Soil Microbiome Dynamics

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Exploring Interactions and Implications for Agricultural Practices

Edited by

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and Wiem Alloun

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CHAPTER 1

PIONEERING SOIL MICROBIOME RESEARCH: THE NEW SCIENCE FRONTIER

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Abstract

The soil microbiome is emerging as a critical frontier in environmental science with profound implications for agriculture, ecosystem management, and climate resilience. This field of research has explored the complex communities of microorganisms living within the soil and their vital roles in nutrient cycling, plant health, and soil structure. Despite significant progress, many aspects of the soil microbiome remain poorly understood, presenting challenges and opportunities for innovation. Recent advances in high-throughput sequencing technologies, metagenomics, and computational biology have provided unprecedented insight into the diversity, function, and dynamics of soil microbial communities. New studies are uncovering how microbial populations interact with plants, influence soil fertility, and contribute to broader ecological processes. As we stand at the verge of a new scientific frontier, soil microbiome research promises to revolutionize sustainable agricultural practices and mitigate the challenges faced in multiple sectors. This idea highlights the transformative potential of soil microbiome research, emphasizing its role in shaping the future of agriculture and food security.

Keywords: soil microbiome, microbial diversity, metabolome, metagenomics.

1.1 Introduction to Soil Microbiome Research.

1.1.1 The Soil Microbiome: An Overview

A microbiome is a colony of microorganisms that prevail in a particular environment with the substances and microbial structures they produce. These microbiomes are found in soils, oceans, humans, animals, and plants among other environments. The microbiome harbors a vast number of microorganisms incorporated into groups, including fungi, bacteria, viruses, blue-green algae, actinomycetes, and protozoa etc among others. Soil microbiomes reside in the root regions of plants, and their functions are crucial in nutrient cycling, carbon sequestration, and sustaining soil fertility (Berg *et al.,* 2020). The varied and diverse characteristics of the soil microbiome result from the range of habitats provided by the soil. The combination of factors, such as temperature, parent material, organisms, and time, contributes to the heterogeneously varying nature of soil and their differences from one geographical location to another. Moreover, in a single soil profile, the environmental conditions within and between soil horizons can vary greatly, offering a variety of homes for microorganisms (Prabhakaran *et al*., 2022). The interaction between soil microbes and plants leads to the formation of symbiotic relationships, which improve plant growth, shield against pathogens, and enhance nutrient uptake. The abundant nitrogen in the atmosphere is converted into an available form by nitrogen-fixing bacteria, which can be absorbed by plants, and the hyphal network of mycorrhizal fungi extends into plant roots, promoting water and mineral absorption. The soil microbiome outperforms phytopathogens in resources and space, or reduces their activity by producing antimicrobial compounds, thus playing a key role in the suppression of diseases (Kumar *et al.,* 2022). The development and composition of the soil microbiome are determined by several factors, such as the plant species harboring them, soil type, field practices, and climatic conditions, making them highly complex. Growing research on the soil microbiome has brought forth its potential in enhancing agricultural productivity, assisting in overcoming obstacles such as climate change and soil degradation, and leading to sustainable agricultural practices. Gaining more knowledge about the soil microbiome would lead to the development of innovative ideas for enhancing the soil microworld, such as improving the population of beneficial microorganisms, minimizing the effects of harmful microorganisms, and assisting food safety and environmental health (Wu *et al.,* 2024).

1.1.2 Historical Context and Milestones in Soil Microbiome Research

Over the past 20 years, increasing our understanding of microbiomes has gained popularity among the general public and in the scientific world, particularly as a field with significant potential for novel medicinal therapies (Berg *et al*., 2020). The discovery of microorganisms in soil and the development of high-throughput sequencing methods to comprehend their variety, functions, and ecological significance have led to major breakthroughs in soil microbiome research in recent decades. Additionally, encouraging findings from microbiome research have increased private investment in businesses and startups as well as the “microbiome market” as a whole (Garg *et al*., 2024). Engineering breakthroughs in microbiome research will be a potential alternative for chemicals in agriculture, horticulture, and aquaculture in the future and will be the foundation for the efficient use of natural resources and enhanced food production (Li *et al*., 2023). Microbiota-based agricultural products are one of the fastest growing aspects of agronomy with 15-18 a Compound Annual Growth Rate (CGAR) and a projected value of approximately 10 billion US dollars by 2025. Furthermore, studies on the microbiome can offer solutions towards the contribution of all life forms on Earth to sustain one of the biggest problems of climate change (Berg *et al*., 2020).

Research on soil microbiomes has predated the development of high-throughput sequencing technologies and contemporary molecular biology techniques. Determining the widespread presence of microorganisms in soil and understanding their functions in soil fertility are the primary goals of early microbiological research (Jiang *et al*., 2023). In 1676, Antonie van Leeuwenhoek, using one of his handcrafted microscopes, became the first person to describe microorganisms, including bacteria, in soil samples. His findings were crude, although the technology available at the time was insufficient to fully explore the intricacy of soil microbiota (Lane, 2015). Until the late nineteenth century, Robert Koch provided the groundwork for microbiological methods that would later play a crucial role in soil microbiology through his revolutionary research on the germ theory of illness. Despite his primary focus on harmful bacteria, his research helped to expand our knowledge of microbial life, particularly that found in soil ecosystems (Drews, 2000). By the early 20th century, soil microbiology had emerged as a formal field, with researchers beginning to develop basic microbiological techniques and focus on soil fertility, decomposition, and nutrient cycling. During the 1910s and the 1920s, research in soil microbiology took a significant turn toward understanding the nitrogen cycle and role of microbes such as *Rhizobium* in soil fertility. *Rhizobium*, a bacterium that forms symbiotic relationships with leguminous plants, is recognized for its ability to fix atmospheric nitrogen, thereby enriching the soil with this vital nutrient (Kupferberg, 2003). This discovery provides new insights into the symbiotic relationships between microbes and plants, thereby shaping the foundations of agricultural microbiology. The period from the 1930s to the 1950s marked a significant leap forward with the introduction of selective media to culture soil bacteria. This breakthrough has allowed scientists to isolate and identify specific microbial species that were previously challenging to study. Bacteria such as *Azotobacter*, which can fix nitrogen independently in the soil, and *Bacillus*, which is known for its role in decomposing organic matter, were isolated and studied. These advances have led to a deeper understanding of the microbial processes that drive soil health, such as nitrogen fixation and breakdown of organic matter into simpler compounds (Aasfar *et al.*, 2021). This era marked a key transition in soil microbiology, shifting from a theoretical understanding of microbial roles in soil fertility to the practical application of microbiological techniques for isolating and studying specific soil microbes.

Accessing the soil microbiome led to the detection and characterization of individual species within the same genus in the 1980s through the development of Polymerase Chain Reaction (PCR) in 1980s allowed the amplification of DNA from environmental samples, paving the way for studying non-culturable microorganisms (Picard *et al.*, 1992). In the 1990s, 16S rRNA sequencing and variation in the ITS region became the standard for identifying bacterial and fungal species, respectively, in any sample. This enabled the detection of a vast array of microbes that could not be previously cultured in the laboratory. *Bacillus subtilis* and *Pseudomonas fluorescens* were identified as key soil bacteria using molecular methods involved in soil nutrient cycling, biocontrol, and plant growth promotion. The advent of next-generation sequencing (NGS) technologies in the 2000s, particularly 16S rRNA and shotgun metagenomic sequencing, has enabled unprecedented depth and breadth of microbiome studies (Soliman *et al.*, 2017). These techniques allow for the sequencing of entire microbial communities directly from environmental samples without the need to culture organisms. This provides insights into the functional potential of microbial communities, such as nutrient cycling, biodegradation, and symbiotic relationships with plants. Soil samples from diverse ecosystems have revealed communities dominated by microbes such as Actinobacteria, Firmicutes, Proteobacteria, and Bacteroidetes (Aguilar-Paredes*et al.*, 2023). Specific species, such as *Streptomyces* (Actinobacteria), are well known for their roles in the decomposition and production of antibiotics (Shivlata and Satyanarayana, 2015). In recent years, there has been a growing focus on understanding the ecological roles of soil microbes, such as Rhizobia, Actinobacteria, Mycorrhizal fungi, and Firmicutes and how they contribute to ecosystem services, such as nutrient cycling, soil structure formation, and resistance to pathogens (Vincze *et al*., 2024). Advances in molecular tools, high-throughput sequencing, and ecological theory have allowed researchers to explore the vast diversity and functional potential of soil microbiomes, offering new insights into their impacts on agriculture, ecosystem services, and environmental health. The continued integration of functional genomics, microbial ecology, and synthetic biology will likely drive future breakthroughs in soil microbiome research (Garg *et al*., 2024).

1.1.3 The Importance of Soil Microbiomes in Ecosystems and Agriculture

Although intensive agricultural methods boost crop yields, they can negatively affect the physical and biological characteristics of soils. The variety and makeup of soil microbial communities are affected by agricultural activities, but the effects of these changes on the functioning of agricultural ecosystems are still not well understood. The most complex and varied environment is soil, which is home to billions of bacteria, millions of fungi, and other microorganisms (Bertola *et al*., 2021). The interaction between the roots and soil microbes has a significant impact on growth and nutrition. The word “rhizosphere” was coined by Lorenz Hiltner, who described it as a microenvironment where bacteria (bacteriorhiza) can interact and significantly affect plant nutrition. Microbial diversity is crucial for the preservation of ecosystems and biological diversity (Chauhan *et al*., 2023). The functioning of ecosystems depends on the interactions between plants and microbes. The root system works closely with a variety of soil microbial populations in addition to aiding in the insertion of a plant into the ground, absorption of water and ions, and nutrient storage. Microbial interactions with roots can involve endophytic or free-living microbes, and can be symbiotic, associative, or coincidental (Shi *et al*., 2024). Mycorrhizal fungi and diazotrophs have symbiotic relationships with the legumes. The interaction between the roots and soil microbes has a significant impact on growth and nutrition. Soil microbiomes are increasingly being used in place of artificial and chemically based fertilizers and pesticides (Rashid *et al*., 2016). Inoculating seeds with advantageous microorganisms that can colonize roots helps protect against plant diseases (O’Callaghan, 2016). Beneficial microorganisms can indirectly reduce plant nutrient deficiency stress by boosting antioxidant enzyme activity and shielding plants from stress-induced ROS build-up (Hasanuzzaman *et al.*, 2020). The rhizosphere is home to a wide array of microbial species that have a number of functions and influence plant growth, such as defending plants from biotic and abiotic stresses, aiding in the cycling of nutrients, and some can even act as phytopathogens. Phytohormones secreted by rhizospheric bacteria, such as exopolysaccharides, quaternary ammonium compounds, trehalose, volatile organic molecules, and proline, increase plant growth and promote tolerance against biotic and abiotic stressors (Bhat *et al.*, 2022).

1.2 The Composition and Diversity of Soil Microbiomes

1.2.1 Microbial Taxonomy and Diversity in Soil

Soil is home to a variety of microbes such as Actinomyces, fungi, plant growth-promoting bacteria (PGPB) and protozoans. Plant growth-promoting rhizobacteria (PGPR) and PGPB are an important group of helpful root-colonizing bacteria in the rhizosphere of plants. PGPBs are classified as symbiotic or free-living bacteria in the soil that can efficiently inhabit the roots and have positive impacts on the host plant. It has been demonstrated that endophytic and rhizospheric bacteria, which are frequently found near plant roots, can function as PGPBs (Fanai *et al.*, 2024). The main distinction is that endophytic PGPB are immune to the impact of fluctuating soil conditions once they have established themselves within host plant tissues. They are a beneficial group of rhizosphere microorganisms that can aid in plant development through a number of mechanisms, such as ACC (1-aminocyclopropane-1-carboxylate) deaminase synthesis, phosphorus solubilization, siderophore synthesis, biological N2 fixation, increased root volume, nutrient uptake, phytohormone synthesis, accumulation of stress-related metabolites such as glycine betaine, poly-sugars, proline, and various volatile organic compounds (VOC), and the upregulation of antioxidant enzymes such as catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione (GSH), ascorbic acid (AsA), glutathione reductase (GR), and α-tocopherol (del Carmen Orozco-Mosqueda *et al.*, 2020). The two main taxonomic groupings that comprise PGPB are Firmicutes and Proteobacteria. Bacillus and Pseudomonas are the two most studied genera of Firmicutes and Proteobacteria, respectively, for promoting plant development. The primary representative genera of the phylum Proteobacteria are strains assigned to the genera *Enterobacter*, *Azospirillum*, *Pseudomonas*, *Burkholderia*, *Rhizobium*, *Serratia*, *Acinetobacter*, *Achromobacter*, *Azotobacter*, *Rahnella* and *Pantoea (*Chauhan *et al.*, 2023). Mycorrhizal fungi can reside on the surface of a plant's root, cortex of the root, or around the epidermal cells of the root. The hyphae produced by the roots of these fungi proliferate in the soil, where they scavenge nutrients, especially phosphates and nitrates, which support plant growth (Wahab *et al.*, 2023). Four primary mycorrhizal types—Ectomycorrhizae, Endomycorrhizae, Ericoid, and Orchidaceous— were identified, based on their structure and function. A specific type of mycorrhiza known as "arbuscular mycorrhiza" (AM) occurs when the symbiotic fungus penetrates the cortical cells of vascular plant roots to produce arbuscules (Pandey *et al.*, 2019). The roots of certain plant species form an ectomycorrhizal symbiotic relationship with a fungal symbiont, also referred to as a mycobiont. When hyphae penetrate the plant host root, a Hartig net is created. Hyphae penetrate and develop transverse to the root axis to form a network that connects the peripheral cells of the root axis. The exchange of carbon and nutrients occurs at the junction of fungus and root cells (Peterson and Massicotte, 2004). Plant-associated fungi, known as rhizosphere fungi, use the nutrients produced by a host plant to create plant-rhizosphere fungal interactions, which are vital to the development of robust ecosystems and environmental sustainability. It is well recognized that a number of PGPF species, including *Trichoderma*, *Fusarium*, *Talaromyces*, *Phytophthora*, and *Penicillium*, improve plant development, innate immunity, and a few key secondary metabolites (Murali *et al.*, 2021).

1.2.2 Factors Influencing Soil Microbial Communities

Numerous biotic and abiotic elements that function both geographically and temporally influence the composition of a given soil microbiome. These include abiotic (soil structure and type, soil moisture, soil pH, soil nutrients, and geographic characteristics) and biotic (plant species, microbial predators, and competitors) factors (Xu *et al.*, 2023). The composition of the microbiome is not always determined by a single factor, although it has been shown that the soil environment has a significant impact on the richness and organization of microbial communities. For example, soil moisture, pH (acidity), and texture have been identified as global determinants of the variety and composition of microbial communities. Certain microbial groupings are more affected by certain conditions than others are. Soil moisture is a reliable indicator of microbial biomass and has been shown to affect the composition of protists (Xu *et al.*, 2023). Microbes form dynamic and intricate colonies that are sensitive to their environment. The rhizosphere and topsoil, which are close to plant roots and have high nutrient availability, are home to most soil microorganisms, with whom they may form symbiotic relationships. Although microbial activity declines with depth, different microorganisms can be found in deeper soil layers (Thepbandit and Athinuwat, 2024). All soils contained a small number of microorganisms and rarer species were found in richer soils. Because other elements are involved, the influence of the aboveground plant community on the microbiome structure varies depending on the context and may not be noticeable for years. In addition, the soil microbiome is susceptible to soil pollution from pesticides, microplastics, and heavy metals (e.g., fertilizer application and industrial pollutants). As they are not broken down by microbes, heavy metals can linger in soils for extended periods of time, disturbing metabolic reactions and the equilibrium of the soil microbiome. The structure and function of the microbiome may also be adversely affected by the accumulation of microplastics in soils (Wang *et al*., 2024).

Bacterial activity, variety, and abundance were generally higher in the rhizosphere than in the bulk soil. A variety of phenolic compounds, organic acids, sugars, amino acids, and other small molecules found in root exudates function as chemoattractants, thereby promoting the development of plant-specific microbiota (Chen and Liu, 2024). The chemical composition of exudates produced by plant roots varies depending on the species used in specific microbial communities. These root exudates affect the rhizosphere by changing the composition of the soil's biochemistry and creating an environment conducive to the development of particular soil microorganisms (Afridi *et al*., 2024). These substances, which provide nourishment to microbes around the roots, include organic acids, sugars, amino acids, polyphenols, flavonoids, hormones, and minerals. Carbohydrates, amino acids, organic acids, flavonols, sugars, lignins, coumarins, anthocyanins, fatty acids, proteins, enzymes, indole compounds, glucosinolates, allomones, and aurones are among the substances released from root exudates (Afridi *et al*., 2024).

1.2.3 Methods for Analyzing Soil Microbiomes: Sequencing and Bioinformatics Approaches

The analysis of soil microbiomes involves a variety of sequencing and bioinformatics methods designed to uncover the complexity, diversity, and functionality of microbial communities in soil (Garg *et al*., 2024). The first step is the extraction of DNA or RNA from soil samples, which is a crucial process that can be challenging owing to the heterogeneity of the soil and the presence of inhibitors. Techniques such as mechanical disruption (e.g., bead-beating) or chemical lysis are commonly employed to release microbial DNA. Once DNA is extracted, 16S rRNA gene sequencing is frequently used to profile bacterial and archaeal communities because the 16S gene is highly conserved among microbes. Similarly, the Internal Transcribed

Spacer (ITS) region of fungi (Wang *et al.*, 2012). This method typically involves PCR amplification of the 16S gene and ITS region, followed by next-generation sequencing (NGS) such as Illumina MiSeq, which generates large datasets of short DNA reads. Bioinformatics tools such as QIIME2, Mothur, and DADA2 were then used to process these reads, including denoising, filtering, and taxonomic classification based on sequence similarity to reference databases such as Greengenes or SILVA (Muhamad Rizal *et al.*, 2020). For a more comprehensive view, shotgun metagenomic sequencing was employed, in which all DNA in a sample was sequenced, offering insights into both the taxonomic composition and functional potential of the microbial community. This approach allows for the identification of functional genes and metabolic pathways, which are crucial for understanding microbial roles in soil processes. Moreover, amplicon sequencing is also used to study non-bacterial groups, such as fungi or viruses, by targeting specific genetic markers, such as the ITS region for fungi (Pérez-Cobas *et al.*, 2020). Metatranscriptomics, which focuses on RNA to capture gene expression, is increasingly used to examine active microbial processes in the soil environment. Bioinformatics pipelines are essential for the analysis of these complex datasets, with tools such as MetaPhlAn for taxonomic profiling and PICRUSt to predict functional profiles from 16S rRNA data (Tyagi and Katara, 2024). The integration of multi-omics data (e.g., genomics, transcriptomics, and metabolomics) and advanced statistical and machine learning techniques allows for a more holistic view of soil microbiomes. Ultimately, these methods help researchers to uncover how soil microbial communities interact with their environment, their role in nutrient cycling, plant growth, and their response to environmental changes (Pinu *et al.*, 2019). The continued development of sequencing technologies and bioinformatics tools is improving the resolution and accuracy of these analyses, offering valuable insights into the ecological importance (Garg *et al.*, 2024). Microbial diversity in soil samples can be analyzed using a culture-independent technique called metagenomics. By directly isolating genetic material (DNA) from specific environments, a variety of uncultured soil microbial species can be identified. Metagenomic analysis of soil microbiomes involves sequencing of the entire genetic material present in a soil sample, providing a comprehensive view of microbial diversity and functionality. Unlike 16S rRNA sequencing, which targets specific genes, metagenomics captures all DNA, including bacteria, archaea, fungi, and other microorganisms, thus allowing for both taxonomic identification and functional profiling. Shotgun sequencing is typically used to fragment DNA, followed by bioinformatic tools to assemble the sequences, annotate them, and identify microbial taxa and functional genes. This approach enables the study of metabolic pathways, enzyme functions, and microbial interactions within soil ecosystems, offering deeper insights into the role of soil microbiomes in nutrient cycling, soil health, and environmental processes (Ejaz *et al.*, 2024).

1.3 Soil Microbiomes and Plant Health

1.3.1 Symbiotic Relationships between Plants and Soil Microbes

Microbes and plants have universal interactions that are essential for the well-being of soil and both partners. Plants engage in a complex process involving a variety of heterotrophic microbes, which may have close relationships ranging from parasitism to symbiosis (Chauhan *et al.*, 2023). The region next to plant roots, known as the rhizosphere, is a microenvironment in which important interactions between plant roots and soil microorganisms occur. These interactions can be advantageous, detrimental, or neutral in nature. Rhizodeposition, the process by which plant roots release different organic compounds, such as sugars, amino acids, organic acids, polysaccharides, vitamins, and secondary metabolites into the soil surrounding the roots, is the main cause of the unique characteristics of the rhizosphere (del Carmen Orozco-Mosqueda *et al.*, 2022). Using these root exudates, the microbial communities that develop establish a niche for themselves, which aids in attracting additional microorganisms and establishing a new niche. Rhizosphere bacteria use root exudates, particularly low-molecular-weight compounds, as substrates for their energy needs, increasing microbial activity and biomass. Recognizing the effects of microorganisms on plants and vice versa requires understanding the interactions between plants and microbes. Recognizing the effects of microorganisms on plants and vice versa requires understanding the interactions between plants and microbes (Mahmud *et al.*, 2021).

1.3.1.1 Rhizobia-Legume Symbiosis

When leguminous plants grow specialized root nodules that contain the most prevalent gram-negative Alphaproteobacteria, rhizobia, plant–rhizobia endosymbiotic interactions occur. The symbiotic relationship between rhizobia and legume roots allows nitrogenase to fix atmospheric nitrogen (Coba de la Peña *et al.*, 2018). Rhizobia include several taxa, including *Ensifer*, *Bradyrhizobium*, *Mesorhizobium*, *Azorhizobium*, and *Rhizobium* (Fahde *et al.*, 2023). Nodules are extremely intricate structures with multiple processes that interact at various points in time. The process of nodule development begins when suitable bacteria in the soil identify signals from plants. Subsequently, the production of Nod factors initiates a gene cascade that results in cell division and bacterial infection (Desbrosses and Stougaar, 2011). Through an infection thread, bacteria move from the nodule primordium to the root hair cells, where they mature into bacteroids that fix atmospheric nitrogen. Bacteroids are enclosed by a symbiosome membrane that produces a microaerobic environment for nitrogen fixation. Additionally, rhizobia exhibit endosymbiotic relationships with parasponia, a non-leguminous plant (Gage, 2004).

1.3.1.2 Plant – Cyanobacteria Symbiosis

Despite being widely distributed, very few cyanobacteria have symbiotic relationships with eukaryotic hosts. The cyanobacteria genus Nostoc is, by far, the most frequently observed species in terrestrial plants (Liaimer *et al., 2016).* Cyanobacteria can colonize various plant organs either extracellularly (in gymnosperms, pteridophytes, and bryophytes) or intracellularly (in angiosperms). Most cyanobacteria linked to mosses are epiphytic. Although only two genera of liverworts display this symbiotic interaction, all hornworts have endophytic cyanobacterial symbioses. Although plants and cyanobacteria almost invariably form symbiotic partnerships in nature, most symbioses between the two organisms are facultative, implying that either partner can be cultured alone (Chauhan *et al*., 2023). The pteridophyte Azolla is the only example of cyanobacteria–plant symbiosis in which the cyanobiont is continuously associated with the host and transmitted from generation to generation. The connection between Azolla and its cyanobiont is preserved by the transfer of cyanobacteria to the progeny for both asexual and sexual reproduction (Bujak and Bujak, 2024).

1.3.1.3 Mycorrhizal Interactions

Hyphae in mycorrhizae extend from the root into the surrounding soil, greatly expanding the available surface area for absorbing water and nutrients. In a mutually advantageous connection, the fungus mobilizes nutrients into the plant in exchange for sugars. Mycorrhizae can be divided into ecto- and endomycorrhizae based on their interactions and where they are found in plant roots (Wahab *et al*., 2023). Arbuscular mycorrhizae (AM), also known as endomycorrhizae, are among the most common ancient relationships between fungi and plant roots. In this case, the fungal partner was always a Glomeromycota member. Although they have evolved a highly effective method for obtaining inorganic nutrients from soil, fungi cannot thrive without their hosts. Arbuscules are highly branched hyphae that enter cortical cells and carry out nutrient exchange. A multifunctional relationship with AM fungi is present in the roots of approximately 70–80% of all vascular plant species (Wang *et al.*, 2017). According to reports, AM fungi work in concert with soil microorganisms, such as phosphate solubilizers, nitrogen fixers, and other PGPRs. The fungus, which is often a member of Basidiomycota or occasionally an Ascomycota, forms a sheath (mantle) outside the root in ectomycorrhizae. Fungal hyphae do not enter the cells; instead, the Hartig net, an intercellular network of hyphae in the root cortex, facilitates nutrient exchange of nutrients (Bücking *et al.*, 2012).

1.3.1.4 Plant – Actinobacteria symbiosis

Actinorhizal plants form a symbiotic relationship with actinobacteria to fix nitrogen in their root nodules. Actinomycetes, including *Frankia sp.*, are associated with a variety of actinorhizal plants (Ghodhbane-Gtari *et al.*, 2021). Across 24 genera and 8 families (*Casuarinaceae*, *Betulaceae*, *Myricaceae*, *Elaeagnaceae*, *Coriariaceae*, *Rhamnaceae*, *Datiscaceae*, and *Rosaceae*), actinorhizal plants comprise more than 200 species (Li *et al.*, 2015). Actinorhizal plants can become infected by *Frankia sp.* either intracellularly through root hair penetration or intercellularly. Actinorhizal nodules, where bacteria are hosted intracellularly and carry out atmospheric nitrogen fixation, are the result of a symbiotic relationship between Actinobacteria and actinorhizal plants. The host plant root exudates promote infection and nodulation, and accelerate *Frankia* development (Cissoko *et al.*, 2018). Actinorhizal symbioses seem to be less developed and less successful in nitrogen fixation than legume–rhizobia symbioses, based on the physiological and structural differences between actinorhizal and legume root nodules. Unlike legume nodules, which resemble stems and have peripheral vascular systems, actinorhizal nodules are modified lateral roots with core vascular systems (Cissoko *et al.*, 2018).

1.3.2 Microbes for plant productivity and disease management

Soil microbes contribute to plant growth, both directly and indirectly. Plants are essential as the main suppliers of energy in the plant-soil subsystem. They support heterotrophic microbial communities by supplying carbon and nutrients through litter deposits and root exudates (Dlamini *et al.*, 2022). However, plant growth can be hampered by a variety of biotic (related to living things) and abiotic (related to non-living causes) stressors. Microorganisms can either trigger the transcription of ACC synthase genes or stimulate indole-3-acetic acid (IAA) production in response to biotic and abiotic stressors (Koza *et al.*, 2022). Consequently, low-molecular-weight osmolytes, such as proline, glycine betaine, and other amino acids, are produced.

Furthermore, by aiding in nitrogen fixation, mineral phosphate solubilization, organic acid production, and the synthesis of essential enzymes, such as ACC deaminase, chitinase, and glucanase, microbes support plant growth under stress (Abdelaal *et al.*, 2021). These microbial processes may improve plant development and reduce the effects of abiotic stress. Boosting gibberellin synthesis, aiding seed germination, and encouraging the growth of different plant elements, such as stems, leaves, flowers, and fruits, and plant growth-promoting microorganisms (PGPM) are essential for improving plant growth. These microbes can enter the plant roots and benefit the plants they inhabit. PGPM stimulates the synthesis of cytokines, which improves root development, increases vascular cambium activity, promotes cell differentiation, and lessens apical dominance (Laishram *et al.*, 2024). Beneficial microorganisms are opening new avenues for long-term disease (pathogen) control, which makes the plant-associated microbiome even more crucial for crop yield. Since they are the main source of soil organic matter, soil microbes provide plant nutrition, and a diverse community of soil microbes protects against pest and disease outbreaks. However, standard agricultural techniques can deplete soil microbes and improve general soil health, which can be avoided by enhancing soil quality in a number of ways(Tian *et al.*, 2020). Certain soil bacteria are crucial for the uptake of nutrients by plants because they supply phosphorus and nitrogen. Additionally, the microbiome aids in the weathering of minerals and the breakdown of resistant organic matter, both of which provide carbon in root exudates and other rhizodeposits. The suppressive qualities of natural soil are greatly enhanced by the soil microbiota, which in turn improves the capacity of soil to impede soil-borne phytopathogens (Wang *et al.*, 2024). Soil-borne phytopathogens reduce nutrient and water intake. These pathogens affect plant growth and survival by causing diseases such as wilts, damping-off, and root rot. Researchers have studied how soil bacteria suppress soil-borne diseases since the 1970s (Dignam *et al.*, 2022). The combined antibacterial activities of chemicals and microorganisms, as well as processes involving antagonistic interactions between pathogens and microbes, can explain these suppressive qualities. The biocontrol-based microbiome is composed of filamentous fungi such as *Aspergillus*, *Trichoderma*, *Penicillium*, and *Gliocladium*; actinomycetes such as Streptomyces; and bacteria such as *Paenibacillus*, *Bacillus*, and *Pseudomonas*. These microorganisms can activate pathways involved in disease suppression (Ayaz *et al.*, 2023).

Soil deterioration, eutrophication, and greenhouse gas emissions are all caused by the unsustainable use of fertilizers, which also changes the process and upsets the Earth's biogeochemical cycles. Because the energy-intensive Haber-Bosch process used to produce N fertilizer depends on fossil fuels, it contributes to global warming and the loss of natural resources, both of which are factors in climate change (Khan *et al*., 2024). Alternative strategies for maintaining soil health and plant nutrition with the lowest amount of mineral fertilizer input are required because the use of mineral fertilizers has detrimental effects. Using organic inputs and adding beneficial, specialized root-associated microorganisms to plants that mineralize bound organic nutrients are two ways to avoid using mineral fertilizers (Khan *et al*., 2023).

1.4 Soil Microbiomes and Carbon Cycling

A greater amount of carbon is found in soil than in the atmosphere and vegetation, making it the largest carbon reservoir on Earth. Numerous facets of our planet are significantly and extensively affected by the loss of carbon from the soil to the atmosphere. Carbon sequestration increases the amount of soil organic carbon that can be stored by removing carbon dioxide from the atmosphere and incorporating it into the soil. Autotrophs and other photosynthetic organisms that take up CO2 from the atmosphere and aid in carbon sequestration make this process possible. The stored carbon is eventually released into the atmosphere by the respiration of both autotrophic and heterotrophic organisms. Microbial communities found in soil are essential for carbon sequestration and emission. Thus, microorganisms use different organic and inorganic forms of carbon as sources of energy and carbon (Wu *et al*., 2024).

Microbial biomass, microbial community structure, microbial by-products, and soil properties such as texture, clay mineralogy, pore size distribution, and aggregate dynamics are some of the variables that affect microbial contribution to carbon sequestration. The degree of microbial participation in the soil carbon sequestration process is determined by the interaction of several variables (Naylor *et al*., 2022). Carbon sequestration in terrestrial ecosystems depends on rhizosphere bacteria found in forests. One of the main sources of soil organic carbon (SOC) is the roots and the interactions between roots and rhizo-microorganisms. The interaction of symbiotic and competitive relationships between soil microorganisms and plant roots controls SOC sequestration of SOC (Solomon *et al*., 2024). Furthermore, soil microorganisms affect carbon sequestration processes and are essential for the succession of plant communities. Numerous bacterial species such as *Bacillus pumilus*, *Bacillus cereus*, *Bacillus mucilaginosus*, and *Bacillus pasteurii* may be involved in the carbon cycle and carbon sequestration processes (Mason *et al*., 2023).

1.5 Agricultural Implications of Soil Microbiome Research

Application of plant growth-promoting rhizobacteria (PGPRs) as an agricultural therapy to reduce niche vacancies and efficiently fill empty niches is a potential management strategy. It has been demonstrated that PGPRs grow especially well in soils with low microbial biomass, increasing the likelihood that inoculations would be successful (de Andrade *et al.*, 2023). When beneficial microbes flourish in this setting, they can rapidly occupy the available space and nutrients from potential pathogen invaders and help achieve long-term niche occupancy. PGPRs help the plant host by enhancing yields, nutrient acquisition, stress tolerance, and disease resistance in addition to "sealing off" open ecological niches and boosting the soil's resilience to pathogen invasion (Basu *et al.*, 2021). Studies have shown that plants inoculated with PGPR and mycorrhizal fungi have received less than 75% of the fertilizers applied, while at the same time yielding identical results to uninoculated plants that have received full fertilizer treatments (Adesemoye et al. 2009). The current challenge for producers is to increase productivity while lowering inputs such as fertilizer and water applications. Furthermore, given the need to grow biofuel crops in regions unsuitable for agricultural production, where drought and salt tolerance may become particularly crucial, these PGPR features hold significant potential for biofuel farming. It is not unexpected that a combination of PGPR medications has been demonstrated to be even more successful than one treatment alone in reducing illness, given the vast range of effects and mechanisms of action. The addition of the PGPR Pseudomonas putida and nodule-inducing *Sinorhizobium meliloti* to the legume *Medicago sativa* is an example of a combined inoculation, which led to increased nodulation and a notable increase in plant biomass (Guiñazú et al. 2009). It has been discovered that exogenous administration of acetoin (3-hydroxy-2-butanone), an elicitor produced from *Bacillus subtilis*, initiates induced systemic resistance (ISR) and shields plants from *Pseudomonas syringae*-driven tomato disease (Rudrappa et al. 2008). By identifying the exact substances and dosages required for use, a non-living application with the same advantages as PGPRs might be developed commercially. These therapies could prevent some of the possible issues that arise while creating commercial PGPR applications, such as low survival owing to competition and unfavorable environmental circumstances (Cummings, 2009).

1.6 Soil Microbiomes in Soil Restoration and Ecosystem Services

As the continuation of life depends on the prolonged and microbially mediated alteration of materials, both in aquatic and terrestrial environments, microorganisms play a crucial role in maintaining the vibrant integrity and equilibrium of the biosphere (Ibrahim *et al.*, 2022). Microbes perform a wide range of functions and are essential for biogeochemical cycling and sustainability. They also produce medications, clean wastewater, and participate in bioremediation (Ayilara and Babalola, 2023). Of all natural settings, soil is arguably one of the most difficult and demanding; its complicated nature is ascribed to the diversity of species and community sizes. In addition to viruses, soil is thought to contain–4-5×10^{30} microbial cells, which is ten times higher than the number found in the seas, according to current global estimates (van Elsas *et al.*, 2012). The productivity of agroecosystems is determined by the soil microbiome and its related processes. Because soil health and microbial variety are essential for sustainable agriculture, current research must concentrate on regulating the soil microbiome. A key component of sustainable energy and food production is the employment of beneficial microorganisms, which enhance plant health and quality and help recycle leftover crops with less negative environmental impacts (Purohit *et al.*, 2024). The majority (≥90%) of the microbial diversity is thought to be unexplored. There are a wealth of new and creative biotechnological advancements and uses in the fields of energy, agriculture, chemicals, mining, materials, food, pharmaceuticals, and environmental protection that correlate to this uncharted diversity (Hernández-Álvarez *et al.*, 2023). Finding the primary ecosystem drivers is one of the most difficult tasks, and modifying these drivers to yield desired results is much more difficult. As these activities are constantly endangering stable agricultural production, researchers worldwide are currently struggling to maximize the functions of microbiomes within the constraints of anthropogenic and natural activities, such as the use of chemical fertilizers, climate change, and new strains of pests and diseases (Dubey *et al.*, 2019). In light of the fact that the world's food demand is expected to double by 2050, achieving this objective will require quick fixes that use the soil microbiota to improve plant nutrient uptake and boost resilience to biotic and abiotic challenges. Hiruma et al. (2016) presented one of the few untapped resources for addressing the sustainability challenges of agriculture in the context of climate change is presented by Hiruma *et al.* (2016). An improved understanding of the complex relationships between plant genotypes, microbiome compositions, and many environmental elements provides vital information for sustainable agriculture.

1.6.1 Restoration of Degraded and Contaminated Soils through Microbial Interventions

Toxic heavy metals (HMs) are released into the environment by industrial processes, such as mining and smelting, drastically lowering soil quality and endangering human and plant health. There is still a pressing need for effective solutions, despite several approaches being used to track and deal with this problem (Adnan *et al.*, 2022). Bioremediation is a promising and reasonably priced method for reducing pollution. Either in-situ (at the location of pollution) or ex-situ (after relocation), microbial communities are used to break down contaminants (Kuppan *et al.*, 2024).

The efficacy of bioremediation can be increased by improving soil characteristics and nutrient bioavailability in addition to managing other process-influencing variables. Furthermore, certain pollutants may be more efficiently degraded by genetic engineering of microbes (Kuppan *et al.*, 2024). The prominent microorganisms used in bioremediation include *Bacillus*, *Pseudomonas*, and *Flavobacterium*. The microbial consortium, composed of *Serratia marcescens* L-11, *Phanerochaete chrysosporium* VV-18, and *Streptomyces rochei* PAH-13, was used for the bioremediation of polyaromatic hydrocarbons (Shaerma et al. 2016). Under controlled conditions, the consortium broke down 60–70% of the PAHs in the broth after seven days. When soil additives, such as compost, paddy straw, and ammonium sulfate, were added under natural conditions, the rate of degradation increased to 56–98% in 7 days and to 83.50–100% in 30 days. With half-lives of 1.71, 4.70, 2.04, and 6.14 days for fluorene, anthracene, phenanthrene, and pyrene, respectively, compost-amended soil degraded the fastest. The capacity of the consortium for PAH oxidation and mineralization was demonstrated by the identification of a variety of degradation products using GC-MS. Soil pollution by heavy metals, mostly from human activities such as mining, manufacturing, and agriculture, has become a major environmental problem on a global scale. Because they are poisonous and nonbiodegradable, heavy metals like chromium (Cr), copper (Cu), and cadmium (Cd) pose major threats to ecosystems and human health. Multiple heavy metals, with intricate relationships and widespread prevalence, are usually associated with soil pollution. According to previous studies, contamination with Cu, Cd, and Cr is most prevalent in mining areas (Nie *et al.*, 2023). Furthermore, Cu contamination from Cu-based fungicides used in both conventional and organic farming emphasizes the need for urgently effective remediation techniques. The common environmental problems of coupled p-chlorophenol (4-CP) and hexavalent chromium [Cr(VI)] contamination were discussed by Sun et al. (2024), who concentrated on the limited understanding of the fate of Cr(VI) and its relationship with amines during dechlorination, which is affected by pH fluctuations (Sun et al. 2024). According to a previous study, *Pseudomonas sp*. PC efficiently breaks down 4-CP and transforms Cr(VI) with elimination efficiency based on the first-order reaction kinetics. A six-month study evaluated bioremediation at the laboratory and field scales (windrow treatment). Although there was less variation in the laboratory data, the polluted soil from a coal tar distillation factory showed comparable rates of deterioration between the two systems. Approximately 85% of PAHs had decomposed in the lab after six months, compared to 90% in the wild. The 3- and 4-ring PAHs degraded 32 and 7.2 times quicker than the 5- and 6-ring PAHs, respectively, and the degradation rates exhibited a negative exponential trend. In the field, four- and 5-ring PAHs degraded more quickly. The original bacterial community was highly diverse, with 13 strains from nine genera. It is primarily composed of Gammaproteobacteria, with smaller amounts of Alpha-, Beta-, and Lactobacillales bacteria (Lors *et al*., 2012).

1.7 Technological Innovations in Soil Microbiome Research

Microbiome engineering, which creates a microbial condition that promotes a desired result such as increased crop yield or improved health, is a frontier in microbiome research. However, understanding what makes a particular microbial community work, whether some species are more significant than others, and how and to what extent the composition and function can be altered are all necessary for effective engineering (Kaul *et al*., 2021). Scientists are using artificial intelligence to sort through the microbiome's intricacy, which includes machine learning and deep learning that have become essential instruments for advancing microbiome research because of their tremendous predictive and informative capabilities (McCoubrey *et al*., 2021). The most widely utilized techniques for microbiome analysis are metagenomic and amplicon sequencing. The amplicon methodology uses readings of particular taxonomic marker genes, such as the ITS region or the 16S rRNA evolutionarily conserved gene, to classify samples. Prokaryotic taxa are typically loosely defined by a predetermined identity threshold that also establishes clusters known as operational taxonomic units (OTUs). ASVs, or amplicon sequence variants, are more recent counterparts of

OTUs. Because ASVs are produced using a denoising technique and do not rely on an artificial dissimilarity criterion, they can even resolve uncommon community members. On the other hand, shotgun metagenomics uses non-specific sequencing to thoroughly catalog all genomes in a sample. Shotgun metagenomic reads can be matched to curated databases for taxonomic or functional annotation using various techniques (Liu *et al.*, 2021).

1.7.1 Shotgun Metagenomic analysis

The genomic DNA of the soil microbial community must be sequenced using molecular shotgun sequencing, also known as whole-metagenome shotgun sequencing. Nonetheless, the availability of genomic data is crucial for functional metagenomics research because of the growing use of high-throughput sequencing techniques (Sharpton, 2014). In metagenomic sequencing, the amplified DNA is randomly broken up into tiny pieces, which are then sequenced using high-throughput sequencing platforms, and the sequenced fragments are then stitched together to form longer contigs or scaffolds. The emergence of several bioinformatics tools (such as the Illumina technique) that may be used to create databases has made shotgun metagenomic analyses feasible. Sequence alignment with a sizable database of annotated sequences is necessary for functional metagenomic algorithms to identify homologs (Navgire *et al.*, 2022). However, many bioinformatics tools for functional profiling are slow. Lind Green's group proposed that metagenomics tools need to be faster and more accurate. Although alternative homology search methods such as RAPSearch2 and DIAMOND have also been developed to reduce run time, homology-based pre-NGS tools such as BLAST match appropriate sequence alignments in a vast database (Pérez-Cobas *et al.*, 2020).

1.7.2 Machine learning

Machine learning (ML), a subset of artificial intelligence (AI) techniques, uses massive datasets to identify, categorize, and forecast trends. ML has been used in microbiome research to address tasks such as phenotyping (i.e., forecasting an environmental or host phenotype), classifying microbial features (i.e., determining the microbiota's abundance, diversity, or distribution), examining the intricate physical and chemical relationships among the microbiome's constituent parts, and keeping an eye out for shifts in the microbiome's composition (McCoubrey *et al.*, 2021).

1.7.3 Deep learning

Deep learning (DL) is a class of machine-learning techniques that uses a variety of artificial neural network designs. Nodes, often referred to as neurons or units, are the building blocks of DL models (Alzubaidi *et al*., 2021). These are functions that convert inputs and send results to other nodes. Node connections produce a network with several layers (hence, the term "deep neural networks") that can be linked together and arranged in various configurations or designs. The fully connected neural network (FCNN), the most fundamental neural network architecture, has nodes from one layer that are fully connected to all the nodes from the layer below (Vakalopoulou *et al*., 2023).

1.8 The Future of Soil Microbiome Research

1.8.1 Emerging Frontiers and Future Directions

Emerging frontiers in soil microbiome research are increasingly focused on deciphering the complex and dynamic interactions between soil microorganisms, their environment, and broader ecosystems (Wang *et al*., 2024). Recent advancements in high-throughput sequencing, metagenomics, and bioinformatics have significantly enhanced our ability to map and analyze the vast diversity of soil microbial communities, providing deeper insights into their functional roles. These technologies help identify the microbial taxa that drive critical processes, such as nutrient cycling, plant growth promotion, disease suppression, and organic matter decomposition (Hiraoka *et al*., 2016). One key area of focus is understanding how microbial diversity influences soil health and ecosystem stability and how specific microbial groups contribute to soil fertility, carbon storage, and water retention. A prominent direction in the field is the exploration of plant-microbe interactions, where beneficial microbes, such as nitrogen-fixing bacteria or mycorrhizal fungi, are being studied for their role in enhancing plant growth, disease resistance, and nutrient uptake. These microbes have the potential to reduce the need for synthetic fertilizers and pesticides, thereby promoting more sustainable agricultural practices (Romero *et al*., 2023). In addition, research is increasingly focusing on the effects of climate change on soil microbiomes, particularly how temperature fluctuations, changes in moisture availability, and altered plant inputs affect microbial activity and community composition. Soil microorganisms may also play a crucial role in climate change mitigation, particularly through their contribution to soil carbon sequestration and ability to enhance soil resilience under changing environmental conditions (Classen *et al*., 2015).

Another emerging frontier is the application of artificial intelligence (AI) and machine learning to soil microbiome data. By integrating AI with large-scale microbiome datasets, researchers are developing predictive models to better understand microbial behavior, soil microbial ecology, and their responses to environmental shifts. This can lead to more accurate predictions of soil health and fertility, thereby providing a foundation for precision agriculture and ecosystem management strategies. Furthermore, the role of soil microbiome in soil restoration and remediation is becoming an increasingly important area of research (Mohseni and Ghorbani, 2024). Scientists are investigating how specific microbial communities can be employed to restore degraded soils, detoxify polluted environments, and promote land reclamation, thereby offering environmentally friendly solutions for sustainable land management. Overall, the future of soil microbiome research lies in unraveling the complex network of interactions that govern soil ecosystems with the goal of developing microbiome-based strategies to address global challenges in agriculture, climate change, and environmental sustainability. By leveraging our growing understanding of microbial communities, scientists are working toward innovative, eco-friendly approaches to improve soil health, enhance crop production, and mitigate the effects of environmental degradation (Iqbal *et al*., 2023).

1.9 Conclusion

Urbanization and rapid population expansion have worsened soil contamination by ECs and harmful heavy metals, endangering human health and sustainable agriculture. Despite these difficulties, bioremediation has become a viable and affordable way to reduce soil contamination and offers a rare opportunity to preserve soil quality and function. As complementary approaches, bioaugmentation and biostimulation accelerate the breakdown of different pollutants and show great promise for use in the field. Future studies combining cutting-edge microbial and genetic engineering technologies with well-optimized biostimulation regimens may enhance the effectiveness and robustness of bioremediation techniques. The actual application of bioremediation technologies will be essential, as they develop to guarantee environmental health and agricultural viability. Environmental factors, microbial competition, and scalability from lab-to-field applications are some of the issues encountered by bioaugmentation, despite its benefits. To increase the efficacy of this remediation technology, further studies are required to completely comprehend the mechanisms of bioaugmentation, optimize procedures, and solve scaling difficulties. The implications of factors such as dosage, frequency, and strain selection on the effectiveness of bioaugmentation have been examined in earlier research, but the underlying mechanisms at the microbial and metabolic levels have not received sufficient attention. Furthermore, microbial remediation studies require long-term creation of suitable ecological conditions to properly evaluate the durability and stability of remediated sites. Despite the fact that it can temporarily lower pollution levels, microbial remediation has long-term impacts on soil health, microbial diversity, and ecosystem resilience. Monitoring changes in microbial populations over long periods is essential, as is any potential build-up or conversion of pollutants into secondary, possibly hazardous substances that could have a negative impact on soil ecosystems.

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