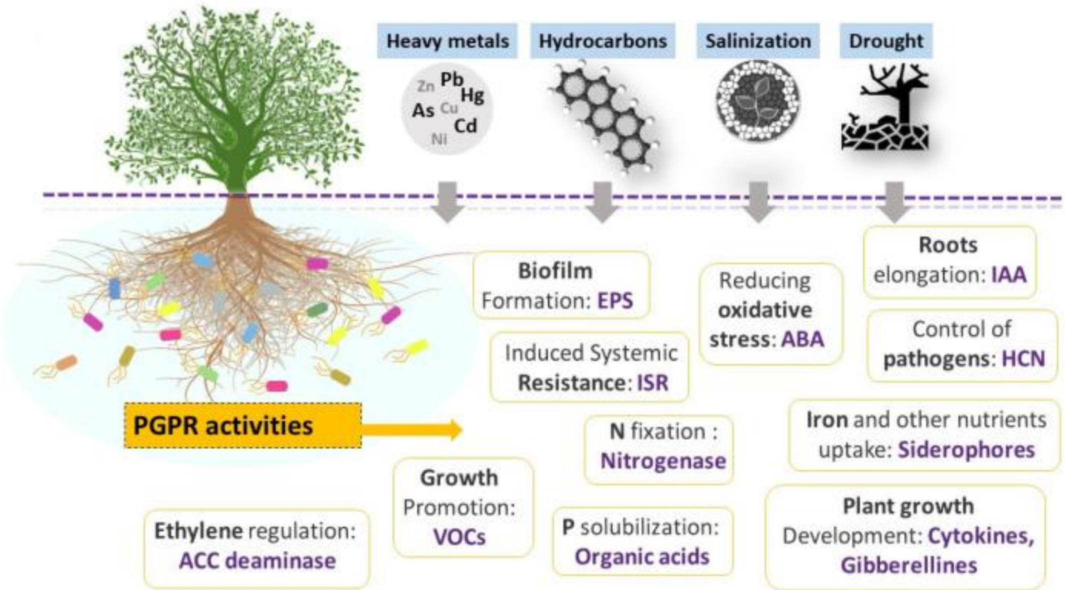

Figure 4. Roles of plant growth-promoting microorganisms (PGPMs) in improving nutrient uptake and resilience.

Among the microorganisms that have demonstrated the greatest effectiveness in encouraging the growth of crops and, consequently, increased productivity, are rhizobacteria and mycorrhizal fungi (Emmanuel and Babalola, 2020; Nanjundappa *et al.*, 2019). Rhizosphere bacteria can improve the capacity of the plants they colonize to take up nutrients from the rhizobia. As a result, they might be viewed as powerful biofertilizers. For example, the most prevalent species of these rhizosphere-promoting bacteria include *Burkholderia, Enterobacter, Klebsiella, Pseudomonas, Arthrobacter, Azospirillum, Azotobacter, Bacillus, Alcaligenes*, and *Serratia* (Rai *et al*., 2020; Kundu *et al*., 2024) and despite being a member of the microbial communities of the rhizosphere, *Streptomyces spp*. has only recently gained attention for their capacity to act as plat growth enhancers (Dias *et al*., 2017). Likewise, Ecto- and endo-mycorrhizal connections (*mycorrhizae*) are essential to ensure plant development and biomass by enhancing nutrient (minerals) and water uptake as well as plant tolerance to abiotic and biotic stresses (Smith and Read 2010).

Furthermore, increased plant output and growth, supported by microbial endophytic populations, are typically linked to better plant health. This is done by directly controlling plant pests and pathogens or by using plants to buffer the situation. According to several research, mycorrhizae and/or rhizobacteria, two types of root-associated microorganisms, may alter plant physiology and make the plant's above-ground portions less vulnerable to assault by phytophagous insects. (Pangesti *et al*., 2013). Plant defense is then carried out by enhancing the expression of sequences controlled by the manufacture of salicylic acid, ethylene, or jasmonate. Other times, helpful bacteria, such as root-colonizing pseudomonads, may directly fight plant-eating insects by releasing volatile organic compounds (VOCs) with insecticidal properties (Kupferschmied *et al*., 2013). As shown in Table 3, microbial communities provide the host plant with significant advantages.

Table 3. Microbial communities provide the host plant with significant advantages.

MULTIPLE MICROBIOME PART	PLANTS	POSITIVE CHARACTERS	REFERENCES
RHIZOSPHERE	*Phragmites karka*	Degradation of the insecticide lindane, formation of the amino acid IAA, the production of ammonia, and activity of the enzyme ACC-deaminase	Singh and Singh, 2019
	Brassica juncea	Inhibit the growth of fungal pathogens	Guan *et al.,* 2008
	Glycine max	Influences rhizosphere phosphorous dynamics and phosphorous dynamics	Tian *et al.,* 2020
	Ipomoea batatas	Fixing of nitrogen and dissolving of phosphate	Margues *et al.,* 2022
ENDOSPHERE	*Berberis aristata*	Bio-control potential	Sharma *et al.*, 2018
	Anadenanthera colubrine	characteristics that encourage plant growth	Alibrandi *et al.,* 2018
	Cymbidium aloifolium	Manufacturing of phytohormones	Jagannath *et al.,* 2019
PHYLLOSPHERE	*Pyrus serotina, Vitis vinifera, Prunus armeniaca and Prunus avium*	Fixation of nitrogen	Liang *et al.,* 2019
	Zea mays	Synthesis of siderophores, indole acetic acid, phosphate solubilization, nitrogen	Abadi *et al.,* 2020

	gas fixation, etc.	
Oryza sativa	Possibility of alleviating a severe drought	Arun *et al*., 2020

3. Botany Basics

3.1 Understanding the Traits of Plants

It is common knowledge that plants differ from other living things in several unique ways. Most of them are known to produce the unique pigment chlorophyll and may be found both on land (terrestrial plants) and in water (aquatic plants). The structures of green-pigmented plants, also known as photoautotrophs, frequently contain large quantities of chlorophylls, which are light-trapping substances. Through a process known as photosynthesis, photoautotrophs can grow and create carbohydrates, particularly sugars, using chlorophyll [which absorbs light], water, light, and some additional factors. The vast bulk of the anabolic equipment required to accomplish this goal is found in the plastids. This characteristic separates photoautotrophs (green-pigmented plants) from heterotrophs, which must obtain their source of energy to survive by directly consuming green plants. As a result, almost every living thing on Earth is reliant on the mechanism of photosynthesis, which is carried out by green plants, either directly or indirectly (Crang *et al*., 2018; Wise and Hoober, 2007).

A great deal of plants is set in a fixed position, which makes them simple for herbivores to devour (Skarpe and Hester, 2008). As a kind of self-preservation, plants have developed biosynthetic pathways that give rise to a variety of hazardous substances, many of which are consumed by people as spices, additives, herbal remedies, colors, preservatives, medications, and stimulants.

Algae, which are technically protists rather than plants, are categorized as "green" plants, similarly, bryophytes, gymnosperms, and angiosperms are known to be the true plants. In addition, because spores are the outcome of meiosis, plants have an evolutionary process known as a discontinuous life cycle. Technically speaking, plants go through mitosis to create gametes, whereas meiosis creates haploid spores. This is distinct from the early stages of embryonic development that occur in numerous protists and the meiotic development process of mammals, which creates gametophytes directly through meiosis. The phrase "alternation of generations" describes these two separate life cycle periods (Crang and Vassilyev, 2003). Figure 5 illustrates the alternation of generations in plants, depicting the life cycle involving both sporophytes and gametophytes, highlighting the transitions between these two phases.

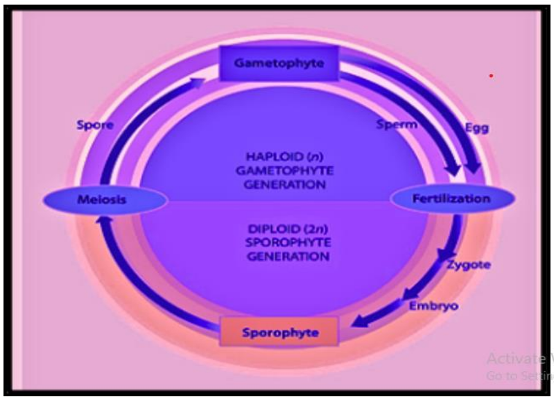

Figure 5. Depicts the phases of alternation of generations in plants, illustrating the life cycle involving sporophytes and gametophytes.

3.2 Plant Anatomy

Over the estimated 475-million-year evolution of terrestrial plants, there has been a tremendous rise in the diversity of plant species. Some plants have the capability of producing seeds, typically referred to as flowering plants (Angiosperms-these plants produce flowers where seeds are formed), on the other hand, non-flowering plants also referred to as gymnosperms are another group that produce cones or other structures to house and release their seeds (Crang *et al*., 2018). Among the four primary angiosperm organs are;

ROOT: The roots of a plant act as a system of anchoring that aids in nutrient, mineral, water, and carbon (heterotrophic) acquisition by plants. Thus, they are connected to every part of the stalk, leaves, and flower through sophisticated circulatory systems. In Figure 6, the illustration depicts seedlings of *Zea mays* (a monocot plant) and *Phaseolus vulgaris* (a eudicot plant) root structures (Dorval *et al*., 2016).

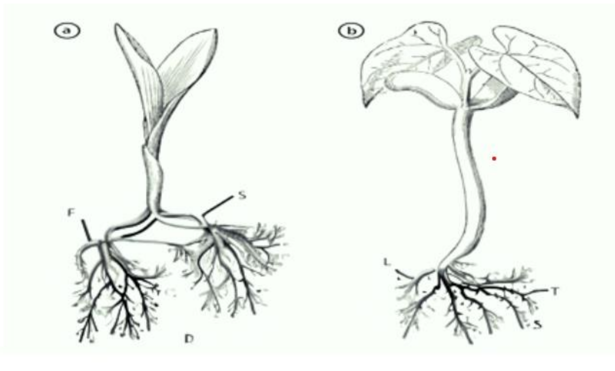

Figure 6. *Zea mays* (a monocot plant) and *Phaseolus vulgaris* (a eudicot plant) seedlings are seen in the illustration. **KEY**: By F-fibrous root, S-stem, L-lateral root, and T-taproot (Dorval *et al*., 2016)

STEM: The plants topmost parts, such as the leaves and flowers, are supported by the stem. The stem's main job is to hold and spread the leaves evenly so that the absorption of sunlight is maximized. Exposure to pollinators like wind, insects, birds, or other animals is a crucial "benefit" that stems offer a plant.

LEAVES: The structures responsible for the plant's photosynthesis are its leaves. Their structure and anatomy have evolved to maximize carbon dioxide intake and light absorption. The surface is virtually flat (to improve sunlight absorption), greenish (due to the presence of many chloroplasts), and minimally translucent (Langer *et al*., 1991)

FLOWERS AND FRUITS: Almost all plant species develop and procreate. However, only angiosperms use fruit and flowers to accomplish this. Fruit is in charge of developing seedlings, and this happens either naturally or by the use of extra agents like the wind, water, animals, or other ways, while a flower must be visible to the forces of wind or attractive to a particular insect pollinator to be pollinated effectively. The two primary groups into which seed plants are conventionally separated are gymnosperms and angiosperms. Compared to non-seed plants, both of these types of seed plants produce much less gametophytes (gametes). Figure 7 illustrates the general structure of a flowering plant, highlighting its roots, stems, leaves, and flowers (Abdulmajeed, 2022).

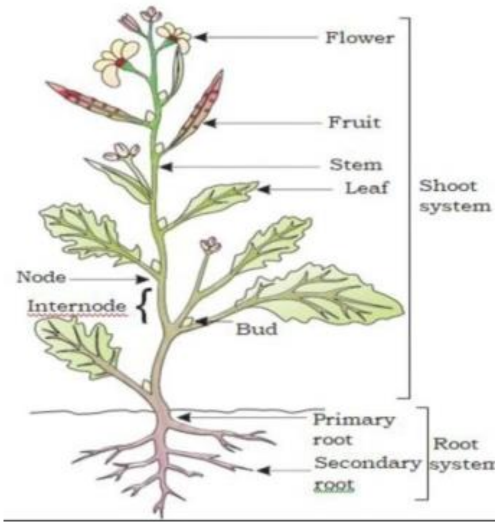

Figure 7. General structure of a flowering plant (Abdulmajeed, 2022).

4. Transmission Pathways And Functional Roles Of The Seed Microbiome

4.1 The Plant Microbiota: Vertical vs. Horizontal Inheritance

The plant microbiome can spread either vertically (acquired straight from the parent) or horizontally (depending on how they were acquired), and this is in harmony with Shade *et al*. (2017) who stated that the horizontal or vertical transmission of any microbiological entity influences how an organism spreads via seeds, and there have only been three major methods identified so far (Shade *et al*., 2017). Three possibilities exist for the seed to get an infection; internally via the maternal plant's xylem or non-vascular tissues (ii) externally via coming into contact with bacterial culture on fruits or crushing debris (iii) florally through the stigma.

In addition, symbioses can be transmitted vertically by mutualistic symbiotic partners, albeit not all mutualists must do so. Also, numerous mutualistic partnerships that can spread horizontally are another example (Frank *et al*., 2017).

Overall, the soil microbiota is a typical repository for biodiversity of bacteria connected to plants and a great majority of these microbes were created specifically to survive in the soil. As a result, the widespread population pool known as soil microbiota contains plant-associated microorganisms, and the bulk of these microorganisms were designed to be gathered in soil conditions using the following techniques:

I) Soil-borne bacteria first circulated in the rhizosphere after which they congregated around the host's rhizoplane in response to root exudates and rhizodeposition.

II) After the host was selected, certain rhizoplane bacteria entered the roots of the host and subsequently colonized the internal tissues (via horizontal transmission). However, the process of microbiological colonization is not yet finished. Through Stems, blooms, and seeds bacteria continued to go to the host's above-ground areas (Zheng and Gong, 2019).

For example, the review conducted by Frank *et al*. (2017) below outlines how bacterial endophytes spread through plants. It addresses both vertical (from parent plant seeds or pollen) and horizontal (from the environment) transmission channels. Furthermore, it also emphasizes several routes, including soil-to-root transfer, propagation through the phyllosphere (above-ground plant surface), and the potential involvement of insects in the transmission of bacteria within plants. As a result, it emphasizes how important these pathways are for passing endophytes from a single generation to the next (Frank *et al*., 2017). The studied transmission pathways and modes are shown graphically in Figure 8.

According to Frank *et al*. (2017), various plants' seeds contain bacteria, proving that bacteria can migrate vertically from one plant to another through pollen and seeds as shown in (Figure 8A). Also, endophytes need a pathway that either passes through xylem vessels or via the shoot apical meristem for their organs of reproduction to emerge from seeds and pass from a single generation to the next to reproduce (Figure 8C).

Additionally, the soil-to-root transmission mechanism, which is assumed to be the main habitat from which bacterial endophytes develop, is the most thoroughly researched horizontal transmission mechanism. Figure 8D demonstrates how permitting soil bacteria to enter the plant's interior sooner enables the rhizosphere, the root system of seedlings and adults, to do this later than the spermosphere, which is the germination environment.

Finally, an additional but less well-researched entrance point for microbes transported via rainwater, bioaerosols from the nearby soil or dust, or other particulates in the air and may penetrate through stomata is the phyllosphere, or surface, of the above-ground plant as shown in (Figure 8E). This region is home to a diverse community of microbes. Thus, all plant life stages likely require stomata as a means of transmission, although foliar endophytes on trees may be especially dependent on them. Furthermore, microbes that enter plants can be transmitted by insects such as sap-feeders, and pollinators, along with other arthropods as shown in (Figures 8F and 8G) (Frank *et al*., 2017).

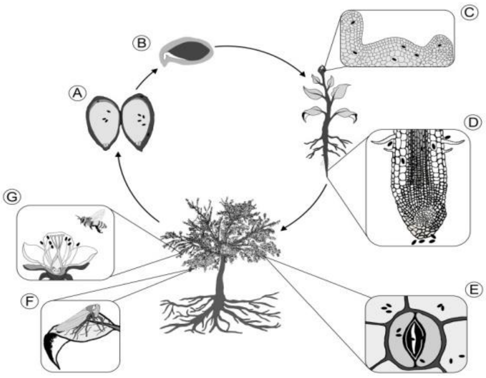

Figure 8. Transmission pathways of bacterial endophytes, from soil to plants and between plant generations (Frank *et al.,* 2017).

5. Methodologies for Studying the Seed Microbiome

5.1 Use of Future-Generation Sequencing Technologies In Seed-Related Microbiome Studies

The separation, characterization, and identification of bacteria from clinical, dietary, or environmental sources formerly relied on methods like the traditional Gram stain and certain biochemical characteristics. Since the human gut microbiota is a diverse community, culture-dependent approaches, despite being the "gold standard," could only detect 0.1% of it. Methods were required to discover or classify microorganisms and forecast the functional relationships of the various microbial populations found in the sample. To this purpose, recent developments in multi-omic technologies have made it possible to profile microbial communities, track population changes in various microbial habitats, and characterize various microbial species (Cao *et al*., 2017).

Next Generation Sequencing (NGS) is a sort of DNA sequencing technology that permits researchers to examine and comprehend the world of microbes from a wider and more in-depth perspective. Traditionally, NGS has been utilized to comprehend the taxonomic makeup of a microbiome associated with food. It utilizes several platforms to identify the sequences of DNA and RNA. Additionally, it has been utilized to characterize the intricate relationships between various microbial communities contained within an individual microbiome at the species- and strain levels as well as their functional interactions (Cao *et al.,* 2017).

For instance, NGS is effective in microbial population monitoring in turfgrass seeds by researchers like Ban *et al.* The 26 different fungal orders that were discovered by NGS include pathogenic strains such as *Boeremia exigua, Claviceps purpurea, Rhizoctonia zeae, and Bipolaris sorokiniana* which cause serious plant diseases. As a result, the work highlights the collaboration between traditional pathogen culturing and NGS for accurate pathogen identification. Additionally, other bacterial orders were used to identify seed-borne bacteria, such as *Acidovorax avenae* and *Erwinia persicina*, highlighting the significance of the study (Ban *et al*., 2021).

Also, guidelines for successfully isolating and cultivating pathogens that affect seeds, as well as examining their physical characteristics, have been established by several institutions, including the International Seed Testing Association, the International Seed Health Initiative, and the United States National Seed Health System (Ellias *et al.,* 2012). A more thorough examination of isolated pathogens has become possible thanks to the widespread usage of inexpensive phenotypic approaches. There are downsides; however, including the inability to grow a wide variety of fungi, prolonged cultivation times, and a lack of sensitivity for spotting illnesses in host seeds with low pathogen levels (Tavanti *et al*., 2005).

Presently, seed-borne disease tracking has been greatly enhanced by molecular methods like PCR, reverse transcription PCR, quantitative PCR, and DNA macroarray employing oligonucleotides. These techniques, however, primarily focus on particular illnesses in seed samples and don't fully characterize the range of microbial populations. A potent method for investigating microbial communities, next-generation sequencing (NGS) provides extensive data sets and thorough insights into a wide range of microorganisms at a reasonable cost. With NGS, a wide range of organisms can be screened in a single sample, enabling the identification of rare species that would otherwise go unnoticed with traditional methods (Ban *et al*., 2021).

6. Mechanisms of Influence on Plant Growth

6.1 Biological Seed Priming and Biological Structural Stimulation of Plant Growth and Defense Responses

A variety of abiotic and biotic variables have an enormous effect on the growth and development of plants, and there are many ways to reduce these pressures. One of the best strategies to encourage plant growth and to give plants systemic tolerance to biotic and abiotic problems is to prime the seeds with beneficial bacteria. Seed priming is the act of treating seeds with microorganisms that help plants grow, and it improves the plant's ability to survive adverse conditions from seed germination onwards.

According to Singh *et al*. (2018), biopriming, also known as seed priming with beneficial microorganisms, promotes the germination of seeds, shields them from a range of plant pathogens, and aids in the enhancement of plant growth. Additionally, a variety of mechanisms involved in bio-priming help to promote morphogenesis and plant immunity. These processes include phytohormone production, stimulated expression of genes that promote plant development, higher nutritional status within the plant, antibiosis, activation of antioxidant production, mycoparasitism, induced phenolic production, and systemic defense activation.

Azotobacter species, Pantoea agglomerans, Rhizobium species, Bacillus subtilis, Paenibacillus polymyxa, Pseudomonas fluorescens, Rhizobium phaseoli, Acinetobacter calcoaceticus, Pseudomonas putida, and Bacillus cereus are a few important bacteria which produce phytohormones and that the seed surface is ideal for the microbial inoculum to colonize due to seed bio-priming (Singh *et al*., 2018).

Similarly, some bacteria promote the growth of plants. These bacteria accomplish this using a variety of techniques, such as biofertilization (improving the plant's access to mineral nutrients), biocontrol (removing pests and weeds that are harmful to the plant), and direct plant root development (for example, by supplying the plant with plant growth hormones). However, for each of these systems, plant-root colonization is a crucial component of the delivery mechanism (Lugtenberg *et al*., 1991).

Lugtenberg *et al*. (1991) believe that three categories can be used to categorize plant-friendly microorganisms. The first class of microbes includes those that are involved in biofertilization or soil microorganisms that can boost the availability of mineral nutrients like phosphorus and nitrogen to the plant. This method of encouraging plant growth has been around for a while. For instance, commercial usage of nitrogen-fixing Rhizobium inocula dates back to the turn of the previous century. The second class of microorganisms comprises those that indirectly encourage the growth of plants by inhibiting the development or activity of plant-pathogenic organisms. This method of disease prevention, which has been used commercially for a long time, is sometimes referred to as biocontrol to distinguish it from treatment with chemical pesticides. Evidence that supports this is the use of *Bacillus thuringiensis* to treat plants which results in the production of a toxin that is fatal to most insects that harm plants. The third category of beneficial microorganisms for plants includes those that directly promote biological plant growth, such as by producing phytohormones in the rhizosphere.

6.2 Challenges and Future Directions

The integration of seed microbiomes into agriculture offers immense promise for sustainable farming, but challenges remain that must be addressed to unlock their full potential. Microbial inoculants, which hold the key to enhancing plant growth and resilience, often show inconsistent performance when transitioning from controlled environments to real-world agricultural systems. Variability in soil types, climate conditions, and interactions with native soil microbiomes can significantly influence their effectiveness (Torres-Abe *et al*., 2024; Hanif *et al*., 2024).

To overcome these hurdles, a deeper understanding of how inoculants interact with indigenous microbial communities and plants is critical. These interactions play a pivotal role in shaping microbial community dynamics and plant health, particularly under stress conditions such as drought or nutrient limitations. Tailoring microbial formulations to specific crops and local environmental contexts could greatly enhance their reliability and impact (Chen *et al*., 2024). Emerging technologies, such as microbial encapsulation and in situ microbiome engineering, offer innovative solutions to improve colonization, stability, and effectiveness in diverse farming conditions (Hanif *et al*., 2024).

Equally important is addressing knowledge gaps about the long-term effects of these microbial applications on soil health and biodiversity. Understanding these impacts is vital not only for ensuring environmental sustainability but also for building resilient agricultural systems capable of meeting future food security demands. Collaborative efforts involving scientists, agronomists, and farmers are essential to bridge the gap between research and practical application, ensuring that seed microbiome technologies are accessible and effective across varying agricultural contexts (Fiodor *et al*., 2023; Torres-Abe *et al*., 2024).

In parallel, supportive policies and educational initiatives must be developed to promote the adoption of sustainable practices. Informing farmers about the benefits and proper use of microbial inoculants can empower them to incorporate these tools into their farming systems (Fiodor *et al*., 2023). By raising awareness and providing resources, we can foster a shift toward a resilient food production system capable of addressing global challenges like climate change and resource depletion, ensuring a sustainable future for agriculture.

7. Conclusion

In conclusion, the seed microbiome is a critical component of plant growth and development, influencing seed germination, plant establishment, disease resistance, and overall productivity. The microbial communities associated with seeds, including bacteria, fungi, and other microorganisms, contribute significantly to plant health and resilience. Recent studies have highlighted the role of the seed microbiome in shaping plant performance, with beneficial microbes such as plant growth-promoting rhizobacteria (PGPR) offering substantial potential for improving crop yields and sustainability. However, despite its importance, the seed microbiome remains underexplored compared to other plant-associated microbiomes. Understanding how environmental factors, plant genotype, and microbial communities interact within seeds is still in its infancy. Moreover, while the presence of beneficial microbes can promote plant growth, the intricate balance with harmful pathogens needs further investigation to optimize seed microbiome management.

There is also a need to develop standardized methodologies for assessing the seed microbiome, as the variability in microbial communities across different plant species and environmental conditions complicates comprehensive studies. Future research should focus on exploring the functional roles of seed-associated microbes, particularly how they interact with the plant's innate defense systems and contribute to stress resilience. Additionally, advancing technologies to manipulate the seed microbiome could lead to novel approaches for sustainable agriculture, reducing reliance on chemical inputs while enhancing crop productivity. By addressing these knowledge gaps, future studies can offer innovative solutions for improving food security and promoting sustainable agricultural practices worldwide.

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