

REVIEW

Microbiome: diversity, distribution, and potential role in sustainable crop production

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Summary: From microbiomes in cheese to soil, many organisms provide enhancement, enrichment, production, and some degradation to the niche they occupy. Although microbial diversity and microbiomes have been known for centuries, it has become a trendy area to investigate with the advent of omics approaches where a vast amount of information can be gathered about the nature and benefits of these microorganisms. This information is crucial given the world's population rise. According to FAO, feeding the world's 9.1 billion people in 2050 will necessitate a 70 percent increase in overall food production. Five steps have been offered to fulfil this increasing global food supply-demand, including decreasing agriculture's footprint, growing more on existing farms, discovering ways to use resources efficiently, modifying our diets, and reducing waste. It is essential to focus on management practices that influence soil health, sustainable productivity, and inorganic inputs to reduce agriculture's footprint. Conventional agriculture has increased agricultural production on a large scale; however, overuse of chemicals has led to food contamination, negative environmental consequences, and disease resistance, all of which have important implications for human health and food security. Microbiome research makes it possible to simultaneously reduce these environmental impacts and steadily increase the quantity and quality of agricultural products. Plant microbiome research focuses on defining the structure and activities of microbial communities in various plant-associated habitats and establishing a relationship between specific microbial taxa and plant performance. The microbes associated with plants in the plant microbiome can provide a variety of advantages, including plant growth promotion, soil fertility and control of pests and plant pathogens. Traditional approaches can only examine a small percentage of the vast unexplored soil microbial world because of their biased detection of microbial genetics and functional diversity through culture methods. Today, with the advent of high-

throughput sequencing techniques and a variety of "omics" approaches, researchers can now identify microbiome structure and dynamics along with host interactions on an extraordinary level. These approaches will be valuable in establishing the relationship between the structure and function of the soil microbial community and gaining a better understanding of environmental and ecological processes, with a focus on plant-microbe ecosystems.

Keywords: Crop improvement, genomics, microbiome, pathogen, sustainable agriculture.

INTRODUCTION

Behind every good cheese is an excellent microbiome (Gobbetti *et al.*, 2018). Cheese is a dynamic ecosystem providing an ideal environment for microorganisms and serves as a model for the behaviour of microbes in complex communities (Wolfe & Dutton, 2013). From factory to field, as cheese microbes (both beneficial and detrimental) contribute to the final flavour, smell, texture, and colour of cheese, soil microbes play a critical role in growing healthy crops and increasing plant yield. The malting industry is another example explaining the relationships between the microbiome and the food industry. Malt quality is highly dependent on the quality of barley grain. Fusarium head blight caused by *Fusarium* spp. is a devastating disease of barley that negatively impacts the malt's quality. The malting industry faces unique challenges with *Fusarium* that are not experienced in other industries. The malting process creates conditions that favour diverse pathogen growth, including *Fusarium* and production of mycotoxins.

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Though *Fusarium* species are central to several quality issues in the malting industry, they are only one component of the microbiome associated with barley and malt. The malt microbiome is the entire community of microorganisms present during the malting process. This community is complex and dynamic, and it is expected that *Fusarium*-related quality issues only manifest themselves when *Fusarium* is competitively dominant within the malt microbiome. Depending on the nature of interactions and the abundance of the microorganisms present in the malt and barley, their effects may be beneficial or detrimental for the process and the final malt quality. Thus, characterization of the microflora during malting and their interactions with each other is an essential step to developing management strategies that will improve malt quality. The diverse nature of microbiomes is given in this paragraph, so the reader appreciates the diversity, complexity and activity microbiomes carry. In the following parts of this review, we will focus on particularly of the soil, the plant, the seed and their microbiomes. These microbiomes dictate how agricultural production systems operate. The operation of a farming system is also dependent on the grower, growers' inputs and all environmental conditions during plant growth. They are so intertwined, it is at times difficult to completely understand what would be the result if one of those parameters changed.

Being one of the most heterogeneous and diverse habitats on the planet, soil hosts the dynamic environments for billions of microorganisms such as bacteria, fungi, actinomycetes, protists and microorganisms such as nematodes, worms, insects, reptiles, and mammals (Bardgett & van der Putten, 2014). Thus, the soil is a biodiversity reservoir, an essential part of our current ecosystem. The conservation of soil biodiversity is critical for both the environment and agricultural industries (Yang *et al.*, 2020), as the loss of soil biodiversity can have a devastating impact on its productivity (Olson *et al.*, 2017).

The term 'microbiome', to signify the range of ecological community of microorganisms that may be commensal, symbiotic, or pathogenic found in and on all multicellular organisms, including plants, was first coined by Joshua Lederberg (Lederberg & McCray, 2001). Microbiome refers to the entire habitat, including the microorganisms (bacteria, archaea, lower and higher eukaryotes, and viruses), their genomes (i.e., genes), and the surrounding environmental conditions (Marchesi & Ravel, 2015). On the other hand, 'microbiota' refers to the assemblage of microorganisms found within a specific environment. The microbes associated with plants can

be classified into epiphytes or epiphytic that exist on the plant surfaces, endophytes or endophytic that are present within the plant's tissue, whether roots or shoots (endosphere), phyllospheric that live on leaves surfaces (phyllosphere), and rhizospheric that inhabits into the soil adjacent to the roots (Rhizosphere) (Berg *et al.*, 2014; Mueller & Sachs, 2015). The term 'rhizosphere' is also defined as the narrow soil region surrounding the roots and is directly influenced by microbes and root secretions (Vishwakarma *et al.*, 2020).

Agricultural products based on the microbiota are among the fastest-growing sectors, with a compound annual growth rate of 15–18% and a predicted value of over 10 billion USD by 2025 (Dunham Trimmer, 2017). Therefore, exploiting soil microorganisms associated with crop plants can be considered one of the most promising long-term solutions to the fundamental issues of ensuring food security while preserving a healthy agroecosystem (Singh & Trivedi 2017; Singh *et al.*, 2020).

Soil microbiome plays vital roles in the dynamics of plant community and has enormous impacts on soil physicochemical characteristics (Lehmann *et al.*, 2017; Sui *et al.*, 2021), nutrients bioavailability, mainly nitrogen or phosphorus (Bartlett *et al.*, 2007; Lurthy *et al.*, 2021), carbon cycle (Jansson & Hofmockel, 2020) and plants physiological processes (Li *et al.*, 2018; Saleem *et al.*, 2019; Abdul Rahman *et al.*, 2021) such that this intricate microbiome is also known as the plant's secondary genome (Berendsen *et al.*, 2012). At the same time, hosts' genotypic attributes, growth stage, soil characteristics and environmental conditions affect the dynamics of the microbiome (Rossmann *et al.*, 2017).

Although only a fraction of the soil microbiome is known, it is still safe to say they play an essential role in agriculture, food production and climate regulation (Babalola *et al.*, 2020; Jansson & Hofmockel, 2020). Thus far, plant-microbe interactions studies have focused mainly on the impacts of a small number of different microbial species, which often reveal contradictory results when utilized in the field (Gadhav *et al.*, 2016; Timmusk *et al.*, 2017), whilst an alternate approach is to emphasis on the whole microbiome (Pineda *et al.*, 2019). For example, Busby *et al.* (2017) stated that introducing more complex soil communities, rather than single species, is essential to maintain a constant high level of crop protection. Thus, microbiome research is important to know the microbial ecology in the soil to support ecosystem functions (Sergaki *et al.*, 2018).

In the past decades, molecular methods have been combined with traditional microbiology approaches to offer new intuitions into soil microbial ecology. In recent years, the development of tools in molecular biology, such as sequencing technologies, has provided researchers with more complete and consistent information about microbial ecology (Lucaciú *et al.*, 2019). For instance, high-throughput sequencing of marker gene amplicons is used to illuminate microbial communities' composition, organization, and spatial distribution in the environment and is increasingly used in microbiome research (Knief, 2014). Moreover, metagenomic approaches can be accompanied by other omics data, such as transcriptomics, proteomics, and metabolomics, to estimate microorganisms' structure and functional potential in soil (Nesme *et al.*, 2014; Lucaciú *et al.*, 2019). Hence, microbiome engineering might be an alternate method of understanding, manipulating, and creating related technology for building microbial communities critical to plant health and production (Prasad *et al.*, 2018).

This review defines some concepts, shows how microbiota benefits the agroecosystem, and then provides an overview of current microbiome research by highlighting new technologies and approaches.

Microbial niches

Rhizosphere microbiome

The rhizosphere microbiome, which is the narrow zone of soil that is influenced by root secretions (Berendsen *et al.*, 2012), includes bacteria, fungi, protists, and oomycetes, is intimately linked to plant's growth, development, and health (Figure 1) (Cai *et al.*, 2017; Wu *et al.*, 2018). Generally, microorganisms in the rhizosphere can be beneficial or detrimental to the host plant (Yu *et al.*, 2019). The harmful microorganisms, such as soil-borne pathogens, diminish plant growth and development, resulting in yield loss and threatening agricultural productivity (Yin *et al.*, 2021). Beneficial microbes, on the other hand, can stimulate plant growth and development by enhancing nutrient availability, producing phytohormones, and increasing abiotic and biotic stress tolerance (Rolli *et al.*, 2015; Jacoby *et al.*, 2017; Yin *et al.*, 2021).

Furthermore, the rhizosphere can be divided into two compartments: the ectorhizosphere or rhizoplane; the outer area of soil surrounding the roots and the endorhizosphere, the region in the root which microbes fed by root-derived compounds may colonize, including

the root cortex, epidermis, and root hairs (Figure 1) (Kloepper *et al.*, 1992; Kumar & Dubey, 2020). In the ectorhizosphere or rhizoplane, microbes that reside on the surface of roots are called epiphytic root microbes. *Actinobacteria*, *Proteobacteria*, *Gammaproteobacteria*, and *Alphaproteobacteria* are known as root epiphytes. In addition, *Burkholderia*, *Pseudomonas*, *Erwinia*, *Sphingomonas* and *Acinetobacter* are the major genera isolated from different plant root surfaces. Few other genera such as *Bacillus*, *Streptomyces*, *Agrobacterium*, *Nocardia* and *Klebsiella* are also found on some root surfaces. Fungi of class *Ascomycota* represent the eukaryotic root epiphytic community (Butani *et al.*, 2021). In the endorhizosphere, endophytic microorganisms, often fungi and bacteria, colonize plant tissue intercellularly and/or intracellularly (Wilson, 1995). Rhizobia, the root-nodule endosymbionts of legume plants, is an endophytic microorganism because of its nitrogen-fixing potential (Gallego-Giraldo *et al.*, 2014). *Microbacterium trichothecenolyticum*, *Brevibacillus choshinensis*, *Endobacter medicaginis*, and *Micromonospora spp* are non-nodulating examples of endophytes (Trujillo *et al.*, 2010; Ramírez-Bahena *et al.*, 2013; Benidire *et al.*, 2017). Endomycorrhizas and ectomycorrhizas are two mycorrhizas that colonize roots as endophytic and ectophytic fungi. The difference between the two types is that ectomycorrhizal fungi's hyphae do not enter individual cells within the root. In contrast, endomycorrhizal fungi's hyphae penetrate the cell wall and invaginate the cell membrane (Allen, 1991). Plant-rhizosphere microbiome interaction is complicated and dynamic (Shi *et al.*, 2016). The root exudates, including organic acids, amino acids, polysaccharides, and other primary and secondary metabolites (Bais *et al.*, 2006), play a critical role in assembling the rhizosphere microbiome (Backer *et al.*, 2018; Zhalnina *et al.*, 2018). The release of root exudates is regulated in response to environmental stimuli, and the composition of root exudates varies widely depending on plant species and physiological stage (Phillips *et al.*, 2004; De-la-Pena *et al.*, 2008; Nguyen, 2009). Root exudates benefit plants by stimulating beneficial microorganisms (e.g., symbionts), improving nutrient uptake, and enabling recognition between self-roots and neighbour-roots (Mommer *et al.*, 2016; Meier *et al.*, 2017). On the other hand, root exudates can stimulate pathogenic microorganisms; for example, watermelon root exudates increase sporulation and spore germination of *Fusarium oxysporum* f. sp. *niveum* (Hao *et al.*, 2010) or microconidia germination of *F. oxysporum* f. sp. *lycopersici* and *F. oxysporum* f. sp. *radicis-lycopersici* increases in the presence of tomato root exudates (Steinkellner *et al.*, 2005). These rhizosphere microorganisms can

also interact with each other, either competitively or synergistically. For example, non-pathogenic strains of *Streptomyces* can control potato scab caused by *Streptomyces scabies* in a bacterial-bacterial pathogens interaction or *Pseudomonas* spp. can control tomato *Fusarium oxysporum* f. sp. *radicis-lycopersici* in a bacterial-fungal pathogens interaction (Whipps, 2001).

An example of antagonist fungal–fungal interaction in the rhizosphere is the interaction between *Phialophora* sp. I-52 and *Gaeumannomyces graminis* var. *tritici* in wheat (Mathre *et al.*, 1998; Whipps, 2001). No clear examples of fungal-bacterial pathogens interaction have been reported (Whipps, 2001).

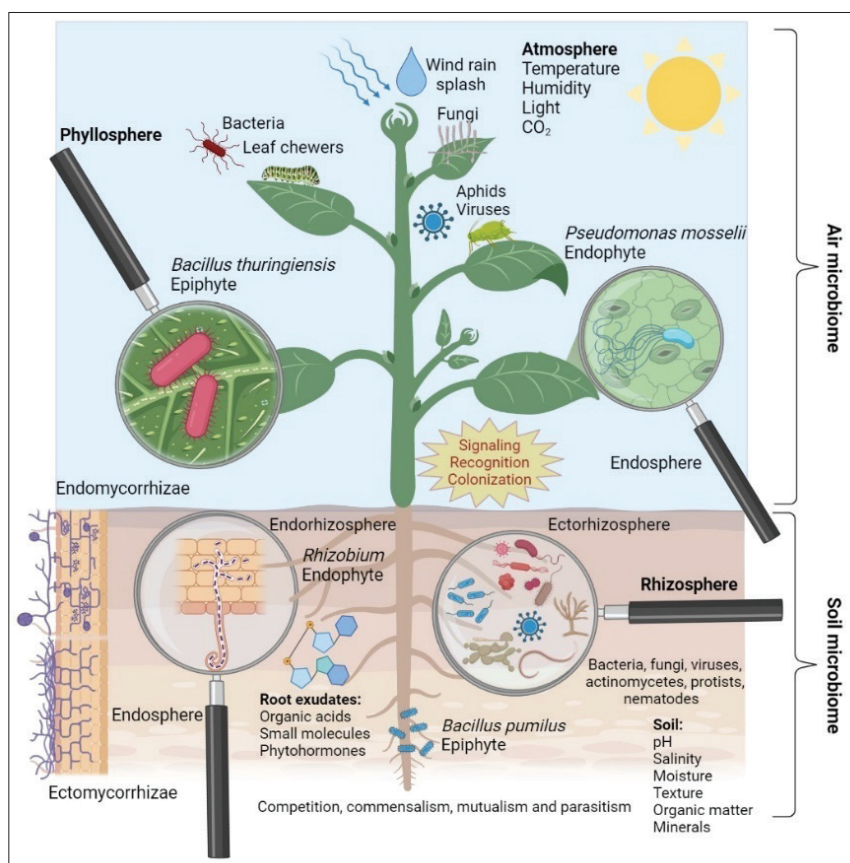


Figure 1: Plant microbiome composition and its association with biotic and abiotic factors

Phyllosphere microbiome

The aerial or aboveground portions of plants, such as stems, leaves, flowers, and fruits, make up the air or aboveground microbiome (Figure 1) (Knief *et al.*, 2010). Leaves as the most dominant part form phyllosphere and can be colonized by these microbial communities both on the surfaces (phylloplane; colonized by epiphytic microorganisms) and inside the leaf tissue (endosphere; colonized by endophytic microorganisms) (Vorholt, 2012), resulting in complex interactions between the plant, microorganisms, and the environment (Bashir *et al.*, 2022). The other aboveground plant-associated

microbial habitats include anthosphere: microbial habitat associated with flowers, carposphere: microbial habitat associated with fruits and caulosphere: microbial habitat associated with stems (Shade *et al.*, 2017). The term phyllosphere itself dated to the mid-1950s and was referred to by Jakoba Ruinen in 1961 (Koskella, 2020). Phyllosphere resides in a diversified and dynamic community of bacteria, fungi, viruses, actinobacteria, cyanobacteria, protozoans, and nematodes (Bashir *et al.*, 2022). Bacteria outnumber other microorganisms in cell number and taxonomic diversity (Andrews & Harris, 2000).

The establishment of the phyllosphere microbiome depends on the leaf-atmosphere environmental interaction with the residing microorganisms in the phyllosphere (Sivakumar *et al.*, 2020). For example, humidity, temperature, nutrient availability (on the plant surface), light/UV intensity, and even soil chemistry determines phyllosphere community composition (Lindow & Brandl, 2003; Leveau, 2015).

Like the rhizosphere, the phyllosphere inhabits both pathogenic and non-pathogenic or even beneficial microorganisms (Montarry *et al.*, 2008; Rastogi *et al.*, 2013). The phyllosphere microbiome can influence plant growth, development, and health (Balint-Kurti *et al.*, 2010; Reed *et al.*, 2010; Gerd *et al.*, 2011). For instance, some phyllosphere bacteria benefit plants by fixing nitrogen (Leveau, 2015), promoting growth (Bringel & Couée, 2015), serving as a barrier against pathogens, and decomposing the pesticides leftover (Venkatachalam *et al.*, 2016). Phyllosphere diazotrophic bacteria utilize carbohydrates excreted by plant leaves (Vorholt, 2012) and fix an appreciable amount of nitrogen which may benefit the plants (Abril *et al.*, 2005; Abadi *et al.*, 2020). Bentley and Carpenter (1984) discovered that diazotrophic epiphytes provided 10–25% of nitrogen to host plants. For example, some phyllospheric bacteria, indole-3-acetic acid (IAA) producers, such as *Streptomyces fradiae*, *Bradyrhizobium*, *Azospirillum* and *Rhizobium*, are the bacteria that interfere with the plant hormonal pool by addition of IAA (Spaepen *et al.*, 2007). Furthermore, beneficial phyllosphere microorganisms interact with roots and leaves to help plants better tolerate abiotic stress (Ripa *et al.*, 2019). For example, inoculation of *Bacillus pumilis* and *Azospirillum lipoferum* increased the abscisic acid concentration in *Arabidopsis thaliana* and maize tissue and stimulated stress-related proteins production (Cohen *et al.*, 2015; Yasmin *et al.*, 2017). In addition, *Beauveria* fungus on rice leaves can safeguard rice enzyme function while also being an ecologically benign bacterium (Du *et al.*, 2014). Generally, the phyllosphere microbiome develops adaptive traits and intimate associations with leaves through mitigating biotic and/or abiotic stress(es) and influencing plant growth and fitness (Vorholt, 2012; Helfrich *et al.*, 2018). However, the effects of phyllosphere beneficial or harmful bacteria, or their combinations, on plant performance are poorly known (Traw *et al.*, 2007; Saleem, 2015).

Seed microbiome

Microbes can interact with seeds at different plant growth and development stages and form seed microbiomes.

The concept of seed microbiome was first developed by Mitter *et al.*, (2017). Microbes can inhabit seed interiors (Endosphere) and seed surfaces or zone of soil under the direct influence of germinating seeds, the so-called spermosphere. Seed microbiota can be in the seed coat, endosperm, and embryo (Figure 2). The seed microbiome makeup can considerably influence seed quality (Links *et al.*, 2014). For example, the negative effect of pathogenic microbes on seed germination is the most common (Munkvold, 2009). For example, Rybakova *et al.*, (2017) discovered a link between pathogen susceptibility and seed microbiome diversity and abundance. By contrast, some seed-borne microbes, on the other hand, can improve germination rates by releasing seed dormancy via cytokinin synthesis (Goggins *et al.*, 2015) or promote plant growth by releasing IAA and 1-aminocyclopropane-1-carboxylate (Chimwamurombe *et al.*, 2016). It has been demonstrated that artificially inserting plant growth-promoting microbes into wheat seeds may improve crop yield (Mitter *et al.*, 2017).

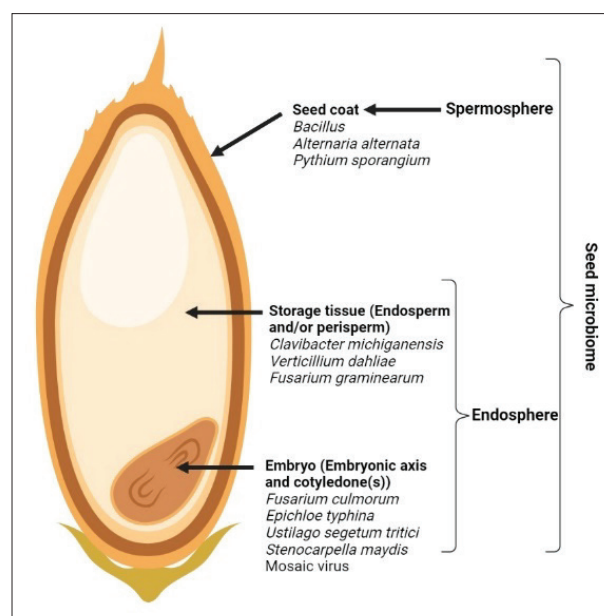


Figure 2: Seed microbiome and localization of some seed-associated microorganisms

Seed microbiomes have a varied makeup, with up to 9000 microbial species (Shade *et al.*, 2017). A variety of endophytic bacteria have been discovered in seed microbiomes. Bacteria colonizing inside seed tissue are mainly from the phyla *Actinobacteria*, *Proteobacteria*, *Firmicutes*, and *Bacteroidetes*. However, the most common genera are *Enterobacter*, *Pantoea*,

Pseudomonas, *Sphingomonas*, and *Acinetobacter* (Hardoim, 2019; Johnston-Monje *et al.*, 2021). Fungi that inhabit the seeds can be categorized as clavicipitaceous endophytes and non-clavicipitaceous endophytes. The former are endosymbionts transmitted by grass seeds and include *Atkinsonella*, *Balansiopsis*, *Balansia*, *Dussiella*, *Myriogenospora*, *Epichloë*, *Parepichloë*. The latter, which are mainly Ascomycetes and Basidiomycetes, can be seen in a variety of seeds and includes *Alternaria*, *Cladosporium*, *Fusarium*, *Aspergillus*, *Undifilum*, *Rhizoctonia*, *Chaetomium*, *Colletotrichum*, *Phialophora*, *Epicoccum*, *Tricothecium*, *Cryptococcus*, and *Filobasidium* (Hardoim, 2019; Johnston-Monje *et al.*, 2021).

Seed microbiome composition is governed by plant species or genotype, environmental conditions, and management procedures (Berg & Raaijmakers, 2018). In a study by Moreira *et al.*, (2021), the seed microbiome of wheat, canola, and lentil lines across two generations were profiled, and crop, genotype, and the environment were reported as the key drivers of the seed microbiome assemblage.

Most seed microbiome research has focused on culturable microbiota, endophytes, and microbial community comparisons across cultivars, geographical regions, and agricultural management methods, whereas seed microbiome persistence across crops and generations, is largely unknown (Khalaf & Raizada 2016; Sánchez-López *et al.*, 2018). Similarly, bacteria have gotten more attention than fungi, and few studies look at both microbiomes (Barret *et al.*, 2015). As a result, our understanding of the seed microbiome is still in its early stages, and its potential for improving plant health and production is mainly unexplored.

Benefits of microbiomes for agroecosystem

Microbiome and plant growth and development

Plant microbiomes form a complex and interconnected microbial network (Huang *et al.*, 2020). Each organism performs a unique role critical to plant health and ecosystem function (Zhou *et al.*, 2010). For instance, Shi *et al.*, (2016) described that increased complexity and connectivity of rhizosphere network are qualities of the rhizosphere bacterial communities.

Plant growth, development and health can be influenced directly by microorganisms that produce phytohormones, improve nutrient uptake and indirectly by triggering the plant immune responses or outcompeting

and suppressing plant pathogens, for instance, through the synthesis of fungal cell wall-degrading enzymes, antibiotics, and siderophores (Gamalero & Glick, 2011; Berendsen *et al.*, 2012; Gu *et al.*, 2020).

Beneficial microorganisms, mainly bacteria named plant growth-promoting microbes (PGPMs), can stimulate plants' growth by altering plants' hormonal and metabolic balance. The secretion of secondary microbial metabolites, which act as hormone-like plant growth regulators, and the synthesis of proteins involved in plant defense signaling enable microbes to colonize plant tissue (Manganiello *et al.*, 2018; Stringlis *et al.*, 2018). Many bacteria and fungi associated with plants can produce IAA, directly impacting plant growth and development (Garnica-Vergara *et al.*, 2016). PGPMs that produce auxins have provoked transcriptional changes in the defence-related hormone. Genes involved in cell wall biosynthesis (Spaepen *et al.*, 2014) cause longer roots (Hong *et al.*, 1991), increase root biomass and reduce stomata size and density (Llorente *et al.*, 2016), and turn on auxin related genes that boost plant growth (Ruzzi & Aroca, 2015). In addition to auxin-mimicking compounds, gibberellins, cytokinins, and defense-related hormones, such as jasmonic acid-isoleucine or salicylic acid, are primarily produced to modulate plants immunity and facilitate microbial colonization (Stringlis *et al.*, 2018). Cytokinins can enhance root exudate production and potentially increase plant-microbe signaling (Ruzzi & Aroca, 2015; Backer *et al.*, 2018). Gibberellin-producing PGPMs species such as *Bacillus cereus*, *Promicromonospora* sp. *Leifsonia soli* and *Enterococcus faecium* have been shown to stimulate shoot growth in plants deficient in gibberellin synthesis (Joo *et al.*, 2005; Kang *et al.*, 2014). This indicates that these species compensate for the absence of plant gibberellins with added bacterial gibberellins (Lee *et al.*, 2015). It was stated that many beneficial microorganisms promote plant growth by lowering plant ethylene levels through the bacterial enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyses the ACC (immediate ethylene precursor) into α -ketobutyrate and ammonia (Glick, 2014). Several studies have demonstrated that inoculating plants with PGPMs, which produce ACC deaminase, improves stress tolerance. This appears to be the case because PGPMs can prevent ethylene levels from rising to suppress plant growth (Ahemad & Kibret, 2014; Pérez-Montaña *et al.*, 2014; Ruzzi & Aroca, 2015).

Although numerous studies have confirmed the role of microorganisms and a healthy microbiome in sustainable agriculture and the environment, plants' intracellular

signalling in response to various phytohormones generated by PGPMs and their interactions with endogenous plant pathways are still poorly understood. This knowledge appears to be required to anticipate the effects of PGPMs application, mainly when we are talking about the microbiome, where several microorganisms are involved and release several phytohormones. Therefore, further research is needed to discover whether biotechnological techniques can provide predictable results.

Microbiome and soil fertility and nutrients use efficiency

As an important component of the soil ecosystem, the soil microbiome plays an essential role in maintaining soil fertility and is used as an ecological indicator to assess soil health. Unfortunately, modern and intensive agriculture drastically affects soil microbial abundance, diversity and activity. Excess chemical application, fertilizers or pesticides and a low amount of soil organic matter are the main threat to the microbiomes. Numerous studies have examined the effects of chemical nitrogenous fertilizers on soil microbiome and found that chemical fertilizers appear to suppress microbial community (Treseder, 2008; Zhou *et al.*, 2017; Xie *et al.*, 2019). For example, Reid *et al.*, (2021) found that rhizobacteria abundance and populations were decreased in wheat grown in soils treated with NPK fertilizer.

Applying beneficial microbes in agroecosystems as a sustainable method for long-term nutrient availability could mitigate the excess use of chemical inputs (Antar *et al.*, 2021). Soil microorganisms, mainly bacteria and fungi, have long been known to contribute to plant nutrition. Nitrogen is an essential mineral nutrient for most plant physiological functions, including photosynthesis, amino acids, and protein biosynthesis (Alori *et al.*, 2017). Some members of the plant microbiome can significantly minimize the requirement for soil nitrogen supplementation, either directly through legume and rhizobium symbiosis or indirectly by supporting nitrogen fixers by their secretions (Naamala & Smith, 2020). Nitrogen fixers microorganisms are classified into two major groups based on their type of association formed with plants: the symbionts and the free-living nitrogen fixers. The symbiotic nitrogen fixers consist of *Rhizobium*, *Sinorhizobium*, *Azoarcus*, *Mesorhizobium*, *Allorhizobium*, *Frankia*, *Bradyrhizobium*, *Azorhizobium*, *Burkholderia*, and some *Achromobacter* strains (Babalola, 2010; Pérez-Montaña *et al.*, 2014; Turan *et al.*, 2016). The free-living nitrogen fixers consisted of *Azoarcus*, *Herbaspirillum*, *Azospirillum*, *Gluconacetobacter*, and *Azotobacter* (Vessey, 2003). In symbionts, the formation of root nodules, specialized structures where atmospheric

nitrogen is reduced into useable forms (primarily NH_3), starts with crosstalk between rhizobia and legume in the form of signal compounds (Naamala *et al.*, 2016) while free-living nitrogen-fixing bacteria thrive in the phyllosphere and rhizosphere of plants (Hardy & Holsten 1973). Foliar and root application of PGPMs has increased nitrogen content (Luziatelli *et al.*, 2019). For example, foliar application of *Azotobacter chroococcum* and *Azospirillum lipoferum* as biofertilizers resulted in considerable increases in aerial plant height, leaf number and fresh weight in lettuce (Hanafy Ahmed *et al.*, 2002). It has also been documented that the presence of *Azotobacter* species in the soil improves nitrogen availability (Din *et al.*, 2019) and phosphorous (Velmourougane *et al.*, 2019).

The soil microbiome has vast potential for increasing soil phosphorus availability and is an important regulator of phosphorus transformation processes (McRose *et al.*, 2021). For example, organic acids like gluconic acid and 2-ketogluconic acid are produced by rhizosphere bacteria such as *Pseudomonas*, *Rhizobium*, *Bacillus*, and *Enterobacter* solubilize phosphates (Werra *et al.*, 2009; Adeleke *et al.*, 2017). Moreover, arbuscular mycorrhizal symbiosis, an essential prerequisite for phosphorus acquisition from the soil, contributes to plant growth and health (Wen *et al.*, 2019).

Soil microorganisms have also been identified to contribute to plant iron nutrition by producing organic compounds called siderophores (Mohanty *et al.*, 2021). Several bacterial species can produce siderophores, including, *Azospirillum*, *Klebsiella*, *Pantoea*, *Pseudomonas*, *Azotobacter*, *Bacillus*, and *Serratia* (Leontidou *et al.*, 2020). In a study, the iron content of sunflower, maize (Masalha *et al.*, 2000), rape, and red clover (Jin *et al.*, 2006) was considerably lower when grown in sterile rather than sterile non-sterile soil. As a result, PGPMs offer a cost-effective and safe alternative technique for increasing soil fertility and enhancing plant growth and development.

Microbiome and abiotic stresses

As the effects of climate change become more apparent over time, severe environmental conditions such as drought, salinity, low and high temperatures, and nutrient deficiency are becoming more frequent. Among these environmental conditions, drought and heat stress cause notable losses in major cereal species such as wheat, barely and maize (Vogel *et al.*, 2019). Under such stressful conditions, plants' metabolism is disturbed by several biochemical factors. To resist such circumstances,

metabolic reconfiguration is essential to satisfy the need for anti-stress factors such as antioxidants, solutes, and proteins (Obata & Fernie, 2012). Hence, employing a long-term strategy to increase plant tolerance to environmental constraints is critical for ensuring and optimizing global food production. The use of PGPMs in a sustainable manner is one of the eco-friendly approaches that can support plants to resist severe environmental conditions (Shah *et al.*, 2021). Most PGPMs can produce phytohormones that stimulate plant growth and crop yield under different abiotic stress (Sarkar *et al.*, 2018; Jochum *et al.*, 2019; Mellidou *et al.*, 2021). In addition, the plant microbiota involved in the production of phytohormones stimulates the production of osmolytes, antioxidants, regulation of stress-responsive genes, and alteration of root morphology, which results in drought tolerance in plants. Therefore, the PGPMs conserve plant growth under drought stress, leading to increased agricultural productivity (Subiramani *et al.*, 2020).

Heat stress impacts plants' various characteristics, including germination, growth, and the production of flowers and seeds through biochemical, physiological, molecular, and morphological changes (Siddiqui *et al.*, 2015). Biochemical changes include changes in amino acids, metabolites, osmolytes, hormones, reactive oxygen species generation and antioxidant enzymes. Molecular alterations include the changes in genes involved in the expression of Osmo protectants, detoxifying enzymes, transporters, and upregulating the expression of heat shock proteins and stress-induced proteins (Khan *et al.*, 2020).

Heat stress tolerance can be enhanced by breeding, tissue culture technologies and nutrients management; however, these approaches are time-consuming, expensive, and have negative environmental consequences (Jan *et al.*, 2018). PGPMs are an alternative and environmentally friendly solution to improve crop productivity by reducing the detrimental effects of heat stress (Park *et al.*, 2017). Several studies have previously described the use of PGPMs to improve heat stress tolerance in plants such as sorghum (Ali *et al.*, 2009), chickpea (Srivastava *et al.*, 2008), wheat (Ali *et al.*, 2011; Abd *et al.*, 2014) and tomato (Issa *et al.*, 2018). Recently Khan *et al.*, (2020) identified thermotolerant *Bacillus cereus* SA1—a bacterium that can produce biologically active metabolites such as gibberellins, indole-3-acetic acid and organic acids – could improve biomass, chlorophyll fluorescence and chlorophyll content in soybean grown under normal and heat stress treatments.

PGPMs could be a practical approach to overcoming the salinity problem. Bacteria species such as *Azotobacter*, *Azospirillum*, *Bradyrhizobium*, *Rhizobium*, *Bacillus*, and *Pseudomonas*, isolated from the saline soils, could be used in salt-stressed farmlands. These salinity resistant PGPMs attach osmotolerance to the plants and provide several benefits such as improved growth, better nutrient uptake, increased chlorophyll content, enhanced vigour and yield (Subiramani *et al.*, 2020). Under salinity stress, *Enterobacter* sp. could help rice seedlings cope with salinity stress (Sarkar *et al.*, 2018). Similarly, salt-tolerant *Pseudomonas fluorescens* increased plant growth in maize (Zerrouk *et al.*, 2016). In wheat, inoculation with *Bacillus aquimaris* improved salt tolerance and plant growth (Upadhyay *et al.*, 2011). Also, *Bacillus subtilis* mitigated salinity stress in white clover (Han *et al.*, 2014).

Microbiome and biotic stresses

Bio-stressors are one of the many challenges that modern agriculture encounters. Plant pathogens such as viruses, bacteria, and fungi are among the primary biotic stressors severely reducing crop production. There are various instances when the plant microbiome, particularly the root and endophytic parts, plays a vital role in suppressing diseases of crops (Mendes *et al.*, 2011; Spence *et al.*, 2014; Cha *et al.*, 2016). For example, Yang *et al.*, (2020) revealed bacterial blight-induced complexed changes in rice leaves' endophytic fungal and bacterial communities. They demonstrated that bacterial blight-associated enrichment of some endophytic bacterial taxa, e.g., *Pantoea* sp. isolates, may play critical roles in controlling the development of bacterial blight disease in rice. Control of *Rhizoctonia solani* of sugar beet was because of *Pseudomonas* spp. (Mendes *et al.*, 2011).

Similarly, Koberl *et al.*, (2013) used a combination of 45 *Bacillus* spp. with *Streptomyces* in managing *Ralstonia* disease in medicinal plants. Inoculation with *Trichoderma harzianum* has been shown to have an antagonistic impact on fungal diseases (Monteiro *et al.*, 2010). Key members of the wheat microbiome can improve fusarium head blight (*Fusarium graminearum*) resistance by interacting with wheat traits to shape the overall wheat phenotype and cultivar performance (Karlsson *et al.*, 2021).

The rhizosphere microbiome can control nematodes by phytohormone synthesis, nitrogen fixation,

phosphorus and potassium solubilization, siderophores containing iron, and creating a gaseous form of nitrogen like ammonia (Mahmud *et al.*, 2021). Microorganisms can also be used in controlling insects. For example, *Metarhizium* is a soil-inhabiting insect-pathogenic fungus worldwide and is currently used as a biocontrol agent against crop pests (Sasan & Bidochka, 2012). Other fungi known as insect pathogens include *Acremonium*, *Beauveria*, *Cladosporium*, *Clonostachys*, and *Isaria* (Wang *et al.*, 2005).

A healthy microbiome can control plants disease through different mechanisms such as accumulating the stress-related phytoalexin metabolites, regulating the defense-related gene expression, inducing the oxidative burst (Gruau *et al.*, 2015), by non-producing lipopeptides and overproducing surfactin (Farace *et al.*, 2015), inducing defences modulated by Ca^{2+} signalling (Vatsa-Portugal *et al.*, 2017) and producing ACC deaminase enzyme that helps plants regulate the stress-related hormone ethylene level (Gamalero *et al.*, 2017).

However, the Phyllosphere microbiome is often overlooked and plays an essential role in plant health (Gao *et al.*, 2021). Recent investigations have found that as the rhizosphere microbiome plays a crucial role in determining aboveground health (Fitzpatrick *et al.*, 2018), infections with aboveground pathogens change

the microbial community in the plant's rhizosphere (Berendsen *et al.*, 2018; Yuan *et al.*, 2018) suggesting that under- and aboveground microbiomes are systematically linked (Gao *et al.*, 2021). However, no comprehensive study of the potential connection between under- and aboveground microbiomes has been performed.

Overall, the plant microbiome acts like a second immune system, protecting the plant against biotic stresses, can promote plant growth, assisting the plants acquire nutrients, or protecting against abiotic stress such as drought, heat, or salinity (Figure 3), finally leads to improved plant health and productivity. Therefore, significant attention must be paid to microbiome studies to help develop and implement beneficial microbes in plant protection and sustainability promotion.

Microbiome research on major crops

Microbiome studies have always been limited by the small number of experiments, variations in sampling and analysis techniques, and small sample sizes within each experiment, but advances in new technologies, for example, high-throughput DNA sequencing coupled with omics analyses, have enabled a revolution in plant microbiome studies and accelerated this area of research. The most general microbial genomics approaches include 16S/18S/ITS amplicon sequencing, metagenomics, meta-transcriptomics, microbial whole-genome sequencing, complete plasmid sequencing, and microbial single-cell sequencing. Using high-throughput and high-resolution genomics technology platforms, microbial genomics techniques can enhance agricultural productivity through soil microbial diversity study, functional microbial genomics, biological product creation, and bacterial genome editing. Next-generation sequencing (such as Illumina HiSeq/MiSeq and Roche 454) and PacBio SMRT sequencing are suitable options for microbial research. PacBio SMRT systems may analyse methylation with PacBio analytical tools and provide long-length readings.

Most of the recent microbiome work involves work on plants in natural and agroecosystems using a combination of field- and lab-based studies, molecular/computational techniques, and functional assay to better understand the plant microbiome, including their community assembly, function transmission and dispersal. DNA sequencing has been applied to overcome challenges in identifying and monitoring plant microbiome (Nezhad, 2014). This method mainly relies on amplifying and sequencing

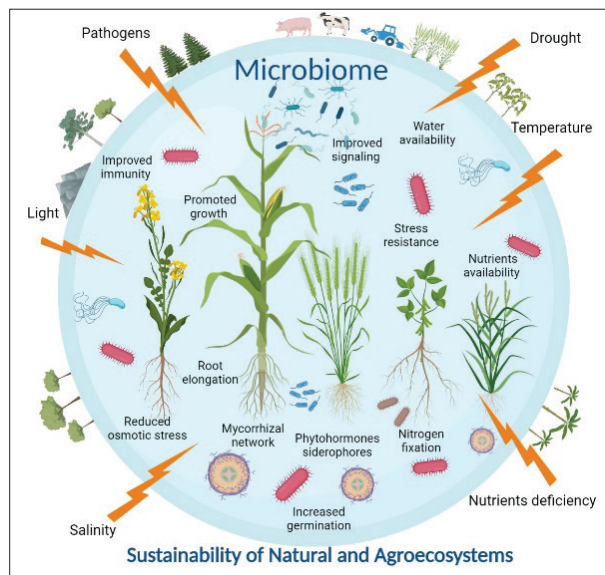


Figure 3: Microbiome for crop improvement and sustainability

small, conserved regions from microbes' genomes, including 16S ribosomal RNA sequences for bacteria and the internal transcribed spacer region or *Elongation Factor 1 alpha (EF1α)* and *Beta-tubulin* genes for fungal species (Raja *et al.*, 2017). In this context, Hu *et al.*, (2019) applied the whole genome shotgun sequencing as a method for the detection of wheat fungal pathogens. They diagnosed fungal pathogens, including *Puccinia striiformis* f. sp. *Tritici* (causal agent of wheat stripe rust), *Zymoseptoria tritici* (causal agent of septoria tritici blotch), and *Pyrenophora tritici repentis* (causal agent of yellow leaf spot). They also identified the bacterial genus *Pseudomonas* co-present with *Puccinia* and *Zymoseptoria* but not *Pyrenophora* infections.

Recently, culture-independent and culture-dependent metagenomics approaches have been employed to investigate the whole rhizosphere microbiome of many crops such as wheat (Ofek-Lalzar *et al.*, 2014), barley (Bulgarelli *et al.*, 2015) and rice (Zhang *et al.*, 2019). According to culture-independent methods, *Proteobacteria* account for over 40% of the bacterial population in the wheat rhizosphere. *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes* are the other dominant phyla (10–15%), with the other phyla accounting for < 5% each (Tkacz *et al.*, 2020; Prudence *et al.*, 2021), whilst culture-dependent techniques revealed that *Actinobacteria* and *Proteobacteria* (25% each) and then *Firmicutes* (10%) are the main phyla in the wheat rhizosphere (Germida & Siciliano, 2001). Furthermore, Comby *et al.*, (2016) reported that Ascomycota (mainly Sordariomycetes or Dothideomycetes) is the most dominant fungal phylum, followed by Basidiomycota (with dominance by Agaricomycetes in which Polyporales and Russulales were top orders), and Zygomycota. In a similar study, MinION oxford nanopore sequencing was used, and the prevalent phyla were recognized as *Proteobacteria* (68%), *firmicutes* (13%), *bacteroidetes* (3%), *actinobacteria* (3%) and *acidobacteria* (3%) (Srivastava *et al.*, 2020).

In a study, Wang *et al.*, (2021) used metagenomic sequencing and analysis and showed a significant microbiome difference between wheat rhizosphere and bulk soil. Similarly, using pyrosequencing of bacterial 16S rRNA genes, Peiffer *et al.*, (2013) reported a substantial variation in bacterial richness, diversity, and relative abundances of taxa between bulk soil in the maize rhizosphere. Beirinckx *et al.*, (2020) identified 12 abundant and enriched bacterial families that colonize maize roots using the same method. The microbiome structure in the bulk soil and soybean rhizosphere as affected by crop sequences was investigated by Bolaji

et al., (2021) using a combination of marker-based Illumina sequencing and bioinformatics analyses. They demonstrated that bacterial species richness and evenness in the soybean rhizosphere soil were similar following canola and soybean compared to a previous corn sequence. On the other hand, fungi richness and evenness were unaffected by crop sequence. Floc'h *et al.*, (2020) used a long-term field experiment. They sampled the rhizosphere of canola grown in different rotation sequences and detected only one core bacterial amplicon sequence variant in the prokaryotic component of the microbiota of canola rhizosphere, a hub taxon identified as cf. *Pseudarthrobacter* sp. Lay *et al.*, (2018) extracted DNA from canola roots and nearby rhizosphere soil and constructed MiSeq amplicon libraries, focusing on bacterial and archaeal 16S rRNA genes and the fungal ITS regions. They found that the root and rhizosphere microbiome of canola differed from wheat and pea. These microbiomes include several putative PGPM, including *Amycolatopsis* sp., *Serratia proteamaculans*, *Pedobacter* sp., *Arthrobacter* sp., *Stenotrophomonas* sp., *Fusarium merismoides*, and *Fusicolla* sp., which correlated positively with canola seed yield.

Unmapped DNA sequencing reads as microbial reads were used to characterize the structure of the rice bacterial microbiome by Roman-Reyna *et al.*, (2020), who identified central bacteria taxa that appear as microbial hubs and may impact the network of host-microbe interactions. They found that the genera *Xanthomonas*, *Pseudomonas*, *Burkholderia* and *Mycoplasma* were the most abundant bacteria in the rice leaf microbiome. They also discovered regions in the rice genome that might be involved in forming these microbial hubs. Using 16S rRNA gene-based metagenomic analysis and Illumina MiSeq sequencing, Oliveira *et al.*, (2022) investigated rice field rhizosphere bacterial diversity and composition. They reported 56 Phyla, with four major Phyla: *Acidobacteria*, *Proteobacteria*, *Bacteroidetes* and *Actinobacteria*.

Therefore, we can use these methods to understand the relationships between microbial communities and plants and increase farm productivity in an environmentally sustainable approach.

CONCLUSION AND OUTLOOK

The plant microbiome and plant-microbe interaction studies can lead to potential farming methods that are both environmentally friendly and agronomically sustainable. Furthermore, microbiome study plays a crucial role in developing biofertilizers, biocontrol

and bioremediation agents in sustainable agriculture. Despite the abundance of research on plant and soil microbiome and plant-microbe interactions, there is not much on the molecular mechanisms that underpin gene activity and signal transduction during beneficial and harmful interactions. Hence, understanding the genetics of microbiota and its interaction with crops using novel technologies such as next-generation sequencing and omics technologies is essential for providing broad and in-depth knowledge of the biological phenomenon to improve plant health, disease control and food quality (Kankanala *et al.*, 2019). Due to genomics tools, our understanding of the plant microbiome has dramatically increased in the post-genomic era. Nonetheless, integrated approaches, such as multi-omics and microbiome engineering methodologies, are still necessary to substantially improve our understanding of the structure and dynamics of microbiomes. Multi-omics data integration could assist in discovering the molecular mechanisms underlying microbiome recruitment, also considering metabolite-metabolite, microbe-microbe, and metabolite-microbe interactions. In addition, integrating efficient approaches with emerging precision agriculture, artificial intelligence, synthetic biology, satellite, and big data can offer a robust framework to achieve the actual potential of plant microbiome in agriculture and environmental science. Nevertheless, numerous obstacles in this field of study must be overcome to understand the microbiome comprehensively. These hurdles are mainly identifying the molecules and compounds responsible for the network communication between plants and microorganisms, taking bacterial and fungal communities to the next level, expanding and validating microbial cultures, understanding plant genotype, microbiome, and environment interactions, taking advantage of host-mediated microbiome member and function selection and developing novel methods and techniques for practical application and manipulation in agricultural settings.

Moreover, there is substantial evidence that plant genetics affects the microbiome. Therefore, plant breeding programs should take the importance of the microbiome as a lifelong strategy. These suggested strategies will offer alternatives for investigating and leveraging plant microbiome to improve global agriculture's sustainability and productivity. The authors believe the microbiome's full use will be realized when major fertilizer companies worldwide take up R&D in this field and produce novel microbial fertilizers that would be the next green revolution. Indeed that should be called the 'true green revolution' where inputs are environmentally friendly, clean and harmless to the fauna

and flora, including our water table. The authors envision the leap from research to products as an agricultural transformation that all world habitants benefit from.

Conflict of interest

The authors declare no conflict of interest in this article.

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